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Shark teeth from the Lower Triassic of Spitsbergen and their histology

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ABSTRACT: The new rich collection of fossil fish remains obtained during the Polish Spitsbergen Expedition of 1998 includes many isolated shark teeth, mostly of the genera *Lissodus*, *Hybodus* and *Acrodus*. The shark microfossils from the Hornsund area (South Spitsbergen) described here and the analysis of the histology of *Lissodus* teeth contribute to a better understanding of the previously described Early Triassic fish fauna from that region (Birkenmajer and Jerzmańska 1979). There is the evidence for coexistence of two types of histology within a single taxon what closes the discussion considering ortho- and osteodentine as a taxonomic factor.

Key words: Arctic, Svalbard, Lower Triassic, shark teeth (Elasmobranchii, Hybodontoidea), histology.

Introduction

The paleontological site described here corresponds to that examined by the Norwegian expedition of Hoel and Røvig in 1917 (*vide* Birkenmajer and Jerzmańska 1979). They found some shark teeth and scales which were subsequently described by Stensiö (1918, 1921). After the Second World War further investigation of the widely understood geology of Svalbard took place, carried out with the participation of Polish scientists. The Polish Spitsbergen Expedition of 1960 (Birkenmajer 1964, p. 14) brought some new material from South Spitsbergen, and the shark remains were described by Jerzmańska (*in* Birkenmajer and Jerzmańska 1979). Later, numerous Polish expeditions were organised to that area, and in 1998 A. Gaździcki and A. Kaim collected samples from the conglomerate of the Lower Triassic Brevassfjellet *Myalina* Bed, cropping out on the southern slope of the Hyrnefjellet Mountain (Figs 1, 2). Dozens of isolated teeth, mostly of chondrichthyan origin, have been obtained from the samples after treating the rocks with acetic acid.

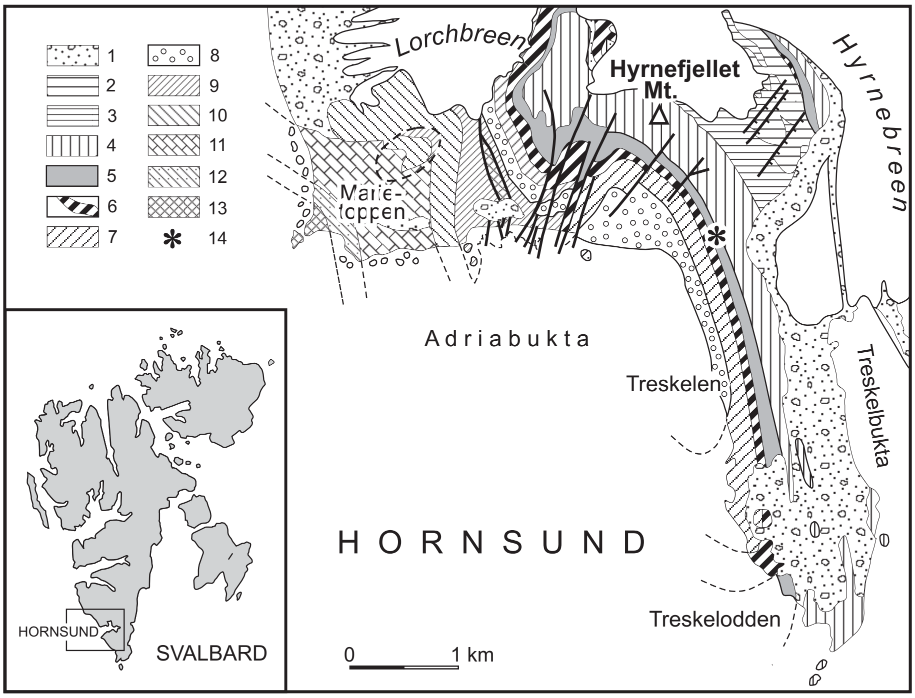

Fig. 1. Geological map of West Spitsbergen (Hornsund area) showing the location of the Hyrnefjellet Mt., where the specimens of shark teeth were collected. 1 – Moraines, partly outwash; 2 – Festningen Sandstone (Hauterivian–Barremian); Ullaberget Series (Lower Neocomian); 3 – Tirolarpasset Series (Volgian–Lower Neocomian); 4 – Middle and Upper Triassic; 5 – Lower Triassic; 6 – Brachiopod Cherty Limestone (Upper Permian); 7 – Treskelodden Beds (Upper Carboniferous–lowermost Permian); 8 – Hyrnefjellet Beds (Middle Carboniferous); 9 – Adriabukta Series (Visean–Namurian A?); 10 – Upper Marietoppen Series (Devonian: Grey Hoek Series?); 11 – Middle Marietoppen Series (Devonian: Stjördalen Division?); 12 – Lower Marietoppen Series (Devonian: Keltiefjellet Division?); 13 – Sofiebogen Formation (Eocambrian–Precambrian); 14 – Shark teeth sampling locality. After Birkenmajer (1964).

This paper is focused on the specimens of the genus *Lissodus* and presents new results on the histology of its teeth. In addition, photographic illustrations and descriptions of other shark microremains collected at the Hyrnefjellet Mt. such as teeth of *Acrodus spitzbergensis* Hulke, 1873 (Fig. 8), *Hybodus microdus* Stensiö, 1921 (Fig. 9A–C), *Hybodus sasseniensis* Stensiö, 1918 (Fig. 9E–F), and *Hybodus* sp. (Fig. 9D) are provided.

Geological setting

All the specimens come from thin layers of the Lower Triassic (Dinerian) fine-grained, iron rich conglomerate, belonging to the 5–6 m thick Brevassfjellet

Fig. 2. Outcrops of the late Paleozoic–early Mesozoic sequence. Hyrnefjellet Mt., Hornsund. Asterisk shows shark teeth sampling locality. *Photo taken by A. Gaździcki, July 1998.*

Myalina Bed (Figs 3, 4), exposed on the SE slope of the Hyrnefjellet Mt. (Figs 1–4) of the Hornsund area in West Spitsbergen. This bed represents the upper part of the Urnetoppen Member of the Vardebukta Formation (Birkenmajer 1964, Harland 1997, Dallmann 1999).

The Vardebukta Formation (Buchan *et al*. 1965) is the oldest lithostratigraphic unit of this rank in the Triassic sequence of Svalbard archipelago (Fig. 3). Both members of the Vardebukta Formation, *viz*. Urnetoppen and Wibebreen, are of marine origin (Birkenmajer and Jerzmańska 1979). The Brevassfjellet *Myalina* Bed marks the horizon by being easily distinguished in the field thanks to an intensely brown-red weathering hue (Fig. 4). The rocks are abound in organic fragments, mainly bivalves (*Myalina*) and trace fossils. The top of the unit is covered by discontinuous intercalations of fine-grained quartz conglomerate 5–10 cm thick. In addition to abundant fish teeth and scales the conglomerate have yielded a few stratigraphically valuable the Lower Triasic (Dienerian) conodonts (Birkenmajer and Trammer 1975).

Material and terminology

The vertebrate material collected by the Paleontological Expedition to Spitsbergen (1998) consists of about 260 isolated ichthyoliths, among them approxi-

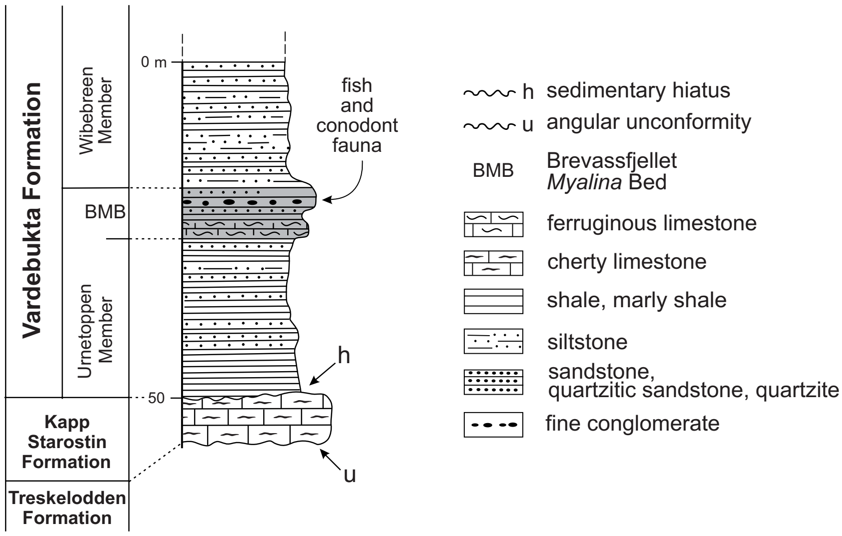

Fig. 3. Position of the fish fauna in the Triassic stratigraphic log of the Hyrnefjellet Mt., Hornsund (after Birkenmajer 1977).

Fig. 4. The Brevassfjellet *Myalina* Bed in the Vardebukta Formation, Hyrnefjellet Mt., Hornsund.

mately 120 shark teeth. The fragmentary character of the fish remains suggests the reworking by the action of currents. The scales and teeth are often abraded and the roots of teeth are usually damaged. This shows that fish bearing conglomerate is a marine bone bed – a concentrate which consists of fossil fragments developed by

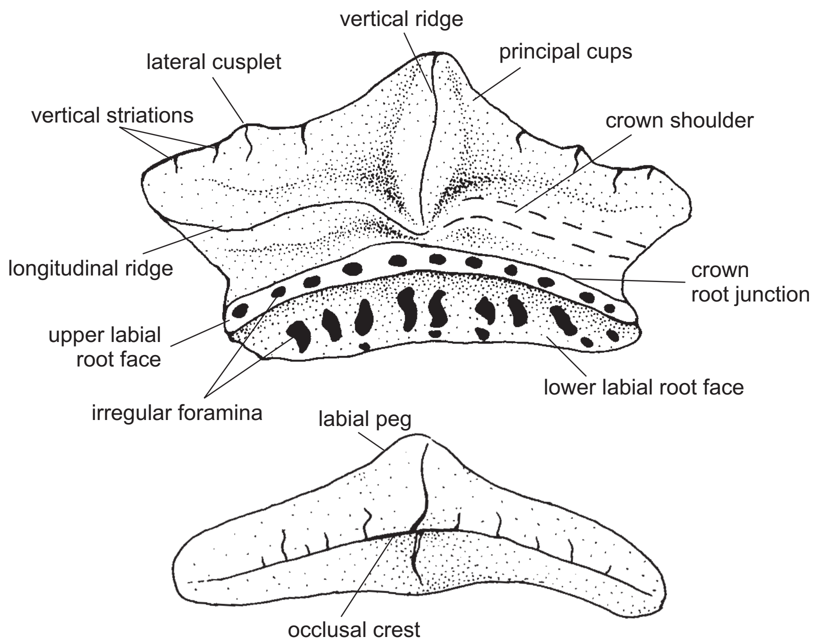

Fig. 5. Descriptive nomenclature of *Lissodus* tooth modified from Duffin (1985).

washing off the finer clay and sand particle from the sediment by bottom currents, being deposited during the formation of offshore sand bars (see Fig. 4).

The descriptive terminology of the shark teeth follows that of Duffin (1985) and a key is shown in Fig. 5.

Illustrated specimens were coated with platinum and photographed using a SEM. The polished surfaces were etched with 1% orthophosphoric acid for 55–65 seconds (Wood 2000), and coated with platinum. During the investigations of histology an energy-dispersive X-ray spectroscopy (EDS) of the filling of the nutrious channels within the teeth of *L. angulatus* was made. The analysis proved that the channels in the root are filled with diagenetic pyrite.

All illustrated specimens are deposited in the Institute of Paleobiology, Polish Academy of Sciences, Warszawa (abbreviated ZPAL P.8).

Systematic paleontology

Class Chondrichthyes Huxley, 1880
Subclass Elasmobranchii Bonaparte, 1838
Order Euselachii Hay, 1902
Superfamily Hybodontoidea Owen, 1846
Family Lonchidiidae Herman, 1977
Genus *Lissodus* Brough, 1935

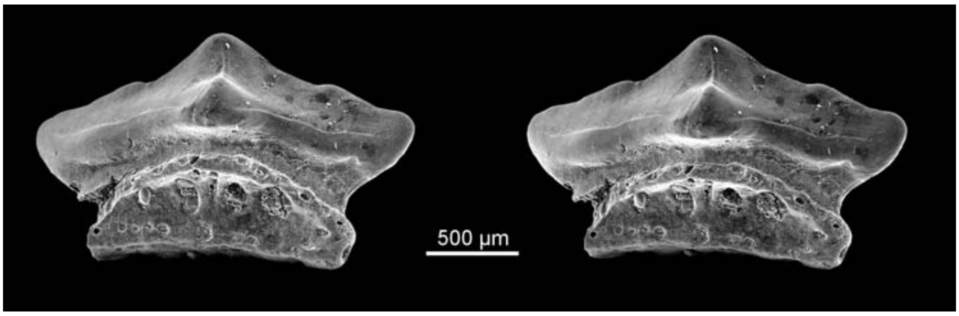

Fig. 6. *Lissodus angulatus* (Stensiö, 1921) – labial view. ZPAL P.8/1-B21. SEM stereo-micrographs. Vardebukta Formation, Lower Triassic (Dinerian); Hyrnefjellet Mt., Hornsund.

Lissodus angulatus (Stensiö, 1921)
(Figs 6, 7, 10)

1921. *Polyacrodus angulatus* Stensiö; Stensiö, 31, text-fig. 13, pl. 1 fig. 27.
1979. *Polyacrodus angulatus* Stensiö; Jerzmańska (*in* Birkenmajer and Jerzmańska), 25, figs 14–17.
1985. *Lissodus angulatus* (Stensiö); Duffin, 119, text-fig. 11 a–c.
1992. *Lissodus angulatus* (Stensiö); Gomez Pallerola, fig. 9 c.
1993. *Lissodus angulatus* (Stensiö); Duffin, text-fig. 6 c.
2001. *Lissodus angulatus* (Stensiö); Duffin, text-fig. 11 a–g.

Material. — About 70 teeth, predominantly complete crowns without roots, seldom with roots preserved ZPAL P.8/1.

Diagnosis (in the sense of Duffin 1985). — The length of the teeth is up to 7 mm with a moderate central principal cusp. The lateral cusplets may be slightly developed although they are usually absent. The labial peg is moderate. The crown is either smooth or ornamented by vertical striations. The striations on the principal cusp bifurcate. A longitudinal ridge is developed along the labial crown shoulder (Fig. 6). The root is lingually-directed. Traces of specialized foramina are frequent along the upper labial root face. The other foramina are irregular but are organized into longitudinal rows on both lower labial and lower lingual root faces.

Description. — Mostly isolated crowns up to 4 mm long, with a moderate principal cusp. The presence of larger crown fragments suggests that some teeth may reach up to 6 mm long.

Lateral cusplets are usually absent, but may show incipient development in the anterior teeth (Fig. 7B). A well developed occlusal crest expands mesiodistally through cusplets apices in a somewhat sinusoidal shape, the whole tooth is curved longitudinally in the same manner (Fig. 7B$_2$). The base of the principal cusp on the labial face widens and is expanded to form the labial peg, which is seen clearly in anterior and lateral teeth (Fig. 7A$_2$, B$_2$, C$_1$). Single well developed vertical ridges (Fig. 7A$_2$, B$_2$, E$_2$) are present on both sides of the crown, descending down the axis of the labial peg, and bifurcating in the posterior teeth on the lingual side at the level of the crown shoulder. In the lateral teeth, on the labial

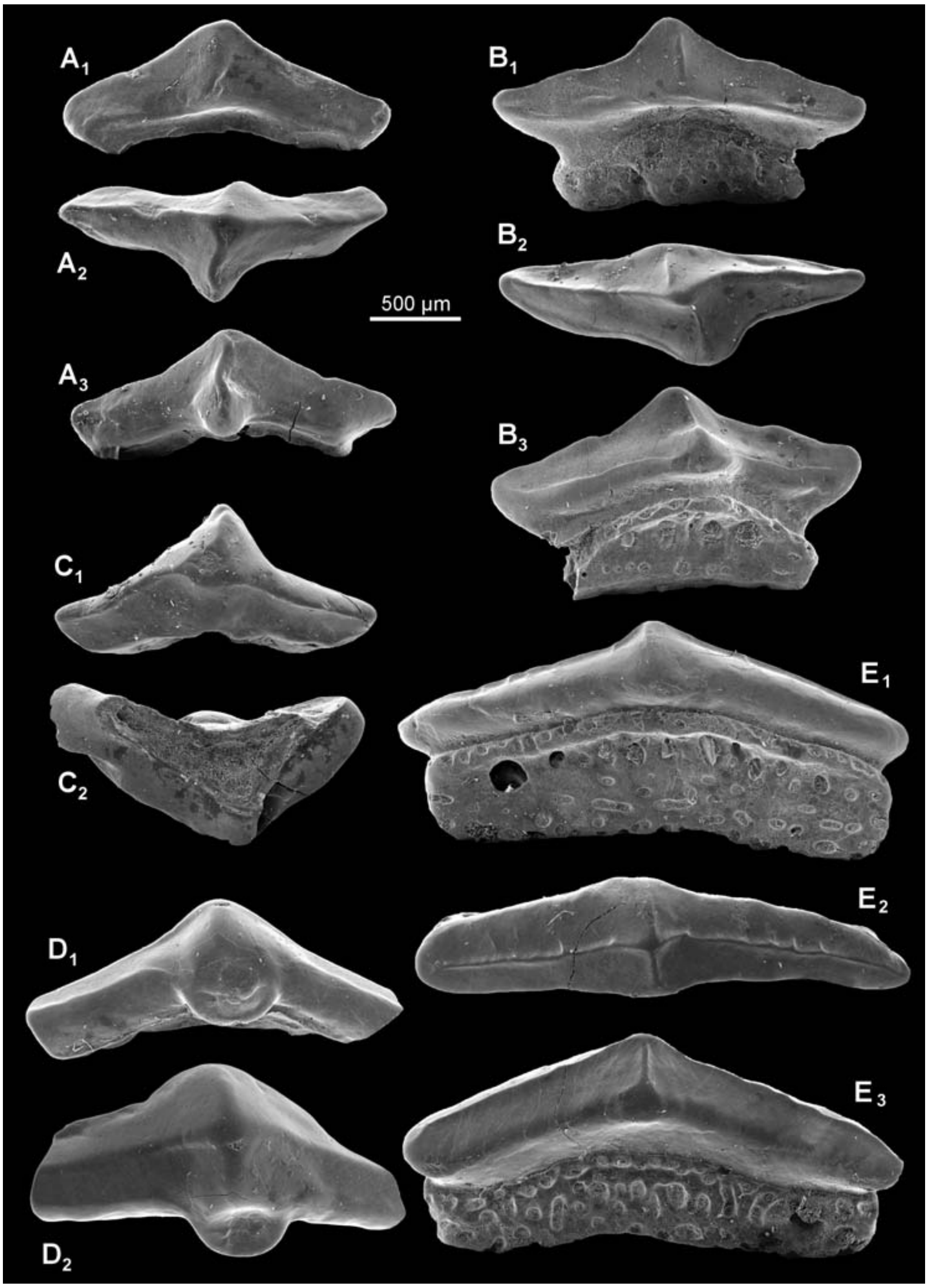

Fig. 7. Teeth of *Lissodus angulatus* (Stensiö, 1921). **A**. ZPAL P.8/1-B25, A_1 – lingual view, A_2 – occlusal view, A_3 – labial view. **B**. ZPAL P.8/1-B21, B_1 – lingual view, B_2 – occlusal view, B_3 – labial view. **C**. ZPAL P.8/1-B48, C_1 – occlusal view, C_2 – basal view. **D**. ZPAL P.8/B210, D_1 – lingual view, D_2 – occlusal view. **E**. ZPAL P.8/1-B22, E_1 – lingual view, E_2 – occlusal view, E_3 – labial view. Vardebukta Formation, Lower Triassic (Dinerian); Hyrnefjellet Mt., Hornsund.

side, the vertical ridge goes through the labial peg terminating at the level of the crown shoulder (Fig. 7A_2, A_3). The crown/root junction is deeply incised around the tooth. The root is narrow and long, and the root attachment is triangular in outline in anterior teeth (Fig. 7C_2). The crown profile is low, the crown surface straight or curved to varying degree, and is at its widest at the base of principal cusps. The surface of the crown may be smooth (Fig. 7B_2, D_2) or ornamented with thin irregularly placed vertical striations on the labial side (Fig. 7E_2). Striations do not appear on the lingual side. A set of longitudinal ridges may be developed along the labial crown shoulder (Fig. 7B_2). The specialised foramina are present on the upper labial root surface. All the other foramina are irregular, often arranged in rows on the lower labial and the lower lingual face of the root as well (Figs 7B_2, E_1).

Remarks. — Jerzmańska (*in* Birkenmajer and Jerzmańska 1979, p. 28) noted that the teeth of this species were similar to the teeth of *L. breve*, but refrained from allocating them to *Lissodus* since details of the histology were lacking. The crown and root morphology of *Polyacrodus angulatus* are unmistakably that of *Lissodus* and the species should be placed in that genus as proposed by Duffin (1985) referring to the Jerzmańska (*in* Birkenmajer and Jerzmańska 1979) description.

Occurrence. — Vardebukta Formation, Lower Triassic (Dinerian): Spitsbergen (Hornsund, Hyrnefjellet Mt.).

Family Acrodontidae Casier, 1959
Genus *Acrodus* Agassiz, 1837
Acrodus spitzbergensis Hulke, 1873
(Fig. 8)

Material. — More than 20 teeth, of which many are complete.

Description. — Isolated teeth, 1.0–7.0 mm long. Tooth features suggest that some teeth reached up to 12 mm. The crowns are oval, low, flat or slightly bent in the vertical plane, the labial surface of the root is prominent, and the lingual surface is concave. The main cusp does not project beyond the labial edge of the crown, but may overhang the lingual part forming a prominent projection over the concave lingual margin. There are also teeth with almost flat crown surfaces. The roots are low and usually broader than the crown. Two separate perpendicular stripes run downward from a well marked longitudinal crest on both the labial and the lingual sides of the crown. The stripes are parallel to each other and in most cases bifurcate near the end of the longitudinal edge. It is worth mentioning that many teeth are unornamented which may be due to intraspecific variation. The occurrence of ornament in those cases is about 4 times more frequent on upper lingual than on the upper labial surface of the crown.

Remarks. — The data provided by Stensiö (1921) makes it clear that all the teeth of *A. spitzbergensis* are characterized by considerable changes in the form of crown and the size ranges up to 3 cm long. Moreover, the teeth from Hornsund are

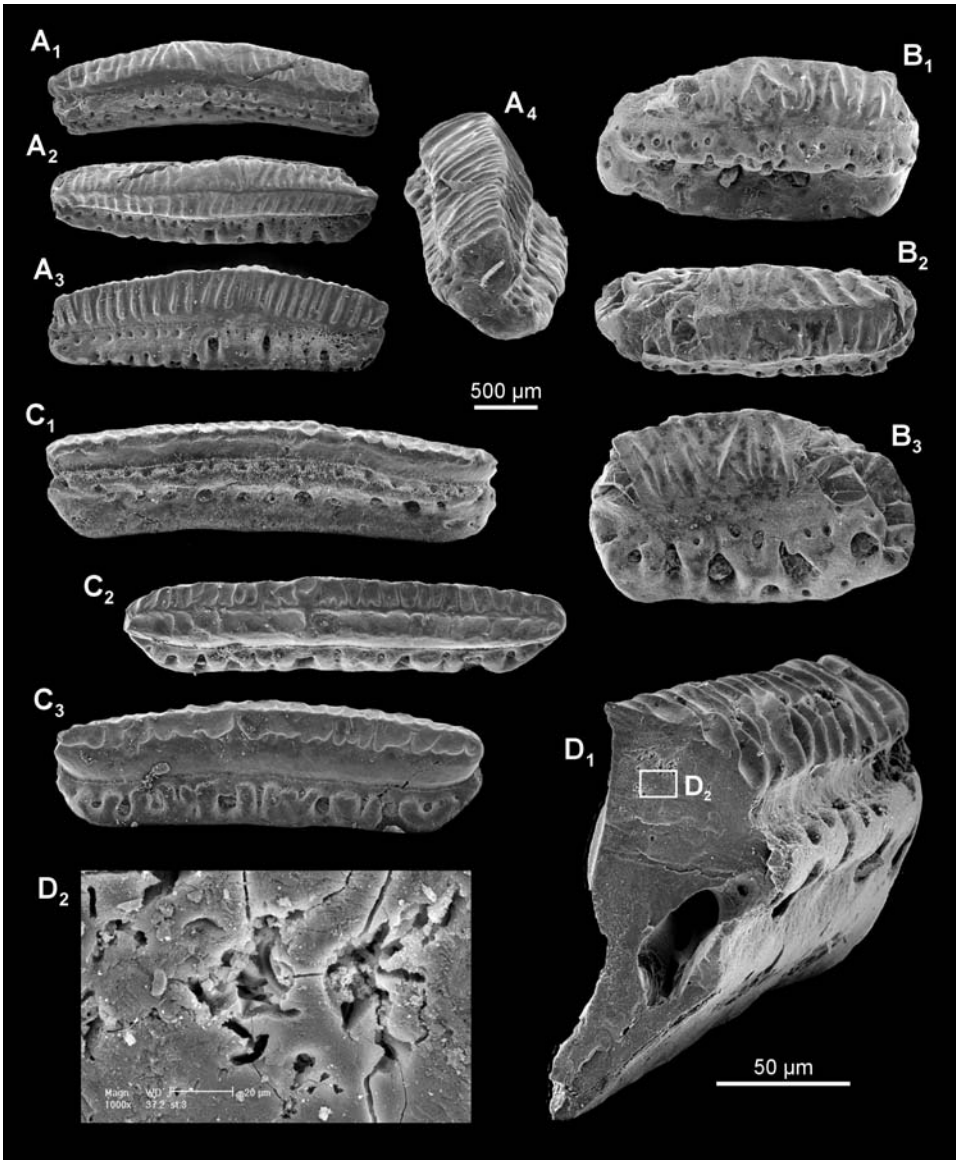

Fig. 8. Teeth of *Acrodus spitzbergensis* Hulke, 1873. **A**. ZPAL P.8/2-B45, A_1 – labial view, A_2 – occlusal view, A_3 – lingual view, A_4 – lateral view. **B**. ZPAL P.8/2-B34, B_1 – labial view, B_2 – occlusal view, B_3 – lingual view. **C**. ZPAL P.8/2-B15, C_1 – labial view, C_2 – occlusal view, C_3 – lingual view. **D**. ZPAL P.8/2-B32, D_1 – cross-section, D_2 – osteodentine. Vardebukta Formation, Lower Triassic (Dinerian); Hyrnefjellet Mt., Hornsund.

evidently smaller than the teeth from Central Spitsbergen as already noted (Birkenmajer and Jerzmańska 1979, p. 24). This difference in size may by due to different stratigraphic position of the teeth: the teeth from Hornsund were collected from the

Lower Dienerian Brevassfjellet *Myalina* Bed (Vardebukta Formation, Urnetoppen Member: upper part), those from Isfjorden – from the Smithian–Spathian Sticky Keep Formation (Birkenmajer and Jerzmańska 1979).

Occurrence. — Vardebukta Formation, Lower Triassic (Dinerian): Spitsbergen (Hornsund, Hyrnefjellet Mt.).

Family Hybodontidae Owen, 1846
Genus *Hybodus* Agassiz, 1837
Hybodus microdus Stensiö, 1921
(Fig. 9A–C)

Material. — More than 20 teeth, usually complete and with preserved root.

Description. — Isolated, small teeth 0.5–2.2 mm. Symphysial and parasymphysial teeth with a large principal cusp and small lateral cusps. Narrow longitudinal depression covered with smooth enamel occurs at the labial side of the crown base. Gradual height reduction of the principal cusp is observed in successive tooth rows: the lateral teeth have low, long crowns with characteristic large lingual process, sometimes less pronounced as a buttress. Root is strongly adjoined to the crown in every tooth.

Remarks. — This description of *Hybodus microdus* based on isolated teeth corresponds to the description by Jerzmańska (*in* Birkenmajer and Jerzmańska 1979). She assumes that there is a greater variation within the species than does Stensiö (1921).

Occurrence. — Vardebukta Formation, Lower Triassic (Dinerian): Spitsbergen (Hornsund, Hyrnefjellet Mt.).

Hybodus sasseniensis Stensiö, 1918
(Fig. 9E–F)

Material. — 5 teeth, including 2 nearly complete, 2 broken central cusps and some fragments of roots with lateral cusps.

Description. — Isolated teeth, 6 mm long with distinct central cusps and one to three lateral cusps. The root at the base of lingual side is usually slightly curved in the vertical plane. The central cusp can be straight, or bent distally or lingually. Some specimens have enameloid or part of the dentine of the central cusp erased which could be – judging by the state of the whole tooth – a result of antemortem wear. The number of lateral cusps depends on the tooth size. Some possess only one cusp on each side of the central cusp: the medium size teeth have up to two, and the largest ones have three cusps, usually placed only on one side of the crown. The lateral cusp grows somehow obliquely to the principal cusp. The ornament consists of numerous vertical stripes almost reaching the central and lateral cusp. The ornamentation is regular, without intervals or deformations. Numerous irregular nutrious foramina are placed randomly all over the surface of the root.

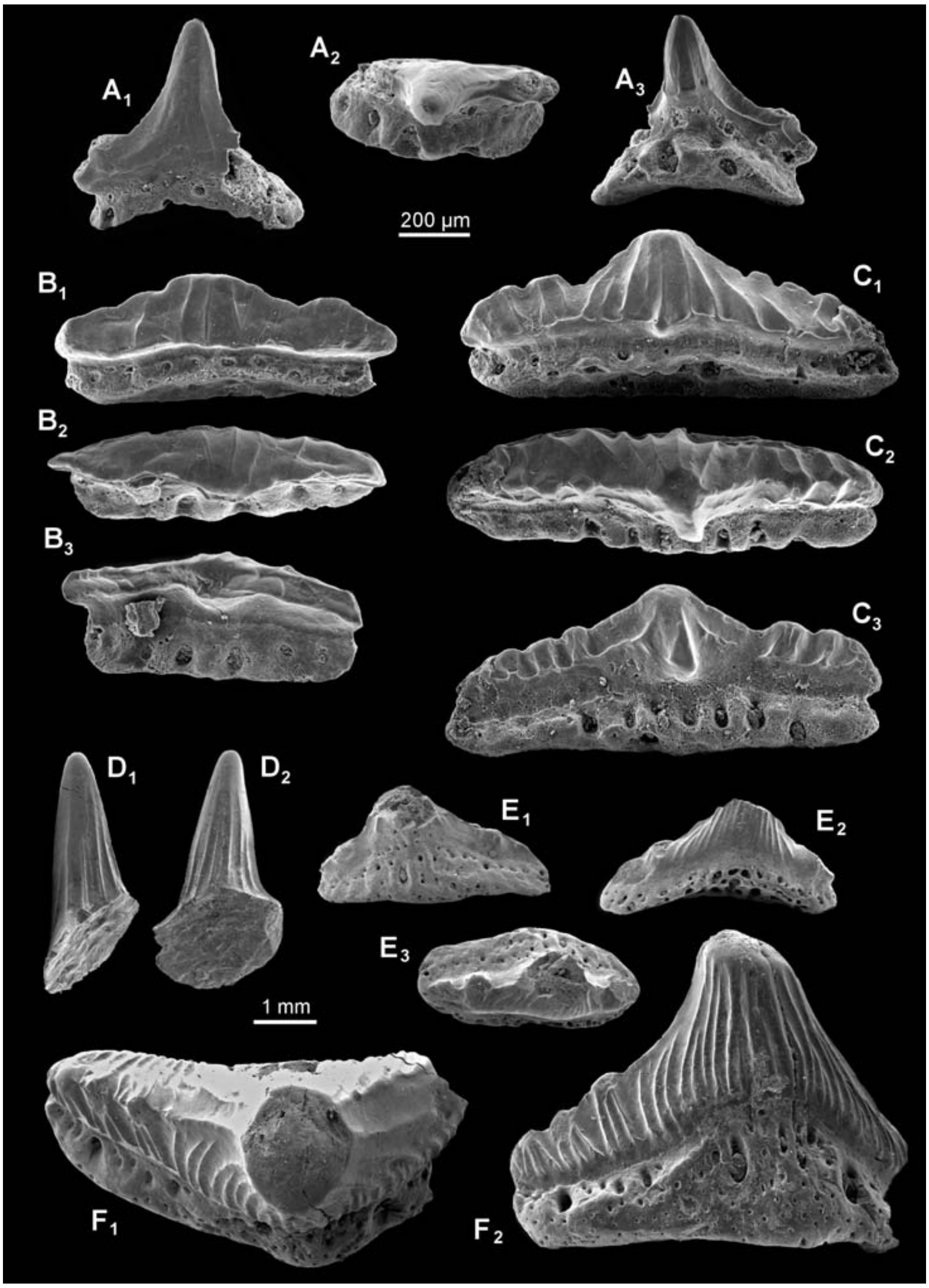

Fig. 9. **A**–**C**. Teeth of *Hybodus microdus* Stensiö, 1921. **A**. ZPAL P.8/3-B17, A_1 – labial view, A_2 – occlusal view, A_3 – lingual view. **B**. ZPAL P.8/3-B35, B_1 – labial view, B_2 – occlusal view, B_3 – lingual view. **C**. ZPAL P.8/3-B14, C_1 – labial view, C_2 – occlusal view, C_3 – lingual view. **D**. *Hybodus* sp. ZPAL P.8/4-B11, D_1 – lateral view, D_2 – lingual view. **E**–**F**. *Hybodus sasseniensis* Stensiö, 1918. **E**. ZPAL P.8/4-B51, E_1 – lingual view, E_2 – labial view, E_3 – occlusal view. **F**. ZPAL P.8/4-B52, F_1 – occlusal view, F_2 – lingual view. Vardebukta Formation, Lower Triassic (Dinerian); Hyrnefjellet Mt., Hornsund.

Remarks. — The species was described by Stensiö (1918) from Vikinghrgda (Sassenfjorden), Isfjorden, and Hornsund in Spitsbergen. The material from Hornsund studied herein contains teeth corresponding to the typical forms of specimens from Isfjorden (Stensiö 1921, pl. 1, figs 3–10) and Hornsund (Stensiö 1918, Birkenmajer and Jerzmańska 1979).

Occurrence. — Vardebukta Formation, Lower Triassic (Dinerian): Spitsbergen (Hornsund, Hyrnefjellet Mt.).

Hybodus sp.
(Fig. 9D)

Material. — Two, incomplete teeth.

Description. — In lateral view, the principal cusp has a sigmoidal shape, straight at the base and slightly crooked labially. It is flattened and its horizontal cross-section is of an ellipsoid shape. Judging by the look of preserved remain we can find their original size as much bigger than any other found there. The real height can be estimated as being approximately 7–10 mm.

Discussion. — Both incompletely preserved fragments of the teeth reveal a prominent affinity to *Hybodus rapax*, described by Stensiö (1921) from Vikinghrgda (Sassenfjorden). The affinities are distinct, but they cannot be placed within the species because of the incompleteness of examinated specimens.

Occurrence. — Vardebukta Formation, Lower Triassic (Dinerian): Spitsbergen (Hornsund, Hyrnefjellet Mt.).

Histology

The most interesting results of the research on shark teeth from Hornsund concern *Lissodus angulatus* which shows two types of histology within a single taxon. This seems to be typical for all representatives of the genus *Lissodus*. In the orthodentine-type teeth, the whole crown underneath the enameloid is formed of orthodentine, and the pulp cavity is often present. In osteodentine-type teeth, a central osteodentine core is always developed, while the orthodentine may be present as a thin layer between the osteodentine and enameloid. The taxonomic importance of *Lissodus* teeth histology has been rather controversial for many years, and its meaning was considered to be important as often as not. Osteodentine-type histology of *Lissodus* known so far by the example of the Late Triassic *L. minimus* (Agassiz, 1839) – see Patterson (1966, pl. 5), was originally considered as typical for all species of *Lissodus.* The present study shows it to be typical only for the lateral and posterior teeth (as suggested by Rees and Underwood 2002, p. 473). Anterior teeth of *Lissodus* dentition have typical orthodentine-type structure with the pulp cavity developed in the central part (Fig. 10B). The type of histology does not depend on the size of teeth. Even diminutive posterior teeth, which are often

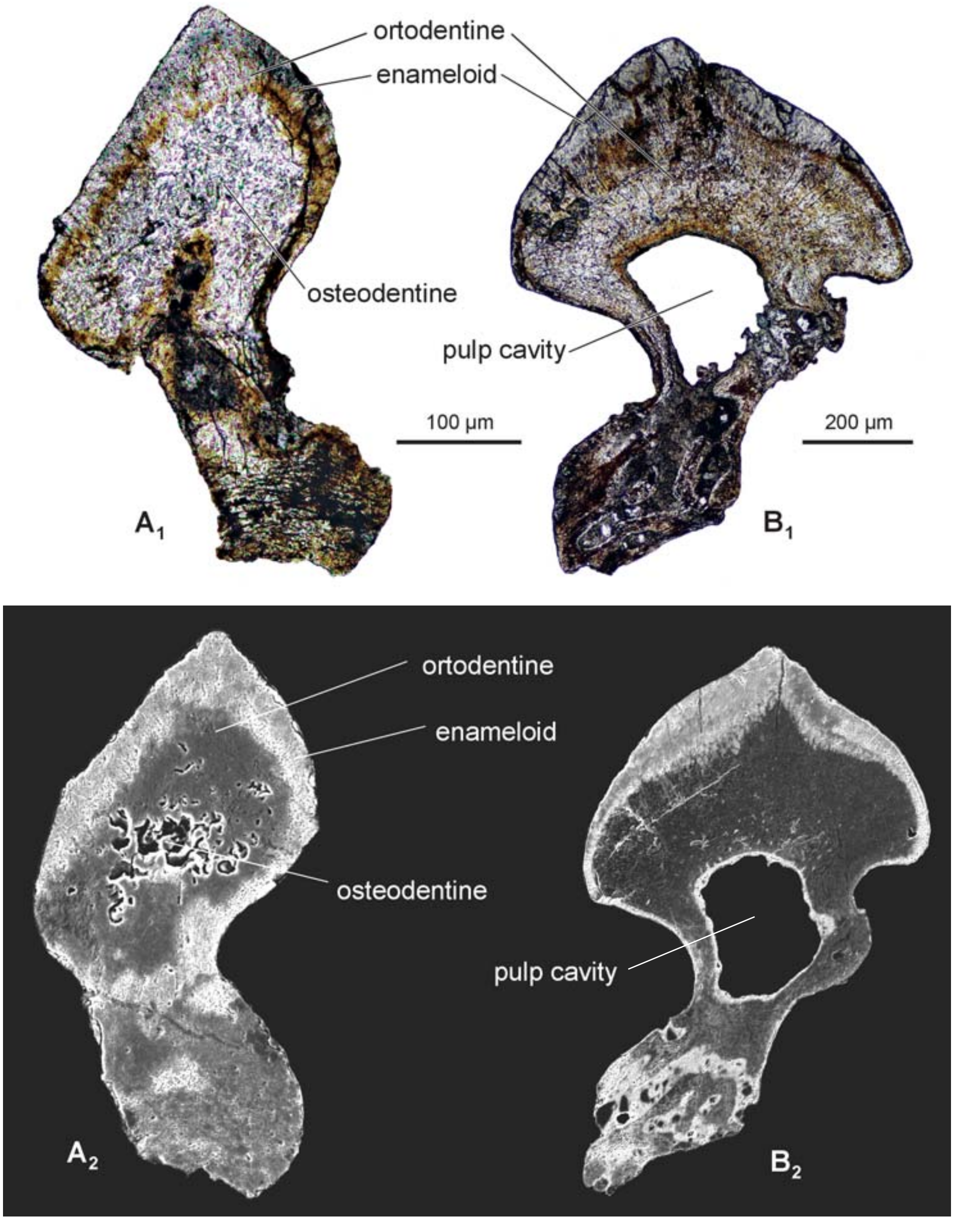

Fig. 10. Vertical sections of *Lissodus angulatus* (Stensiö, 1921) teeth from the Vardebukta Formation, Lower Triassic (Dinerian), Hyrnefjellet Mt., Hornsund. **A**. ZPAL P.8/1-BB1 – posterior tooth. **B**. ZPAL P.8/1-BB2 – anterior tooth. A_1–B_1 – thin sections, A_2–B_2 – SEM micrographs.

smaller than anterior ones, still have a well developed osteodentine core (Fig. 10A). It is clear now that the lack of osteodentine cannot be explained by insufficient space inside narrow and small teeth – see Rees and Underwood (2002). The case of the Early Permian *Lissodus zideki* (Johnson, 1981) is very similar, where two types of histology are present within one taxon. It is also worth of note, that the osteodentine core of *L. zideki* is relatively small compared to that in the teeth of the Early Triassic *L. angulatus.* In the latter the osteodentine occupies almost the whole crown, while in *L. zideki* the orthodentine makes a quite thick layer between enameloid and osteodentine core. Future studies should reveal whether that difference has an evolutionary meaning.

All the specimens described in this paper possess only one layer of an SCE (single crystallite enameloid) with randomly oriented crystallites. The only exception is *Hybodus* sp. where the enameloid shows an area where the crystallites are perpendicularly oriented to the surface of the crown. Similar enameloid in hybodonts was described by Johns *et al*. (1997, pl. 38), and Dorka (2001). While in the teeth of neoselachians enameloid cover consists of three layers marked as SCE, PFE and TFE (Reif 1973, see also Rees 2001), in the hybodonts teeth it is limited only to SCE (Reif 1973, Rees 1998).

The existence of two types of histology within a single taxon closes the discussion considering ortho- and osteodentine as a taxonomically valid feature.

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