Early Jurassic selachians from the Hasle Formation on Bornholm, Denmark

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A selachian fauna from the early Pliensbachian (*Uptonia jamesoni* to *Prodactylioceras davoei* zones) is recorded from the Hasle Formation on the island of Bornholm. Three hybodont sharks, *Hybodus reticulatus*, *H. delabechei* and *Lissodus hasleensis* sp. n., and three neoselachians, *Synechodus occultidens*, *Paraorthacodus* sp. and *Agaleus dorsetensis*, are recognized in the fauna. The enameloid ultrastructure of teeth of *A. dorsetensis* was examined and found to be comprised of at least two layers, confirming a neoselachian affinity, based on the overall tooth morphology. The palaeogeographical and stratigraphical records of the previously described species are extended. Pliensbachian selachian faunas are not well investigated and the described species in the Hasle fauna are all known from Sinemurian deposits elsewhere.

Key words: Selachians, hybodonts, neoselachians, palaeobiogeography, palaeoecology, Pliensbachian, Early Jurassic, Bornholm, Denmark.

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Introduction

Early Jurassic selachian faunas are dominated by two groups, the euselachian hybodonts and the neoselachian palaeospinacids. The earliest certain records of hybodont sharks are from the Viséan, Early Carboniferous (Duffin 1985). They may originate, however, as far back as the mid-Devonian (Zangerl 1981). The latest records are from the Maastrichtian, Late Cretaceous (Cappetta *et al.* 1993). The most characteristic external features of a hybodont shark are the large dorsal fin spines and, in males, one or two pairs of cephalic spines, the latter feature being exclusive to the group. They inhabited rivers, estuaries and lagoons as well as coastal marine environments. Fluviatile environments appear to be more frequently inhabited in the Early Cretaceous, or even the Late Jurassic, onwards. The decrease of hybodonts in marine environments was probably due to overwhelming competition with the rapidly diversifying neosela-

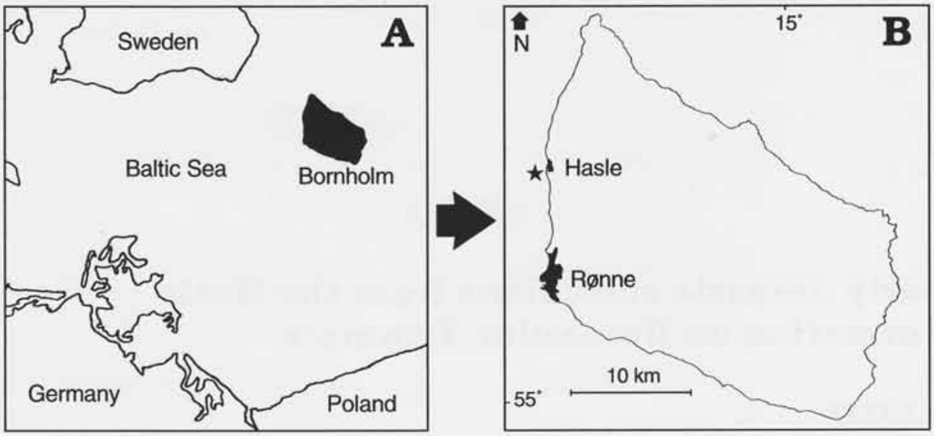

Fig. 1. **A**. General location of the island of Bornholm. **B**. The coastal cliff section with the type locality of the Hasle Formation marked with a star.

chians. The enameloid of hybodont teeth consists of only one layer (single-crystallite enamel of Reif 1973), whereas most neoselachians have three layers making the teeth more resistant to breakage. The simple enameloid structure in hybodont teeth may explain why hybodonts rarely developed a cutting-type dentition with labio-lingually flattened teeth.

Palaeospinacid sharks are an extinct group of neoselachians, possibly ranging from the Early Triassic (Thies 1982). The earliest certain records are from the Ladinian, Middle Triassic, of Canada (Johns *et al.* 1997). The latest occurrences are from the Late Palaeocene (Cappetta *et al.* 1993). Externally, palaeospinacid sharks are characterised by an elongated body with a subterminal mouth and two dorsal fin spines (Cappetta 1987). The vertebral centra are calcified and there are many diagnostic cranial features, as well as an amphistylic jaw suspension (see Maisey 1985). Palaeospinacid teeth form a clutching type dentition and the root of the teeth is at a pseudopolyaulacorhize stage (Cappetta 1987). They have been the subject of a heated debate in recent years (Thies 1991, 1993; Cappetta 1987, 1992; Duffin & Ward 1993). The most important result of this controversy came in 1993 when Duffin & Ward, in a paper on the palaeospinacids of Lyme Regis, concluded that the type species of *Palaeospinax*, *P. priscus*, is a *nomen dubium* since its holotype consists of a single row of vertebrae, lacking generic or specific characters. Species previously referred to *Palaeospinax* were reassigned to either of the two remaining valid genera in the family, *Paraorthacodus* and *Synechodus*.

Geology and biostratigraphy

The island of Bornholm (Fig. 1) is part of the Fenno-Scandian Border Zone and constitutes a fault block mosaic (Gravesen *et al.* 1982). Sporadic outcrops of Early Jurassic strata are exposed in the south-western part of the island and are dominated by deltaic and lacustrine deposits. However, due to an early Pliensbachian transgression (Hallam 1975), the limonitic sandstones and siltstones of the Hasle Formation were primarily deposited in a shallow marine environment. The dominating sedimentary structures of the formation include hummocky cross-stratification and thin, poorly sorted, gravel laminae, representing erosional surfaces (Gravesen *et al.* 1982). Deposition took place at a depth of 10–40 meters on the open shelf, one or two kilometres from the coast line (Surlyk & Noe-Nygaard 1986). The sedimentary structures show that sedimentation was active during storms that were either frequent or so vigorous that they eroded all fair-weather deposits.

The age of the formation has been determined by means of ammonites to include the zones of *Uptonia jamesoni* to *Prodactylioceras davoei* in the early Pliensbachian (Gravesen *et al.* 1982). Invertebrate fossils are very scarce in the section yielding selachian remains and it has not been possible to make a more precise age determination.

Material and methods

All fossils described herein were collected during the last decade at the type locality of the Hasle Formation, situated along the coast, south of the harbour in the town of Hasle (Fig. 1B). The strata are exposed along the shore for approximately 700 meters. The sandstones are often too consolidated to make bulk processing successful. As a result, most of the selachian material in this study was obtained through surface picking. In places, weathering has softened the sandstone allowing some bulk sampling. In total 18 kg were gently wet sieved and the residue above 500 μm was picked.

Prior to photography, the large teeth were coated with ammonium chloride, while small teeth were coated with gold and photographed using a SEM.

The ultrastructure of the teeth was examined with a SEM after etching the teeth with 5 N hydrochloric acid (HCl) for 10 to 30 seconds and then coating them with gold (see Reif 1973: p. 232).

Systematic palaeontology

General systematics, taxonomy and descriptive terminology for palaeospinacids follow those of Cappetta (1987). Descriptive terminology for *Agaleus* follows that of Duffin & Ward (1983) and terminology for hybodonts is modified from Duffin (1985) and shown in Fig. 2.

All illustrated specimens are deposited in the type collection of the Division of Historical Geology and Palaeontology, Lund University, Sweden and prefixed LO (Lund Original). The suffix 'T' denotes holotype and 't' denotes other illustrated specimens.

Cohort Euselachii Hay, 1902

Superfamily Hybodontoidea Zangerl, 1981

Remarks. — As a result of the extreme rarity of skeletal remains or even associated teeth from single individuals, the interrelationships and taxonomy of hybodonts is complicated. A revision of hybodont

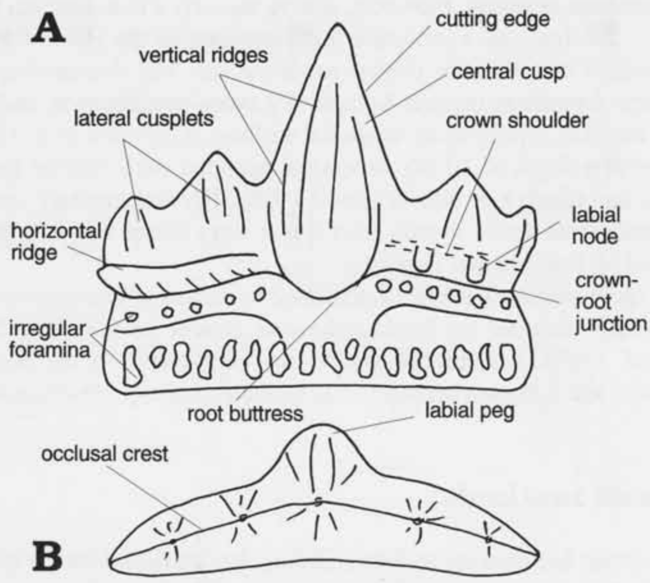

Fig. 2. A generalized hybodont shark tooth in labial (**A**) and occlusal (**B**) views, showing descriptive terms used in the text.

taxonomy and systematics is greatly needed, as a few genera may be paraphyletic or even polyphyletic. This is, however, beyond the scope of this paper and I will consequently follow the current taxonomy.

Family Hybodontidae Owen, 1846
Genus *Hybodus* Agassiz, 1837

Type species: *Hybodus reticulatus* Agassiz, 1837 from the Sinemurian, Early Jurassic of Lyme Regis, England.

Hybodus reticulatus Agassiz, 1837

Fig. 3G–L.
Hybodus reticulatus Agassiz 1837: p. 50, pl. 22: 22–23.
Hybodus reticulatus Agassiz, 1837; Woodward 1889: p. 266–268, pl. 10: 16–18.
Hybodus reticulatus Agassiz, 1837; Malling & Grönwall 1909: p. 294, pl. 11: 12.
Hybodus reticulatus Agassiz, 1837; Maisey 1987: p. 1–39, figs 1–7, 9–13, 18.
Hybodus reticulatus Agassiz, 1837; Duffin 1993: p. 49, fig 1d.
Hybodus reticulatus Agassiz, 1837; Delsate & Duffin 1993: p. 110, pl. 1: 1

Material. — 21 incomplete crowns, LO 7953t, LO 7954t and LO 7955t, all others unnumbered.

Description. — The teeth have a high central cusp and two to three pairs of lateral cusplets. All teeth are approximately as high as they are wide. The largest tooth measures 11 mm in height. The central cusp and the lateral cusplets are slender with circular to oval cross section. The cusp and the cusplets of lateral teeth are slightly inclined posteriorly. The cusplets vary from being very small elevations of the occlusal crest to reaching approximately one quarter of the height of the central cusp. Ornamentation consists of weak vertical ridges, occasionally bifurcating, covering the crown except for the apex of the central cusp. The cutting edges are moderately strong. The labial and lingual sides are equally convex. Monognathic heterodonty in this species is manifested by differen-

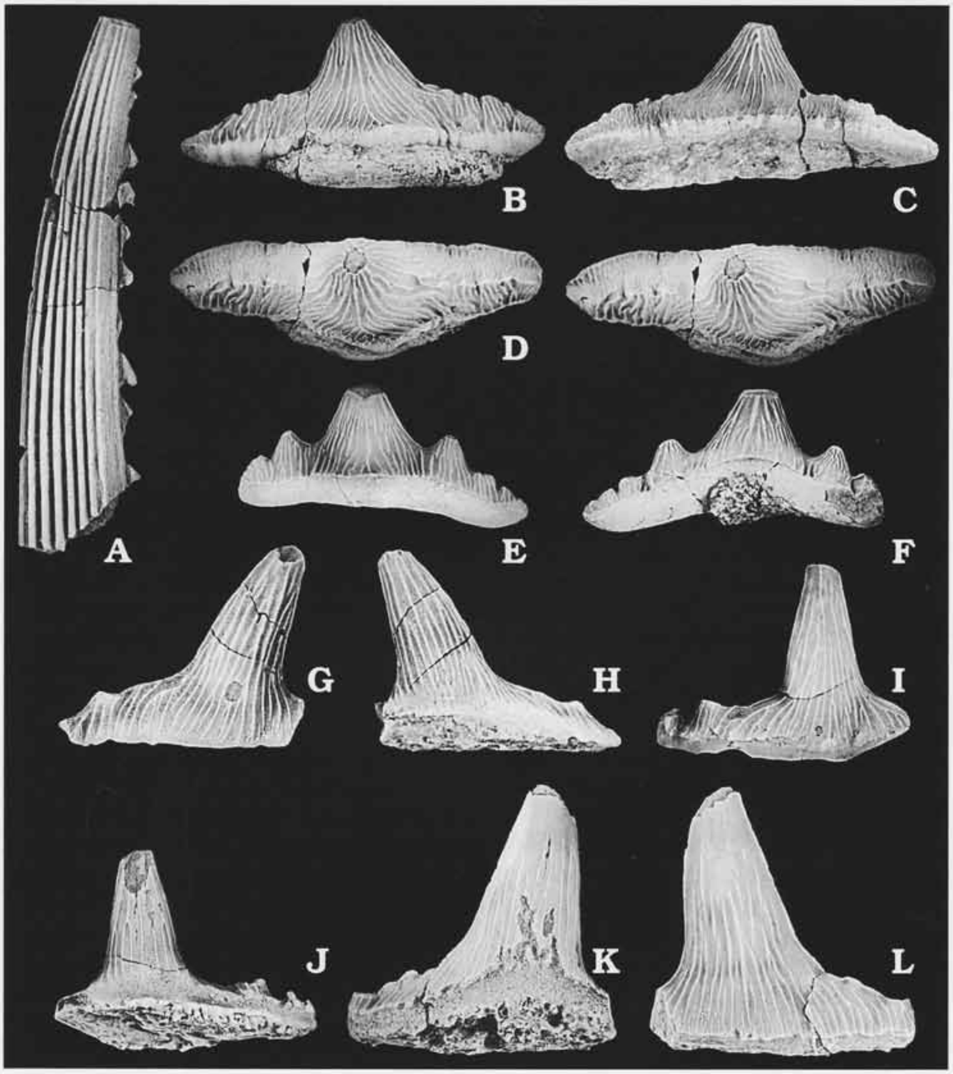

Fig. 3. *Hybodus* teeth and hybodont fin spine. **A**. Hybodont fin spine, LO 7963t × 1.8. **B–F**. *H. delabechei* Charlesworth, 1839 × 1.6. **B–D**. LO 7956t in labial (**B**), lingual (**C**), and occlusal (**D**) views (stereo pair). **E**, **F**. LO 7957t in labial (**E**) and lingual (**F**) views. **G–L** *H. reticulatus* Agassiz, 1837 × 3.5. **G**, **H**. LO 7953t in labial (**G**) and lingual (**H**) views. **I**, **J**. LO 7954t in labial (**I**) and lingual (**J**) views. **K**, **L.** LO 7955t in lingual (**K**) and labial (**L**) views.

ces in height of the lateral cusplets. Lateral teeth are furthermore lower and inclined posteriorly. The crown–root junction is slightly incised. The root is not preserved in specimens from the Hasle material.

Discussion. — Associated dentitions and cranial material of this species are known from Lyme Regis, southern England (Maisey 1987). The skull material is often crushed and partly covering the dentitions. Furthermore, the teeth are often embedded in the sediment and the range of dental variation cannot be determined (Maisey 1987).

Hybodus delabechei Charlesworth, 1839

Fig. 3B–F.
Hybodus delabechei Charlesworth 1839: pp. 242–247, pl. 4.
Hybodus pyramidalis Agassiz 1843: p. 182, pl. 22a: 20–21.
Hybodus delabechei Charlesworth, 1839; Woodward 1889a: pp. 259–264, pl. 8: 1–5, 10: 1–5.
Hybodus delabechei Charlesworth, 1839; Woodward 1889b: pp. 58–61, pl. 1: 1–8.
Hybodus delabechei Charlesworth, 1839; Casier 1959: pp. 8–9, pl. 1: 1.
Hybodus delabechei (Charlesworth, 1839); Duffin 1993: p. 49, fig. 1e.

Material. — Three complete crowns, LO 7956t, LO 7957t and unnumbered.

Description. — The teeth are very large and the largest crown in the Hasle material is 29 mm wide. There is a moderately low and pyramidal central cusp. The teeth from Hasle have three or four pairs of lateral cusplets varying in size from being only small elevations of the occlusal crest to reaching half the height of the central cusp. The occlusal crest is weak on the central cusp and more pronounced on the lateral cusplets. There is a wide base of the crown on two of the teeth studied. The base of the crown is ornamented with a horizontal ridge. The third tooth lacks this wide base. The first pair of lateral cusplets is well separated from the central cusp. There are strong vertical ridges covering the crown. Branching of the ridges occurs frequently. Only a small part of the root is preserved. The teeth vary in height and number of the lateral cusplets and development of the wide base of the crown. It cannot be determined, at this time, if the heterodonty is monognathic or dignathic in nature, even though the former seems more likely.

Discussion. — The general tooth morphology in *Hybodus delabechei* is quite different from that of *H. reticulatus*, the type species of *Hybodus*, and the former taxon may in fact belong to a separate genus. The strong overhang of the root by the crown and the wide base of the teeth are features not present on the teeth of *H. reticulatus*. There is also a significant difference in the morphology of the central cusp and the lateral cusplets. They are far more slender and taller in *H. reticulatus*. Until the well preserved hybodont remains from Lyme Regis have been properly described, the taxonomy of Early Jurassic hybodonts will remain complicated.

Family Polyacrodontidae Glikman, 1964
Genus *Lissodus* Brough, 1935

Type species: *Hybodus africanus* Broom, 1909 from the Lower Triassic of Bekkers Kraal, South Africa.

Remarks. — This genus, recently revised by Duffin (1985), includes species with very different tooth morphologies and heterodonty patterns. The presence of a labial peg and a low crown are the only characters available for distinguishing this genus from other hybodontiform genera (Duffin 1985). Many species of *Polyacrodus*, another hybodontiform genus, also possess low-crowned teeth with a labial peg. The type species of *Lissodus*, *L. africanus*, has wide teeth with a moderately strong labial peg and a triangular crown-root junction in basal view. These features are not present on all nominal *Lissodus* species. Generally, species referred to *Lissodus* can be divided into two morphological groups. One group, including the type species and e.g. *L. leiodus* (Woodward, 1887), *L. nodosus* (Seilacher, 1943) and *L. wardi* Duffin, 1985, has wide and low crushing teeth that are weakly ornamented. The other group, that includes *L. rugianus* Ansorge, 1990, *L. striatus* (Patterson, 1966) and *L. multicuspidatus* Duffin & Thies, 1997, among others, possess narrow teeth, often ornamented with vertical ridges and probably better adapted for cutting. The assignment of many species to *Lissodus* is uncertain and the genus may be paraphyletic.

Lissodus hasleensis sp. n.

Fig. 4A–G.
Acrodus minimus Agassiz, 1839; Malling & Grönwall 1909: p. 294–295, pl 11: 13.

Etymology: Named after the Hasle Formation.

Holotype: LO 7958T, a complete antero-lateral tooth.

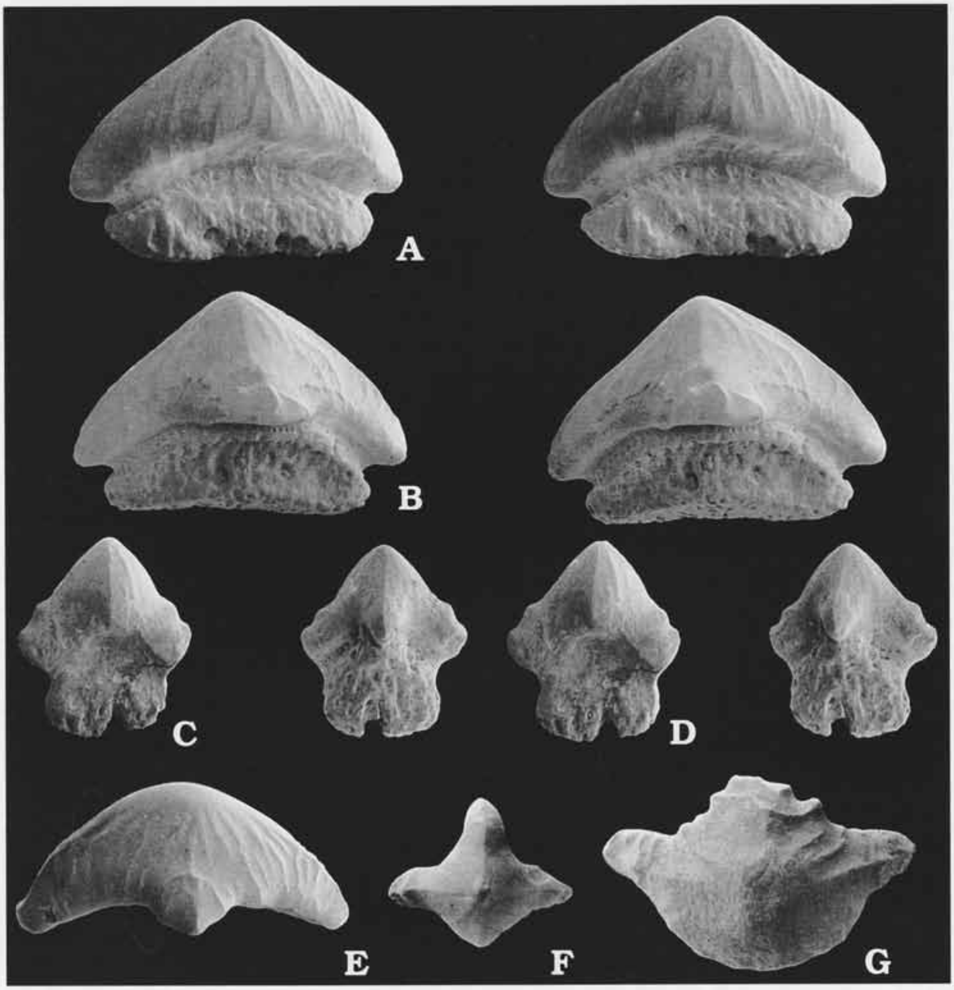

Fig. 4. *Lissodus hasleensis* sp. n., SEM micrographs × 8.5. **A**, **B**. LO 7958T, Antero-lateral tooth in lingual (**A**) and labial (**B**) views (stereo pairs). **C**, **D**. LO 7959t, Anterior tooth in lingual (**C**) and labial view (**D**) (stereo pairs). **E**. LO 7960t, lateral tooth in labial view. **F**. LO 7961t, anterior tooth in occlusal view. **G**. LO 7962t, lateral tooth in occlusal view.

Paratype: LO 7959t, a complete anterior tooth.

Type stratum: A gravel layer in the lower part of the Hasle Formation at its type locality south of Hasle town on Bornholm, Denmark. Precise position within the formation unknown.

Material. — Four complete teeth (LO 7958T, LO 7959t and two unnumbered) and 35 crowns (LO 7960t, LO 7961t, LO 7962t, all others unnumbered).

Diagnosis. — Species of *Lissodus* that differs from *L. minimus* in having anterior teeth that are not as wide and lacking the expanded lingual side, thus giving teeth of *L. minimus* a diamond shape in occlusal view. The lateral teeth of *L. minimus* are likewise more elongated and they have a weak labial peg as opposed to the strong peg in *L. hasleensis*. Furthermore, the number of lateral cusplets on each side of the cusp may reach five in *L. minimus*, whereas no teeth of *L. hasleensis* have more than two. Anterior teeth of *L. nodosus* have a more robust labial peg than anterior teeth of *L. hasleensis*. On lateral teeth of *L. nodosus* there are labial nodes and a small labial peg whereas lateral teeth of *L. hasleensis* lack labial nodes and have a well developed labial peg. Teeth of *L. wardi* are lower, lack lateral cusplets and are much wider compared to teeth of *L. hasleensis*.

Description. — The teeth are up to 9 mm wide and form a clutching-grinding type dentition. The teeth show considerable monognathic heterodonty. Anterior teeth have a moderately high crown with a poorly demarcated central cusp. Small elevations on the occlusal crest form up to two pairs of lateral cusplets in anterior teeth. Lateral cusplets may be lacking in the smooth-crowned, rounded, lateral teeth. Anterior teeth have a few, weak, vertical ridges, primarily on the lingual side. The ridges are present foremost on the lower part of the crown in laterals. They descend from the central cusp and, distally, from the occlusal crest; they rarely branch. There is a pointed labial peg, which is strong in anterior teeth. Lateral teeth have three or four nodes forming a wavy edge on the well developed labial peg. All teeth have a moderate occlusal crest. The crown shoulder is weakly developed in anterior teeth. In lingual and labial view, the distal parts of the crown are bent down towards the root. The crown overhangs the root on all sides because the proximal part of the root is more narrow than the distal part. The root is typically hybodont in structure. On the lingual side of the root, there are many irregular foramina close to the basal face of the root and one row of smaller foramina close to the crown-root junction. The labial face of the root shows the same pattern as the lingual face. There is a root buttress on the labial side of anterior teeth. The root is much higher in anterior teeth than it is in lateral teeth. The basal face of the root is flat and penetrated by numerous irregular foramina.

Discussion. — This species is part of the same species-group as *L. minimus* Agassiz, 1839 from the Rhaetic of England, *L. nodosus* (Seilacher, 1943) from the Middle to Late Triassic of Germany and *L. wardi* Duffin, 1985 from the Bathonian, Middle Jurassic of England. These taxa share the same heterodonty pattern as *L. hasleensis*.

Hybodont fin spines

Fig. 3A.

Material. — One incomplete spine, LO 7963t, and one fragment.

Description. — The most complete spine measures 39 mm in height. A large part of the base is missing as is the tip of the spine. It is ornamented with continuous costae on the lateral sides. At the base of the spine there are six costae and only four close to the apex. There is one strong costa on the anterior edge. On the posterior side there is one row of hook-denticles. The denticles are arranged in a single row without any inclination.

Discussion. — Fin spines from hybodont sharks are poorly investigated and it is difficult to assign isolated spines to a certain species. It is most likely that the spines are from *L. hasleensis*, since it is the most common taxon in the Hasle fauna. Furthermore, the spines are quite small, corresponding to the size of spines from other *Lissodus* species with approximately the same tooth size. The other possibility is that the spines are from juvenile *H. reticulatus*, as small teeth of this species are present in the material. However, the denticles on the posterior side are not situated along a straight line in spines of *H. reticulatus* from Lyme Regis (see Agassiz 1843).

Cohort Neoselachii Compagno, 1977
Order Synechodontiformes Duffin & Ward, 1993
Family Paleospinacidae Regan, 1906
Genus *Synechodus* Woodward, 1888

Type species: *Hybodus dubrisiensis* Mackie, 1863 from the Cenomanian, Late Cretaceous of England.

Synechodus occultidens Duffin & Ward, 1993

Fig. 5C, D.

Palaeospinax priscus (Agassiz, 1843); Thies 1983: p.12–14, text fig. 4a.

Synechodus occultidens sp. nov.; Duffin & Ward 1993: p. 72–77, pl. 8a, 9, 10b, 11, 12, text fig 10.

Material. — Four incomplete teeth lacking two or more of the lateral cusplets, LO 7964t and unnumbered.

Description. — The teeth are small with a high and slender cusp. The most complete one measures 2.1 mm in height and 2.0 mm in width. There are two minute lateral cusplets preserved. They are closely spaced, but well separated from the cusp. The cusp is oval in cross section and inclined lingually. The cutting edges on the cusp are poorly developed, but continuous. On the lingual side there are weak vertical folds close to the root. The surface is smooth on the labial side. The lingual side is slightly convex. There is a strong overhang of the root by the crown at the labial crown-root junction. The root extends lingually more than the crown.

Discussion. — Duffin & Ward (1993) mentioned that the two species *Synechodus occultidens* and *S. enniskilleni*, described by them, may in fact be one and the same species and a case of gynandric heterodonty. Until more complete material, showing both dentition and the pelvic region, is found, this hypothesis can not be verified. The teeth from the two species are primarily separated from each other by differences in the development of vertical folds and the height of the lateral cusplets. It seems unlikely that gynandric heterodonty is the case, since, in many deposits, only one dental morphology of *Synechodus* is found, e.g. the Early–Middle Norian of British Columbia (Johns *et al.* 1997) and the Late Campanian of Wyoming (Case 1987). It is usually not the amount of ornamentation that separates the male and female dentitions in extant selachians with gynandric heterodonty. Both *S. occultidens* and *S. enniskilleni* are known from more or less complete dentitions from Lyme Regis (Duffin & Ward 1993). The size of the teeth in this study is approximately the same as in the English material, indicating a body length of some 30 to 40 cm.

Genus *Paraorthacodus* Glikman, 1957

Type species: *Sphenodus recurvus* Trautschold, 1877 from the Cenomanian, Late Cretaceous of the Volga area, Russia.

Paraorthacodus sp.

Fig. 5A–B, E–F.

Material. — Two incomplete teeth, LO 7965t and LO 7966t.

Description. — The material comprises one anterior and one lateral tooth. The cusp of the anterior tooth is tall, measuring 3.4 mm in height, and have prominent cutting edges. There are weak, but dense, vertical folds ascending from the crown base and reaching one third of the height of the cusp on the lingual side. On the labial side, they cover only a small portion of the crown, close to the root. The lateral tooth has three of lateral cusplets on the proximal side, the tallest one reaches half the height of the moderately high cusp. Relatively strong vertical folds ascend from the base of the crown to its apex. The cutting edges are also strong. The labial side is almost flat while the lingual side is markedly convex in both teeth. The crown and the root are flushed in the same plane labially. Only a small portion of the root, lacking diagnostic features, is preserved on each tooth.

Discussion. — These early Pliensbachian teeth resemble teeth of *P. kruckowi* (Thies, 1983) from the Aalenian of Germany, previously the oldest record of the genus. However, the proximal pair of lateral cusplets appears to be situated further away from the cusp in *P. kruckowi*. The material from Hasle is not sufficiently well preserved to make a certain determination.

Incertae ordinis

Discussion. — Duffin & Ward (1983) assigned *Agaleus* to the order Orectolobiformes Applegate, 1972, a view shared by Cappetta (1987). This assignment is questionable. The teeth of *Agaleus dorsetensis* are much larger than those of any other Jurassic orectolobiform. The Jurassic record of typical orectolobiforms

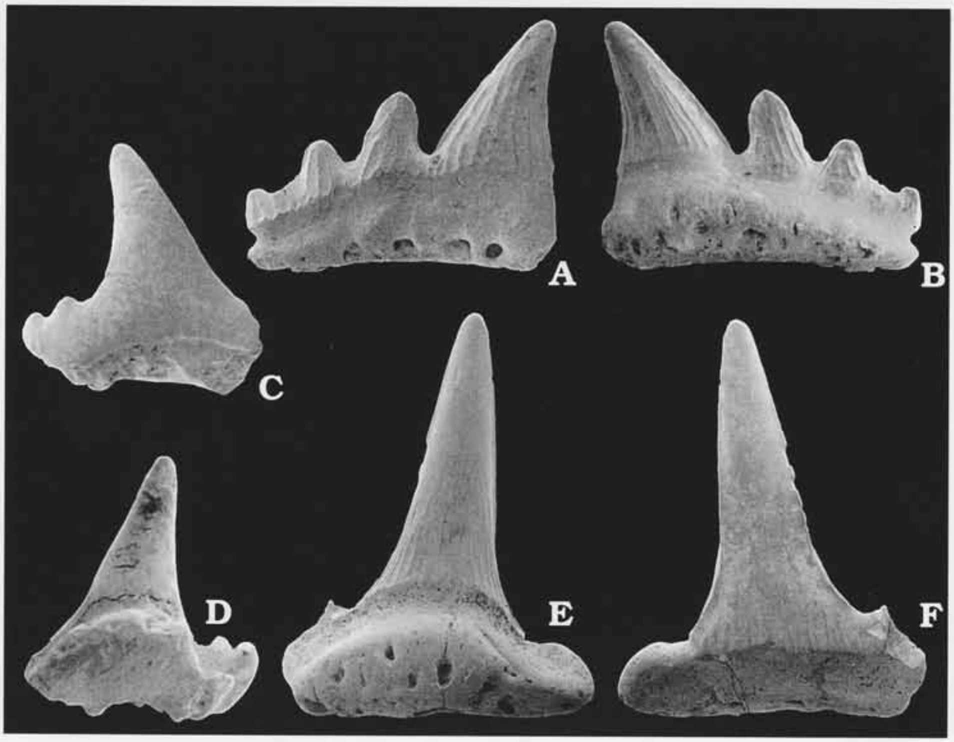

Fig. 5. Palaeospinacid sharks teeth, SEM micrographs. **A**, **B**. *Paraorthacodus* sp. × 15. LO 7965t, in labial (**A**) and lingual (**B**) views. **C**, **D**. *Synechodus occultidens* Duffin & Ward, 1993 × 15. LO 7964t in labial (**C**) and lingual (**D**) views. **E**, **F**. *Paraorthacodus* sp. × 11. LO 7966t, in lingual (**E**) and labial (**F**) views.

comprises only small-toothed species with teeth rarely exceeding 2 mm in height. Teeth of orectolobiform sharks have been found in Toarcian, Aalenian, Callovian and Tithonian deposits (Cappetta 1987; Cappetta *et al.* 1993). It seems somewhat unlikely that the oldest known member of the group would be so much larger than its Jurassic descendants. The teeth of *Agaleus* are also quite specialised with an apparently advanced root morphology, including a labial root buttress. Later orectolobiform sharks lack some of the unique features in *Agaleus*, like the longitudinal ridge on the base of the crown. Teeth of *Agaleus* lack a lingual uvula, a feature present on teeth of typical Jurassic orectolobiforms.

Incertae familiae

Genus *Agaleus* Duffin & Ward, 1983

Type species: *Agaleus dorsetensis* Duffin & Ward, 1983 from the Sinemurian, Early Jurassic of Lyme Regis, England.

Agaleus dorsetensis Duffin & Ward, 1983

Fig. 6A–F.

Otodus? sp.; Malling & Grönwall 1909: p. 295.

Agaleus dorsetensis sp. nov.; Duffin & Ward 1983: pp. 840–844, text-figs 1, 3.

Material. — Four teeth (LO 7967t, the others unnumbered) and fragments.

Description. — The teeth of this species are characterised by their large, and strongly lingually curved, cusp. It is flanked by one pair of slightly less inclined lateral cusplets. The length from the

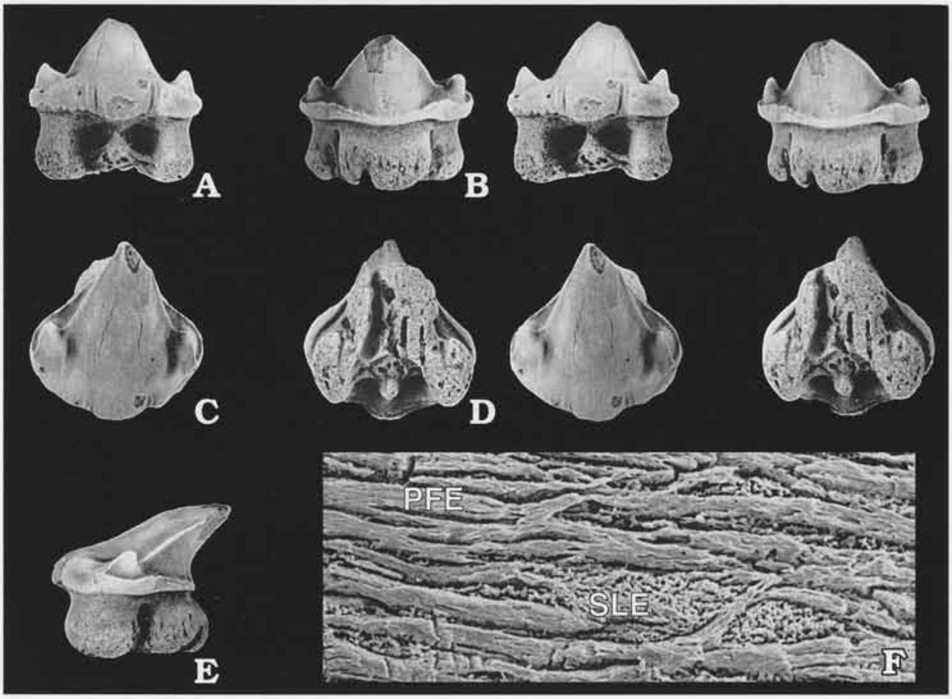

Fig. 6. *Agaleus dorsetensis* Duffin & Ward, 1983. **A**–**E**. LO 7967t in labial (**A**), lingual (**B**), occlusal (**C**), basal (**D**) views (stereo pairs) and in lateral view (**E**); × 3. **F**. SEM micrograph showing the ultrastructure including shiny layered enameloid (SLE) and parallel fibred enameloid (PFE) × 500.

apex of the cusp to the labial base of the crown is 7 to 10 mm. The cutting edges are prominent on the cusp and weaker on the lateral cusplets. Both the cusp and the lateral cusplets have a conical shape. The lateral cusplets are well separated from the cusp but the cutting edges are connecting them. On one specimen there are a few weak vertical folds on the lower labial part of the crown, on the other specimens the crown surface is smooth. There is a longitudinal ridge near the base of the crown and the crown overhangs the root on all sides. The overhang is extended on the middle part of the labial side, forming a small basal flange. The root is as high as the crown, and has hemiaulacorhize vascularization. The basal face of the root has a V-shape. There is a root buttress on the labial side beneath the basal flange. Large specialised foramina are present on the sides of the root buttress and on the flanks of the root in lingual view. The basal half of the root is penetrated by numerous small irregular foramina.

Ultrastructure. — The ultrastructure of the teeth of this species has not previously been investigated. There is an outer layer of shiny layered enameloid (SLE on Fig. 6 F) and one layer of parallel fibred enameloid (PFE on Fig. 6 F). Whether there is an inner layer of randomly fibred enameloid or not remains to be determined.

Comparisons with other Early Jurassic selachian faunas

Shark faunas from the Pliensbachian stage are poorly known. To the best of my knowledge, the Hasle fauna is the only one recorded of this age. The Sinemurian, on the other hand, has yielded shark faunas from a few localities in north-western Europe. The well known deposits at Lyme Regis in southern England have yielded ten species of selachians (Duffin & Ward 1983; Duffin 1993). Seven of these are hybodonts, including two species of *Acrodus* and five species of *Hybodus*. The five nominal *Hybodus*-species have not been sufficiently investigated and there may be synonyms among them. The remaining three species are neoselachians, including *Synechodus enniskilleni, S. occultidens* and *Agaleus dorsetensis*. The lack of small-toothed hybodonts in the Lyme Regis fauna is possibly artifactual, due to the nature of the sediment, which makes processing of bulk samples difficult. The remains of the small-toothed palaeospinacids have all been found associated at Lyme Regis. Two hybodont taxa from Lyme Regis, *Hybodus reticulatus* and *H. delabechei*, are present in the fauna from Hasle, as well as two neoselachians, *Synechodus occultidens* and *Agaleus dorsetensis*. Delsate & Duffin (1993) described a Sinemurian shark fauna from southern Belgium, including seven species, of which four are hybodonts and three are neoselachians. Two species of this fauna are also present in the Hasle fauna: *H. reticulatus* and *S. occultidens*. Casier (1959) described shark teeth of early Sinemurian age from localities near Virton, Belgium. Due to the scarcity of material and the collecting techniques employed, only three species, all large hybodonts, *H. delabechei*, *Acrodus nobilis* and *A. undulatus*, were found. Only one of these, *H. delabechei*, was also recognised in the Hasle fauna.

Palaeoecology

The teeth of *H. delabechei* suggest that it may have been feeding on shelly invertebrates to a larger extent than *H. reticulatus*, which has a more pronounced tearing-type dentition. The latter suggests a fish diet. Martill (1991) proposed that *Hybodus* was a scavenger, based on the fact that isolated crowns are often found associated with remains of marine reptiles. This is a reasonable explanation for at least some species of *Hybodus*, since many extant sharks consume carrion as part of their diet (Compagno 1984). The other hybodont in this study, *Lissodus hasleensis*, was a smaller, and most likely bottom-dwelling shark with a diet most probably consisting of molluscs, arthropods and echinoderms. There are striking similarities in the dentition between *L. hasleensis* and the Recent Port Jackson shark, *Heterodontus portusjacksoni* (Meyer, 1793). In the latter, there are enlarged lateral crushing teeth. Port Jackson sharks feed primarily on benthic invertebrates, of which sea urchins is the favourite food source. Crustaceans, molluscs and polychaetes are also part of their diet (Compagno 1984). It is likely that several teeth in each of the anterior files of *L. hasleensis* were in use at the same time both to catch and hold the prey, a common feature in clutching type dentitions. The slender anterior teeth of the palaeospinacids indicate that they preyed, to a larger extent, on smaller fish and invertebrates without shells. *Agaleus dorsetensis* may possibly have been a suction feeder as its anterior teeth are similar to those of extant nurse sharks of the family Ginglymostomatidae Gill 1862, which are suction feeders with a diet of various benthic invertebrates.

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Wczesnojurajskie żarłacze z formacji Hasle na Bornholmie (Dania)

JAN REES

Streszczenie

Opisano faunę żarłaczy z odsłonięć formacji Hasle (wczesny pliensbach – piętra *Uptonia jamesoni* do *Prodactylioceras davoei*) na wyspie Bornholm. Hybodontoidea reprezentowane są przez *Hybodus reticulatus, H. delabechei* i *Lissodus hasleensis* sp. n., a Neoselachii przez dwa gatunki z rodziny Palaeospinacidae: *Synechodus occultidens* i *Paraorthacodus* sp., oraz *Agaleus dorsetensis*, domniemanego przedstawiciela brodatokształtnych (Orectolobiformes).

Nowy hybodont *Lissodus hasleensis* był niewielkim, zapewne przydennym rekinem. Typem heterodoncji przypomina współczesnego rogatka australijskiego (*Heterodontus portusjacksoni*), żywiącego się głównie bentonicznymi bezkręgowcami, zwłaszcza jeżowcami.

Ultrastruktura enameloidu zębów *A. dorsetensis* okazała się być co najmniej dwuwarstwowa, co potwierdza przynależność do Neoselachii, na którą wskazywała morfologia zębów. Wątpliwe jest jednak zaliczanie *Agaleus* do rzędu Orectolobiformes. Typowe brodatokształtne znane są z jury na podstawie zębów rzadko przekraczających 2 mm wysokości, tymczasem u *Agaleus* mogą one dochodzić do 8 mm. Wydaje się mało prawdopodobne, by najstarszy przedstawiciel grupy był aż o tyle większy od swych jurajskich potomków. Zęby *Agaleus* mają też cechy swoiste, np. zgrubienie na podstawie po stronie wargowej oraż podłużny grzebień u nasady korony, których brak u typowych jurajskich brodatokształtnych. Brak natomiast u *Agaleus* typowego dla nich „języczka" po stronie językowej.

Rozszerzeniu ulegają zasięgi paleogeograficzne i stratygraficzne wcześniej opisywanych gatunków. Fauny żarłaczowe z pliensbachu są dotąd słabo rozpoznane i gatunki opisane z formacji Hasle znane były dotychczas z osadów synemurskich innych terenów.