

A study of the sharks and rays from the Lillebælt Clay (Early–Middle Eocene) of Denmark, and their palaeoecology

AGNETE WEINREICH CARLSEN & GILLES CUNY



Carlsen, A.W. & Cuny, G. 2014. A study of the sharks and rays from the Lillebælt Clay (Early–Middle Eocene) of Denmark, and their palaeoecology. © 2014 by Bulletin of the Geological Society of Denmark, Vol. 62, pp. 39–88. ISSN 2245-7070. (www.2dgf.dk/publikationer/bulletin).

Elasmobranch assemblages from the Eocene Lillebælt Clay Formation (Late Ypresian to Middle Lutetian) at Trelde Næs in Denmark yielded teeth of 31 different genera/species from surface collecting as well as from bulk sampling. The fauna is dominated by lamniform pelagic sharks and deep-water genera like Hexanchiformes, *Centrophorus*, *Isistius*, *Echinorhinus* and *Pristiophorus*. *Coupatezia miretrainsensis*, *Centrophorus* aff. *granulosus* and *Chlamydoselachus* cf. *fiedleri* are reported for the first time from the Ypresian. The record of *Coupatezia miretrainsensis* extends its stratigraphic record from the Lutetian back to the Late Ypresian, whereas the record of *Centrophorus* aff. *granulosus* extends the origin of the *Centrophorus granulosus* group back to the Late Ypresian from its hitherto known origin in the Lutetian. The possible presence of the sparsely known Bartonian genus *Turania* awaits further sampling to be confirmed. The Ichthyofauna suggests deposition in a deep-water environment in subtropical to temperate waters on the middle or outer continental shelf and upper slope at water depth down to 350 m. This is in agreement with depositional depths inferred from fossil molluscs and fish otoliths from Trelde Næs.

Keywords: Denmark, Lillebælt Clay Formation, Eocene, Elasmobranchii, fossil teeth, palaeoecology.

Agnete Weinreich Carlsen [agnetecarlsen@mail.dk], Natural History Museum of Denmark, University of Copenhagen, Øster Voldgade 5-7, DK-1350 København K, Denmark. Gilles Cuny [gilles.cuny@gmail.com], Natural History Museum of Denmark, University of Copenhagen, Øster Voldgade 5-7, DK-1350 København K, Denmark; current address: UMR CNRS 5276 LGLTPE, Université Claude Bernard, Lyon 1, Campus de la Doua Bâtiment Géode, 2 rue Raphaël Dubois, F-69622 Villeurbanne Cedex, France.

Received 25 February 2014
Accepted in revised form
13 August 2014
Published online
19 November 2014

The vertebrate fauna from the Eocene of Denmark is still imperfectly known. Bonde (1966) reported *Palaeohypotodus rutoti* under the name *Odontaspis rutoti* and *Striatolamia macrota* under the name *Odontaspis* (*Synodontaspis*) *macrota* 'premut. striata' and several fossils of bony fish from the Fur Formation (Early Eocene) in the Limfjord area in Northern Jutland. So far, very little information has been published about the vertebrate fossils from the Eocene Lillebælt Clay Formation in Eastern Jutland (see Hansen *et al.* 2013).

The Lillebælt Clay Formation has been described as sparsely fossiliferous, but a great deal of fossilised invertebrates has been found. Bonde (1968) reported echinoderms, molluscs, crustaceans, brachiopods, annelids, radiolarians and foraminifers from the Lillebælt Clay at Trelde Næs. The molluscan fauna from Trelde Næs has been described in detail by Schnetler and Heilmann-Clausen (2011). The fauna contains

75 species mostly embedded in concretions with a provenance from L4 to the lower part of the Søvind Marl Formation. This molluscan fauna suggests deposition depths between 100 and 300 m (Schnetler & Heilmann-Clausen 2011).

Associated skeletal and dental remains of a fossil odontaspidid shark have recently been described from Trelde Næs (Hansen *et al.* 2013). In spite of the rarity of macrofossils, intensive collecting by amateurs has resulted in the recovery of much material including many shark teeth and teeth of bony fish.

The aim of this paper is to describe the elasmobranch fossil teeth from the Lillebælt Clay Formation, Eocene of Denmark. This fauna, although well-known by avocational palaeontologists in Denmark, has rarely been described in the scientific literature. Moreover, the composition of the fauna gives information on the depositional environment of the Lillebælt

Clay Formation. Three private collections have been available for this study. Unfortunately, most of the material is collected from the surface of the beach and its exact provenance is therefore quite vague. Three collectors have also screen-washed bulk material from layer L2 of the Lillebælt Clay and the provenance of this material is therefore more precisely known, dating from the Late Ypresian. The material described by Hansen *et al.* (2013) comes from layer L5 and is therefore slightly younger (Lower Lutetian) than the assemblage from layer L2.

Geological setting

Trelde Næs is a peninsula in Eastern Jutland near the town of Fredericia (Fig. 1). During the Eocene, the Danish area was covered by the North Sea and clays and marls were deposited. When the Lillebælt Clay was deposited, a land bridge closed the North Sea from the warm Atlantic Ocean and pure clays were deposited at Trelde Næs (Heilmann-Clausen & Surlyk 2006, fig. 10-2). The fine-grained clays of the Lillebælt Clay Formation and the lower part of the Søvind Marl

are exposed in outcrops on the SE-coast of Trelde Næs (Fig. 1) (Heilmann-Clausen *et al.* 1985). Small outcrops of Søvind Marl have been observed at Kirstinebjerg and Østerskov (Schnetler & Heilmann-Clausen 2011). Schnetler (1985) claimed to have observed small temporary exposures of the Late Oligocene Brejning Formation at Trelde Næs but gave no evidence for it. In wet periods large amounts of water are absorbed by the clay which becomes unstable and may form landslides. The Lillebælt Clay is generally poor in fossil material, but extensive sampling has revealed a great variety of fossils including snails, bivalves, crabs and shark teeth.

Stratigraphy

The Lillebælt Clay Formation has been extensively logged by Heilmann-Clausen *et al.* (1985) and it is formally divided into six lithological units named from the base L1 to L6. At Trelde Næs L2 to L6 is more or less exposed in outcrops and their stratigraphy is illustrated by Heilmann-Clausen *et al.* (1985, fig. 14). L2 is a grey-green extremely fine-grained, waxy, non-calcareous clay, probably deposited very slowly far from the coast (Heilmann-Clausen & Surlyk 2006). In



Fig. 1. The Trelde Næs peninsula showing the location of Kirstinebjerg, Fredericia Fælle, Vesterskov and Østerskov. The inserted map of Denmark shows the position of Trelde Næs (red square) and the Eocene outcrops (in black) below the Quaternary. Partly from Schnetler & Heilmann-Clausen (2011) and Hansen *et al.* 2013. Google map.

the lower part of L2, two black layers are seen. Both layers are rich in organic material and this could indicate anoxic bottom waters due to blooming of planktonic organisms. Two closely spaced ash layers just below the lowermost black layer form an important marker within L2. Layer L2 was deposited in the Late Ypresian. The transition to L3 is marked by a carbonate-cemented horizon with signs of bioturbation, which could indicate oxygen-rich bottom water. The boundary between L2 and L3 marks the transition to the Lutetian (Schnetler & Heilmann-Clausen 2011). L3 contains mainly red-brown clay beds and one ash bed. L4 consists of greenish clay and a concretionary layer is present near the base. L5 consists of dark grey-green, slightly calcareous clay. In L6, bioturbation is frequent and there are intervals of marls suggesting warmer waters. Several concretionary layers are present in L6. At Trelde Næs the Lillebælt Clay Formation is overlain by the lower part of the late Lutetian Søvind Marl Formation which has an increased calcareous content.

The Lillebælt Clay Formation in Jutland is usually glacially folded. At Kirstinebjerg the strata form an asymmetrical anticline (Fig. 2).

Palaeo-water depths

In the Lillebælt Clay Formation the grain-size is extremely small, with almost 90% in the clay fraction < 63 μ m (Heilmann-Clausen *et al.* 1985), indicating sedimentation in deep waters far from the coast. The distance to the nearest palaeo-coast in Sweden was about 300 km at the time (Thomsen *et al.* 2012). The water depth in the Danish area during the time period when the Trelde Næs sediments were deposited was probably decreasing from 500 to 400 m due to a global

decrease in the sea level (Heilmann-Clausen & Surlyk 2006, fig. 10-2). The global sea level was, however, still high due to the ice free world (Heilmann-Clausen & Surlyk 2006). The North Sea Basin was divided into the Norwegian–Danish Basin and the north-west German Basin by the Precambrian Ringkøbing–Fyn High (Heilmann-Clausen & Surlyk 2006, fig. 6-2). The Ringkøbing–Fyn High consists of a series of elevated basement blocks extending from the North Sea across Denmark to the Baltic Sea (Michelsen 1994). Trelde Næs is located on the northern border of this structure. Based on boreholes, Dinesen *et al.* (1977) constructed contour maps of the Eocene and Danian surface in Jutland and Fyn and found that the Danian as well as the Eocene surface in the Trelde Næs area was elevated by at least 150 m compared to central and north-western Jutland. There are no available data specifically on the Ypresian/Lutetian palaeo-bathymetry in the Fredericia area, but the paper mentioned above could support the idea that the water depth was lower in the Trelde Næs area than in central and north-western Jutland and probably in the North Sea Basin as a whole.

Stable isotope ($\delta^{13}\text{C}$, $\delta^{18}\text{O}$) and biostratigraphic data on benthic foraminifera from the Middle Ypresian Røsnæs Clay Formation at Albæk Hoved (situated 15 km north-east of Trelde Næs) suggest the palaeo-depth to have been from 600 to 1000 m (Schmitz *et al.* 1996). The Røsnæs Clay was deposited in a period where the English Channel was open and the sea level was higher than when the Trelde Næs sediments were deposited (Heilmann-Clausen & Surlyk 2006, fig. 10-2).

Based on the molluscan fauna of Trelde Næs, Schnetler & Heilmann-Clausen (2011) suggested the palaeodepth to have been from 100 to 300 m.



Fig. 2. The locality at Kirstinebjerg. The first author and Mogens Madsen sampling from the upper black layer in L2.

Material and methods

The present study is based on four separate collections.

1) Ole Barsøe Hansen (OBH), Kolding, has collected shark teeth during the last 20–30 years. All the teeth were surface collected from between the pebbles on the beach at the foot of the steep clay banks along the south-east coast of Trelde Næs. The examined part of the collection consists of a total of 1931 teeth. The majority of the teeth (1748) are from Lamniformes. Of the total number of teeth, 39% are identified to genus or species, 30% are identified only to family or order, and the remaining 31% of the teeth are so damaged that identification was not attempted. The precise stratigraphic origin of these teeth is unknown but they are from layer L2 to L6 and Søvind Marl, the layers outcropping in the area.

2) Mogens Madsen (MM), Fredericia, has collected shark teeth during 4–5 years. His collection consists of 170 teeth of which 98 were hand collected from the beach and 72 were extracted from bulk samples taken from the Lillebælt Clay, layer L2 at Kirstinebjerg (GPS coordinates: 09°48'09.03"E, 55°35'52.6"N). The bulk material was collected over the years and a total of approximately 100 kg of clay has been processed. The clay was dried, dissolved in warm water and screen washed through a 1 mm sieve. The residues were dried and searched for teeth by MM using a binocular microscope. About 63 % of the teeth are identified to genus or species.

3) Sten Lennart Jakobsen (SL), Copenhagen, has taken a bulk sample of approximately 20 kg of clay also from L2 at Kirstinebjerg. The clay was dried, dissolved in warm water, treated with tetrasodiumpyrophosphate ($\text{Na}_4\text{P}_2\text{O}_7$) and screen washed through a 0.25 mm sieve. The dry residue was searched using a binocular microscope (Euromex) by the first author. Sixteen shark teeth were retrieved and of these 13 teeth are identified to genus or species.

4) The first author's (AWC) collection, Copenhagen. In 2012 a total bulk sample of 40.9 kg was taken from L2 at Kirstinebjerg (Fig. 2). The clay was dried, dissolved in warm water, treated with tetrasodiumpyrophosphate ($\text{Na}_4\text{P}_2\text{O}_7$) and screen washed through a 0.25 mm sieve. The clay from the black layer was difficult to disintegrate and was thereafter treated with hydrogen peroxide (H_2O_2). The dry residue was searched using a binocular microscope (Euromex) and 97 shark teeth and teeth fragments were retrieved. Of these, 31 teeth are identified to genus or species.

All illustrated teeth are housed in the Natural History Museum of Denmark in Copenhagen under the catalogue numbers DK728 (Mogens Madsen), DK729 (Ole Barsøe Hansen), DK730 (Sten Lennart Jakobsen) and DK731 (Agnete Weinreich Carlsen) after they

have been declared 'Danekræ' in 2013 (Christensen & Hald 1991). The remaining teeth in Lot MM (Mogens Madsen), Lot OBH (Ole Barsøe Hansen), Lot SL (Sten Lennart Jakobsen) and Lot AWC (Agnete Weinreich Carlsen) are all housed in their respective private collections.

Teeth larger than 5 mm have been photographed with a Nikon D7000. Smaller teeth have been photographed with a JEOL Scanning Electron Microscope (SEM) JSM 6335F. A few small teeth were photographed with an Olympus digital image acquisition system DP12 mounted on an Olympus SZ40 binocular microscope.

Besides the shark teeth, the bulk samples contained a large amount of teeth and a few vertebrae of bony fish. They are not the subject of this work.

Systematic palaeontology

Class Chondrichthyes Huxley 1880

Subclass Elasmobranchii Bonaparte 1838

Subcohort Neoselachii Compagno 1977

Superorder Galeomorphii Compagno 1973

Order Lamniformes Berg 1958

Family Mitsukurinidae Jordan 1898

Genus *Anomotodon* Arambourg 1952

Anomotodon sheppeyensis Casier 1966
Fig. 3A–F

Material. 73 anterior and 27 lateral teeth, including DK729aa, DK729ab and Lot OBH10.0.

Description. Forty-seven anterior teeth are severely worn out. Their ornamentation is probably lost and the cutting edges are indistinct, whereas 26 anterior teeth and 27 lateral teeth with triangular crowns are well preserved.

Anterior teeth measure 10 to 21 mm apico-basally, and 6 to 10 mm mesio-distally. The crown is slender, erect and more or less inclined lingually. The lingual face is strongly convex mesio-distally and ornamented with folds in the basal two thirds of the cusp. The folds are parallel in the basal part and become more interdigitated nearer to the apex. The lingual crown–root junction is characterised by a very marked depressed

neck. The labial face is smooth and slightly convex mesio-distally. At the labial crown–root junction there is a small median crest. The enameloid expands over the upper labial part of the root lobes. The cutting edges are well developed and expand down along the short oblique heels. The root height is one third of the total height. The lobes are close and symmetric with an angle between them of about 70° in the most anterior teeth, widening to 110° in the more posterior teeth where the lobes are getting more asymmetric. The mesial lobe is longer, more pointed and more

labio-lingually flattened than the distal lobe. The lingual protuberance is strong and a deep, long nutritive groove is present.

Twenty-seven teeth have a triangular crown and are considered to be laterals. They measure 6–10 mm apico-basally and 6–10 mm mesio-distally. Fourteen are from the upper jaw and thirteen from the lower jaw. The upper teeth have a triangular, asymmetric crown, whereas the lower teeth have a triangular symmetric crown (Cunningham 2000). The cutting edges are well developed and expand over the long,

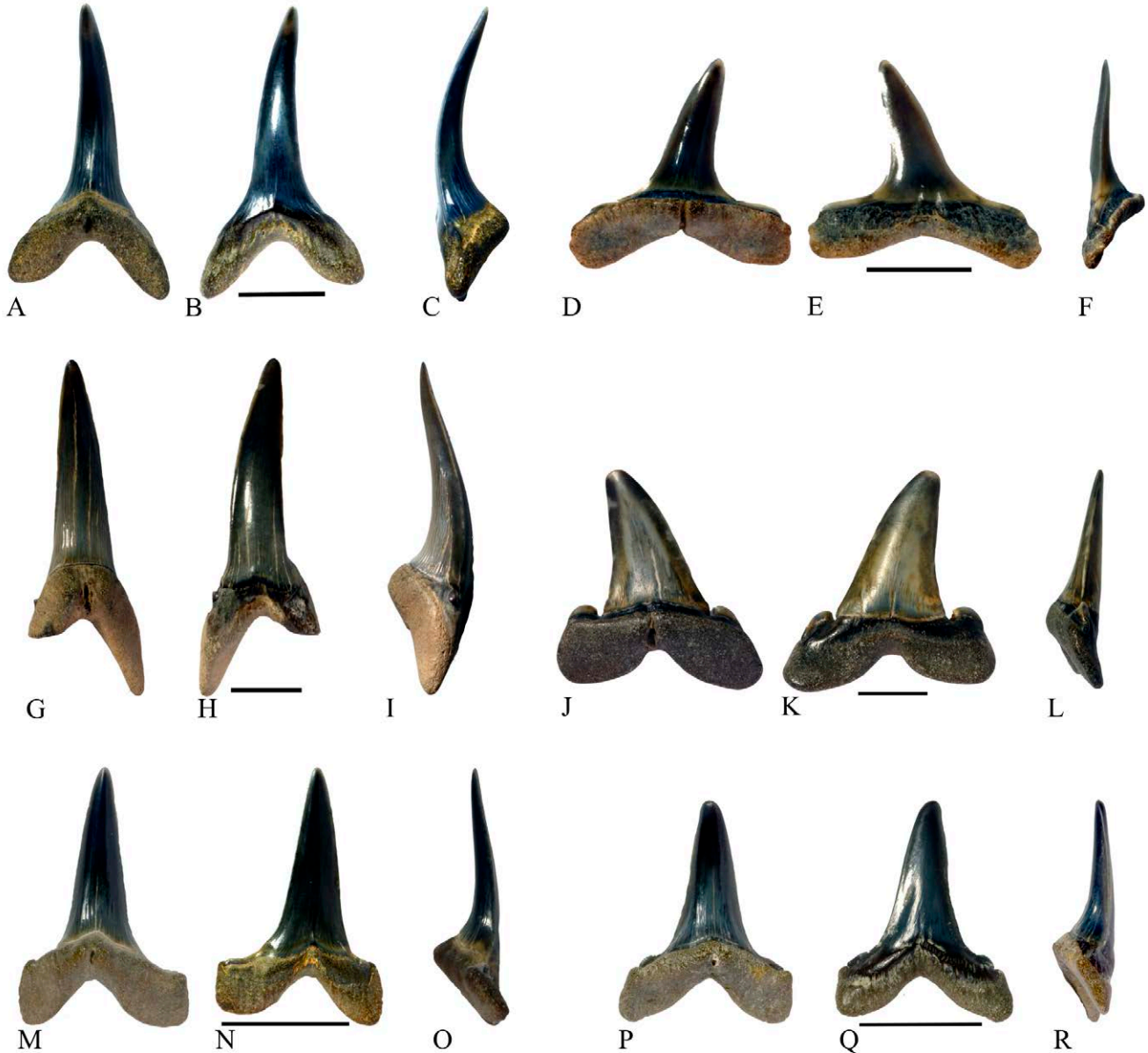


Fig. 3. A–F, *Anomotodon sheppeyensis*. A–C, anterior tooth DK729aa. A, lingual view; B, labial view; C, distal view. D–F, lateral tooth DK729ab. D, lingual view; E, labial view; F, mesial view. Scale bars 5 mm. G–L, *Striatolamia macrota*. G–I, anterior tooth DK729ba. G, lingual view; H, labial view; I, mesial view. J–L, lateral tooth DK729bb. J, lingual view; K, labial view; L, mesial view. Scale bars 10 mm. M–R, *Woellsteinia kozlovi*. M–O, anterior tooth DK729ca. M, lingual view; N, labial view; O, distal view. P–R, lateral tooth DK729cb. P, lingual view; Q, labial view; R, distal view. Scale bars 10 mm.

low horizontal heels. On the upper teeth, the mesial cutting edge has a sinusoidal shape, concave in the basal half and convex in the apical part. The distal cutting edge is strongly concave near the base and almost straight apically. The root lobes are widely spread with straight mesial and distal edges in the upper teeth and more rounded edges in the lower teeth. The linguo-basal face of the root is flat in most of the teeth and the basal edge is arc-shaped. The lingual protuberance is strong with a nutritive groove.

Comparison. Among Mitsukurinidae and Odontaspidae, the presence of lingual ornamentation can be observed in teeth of *Mitsukurina* Jordan 1898, *Woellsteinia* Reinecke, Stapf & Raisch 2001, *Striatolamia* Glikman 1964b and *Turania* Kozlov 2001. However, lateral teeth of *Mitsukurina* and anterior and lateral teeth of *Striatolamia* and *Turania* have cusplets (Cappetta 2012). The morphology of teeth of *Woellsteinia* is close to the Trelde Næs teeth, but they are significantly larger and have a more robust crown (Reinecke *et al.* 2001) than teeth of *Anomotodon* (Cappetta 1976).

The type species of *Anomotodon*, *A. plicatus* Arambourg 1952, is recorded from the late Cretaceous. Its teeth are smaller (less than 11 mm apico-basally in the anterior teeth) than the Trelde Næs teeth (Arambourg 1952). *Anomotodon novus* Winkler 1876b is known from the Eocene of the Paris Basin and the Paleogene of the North Sea Basin in Germany (Dutheil *et al.* 2006; Diedrich 2012). Teeth of *A. novus* are separated from the Trelde Næs teeth by their smaller size and often smooth lingual face (Cappetta 1976; Eeckhaut and De Schutter 2009) whereas another Eocene species, *A. multidenticulatus* Long 1992, is separated by having teeth with small cusplets on the heels (Long 1992). The Trelde Næs teeth are significantly smaller than teeth of the Cretaceous *A. hermani* Siverson 1992, which are up to 30 mm high and have strong folds covering most of the lingual face (Siverson 1992). Cappetta (1976) redescribed teeth of *Anomotodon sheppeyensis* from the Eocene (Ypresian) of the London Clay. The Trelde Næs teeth agree with the teeth of the latter species (Rayner *et al.* 2009, p. 114).

Genus *Striatolamia* Glikman 1964b

Striatolamia macrota (Agassiz 1843)

Fig. 3G–L

Material. 14 anterior, 14 antero-lateral and 18 lateral teeth, including DK729ba, DK729bb and Lot OBH11.0.

Description. Long and slender teeth with a sigmoidal profile of the crown in mesial or distal view are supposed to be from anterior files. They measure up to

50 mm apico-basally and up to 16 mm mesio-distally. Most of the teeth lack parts of the root lobes. The lingual crown face is strongly convex mesio-distally. The labial face is convex at the base and almost flat in the apical part. The lingual face is ornamented with fine parallel folds in the basal three fourths. The folds are missing close to the cutting edges. In some of the teeth, the ornamentation is missing. The cutting edges are well developed and do not reach the crown base. Very small (about 0.5 mm high) lateral cusplets appear on both sides of the main cusp. The cusplets are pointed and well separated from the main cusp when seen in labial view. The enameloid is interrupted between the cusp and the cusplet. The root is strong and represents two fifth of the total tooth height. The root lobes are long and pointed with a mesio-distal flattening and an acute angle between the lobes. The lingual protuberance is pronounced and bears a shallow furrow.

The teeth supposed to be from the antero-lateral files are better preserved than the anterior teeth. They are shorter apico-basally, the cusp is more or less inclined distally and the root lobes are with an obtuse angle, increasing in the more lateral positions. The lingual root face is almost flat in mesial view. Most of the teeth are ornamented in the same way as the anterior teeth. The cutting edges are longer and almost reach the crown base. The cusplets are still very small (about 0.5 mm high) and the cutting edge between the cusp and the cusplets is interrupted.

The teeth supposed to be from the lateral files have a triangular labio-lingually flattened and distally inclined crown. The largest tooth measures 30 mm apico-basally and 30 mm mesio-distally. Only a few teeth are faintly ornamented; the cutting edges are well developed and reach the crown base. On the labial face, there is a triangular depression at the base of the crown and the crown–root boundary is straight. The cusplets are proportionally larger than in the anterior teeth. They are rounded and clearly pectinated. In labial view they are clearly separated from the main cusp and the cutting edge between the cusp and the cusplet is interrupted. In one tooth there are two distal cusplets not fully separated. The roots are robust with widely spread lobes separated by a rounded indentation. The root lobes are more or less rectangular. The lingual protuberance is weak and bears a shallow groove, sometimes with a foramen.

Comparison. The Trelde Næs teeth resemble teeth of *Carcharias* Rafinesque 1810 in many ways, but the very small cusplets on the anterior teeth are characteristic of teeth of *Striatolamia* (Ferrusquia-Villafranca *et al.* 1999; Cunningham 2000). The cutting edges remain on the border of the teeth of *Striatolamia*, whereas in teeth of *Carcharias* they are labially displaced at the base

(Mannering & Hiller 2008). Teeth of *Anomotodon* and *Woellsteinia* are also ornamented but their teeth are considerably smaller and do not have cusplets. Teeth of *Mitsukurina* have ornamentation but no cusplets on the anterior teeth.

Striatolamia striata Winkler 1876a is reported from the Upper Paleocene in the Paris Basin in France (Dutheil *et al.* 2006) and *Striatolamia macrota* is reported from the Lower Eocene (Ypresian) of the Isle of Sheppey, England (Agassiz 1843), France (Adnet 2006a; Dutheil *et al.* 2006), the German North Sea Basin (Diedrich 2012), Antarctica (Long 1992) and Belgium (Eeckhaut & De Schutter 2009). The well-developed ornamentation on teeth of *Striatolamia striata* (Cappetta 2012) separates them from the Trelde Næs teeth. The Trelde Næs teeth are similar to those of *Striatolamia macrota*.

The taxonomic relationships of *Striatolamia macrota* have been debated. Adnet (2006a) and Eeckhaut & De Schutter (2009) place these teeth in their own genus *Striatolamia* in the family Odontaspidae, but often as Odontaspidae *incertae sedis*, although they give no reasons for this. Long (1992) and Purdy (1998) argue for the genus *Carcharias* because of their morphology close to teeth of *Carcharias taurus* and Long (1992) finds no reason for retaining the genus *Striatolamia*. Siverson (1995), however, points out that the similarities between teeth of *Striatolamia macrota* and those of the extant *Carcharias taurus* Rafinesque 1810 could be the result of convergent evolution. With the discovery of the oldest species of *Striatolamia*, *Striatolamia cederstroemi* (Siverson 1995; Upper Danian from Sweden), which had teeth with small cusplets only on the anterior teeth, the traditional assignment of *Striatolamia* to the Odontaspidae became less well supported. Cappetta and Nolf (2005) relate *Striatolamia* to the family Mitsukurinidae because of the ornamentation pattern of the teeth. It all depends on which characters are considered most important: the tooth shape and cusplets or the ornamentation. We follow here Cappetta and Nolf (2005) as well as Siverson (1995) and assign *Striatolamia* to the family Mitsukurinidae.

Genus *Woellsteinia* Reinecke, Stapf & Raisch 2001

Woellsteinia kozlovi Adnet 2006a

Fig. 3M–R

Material. 8 anterior and 14 lateral teeth, including DK729ca, DK729cb and Lot OBH12.0.

Description. Anterior teeth measure up to 22 mm apico-basally and 14 mm mesio-distally. One of the teeth is very small (14 mm apico-distally) and could be a parasymphyseal tooth. The crown is robust with

a broad base and is narrowing towards the apex. The crown is erect or inclined slightly distally. In mesial view the crown is straight except in three cases where the tip is slightly lingually inclined. The labial face is smooth and slightly convex. The enameloid extends like an apron over the proximal half of the labial face of the root lobes and in the best preserved teeth; this apron is ornamented with vertical ridges. The labial crown–root junction has an upright median V-shaped depression pointing towards the crown tip. The lingual face is strongly convex. In the basal two thirds, it is ornamented with longitudinal folds. A narrow dental rim is present at the crown base. The cutting edges are well developed and extend over the short oblique heels, in some cases with irregular bumps on the heels. Real cusplets are not present. The root height is approximately one third of the total height. It has two slightly asymmetric lobes; the distal one is longer and more rounded than the mesial one. The angle between the lobes is about 90°. The lingual protuberance is large with a nutritive foramen in a poorly developed groove.

The lateral teeth are smaller than the anterior teeth. They measure up to 17 mm apico-basally and up to 16 mm mesio-distally. They have a more triangular and robust crown which is straight in mesial view. The lingual ornamentation is less pronounced than in the anterior teeth and missing in the more worn teeth. The crown is distally inclined in the lower laterals with a concave distal cutting edge. The heels are long and almost horizontal and the cutting edges expand over the heels. The root is robust and the root lobes are well separated with an obtuse angle. Some of the root lobes are ear-shaped and some are more rectangular. They are all flattened labio-lingually. The lingual protuberance is less developed than in the anterior teeth and the nutritive groove is shallow.

Comparison. When compared to teeth of Odontaspidae, the teeth from Trelde Næs separate easily because they do not have lateral cusplets (Cappetta 2012). The presence of lingual ornamentation can be observed in teeth of *Anomotodon*, *Mitsukurina*, *Woellsteinia*, *Striatolamia* and *Turania*. However teeth of *Mitsukurina*, *Striatolamia* and *Turania* have cusplets (Cappetta 2012). The morphology of the Trelde Næs teeth is close to teeth of *Anomotodon* but the Trelde Næs teeth are larger and have a more robust crown. The ornamented labial apron is only described in teeth of *Woellsteinia* (Reinecke *et al.* 2001).

Two species are reported from the Eocene; *Woellsteinia kozlovi* Adnet 2006a and *Woellsteinia hermani* (Zhelezko & Kozlov 1999). The last species has no folds on the teeth (Mannering & Hiller 2008). The Trelde Næs teeth have folds and seem therefore clos-

est to teeth of *Woellsteinia kozlovi* which also have a more robust crown than teeth of *Woellsteinia hermani* (Reinecke *et al.* 2001). The genus *Woellsteinia* has been reported from Germany (Reinecke *et al.* 2001), south-western France (Adnet 2006a) and Asia (Zhelezko & Kozlov 1999).

Family Lamnidae Müller and Henle 1838

Genus *Isurolamna* Cappetta 1976

Isurolamna affinis (Casier 1946)

Fig. 4A–F

Material. 45 anterior and 171 lateral teeth, including DK729da, DK729db and Lot OBH13.0.

Description. The anterior teeth measure from 13 to 20 mm apico-basally and from 9 to 11 mm mesio-distally. The crown is slender and lingually inclined in 28 teeth, whereas it is slightly distally inclined in 17 teeth. The lingual face is strongly convex, the labial face almost flat with a median depression adjacent to the almost straight crown–root junction. The enameloid is smooth on both faces. The cutting edges are worn, but when preserved they stop before the base of the crown. There is one pair of very small cusplets. In one of the best preserved teeth they are triangular, divergent and separated from the main cusp. The root shows two rounded lobes and the angle between the lobes varies from 90° to 120°. The basal root edge is arcuate. The lingual protuberance is marked and has a shallow, short nutritive groove or a round foramen.

The lateral teeth measure from 8 to 12 mm apico-basally and from 8 to 12 mm mesio-distally. The crown is triangular and straight in some of them and distally inclined in others. The crown is flattened labio-lingually with a convex lingual face and a flat labial face. The labial crown–root junction is straight. The cutting edges are well preserved and reach the base of the crown. On most of the teeth there is one pair of well-developed triangular cusplets, well separated from the main cusp in lingual view. On twenty teeth, the cusplets are doubled. The root lobes are rectangular or rounded, often with straight mesial and distal edges. The basal root edge is arcuate or straight with a small depression medially. The lingual protuberance is low and a shallow short nutritive groove is present on most of the teeth.

Comparison. The genus *Isurolamna* is characterized by a strong heterodonty, anterior teeth being of isuroid morphology and lateral teeth of lamnid morphology (Cappetta 1976). The Trelde Næs anterior teeth are sepa-

rated from teeth of Odontaspidae because of the very vestigial or lacking nutritive groove. They resemble teeth of *Isurus* Rafinesque 1810. The lateral teeth resemble teeth of Lamnidae because of the shallow and short nutritive groove. The Trelde Næs teeth are very similar to teeth of *Isurolamna* (Adnet 2006a). Two species are known from the Lower Eocene, *Isurolamna inflata* Leriche 1905 and *Isurolamna affinis* (Cappetta 2012). Teeth of *Isurolamna affinis* have very vestigial or lacking lateral cusplets on the anterior teeth and have a tendency to doubling of the cusplets on the lateral teeth, whereas teeth of *Isurolamna inflata* have regular but small cusplets on the anterior teeth and just one pair of cusplets on the lateral teeth (Adnet 2006a). *Isurolamna bajarunsai* Glikman & Zhelezko 1985 is known from the Middle Eocene of Kazakhstan. Its teeth differ from the Trelde Næs teeth by being significantly larger (Adnet 2006a). The Trelde Næs teeth seem closest to teeth of *Isurolamna affinis* and are similar to teeth figured by Casier (1966) and Cappetta (2012 fig. 203A–G).

Isurolamna affinis is known from the Ypresian of England (Casier 1966), the Eocene of south-western France (Adnet 2006a), the Eocene of Belgium (Nolf 1988; Eeckhaut & De Schutter 2009) and the Ypresian/Lutetian of North Germany (Diedrich 2012).

Genus *Macrorhizodus* Glikman 1964b

Macrorhizodus cf. nolfi Zhelezko 1999 in Zhelezko & Kozlov (1999)

Fig. 4G–L

Material. 20 anterior, 34 antero-lateral and 45 lateral teeth, including DK729ea, DK729eb and Lot OBH14.0.

Description. Specimens from the anterior files are long and robust. They measure from 30 to 48 mm apico-basally and from 15 to 23 mm mesio-distally. The cusp is stout with a lingual inclination in mesial view. The labial face is smooth and slightly convex, flatter at the base. The crown–root junction is curved and the enameloid extends a little over the labial root lobes. On most of the teeth there is a slight overhang of the enameloid to the root. The lingual face is strongly convex and smooth. The neck is narrow but marked and on half of the teeth there is a small crest basal to the neck. The cutting edges are marked and extend to the base of the crown. The root is very strong. The root lobes are long and the angle between the lobes varies from 45° to 90°. The root lobes are pointed and on the best preserved tooth there is a crest along the lingual margins of the root. In mesial view the root lobes are arched with the concavity located lingually. The lingual protuberance is strong and a single foramen is present on the best preserved teeth.

In teeth from the antero-lateral files the cusp is erect in mesial view and more triangular and shorter than in the anterior teeth. The specimens, which are probably from the antero-lateral files, are up to 28 mm apico-distally and up to 21 mm mesio-distally. The root lobes are more separated and of unequal length; the mesial lobe is longer and more pointed than the distal lobe.

The upper lateral teeth have a distally inclined crown with a concave distal cutting edge, and the lower lateral teeth have a symmetric crown with almost straight cutting edges (Shimada 2005). The crown is considerably lower (22 mm apico-distally) in the lateral teeth compared to the anterior teeth. It is triangular with some concavity at the labial base. In mesial view, the crown is straight. Most of the teeth have a short heel and the cutting edge follows that heel. In a few of them, there are vestigial cusplets or a bump on the heel. The labial crown-root junction is straight with a little overhang of the enameloid. The root is strong, the linguo-basal and the labial faces are flat and the lobes are widely spread and almost rectilinear. The basal edge is more or less concave. The lingual protuberance is weak and a foramen is present on the best preserved teeth.

Comparison. The Trelde Næs teeth have no cusplets which excludes them from the Odontaspidae. They have a robust design which excludes them from the Mitsukurinidae, and the enameloid is smooth as in teeth of Lamnidae (Cappetta 2012). *Macrorhizodus* was considered as a synonym of *Isurus* by Cappetta (1987), but its tooth design and morphology is different from the latter. The cutting edge is complete in teeth of *Macrorhizodus* whereas in teeth of *Isurus* it generally does not reach the base (Cappetta 2012). The Trelde Næs teeth compare very well with teeth of *Macrorhizodus*.

Macrorhizodus nolfi is described from the Lower Eocene (Zhelezko & Kozlov 1999; Rayner *et al.* 2009) and *Macrorhizodus praecursor* from the Eocene of Belgium (Leriche 1905). *Macrorhizodus (Oxyrhina) praecursor* was described by Leriche (1905) as the Eocene variation of the Oligocene *Macrorhizodus (Oxyrhina) desori* (Agassiz 1843), although there is no illustration of these teeth presented by the latter author. *Macrorhizodus nolfi* is the only species characterised by teeth with very small and vestigial lateral cusplets or bumps on the heels of the lateral teeth (Adnet 2006a). A few of the lateral teeth from Trelde Næs have very small cusplets or bumps on the heel and it is therefore suggested that they are close to teeth of *Macrorhizodus nolfi*. This is in

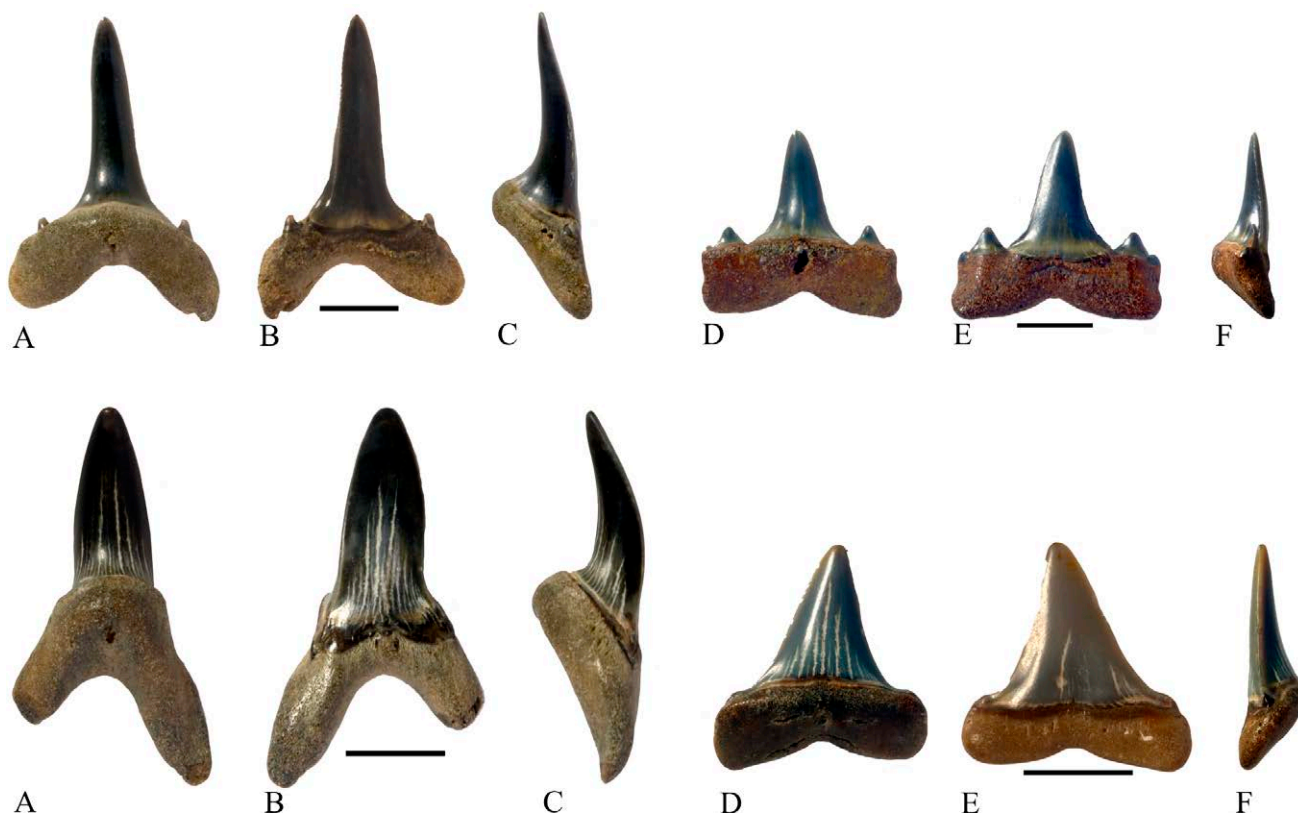


Fig. 4. A–F, *Isurolamna affinis*. A–C, anterior tooth DK729da. A, lingual view; B, labial view; C, mesial view. D–F, lateral tooth DK729db. D, lingual view; E, labial view; F, mesial view. Scale bars 5 mm. G–L, *Macrorhizodus cf. nolfi*. G–I, anterior tooth DK729ea. G, lingual view; H, labial view; I, mesial view. J–L, lateral tooth DK729eb. J, lingual view; K, labial view; L, mesial view. Scale bars 10 mm.

accordance with the age of the Lillebælt Clay Layer 2 to 6 interval which is dated to Ypresian/Lutetian (Heilmann-Clausen *et al.* 1985). However, the provenance of the Trelde Næs teeth is not known precisely because they were sampled from the beach. *Macrorhizodus nolfi* has been recorded in the Lower Eocene of the London Clay (Casier 1966; Rayner *et al.* 2009) and the Ypresian of Kazakhstan (Zhelezko & Kozlov 1999).

Family Xiphodolamiidae Glickman 1964a

Genus *Xiphodolamia* Leidy 1877

Xiphodolamia ensis Leidy 1877

Fig. 5A–C

Material. DK729f, one antero-lateral tooth.

Description. The tooth measures 13 mm apico-basally and 7 mm mesio-distally. The crown is slightly lingually inclined and bent distally at about 30°. The crown is slender with smooth enamel. The lingual face is strongly convex, the labial face slightly convex. The mesial cutting edge is partly worn, but it reaches the crown foot. The distal cutting edge is located only on the apical half of the tooth. A short distal heel is present. There are no cusplets.

The root is strong and high (5 mm apico-basally), wider mesio-distally than the base of the cusp and divided into two well defined square lobes. The distal lobe is twice the size of the mesial lobe measured mesio-distally. The lobes are close together. The lingual protuberance is marked and with a small foramen. The linguo-basal face of the root is flat as well as the labial face. The basal edges of the root lobes are straight.

Comparison. The square shape of the root of DK729f separates it from teeth of other lamniform sharks. The position of the cutting edges is unique in teeth of *Xiphodolamia* (Adnet *et al.* 2009). Five species of *Xiphodolamia* are mentioned by Cappetta (2012); *Xi-*

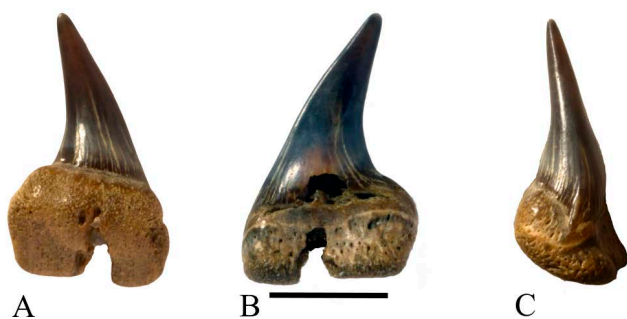


Fig. 5. A–C, *Xiphodolamia ensis*. Antero-lateral tooth DK729f. A, lingual view; B, labial view; C, mesial view. Scale bar 5 mm.

phodolamia ensis, *Xiphodolamia barbadica*, *Xiphodolamia eocaena*, *Xiphodolamia zignoi* and *Xiphodolamia serrata*. They are probably synonyms except for *Xiphodolamia serrata*, which possesses serrated cutting edges (Adnet *et al.* 2009; Cappetta 2012). DK729f is probably from one of the antero-lateral files because of the complete mesial cutting edge and the apically placed distal cutting edge (Adnet *et al.* 2009). DK729f separates from teeth of *Xiphodolamia serrata* by the absence of serration on the cutting edges. It resembles teeth figured as *Xiphodolamia ensis* by Woodward (1899 pl. 1 fig. 8), Adnet *et al.* (2009, fig. 2) and Rayner *et al.* (2009 p. 105). *Xiphodolamia ensis* is known for instance from the Early Ypresian London Clay (Rayner *et al.* 2009), the Eocene of Belgium (Eeckhaut & De Schutter 2009) and the Ypresian/Lutetian of North Germany (Diedrich 2012).

Family Alopiidae Bonaparte 1838

Genus *Alopias* Rafinesque 1810

Alopias crochardi Ward 1978

Fig. 6A–F

Material. 24 anterior and 24 lateral teeth, including DK729ga, DK729gb, MM0070, MM0058 and Lot OBH16.0.

Description. Teeth measure up to 13 mm apico-basally and 11 mm mesio-distally. The cusp is pointed, symmetric and slender with a lingual inclination in the anterior teeth. The lingual face is smooth and convex. The lingual crown–root junction is marked by a pronounced neck. Labially the crown enameloid expands in a thin layer over the root lobes. The labial crown face is slightly convex and in some teeth there is a medial depression basally. In most of the teeth the cutting edges are worn, but when they are present they are sharp and reach the base of the crown and become fainter over the short heels. The root is bi-lobed with a semi-circular basal face. The lobes are slim and rounded. The lingual protuberance is strong with a shallow nutritive groove.

The lateral teeth are smaller in size and straighter in mesial view and the crown is more triangular and bent distally compared to the anterior teeth. The mesial border in the most lateral teeth has a sinusoidal shape with a small bump over the heel. The distal border is strongly concave at the base and slightly convex near the apex. There are no cusplets but in a few teeth the heels have low callosities. The root is bi-lobed with a semi-circular basal edge in most of the teeth. The lobes are linguo-labially flattened and the mesial lobe is the longest. The linguo-basal face of the root is flat. The lingual protuberance is well developed and in most of the teeth the nutritive groove is long and deep.

Comparison. The Trelde Næs teeth have no cusplets which separates them from teeth of Odontaspidae and *Usakias* Zhelezko & Kozlov 1999. The crown face is smooth unlike on most of the teeth of Mitsukurinidae (Cappetta 2012). The teeth compare well to the general description of teeth of *Alopias* by Ward (1978).

There are three living species of *Alopias*: *Alopias superciliosus* Lowe 1841, *Alopias vulpinus* Bonnaterre, 1788 and *Alopias pelagicus* Nakamura 1935. *Alopias superciliosus* has teeth with a slender gracile crown and a well-developed lingual groove on the root, *Alopias vulpinus* has teeth with a broader triangular crown and no lingual groove on the root, and *Alopias pelagicus* has teeth with small denticles on the distal heel (Ward 1978). The teeth from Trelde Næs are closest to the *Superciliosus* group.

At least four species have been described from the lower Eocene: *Alopias crochardi* Ward 1978, *Alopias leeensis* Ward 1978, *Alopias denticulatus* Cappetta 1981 and *Alopias alabamensis* White 1956. Teeth of *Alopias denticulatus* have small vestigial cusplets, and teeth of *Alopias alabamensis*, *Alopias latidens alabamensis* and *Alopias leeensis* have a broad crown (Ward 1978; Zalmout *et al.* 2012 fig. 4 AA and BB). The teeth from Trelde Næs are very similar to teeth of *Alopias crochardi* (Rayner *et al.* 2009, p. 113), but we cannot rule out the possibility that some of the teeth attributed to *Alopias crochardi* represent worn teeth of *Alopias denticulatus* (see the discussion below on the teeth of *Usakias* sp.).

Genus *Usakias* Zhelezko & Kozlov 1999

Usakias sp.

Fig. 6G–L

Material. 47 anterior and antero-lateral and 16 lateral teeth, including DK729ha, DK729hb and Lot OBH17.0. All the teeth are more or less worn.

Description. The anterior and antero-lateral teeth measure up to 14 mm apico-basally and up to 11 mm mesio-distally. The anterior teeth have a straight crown in lingual view and the antero-lateral teeth are slightly inclined distally. The crown is slim, triangular and lingually inclined, but not of sigmoidal shape. The lingual face is strongly convex, the labial face is slightly convex often with a basal triangular depression. The enameloid is smooth on both faces. On the labial face the enameloid extends over the apical part of the root lobes. The lingual crown–root junction is well marked by a depressed neck. At the labial crown–root junction, the enameloid is overhanging the root, sometimes as a bulge. The cutting edges, when preserved, are sharp and stop well before the crown base. There is one pair of small cusplets emerging from the labial extension over the root lobes. They are worn on most of the teeth, but when well-preserved they are pointed and hook-shaped.

The root is bi-lobed and symmetric in the anterior teeth and slightly asymmetrical in the antero-lateral

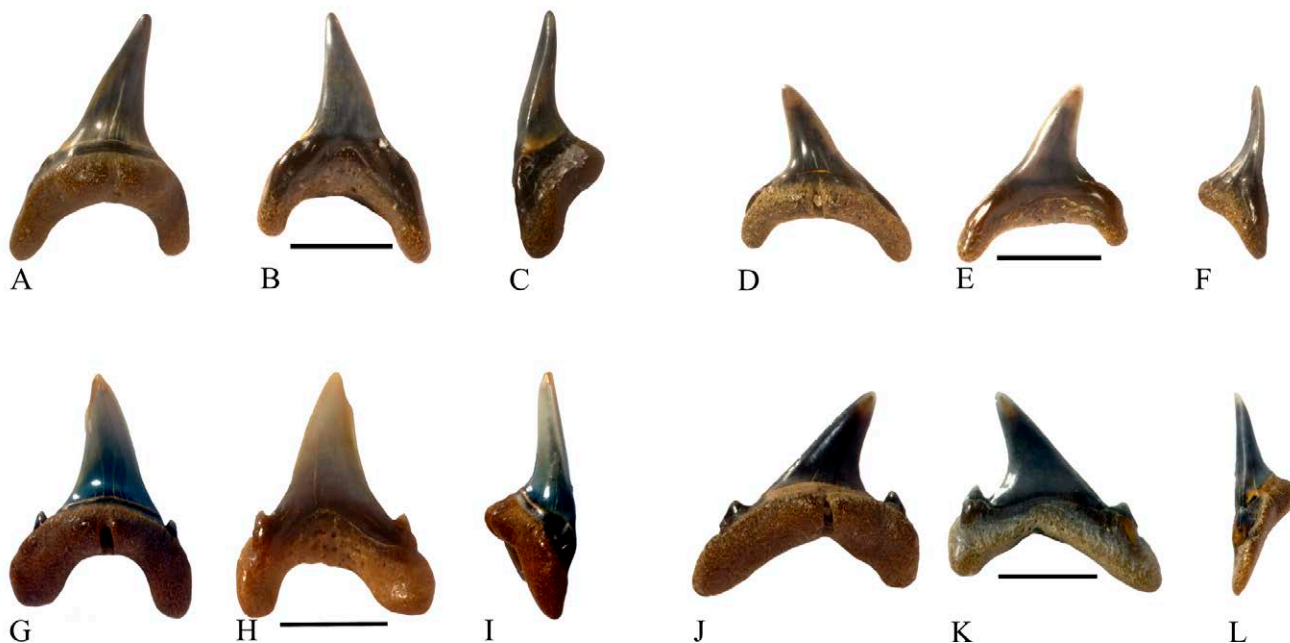


Fig. 6. A–F, *Alopias crochardi*. A–C, anterior tooth DK729ga. A, lingual view; B, labial view; C, mesial view. D–F, lateral tooth DK729gb. D, lingual view; E, labial view; F, mesial view. G–L, *Usakias* sp. G–I, anterior tooth DK729ha. G, lingual view; H, labial view; I, mesial view. J–K, lateral tooth DK729hb. J, lingual view; K, labial view; L, mesial view. All scale bars 5 mm.

teeth, the mesial lobe being longer than the distal one. The root lobes are slim and rounded, and the basal root edge is semi-circular. The lingual protuberance is strong with a long and sometimes deep nutritive groove.

The lateral teeth are of the same size and have a distally inclined crown which is straight in mesial view. The cutting edges run to the base of the crown where they are in continuity with the cutting edge of the low broad cusplets. The root lobes are more spread out and the lingual protuberance is weaker than in the anterior and antero-lateral teeth; they still bear a nutritive groove.

Comparison. The Trelde Næs teeth morphology is typical for teeth of Alopiidae with a labial enameloid extension over the root and a C-shaped root. They separate from teeth of *Alopias* by having well developed cusplets and incomplete cutting edges on the anterior teeth. *Alopias denticulatus* also has cusplets, but they are vestigial and not hook-shaped (Adnet 2006a), contrary to the teeth from Trelde Næs which all have well developed cusplets. Zhelezko & Kozlov (1999) erected the genus *Usakias* for alopiid teeth with cusplets and included *Alopias denticulatus*

but excluded *Alopias crochardi* where cusplets are not present. However, Adnet (2006a) preferred to retain *Alopias denticulatus* as different from *Usakias* based on the size and shape of the cusplets.

The Trelde Næs teeth are worn and it is not possible to assign them with confidence to a specific species and particularly to *Usakias asiaticus* Kozlov 2000, the unique species in the Lower Eocene, and it is even possible that some of them are teeth of *Alopias denticulatus*.

Usakias is known from the Lower and Middle Eocene of Kazakhstan (Zhelezko & Kozlov 1999), North Germany (Diedrich 2012) and Belgium (Eeckhaut & De Schutter 2009).

Family Otodontidae Glikman 1964b

Genus *Carcharocles* Jordan and Hannibal 1923

Carcharocles auriculatus (Blainville 1818)

Fig. 7A–F

Material. 26 teeth, most of them fragmentary, including DK729ia, DK729ib, Lot OBH18.0 and Lot MM10.0.

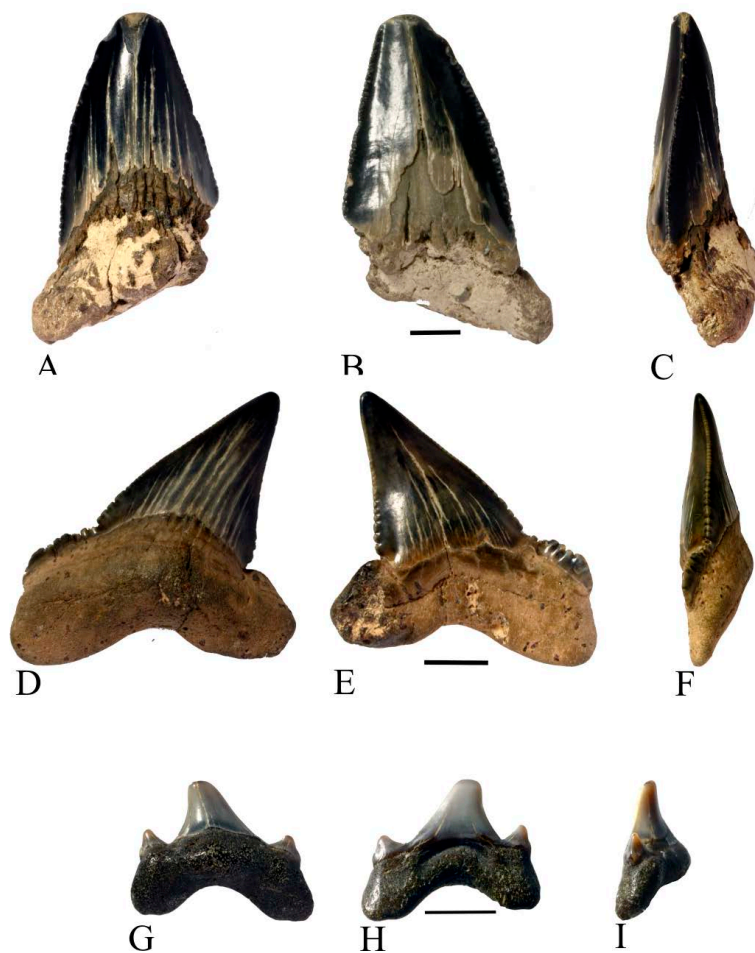


Fig. 7. A–F, *Carcharocles auriculatus*. A–C, anterior tooth DK729ia. A, lingual view; B, labial view; C, mesial view. D–F, lateral tooth DK729ib. D, lingual view; E, labial view; F, mesial view. Scale bars 10 mm. G–I, *Otodus* cf. *obliquus*. Lateral tooth DK729j. G, lingual view; H, labial view; I, mesial view. Scale bar 5 mm.

Description. The largest tooth measures approximately 65 mm apico-basally. One of the root lobes and the cusplets are missing. The intact tooth would have been about 45 mm mesio-distally. Both crown faces are smooth and convex, the lingual face more so than the labial face. The crown is rather narrow and almost symmetrical, very robust and triangular. The cutting edges are irregularly serrated from the apex to the base of the crown. On the lingual face, the band at the base of the crown is clearly chevron-shaped. This tooth is believed to be from the anterior files because of its symmetrical shape.

The best preserved tooth measures 38 mm apico-distally and 42 mm mesio-distally. Only a small part of the distal lobe of the root is missing on the labial side. The crown is robust, triangular and inclined 45° distally. The lingual face is more convex than the labial face, especially near the base. The crown is more linguo-labially compressed than in the anterior tooth. The cutting edges are irregularly serrated from the base to the apex. The mesial cutting edge is convex, whereas the distal one is slightly concave. At the base of the mesial cutting edge, there is a broad cusplet with six irregular serrations. The distal cusplet is worn out. On the lingual face, the band at the base of the crown is clearly chevron-shaped. The root is nearly half the size of the total height of the tooth. It shows two widely separated rounded lobes. The mesial lobe is larger and thicker than the distal lobe. The basal edge is arc-shaped in lingual view. The lingual protuberance is not very salient and lacks a nutritive foramen. This tooth is believed to be from the lateral files because of its asymmetric crown.

Two smaller teeth (18–20 mm apico-basally) have an even more inclined crown and their lingual band is not clearly chevron-shaped. These teeth are believed to be from the posterior files.

Comparison. The teeth are very large and thereby separated from most other teeth just by their size. Teeth of *Otodus obliquus* Agassiz 1843 are also large, but they are not serrated as the Trelde Næs teeth are. The only genus with teeth similar to these teeth is *Carcharocles*.

It is believed by most authors (Cappetta 2012) that *Carcharocles* belongs to the Otodontidae, but still a few authors refer these very large teeth to the Lamnids (Purdy *et al.* 2001). Cappetta (2012) considers *Carcharocles* to be a subgenus of *Otodus*. In our opinion this is to make it more complicated than necessary. The transition from the non-serrated teeth of *Otodus obliquus* to the regularly serrated teeth of *Carcharocles megalodon* Agassiz 1843 is best described by the acquisition of partial serration in teeth of *Otodus subserratus* (Agassiz 1843) to full irregular serration in teeth of *Carcharocles auriculatus* and subsequent loss of the

side cusplets in teeth of *Carcharocles megalodon* where the serration is regular. Teeth with fine but irregular partial serration have been called *Otodus obliquus* var. *mugodzharcicus* Zhelezko in Zhelezko & Kozlov 1999, but they are probably synonymous with *Carcharocles aksuaticus* Menner 1928, which occupies the morphospace between *Otodus obliquus* and *Carcharocles auriculatus* (<http://www.elasmo.com/>). The Trelde Næs teeth are separated from the partially serrated teeth of *Otodus obliquus* var. *mugodzharcicus* by their completely serrated cutting edges. They seem closest to teeth of *Carcharocles auriculatus* because of the narrow crown in the anterior teeth, their broad cusplets and the complete and irregular serration of the cutting edges on the main cusp as well as on the cusplets (Cappetta 2012). *Carcharocles auriculatus* is known from the Early to Late Eocene (Ward & Wiest 1990; Long 1992; Eeckhaut & De Schutter 2009; Diedrich 2012).

Genus *Otodus* Agassiz 1843

Otodus cf. *obliquus* Agassiz 1843

Fig. 7G–I

Material. 3 worn lateral teeth, including DK729j and Lot OBH19.0.

Description. The teeth measure about 11 mm apico-basally and 13 mm mesio-distally. The crown is triangular, broad and inclined distally at about 20°. In mesial view it is almost straight. The lingual face is strongly convex, the labial face almost flat. The enameloid is smooth. The cutting edges are not serrated and reach the base of the crown. The labial crown–root junction is arcuate and the enameloid overhangs the root slightly. The lingual crown–root junction is marked by a broad, slightly chevron-shaped neck. There is one pair of cusplets; they are 2 mm high, diverging and pyramid-shaped. The root is very strong (about 50% of the total height of the tooth). The lobes are round, more or less spread out and with labio-lingually flattened extremities. The basal root edge is C-shaped. The lingual protuberance is not very marked and there is no nutritive groove, but a small foramen is present.

Comparison. The Trelde Næs teeth resemble teeth of *Cretalamna* Glikman 1958, but they have a more robust root and a wider crown. The Trelde Næs teeth compare well with teeth of *Otodus*. They are much worn and cannot be identified to species level with confidence.

Otodus appeared in the lower Paleocene (Zhelezko & Kozlov 1999) and is known from the Ypresian of the London Clay in England (Rayner *et al.* 2009) and from northern Africa in Morocco (Arambourg 1952; Noubhani & Cappetta 1997). *Otodus obliquus* is mostly

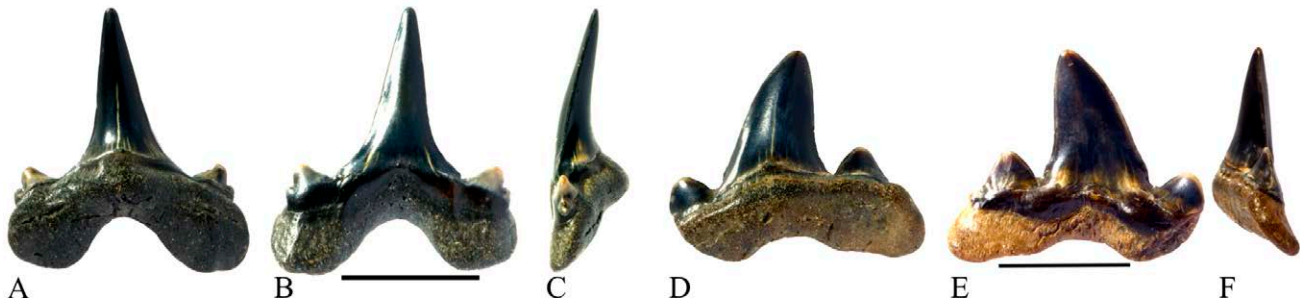


Fig. 8. A–F, *Cretalamna* aff. *appendiculata*. A–C, anterior tooth DK729ra. A, lingual view; B, labial view; C, distal view. D–F, lateral tooth DK729rb. D, lingual view; E, labial view; F, distal view. Scale bars 10 mm.

restricted to the Eocene but has also been mentioned from the Late Paleocene of Kazakhstan (Kordikova *et al.* 2001) and Denmark (Reinecke & Engelhard 1997).

Genus *Cretalamna* Glikman 1958

Cretalamna aff. *appendiculata* (Agassiz 1843)

Fig. 8A–F

Material. 1 anterior and 2 worn lateral teeth, including DK729ra, DK729rb and Lot OBH29.0.

Description. The anterior tooth measures 19 mm apico-basally and 17 mm mesio-distally. The crown is not very broad, triangular and upright in lingual view and with a slight lingual inclination. The lingual face is convex, the labial face less so with a shallow depression basally. The enameloid is smooth. There are two pairs of low cusplets. The inner ones are triangular and diverging, the outer ones vestigial and not fully separated from the inner ones. The root is low with two rounded lobes. The basal edge of the root is U-shaped. The lingual protuberance is not very strong and there is no nutritive groove.

The lateral teeth measure 11 to 16 mm apico-basally and 9 to 18 mm mesio-distally. The crown is stout with a strongly convex lingual face; the labial face is slightly convex in the apical half and with a median depression in the basal part. The crown is inclined at about 10° distally. The mesial cutting edge is convex, the distal one straight. The cutting edges are not serrated and reach the base of the crown. The enameloid is smooth. There is one pair of 2–3 mm high diverging cusplets which are triangular and pectinated with cutting edges. The lingual crown–root junction is marked and slightly chevron shaped. The labial crown–root junction is medially concave. The enameloid covers and overhangs the apical third of the root under the cusplets. The root is low with widely spread round root

lobes. The tip of the mesial root lobe is missing on the largest tooth. The basal edge of the root is medially concave and U-shaped. The lingual protuberance is not very prominent and there is no sign of a nutritive groove or foramen.

Comparison. The Trelde Næs teeth resemble teeth of *Otodus obliquus* but are considerably smaller. *Otodus* is characterized by a robust root and a wide crown in contrast to teeth of *Cretalamna* where the root is lower and the cusp more narrow (Ward personal communication 2013). The morphology of the Trelde Næs teeth shares with those of *Cretalamna* a narrow crown on the anterior tooth, a broad triangular cusplets and a lack of a nutritive groove on the low root (Shimada 2007). Teeth of *Cretalamna appendiculata* have one pair of cusplets whereas teeth of *Cretalamna maroccana* Arambourg 1935 have two pairs of cusplets. However, isolated teeth of *Cretalamna appendiculata* type are notoriously difficult to identify at species level (Siverson *et al.* in press).

Traditionally *Cretalamna* is assigned to the family Cretoxyrhinidae but its exact relationships are uncertain; it has been suggested (Siverson 1999; Shimada 2007; Underwood & Cumbaa 2010; Siverson *et al.* in press) that *Cretalamna* should instead be assigned to the Otodontidae, based on the striking similarities in the tooth morphology between the *Otodus obliquus* group and the Late Cretaceous *Cretalamna*. *Cretalamna* is known from the Lower Cretaceous to the Priabonian, and in the Lower Eocene chiefly by the species *Cretalamna appendiculata* (Cappetta 2012) which has been reported from the Early Ypresian London Clay (Rayner *et al.* 2009), the Ypresian/Lutetian of south-western France (Adnet 2006a) and the Ypresian/Lutetian of Morocco (Noubhani & Cappetta 1997). However, the species *Cretalamna appendiculata* appears to be restricted to the Late Cretaceous (Siverson *et al.* in press) and the Eocene specimens are likely to belong to a different species, not yet named.

Family Odontaspidae Müller & Henle
1839

Genus *Palaeohypotodus* Glikman 1964b

Palaeohypotodus rutoti (Winkler 1876a)
Fig. 9A–F

Material. Two teeth: DK729ka and DK729kb.

Description. The anterior tooth (DK729ka) measures 22 mm apico-basally and 8 mm mesio-distally. The crown is slender and very slightly distally inclined in labial view and lingually inclined with a sigmoidal shape. The cutting edges stop just before the base of the main cusp and are labially displaced near the base.

There are coarse striations at the base of the labial face along the crown–root junction. Otherwise the enameloid is smooth. There are two cusplets separated from the main cusp on the mesial side. On the distal side, the root and the cusplets are not preserved. The inner cusplet is high (3 mm), pointed and lingually inclined. The outer cusplet is smaller and hook-shaped. The preserved root lobe is long, almost vertical, and mesio-distally compressed. The lingual protuberance is strong with a long deep nutritive groove.

The lateral tooth (DK729kb) measures 8 mm apico-basally and 8 mm mesio-distally. The crown is slender, triangular and upright. It is lingually inclined in mesial view. The lingual face is more convex than the labial face. The cutting edges are not serrated and do not reach the base of the cusp. Two cusplets are present



Fig. 9. A–J, *Palaeohypotodus rutoti*. A–C, anterior tooth DK729ka. A, lingual view; B, labial view; C, mesial view. D–F, lateral tooth DK729kb. D, lingual view; E, labial view; F, distal view. G–L, *Odontaspis* cf. *winkleri*. G–I, anterior tooth DK729la. G, lingual view; H, labial view; I, mesial view. J–L, lateral tooth DK729lb. J, lingual view; K, labial view; L, mesial view. All scale bars 5 mm.

on each side of the main cusp. The inner ones are high (almost half the height of the main cusp) and pointed, bending lingually. The outer ones are very small and diverge from the main cusp. Several vertical bulges or strong folds are present at the labial base of the cusp and the cusplets, otherwise the enameloid is smooth. The root is high, half the total height of the tooth. The lobes are long and rounded and the basal edge is arch-shaped. The lingual protuberance is marked and bears a deep nutritive groove.

Comparison. Basal labial ridges are seen on teeth of *Hispidaspis* Sokolov 1978 and *Cenocarcharias* Cappetta & Case 1999 but DK729ka–b can be separated from these by their very high cusplets (Cappetta 2012). Teeth of *Johnlongia* Siverson 1996 also have labial coarse ornamentation and high cusplets but separate from DK729ka–b because their ornamentation, contrary to the latter, covers a great part of the labial face of the cusp (Cappetta 2012). Labial ornamentation can sometimes be seen on teeth of *Odontaspis*, but it is never as coarse as in DK729ka–b (Cappetta & Nolf 2005; Mannering & Hiller 2008).

It is always difficult to identify a genus from just two teeth, but DK729ka–b seem very close to *Palaeohypotodus*. Cappetta & Nolf (2005) refer to this genus as being monospecific.

Palaeohypotodus rutoti has been described from the Early Eocene of Belgium (Iserbyt & De Schutter 2012), the Paleocene and Eocene of France (Cappetta & Nolf 2005), the Late Paleocene of North America (Ward & Wiest 1990), the Upper Danian of Greenland (Bendix-Almgreen 1969), the Early Eocene London Clay of England (Rayner *et al.* 2009) and the Eocene of Antarctica (Long 1992).

Genus *Odontaspis* Agassiz 1838

Odontaspis cf. *winkleri* Leriche 1905

Fig. 9G–L

Material. 6 anterior and 3 lateral teeth, including DK729la, DK729lb and Lot OBH21.0.

Description. The teeth measure from 10 to 25 mm apico-basally and from 8 to 15 mm mesio-distally. The crown is very slim, upright in lingual view and lingually inclined in mesial view. The lingual face is more convex than the labial face. The cutting edges are not serrated and do not reach the base of the crown on the six anterior teeth. On the three lateral teeth, they stop just at the base of the crown and there are coarse serrations on the basal 1 mm of the cutting edge. The lingual crown face is smooth. The enameloid on the labial crown face expands over the apical part of the root lobes and on three teeth there are faint vertical

fold in the enameloid extension at the base of the cusplets. There are two pairs of cusplets; the inner ones are high (2–4 mm) and the outer ones vestigial. The inner cusplets are pointed, slightly lingually inclined, without cutting edges and circular at the base.

The root lobes are long and slim with an arcuate basal edge. The angle between the lobes varies from 80° to 110°. The lingual protuberance is very marked and there is a deep nutritive groove with one foramen.

Comparison. When compared with those of other odontaspids, the Trelde Næs teeth separate from those of *Carcharias*, *Jaekelotodus* Menner 1928, *Hypotodus* Jaekel 1895 and *Sylvestrilamia* Cappetta & Nolf 2005, which never possess cusplets as high as the Trelde Næs ones. Well-developed cusplets are present in teeth of *Odontaspis*, *Brachycarcharias* Cappetta & Nolf 2005, *Orpodon* Cappetta & Nolf 2005 and *Palaeohypotodus* (Cappetta 2012). However, teeth of *Brachycarcharias* have a broader crown and a lingually ornamented crown face (Cappetta & Nolf 2005) and teeth of *Orpodon* are much smaller. Teeth of *Palaeohypotodus* have a pronounced coarse labial ornamentation at the base of the crown (Cappetta 2012), whereas the labial ornamentation on the Trelde Næs teeth is faint and restricted to the base of the cusplets. The incomplete cutting edges are characteristic of anterior teeth of *Odontaspis* (Mannering & Hiller 2008). Basal serrations on the cutting edge are present on teeth of *Mennerotodus* Zhelezko 1994, *Hispidaspis*, *Palaeohypotodus* and *Jaekelotodus* (Cappetta 2012), but can also be seen on the lateral teeth of *Odontaspis winkleri* (Ward personal communication 2013). The slender crown, relatively high cusplets, short cutting edges and labial folds are seen on teeth of *Odontaspis winkleri* and *Odontaspis speyeri* Darteville & Casier 1943; however the more slender teeth of *Odontaspis winkleri* compare best to the Trelde Næs teeth (Leriche 1905, Arambourg 1952, Mannering & Hiller 2008).

Odontaspis winkleri is known from the Eocene of Belgium (Leriche 1905; Nolf 1988; Eeckhaut & De Schutter 2009), the Lower Eocene of England (Casier 1966, Rayner *et al.* 2009), the Ypresian/Lutetian of France (Adnet 2006a; Dutheil *et al.* 2006) and North Germany (Diedrich 2012).

Genus *Jaekelotodus* Menner 1928

Jaekelotodus robustus (Leriche 1921)

Fig. 10A–F

Material. 5 anterior and 6 lateral teeth, including DK729ma, DK729mb and Lot OBH22.0.

Description. The anterior teeth measure from 24 to 33 mm apico-basally and from 16 to 20 mm mesio-distally. The crown is triangular, symmetric, stout and slightly lingually inclined. The lingual face is strongly convex, the labial face almost flat with a basal median depression. The enameloid expands over the apical part of the root lobes on the labial face and the enameloid overhangs the root. The labial crown-root junction is V-shaped. The cutting edges are sharp and reach the crown base. There are two pairs of cusplets on three teeth, one pair on the other two teeth. The cusplets are 2–3 mm high, pointed, hook-shaped and inclined lingually. When present the second pair of cusplets is very small and not completely separated from the inner cusplets.

The lateral teeth measure from 16 to 22 mm apico-basally, and from 17 to 22 mm mesio-distally. The crown is erect in mesial view and more or less distally inclined. The lingual face is convex, the labial face flat with a basal median depression. The enameloid is overhanging the root on the labial face. The crown-root junction is concave in its median part. The cutting edges are sharp and reach the crown base. The distal edge is concave, the mesial one straight or convex.

There are two pairs of cusplets on all the lateral

teeth. The inner ones are pointed and lingually inclined; the outer ones are vestigial and not completely separated from the inner ones. The root has two widely spread rounded lobes, labio-lingually flattened at their extremities. The basal root edge is arcuate with a median concavity in three specimens. The lingual protuberance is not very prominent and there is a shallow nutritive groove with a small foramen.

Comparison. The cusplets are short on the Trelde Næs teeth and thereby they are separated from teeth of *Odontaspis*, *Orpodon*, *Palaeohypotodus* and *Brachycarcharias*. Teeth of *Hypotodus* also have one or two pairs of hooked short cusplets, but they differ from the Trelde Næs teeth by their cutting edge, which never reaches the crown base (Cappetta 2012). The very robust crown and the complete cutting edge are only seen in teeth of *Jaekelotodus*. Two species of *Jaekelotodus* are described from the Paleogene (Nolf 1988; Cappetta & Nolf 2005), *Jaekelotodus trigonalis* Jaekel 1895 and *Jaekelotodus robustus*. Teeth of *Jaekelotodus trigonalis* separate from teeth of *Jaekelotodus robustus* by always having two pairs of cusplets on the anterior teeth and having higher cusplets on the lateral teeth (Cappetta and Nolf 2005). The Trelde Næs teeth have one or two

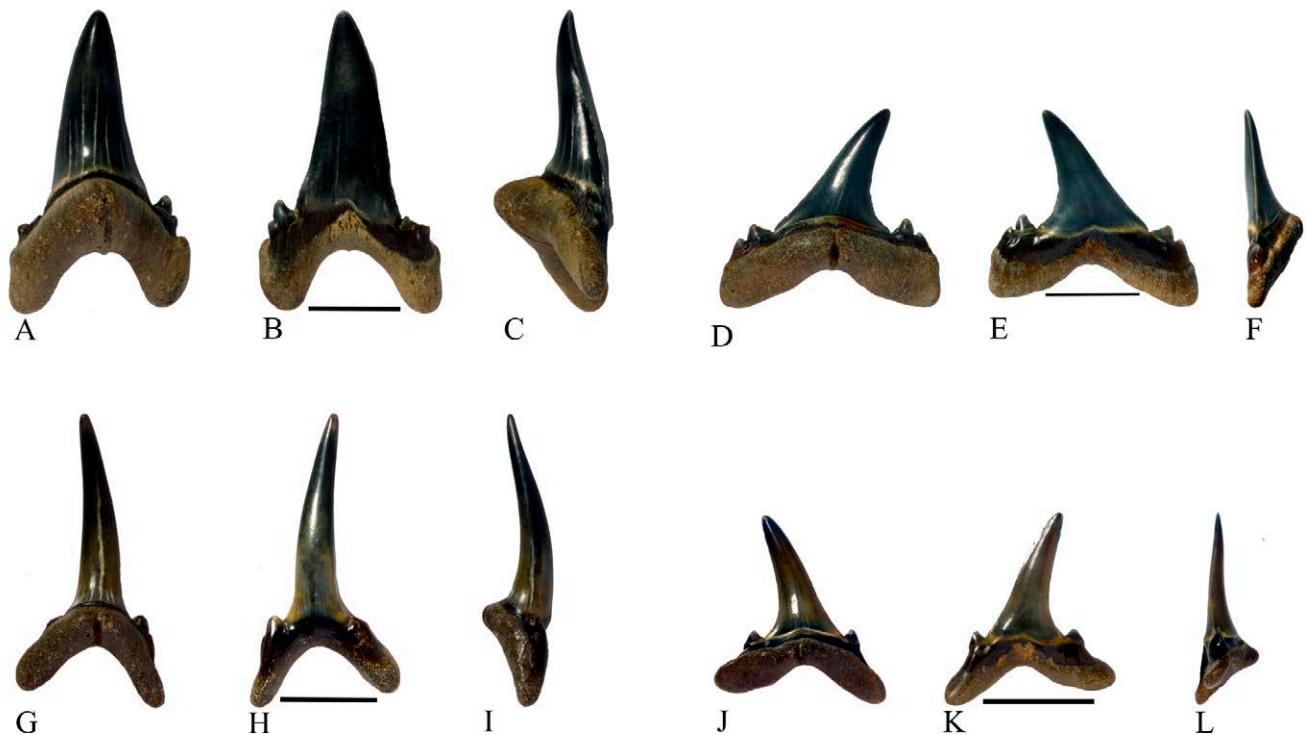


Fig. 10. A–F, *Jaekelotodus robustus*. A–C, anterior tooth DK729ma. A, lingual view; B, labial view; C, distal view. D–F, lateral tooth DK729mb. D, lingual view; E, labial view; F, mesial view. G–L, *Carcharias* sp. sensu Cappetta & Nolf 2005. G–I, anterior tooth DK729na. G, lingual view; H, labial view; I, mesial view. J–L, lateral tooth DK729nb. J, lingual view; K, labial view; L, distal view. All scale bars 10 mm.

cusplets on the anterior teeth and seem closest to teeth of *Jaekelotodus robustus*.

Jaekelotodus robustus is known from the Eocene of Belgium (Nolf 1988; Eeckhaut & De Schutter 2009), the Eocene of North Germany (Diedrich 2012) and the Eocene of England (Casier 1966; Rayner *et al.* 2009).

Genus *Carcharias* Rafinesque 1810

Carcharias sp. sensu Cappetta & Nolf 2005

Fig. 10G–L

Material. 8 anterior and 6 lateral teeth, including DK729na, DK729nb and Lot OBH23.0.

Description. The anterior teeth measure from 12 to 32 mm apico-basally and from 7 to 15 mm mesio-distally. Two teeth are significantly smaller and better preserved than the other ones, which are worn. The crown is high and narrow, almost upright in labial view and more or less lingually inclined. The lingual face is strongly convex, the labial face slightly convex. The enameloid is smooth except for one tooth where there are faint signs of ornamentation on the lingual face. The cutting edges are worn on most of the teeth, but when preserved they are sharp and do not reach the base of the crown. There is one pair of small cusplets which are pointed, hook-shaped and lingually inclined. The lingual crown–root junction is marked by a distinct neck, the labial enameloid overhangs the root to some degree and the junction is arcuate. The enameloid extends over the apical part of the labial root lobes. The root is with two long rounded lobes, the angle between which is about 90°. The lingual protuberance is marked and with a long nutritive groove. The two small teeth are either from a juvenile or from the upper intermediate file.

The lateral teeth are almost the same size and measure about 15 mm apico-basally and 15 mm mesio-distally. They are better preserved than the anterior teeth. The crown is more or less distally inclined and the labial face is almost flat. On one tooth, there are very fine lingual striations. In mesial view the crown is straight. The cutting edges reach the base of the crown. The cusplets are triangular in labial view, pointed and slightly lingually inclined. On the best preserved tooth, there is no interruption of the cutting edge between the main cusp and the cusplets. The root is low with widely spread symmetric and rounded lobes. The lingual protuberance is not very strong and there is a long deep nutritive groove.

Comparison. The Trelde Næs teeth differ from teeth of most other Odontaspidae because of the lingual ornamentation which is only seen on teeth of *Turania*,

Brachycarcharias, *Sylvestrilamia* and sometimes *Carcharias*. Teeth of *Brachycarcharias* have a more robust crown and longer cusplets than the Trelde Næs teeth, and anterior teeth of *Sylvestrilamia* are less than 20 mm high (Cappetta & Nolf 2005). Teeth of *Turania* have strong ornamentation covering most of the lingual crown face (Cappetta 2012). The Trelde Næs teeth are close to the teeth described as *Carcharias* sp. by Cappetta & Nolf (2005). They have only faint ornamentation, which probably results from wear. The cutting edges are fairly long on the Trelde Næs teeth and thereby differ from the Miocene *Carcharias acutissima* Agassiz 1843 figured by Cappetta (2012, fig. 183) where the cutting edges are short. The genus *Carcharias* is known from the Late Cretaceous to the Recent (Cappetta 2012).

Genus *Turania* Kozlov 2001

Turania sp.

Fig. 11A–F

Material. 4 anterior and 1 lateral teeth, including DK729oa, DK729ob and Lot OBH24.0.

Description. The anterior teeth measure from 23 to 27 mm apico-basally and from 14 to 15 mm mesio-distally. The crown is very slender and upright in labial view and lingually inclined in mesial view. The lingual face is convex, whereas the labial face is slightly convex with a slight median depression basally. The enameloid on the lingual face is ornamented with strong longitudinal folds covering most of the crown except the tip. The labial face is smooth. The cutting edges are well developed and reach the base of the crown on one tooth and stop before the base on three teeth. The lingual crown–root junction is marked with a distinct neck. On the labial face, the enameloid expands basally over the root lobes, overhangs the root, and the crown–root junction is V-shaped. There is one pair of well separated small pointed cusplets slightly diverging and lingually bent. There are no cutting edges on the cusplets. The root has two long symmetrical lobes; the angle between the lobes varies from 70° to 90°. The lobe extremities are pointed and flattened labio-lingually. The lingual protuberance is well developed and there is a deep nutritive groove.

The lateral tooth measures 16 mm apico-basally and 12 mm mesio-distally. The crown is upright in labial view and slightly lingually bent. The cutting edges reach the base of the crown. The lingual crown face is ornamented, the labial face is smooth. The lingual crown–root junction is marked with a distinct neck, the labial one is straight. There is one pair of cusplets, which are well separated from the crown and of tri-

angular shape with signs of worn cutting edges. The root is low with two widely spread rounded flat root lobes. The lingual protuberance is low with a shallow nutritive groove and one foramen.

Comparison. The Trelde Næs teeth differ from teeth of most other Odontaspididae because of the lingual ornamentation which is only seen on teeth of *Turania*, *Sylvestrilamia*, *Brachycarcharias* and sometimes *Carcharias*. Teeth of *Brachycarcharias* have a more robust crown and longer cusplets than the Trelde Næs teeth, and anterior teeth of *Sylvestrilamia* are less than 20 mm high (Cappetta & Nolf 2005). The Trelde Næs teeth are close to the teeth described as *Turania* (Cappetta 2012). They are also close to teeth of *Striatolamia*, but these teeth have very small cusplets and weaker ornamentation. *Turania* is described from the Lower Bartonian of Kazakhstan (Kozlov 2001). Cappetta (2012) consider that the validity of the genus is not established with certainty.

Genus *Hypotodus* Jaekel 1895

Hypotodus verticalis (Agassiz 1843)

Fig. 11G–L

Material. 6 antero-lateral and 1 lateral teeth, including DK729pa, DK729pb and Lot OBH25.0

Description. The antero-lateral teeth measure from 17 to 24 mm apico-basally and from 12 to 14 mm mesio-distally. The crown is triangular, upright and in two specimens lingually inclined. The enameloid is smooth on both faces. The lingual face is convex, the labial face less so, sometimes with a small short basal median ridge. The cutting edges are marked and they almost reach the base of the crown. The labial crown–root junction is concave apically. There is no significant enameloid overhang of the root. There is one pair of cusplets. They are small (1–2 mm high), hook-shaped, pointed and directed lingually and in

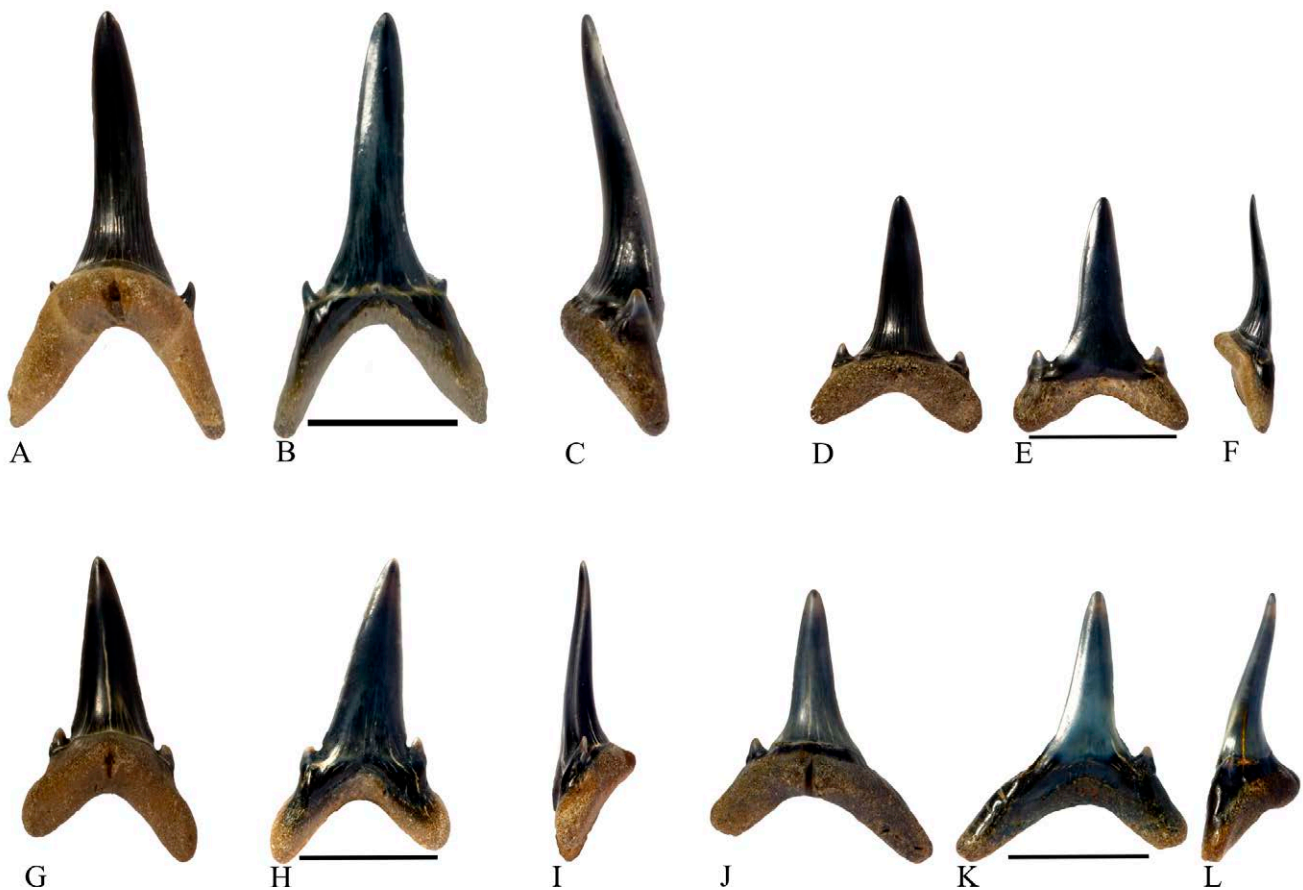


Fig. 11. A–F, *Turania* sp. A–C, anterior tooth DK729oa. A, lingual view; B, labial view; C mesial view. D–F, lateral tooth DK729ob. D, lingual view; E, labial view; F, mesial view. G–L, *Hypotodus verticalis*. G–I, anterior tooth DK729pa. G, lingual view; H, labial view; I, distal view. J–L, lateral tooth DK729pb. J, lingual view; K, labial view; L, distal view. All scale bars 10 mm.

some teeth medially. The cusplets are separated from the main cusp by a deep and narrow notch in lingual view. The root lobes are asymmetric, long and flattened in the extremities. The angle between the lobes varies from 80° to 110°. The basal root edge is more or less angled. The lingual protuberance is marked and has a long and shallow nutritive groove.

The lateral tooth measures 18 mm apico-basally and 13 mm mesio-distally. The crown is triangular, upright in lingual view and straight in mesial view. The lingual face is convex, the labial face almost flat and slightly hollowed at the base with a vertical small ridge. The cutting edges almost reach the base of the crown. The distal cusplet is worn away; the mesial one is small, pointed and triangular. The cusplet is separated from the crown by a notch.

The root lobes are long and asymmetrical. The distal lobe is the longest. The angle between the lobes is about 120°. The lobes are round and the basal root edge is arcuate. The lingual protuberance is marked and there is a long and deep nutritive groove.

Comparison. The Trelde Næs teeth have small cusplets and thereby separate from teeth of *Odontaspis*, *Orpodon*, *Brachycarcharias* and *Palaeohypotodus*. They also have smooth enameloid and thereby separate from teeth of *Carcharias*, *Turania*, *Brachycarcharias*, *Sylvestrilamia* and most Mitsukurinidae. The cutting edges stop before the base of the crown in the Trelde Næs teeth whereas they reach the base in teeth of *Jaekelotodus*,

Isurolamna, *Sylvestrilamia* and *Brachycarcharias*. Teeth of *Hypotodus* are characterized by small hook-shaped cusplets which are separated by a deep notch from the crown, smooth enameloid and cutting edges not reaching the base (Cappetta 2012).

Cappetta & Nolf (2005) revised the Odontaspidae and restricted the genus *Hypotodus* to only one species *Hypotodus verticalis*. *Hypotodus verticalis* is known from the Lower Eocene (Ypresian) of England (Agassiz 1843; Casier 1966, Rayner *et al.* 2009), the Eocene of Belgium (Nolf 1988; Eeckhaut & De Schutter 2009) and the Ypresian of France (Adnet 2006a; Dutheil *et al.* 2006; Adnet & Cappetta 2008).

Odontaspidae genus and species indet. 1

Fig. 12A–C

Material. 6 anterior teeth, including DK729qa and Lot OBH26.0.

Description. The teeth measure from 21 to 34 mm apico-basally and from 10 to 17 mm mesio-distally. The crown is very slim and inclined lingually and not of sigmoidal shape. The lingual and labial faces are strongly convex and smooth, so that the crown is almost circular at its base. There is a small vertical ridge at the base of the labial face. The cutting edges are blunt and indistinct. The cusplets are high (up to 5 mm). They are slim, pointed and inclined lingually.

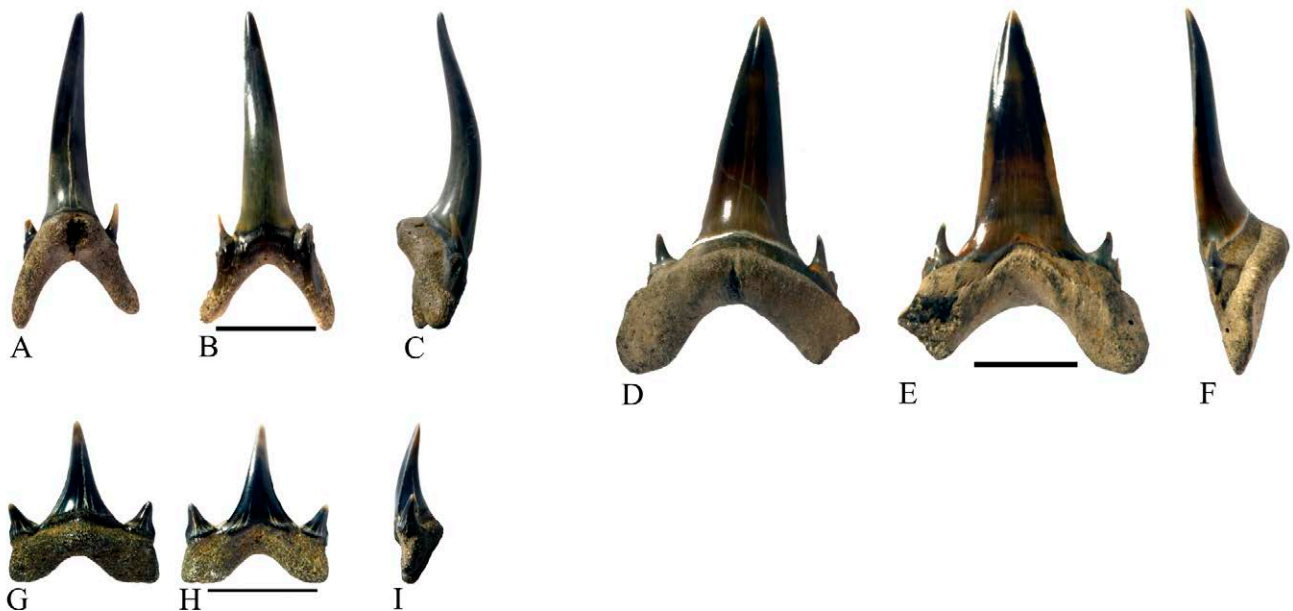


Fig. 12. A–C, Odontaspidae genus et species indet. 1, anterior tooth DK729qa. A, lingual view; B, labial view; C, distal view. D–F, Odontaspidae genus et species indet. 2, anterior tooth DK729qc. D, lingual view; E, labial view; F, mesio-distal view. G–I, Lamniformes family indet., lateral tooth DK729qb. G, lingual view; H, labial view; I, mesio-distal view. All scale bars 10 mm.

They have no cutting edges and are circular at the base. On two teeth, there seems to have been an accessory cusplet. On one tooth there are, labially, very coarse vertical folds at the base of the cusp and the cusplets. The root is symmetrical with long slender root lobes with an angle between the lobes of 70° to 90°. The lingual protuberance is strong with a deep nutritive groove.

Comparison. The Trelde Næs anterior teeth cannot with confidence be placed in a specific genus. They are without doubt of odontaspimid morphology. They bear some resemblance to *Odontaspis*, but the crown lacks clear cutting edges.

Odontaspididae genus and species indet. 2

Fig. 12D–F

Material. 1 anterior tooth, DK729qc.

Description. The tooth measures 35 mm apico-basally and 25 mm mesio-distally. The crown is labio-lingually flattened, triangular, symmetrical and slightly sigmoidal in mesial view. The lingual face is convex, whereas the labial face is flat with a shallow median depression at the base and no overhang of the root. The enameloid is smooth. The cutting edges are almost straight, very sharp and stop just before the base of the crown. The labial crown-root junction is slightly V-shaped and the lingual one is marked by a broad neck. There are two pairs of cusplets. The inner ones

are 4 mm high, slender with cutting edges and inclined lingually. The outer cusplets are vestigial and not fully separated from the inner ones. The root has two rounded lobes with flattened extremities. The tip of one of the root lobes is not preserved. The angle between the root lobes is 90° and the basal root edge is arc-shaped. The lingual protuberance is not very strong and there is a deep nutritive groove.

Comparison. The Trelde Næs tooth is without doubt of odontaspimid morphology. It resembles teeth of *Jaekelotodus*, but the crown is flatter and the root less strong (Cappetta 2012). It cannot be identified with confidence at genus or species level.

Odontaspididae genus and species indet. 2 is easily separated from Odontaspididae genus and species indet. 1 by the robustness its crown compared with the gracile, clutching-piercing teeth of Odontaspididae genus and species indet. 1.

Lamniformes family indet.

Fig. 12G–I

Material. 12 lateral teeth, including DK729qb and Lot OBH28.0.

Description. The teeth measure from 10 to 18 mm apico-basally and from 11 to 14 mm mesio-distally. The crown is low, triangular and inclined distally in five teeth. The remaining teeth have erect crowns in

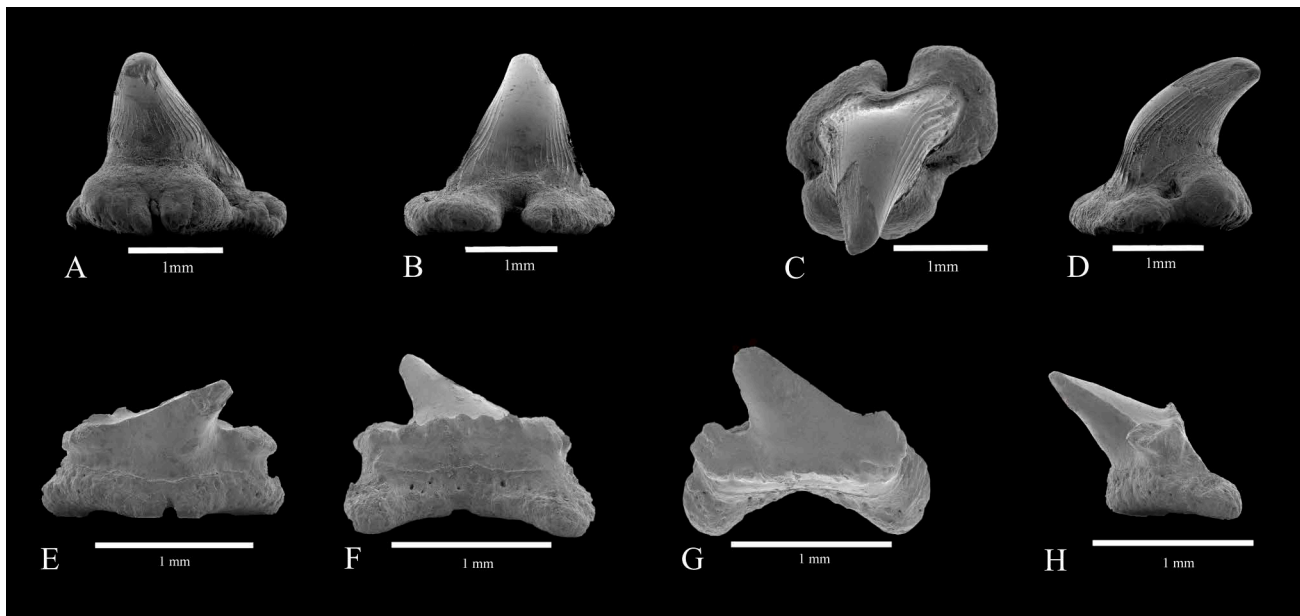


Fig. 13. **A–D**, *Megascyliorhinus cooperi*. Anterior tooth DK728a. **A**, lingual view; **B**, labial view; **C**, apical view; **D**, mesio-distal view. **E–H**, *Fountizia* sp. Lateral tooth DK728b. **E**, lingual view; **F**, labial view; **G**, apical view; **H**, distal view.

labial view and slightly lingually inclined crowns in mesial view. The enameloid is smooth. The lingual face is convex, the labial face less so with a median basal triangular depression. The cutting edges are sharp and reach the base of the crown. There is one pair of cusplets on seven teeth and two pairs on five teeth. The cusplets are up to 2 mm high, triangular, diverging and with a sharp cutting edge. When the cusplets are doubled, the outer ones are vestigial and not separated from the inner one. The lobes of the root are rounded and more or less spread out. The basal root edge is angled in some teeth and arc-shaped in others. The lingual protuberance is not very strong; there is no nutritive groove, but on some of the teeth a small foramen is present.

Comparison. The teeth could have some affinity to Lamnidae and Otodontidae, which often lack a distinct furrow on their teeth (Cappetta 2012). However, teeth of Otodontidae have a more robust root than the Trelde Næs teeth. The cusplets on teeth of Lamnidae are not as developed as on the Trelde Næs teeth (Cappetta 2012). These lateral teeth cannot therefore be ascribed with confidence to a specific family.

Order Carcharhiniformes Compagno 1973

Family Scyliorhinidae Gill 1862

Subfamily Megascyliorhininae Pfeil 1984

Genus *Megascyliorhinus* Cappetta & Ward 1977

Megascyliorhinus cooperi Cappetta & Ward 1977 Fig. 13A–D

Material. 1 anterior tooth (DK728a) and 1 lateral tooth (MM3110).

Description. DK728a measures 3 mm apico-basally, but the tip of the crown is missing, and 2.5 mm mesio-distally. The crown is stout and strongly inclined lingually. The labial face is convex and in the basal part there is a depression at the crown–root junction. The enameloid is ornamented with parallel folds at the base and in the mesial and distal regions of the crown. The central part of the labial face is smooth. There are no visible cutting edges. The lingual face of the crown is strongly convex and ornamented in the basal half.

The root is divided into two lobes by a deep groove. The root base is flat and broader than the base of the cusp. The labial part of the root has asymmetric rounded lobes; the lingual part is more narrow and continuous with a strong lingual protuberance. The limit between the lingual and the labial part of the root

is marked by a narrow depression with a deep hole on the mesial as well as on the distal side of the root. This is best seen in apical view. There are no cusplets.

MM3110 measures 2 mm apico-basally and 1.8 mm mesio-distally. The crown is almost symmetrical. It is stout, conical, pointed and inclined lingually. The lingual face is convex and worn without visible ornamentation. The labial face is strongly convex with a bulge in the basal part of the crown and a depression at the crown–root junction. The enameloid has folds on the basal one third, especially in the mesial and distal regions of the cusp. The cusp has no visible cutting edges. There is one slender, pointed, 1 mm long cusplet which is well separated from the main cusp. It is lingually bent. The other cusplet is broken off together with a part of the root.

The root is low with a flat basal face divided into two rounded lobes by a lingual groove. The labial half of the root is broader than the lingual half, which is continuous with a pronounced lingual protuberance. The limit between the lingual and the labial part of the root is marked by a deep narrow lateral depression with a deep oval hole.

Comparison. The subfamily Megascyliorhininae is characterised by teeth with a high conical cusp with little marked cutting edges and ornamentation on the labial and lingual faces of the cusp. Cusplets are often present on the lateral teeth. The basal root face is flat with a deep furrow (Cappetta & Ward 1977). Teeth of *Megascyliorhinus miocaenicus* Antunes & Jonet 1970 from the Miocene of France are close to the Trelde Næs teeth but have a stouter crown with lesser lingual inclination (Cappetta & Ward 1977). Teeth of *Megascyliorhinus trelewensis* Cione 1986 from the Oligocene of Argentina differ from the Trelde Næs teeth by being larger with an incomplete basal furrow and the presence of lateral cutting edges (Cione 1986). The Trelde Næs teeth closely resemble teeth of *Megascyliorhinus cooperi* known from the Ypresian of the London Clay in England (Cappetta & Ward 1977; Rayner *et al.* 2009) and from the Middle Eocene of France (Adnet 2006a, Plate 31). *Megascyliorhinus cooperi* is also known from the Oligocene to Pliocene of New Zealand (Keyes 1984).

Scyliorhinidae incerta subfamilia

Genus *Fountizia* Noubhani & Cappetta 1997

Fountizia sp. Fig. 13E–H

Material. 1 well preserved tooth (DK728b) and 1 tooth lacking the crown (MM0072).

Description. DK728b measures 1.5 mm mesio-distally and 1.5 mm apico-basally, whereas MM0072 measures 2 mm mesio-distally and 1.5 mm apico-basally. DK728b has a triangular stout crown slightly bent distally and lingually inclined. The cutting edges reach the base of the crown and are continuous with one low cusplet on each side of the crown. The distal cutting edge is concave, the mesial one almost straight. The cusplets are worn. The lingual crown face is smooth and strongly convex. The crown-root junction is marked and almost straight. The labial crown face is moderately convex and at the crown-root junction and under the heels there are eight coarse vertical folds on a prominent horizontal crest which overhangs the root. The ornamentation does not extend to the crown face. These folds are worn on MM0072 but the crest is preserved.

The root is strong with a strong lingual protuberance and divided into two lobes by a deep furrow. The root lobes are kidney-shaped in basal view and slightly concave. Seen in labial view, the basal border of the root is concave on both teeth; seen apically the labial border is concave as well. There are several foramina along the basal margin on the labial face of the root.

Comparison. The Trelde Næs teeth are probably from the lateral files because of their distally inclined cusp (Cappetta 1976). They are separated from other scyliorhinid teeth by the presence of coarse folds at the base of the labial crown face. This character is also seen on teeth of *Premontreia* Cappetta 1992, but these teeth are larger and have a lower and more rectangular root contrary to the Trelde Næs teeth where the root is with rounded lobes (Cappetta 2012). The Trelde Næs teeth are assigned to the genus *Fountizia* because of the confinement of the ornamentation to the base of the crown combined with the rounded root lobes (Cappetta 2012).

Teeth of *Fountizia poudenxae* Adnet 2006a and *Fountizia zhelezkoi* Malyshkina 2006 differ from the Trelde Næs teeth by having folds on both sides of the cusp. Teeth of *Fountizia arba* Noubhani & Cappetta 1997 are significantly smaller and lack folds on the labial crest

at the crown-root junction. Teeth of *Fountizia gadaensis* Noubhani & Cappetta 1997 differ from the Trelde Næs teeth by having a more lingually inclined crown and more cusplets which are situated higher on the crown (Noubhani & Cappetta 1997). The Trelde Næs teeth resemble teeth of *Fountizia abdouni* Noubhani & Cappetta 1997 as well as of *Fountizia pattersoni* Cappetta 1976, but with only two more or less well preserved lateral teeth it is not possible to assign the Trelde Næs teeth to a specific species.

Fountizia is known from the Early Eocene London Clay (Rayner *et al.* 2009), the Ypresian/Lutetian of south-western France (Adnet 2006a), the Ypresian Paris Basin in France (Dutheil *et al.* 2006) and the Ypresian/Lutetian of Morocco (Noubhani & Cappetta 1997).

Family Carcharhinidae Jordan & Everman 1896

Genus *Physogaleus* Cappetta 1980a

Physogaleus cf. *secundus* Winkler 1876b

Fig. 14A–B

Material. 3 lower and 8 upper teeth, including DK729s (upper lateral tooth), MM0053 (upper lateral tooth) and Lot OBH30.0.

Description. DK729s measures 9 mm mesio-distally, 7 mm apico-basally and 3 mm labio-lingually. The tooth is labio-lingually compressed. The main cusp is triangular and inclined distally at about 65° to the crown-root boundary. The mesial edge is long and almost straight with two small irregular bumps. In the middle of the cutting edge, a small part is missing due to wear. The mesial third of the cutting edge has faint signs of serration. The distal cutting edge is straight and short, creating a notch with the distal heel. The heel is marked and three triangular cusplets are present, decreasing in size distally. The lingual face of the main cusp is convex, whereas the labial face is almost flat in the apical half and convex basally along the straight crown-root junction. The enameloid is smooth. The root is low with a slightly concave basal face. It is divided into two almost triangular (in basal view) lobes by a deep furrow. The lingual protuberance is marked. In labial view the root is rectangular.

The three lower antero-lateral teeth measure 10 mm mesio-distally, 10 mm apico-basally and 4 mm labio-lingually. The crown is high and inclined about 45° distally. The mesial heel is long and the shape of the mesial cutting edge is sinusoidal without serration. The distal cutting edge is concave and there are three cusplets on the distal heel. The lingual face of

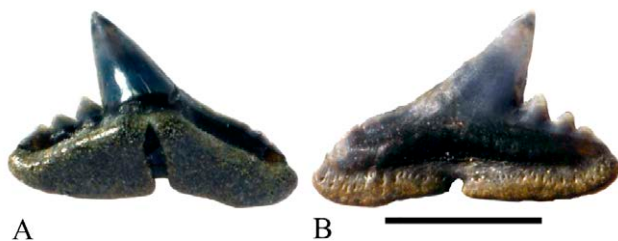


Fig. 14. A–B, *Physogaleus* cf. *secundus*, upper lateral tooth DK729s. A, lingual view; B, labial view. Scale bar 5 mm.

the crown is strongly convex, the labial face is slightly convex and the enameloid overhangs the root. The root is bulky with a pronounced lingual protuberance. It is divided into two lobes by a long deep furrow. Seen basally the root lobes are triangular. The basal edge of the root is almost straight in labial view.

The eight upper lateral teeth differ from the lower teeth in having a wider triangular and more robust crown and the basal edge of the root is slightly concave.

Comparison. The Trelde Næs teeth separate from teeth of *Scoliodon* Müller & Henle 1837 by having cusplets on the distal heel and from teeth of *Rhizoprionodon* Whitley 1929 which are smaller (less than 4 mm) and also lack cusplets on the distal heel (Cappetta 1980a). Teeth of *Galeocerdo* Müller & Henle 1837 and *Carcharhinus* Blainville 1816 are larger than the Trelde Næs teeth and also differ by having complete serrated cutting edges, whereas teeth of *Abdounia* Cappetta 1980a have mesial as well as distal cusplets (Cappetta 2012). The Trelde Næs teeth fit well with the description of teeth of the genus *Physogaleus* (Cappetta 1980a). The position of the figured Trelde Næs tooth in the jaws is interpreted from Cappetta (2012, fig. 297).

Three species of *Physogaleus* have been reported from the Paleogene of Europe (Dutheil *et al.* 2002; Adnet 2006a): *Physogaleus secundus*, *Physogaleus tertius*

Winkler 1874 and *Physogaleus latus* Storms 1894. The teeth of the three species are almost similar and can probably only be separated by their size. Teeth of *Physogaleus secundus* are rather large and have more developed distal cusplets compared to *Physogaleus tertius*; Teeth of *Physogaleus latus* are close to teeth of *Physogaleus secundus* but are two or three times larger. The Trelde Næs teeth seem closest to teeth of *Physogaleus secundus*.

Superorder Squalomorphii Compagno 1973

Order Hexanchiformes Berg 1940

Suborder Chlamydoselachoidei Berg 1958

Family Chlamydoselachidae Garman 1884

Genus *Chlamydoselachus* Garman 1884

Chlamydoselachus cf. fiedleri Pfeil 1983

Fig. 15A–F

Material. 1 antero-lateral tooth (DK728c).

Description. DK728c measures 3 mm apico-basally. The distal cusp is lacking. The median cusp is slightly

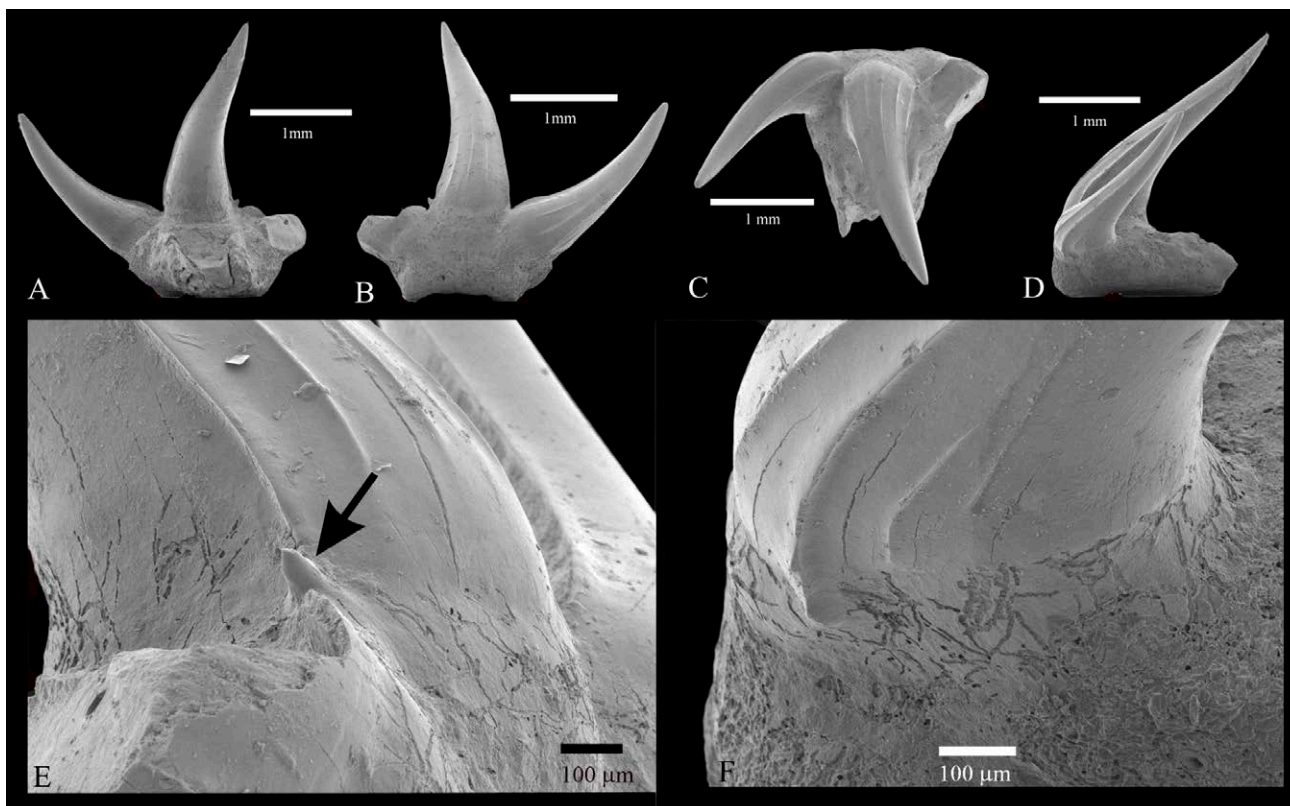


Fig. 15. A–F, *Chlamydoselachus cf. fiedleri*. Antero-lateral tooth DK728c. A, lingual view; B, labial view; C, apical view; D, mesial view; E, detail of intermediary cusplet; F, detail of microborings.

sigmoidal in lingual view and the angle between the median cusp and the base of the root is about 60° in mesial view. The mesial cusp is slightly more lingually inclined. The angle between the median cusp and the preserved mesial cusp is about 45° in lingual view. The lingual face of the cusps is strongly convex with a smooth enameloid. Four almost parallel sharp longitudinal ridges are present on the basal half of the labial face of the cusps. The cutting edges are sharp and reach the base of the crown on both cusps. There is no gap between the base of the median and lateral cusps and a very small intermediate cusp is present distally at the base of the median cusp. The crown-root junction on the lingual face of the median cusp is marked by a broad neck. There are many microborings at the base of the mesial cusp.

The root measures 1.8 mm labio-lingually and 1.2 mm mesio-distally. It is low and broader labially than lingually. The apical surface of the root is divided by a deep trough flanked by a marked mesial and distal crest. The lingual edge has a broad shallow incision forming two short lobes. The basal surface of the root is almost flat in the lingual part and is slightly concave

in the labial part, forming a shallow depression when seen in labial view. Several very small foramina are present on the basal surface of the root, none on the apical surface.

Comparison. Chlamydoselachidae contains two genera; *Chlamydoselachus* and *Proteoثرinax* (former *Thrinax* Pfeil 1983). Absence of intermediate cusplets is seen in teeth of *Proteoثرinax* (Pfeil 1983; Cappetta 2012) and *Chlamydoselachus goliath* Antunes & Cappetta 2002 from the Late Cretaceous of Angola (Antunes & Cappetta 2002), *Chlamydoselachus keyesi* from the Paleocene of New Zealand (Mannering & Hiller 2008), *Chlamydoselachus lawleyi* Davis 1887 from the Pliocene of Italy (Pfeil 1983) and sometimes in the recent *Chlamydoselachus anguineus* Garman 1884. DK728c separates from *Proteoثرinax* by having an ornamented crown with full cutting edges. Teeth of *Chlamydoselachus goliath* are significantly larger than DK728c and have upright cusps which lack ornamentation (Antunes & Cappetta 2002). Teeth of *Chlamydoselachus lawleyi* differ from DK728c by having a gap between the median cusp and the lateral cusps (Pfeil 1983). Teeth of *Chlamydoselachus*

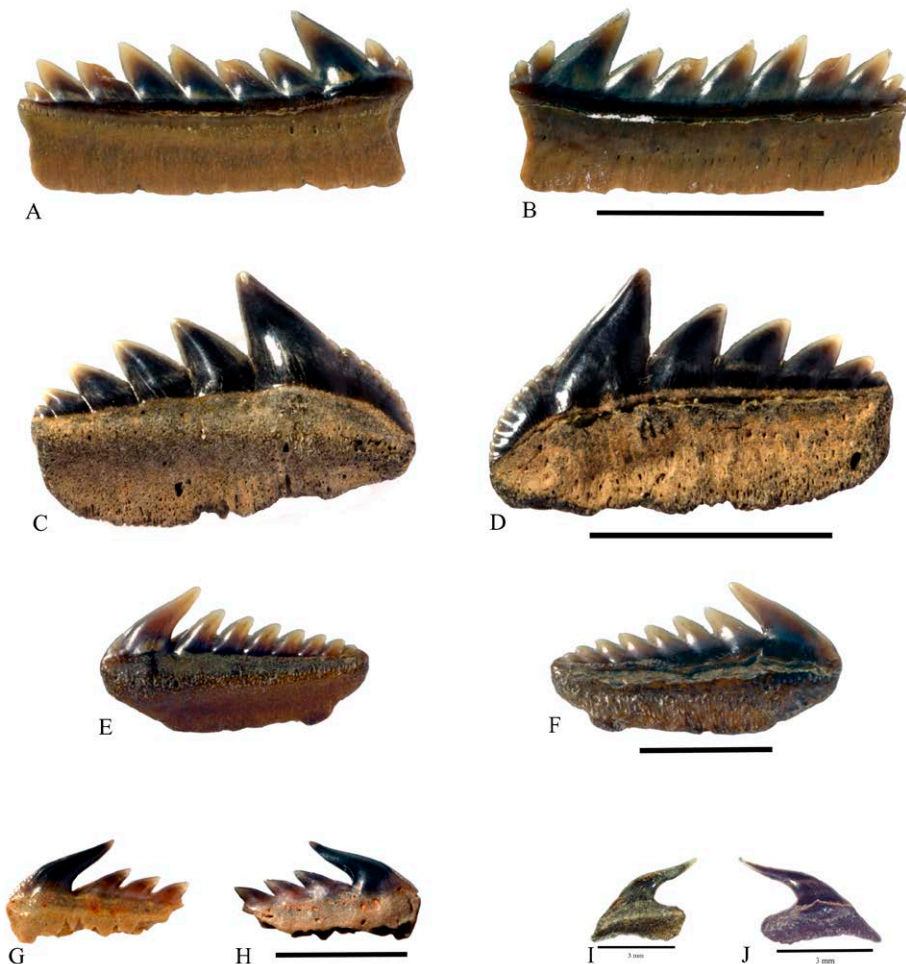


Fig. 16. A–B, *Heptanchias howelli*. Lower tooth DK729t. A, lingual view; B, labial view. Scale bar 10 mm. C–D, *Notorynchus serratissimus*. Lower tooth DK729u. C, lingual view; D, labial view. Scale bar 10 mm. E–F, *Hexanchus cf. agassizi*. Lower tooth DK729v. E, lingual view; F, labial view. Scale bar 5 mm. G–J, *Weltonia burnhamensis*. G–H, lower tooth DK729x. G, lingual view; H, labial view. Scale bar 5 mm. I–J, upper tooth DK728d. I, lingual view; J, labial view. Scale bar 3 mm.

fiedleri from the Lutetian of Austria and Denmark have intermediary cusplets. However Pfeil (1983, fig 54) describe a juvenile tooth of *Chlamydoselachus fiedleri* of very small size, lacking intermediary cusplets and only striated on the labial face of the cusps. It differs from DK728c only by having a labio-lingually shorter root. Teeth of *Chlamydoselachus keyesi* from the Paleocene of New Zealand (Mannering & Hiller 2008) are also close to DK728c as they lack intermediate cusps, are coarsely striated on the labial face of the cusps and have lingually bent cusps. However their root is different from DK728c, being shorter labio-lingually, and the teeth are significantly larger. DK728c is very small and could represent a tooth from a juvenile. It has characters common with *Chlamydoselachus fiedleri* as well as with *Chlamydoselachus keyesi*. Because of its short root, it cannot be assigned with confidence to one of these two species, but it seems closest to *Chlamydoselachus fiedleri*.

Chlamydoselachus thompsoni Richter & Ward 1990 is known from the Cretaceous of Antarctica and differs from DK728c by its larger size and ornamentation of both faces of the crown. The genus *Chlamydoselachus* is known from the Late Cretaceous of Antarctica and Angola (Richter & Ward 1990; Antunes & Cappetta 2002), the Paleocene of New Zealand (Consoli 2008; Mannering & Hiller 2008) until recent. The species *Chlamydoselachus fiedleri* has been reported from the Eocene (Lutetian) of Austria and Denmark (Pfeil 1983).

Suborder Hexanchoidei Garman 1913

Family Heptranchidae Barnard 1925

Genus *Heptranchias* Rafinesque 1810

Heptranchias howelli Reed 1946

Fig. 16A–B

Material: 1 complete lower tooth (DK729t), 17 lower teeth of which one is complete (Lot OBH31.0), 1 broken tooth (MM5012b).

Description. The largest tooth measures 17.5 mm mesio-distally, 8.5 mm apico-basally and 4.5 mm labio-lingually. The teeth have one primary cusp and five to seven accessory cusps. The primary cusp is significantly larger in height than the other cusps. The accessory cusps increase in height distally until the third and fourth one, which are similar in size. The last three cusps decrease in height distally. Small cusplets are seen at the base of the mesial cutting edge of the primary cusp, increasing in size apically. Their number varies from one to three. The mesial cutting

edge on the primary cusp is slightly convex and the distal cutting edge is straight. The cutting edges on the accessory cusps are slightly convex. The lingual face is convex, whereas the labial face is almost flat. All the cusps are inclined about 45° distally. The crown–root junction is distinct and almost parallel to the root base. The root height is 5 mm in the largest tooth and the root is rectangular with a straight basal edge. There is a relatively deep depression in the mesial edge seen in labial view, whereas the distal one is straight or convex. The root is compressed linguo-labially. The labial face of the root is flat with many small foramina. The lingual face is composed of two concave faces forming a longitudinal protuberance at their junction. In the mesial part, three small, but distinct foramina open on the lingual face. In apical view the tooth is slightly concave to the lingual side.

Comparison. The teeth are believed to come from an antero-lateral file of the lower jaw because of their comb-shape. The Trelde Næs teeth separate from those of Hexanchidae by the irregular decrease in size of the accessory cusps. This is typical for Heptranchidae (Cappetta 2012). The Trelde Næs teeth are typical for teeth of *Heptranchias* and separate easily from those of the very different *Paraheptranchias* Pfeil 1981 where small cusplets are present between the main cusps (Cappetta 2012).

Teeth of *Heptranchias perlo* Bonnaterre, 1788 usually have a single mesial cusplet on the upper teeth (Long 1992) and two or more mesial cusplets on the lower lateral teeth (Compagno *et al.* 2005). Teeth of the Oligocene *Heptranchias ezoensis* Applegate & Uyeno 1968 and *Heptranchias tenuidens* Leriche 1938 differ from the Trelde Næs teeth by their reduced number and considerable size of mesial cusplets (Cappetta 1981). *Heptranchias howelli*, which has teeth with up to five mesial cusplets, is known from the Eocene (Cappetta 1981; Long 1992; Noubhani & Cappetta 1997; Kriwet 2005; Adnet 2006a). The Trelde Næs teeth, having one to three mesial cusplets, are very similar to the teeth described from Morocco as teeth of *Heptranchias howelli* (Cappetta 1981). Siverson (1995) describes teeth of *Heptranchias sp.* from the Danian of Sweden. His figures and description are also close to the Trelde Næs teeth but the Swedish teeth look more compact with a deeper root.

Family Hexanchidae Gray 1851

Genus *Notorynchus* Ayres 1855

Notorynchus serratissimus (Agassiz 1843)

Fig. 16C–D

Material. 24 lower teeth, 7 of which are well preserved, including DK729u, MM5012a and Lot OBH32.0.

Description. The best preserved tooth measures 20 mm mesio-distally and 12 mm apico-distally. The teeth are linguo-labially flattened and comb-shaped. The main cusp is larger than the accessory cusps which gradually decrease in size distally. On the basal half of the mesial edge of the main cusp, a long heel bears five to ten small cusplets which decrease in size mesially. There are four to five accessory cusps. The cutting edges of the main cusp are both straight. On the accessory cusps, the mesial cutting edges are convex and the distal ones straight. All the cusps lean distally. The main cusp is the most upright with an angle between the cusp and the root base measuring more than 45°. The accessory cusps lean more distally the further distally they are situated. The lingual face of the cusps is more convex than the labial face. The root-crown junction is distinct and concave towards the root base. The root is high and almost rectangular. The mesial and distal edges of the root are straight or with a small depression in labial view. The labial face of the root is flat with many small, mostly oval openings. The lingual root face has a pronounced lingual protuberance parallel to the basal edge, and several openings of various sizes are present on the linguo-basal face. Seen apically most of the teeth are slightly oblique with a lingual concavity.

Comparison. The Trelde Næs teeth are from the lower jaw because of their comb-shape. They have a regular decrease in size of the accessory cusps and thereby separate from teeth of Heptranchidae (Cappetta 2012). They have a mesial heel with small cusplets which separates them from teeth of *Hexanchus* Rafinesque 1810 where the basal half of the mesial edge of the main cusp is more or less serrated and no heel is present (Ward 1979). Teeth of *Pachyhexanchus* Cappetta 1990a also have a long mesial heel, but it is never serrated (Cappetta 2012). Teeth of the Cretaceous *Gladioserratus* Underwood *et al.* 2011a are close to the Trelde Næs teeth, but differ by having serrae of even size on the mesial heel whereas the serrae on the Trelde Næs teeth decrease in size mesially.

The Trelde Næs teeth separate from teeth of the Oligocene *Notorynchus kempfi* Ward 1979 which is larger and has finer mesial serrations and more accessory cusplets, and from teeth of the Oligocene–Miocene *Notorynchus primigenius* Agassiz 1843 that are even larger with a more pointed and upright main cusp (Ward 1979). The Trelde Næs teeth closely resemble teeth of *Notorynchus serratissimus*, which has been reported from the Early Eocene of England (Casier

1966; Cappetta 1976; Rayner *et al.* 2009) and Belgium (Leriche 1905; Nolf 1988; Eeckhaut & De Schutter 2009).

Genus *Hexanchus* Rafinesque 1810

Hexanchus cf. *agassizi* Cappetta 1976

Fig. 16E–F

Material. 6 teeth from the lower jaw, including DK729v, Lot OBH33.0 and Lot MM0078.

Description. The best preserved tooth measures 11 mm mesio-distally, 6 mm apico-basally and 1.7 mm labio-lingually. The tooth is worn. It is comb-shaped with a main cusp and seven accessory cusps regularly decreasing in size distally. All cusps are leaning apico-distally. The mesial cutting edge of the main cusp has no serration and no heel. It is convex in the basal two thirds and straight near the apex. The distal cutting edge is concave in the basal part and convex in the apical part. The lingual face is convex, the labial face almost flat. The main cusp is slightly larger than the first accessory cusp. The accessory cusps have convex mesial and almost straight distal cutting edges. The root-crown junction is distinct and parallel to the moderately developed lingual protuberance. On the mesial edge of the root there is a small depression. The distal edge is incomplete. The labial face of the root is flat. On the lingual protuberance there are two small foramina opening basally to the main and the first accessory cusp. The basal edge of the root is straight.

Comparison. The Trelde Næs teeth separate from teeth of Heptranchidae by the regularly decreasing size of the accessory cusps (Cappetta 2012). Teeth of *Notorynchus* always have cusplets on the mesial heel, whereas the mesial serration on teeth of *Hexanchus* are less developed or even missing (Ward 1979). Teeth of *Pachyhexanchus* have a mesial non-serrated heel, contrary to *Hexanchus* where no heel is present (Cappetta 2012). The Trelde Næs teeth have no visible serration, but this could partly be a result of wear. The acrocone cusp on the Trelde Næs teeth is larger than the first accessory cusp, but not as large as in teeth of *Weltonia* Ward 1979, where it is at least 50% larger than the first accessory cusp (Ward 1979).

Ward (1979) describes the teeth of *Hexanchus agassizi*, *Hexanchus collinsonae* and *Hexanchus hookeri* from the Lower Eocene of England. Teeth of *Hexanchus collinsonae* and *Hexanchus hookeri* separate from teeth of *Hexanchus agassizi* by their stouter roots and coarser serration (Ward 1979). *Hexanchus collinsonae* and *Hexanchus hookeri* may be ontogenetic states of *Hexanchus agassizi* (Adnet 2006b). The Trelde Næs teeth are most

likely lower teeth of *Hexanchus agassizi* having no visible serration. *Hexanchus agassizi* is known from south-western France and from the London Clay of England (Adnet 2006a; Rayner *et al.* 2009).

Genus *Weltonia* Ward 1979

Weltonia burnhamensis Ward 1979

Fig. 16G–J

Material. 1 lower tooth (DK728c) and 1 upper tooth (DK728d).

Description. DK728c is comb-shaped and thus probably from the lower jaw. The main cusp and three accessory cusps are preserved. The tooth is 7 mm long mesio-distally and 4 mm high apico-basally. The basal half of the root and the distal part of the tooth is missing so that the tooth was probably larger than the given measurements. The main cusp is of sigmoidal shape. The basal two thirds of its mesial cutting edge are convex with coarse serration on its basal half. The apical one third is concave. The basal one third of the distal cutting edge is strongly concave, the apical two thirds slightly convex. The lingual face is convex, the labial face almost flat. The main cusp is significantly larger than the first accessory cusp and the two cusps are well separated. The main cusp is distally inclined at about 45°. The three accessory cusps decrease regularly in size distally and all lean about 45° distally. The mesial cutting edges are convex, the distal ones almost straight. The lingual faces are convex, the labial faces almost flat. The basal part of the root is missing but a weak longitudinal lingual protuberance parallel to the crown–root boundary is preserved. The preserved labial root face is flat. The mesial edge of the root is depressed. Several foramens of various sizes are seen on both root surfaces.

DK728d measures 3 mm apico-basally and 4 mm mesio-distally. There is one slender, very sigmoidal cusp, which is inclined distally at about 70°. Both faces of the cusp are convex. The mesial cutting edge is sharp, the distal one blunt. The root is flat with a moderate lingual protuberance. On the labial face, the crown–root junction is marked by a deep depression in the middle part of the tooth. This tooth is with only one cusp and thereby probably from the upper jaw.

Comparison. The lower tooth is typical of Hexanchidae because of the regular decrease of the size of the accessory cusps (Cappetta 2012). It is separated from teeth of *Hexanchus*, *Notorynchus* and *Pachyhexanchus* by its high sigmoidal main cusp which is well separated from the second cusp (Ward 1979). Two species of *Weltonia* are described: *Weltonia burnhamensis* and *Weltonia ancistrodon* Arambourg 1952. The Trelde Næs tooth separates from teeth of *Weltonia ancistrodon* which have a very high main cusp (Arambourg 1952; Cappetta 2012, fig. 85G). On the other hand it agrees well with teeth of *Weltonia burnhamensis*. This species is known from the Ypresian of England (Casier 1966; Rayner *et al.* 2009).

Order Squatiniformes Buen 1926

Family Squatinidae Bonaparte 1838

Genus *Squatina* Dumeril 1806

Squatina cf. prima Winkler 1874

Fig. 17A–C

Material. 1 well-preserved tooth (DK729y) and 3 worn teeth (Lot OBH35.0).

Description. The best preserved tooth is broader than high: 11 mm mesio-distally and 4 mm apico-basally. The cusp is slender, erect, triangular and symmetric in labial view. The labial as well as the lingual face of the cusp are convex and smooth. The labial face is extended basally in a small rounded apron. The lingual protuberance is strong and covered with enameloid medially forming a triangular uvula. The cutting edges on the crown are sharp and expand over the long, low heels. The root is flat and perpendicular to the cusp and of triangular shape in basal view. The root is hollowed in its labial median area where one opening is present. The medio-lingual duct is covered and a medio-lingual foramen opens at the extremity of the lingual protuberance. Below the crown–root boundary there are several small foramina on the lingual face of the root. The root vascularisation is hemiaulacorhize. This means that there is a connection between the central foramen on the root base



Fig. 17. A–C, *Squatina cf. prima*. Lateral tooth DK729y. A, lingual view; B, labial view; C, apical view. Scale bar 5 mm.

and the foramen on the lingual protuberance via the medio-internal canal which runs parallel to the surface (Cappetta 2012).

The other three teeth are smaller with a relatively higher and slightly lingually inclined cusp. The basal face of the root is concave in two teeth.

Comparison. The Trelde Næs teeth separate from teeth of *Pseudorhina* Jaekel 1898, which are very small, less than 1.5 mm in total width, and with a much wider labial apron (Cappetta 2012). Teeth of *Squatina* are also similar to teeth of *Orectolobus* Bonaparte 1834 but the heels are elevated and sometimes form distal denticles in the latter (Long 1992).

The Trelde Næs teeth belong to the genus *Squatina* because of their triangular root, their rounded labial apron, their long heels with sharp cutting edges and their triangular crown. The conservative nature of the *Squatina* dentition makes it difficult to identify isolated teeth at species level and their stratigraphic position becomes of importance. *Squatina hassei* Leriche 1929 is the preferred identification for the Cretaceous sharks. Teeth of this species are small (5 mm) with a short cusp and steeply sloping shoulders. *Squatina prima* is the Paleogene species employed for this genus. Its teeth have a slender crown and low shoulders (Casier 1966; Adnet 2006a). *Squatina subserrata* Münster 1846 is the Pliocene–Miocene species and is characterized by robust teeth (<http://elasma.com>). The Trelde Næs teeth are very similar to teeth of *Squatina prima* because of the slender crown, the low shoulders and the medium size (Casier 1966; Adnet 2006a).

Order Squaliformes Goodrich 1909

Family Centrophoridae Bleeker 1859

Genus *Centrophorus* Müller & Henle 1837

Centrophorus aff. *granulosus* Bloch & Schneider 1801

Fig. 18A–D

Material. 22 teeth, including DK731, Lot AWC10.0, Lot SL0001 and Lot MM3118.0

Description. The teeth are small, less than 3 mm apico-basally. The height (apico-basally) is larger than the width (mesio-distally). The teeth are labio-lingually flattened with a very distally inclined triangular crown. The labial and lingual faces are slightly convex with smooth enameloid. The mesial cutting edge is slightly sigmoid and coarsely serrated, whereas the distal one is straight without serrae. The distal heel is low and rounded and separated from the crown by a deep notch. A flat apron on the labial face extends down over the root, not reaching the base of the root. The apron is triangular and thick with distinct edges. On the lingual face the uvula is marked and of triangular shape. The root is labio-lingually compressed. The basal edge is more or less straight. The mesial edge is curved with a depression in which the adjacent mesial tooth is interlocked. In the bottom of the depression a wear facet is present in the largest teeth. The distal edge of the root is rounded to accom-

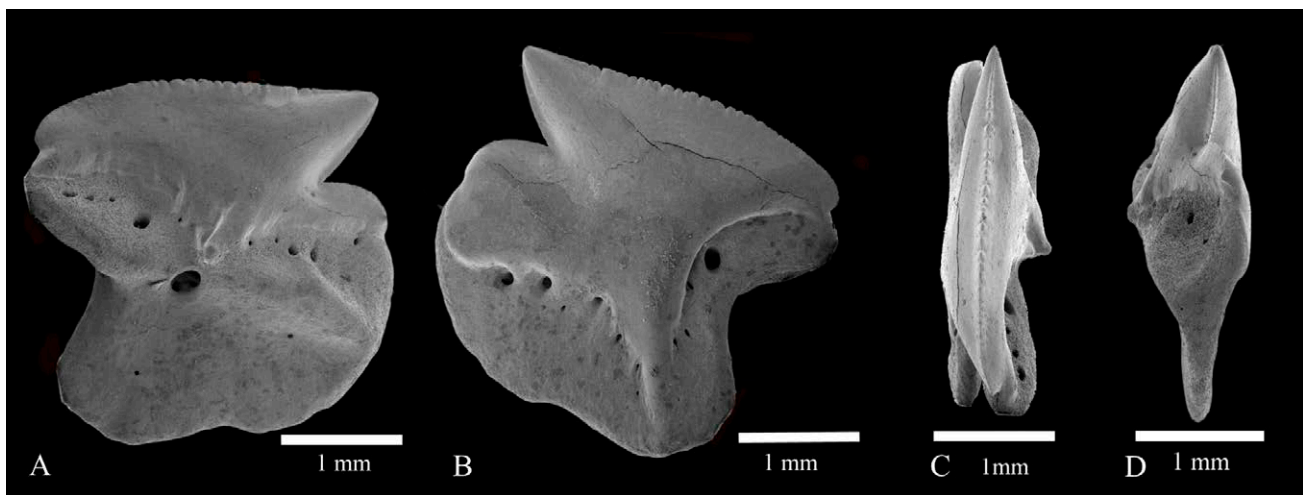


Fig 18. A–D, *Centrophorus* aff. *granulosus*. DK731. A, lingual view; B, labial view; C, apical view; D, distal view.

moderate the adjacent distal tooth. The labial root face is flat and several large foramina open close to the crown–root junction. The lingual root face is divided by a prominent longitudinal protuberance parallel to the crown base. The uvula extends basally to the protuberance and a large foramen opens just basal to the tip of the uvula. From this foramen, a shallow furrow is present in mesio-basal direction, reaching the root base. On both sides of the uvula, the root has a shallow depression and a few foramina open on the lingual face of the root.

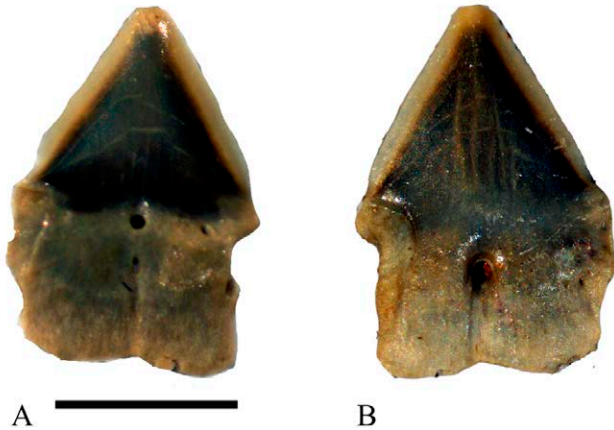


Fig. 19. A–B, *Isistius trituratorus*. Anterior tooth DK730. A, lingual view. B, labial view. Scale bar 2 mm.

Comparison. The basal root compression, the shape and size of the labial apron and the lingual protuberance separates the Trelde Næs teeth from those of all the squaliform families except Centrophoridae, which includes the genus *Centrophorus* and *Deania* Jordan & Snyder 1902 (Cappetta 2012). The Trelde Næs teeth have serrated mesial cutting edges and only one opening, an infundibulum, just below the tip of the uvula, whereas teeth of *Deania* have unserrated cutting edges and two lingual openings (De Schutter & Wijnker 2002).

Many species of the genus *Centrophorus* have been described. The recent species *Centrophorus squamosus* Bonnaterre, 1788 has teeth with ornamentation on the uvula and serration on the mesial as well as the distal cutting edge (Marsili & Tabanelli 2007), whereas the Trelde Næs teeth are only serrated on the mesial cutting edge. The Trelde Næs teeth closely resemble teeth of *Centrophorus granulosus* as figured by Cappetta (2012, fig. 98 F–G) and *Centrophorus* aff. *granulosus* as figured by Adnet (2006a, Plate 4, fig. 4–7). *Centrophorus* is known from the Upper Cretaceous to recent (Adnet & Cappetta 2001; Klug & Kriwet 2010). *Centrophorus* aff. *granulosus* is known from the Lutetian of south-western France (Adnet 2006a).

Family Dalatiidae Gray 1851

Genus *Isistius* Gill 1865

Isistius trituratorus Winkler 1876b

Fig. 19A–B

Material. 9 lower teeth, including DK730 (1 well preserved tooth), Lot MM0002 (5 well preserved teeth) and Lot AWC11.0 (3 fragmentary teeth).

Description. The largest tooth is 4 mm high apico-basally, 3 mm broad mesio-distally and strongly flattened labio-lingually. The crown is symmetric and triangular with unserrated cutting edges and without heels. Both faces are slightly convex. On the labial face a thin apron is present with a poorly marked basal boundary near the ‘button-hole’. This hole is an oval infundibulum, and a furrow reaches from its basal edge to the basal edge of the root. The labial root face is flat. The basal margin of the root is slightly indented in the centre. The root is square with straight mesial and distal margins. The lingual face is flat and at the crown–root boundary there is a poorly developed lingual protuberance parallel with the root base. Two axial foramina open lingually, a round one just below the crown and an oval one in the middle of the root. A shallow furrow stretches from this hole to the base of the root. The overlap depressions on the mesial and the distal root edges that accommodate the adjacent tooth are long and marked; especially the mesial one is deep. All teeth are from the lower jaw because of their triangular crown.

Comparison. The Trelde Næs teeth are placed in the Dalatiidae because of their triangular crown and their ‘button-hole’. The genus *Isistius* is the only genus with teeth with a symmetric crown without heels and a square root. Two fossil species of *Isistius* have been described from the Eocene to Lower Pliocene; *Isistius trituratorus* and *Isistius triangulus* Probst 1879 (Cappetta 2012). From the most ancient to the most recent species, the opening of the ‘button-hole’ seems to have a successively lower position on the labial face of the root, and the root becomes higher (Cappetta 2012). The Trelde Næs teeth have smooth cutting edges on the crown and thereby separate from teeth of *Isistius triangulus* which have serrated cutting edges (Longbottom 1979; Adnet 2006a). Teeth of living *Isistius brasiliensis* Quoy & Gaimard 1824 have higher roots than those of *Isistius trituratorus* (Arambourg 1952). The Trelde Næs teeth are very similar to teeth of *Isistius trituratorus*, which lack serration (Arambourg 1952).

Isistius trituratorus is known from the Lower Eocene of England (Casier 1966; Cooper 1977; Rayner *et al.*

2009), the Eocene of Belgium (Nolf 1988; Eeckhaut & De Schutter 2009; Iserbyt & De Schutter 2012) and Morocco (Arambourg 1952; Ward & Wiest 1990; Noubhani & Cappetta 1997) and the Lutetian of France (Adnet 2006a).

Order Echinorhiniformes Buen 1926

Family Echinorhinidae Gill 1862

Genus *Echinorhinus* Blainville 1816

Echinorhinus cf. *priscus* Arambourg 1952

Fig. 20A–F

Material. 39 teeth, including DK728e, DK728f, Lot AWC12.0, Lot MM0067.0 and Lot SL0006.

Description. The largest and best preserved tooth measures 6 mm mesio-distally, 3.5 mm apico-basally and 0.5 mm labio-lingually. The crown is triangular and bent distally. The most mesial part of the cutting edge is convex, the middle part is straight and the distal part is slightly concave. The distal cutting edge is slightly

convex. The distal heel is low and short and separated from the main cusp by a deep notch. The cutting edges are worn but faint signs of irregular serration are preserved in most of the teeth. Both labial and lingual crown faces are slightly convex. In most of the teeth the crown tip extends beyond the distal border of the root. The root is strongly compressed labio-lingually. In labial view it is rectangular with straight distal, mesial and basal borders. The crown–root junction is almost straight on both sides of the tooth. The labial root face is flat and there are several small foramina opening along the crown–root junction. The lingual root face is flat and the crown–root junction forms a longitudinal shallow protuberance with many small foramina. In most of the teeth there is a vertical furrow in the central part of the lingual root face; a few teeth have two parallel furrows.

Comparison. The Trelde Næs teeth belong to Echinorhiniformes because of their strong labio-lingual compression and their simple, distally inclined cusp and no overlapping of the teeth (Cappetta 2012). They differ from teeth of *Pseudoechinorhinus* Pfeil 1983 and *Paraechinorhinus* Pfeil 1983 where the cusp is more upright and not bent (Cappetta 2012, fig. 94). Teeth of



Fig. 20. A–D, *Echinorhinus* cf. *priscus*. Lateral tooth DK728e. A, lingual view; B, labial view; C, apical view; D, distal view. E–F, *Echinorhinus* cf. *priscus*. Anterolateral tooth DK728f. E, lingual view; F, labial view.

Gibbechinorhinus Cappetta 1990b are very large (up to 24 mm mesio-distally) and *Orthechinorhinus* Adnet 2006a have very small (less than 3 mm mesio-distally) teeth of tearing type (Cappetta 2012).

The Trelde Næs teeth separate easily from teeth of the living *Echinorhinus brucus* Bonnaterre, 1788 and *Echinorhinus cookei* Pietschmann 1928 which have cusplets on the mesial side of the main cusp and on the heel.

Pfeil (1983) gave exhaustive descriptions of known species of *Echinorhinus*. Most of the Cretaceous species lack cusplets (Adnet *et al.* 2012). Among the Tertiary species only teeth of *Echinorhinus priscus* known from the Lower Eocene of Morocco and Austria (Noubhani & Cappetta 1997; Pfeil 1983) and *Echinorhinus weltoni* Pfeil 1983 known from the Upper Eocene always lack side cusplets. All the Oligocene, Miocene and Pliocene species have teeth with either mesial or distal cusplets or both (Pfeil 1983). The Trelde Næs teeth are serrated in a way similar to teeth of *Echinorhinus weltoni* but differ from the latter by having longer distal crown tips extending beyond the root (Pfeil 1983). The Trelde Næs teeth are also close to teeth of *Echinorhinus priscus*, but in the latter no serration has been described (Arambourg 1952; Pfeil 1983). It seems therefore that the Trelde Næs teeth possess characters from both Eocene species but they seem closest to teeth of *Echinorhinus priscus* where long distal crown tips are described (Pfeil 1983).

Order Pristiophoriformes Berg 1958

Family Pristiophoridae Bleeker 1859

Genus *Pristiophorus* Müller & Henle 1837

Pristiophorus cf. *lanceolatus* Davis 1888

Fig. 21A–D

Material. 1 rostral tooth, DK729z.

Description. DK729z is an almost intact rostral tooth where a tiny part of the apex of the enameloid cap is missing. The tooth is worn. The total height from apex to base is 4.5 mm: 2.5 mm for the cap and 2 mm for the peduncle. The cap is dorso-ventrally flattened with slightly convex dorsal and ventral faces. The base of the peduncle is perpendicular to the cap. The enameloid is smooth and the cutting edges are rounded and almost parallel in dorsal view, except for the apical fifth where they gradually taper to the apex. The tooth lacks transverse ridges. At the cap–peduncle junction there is a bulge forming a collar above the constricted peduncle.

The peduncle widens rapidly basally and measures 3.1 mm (antero-posteriorly) at the flat base. Seen basally there is a deep anterior–posterior rectangular groove opening to the pulp cavity. The posterior margin is concave and slightly bi-lobed (one of the lobes is missing). The anterior margin is convex and there is a deep furrow from the central hole to the front of the peduncle.

Comparison. DK729z is a rostral tooth of Pristiophoridae because of its lack of transverse ridges and its open pulp cavity that separate it from rostral teeth of Pristoidei (Slaughter & Springer 1968; Cappetta 2012). Rostral teeth of Sclerorhynchoidei are, like the rostral teeth of Pristiophoridae, not imbedded in alveoli, but teeth of the former have a closed basal face (Cappetta 2012).

Three genera of Pristiophoridae have been described. Rostral teeth of *Pristiophorus* differ from rostral teeth of the extant *Pliotrema* Regan 1906 and the extinct *Ikamauius* Keyes 1979 by lacking barbs on the cutting edges (Keyes 1982). DK729z does not have parallel crown edges like rostral teeth of *Pristiophorus lineatus* Applegate & Uyono 1968 but slightly tapering

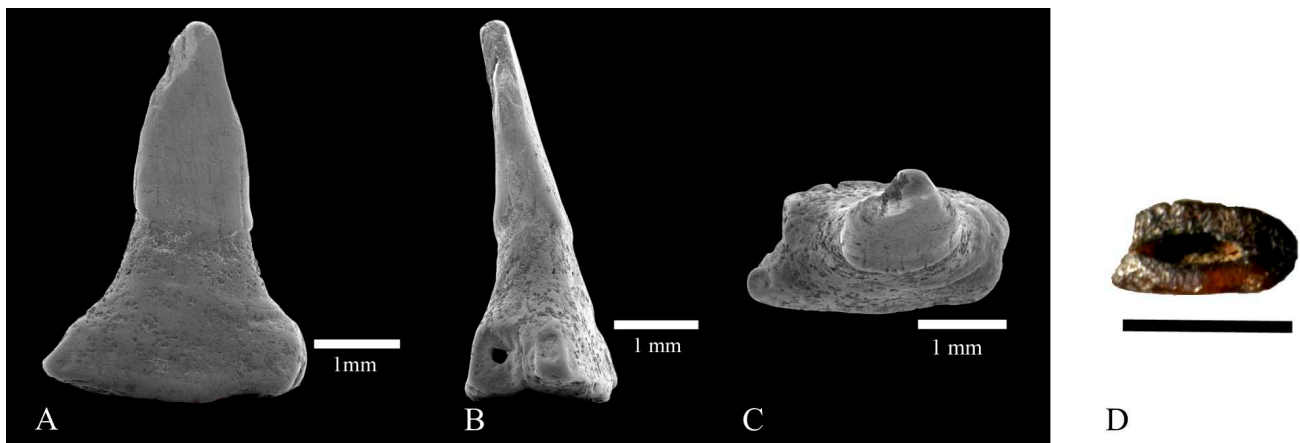


Fig. 21. A–D, *Pristiophorus* cf. *lanceolatus*. Rostral tooth DK729z. A, dorsal view; B, posterior view; C, apical view; D, basal view.

crown edges, and it lacks ornamentation on the crown like rostral teeth of *Pristiophorus lanceolatus* (Keyes 1982). It separates from rostral teeth of the Cretaceous *Pristiophorus tumidens* Woodward 1932, the Miocene *Pristiophorus suevicus* Jaekel 1890 and the Eocene *Pristiophorus lapicidinensis* Adnet 2006a which all have ornamentation on the crown (Long 1992; Gottfried & Rabarison 1997; Adnet 2006a).

Comparisons are difficult because of the low number of figured teeth for the different species in the literature and the fact that only one worn tooth is available from Trelde Næs. *Pristiophorus lineatus* is known from the Oligocene of Japan (Cappetta 2012), and *Pristiophorus lanceolatus* is known from the Eocene of Antarctica (Long 1992; Kriwet 2005) and the Oligocene of New Zealand (Keyes 1982). The Trelde Næs rostral tooth is closest to teeth of *Pristiophorus lanceolatus*. Similar teeth have been found in the Eocene of Oregon (Welton 1972), the Eocene of Antarctica (Long 1992) and the Pliocene of Italy (Cigala-Fulgosi 1986).

Superorder Batomorphii Cappetta 1980b

Order Myliobatiformes Compagno 1973

Superfamily Dasyatoidea Jordan 1888

Family *incertae sedis*

Genus *Coupatezia* Cappetta 1982

Coupatezia miretrainensis Adnet 2006a

Fig. 22A–D

Material. 3 lateral male teeth, including DK728g, MM1010 and MM0046.

Description. The teeth are very small and measure about 2 mm mesio-distally, 2 mm labio-lingually and 1.8 mm apico-basally. They have a slender, pointed lingually and slightly distally inclined cusp. The labial

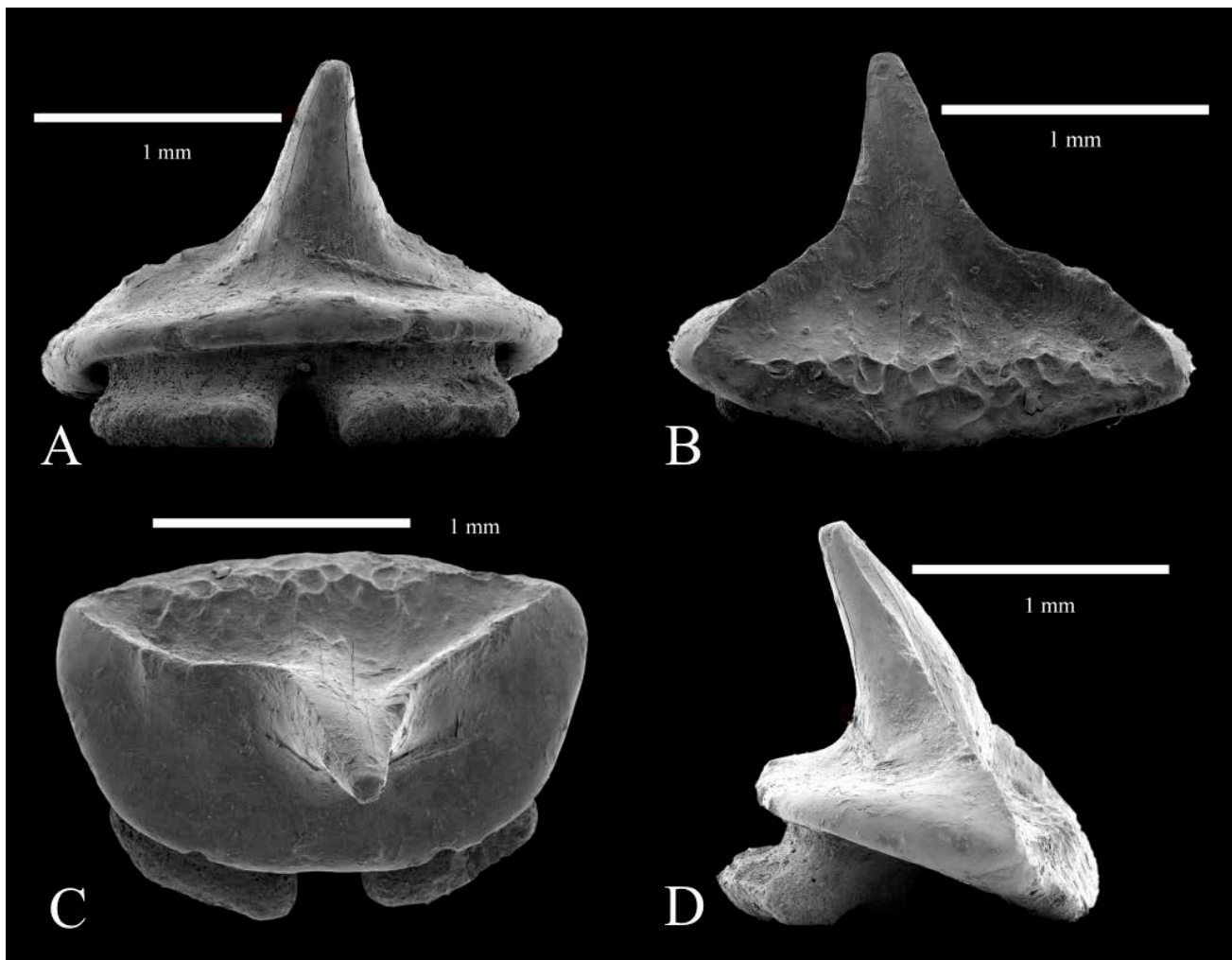


Fig. 22. A–D, *Coupatezia miretrainensis*. Male lateral tooth DK728g. A, lingual view; B, labial view; C, apical view; D, mesio-distal view.

face of the cusp is flat in the upper part and slightly concave in the basal part and without a median ridge. The edge of the labial visor is convex, broad and rounded with a flat horizontal basal face. The enameloid on the basal part of the labial face and the visor has coarse, vermicular and irregular ornamentation. The lingual crown face is strongly convex mesiodistally with 10–15 very faint longitudinal ridges or cracks on the enameloid, which are possibly a result of wear. The lingual visor is short and semi-circular when seen in apical view. The labial and lingual crown faces are separated by labially displaced and very prominent cutting edges which reach the crown base.

The root is low and displaced lingually. Its basal face is flat. It is divided in two triangular lobes by a deep and broad furrow with a large central foramen. The lingual edges of the root extend slightly beyond the crown foot and are visible in apical view. The lingual and the labial borders of the root are respectively oblique and parallel.

Comparison. The Trelde Næs teeth separate from teeth of *Raja* Agassiz 1843 by having ornamentation on the labial face of the cusp (Ward 1984). Furthermore the root is more developed in teeth of *Raja* and the basal side of the labial visor is convex. The Trelde Næs teeth also differ from teeth of *Torpedo* Forskål, 1775 and *Narcine* Henle 1834 by having ornamentation (Adnet 2006a). The Trelde Næs teeth have some resemblance with teeth of *Taeniura lymna* Forskål, 1775 known from the Miocene to the recent (Cappetta 2012) but they differ by having ornamentation near and on the basal labial margin of the cusp (Cappetta 2012). Labial ornamentation is seen on teeth of *Merabatis* Arambourg 1952 but these teeth are characterized by the complete concealment of the root by the visors in apical view, contrary to teeth of *Coupatezia* where the root is visible in apical view. Furthermore, teeth of *Raja* and *Merabatis* have a more or less sharp median labial vertical crest which is not present on the Trelde Næs teeth. *Coupatezia* has been described from the Upper Cretaceous of Morocco (Arambourg 1952; Noubhani & Cappetta 1997) to the Lutetian and Bartonian of France (Adnet 2006a). The species *Coupatezia miretrainensis* differ from the other species by its vermicular labial ornamentation and its relatively thin labial visor (Adnet 2006a). The Trelde Næs teeth are similar to lateral male teeth of *Coupatezia miretrainensis* figured by Adnet (2006a, plate 37, fig. 4a–4c). The Trelde Næs teeth are believed to be from male individuals because of the pointed cusp, contrary to the low cusp in female teeth. The slightly asymmetric cusp suggests a lateral position in the jaw.

Table 1. List of elasmobranchs found at Trelde Næs.

Numbers indicate the number of teeth used in the descriptions

	Surface material Lillebælt Clay layer L2–L6 and Søvind Marl	Bulk material Lillebælt Clay layer L2
Superorder Galeomorphii		
Order Lamniformes		
<i>Anomotodon sheppeyensis</i>	100	
<i>Striatolamia macrota</i>	46	
<i>Woellsteinia kozlovi</i>	22	
<i>Isurolamna affinis</i>	216	
<i>Macrorhizodus</i> cf. <i>nolfi</i>	99	
<i>Xiphodolamia ensis</i>	1	
<i>Alopias crochardi</i>	46	2
<i>Usakias</i> sp.	63	
<i>Carcharocles auriculatus</i>	34	
<i>Otodus</i> cf. <i>obliquus</i>	3	
<i>Palaeohypotodus rutoti</i>	2	
<i>Odontaspis</i> cf. <i>winkleri</i>	9	
<i>Jaekelotodus robustus</i>	11	
<i>Carcharias</i> sp. sensu Cappetta & Nolf 2005	14	
<i>Turania</i> sp.	5	
<i>Hypotodus verticalis</i>	7	
Odontaspidae genus indet. 1	6	
Odontaspidae genus indet. 2	1	
<i>Cretalamna</i> aff. <i>appendiculata</i>	3	
Lamniformes family indet.	12	
Order Carchariniformes		
<i>Megascyliorhinus cooperi</i>	2	
<i>Fountizia</i> sp.		2
<i>Physogaleus</i> cf. <i>secundus</i>	10	1
Superorder Squalomorphii		
Order Hexanchiformes		
<i>Chlamydoselachus</i> cf. <i>fiedleri</i>		1
<i>Heptranchias howelli</i>	18	1
<i>Notorynchus serratissimus</i>	23	1
<i>Hexanchus</i> cf. <i>agassizi</i>	4	2
<i>Weltonia burnhamensis</i>	1	1
Order Squatiniformes		
<i>Squatina</i> cf. <i>prima</i>	4	
Order Squaliformes		
<i>Centrophorus</i> aff. <i>granulosus</i>		22
<i>Isistius trituratorus</i>		9
Order Echinorhiniformes		
<i>Echinorhinus</i> cf. <i>priscus</i>		39
Order Pristiophoriformes		
<i>Pristiophorus</i> cf. <i>lanceolatus</i>	1	
Superorder Batomorphii		
Order Myliobatiformes		
<i>Coupatezia miretrainensis</i>		3

Palaeoecology and palaeoenvironment

Inferences on the palaeoecology of the Trelde Næs sharks and rays may be made by considering the occurrence and behaviour of related living forms, based on information in the literature (Compagno 2003; Compagno et al. 2005; <http://www.fishbase.com>). Of the 31 identified genera recorded from Trelde Næs so far, twelve genera are represented by extant genera, and fourteen are members of extinct families. The last five are members of extinct families and can only be related to modern superfamily or order. When there are no close living relatives, the palaeoecology may be considered exclusively from the tooth morphology and the fossil record.

The Trelde Næs shark and ray teeth material is divided into two sets according to the sampling method (Table 1): 1) Teeth retrieved from screen washed bulk samples where the provenance is known to be from the Lillebælt Clay Formation layer L2; 2) Teeth retrieved from surface sampling whose origin can therefore only be delimited to the Lillebælt Clay Formation layer L2 to L6 and the Lower Søvind Marl Formation.

For the purpose of this project, deep-water chondrichthyans have been defined as those sharks and rays whose distribution is predominantly at, or spend the majority of their lifecycle at depths below 200 m. This depth is generally recognized as the continental and insular shelf edge, and therefore deep-water species are those occurring on or over the continental and insular slopes and beyond, including the abyssal plains and oceanic seamounts (Kyne & Simpfendorfer 2007).

Screen washed material

This material (Table 1) contains only small teeth of Lamniformes, Carchariniiformes, Hexanchiiformes, Squaliiformes, Echinorhiniiformes and Myliobatiiformes, and includes thirteen different genera retrieved from a relatively small bulk size of approximately 160 kg.

Lamniformes are represented by two teeth of *Alopias crochardi*. The tooth morphology of the fossil species *Alopias crochardi* is closest to that of *Alopias superciliosus*. These pelagic sharks live worldwide in warm to temperate oceans and have been observed down to a depth of 730 m (<http://www.fishbase.org>).

Carchariniiformes are represented by *Megascyliorhinus cooperi*, *Fountiztia* sp. and *Physogaleus* cf. *secundus*. These genera have no close living relatives.

Megascyliorhinus cooperi is described as belonging

to the family Scyliorhinidae (Cappetta & Ward 1977) in the extinct subfamily Megascyliorhininae. Teeth of *Megascyliorhinus* differ from teeth of other Scyliorhinids by lacking cusplets on the anterior teeth, but Cappetta & Ward (1977) pointed out broad similarities between the teeth of *Megascyliorhinus* and the teeth of *Scyliorhinus* Blainville 1816. The latter genus is benthic and nocturnal with a depth range from 10 to 780 m (<http://www.fishbase.org>). Cappetta & Ward (1977) suggested a depth range of 150 to 200 m for *Megascyliorhinus*, whereas Adnet (2006a) suggested it

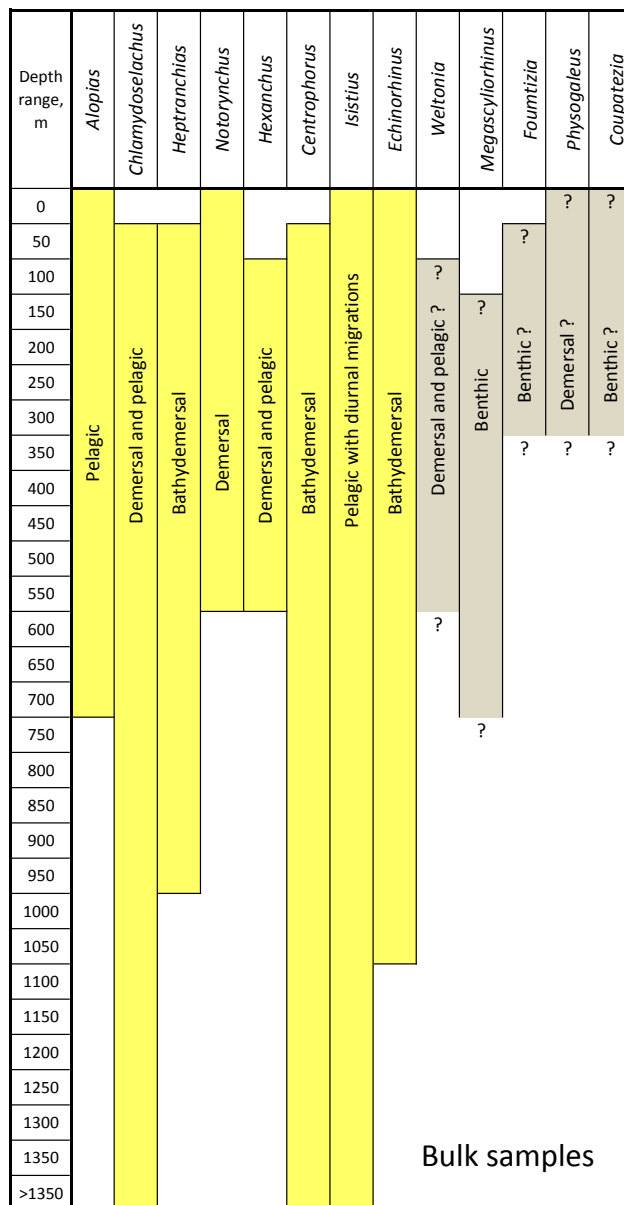


Fig. 23. Suggested depth range (metres) of the sharks and rays found in the Lillebælt Clay Formation layer L2 (bulk samples). The yellow columns indicate recent genera. The grey columns indicate fossil genera without close living relatives and where the depth range is uncertain.

to be deeper as it has been found together with other deep-water species.

Teeth of *Fountizia* have ornamented crowns with small cusplets and a pronounced horizontal labial crest, characters found among Scyliorhinidae and Triakidae (Compagno 2003). The habitat of *Fountizia* is unknown, but the fact that it has been found together with other deep-water genera such as *Centrophorus* in south-western France (Adnet 2006a) could suggest a depth range of a few hundred metres.

Physogaleus cf. *secundus* is described as belonging to the family Carcharhinidae. Cappetta (1980a) suggested that *Physogaleus* might be an ancestor to *Scoliodon*, *Rhizoprionodon* and *Loxodon*, but the morphology of its teeth seems closest to that of *Rhizoprionodon* (Compagno *et al.* 2005, drawings p. 317–320). *Rhizoprionodon* probably lives near the bottom and is very common in coastal water and on continental shelves with a depth range down to 350 m (Compagno *et al.* 2005).

Hexanchiformes are represented by *Chlamydoselachus* cf. *fiedleri*, *Heptranchias howelli*, *Notorynchus serratisimus*, *Hexanchus* cf. *agassizi* and *Weltonia burnhamensis*.

The recent species of *Chlamydoselachus* live near the bottom as well as in the midwaters with a depth range of 50 to 1200 m and they have been found on the continental shelf and upper slopes (<http://www.fishbase.org>). *Heptranchias perlo* is the only recent species of the genus *Heptranchias*. It is found near the bottom on the outer continental and insular shelves and upper slopes in depths of 50 to 400 m, as well as inshore, down to 1000 m (<http://www.fishbase.org>). *Notorynchus cepedianus* is the only recent species of the genus *Notorynchus*. It is found on the continental shelf, often in shallow water, but its depth range is from 1 to 570 m. It lives near the bottom but can also be seen near the surface (<http://www.fishbase.org>).

There are two recent species of *Hexanchus*. They both live near the bottom and in open waters, occasionally moving to the surface at night. Their depth range is usually from 90 to 600 m (<http://www.fishbase.org>). *Weltonia* is described as belonging to the family Hexanchidae and has no living relatives at genus level. There are two fossil species of *Weltonia*: *Weltonia burnhamensis* and *Weltonia ancistrodon*, known respectively from the London Clay (Casier 1966; Ward 1979) and Morocco (Arambourg 1952; Noubhani & Cappetta 1997). The fact that *Weltonia* has been found together with other hexanchids in the above-mentioned locations justifies the assumption that *Weltonia* was also living in deep waters.

Squaliformes are represented by *Centrophorus* aff. *granulosus* and *Isistius trituratorus*. The recent species of *Centrophorus* are all deep-water species living on the outer slope near the bottom. The depth range varies, but the common range is 100 to 800 m although some

species have been found at depths of 2400 m (<http://www.fishbase.org>).

The recent species of *Isistius* are also deep-water species down to over 1350 m, found in tropical to temperate waters with diurnal migration to the surface at night (<http://www.fishbase.org>).

Echinorhiniformes are represented by *Echinorhinus* cf. *priscus*. The modern species of *Echinorhinus* are deep-water sharks, found on continental and insular shelves and upper slopes and sometimes also in shallow water. They live in temperate water down to 900 m. (<http://www.fishbase.org>).

Only one species of Batomorphii was found: *Coupatezia miretrainensis*. The tooth morphology of *Coupatezia* has some similarities to teeth of Dasyatidae, in particular *Dasyatis pastinaca* (common stingray) (Cappetta 2012). This species lives today on muddy bottoms down to 200 m in subtropical waters (<http://www.fishbase.org>). Teeth of *Coupatezia* also show some similarities with teeth of *Taeniura* (Cappetta 2012, fig. 414), but this genus is reef-related in tropical waters (<http://www.fishbase.org>).

Adnet (2006a) suggested that some species of *Coupatezia* were living in deep waters, and the fact that teeth of *Coupatezia* have been found in deep-water sediments together with teeth of several other deep-water genera (Adnet *et al.* 2008) supports this idea. It was probably found down to about 350 m, but this remains uncertain.

Summary. All the species with recent close relatives present in layer L2 can be found in water depths down to 600 m or more (Fig. 23). The pelagic species (*Alopias* and *Isistius*) give no information on the water depth because they feed at various depths in the water column. The demersal and bathydemersal species (*Chlamydoselachus*, *Heptranchias*, *Notorynchus*, *Hexanchus*, *Centrophorus* and *Echinorhinus*) all live and feed near the bottom and thereby suggest a maximum water depth about 600 m, but they are also found in shallower waters. This agrees with the water depth in the Danish area given in Heilmann-Clausen & Surlyk (2006) as probably being about 500 m during the Late Ypresian. The habitat and depth range of the five genera without close living relatives (*Weltonia*, *Megascyliorhinus*, *Fountizia*, *Physogaleus* and *Coupatezia*) is difficult to infer with confidence. We consider them all to have been benthic or demersal. It seems that the depositional environment for the teeth from the bulk sample was a marine deep-water environment with depth below 100 m but probably not deeper than 350 m (Fig. 23). This agrees with the water depth of 100 to 300 m inferred from the molluscan fauna from Trelde Næs (Schnetler & Heilmann-Clausen 2011). An explanation for the discrepancy between the depth given

by Heilmann-Clausen & Surlyk (2006) and the present fossil record could be that Trelde Næs is located in the vicinity of the Ringkøbing–Fyn High in the North Sea Basin. Another explanation for the difference from the expected 500 m would be that teeth of *Foumtizia*, *Physogaleus* and *Coupatetia* have been transported by currents from shallower waters out into a deeper basin. This explanation seems less probable because the nearest coastline was about 300 km from the deposition site at Trelde Næs (Thomsen *et al.* 2012).

Surface collected material

This material consists mainly of teeth of Lamniformes (about 90%). There are only very few small teeth in this material, probably because of the collecting method, but this does not mean that the small and very small teeth are absent from the sediments. The far most abundant teeth are from Mitsukurinidae, Lamnidae and Alopiidae (Table 1).

Seventeen species of Lamniformes in seven families were identified. Mitsukurinidae are represented by *Anomotodon sheppeyensis*, *Striatolamia macrota* and *Woellsteinia kozlovi*. There is only one living species in this family, *Mitsukurina owstoni* Jordan 1898. This shark is a pelagic shark with a worldwide distribution in tropical and warm waters with a depth range from 30 to 1300 m. It has been found on outer continental shelves and upper slopes, but rarely in shallow water close inshore (<http://www.fishbase.org>). Teeth of *Anomotodon sheppeyensis* have been found in the London Clay deep-water sediments (Rayner *et al.* 2009) and the deep-water sediments of south-western France (Adnet 2006a). However, teeth of other species of *Anomotodon* have been found in shallow-water deposits in Antarctica (Kriwet 2005) and Southern Chile (Otero *et al.* 2012). Teeth of *Striatolamia macrota* are known from the Early Ypresian London Clay (Rayner *et al.* 2009), the Ypresian/Lutetian of south-western France (Adnet 2006a; Adnet *et al.* 2008) and the Ypresian/Lutetian of North Germany (Diedrich 2012). All these environments are considered to be deep-water environments. However, teeth of *Striatolamia macrota* have also been found in marine shallow-water deposits of the Eocene of Belgium (Nolf 1988), Antarctica (Kriwet 2005), Southern Chile (Otero *et al.* 2012) and Maryland, USA (Ward & Wiest 1990). Teeth of *Woellsteinia* have only been found in deep-water deposits from south-western France (Adnet 2006a) and from New Zealand (Mannering & Hiller 2008). The fossil record of the Mitsukurinidae suggests therefore a pelagic behaviour and a worldwide distribution of fossil genera.

Lamnidae are represented by *Isurolamna affinis* and *Macrorhizodus* cf. *nolfi*. Today, the family encompasses *Carcharodon*, *Isurus* and *Lamna*. They are all pelagic with

a depth range from 0 to 750 m, but sometimes visit temperate shallower waters (<http://www.fishbase.org>).

Teeth of *Isurolamna affinis* have been found in deep-water sediments from the London Clay (Rayner *et al.* 2009), south-western France (Adnet 2006a), North Germany (Diedrich 2012) and shallow open marine waters from Belgium (Nolf 1988; Eeckhaut & De Schutter 2009). Teeth of *Macrorhizodus nolfi* have been found in the deep-water sediments from the Early Ypresian London Clay (Rayner *et al.* 2009) and also in Ypresian deposits of Kazakhstan (Zhelezko & Kozlov 1999), for which the palaeobathymetry is not known. Teeth of *Macrorhizodus praecursor* have been found in deep-water deposits in south-western France (Adnet 2006a), Germany (Diedrich 2012) as well as in shallow open marine water deposits in Belgium (Nolf 1988), Egypt (Underwood *et al.* 2011b), Antarctica (Kriwet 2005) and Chile (Otero *et al.* 2012). This suggests that *Isurolamna* as well as *Macrorhizodus* were pelagic sharks like the recent lamnids.

Xiphodolamiidae are represented by *Xiphodolamia ensis* which has no recent relatives. Adnet *et al.* (2009) considered this genus as Lamnidae *incertae sedis*, but Cappetta (2012) has elevated the subfamily Xiphodolaminae Glikman 1964a to the rank of family because of its very special dental morphology. Adnet *et al.* (2009) regarded *Xiphodolamia* as an old lineage derived from the stem group of Lamnidae, close to the Isuroid sharks. Fossil teeth of *Xiphodolamia* are rare in coastal deposits but occur in deep-water deposits like the London Clay (Rayner *et al.* 2009), North Germany (Diedrich 2012), but also in shallow-marine water in Belgium (Nolf 1988; Eeckhaut & De Schutter 2009). This led Adnet *et al.* (2009) to suggest that *Xiphodolamia* probably lived in rather deep and/or open waters.

Alopiidae are represented by *Alopias crochardi* and *Usakias* sp. The closest recent relative to *Alopias crochardi* is presumed to be *Alopias superciliosus*, which is a pelagic species distributed worldwide in warm and temperate waters down to 730 m (<http://www.fishbase.org>). Teeth of *Usakias* are morphologically close to teeth of *Alopias* and there is no reason to think that its habitat differed from the habitat of *Alopias*. Teeth of *Usakias* have been found in deep-water sediments in North Germany (Diedrich 2012) and shallow-marine water sediments in Belgium (Eeckhaut & De Schutter 2009).

Otodontidae is an extinct family represented by *Carcharocles auriculatus* and *Otodus* cf. *obliquus*. Based on the size and morphology of teeth of *Carcharocles auriculatus*, this shark must have been a very large predator. Its teeth have been found worldwide (Cappetta 2012). This suggests that it had a pelagic behaviour and its teeth have been found in deep as well as shallow-marine deposits. Teeth of *Otodus* cf. *obliquus* are morphologically very close to teeth of *Carcharocles*

and it is parsimonious to infer a similar habitat. *Otodus* had the same distribution as *Carcharocles* (Cappetta 2012) and has been found in deep-water sediments in the London Clay (Rayner *et al.* 2009), the Paris Basin in France (Dutheil *et al.* 2006) and North Germany (Diedrich 2012).

Cretalamna aff. *appendiculata*. From the morphology and size of their teeth, they are believed to have been large predatory sharks, and their teeth have been found worldwide (Cappetta 2012). Teeth of *Cretalamna* aff. *appendiculata* have been found in deep-water sediments from the Northern hemisphere in the London Clay (Rayner *et al.* 2009), southwestern France (Adnet 2006a) and sediments from Morocco (Noubhani & Cappetta 1997).

Odontaspidae are represented by six different genera: *Palaeohypotodus*, *Odontaspis*, *Jaekelotodus*, *Car-*

charias, *Turania* and *Hypotodus*, whereas the family encompasses today only *Odontaspis* and *Carcharias*.

Odontaspis is found on or near the bottom of the continental and insular shelves and upper slopes and are considered deep-water species, possibly pelagic (Compagno *et al.* 2005), with a depth range from 1 to over 1000 m (<http://www.fishbase.org>).

Carcharias lives in the neritic zone in water depth down to 200 m. It is a common littoral shark found inshore from the surf zone and in shallow bays to the outer continental shelves. It often occurs on or near the bottom but also in midwaters or at the surface. It is known to migrate between oceans, moving to cooler water in summer, and is distributed worldwide in the subtropical zone (<http://www.fishbase.org>).

The different lifestyles of *Odontaspis* and *Carcharias* lead Cvancara & Hoganson (1993) to place *Carcharias*

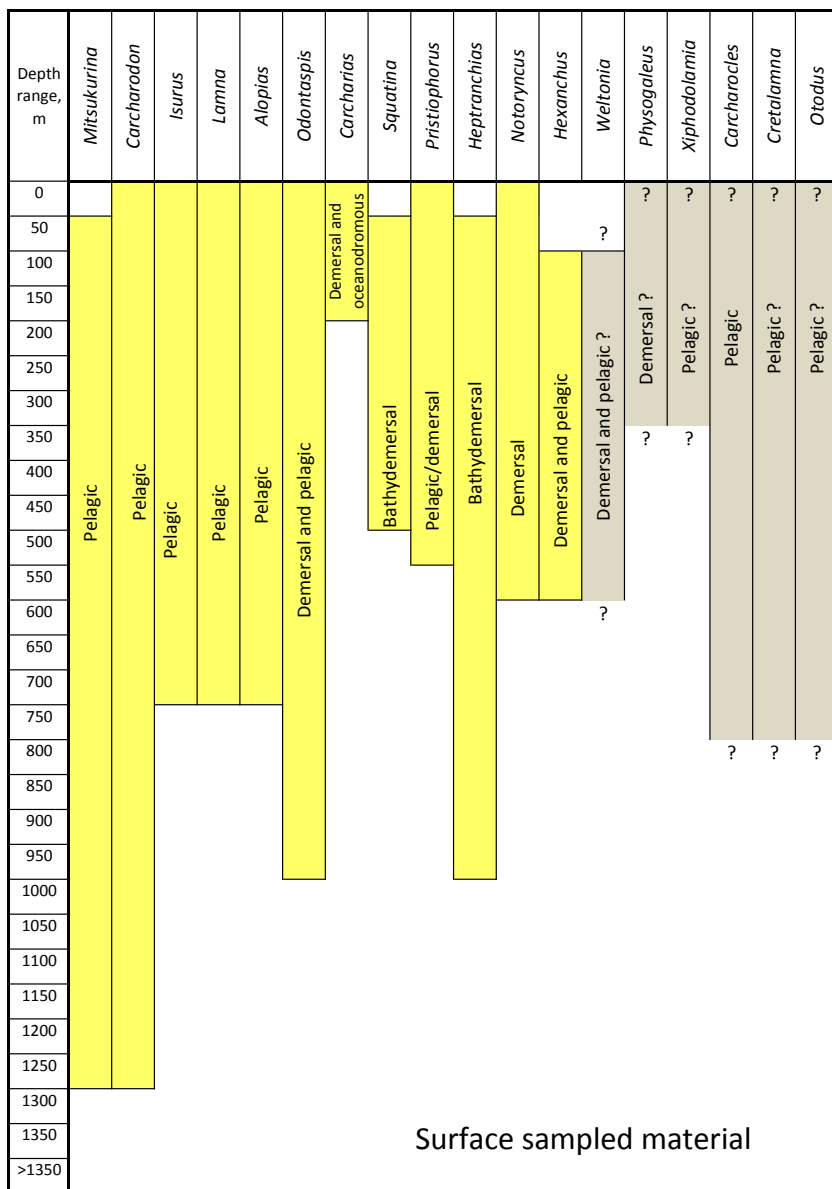


Fig. 24. Suggested depth range (metres) of the sharks found in the Lillebælt Clay Formation layers L2 to L6 and Lower Søvind Marl Formation (surface samples). The yellow columns indicate recent genera. The grey columns indicate fossil genera without close living relatives and where the depth range is uncertain.

in its own family Carchariidae. This has recently been confirmed by molecular DNA-studies which found that *Odontaspis* and *Carcharias* are not closely related (Vélez-Zuazo & Agnarsson 2011). However, these results have not yet been commonly accepted, and we conservatively keep all six genera in the family Odontaspidae.

Teeth of *Palaeohypotodus*, *Jaekelotodus*, and *Hypotodus* have morphology close to teeth of *Odontaspis* and probably lived in the same type of habitat as deep-water demersal species. *Palaeohypotodus* has been found in deep- and shallow-marine sediments from both hemispheres, whereas *Jaekelotodus* and *Hypotodus* have only been found in sediments from the Northern hemisphere (Cappetta 2012). Teeth of *Carcharias* sp. sensu Cappetta & Nolf 2005 have been found in deep-water sediments (Cooper 1977; Adnet 2006a; Dutheil *et al.*

2006; Mannering & Hiller 2008; Diedrich 2012) as well as in shallow-water sediments (Eeckhaut & De Schutter 2009) from both hemispheres. Teeth of *Turania* have so far only been found in Bartonian sediments (the deposition depth of which is unknown) in Kazakhstan (Kozlov 2001), but this taxon must be considered with caution as discussed above.

It is concluded that the fossil Odontaspidae were all deep-water species, possibly pelagic, and lived near the bottom in the epicontinental seas and in the open sea. Fossil teeth of *Carcharias* are not uncommon in deep-water sediments and it is a possibility that the genus today has adapted to shallower water than was the case in the Eocene.

Hexanchiformes (except *Chlamydoselachus*) and *Physogaleus* cf. *secundus* were present in the surface sample as well as in the bulk samples.

							Trelde Næs						
							Danian	Selandian	Thanetian	Ypresian	Lutetian	Bartonian	Priabonian
							Paleocene			Eocene			
Genera							Early	Late		Early	Middle	Late	
<i>Anomotodon</i>													
<i>Striatolamia</i>													
<i>Woellsteinia</i>													
<i>Isurolamna</i>													
<i>Macrorhizodus</i>													
<i>Xiphodolamia</i>													
<i>Alopias</i>													
<i>Usakias</i>													
<i>Carcharocles</i>													
<i>Otodus</i>													
<i>Palaeohypotodus</i>													
<i>Odontaspis</i>													
<i>Jaekelotodus</i>													
<i>Carcharias</i>													
<i>Turania</i>													
<i>Hypotodus</i>													
<i>Cretalamna</i>													
<i>Megascyliorhinus</i>													
<i>Fountizia</i>													
<i>Physogaleus</i>													
<i>Chlamydoselachus</i>													
<i>Heptranchias</i>													
<i>Notorynchus</i>													
<i>Hexanchus</i>													
<i>Weltonia</i>													
<i>Squatina</i>													
<i>Centrophorus</i>													
<i>Isistius</i>													
<i>Echinorhinus</i>													
<i>Pristiophorus</i>													
<i>Coupatezia</i>													

Fig. 25. Known stratigraphic distribution of the genera present in the total Trelde Næs fauna during the Paleocene and the Eocene. Data from Cappetta (2012).

Squatiniiformes are represented by *Squatina* cf. *prima*. The recent species of *Squatina*, except *Squatina dumeril*, live on the continental shelf and the upper slope near or on the bottom with a depth range of approximately 10–500 m (<http://www.fishbase.org>). Fossil teeth of *Squatina* have been found in deep-sea and shallow-marine sediments worldwide (Nolf 1988; Ward & Wiest 1990; Noubhani & Cappetta 1997; Kriwet 2005; Adnet 2006a; Dutheil *et al.* 2006; Eeckhaut & De Schutter 2009; Rayner *et al.* 2009; Underwood *et al.* 2011b). This shark first appeared in the upper Jurassic and has had a very long time to spread worldwide in spite of its benthic behavior.

Pristiophoriformes are represented by one rostral tooth of *Pristiophorus* cf. *lanceolatus*. The recent species of *Pristiophorus* all live on the continental shelf and the upper slope. Two species are pelagic, the others are

demersal and live on or near the bottom. The depth range of the genus is approximately 0–500 m (<http://www.fishbase.org>). In the fossil record, *Pristiophorus* has a worldwide distribution (Compagno *et al.* 2005). The genus has been found in the deep-water sediments of southwestern France (Adnet 2006a) and shallow-marine sediments of Egypt (Underwood *et al.* 2011b) and Antarctica (Kriwet 2005). *Pristiophorus lanceolatus* has been described from Antarctica (Long 1992), but may have been distributed worldwide (Long 1992).

Summary. The teeth from the surface material (Fig. 24) come from a long time period (about 5.1 Ma), from the Upper Ypresian to the Middle Lutetian.

Mitsukurina, Carcharodon, Isurus, Lamna and Alopias are pelagic and cannot contribute to estimation of

Species	Trelde Næs						
	Danian	Selandian	Thanetian	Ypresian	Lutetian	Bartonian	Priabonian
	Paleocene			Eocene			
Early	Late		Early	Middle	Late		
<i>Anomotodon sheppeyensis</i>							
<i>Striatolamia macrota</i>							
<i>Woellsteinia kozlovi</i>							
<i>Isurolamna affinis</i>							
<i>Macrorhizodus</i> cf. <i>nolfi</i>							
<i>Xiphodolamia ensis</i>							
<i>Alopias crochardi</i>							
<i>Usakias</i> sp.							
<i>Carcharocles auriculatus</i>							
<i>Otodus</i> cf. <i>obliquus</i>							
<i>Palaeohypotodus rutoti</i>							
<i>Odontaspis</i> cf. <i>winkleri</i>							
<i>Jaekelotodus robustus</i>							
<i>Carcharias</i> sp. sensu Cappetta & Nolf 2005							
<i>Turania</i> sp.							
<i>Hypotodus verticalis</i>							
<i>Cretalamna</i> aff. <i>appendiculata</i>							
<i>Megascyliorhinus cooperi</i>							
<i>Foumtizia</i> sp.							
<i>Physogaleus</i> cf. <i>secundus</i>							
<i>Chlamydoselachus</i> cf. <i>fiedleri</i>							
<i>Heptranchias howelli</i>							
<i>Notorynchus serratissimus</i>							
<i>Hexanchus</i> cf. <i>agassizi</i>							
<i>Weltonia burnhamensis</i>							
<i>Squatina</i> cf. <i>prima</i>							
<i>Centrophorus</i> aff. <i>granulosus</i>							
<i>Isistius triturratus</i>							
<i>Echinorhinus</i> cf. <i>priscus</i>							
<i>Pristiophorus</i> cf. <i>lanceolatus</i>							
<i>Coupatzia miretraiensis</i>							

Fig. 26. Stratigraphic distribution of the Trelde Næs species. Yellow colour indicates stratigraphic distribution of the species known from the literature. Grey colour indicates species found in the bulk samples. Green colour indicates presence only known from Trelde Næs.

the water depth at which the sediment was deposited because they feed at various depths in the water column. *Odontaspis*, *Squatina*, *Pristiophorus*, *Heptanchias*, *Notorynchus* and *Hexanchus* are demersal in waters down at least to 500 m. This could agree with the water depth in the Danish area given in Heilmann-Clausen & Surlyk (2006) as probably around 500 m, with the exception of *Carcharias* which today lives in shallower water. It is in this connection notable that *Carcharias*

has been found in several deep-water deposits, and the presence of *Carcharias* can therefore not be considered as a contradiction to the water depth given by Heilmann-Clausen & Surlyk (2006).

The habitat of the six fossil genera without close living relatives (*Weltonia*, *Physogaleus*, *Xiphodolamia*, *Cretalamna*, *Carcharocles* and *Otodus*) is difficult to infer with confidence (Fig. 24). It appears likely that the teeth from the surface sample were deposited in a marine

	<i>Anomotodon sheppeyensis</i>	<i>Striatolamia macrata</i>	<i>Woelksteinia kozlovi</i>	<i>Isurrolamia affinis</i>	<i>Macrorhizodus cf. nolfi</i>	<i>Xiphodolamia ensis</i>	<i>Alopias crochardi</i>	<i>Usakias</i> sp.	<i>Carcharocles auriculatus</i>	<i>Otodus (Otodus) cf. obliquus</i>	<i>Palaeohypotodus rutoti</i>	<i>Odontaspis cf. winkleri</i>	<i>Jaekelotodus robustus</i>	<i>Carcharias</i> sp.	<i>Turanina</i> sp.	<i>Hypotodus verticalis</i>	<i>Cretalamna aff. appendiculata</i>	<i>Megascyllorhinus cooperi</i>	<i>Foumitzia</i> sp.	<i>Physogaleus cf. secundus</i>	<i>Chlamydoselachus aff. fiedleri</i>	<i>Heptanchias howelli</i>	<i>Notorynchus serratissimus</i>	<i>Hexanchus cf. agassizi</i>	<i>Weltonia burnhamensis</i>	<i>Squatina cf. prima</i>	<i>Centrophorus aff. granulosus</i>	<i>Isistius trituratorus</i>	<i>Echinorhinus cf. priscus</i>	<i>Pristiophorus cf. lanceolatus</i>	<i>Coupatzeia miretrainsensis</i>			
	Lamniformes																Carchariniformes				Hexanchiformes													
Trelde Næs Ypresian/Lutetian	100	46	22	216	99	1	48	63	34	3	2	9	11	14	5	7	3	2	2	11	1	19	24	6	2	4	22	9	39	1	3	31		
(a) London Clay Early-Middle Ypresian	•	•		•	•	•	•			•	•	•	•	•		•	•	•	•			•	•	•	•	•	•	•					21	
(b) SW France Ypresian/Lutetian	•	•	•	•								•				•	•	•	•			•		•		•	•						15	
(c) Belgium Eocene		•		•			•	•			•	•	•	•		•			•			•				•	•						14	
(d) North Germany Ypresian/Lutetian		•		•			•	•	•			•	•	•		•							•				•							10
(e) France Paris Basin Early Ypresian										•	•	•		•		•																		5
(f) Morocco Ypresian/Lutetian		•								•		•		•		•				•		•				•	•	•						11

Fig. 27. List of faunas used for comparison on species level. (a): Rayner *et al.* (2009); Cooper (1977). (b): Adnet (2006a); Adnet *et al.* (2008). (c): Nolf (1988); Eeckhaut & De Schutter (2009). (d) : Diedrich (2012). (e): Dutheil *et al.* (2006). (f): Ward & Wiest (1990); Noubhani & Cappetta (1997). Numbers in row 3 indicate the number of teeth used for description/identification in the Trelde Næs fauna. • indicates presence of the same species as in the Trelde Næs fauna. Numbers in the right column indicate the sum of the species in common with the Trelde Næs fauna.

	<i>Anomotodon</i>	<i>Striatolamia</i>	<i>Woelksteinia</i>	<i>Isurrolamia</i>	<i>Macrorhizodus</i>	<i>Xiphodolamia</i>	<i>Alopias</i>	<i>Usakias</i>	<i>Carcharocles</i>	<i>Otodus (Otodus)</i>	<i>Palaeohypotodus</i>	<i>Odontaspis</i>	<i>Jaekelotodus</i>	<i>Carcharias</i>	<i>Turanina</i>	<i>Hypotodus</i>	<i>Cretalamna</i>	<i>Megascyllorhinus</i>	<i>Foumitzia</i>	<i>Physogaleus</i>	<i>Chlamydoselachus</i>	<i>Heptanchias</i>	<i>Notorynchus</i>	<i>Hexanchus</i>	<i>Weltonia</i>	<i>Squatina</i>	<i>Centrophorus</i>	<i>Isistius</i>	<i>Echinorhinus</i>	<i>Pristiophorus</i>	<i>Coupatzeia</i>			
	Lamniformes																Carchariniformes				Hexanchiformes													
Trelde Næs Ypresian/Lutetian	100	46	22	216	99	1	48	63	34	3	2	9	11	14	5	7	3	2	2	11	1	19	24	6	2	4	22	9	39	1	3	31		
(a) London Clay Early-Middle Ypresian	•	•		•	•	•	•			•	•	•	•	•		•	•	•	•			•	•	•	•	•	•	•					22	
(b) SW France Ypresian/Lutetian	•	•	•	•	•		•					•				•	•	•	•			•		•		•	•	•					22	
(c) Belgium Eocene	•	•		•	•	•		•	•		•	•	•	•		•			•				•			•	•							17
(d) North Germany Ypresian/Lutetian	•	•		•	•	•		•	•	•		•	•	•		•																		12
(e) France Paris Basin Early Ypresian	•	•		•						•	•	•		•		•										•								10
(f) Morocco Ypresian/Lutetian		•		•			•			•		•		•		•				•		•		•	•	•	•	•	•					17

Fig. 28. List of faunas used for comparison on genus level. (a) Rayner *et al.* (2009); Cooper (1977). (b): Adnet (2006a); Adnet *et al.* (2008). (c): Nolf (1988); Eeckhaut & De Schutter (2009). (d): Diedrich (2012). (e): Dutheil *et al.* (2006). (f): Ward & Wiest (1990); Noubhani & Cappetta (1997). Numbers in row 3 indicate the number of teeth used for description/identification in the Trelde Næs fauna. • indicates presence of the same genus as in the Trelde Næs fauna. Numbers in the right column indicate the sum of the genera in common with the Trelde Næs fauna.

deep-sea environment below 100 m. The precise depth is unknown, but a depth between 100 and 350 m will satisfy almost all the species present in the studied surface sample. Based on the molluscan fauna from Trelde Næs, Schnetler & Heilmann-Clausen (2011) suggested deposition of the Lillebælt Clay in water depth between 100 and 300 m, which agrees with the data based on shark teeth distribution. The discrepancy between the water depth given by Heilmann-Clausen & Surlyk (2006) and the present work and the work of Schnetler & Heilmann-Clausen (2011) might be explained by the localisation of Trelde Næs in the vicinity of the Ringkøbing-Fyn High if this structure was expressed as an elevation of the sea floor.

It is concluded that in the period when the Lillebælt Clay Formation layers L2–L6 and the lower Søvind Marl Formation were deposited, the elasmobranch fauna was dominated by pelagic species and deep-water species living in warm to temperate water on the middle or outer continental shelf and upper slope. The average water depth in the period is estimated to have been between 100 and 350 m. It must be emphasized that the data on the species without close living relatives are uncertain. The fall in the sea level in the Danish area as given by Heilmann-Clausen & Surlyk (2006, fig 10-2) to have been about 100 m, from 500 m to 400 m in the actual period, cannot be confirmed by the present work, probably due to the sparsely known habitat of the fossil species without close living relatives.

Biostratigraphy

During the Late Ypresian and the Lutetian, the North Sea Basin was covered by a large epicontinental sea which covered Denmark, southeast England, north-west Germany, Holland, Belgium and part of France. From the Arctic Sea, a seaway opened into central Asia via the Turgai Strait.

Many of the genera present in the Trelde Næs fauna were already established in the Paleocene, see Fig. 25 (Cappetta 2012), and could have spread via the open seaways. In the Late Ypresian and Early Lutetian, a land bridge between the European continent and Great Britain blocked the direct passage between the North Sea and the Atlantic Ocean (Heilmann-Clausen & Surlyk 2006, fig 10-2), giving possibility for development of allopatric species of the same genera in the Trelde Næs fauna and in the faunas close to the Atlantic Sea.

Woellsteinia, *Macrorhizodus*, *Xiphodolamia*, *Alopias*, *Usakias*, *Carcharocles* and *Megascyliorhinus* first appeared at the beginning of the Eocene. *Weltonia* is restricted to the Thanetian and the Ypresian. *Isistius* first appeared

in the Late Paleocene. *Turania*, if valid, has only been reported from the Bartonian. *Otodus*, *Palaeohypotodus* and *Weltonia* became extinct at the end of the Ypresian (Cappetta 2012).

The bulk sample from Trelde Næs has a known provenance from the Late Ypresian layer L2. It is seen from Fig. 26 that 10 of the recorded 13 species from L2 are known from the literature to be present in the Ypresian. Three species: *Chlamydoselachus* cf. *fiedleri*, *Coupagezia miretrainensis* and *Centrophorus* aff. *granulosus* have not earlier been described from the Ypresian.

The genus *Chlamydoselachus* is known from the Late Cretaceous to the present (Cappetta 2012), but, as the identification of the species *Chlamydoselachus* cf. *fiedleri* is tentative, it does not seem justified to extend the stratigraphic distribution of this species to the Ypresian; however if we consider that this species occurred in the Lutetian of Denmark (Pfeil 1983) it will not be unexpected to find this taxon in the Upper Ypresian too.

Coupagezia is also a genus that goes back to the Late Cretaceous. The presence of the species *Coupagezia miretrainensis* was so far restricted to the Lutetian (Adnet 2006a). Its discovery in L2 therefore extends its stratigraphic distribution to the Late Ypresian.

Adnet (2006a) described teeth of *Centrophorus* aff. *granulosus* from the Lutetian of southwestern France and suggested they were at the origin of the *Centrophorus granulosus* group. These teeth are similar to the Trelde Næs teeth and based on this similarity it seems justified to extend the origin of the *Centrophorus granulosus* group back to the Late Ypresian.

From Fig. 26 it can be seen that *Pristiophorus* cf. *lanceolatus* appeared in the Lutetian and therefore probably has come from L3–L6 or the Søvind Marl.

Turania is a doubtful genus which has until now only been known from Bartonian sediments (Kozlov 2001). Its presence in the Trelde Næs surface sample is difficult to explain. One possibility is that the five teeth in reality belongs to *Carcharias*, another possibility is that Trelde Næs contains sediments from the Bartonian. The latter seems less probable because extensive logging at Trelde Næs has never revealed Bartonian sediments (Heilmann-Clausen *et al.* 1985). Schnetler (1985) claimed to have observed small temporary exposures of the Late Oligocene Brejning Formation, but gave no evidence for it. In the present state of our knowledge, an extension of the stratigraphic distribution of *Turania* cannot be demonstrated. All the remaining species are already known from the Ypresian.

Macrorhizodus nolfi, *Xiphodolamia ensis*, *Alopias crochardi*, *Otodus obliquus*, *Palaeohypotodus rutoti*, *Notorynchus serratissimus* and *Weltonia burnhamensis* became extinct at the end of the Ypresian and therefore their

teeth must have been washed out from the Late Ypresian layer L2 for them to appear in the surface sample.

Anomotodon sheppeyensis, *Striatolamia macrota*, *Woellsteinia kozlovi*, *Isurolamna affinis*, *Usakias* sp., *Carcharocles auriculatus*, *Odontaspis* cf. *winkleri*, *Jaekelotodus robustus*, *Carcharias* sp. *sensu* Cappetta & Nolf 2005, *Hypotodus verticalis*, *Cretalamna* aff. *appendiculata*, *Physogaleus* cf. *secundus* and *Squatina* cf. *prima* are all present in the surface sample. These species are known from the Lutetian as well as from the Ypresian (Fig. 26). These teeth could have been washed out from any of the layers at Trelde Næs, and the idea that some of the sediments are of Lutetian age (Heilmann-Clausen *et al.* 1985) can be supported.

Palaeogeography

The teeth of the Trelde Næs fauna were deposited in a 5.1 My long period from the Late Ypresian to the Middle Lutetian. It is therefore compared with other faunas deposited during approximately the same time span. It does not seem justified to consider the two samples from Trelde Næs separately.

Fossil North European Eocene elasmobranch faunas are reported from the London Clay (Cooper 1977; Rayner *et al.* 2009); France (Adnet 2006a; Dutheil *et al.* 2006; Adnet *et al.* 2008); North Germany (Diedrich 2012) and Belgium (Nolf 1988; Eeckhaut & De Schutter 2009). In the Mediterranean area, the Tethys Sea sediments have yielded elasmobranch faunas from Morocco (Arambourg 1952; Noubhani & Cappetta 1997). Figs. 27–28 give an overview of the species and genera in common with the Trelde Næs fauna.

North European faunas

Of the 31 different species found at Trelde Næs, 21 species (Fig. 27) and 22 genera (Fig. 28) are in common with species and genera in the Early/Middle Ypresian London Clay (Cooper 1977; Rayner *et al.* 2009). Nine of the Trelde Næs genera are not recorded from the London Clay. *Chlamydoselachus*, *Heptranchias*, *Centrophorus*, *Echinorhinus*, *Pristiophorus* and *Coupagezia* are all considered demersal/benthic deep-water genera and their absence in the London Clay may suggest that the London Clay was deposited in shallower (but still deep) waters than the Trelde Næs fauna. This opinion is supported by Schwartzhans (2007) who examined the fossil fish otoliths from Trelde Næs layer L3–L6 and found the deposition depth to have been shallower in the London Clay and even shallower in the Belgian Eocene than at Trelde Næs. *Anomotodon* and *Woellsteinia* have a very similar dental morphology

and the absence of *Woellsteinia* in the London Clay does not seem significant. The same can be said about *Usakias* which is close to *Alopias*. Teeth of *Carcharocles auriculatus* are not present in the London Clay where *Carcharocles* is represented by *Carcharocles aksuaticus* under the name *Otodus obliquus* var. *mugodzhharicus* (Rayner *et al.* 2009). This is not surprising because the London Clay species is the precursor of *Carcharocles auriculatus* and the London Clay is from the Early/Middle Ypresian when *Carcharocles aksuaticus* was representing the genus (<http://elasma.com/>). *Carcharias* sp. *sensu* Cappetta & Nolf 2005 and *Turania* sp. have a very similar dental morphology and appeared respectively in the Paleocene and the Bartonian. *Carcharias* sp. *sensu* Cappetta & Nolf 2005 is present in the London Clay (Cooper 1977), where it was described under the name *Synodontaspis hopei*. It is not surprising that *Turania* is absent from the older London Clay. *Turania* is a little known genus, and it has so far only been described from the Bartonian of Kazakhstan (Kozlov 2001). It was probably a migrating shark and could have spread from the North Sea to Asia via the Turgai Strait, but the presence of *Turania* at Trelde Næs requires further proof to be reliable.

The Ypresian/Lutetian deep-water fauna from southwestern France (Adnet 2006a; Adnet *et al.* 2008) has 15 species (Fig. 27) and 22 genera (Fig. 28) in common with the Trelde Næs fauna. The deep-water genera *Chlamydoselachus*, *Heptranchias*, *Hexanchus*, *Centrophorus*, *Echinorhinus*, *Coupagezia* and *Pristiophorus* are present; this suggests deposition in deep water with a depth similar to that of Trelde Næs.

The Eocene fauna from Belgium (Nolf 1988; Eeckhaut & De Schutter 2009) has 14 species (Fig. 27) and 17 genera (Fig. 28) in common with the Trelde Næs fauna. Most of the pelagic Lamniformes are present, but most of the deep-sea species are missing from the Belgian fauna; this could suggest deposition in shallower marine waters than at Trelde Næs, as Schwartzhans (2007) also inferred based on the fish otoliths from Trelde Næs.

The Ypresian/Lutetian North German fauna (Diedrich 2012) is characterised by Lamniformes of which 12 are in common with the 17 lamniform genera of the Trelde Næs fauna (Fig. 28). There are no small teeth in the German fauna which is probably due to the sampling method (sieving with a mesh size of 4 mm).

The Ypresian fauna from the Paris Basin (Dutheil *et al.* 2006) is dominated by Lamniformes, *Foumtizia* and *Squatina* (Fig. 28). Most of the deep-sea genera are missing. This may again suggest deposition in shallower waters than at Trelde Næs.

It is remarkable that the Trelde Næs fauna contains 39 teeth of *Echinorhinus* which is otherwise only found in the Ypresian/Lutetian of southwestern France (Ad-

net 2006a) and in Austria (Pfeil 1983) and Morocco in the Tethys Sea (Arambourg 1952; Noubhani & Cappetta 1997).

Tethyan fauna

In the Moroccan fauna from the southern Tethys Sea (Ward & Wiest 1990; Noubhani & Cappetta 1997), 11 species (Fig. 27) and 17 genera (Fig. 28) are in common with the Trelde Næs fauna. Most of the lamniform genera and deep-sea genera are represented, some of them as different species. This could be caused by the considerable distance between the locations.

Summary

In summary, the Trelde Næs fauna seems most similar to the fauna from the Early/Middle Ypresian London Clay and the fauna from the Ypresian/Lutetian deposits in southwestern France. The deep-water sharks are less common in the London Clay sediments than in the Trelde Næs and the southwestern France sediments. This could support the idea that the water depth was lower, at about 200 m, during deposition of the London Clay as suggested by Casier (1966). Trelde Næs is considered to have been far from the coast (Heilmann-Clausen & Surlyk 2006) and probably the London Clay was deposited closer to the coast line. This view is supported by the higher content of sand in the London Clay deposits (Casier 1966). The Trelde Næs fauna also has a strong affinity to the southwestern France fauna where the deposition depth seems to have been similar. At genus level there is also a relative strong affinity to the other North European faunas and to the fauna from Morocco. Differences in faunal associations are not only governed by phylogenetic evolution but also by sea level differences, salinity and availability of suitable prey to sustain the predatory sharks and rays.

Conclusions

Bulk samples and surface samples from Trelde Næs sediments have yielded 30 different genera/species of sharks and one species of ray (*Coupagezia miretrainensis*).

The vast majority of the teeth come from lamniform sharks, but this is probably due to sampling bias.

Teeth of 18 demersal/benthic deep-water genera are present.

Based on the elasmobranch fauna, the deposition depth was probably between 100 and 350 m.

The Trelde Næs fauna is most similar to the fauna from the Early/Middle Ypresian London Clay. The two faunas have 22 genera and 21 species in common. Six of the deep-water genera at Trelde Næs are missing in the London Clay. This suggests a shallower depositional environment of the London Clay compared to Trelde Næs.

The Trelde Næs fauna is also close to the Ypresian/Lutetian fauna from southwestern France. The two faunas have 22 genera and 15 species in common. Fourteen deep-water genera are present in southwestern France. This suggests a depositional environment similar to that of Trelde Næs.

A tooth of *Chlamydoselachus* cf. *fiedleri* is reported for the first time in the Late Ypresian of Denmark. The identification of the species is still to be considered with caution and it is not justified to extend the stratigraphic distribution of this species to the Late Ypresian.

Coupagezia miretrainensis is reported for the first time in the Late Ypresian of Denmark, extending its stratigraphic distribution from the Lutetian to the Late Ypresian.

Centrophorus aff. *granulosus* is reported for the first time in the Late Ypresian of Denmark. On the basis of similar teeth described by Adnet (2006) it seems justified to extend the origin of the *Centrophorus granulosus* group back to the Late Ypresian from its hitherto known origin in the Lutetian.

The presence of teeth of *Turania* in the Ypresian/Lutetian of Denmark, hitherto only known from the Bartonian, is puzzling. Further sampling from the Trelde Næs sediments might allow confirmation or disproof of its presence.

The faunal assemblage from Trelde Næs confirms an Ypresian age of layer L2 in the Lillebælt Clay Formation.

The faunal assemblage from Trelde Næs confirms that the Lillebælt Clay Formation probably also contains sediments of Lutetian age.

Acknowledgements

This work has only been possible by the kindness of Mogens Madsen (Fredericia) and Ole Barsøe Hansen (Kolding) who generously made their private collections available to the authors. David Ward (Orpington, England) has helped with the identification of some of the teeth. Sten Lennart Jakobsen (Copenhagen) provided help with the photographic work and processing of the sediment.

References

- Adnet, S. 2006a: Nouvelles faune de sélaciens (Elasmobranchii, Neoselachii) de l'Eocène Moyen des Landes (Sud-Ouest, France). Implication de la connaissance des communautés d'eaux profondes. *Paleo Ichthyologica* 10, 1–128.
- Adnet, S. 2006b: Biometric analysis of the teeth of fossil and recent hexanchid sharks and its taxonomic implications. *Acta Palaeontologica Polonica* 51(3), 477–488.
- Adnet, S. & Cappetta, H. 2001: A paleontological and phylogenetic analysis of squaliform sharks (Chondrichthyes: Squaliformes) based on dental characters. *Lethaia* 34, 234–248.
- Adnet, S. & Cappetta, H. 2008: New fossil triakid sharks from the early Eocene of Prémontré, France, and comments on fossil record of the family. *Acta Paleontologica Polonica* 53(3), 433–448.
- Adnet, S., Cappetta, H. & Reynders, J. 2008: Contribution of Eocene sharks and rays from Southern France to the history of deep-sea selachians. *Acta Geologica Polonica* 58(2), 257–260.
- Adnet, S., Guinot, G., Cappetta, H. & Welcomme, J.-L. 2012: Oldest evidence of bramble sharks (Elasmobranchii, Echinorhinidae) in the Lower Cretaceous of southeast France and the evolutionary history of orbitostylic sharks. *Cretaceous Research* 35, 81–87.
- Adnet, S., Hosseinzadeh, R., Antunes, M.T., Balbino, A. C., Kozlov, V.A. & Cappetta, H. 2009: Review of the enigmatic Eocene shark genus *Xiphodolamia* (Chondrichthyes, Lamniformes) and description of a new species recovered from Angola, Iran and Jordan. *Journal of African Earth sciences* 55, 197–204.
- Agassiz, L. 1833–1844: Recherches sur les poissons fossiles. Tome 3 contenant l'histoire des placoides, 422 pp. Petitpierre, Neuchâtel et Soleure.
- Antunes, M.T. & Cappetta, H. 2002: Sélaciens du Crétacé (Albien–Maastrichtien) d'Angola. *Palaeontographica Abteilung A* 264(5–6), 85–146.
- Antunes, M.T. & Jonet, S. 1970: Requins de l'Helvétien supérieur et du Tortonien de Lisbonne. *Revista Faculdades Ciências naturais. Universidade Lisboa* 16(1), 119–280.
- Applegate, S.P. & Uyeno, T. 1968: The first discovery of a fossil tooth belonging to the shark genus *Heptranchias*, with a new *Pristiophorus* spine, both from the Oligocene of Japan. *Bulletin of the National Science Museum, Ser. C (Geol. & Paleont.)* 11(1), 195–200.
- Arambourg, C. 1935: Note préliminaire sur les vertébrés fossiles des phosphates du Maroc. *Bulletin de la Société géologique de France* 5(5), 413–439.
- Arambourg, C. 1952: Les vertébrés fossiles des gisements de phosphates (Maroc-Algérie-Tunisie). Notes et Mémoire. Service géologique de Maroc 92, 1–372.
- Ayres, W.O. 1855: Description of new species of California fishes. *Proceedings of the California Academy of Natural Science* 1(1), 23–77.
- Barnard, K.H. 1925: Monograph of the fishes of South Africa Part 1. *Annals of South African Museum* 21(1), 1–418.
- Bendix-Almgreen, S.E. 1969: Notes on the upper Cretaceous and lower Tertiary fish faunas of Northern West Greenland. *Bulletin of the Geological Society of Denmark* 19, 204–217.
- Berg, L.S. 1940: Classification of fishes, both recent and fossil. *Travaux de L'Institut Zoologique de l'Académie des Sciences de l'URSS Tome V*, 2, 87–345.
- Berg, L.S. 1958: System der Rezenten und Fossilen Fischartigen und Fische. *Hochschulbücher für Biologie XI+* 310 pp. Berlin.
- Blainville, H.M.D. de 1816: Prodromes d'une nouvelle distribution systématique du règne animal. *Bulletin de la Société Philomathique de Paris* 8, 105–112 + 121–124.
- Blainville, H.M.D. de 1818: Sur les ichthyolites ou les poissons fossiles. *Nouveau Dictionnaire d'Histoire Naturelle* 27, 310–395. Deterville, Paris.
- Bleeker, P. 1859: Enumeratio specierum piscium hucusque in Archipeloga indico observatum, adjectis habitationibus citatibusque, ubi descriptiones earum recentiores reperiuntur, nec non speciebus Musei Bleekeriani Bengalensibus, Japonicis, Capensibus Tasmanicisque. *Acta Societas Scientiarum Indo-Neerlandicae* 6, p. I–XXXVI + 1–176.
- Bloch, H.M. & Schneider, J.G. 1801: M. E. Blochii Systema Ichthyologiae iconibus ex illustratum. Post obitum auctoris opus inchoatum absolvit, correxit, interpolavit Jo. Gottlob Schneider, Saxo. 584 pp.; Berolini (Sumtibus Austoris Impresum et Bibliopolio Sanderiano Commissum).
- Bonaparte, C.L. 1834: Iconografia della fauna italiana per le quattro classi degli animali vertebrati. Tomo III. Pesci. Roma: Fasc. 12–14, puntata 59–79.
- Bonaparte, C.L. 1838: Selachorum tabula analytica. *Nuovi annali delle scienze naturali, Bologna* 2, 195–214.
- Bonde, N. 1966: The fishes of the Mo-Clay Formation. *Meddelelser fra Dansk Geologisk Forening* 16, 198–202.
- Bonde, N. 1968: Nyligt fundne fossiler fra det 'plastiske ler'. *Meddelelser fra Dansk Geologisk Forening* 18, 148–151.
- Bonnaterre, J.P. 1788: Ichthyologie. Tableau encyclopédique et méthodique des trois règnes de la nature. Paris, 215 pp., pl. A–B + 1–100.
- Buen, F. de 1926: Catálogo ictiológico del Mediterráneo Español y de Marruecos, recopilando lo publicado sobre peces de las costas mediterráneas y próximas del Atlántico (Mar de España). Resultados de las Campañas Realizadas por Acuerdos Internacionales, *Instituto Español de Oceanografía* 2, 1–221.
- Cappetta, H. 1976: Sélaciens nouveaux du London Clay de L'Essex (Yprésien du Basin du Londres). *Geobios* 9(5), 551–575.
- Cappetta, H. 1980a: Modification du statut générique de quelques espèces de sélaciens crétacés et tertiaires. *Palaeovertebrata* 10(1), 29–42.
- Cappetta, H. 1980b: Les Sélaciens supérieur du Liban. I. Requins. *Palaeontographica Abt. A* 168(1–4), 69–148.
- Cappetta, H. 1981: Addition a la faune de sélachiens fossiles du Maroc. I: Sur la présence des genres *Heptranchias*, *Alopias* et *Odontorhynchus* dans l'Yprésien des Ouled Abdoun. *Geobios* 14(5), 563–575.
- Cappetta, H. 1982: Révision de *Cestracion duponti* Winkler 1874 (Selachii, Batomorphii) du Bruxellien de Woluwe-Saint-Lambert

- (Eocène moyen de Belgique). Meddelingen Van De Werkgroep Voor Tertiaire En Kwartaire Geologie 19(4), 113–125.
- Cappetta, H. 1987: Chondrichthyes II: Mesozoic and Cenozoic elasmobranchii. In: Schulze, H-P (ed.): Handbook of paleoichthyology 3B. 193 pp. Gustav Fischer Verlag, Stuttgart and New York.
- Cappetta, H. 1990a: Hexanchiforme nouveau (Neoselachii) du Crétacé inférieur du Sud de la France. *Palaeovertebrata* 20(1), 33–54.
- Cappetta, H. 1990b: Echinorhinidae nouveau (Neoselachii, Squaliformes) du Crétacé supérieur du Negev (Israël). *Neues Jahrbuch für Geologie und Palaontologie, Monatshefte* 1990(12), 741–749.
- Cappetta, H. 1992: Carcharhiniformes nouveaux (Chondrichthyes, Neoselachii) de l'Yprésien du Bassin de Paris. *Géobios* 25(5), 639–646.
- Cappetta, H. 2012: Chondrichthyes – Mesozoic and Cenozoic Elasmobranchii: Teeth. In: Schultze, H-P (ed.): Handbook of Paleoichthyology 3E, 512 pp. Verlag Dr. Friedrich Pfeil, München.
- Cappetta, H. & Case, G.R. 1999: Additions aux faunes de séla-ciens du Crétacé du Texas (Albien supérieur–Campanien). *Palaeo Ichthyologica* 9, 5–111.
- Cappetta, H. & Nolf, D. 2005: Révision de quelque Odontaspidae (Neoselachi: Lamniformes) du Paléocène et de l'Eocène du Bassin de la mer du Nord. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre* 75, 237–266.
- Cappetta, H. & Ward, D. 1977: *Megascyliorhinus cooperi* gen. nov. sp. nov., a new shark from the London Clay (Eocene) of Essex, England. *Palaeontology* 20(1), 195–202.
- Casier, E. 1946: La faune ichthyologique de l'Yprésien de la Belgique. *Mémoires du Musée Royal d'Histoire Naturelle de Belgique* 104, 1–267.
- Casier, E. 1966: Faune ichthyologique du London Clay. 496 pp. London : British Museum of Natural History.
- Christensen, E.J. & Hald, N. 1991: Danekræ, et nyt begreb i dansk museumslovgivning. *Arkæologiske Udgravninger i Danmark* 1990, 7–16.
- Cigala-Fulgosi, F. 1986: A deep water elasmobranch fauna from a lower Pliocene outcropping (Northern Italy). In: Uyeno, T., Arai, R., Taniuchi, T. & Matsura, K. (eds): Proceedings of the second international conference on Indo-Pacific fishes. Ichthyological Society of Japan, Tokyo: 133–139.
- Cione, A.L. 1986: A new *Megascyliorhinus* (Chondrichthyes, Galeomorphii) from the Middle Tertiary of Patagonia. *Journal of Vertebrate Paleontology* 6(2), 105–112.
- Compagno, L.J.V. 1973: Interrelationships of living elasmobranchs. In: Greenwood, P.H., Miles, R.S. & Patterson, C. (eds): Interrelationships of fishes. *Zoological Journal of the Linnean Society* 53 Suppl. 1, 15–61.
- Compagno, L.J.V. 1977: Phyletic relationships of living sharks and rays. *American Zoologist* 17, 303–322.
- Compagno, L.J.V. 2003: Sharks of the order Carcharhiniformes, 486 pp. The Blackburn Press.
- Compagno, L.J.V., Dando, M. & Fowler, S. 2005: Sharks of the world. 368 pp. Princeton University Press, Princeton and Oxford.
- Consoli, C.P. 2008: A rare Danian (Early Paleocene) *Chlamydose-lachus* (Chondrichthyes: Elasmobranchii) from the Takatika Grit, Chatham Islands, New Zealand. *Journal of Vertebrate Paleontology* 28(2), 285–290.
- Cooper, J. 1977: The palaeontology of the London Clay (Lower Eocene) of the Herne Bay coastal section, Kent, England. *Proceedings of the Geological Association* 88(3), 163–178.
- Cunningham, S.B. 2000: A comparison of isolated teeth of early Eocene *Striatolamia macrotia* (Chondrichthyes, Lamniformes), with those of a Recent sand shark, *Carcharias taurus*. *Tertiary Research* 20(1–4), 17–34.
- Cvancara, A.M. & Hoganson, J.W. 1993: Vertebrates of the Cannonball Formation (Paleocene) in North and South Dakota. *Journal of Vertebrate Paleontology* 13(1), 1–23.
- Dartevelle, E. & Casier, E. 1943: Les poissons fossiles du Bas-Congo et des régions voisines. *Annales du Musée du Congo Belge, Sér. A (Minéralogie Géologie, Paléontologie)* 3, 2(1), 1–200.
- Davis, J.W. 1887: Note on a fossil species of *Chlamydose-lachus*. *Proceedings of the Zoological Society of London* 1887, 542–544.
- Davis, J.W. 1888: On fossil fish-remains from the Tertiary and Cretaceous-Tertiary formations of New-Zealand. *Scientific transactions of the Royal Dublin Society* 4(2), 1–48.
- De Schutter, P.J. & Wijnker, E. 2002: Large *Centrophorus* (Chondrichthyes, Squaliformes) of the Belgian Neogene continental shelf. *Geologica Belgica* 15(1–2), 26–36.
- Diedrich, C.G. 2012: Eocene (Lutetian) Shark-rich coastal paleoenvironments of the Southern North Sea Basin in Europe: Biodiversity of the Marine Fürstenau Formation including early white and megatooth Sharks. *International Journal of Oceanography* 2012, 1–22.
- Dinesen, A., Michelsen, O. & Lieberkind, K. 1977: A survey of the Paleocene and Eocene deposits in Jylland and Fyn. *Geological Survey of Denmark, series B* (1), 1–14.
- Dumeril, A.H.A. 1806: *Zoologie analytique, ou méthode naturelle de classification des animaux*. Paris, 1–344.
- Dutheil, D.B., Moreau, F. & Delhay-Prat, V. 2002: Cycle sédimentaire et vertébrés d'une formation peu connue du Bassin de Paris, l'unité des Sables de Bourguillemont (Oise, France) (Paléocène supérieur). *Geodiversitas* 24(4), 753–764.
- Dutheil, D.B., Moreau, F. & De Plöeg, G. 2006: Les ichthyofaunes du gisement à ambre de Le Quesnoy (Paléocène et Éocène du bassin de Paris, France). *Cossmanniana* 11(1–4), 1–13.
- Eeckhaut, G. & De Schutter, P. 2009: The elasmobranch fauna of the Lede Sand Formation at Oosterzele (Lutetian, Middle Eocene of Belgium). *Palaeofocus* 1, 1–57.
- Ferrusquia-Villafranca, I., Applegate, P.S. & Espinosa-Arrubarrena, L. 1999: First Paleogene selachifauna of the Middle American–Caribbean–Antillean Region, La Mesa de Copoya, West-Central Chiapas – Mexico. *Systematics and paleontological significance*. *Revista Mexicana de Ciencias Geológicas* 16(1), 155–174.

- Forskål, P. 1775: Descriptiones animalium, avium, amphibiorum, piscium, insectorum, vermium / quae in itinere orientali observavit Petrus Forskål. 1–20 + i–xxxiv + 1–164. Hauniae (ex officina Mölleri).
- Garman, S. 1884: An extraordinary shark. Bulletin of the Essex Institute 16, 47–55.
- Garman, S. 1913: The Plagiostomia (sharks, skates and rays). Memories of the Museum of Comparative Zoology at Harvard College 36, XIII + 528 pp.
- Gill, T.N. 1862: Analytical synopsis of the order of Squali; a revision of the nomenclature of the genera. Annals of the Lyceum of the Natural History of New York 7, 371–408.
- Gill, T.N. 1865: Synopsis of the eastern American sharks. Proceedings of Academy of Natural Sciences of Philadelphia 16(5), 258–265.
- Glikman, L.S. 1958: [Rates of evolution in Lamnoid sharks]. Doklady Akademii Nauk SSSR 123(3), 568–571 (in Russian).
- Glikman, L.S. 1964a: [Subclass Elasmobranchii]. In: Obruchev. D.V. (ed.): Osnovi Paleontologii (Agnatha, Pisces), 195–237, Moscow (Nauka) (in Russian).
- Glikman, L.S. 1964b: [Sharks of the Palaeogene and their stratigraphic significance]. Doklady Akademii Nauk SSSR, Moscow, 228 pp. (in Russian).
- Glikman, L.S. & Zhelezko, V.I. 1985: [Paleogene sharks of the Mangyschlak Plateau and the Eocene/Oligocene boundary]. Bulletin MOIP. Otdelenie geologicheskoe 60(5), 86–99. (in Russian).
- Goodrich, E.S. 1909: Vertebrata Craniata. 1. Cyclostomes and fishes. In: Lankester E.R. (ed.), A Treatise on Zoology, part 9, XVI + 518 pp.. London: Adam a. Charles Black.
- Gottfried, M.D. & Rabarison, J.A. 1997: First Mesozoic Gondwanan record of a sawshark (Chondrichthyes, Pristiophoriformes), from the Late Cretaceous of Madagascar. Journal of Vertebrate Paleontology 17(4), 750–751.
- Gray, J.E. 1851: List of the specimens of fish in the collection of the British Museum. Part I. Chondropterygii. X + 160 pp. British Museum (Natural History), London.
- Hansen, B.B., Cuny, G., Rasmussen, B.W., Shimada, K., Jacobs, P. & Heilmann-Clausen, C. 2013: Associated skeletal and dental remains of a fossil odontaspimid shark (Elasmobranchii: Lamniformes) from the Middle Eocene Lillebælt Clay Formation in Denmark. Bulletin of the Geological Society of Denmark 61, 37–46.
- Heilmann-Clausen, C. & Surlyk, F. 2006: Koralrev og lerhav. In: Larsen, G. (ed.) Naturen i Danmark, Geologien, 549 pp. Copenhagen: Gyldendal.
- Heilmann-Clausen, C., Nielsen, O.B. & Gersner, F. 1985: Lithostratigraphy and depositional environments in the Upper Paleocene and Eocene of Denmark. Bulletin of the Geological Society of Denmark 33, 287–323.
- Henle, F.G.J. 1834: Ueber *Narcine*, eine neue Gattung elektrischer Rochen nebst einer Synopsis der elektrischen Rochen, 44 pp. Berlin: G. Eichler.
- Huxley, T.H. 1880: On the application of the laws of evolution to the arrangement of the Vertebrata, and more particularly of the Mammalia. Proceedings of the Zoological Society of London 1880, 649–662.
- Iserby, A. & De Schutter, P.J. 2012: Quantitative analysis of Elasmobranch assemblages from two successive Ypresian (early Eocene) facies at Marke, Western Belgium. Geologica Belgica 15(3), 146–153.
- Jaekel, O. 1890: Über die systematische Stellung und über fossile Reste der Gattung Pristiophorus. Zeitschrift der Deutschen Geologischen Gesellschaft 42, 86–120.
- Jaekel, O. 1895: Unter-tertiäre Salachier aus Südrussland. Mémoires du Comité géologique de St. Petersburg 9(4), 19–35.
- Jaekel, O. 1898: Ueber die verschiedenen Rochentypen. Sitzungsberichte der Gesellschaft naturforschender Freunde zu Berlin 1898, 44–53.
- Jordan, D.S. 1888: Description of two new species of fishes from South America. Proceedings of the Academy of Natural Sciences of Philadelphia 39, 387–388.
- Jordan, D.S. 1898: Description of a species of fish (*Mitsukurina owstoni*) from Japan, the type of a distinct family of lamnoid sharks. Proceedings of the California Academy of Science 3(1) 6, 199–202.
- Jordan, D.S. & Evermann, B.W. 1896: The fishes of North and Middle America, a descriptive catalogue of the species of fish-like vertebrates found in the waters of North America, north of the isthmus of Panama. Part I. Bulletin of the United States National Museum 47, I–LX + 1–1240.
- Jordan, D.S. & Hannibal, H. 1923: Fossil sharks and rays of the Pacific slope of North America. Bulletin of the Southern California Academy of Science 22, 27–63.
- Jordan, D.S. & Snyder, J.O. 1902: Descriptions of two new species of squaloid sharks from Japan. Proceedings of the United States National Museum 25, 79–81.
- Keyes, I.W. 1979: *Ikamauius*, a new genus of fossil sawshark (Order Selachii: Family Pristiophoridae) from the Cenozoic of New Zealand. New Zealand Journal of Geology and Geophysics 22(1), 125–129.
- Keyes, I.W. 1982: The Cenozoic sawshark *Pristiophorus lanceolatus* (Davis) (Order Selachii) of New Zealand and Australia, with a review of the phylogeny and distribution of world fossil and extant Pristiophoridae. New Zealand Journal of Geology and Geophysics 25(4), 459–474.
- Keyes, I.W. 1984: New records of fossil elasmobranch genera *Megascyliorhinus*, *Centrophorus*, and *Dalatias* (Order Selachii) in New Zealand. New Zealand Journal of Geology and Geophysics 27(2), 203–216.
- Klug, S. & Kriwet, J. 2010: Timing of deep-sea adaptation in dogfish sharks: insights from a supertree of extinct and extant taxa. Zoologica Scripta 39(4), 331–342.
- Kordikova, E.G., Polly, P.D., Alifanov, V.A., Rocek, Z., Gunnell, G.F. & Averianof, A.O. 2001: Small vertebrates from the Late Cretaceous and Early Tertiary of the Northeastern Aral Sea region, Kazakhstan. Journal of Paleontology 75, 390–400.
- Kozlov, V.A. 2000: [Systematics and evolution of sharks from the family Alopiidae (based on the materials from Palaeogene deposits of Middle Asia and western Kazakhstan)]. Materi-

- aly po stratigrafii i Paleontologii Urals 4, 142–147 (in Russian).
- Kozlov, V.A. 2001: Additions to the Paleogene elasmobranch fauna of western Kazakhstan. *Turania*, a new shark genus (Odontaspidae) and a new ray species (genus *Archaeomanta*, Mobulidae). Russian Academy of Science, Urals Branch, 83–86 (in Russian).
- Kriwet, J. 2005: Additions to the Eocene selachian fauna of Antarctica with comments on Antarctic selachian diversity. *Journal of Vertebrate Paleontology* 25(1), 1–7.
- Kyne, P.M. & Simpfendorfer, A.C. 2007: A Collation and summarization of available data on deepwater Chondrichthyans: Biodiversity, Life History and Fisheries. IUCN SSC Shark Specialist Group for the Marine Conservation, Biology Institute, 1–137.
- Leidy, J. 1877: Description of vertebrate remains, chiefly from the Phosphate Beds of South Carolina. *Journal of the Academy of Natural Sciences of Philadelphia* 8(2), 209–261.
- Leriche, M. 1905: Les poissons Eocène de la Belgique. *Mémoires de Musée Royal d'Histoire Naturelle de Belgique* 3(3), 59–228.
- Leriche, M. 1921: Sur les restes de Poissons remaniés dans le Néogène de la Belgique. Leur signification au point de vue de l'histoire géologique de la Belgique pendant le tertiaire supérieur. *Bulletin de la Société Belge de Géologie* 30, 115–120.
- Leriche, M. 1929: Sur une forme nouvelle du genre *Chlamydoselachus* (*C. tobleri*) rejetée par le volcan de boue de Chagonary (île de la Trinité, Petites-Antilles). *Bulletin de la Société Belge de Géologie, de Paléontologie et d'Hydrologie* 38(1), 55–58.
- Leriche, M. 1938: Contribution à l'étude des poissons fossiles des pays riverains de la Méditerranée américaine (Venezuela, Trinité, Antilles, Mexique). *Mémoires de la Société Paléontologique Suisse* 61(1), 42 pp.
- Long, D.J. 1992: Sharks from the La Meseta Formation (Eocene), Seymour Island, Antarctic Peninsula. *Journal of Vertebrate Paleontology* 12(1), 11–32.
- Longbottom, A.E. 1979: Miocene shark's teeth from Ecuador. *Bulletin of the British Museum (Natural History), (Geology)* 32(1), 57–70.
- Lowe, R.T. 1841: A paper from the Rev. R.T. Lowe, M.A., describing certain new species of Madeiran fishes, and containing additional information relating to those already described. *Proceedings of the Zoological Society of London* 8, 36–39.
- Malyschkina, T. 2006: Late Eocene scyliorhinid sharks from the Trans-Urals, Russia. *Acta Palaeontologica Polonia* 51(3), 465–475.
- Mannering, A.A. & Hiller, N. 2008: An early Cenozoic neoselachian shark fauna from the Southwest Pacific. *Palaeontology* 51(6), 1341–1365.
- Marsili, S. & Tabanelli, C. 2007: Bathyal sharks from the middle Pliocene of the Romagna Apennines (Italy). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 244(2), 247–255.
- Menner, V.V. 1928: [Les séliaciens du Paléogène de Manghyschlack d'Emba et du versant oriental d'Oural]. *Bulletin de la Société imperiale des Naturalistes de Moscou. Section géologique* 6(3-4), 292–338. (in Russian with French summary).
- Michelsen, O. 1994: Stratigraphic correlation of the Danish onshore and offshore Tertiary successions based on sequence stratigraphy. *Bulletin of the Geological Society of Denmark* 41, 145–161.
- Müller, J. & Henle, F.G.J. 1837: Gattungen der Haifische und Rochen, nach einer von ihm mit Herrn Henle unternommenen gemeinschaftlichen Arbeit über die Naturgeschichte der Knorpelfische. *Berichte Akademie der Wissenschaften* 1837(2), 111–118.
- Müller, J. & Henle, F.G.J. 1838–41: Systematische Beschreibung der Plagiostomen, 200 pp. Veit & Co., Berlin.
- Münster G. Von. 1846: Ueber die in der Tertiär-Formation des Wiener Beckens vorkommenden Fisch-Ueberreste, mit Beschreibung einiger neuen merkwürdigen Arten. *Beiträge zur Petrefaktenkunde* 7, 1–31.
- Nakamura, H. 1935: On the two species of the thresher shark from Formosan waters. *Memoirs Faculty Science Taihoku Imperial University Formosa* 14(1), 1–6.
- Nolf, D. 1988: Fossiles de Belgique. Dent de requins et de raies du Tertiaire de la Belgique. 188 pp. Brussels: Institut royal des sciences naturelles de Belgique.
- Noubhani, A. & Cappetta, H. 1997: Les Orectolobiformes, Carcharhiniformes et Myliobatiformes (Elasmobranchii, Neoselachii) des bassins à phosphate du Maroc. (Maastrichtien–Lutétien basal). *Systématique, biostratigraphie, évolution et dynamique des faunes. Palaeo Ichthyologica* 8, 1–327.
- Otero, R.A., Torres, T., Le Roux, J.P., Hervé, F., Fanning, C.M., Yury-Yáñez, R.E. & Rubilar-Rogers D. 2012: A Late Eocene age proposal for the Loreto Formation (Brunswick Peninsula, southernmost Chile), based on fossil cartilaginous fishes, paleobotany and radiometric evidence. *Andean Geology* 39(1), 180–200.
- Pfeil, F.H. 1981: Eine nektonische Fischfauna aus dem unteroligozänen Schönecker Fischschiefer des Galon-Grabens in Oberbayern. *Geologica Bavarica* 82, 357–388.
- Pfeil, F.H. 1983: Zahnmorphologische Untersuchungen an rezenten und fossilen Haien der Ordnungen Chlamydoselachiformes und Echinorhiniformes. *Palaeo Ichthyologica* 1, 1–315.
- Pfeil, F.H. 1984: Neoselachian teeth collected from phosphate-bearing greensand on Chatham Rise east of New Zealand. *Geologisches Jahrbuch* 65, 107–115.
- Pietschmann, V. 1928: Neue Fischarten aus dem Pazifischen Ozean. *Anzeiger der Akademie der Wissenschaften in Wien*, 65(27), 297–298.
- Probst, J. 1879: Beiträge zur Kenntniss der fossilen Fische aus der Molasse von Baltringen. *Hayfische. Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg* 35, 127–191.
- Purdy, R.W. 1998: Chondrichthyan fishes from the Paleocene of South Carolina. *Transactions of the American Philosophical Society* 88, 122–146.
- Purdy, R.W., Schneider, V.P., Applegate, S.P., McLellan, J.H., Meyer, R.L., & Slaughter, B.H. 2001: The neogene sharks, rays and bony fishes from Lee Creek Mine, Aurora, North Caro-

- lina. *Smithsonian contributions to paleobiology* 90, 71–202.
- Quoy, J.R.C. & Gaimard, J.P. 1824: Description des Poissons. Chapitre IX. In: Freycinet, L. de, Voyage autour du Monde entrepris par ordre du roi, exécuté sur les corvettes de L. M. "L'Uranie" et "La Physicienne," pendant les années 1817, 1818, 1819 et 1820. Paris. Description des Poissons. Chapter IX.: 192–401 [1–328 in 1824; 329–616 in 1825].
- Rafinesque, C.S. 1810: Caratteri di alcuni nuovi generi e nuovi spedie di animali e piante della Sicilia, con varie osservazione sopra i medesimi. Part 1. I–IV + 3–69 p. Palermo (Sanfilippo).
- Rayner, R., Mitchell, T., Rayner, M. & Clouter, F. 2009: London Clay fossils of Kent and Essex, 228 pp. Medway Fossil and Mineral Society.
- Reed, M.D. 1946: A new species of fossil shark from New Jersey. *Notula Naturae of the Academy of Natural Sciences of Philadelphia* 172, 1–3.
- Regan, C.T. 1906: Descriptions of new or little known fishes from the coast of Natal. *Annals of the Natal Government Museum* 1(1), 1–6.
- Reinecke, T. & Engelhard, P. 1997: The selachian fauna from Geschiebe of the Lower Selandian basal conglomerate (Thanetian, Late Paleocene) in the Danish subbasin (Sealand, Scania, western Baltic Sea). *Erratica* 2, 3–45.
- Reinecke, T., Stapf, H. & Raisch, M. 2001: Die Selachier und Chimären des Unteren Meeressandes und Schleisandes im Mainzer Becken (Rupelium, Unteres Oligozän). *Paleontos* 1, 1–73.
- Richter, M. & Ward, D.J. 1990: Fish remains from the Santa Marta Formation (Late Cretaceous) of James Ross Island, Antarctica. *Antarctic Science* 2(1), 67–76.
- Schmitz, B., Heilmann-Clausen, C., King, C., Steurbaut, E., Andreasson, F.P., Corfield, R.M. & Cartlidge, J.E. 1996: Stable isotope and biotic evolution in the North Sea during the early Eocene: the Albæk Hoved section Denmark. *Special Publication, Geological Society (London)* 101, 275–306.
- Schnetler, K.I. 1985: Two new Upper Oligocene gastropods from the North Sea Basin. *Bulletin of the Geological Society of Denmark* 34, 199–204.
- Schnetler, K.I. & Heilmann-Clausen, C. 2011: The molluscan fauna of the Eocene Lillebælt Clay, Denmark. *Cainozoic Research* 8(1–2), 41–99.
- Schwartzhans, W. 2007: Otoliths from casts from the Eocene Lillebælt Clay Formation of Trelde Næs near Fredericia (Denmark), with remarks on the diet of stomatopods. *Neues Jahrbuch für Geologie und Paläontologie* 246(1), 69–81.
- Shimada, K. 2005: Phylogeny of lamniform sharks (Chondrichthyes: Elasmobranchii) and the contribution of dental characters to lamniform systematics. *Paleontological Research* 9(1), 55–72.
- Shimada, K. 2007: Skeletal and Dental Anatomy of Lamniform Shark, *Cretalamna appendiculata*, from Upper Cretaceous Niobrara Chalk of Kansas. *Journal of Vertebrate Paleontology* 27(3), 584–602.
- Siverson, M. 1992: Biology, dental morphology and taxonomy of lamniform sharks from the Campanian of the Kristianstad Basin, Sweden. *Palaeontology* 35(3), 519–554.
- Siverson, M. 1995: Revision of the Danian Cow Sharks, Sand Tiger Sharks, and Goblin Sharks (Hexanchidae, Odontaspidae and Mitsukurinidae) from Southern Sweden. *Journal of Vertebrate Paleontology* 15(1), 1–12.
- Siverson, M. 1996: Lamniform sharks of the mid Cretaceous Alinga Formation and Beedagong Claystone, Western Australia. *Palaeontology* 39(4), 813–849.
- Siverson, M. 1999: A new large lamniform shark from the uppermost Gearle Siltstone (Cenomanian, Late Cretaceous) of Western Australia. *Transactions of the Royal Society of Edinburgh: Earth Sciences* 90, 49–65.
- Siverson, M., Lindgren, J., Newbrey, M.G., Cederström, P. & Cook T.D. 2014: Late Cretaceous (Cenomanian–Campanian) mid-palaeolatitude sharks of *Cretalamna appendiculata* type. *Acta Palaeontologica Polonica*, in press, 1–49.
- Slaughter, B.H. & Springer, S. 1968: Replacement of Rostral Teeth in Sawfishes and Sawsharks. *Copeia* 1968(3), 499–506.
- Sokolov, M. 1978: Sharks as guide-fossils for the zonation and subdivision of the Cretaceous beds of Tourousk. *Nedra, Moskva* 61, 1–60.
- Storms, R. 1894: Troisième note sur les poissons du terrain rupélien. *Bulletin de la Société Belge de Géologie, de Paléontologie et d'Hydrologie* 8, 67–82.
- Thomsen, E., Abrahamsen, N., Heilmann-Clausen, C., King, C. & Nielsen, O.B. 2012: Middle Eocene to earliest Oligocene development in the eastern North Sea Basin: Biostratigraphy, magnetostratigraphy and palaeoenvironment of the Kysing-4 borehole, Denmark. *Palaeogeography, Palaeoclimatology, Palaeoecology* 350–352, 212–235.
- Underwood C.J. & Cumbaa S.L. 2010: Chondrichthyans from a Cenomanian (Late Cretaceous) bonebed, Saskatchewan, Canada. *Palaeontology* 53(4), 903–944.
- Underwood, C.J., Goswami, A., Prasad, G.V.R., Omkar, V. & Flynn, J.J. 2011a: Marine vertebrates from the "Middle" Cretaceous (Early Cenomanian) of South India. *Journal of Paleontology* 31(3), 539–552.
- Underwood, C.J., Ward, D.J., King, C., Antar, S.M., Zalmout, I.S. & Gingerich, P.D. 2011b: Shark and ray faunas in the Middle and Late Eocene of the Fayum Area, Egypt. *Proceedings of the Geologists' Association* 122, 47–66.
- Vélez-Zuazo, X. & Agnarsson, I. 2011: Shark tales: A molecular species-level phylogeny of sharks (Selachimorpha, Chondrichthyes). *Molecular Phylogenetics and Evolution* 58, 207–217.
- Ward, D.J. 1978: Additions to the fish fauna of the English Palaeocene. 1. Two new species of *Alopias* (Tresher Shark) from the English Eocene. *Tertiary Research* 2(1), 23–28.
- Ward, D.J. 1979: Additions to the fish fauna of the English Paleogene. 3. A review of the Hexanchid sharks with a description of four new species. *Tertiary Research* 2(3), 111–129.
- Ward, D.J. 1984: Additions to the fish fauna of the English Palaeogene. 5. A new species of *Raja* from the London Clay. *Tertiary Research* 6(2), 65–68.

- Ward, D.J. & Wiest, R.L. 1990: A Checklist of Paleocene and Eocene sharks and rays (Chondrichthyes) from the Pamunkey Group, Maryland and Virginia, USA. *Tertiary Research* 12(2), 81–88.
- Welton, B.J. 1972: Fossil sharks in Oregon. *The Ore Bin* 34(10), 161–172.
- White, E.I. 1956: The Eocene fishes of Alabama. *Bulletins of American Paleontology* 36(156), 123–150.
- Whitley, G.P. 1929: Additions to the check-list of the fishes of New South Wales. No. 2. *Australian Zoologist* 5(4), 353–357.
- Winkler, T.C. 1874: Mémoire sur des dents de poissons du terrain bruxellien. *Archives du Musée Teyler* 3(4), 295–304.
- Winkler, T.C. 1876a : Mémoire sur quelques restes de poissons du système heersien. *Archives du Musée Teyler* 4(1), 1–15.
- Winkler, T.C. 1876b: Deuxième mémoire sur des dents de poissons fossiles du terrain bruxellien. *Archives du Musée Teyler* 4(1), 16–48.
- Woodward, A.S. 1899: Notes on the teeth of sharks and skates from English Eocene formations. *Proceedings of the Geologists' Association* 16, 1–14.
- Woodward, A.S. 1932: A Cretaceous pristiphorid shark. *Annals and Magazine of Natural History, (Series 10)* 10, 476–479.
- Zalmout, I.S.A., Antar, M.S.M., Shafy, A.E., Metwally, M.H., Hatab, E.E. & Gingerich, P.D. 2012: Priabonian sharks and rays (Late Eocene: Neoselachii) from Minqar Tabaghbagh in the Western Qattara Depression, Egypt. *Contributions from the Museum of Paleontology, University of Michigan* 32(6), 71–90.
- Zhelezko, V.I. 1994: Sharks of family Jaekelotodontidae of European and middle Asian paleobiogeographic provinces. *Bulletin Moscow Society of Naturalists* 69(6), 47–62 (in Russian).
- Zhelezko, V.I. & Kozlov, V.A. 1999: Elasmobranchii and Paleogene biostratigraphy of Transurals and central Asia. *Russian Academy of Sciences, Urals Branch* 3, 1–323 (in Russian).

Web sites

<http://www.elasmo.com/>
<http://www.fishbase.org/>