

A new Pliensbachian (Early Jurassic) neoselachian shark fauna from southern Sweden

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Hettangian to Pliensbachian neoselachian tooth assemblages from marine deposits in northwest Europe are dominated by palaeospinacids. In the Toarcian, elasmobranch faunas tend to be more diverse and several other neoselachian groups have their first occurrence. A small, but surprisingly diverse, neoselachian tooth assemblage, comprising seven taxa, has been extracted from Pliensbachian sediments within the Rya Formation in southern Sweden. The fauna includes five synechodontiform species; *Synechodus occultidens*, *S. enniskilleni*, '*Synechodus*' sp., *Paraorthacodus* sp., and *Sphenodus* sp. The remaining two species include Hexanchidae indet. and *Agaleus dorsetensis*. The exclusively Early Jurassic *A. dorsetensis* is separated from all other neoselachians on the basis of tooth morphology and is here included in the new, monotypic family Agaleidae nov. The assemblage from the Rya Formation is the first selachian fauna to be recorded from the Jurassic of Sweden and it has a composition quite different from contemporary faunas found in other areas of Europe. The neoselachian part of the fauna is more diverse while hybodont sharks are represented solely by a single species.

Key words: Neoselachians, Pliensbachian, Early Jurassic, Rya Formation, Scania, Sweden.

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Introduction

In the Early Jurassic, neoselachian diversity was quite low in northwest Europe, particularly in pre-Toarcian times. Only two groups, the galeomorph *Agaleus* Duffin & Ward, 1983 and members of the family Palaeospinacidae Regan, 1906, occur frequently in Sinemurian and Pliensbachian sediments. Palaeospinacids were already established in the Middle Triassic (Johns *et al.* 1997) and they became extinct in the late Paleocene (Cappetta *et al.* 1993). The genus *Synechodus* Woodward, 1888, is fairly common in the Early Jurassic and known from both articulated dentitions (Duffin

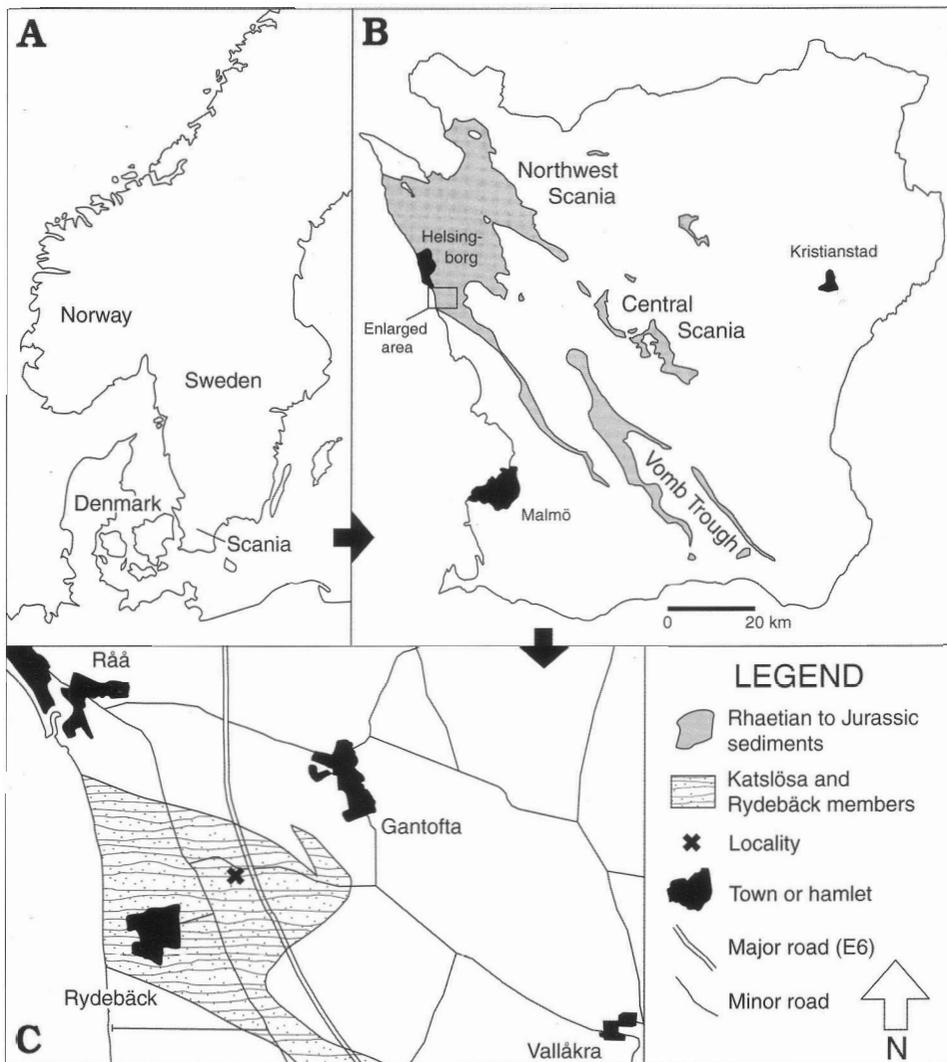


Fig. 1. Map showing the location of Scania in Scandinavia (A) and the extension of Rhaetian to Jurassic strata as surface bedrock in Scania (B) based on map Ba 43 from the Swedish Geological Survey. Detail map (C) shows the extension of the Katslösa and Rydebäck members as surface bedrock in the area (based on map Af 149 from the Swedish Geological Survey) and the shark yielding locality.

1987; Thies 1992; Duffin & Ward 1993) and isolated teeth (Thies 1983; Delsate & Duffin 1993; Rees 1998). Remains of the other palaeospinacid genus, *Paraorthacodus* Glikman, 1957, are less frequently found in Early Jurassic sediments, but isolated teeth have been recorded (Biddle 1993; Rees 1998). Palaeospinacids were spread over large parts of Europe in the Early Jurassic and their remains have been found in England (Duffin & Ward 1993), Denmark (Rees 1998), Belgium (Delsate & Duffin 1993), France (Lamaud 1979; Biddle 1993) and Italy (Duffin 1987). The previous records show that these sharks were a frequent element in Early Jurassic shark faunas, while

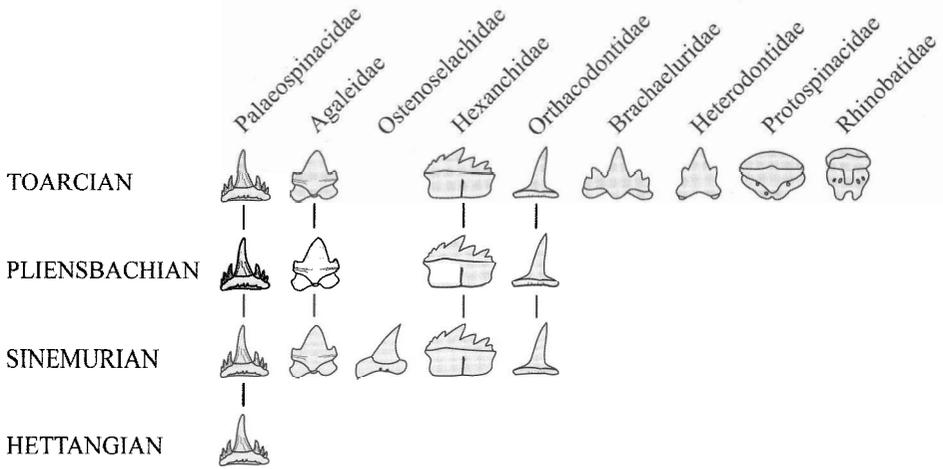


Fig. 2. Stratigraphical distribution of neoselachian families in the Early Jurassic.

the present work reveals that their diversity was quite high as early as the Pliensbachian. The other synechodontiform family, the Orthacodontidae de Beaumont, 1960, including only the genus *Sphenodus* Agassiz, 1843 (see Cappetta 1987), first appears in the Sinemurian (de Beaumont 1960). This record, from Switzerland, was previously the only pre-Toarcian occurrence of the genus.

Agaleus dorsetensis Duffin & Ward, 1983 is seemingly an exclusively Early Jurassic neoselachian, ranging from the Sinemurian to the Toarcian. So far, it is known only from isolated teeth, found in England (Duffin & Ward 1983), Denmark (Rees 1998), Belgium (Delsate & Duffin 1993) and France (Lamaud 1979; Biddle 1993). Originally, *Agaleus* was included in the Orectolobiformes (Duffin & Ward 1983) but the teeth display unique characters not present in unquestionable orectolobiforms (Rees 1998). In this work, *Agaleus* is included in the new monotypic family Agaleidae (see below).

An enigmatic neoselachian, *Osteoselache stenosoma* Duffin, 1998, is known from the Sinemurian of northern Italy. This shark is included in the monotypic family Osteoselachidae Duffin, 1998. Although this species is known from several complete specimens, the teeth are poorly known (Duffin 1998). *Osteoselache stenosoma* has no known relatives, extinct or living.

The earliest known member of the family Hexanchidae Gray, 1851 is *Hexanchus arzoensis* (de Beaumont, 1960), occurring in the Sinemurian of Switzerland. The only other pre-Toarcian hexanchid, *Hexanchus? wiedenrothi* Thies, 1983, was reported from the Pliensbachian of northern Germany.

Toarcian neoselachians are much more investigated, particularly from continental Europe, and the faunas include first occurrences of several modern groups (Fig. 2). The families Heterodontidae Gray, 1851, Brachaeluridae Applegate, 1972 and Rhinobatidae Müller & Henle, 1838 all have their first appearances in Toarcian strata (Cappetta *et al.* 1993), as well as the orectolobiform *Annea* Thies, 1983 (Delsate & Thies 1995). Two other taxa with unknown higher relationships are also present in the Toarcian, the Protospinacidae Woodward, 1919 (Delsate *et al.* 1989) and the galeomorph *Jurobatus* Thies, 1983 (Thies 1993a).

Geology and stratigraphy

Rhaetian to Early Jurassic sediments in southern Sweden are found in three areas, northwest Scania, the Vomb Trough and central Scania (Fig. 1). The most complete succession of strata is present in northwest Scania. Here, Rhaetian and Early Jurassic sediments have been studied for a long time, both in natural outcrops and quarries, and the stratigraphy is well understood. The Höganäs Formation comprises Rhaetian to Hettangian strata while Sinemurian to Toarcian sediments are included in the Rya Formation (Norling in Bergström *et al.* 1982). The sediments of the Rya Formation are primarily of marine origin. In southern Sweden, the Early Sinemurian is characterised by the deposition of transgressive strata due to the Tethyan transgression (Norling & Bergström 1987). There was a brief period of continental deposition in the late Sinemurian, as indicated by a coalseam and a rootlet bed (Norling *et al.* 1993). After this interruption, marine sedimentation was resumed (Guy-Ohlson & Norling 1994) and continued throughout most of the Early Jurassic (Norling *et al.* 1993). The Rya Formation is divided into the Döshult, Pankarp, Katslösa and Rydebäck members. Clay, silt and sand of the Katslösa member and the Early Jurassic part of the Rydebäck member were primarily deposited in quiet marine environments below the wave base (Norling *et al.* 1993). Sediments of the two members are highly fossiliferous (Troedsson 1951; Norling *et al.* 1993). The Katslösa member have been dated to include parts of the latest Sinemurian *Echioreras raricostatum* zone and the early Pliensbachian *Uptonia jamesoni*, *Tragophylloceras ibex* and *Prodactylioceras davoei* zones (Norling *et al.* 1993). A large section of the Katslösa member was studied by Troedsson (1951), but since no bulk samples were collected and processed, only a few shark teeth were recorded. The teeth are poorly preserved and they probably belong to hybodont sharks. The Rydebäck member ranges from the late Pliensbachian *Amaltheus margaritatus* zone well into the Aalenian (Norling *et al.* 1993). Towards the end of the Early Jurassic, there is a regressional tendency within the member.

The temporary exposure yielding the material dealt with herein, was created during construction of a railroad bridge above the road between the hamlets of Rya and Katslösa in northwestern Scania (Fig. 1). It is located at 55° 58' 32'' N, 12° 47' 36'' E and the coordinates of the Swedish National Grid are 620935 131145. Unfortunately, Jurassic strata are no longer accessible here since the constructions are completed. The section comprised poorly lithified, dark grey silts and claystones. Within the sediments, there are minor concentrations of shell debris and the occasional coal lens. No sedimentary structures have been preserved as the sediments are completely bioturbated. Fish remains include, apart from neoselachians, teeth of the hybodont shark *Hybodus reticulatus* Agassiz, 1837, fragmentary chimeroid remains and teeth and scales of actinopterygians. No age-diagnostic ammonites were found, but the well preserved foraminiferal fauna indicates late Pliensbachian age, corresponding to the ammonite zones of *Amaltheus margaritatus* and *Pleuroceras spinatum*, although some foraminifera would correspond to the *Prodactylioceras davoei* zone (Norling personal communication). It is possible that the bulk samples include sediments from more than one ammonite zone. Other fossils found include frequent belemnites, gastropods, bivalves, echinoderms and ostracods.

Material and methods

Bulk samples of sediment were collected in November 1997 during construction of the railroad bridge. Sampling was focused on the shell debris concentrations and 171 kg of these were collected. In addition, the samples included 388 kg of the less fossiliferous silt and clay. The material was dried and washed in a clay washing machine built in accordance with Ward (1981). The remaining material, primarily poorly lithified siltstones, was frozen in several cycles and the residues picked to the 355 µm fraction. Shell debris was dissolved in buffered acetic acid. Neoselachian teeth are rare and usually broken, probably due to compaction, since the teeth are not abraded. Some teeth display endolithic bioerosion. This type of damage is particularly common on smaller specimens.

Photographed specimens were coated with gold and photographed using a SEM. All illustrated specimens are housed in the type collection of the Division of Historical geology and Palaeontology at Lund University, Sweden, abbreviated LO, except HU0-CRL-30, kept at the Centre de Recherches Lorraines in Ethe, Belgium.

Faunal discussion

Apart from a few teeth of the hybodont *Hybodus reticulatus*, the shark fauna from the Rya Formation is exclusively neoselachian. Other Sinemurian and Pliensbachian faunas in Europe have a different composition where larger hybodonts constitute a significant part of the fauna. Two genera of large hybodonts, *Hybodus* Agassiz, 1837 and *Acrodus* Agassiz, 1837, are particularly common in the Sinemurian fauna of Lyme Regis, southern England. A total of seven nominal species of these two genera are present, although there may be synonyms among them. Sinemurian faunas from Belgium (Casier 1959; Delsate & Duffin 1993) also include teeth of *Acrodus* and there is a single record from the Sinemurian of the Vomb Trough (Fig. 1) in Sweden (Moberg 1888). However, this genus appears to have become extinct by the Pliensbachian as it is lacking in Denmark (Rees 1998), France (Biddle 1993), Belgium (Delsate personal communication) and Sweden (herein). Alleged later Jurassic and Cretaceous species of *Acrodus* (e.g. 'A.' *dolloi* Leriche, 1911, 'A.' *levis* Woodward, 1887 and 'A.' *leiodus* Woodward, 1887) all belong to other genera. The synechodontiform Rya Formation assemblage, including five taxa, is the most diverse assemblage ever found. It is possible that the synechodontiforms in the Early Jurassic flourished in the near absence of other neoselachians. In the Lyme Regis fauna, neoselachians are rare. Only three species are found, two *Synechodus*-species and *Agaleus dorsetensis*, where the former two are known solely from articulated specimens. This is a sampling artefact as the Lyme Regis sediments are unsuitable for bulk sampling. Sinemurian and Pliensbachian tooth assemblages obtained by bulk sampling usually include one or two synechodontiform species and often *A. dorsetensis* (Delsate & Duffin 1993; Biddle 1993; Rees 1998). The Rya Formation fauna is the first Swedish shark fauna to be described from the Jurassic. Previously, only scattered remains have been found (e.g., Moberg 1888; Troedsson 1951), due to the fact that no bulk sampling have been undertaken. This is the northernmost locality for all the species found.

Systematic palaeontology

Systematics and descriptive tooth terminology largely follow that of Cappetta (1987), while descriptive terms for the placoid scales are from Duffin & Ward (1993).

Subcohort Neoselachii Compagno, 1977

Order Hexanchiformes Buen, 1926

Family Hexanchidae Gray, 1851

Hexanchidae indet.

Fig. 3A–C.

Material.— A single incomplete tooth, LO8252t.

Description.— The specimen consists of the mesial part of a tooth. The acrocone is slender and not curved. On the mesial cutting edge, there are only small irregularities, no serrations or cusplets are present. The root is higher than the acrocone, and labio-lingually flattened. On the lingual side of the root, there is a large number of small foramina, primarily on the basal part.

Discussion.— As stated above, Early Jurassic hexanchids are extremely rare. The record comprises a mixture of what appears to be more advanced hexanchids, like *Hexanchus arzoensis* (de Beaumont, 1960), and hexanchids not closely related to modern forms, in particular members of the genus *Welcommia* Cappetta, 1990 (see Delsate & Godefroit 1995), known from the Toarcian. The incomplete tooth from the Swedish Pliensbachian can not be referred to any genus with confidence, although it appears to be close to *Hexanchus*. The thin root is quite different from the markedly thicker root in *Welcommia*.

Incertae ordinis

Family Agaleidae nov.

Type genus: *Agaleus* Duffin & Ward, 1983, known from Sinemurian to Toarcian strata in western and northern Europe (Fig. 5).

Diagnosis.— Anterior teeth (Fig. 4A–D, H–K) are characterised by a large central cusp that is lingually inclined. It is flanked by a single pair of lateral cusplets. The cutting edges are prominent. There is a horizontal ridge on the crown base. The ridge may be lacking labially. The root is high and has a large lingual lobe and two slightly smaller labial lobes. A labial protuberance is present between the two labial lobes. It is situated close to the crown-root junction and is approximately half the height of the whole root. Lateral teeth (Fig. 4E–G) are lower, lacking both a pronounced cusp and lateral cusplets. There is a mesial cutting edge on the crown and the horizontal ridge on the base of the crown is not as distinct as in anterior teeth. The heterodonty pattern is probably disjunct monognathic.

Discussion.— Superficially, the overall tooth morphology of agaleids is similar to that of some orectolobiforms, e. g. members of the Orectolobidae Jordan & Fowler, 1903 and the Brachaeluridae. Teeth of Agaleidae are clearly different though, particularly in the presence of a horizontal ridge at the base of the crown and the combination of a labial root buttress and a high root. The higher relationships of the new family are not clear, but it is most likely a member of the Galeomorpha (Duffin & Ward 1983). The presence of cusplets in anterior teeth in combination with a hemiaulacorhize stage of root vascularisation, is not present outside the Galeomorpha.

Genus *Agaleus* Duffin & Ward, 1983

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

Agaleus dorsetensis Duffin & Ward, 1983

Figs. 3D–G, 4H–K.

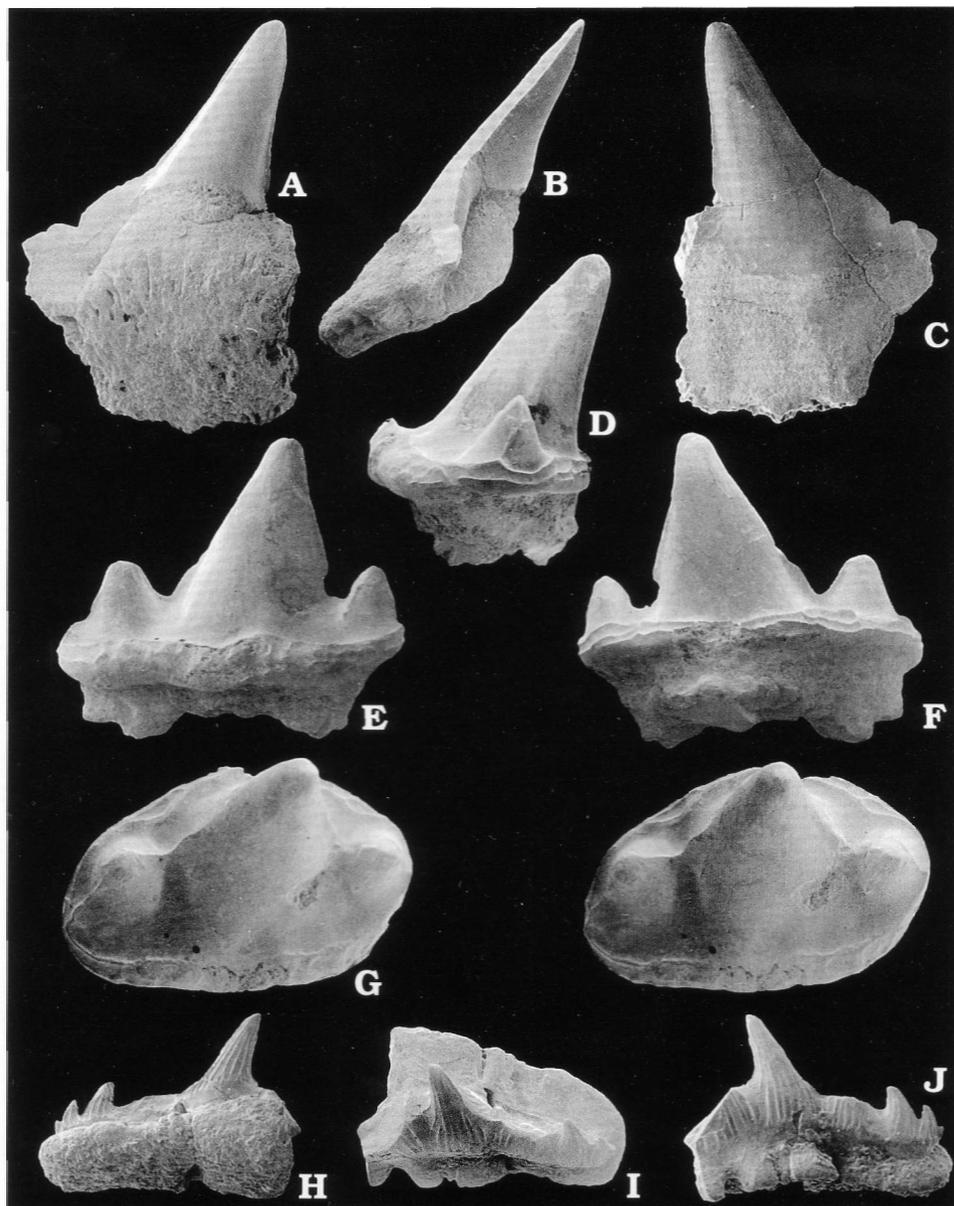


Fig. 3. Hexanchidae indet., *Agaleus dorsetensis* Duffin & Ward, 1983 and *Paraorthacodus* sp., SEM micrographs $\times 9$. A–C. LO8252t, Hexanchidae indet. in lingual (A), mesial (B) and labial (C) views. D–G. LO8253t, *A. dorsetensis* in lateral (D), labial (E), lingual (F) and occlusal (G) views (stereo pair). H–J. LO8258t, *Paraorthacodus* sp. in lingual (H), occlusal (I) and labial (J) views.

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

Ginglymostoma(?) sp.; Lamaud 1979: pp. 121–122, figs. 6–9.

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

Agaleus dorsetensis Duffin & Ward, 1983; Siverson 1991: p. 19.

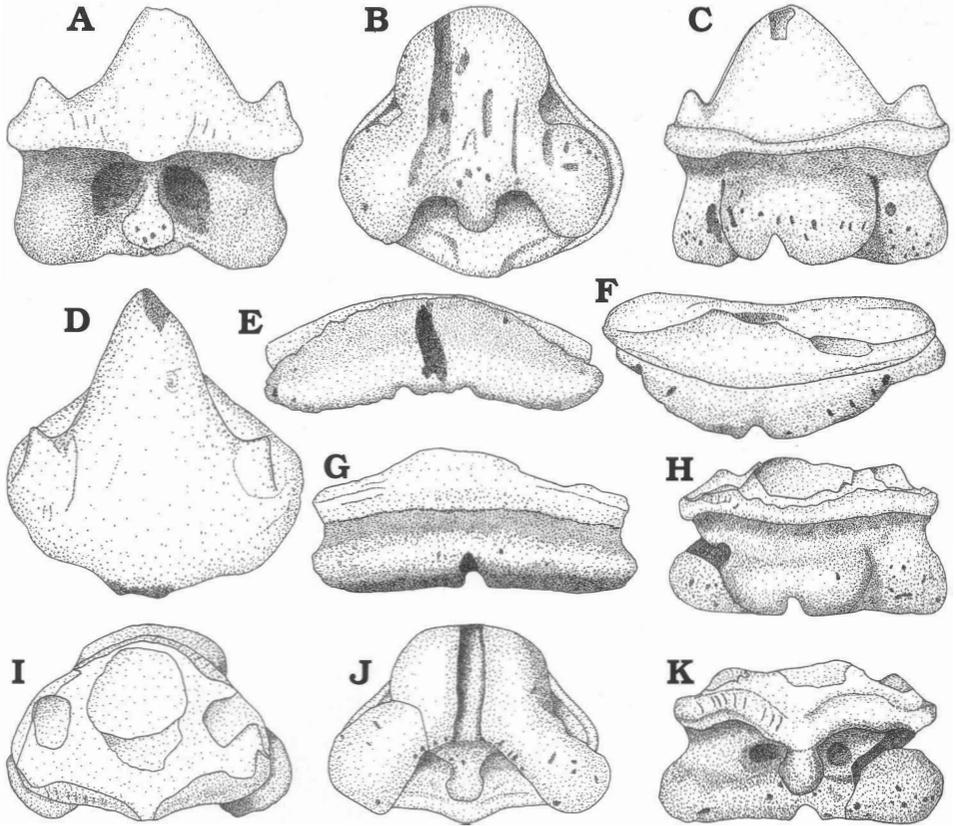


Fig. 4. Teeth of Agaleidae. A–D. *Agaleus dorsetensis* Duffin & Ward, 1983, LO7967t, complete anterior tooth from the Pliensbachian of Bornholm, Denmark in labial (A), basal (B), lingual (C) and occlusal (D) views $\times 4$. E–G. *Agaleus* sp., HU0-CRL-30, complete lateral tooth from the Sinemurian of southern Belgium in basal (E), occlusal (F) and lingual (G) views $\times 12$ (drawn from Delsate & Duffin 1993). H–K. *A. dorsetensis*, LO8254t, broken anterior tooth from the Pliensbachian of southern Sweden in lingual (H), occlusal (I), basal (J) and labial (K) views $\times 4.5$.

Agaleus dorsetensis Duffin & Ward, 1983; Biddle 1993: pp. 62–63, figs. 1–4.

Agaleus dorsetensis Duffin & Ward, 1983; Rees 1998: pp. 448–449, fig. 6.

Material.— Four incomplete teeth, LO8253t, LO8254t and unnumbered.

Description.— These robust teeth have a high central cusp and a single pair of lateral cusplets, all of which are inclined, but not recurved, lingually. On one tooth, there is an accessory cusplet present outside of one of the lateral cusplets. The cutting edges are strong. There is a horizontal ridge on the base of the crown, occasionally ornamented with small vertical folds. A small basal flange may be present on the labial side. Below the crown-root junction, the root is incised. The root (only preserved in one tooth) is characterised by two labial lobes, with a root buttress in between, and a single lingual lobe. The root vascularisation is at the hemiaulacorhize stage and comprises a single groove in the basal part of the root. Two large foramina are present on each side of the labial root buttress. Small foramina are randomly distributed on the lower part of the root.

Discussion.— So far, only one species of *Agaleus* has been described (i.e., *A. dorsetensis*) and most *Agaleus* teeth found have been assigned to it. The heterodonty pattern and intraspecific varia-

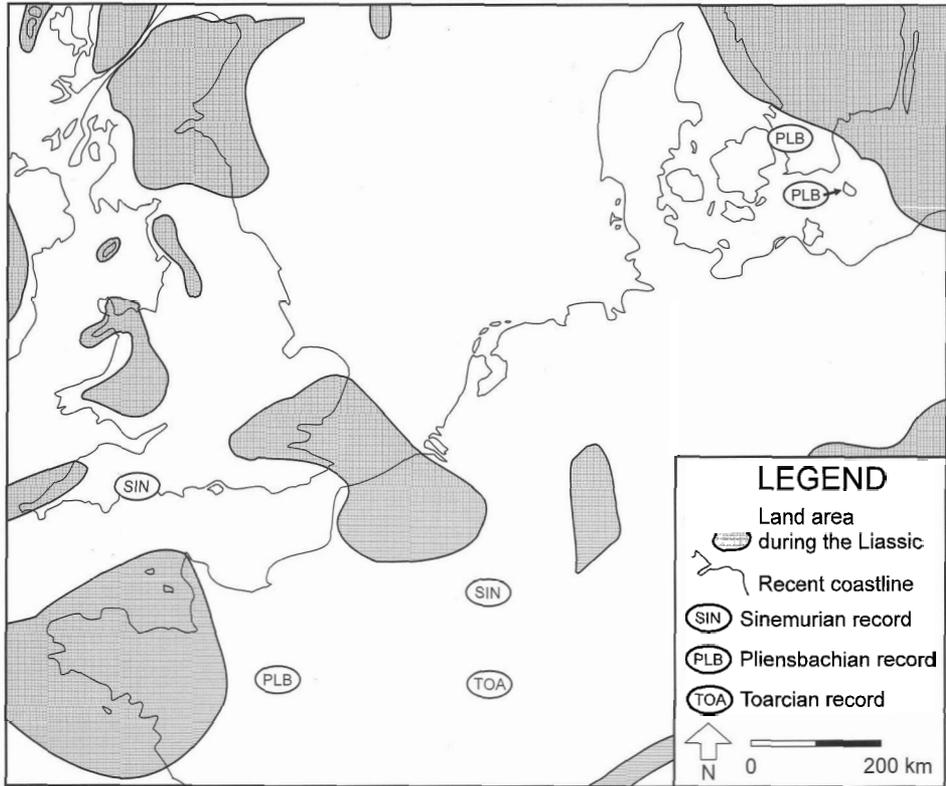


Fig. 5. Palaeogeographical map of northwest Europe with the occurrences of *Agaleus*. Palaeogeography from Ziegler (1990) and data on the *Agaleus* occurrences from Lamaud (1979), Duffin & Ward (1983), Biddle (1993), Delsate & Duffin (1993) and Rees (1998).

tion in *A. dorsetensis* have not been fully understood as isolated teeth are never found in great abundance. The Swedish material provides some information on intraspecific variation. In contrast to the type material from southern England (see Duffin & Ward 1983: text-figs. 1, 3) and the Danish material (Rees 1998: fig. 6), the horizontal ridge on the base of the crown is present on all sides in the Swedish material. Obviously, these teeth lack the basal flange. The ridge is lacking on the labial side in the English and Danish teeth mentioned above, leaving room for the basal flange. Furthermore, the cusp and cusplets are nearly straight in the Swedish material, lingually inclined but not curved as in the type material. The basal groove on the root appears to be more developed in the Swedish material.

Order Synchodontiformes Duffin & Ward, 1993

Family Orthacodontidae de Beaumont, 1960

Genus *Sphenodus* Agassiz, 1843

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

Remarks.— The earliest record of this genus, *S. helveticus*, was described from the Sinemurian of Switzerland by de Beaumont (1960) who based the species on a number of incomplete teeth. As only complete teeth can allow a correct definition of a species of *Sphenodus* (Cappetta 1987), it has been

suggested that the material of *S. helveticus* comprises a mixture of teeth from the two genera *Sphenodus* and *Paraorthacodus* (Cappetta *et al.* 1993). As *Sphenodus* is probably the sister-group of the palaeospinacids (Duffin & Ward 1993), it is likely that early forms would have a morphology approaching that of some early palaeospinacids.

Sphenodus sp.

Fig. 6A–I.

Material.— Two complete teeth, one anterolateral (LO8255t) and one posterior (LO8256t), and four isolated cusps (LO8257t and unnumbered).

Description.— The crown of the anterolateral tooth is smaller than the root and lingually inclined. The labial face of the slender cusp is quite flat and basally ornamented with densely spaced folds. On the strongly convex lingual face, the folds are as densely spaced, but here they reach half the height of the cusp. Although the tooth is slightly worn, it is clear that no lateral cusplets are present. Cutting edges are prominent, particularly on the lower part of the cusp. The crown and the root are flushed in the same plane labially while the root is more extended lingually. The root lacks foramina, apart from four prominent grooves on the basal labial rootface. This tooth measures 5.8 mm in width and 5.0 mm in height. The posterior tooth is very low and has two pairs of low lateral cusplets. The whole crown is lingually inclined. Vertical folds are completely covering the crown. They are quite coarse and rarely bifurcating, only on the lower parts. The root is higher than the crown, and the lower part projects lingually. Two small foramina are present on the central part of the root on the labial side. This posterior tooth measures 3.9 mm in width and 1.7 mm in height. The isolated cusps provide some information on heterodonty. Two cusps are wider at the base, and have a more flattened labial face than the complete anterolateral tooth. A single large cusp indicates that the teeth could be at least twice the size of the complete anterolateral tooth.

Discussion.— A few characters separate these teeth from those of younger species of *Sphenodus*. The vertical folds are more pronounced than in teeth of later species of the genus. The cutting edges and the labio-lingual flattening of the cusp are features less developed on these Pliensbachian teeth compared to younger *Sphenodus*-species. As noted by Thies (1993b), Jurassic species of *Sphenodus* may have a pseudopolyaulacorhize root, although some later species have an anaulacorhize root, e. g. *S. lundgreni* Davis, 1890 from the Danian of Sweden and Denmark. There is a need for a revision of the genus (Duffin & Ward 1993) as some nominal species may be junior synonyms or nomina dubia.

Family Palaeospinacidae Regan, 1906

Genus *Paraorthacodus* Glikman, 1957

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

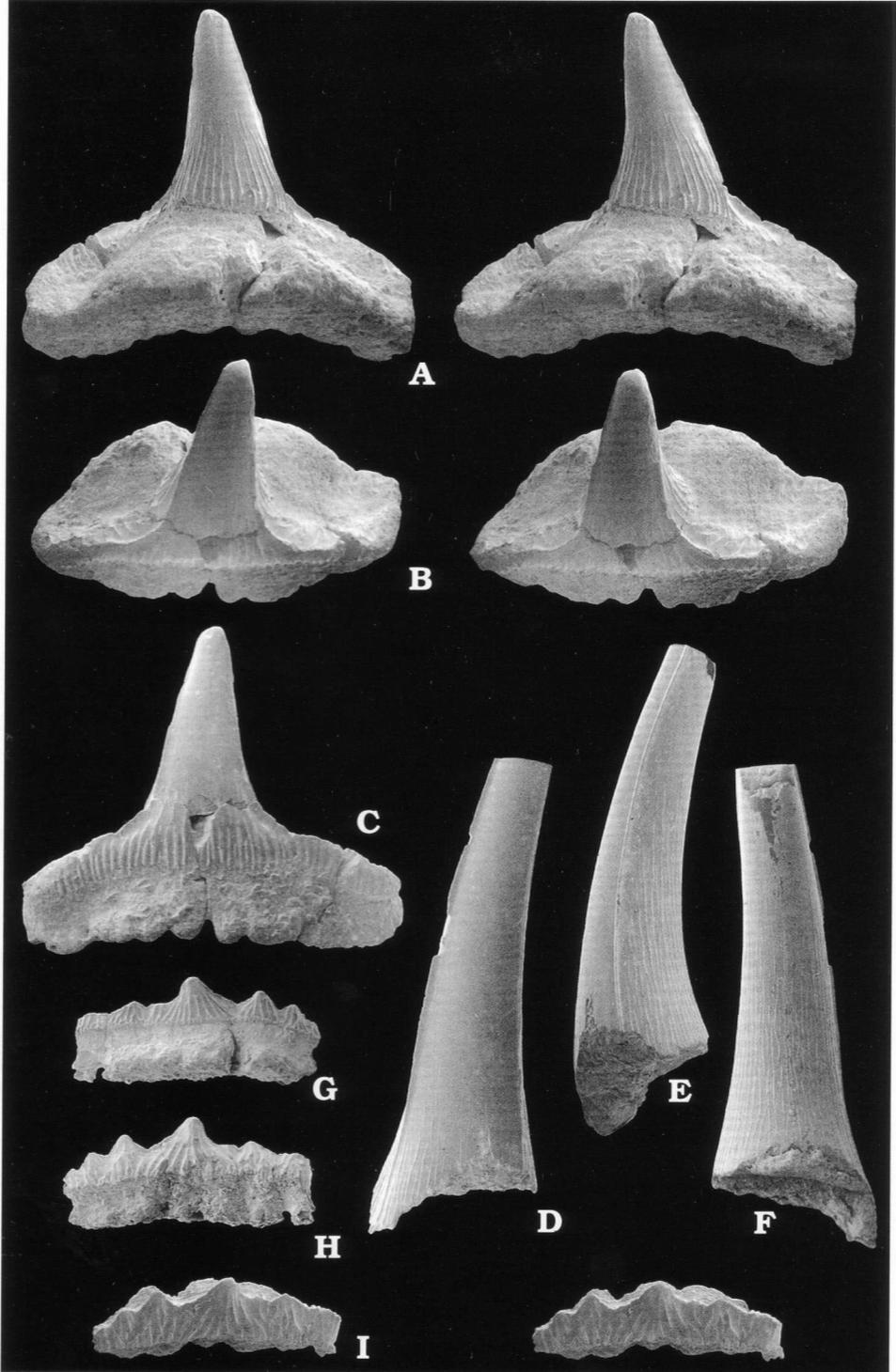
Paraorthacodus sp.

Fig. 3H–J.

Material.— Three broken teeth, LO8258t and unnumbered.

Description.— These broken teeth have up to four lateral cusplets, at least on one side. The most proximal cusplet is high and slender. The crown is almost completely covered with fairly strong vertical folds. The crown-root junction on the labial side is incised and the root projects both labially and lingually, particularly in the latter direction. The root vascularisation is of the pseudopolyaulacorhize

Fig. 6. *Sphenodus* sp., SEM micrographs $\times 9$. A–C. LO8255t, anterolateral tooth in lingual (A) and occlusal (B) view (both stereo pairs) and in labial (C) view. D–F. LO8257t, isolated cusp in labial (D), lateral (E) and lingual (F) views. G–I. LO8256t, posterior tooth in lingual (G), labial (H) and occlusal (I) views (stereo pair).



type with strongly marked grooves on the basal labial side. The largest broken tooth measures 4.2 mm in width.

Discussion.— This is one of the earliest records of this genus. It was previously known from two Pliensbachian sites in France (Biddle 1993) and Denmark (Rees 1998). The size of the broken teeth in this study indicates a larger tooth size than previously recorded in the Pliensbachian.

Genus *Synechodus* Woodward, 1888

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

Remarks.— The nominal *Palaeospinax priscus* (Agassiz, 1843) from the Early Jurassic of Lyme Regis, southern England is based on a specimen comprising only a row of vertebrae and a few scales. As the vertebral column has limited taxonomic value (Maisey 1977) and the scales belong to the placoid morphotype, present in most neoselachians, Duffin & Ward (1993) rightly considered *P. priscus* and consequently also *Palaeospinax* nomina dubia. The latter authors (Duffin & Ward 1993) described two new species from the material previously referred to *P. priscus* and included them in the genus *Synechodus*. Both species, *S. occultidens* and *S. enniskilleni*, were referred to *Synechodus* because of a dentition very similar to that of *S. dubrisiensis* (Mackie, 1863), the type species of *Synechodus*. Maisey (1977) had previously compared the anatomy of 'Palaeospinax' to that of *Synechodus* and concluded that the jaws and dentitions of the two nominal genera are very similar. There is a postcranial difference often noted, both Early Jurassic species possess dorsal fin spines while these are lost in *S. dubrisiensis*. However, the loss of a single primitive character does not validate a separation between the two (Maisey 1985; Duffin & Ward 1993) and nominal species of 'Palaeospinax' is at present best included in *Synechodus* or the other valid palaeospinacid genus, *Paraorthacodus*.

Synechodus occultidens Duffin & Ward, 1993

Fig. 7A–F.

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

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

Synechodus occultidens Duffin & Ward, 1993; Rees 1998: p. 447, fig. 5c, d.

Material.— 15 incomplete teeth, LO8259t, LO8260t, LO8261t and unnumbered.

Description.— The anterior teeth are characterised by the smooth enameloid covering large parts of the crown, particularly on the labial side. The ornamentation consists only of weak folds near the base of the crown, both on the labial and the lingual sides. The folds usually reach higher up on the lingual side. The central cusp is moderately high and wide at the base. At least two pairs of small lateral cusplets are present in anterior teeth. The cutting edges are weak. There is a strong overhang over the root by the crown on the labial side. The root is projected lingually and have, apart from typically palaeospinacid grooves on the basal labial side, a few irregularly placed foramina on the lingual side. The largest anterior tooth in this material measures 3.0 mm in width, even though it lacks lateral cusplets on one side. Anterolateral teeth have a posteriorly inclined cusp but are otherwise similar to anterior teeth. Posterior teeth have a lower crown and are more mesio-distally expanded. They are often ornamented with weak folds covering the entire crown. The cusp is wide at the base and there are three pairs of low cusplets. The root projection in posterior teeth is weaker and the crown overhang is not as pronounced as in the anterior teeth.

Discussion.— On the posterior tooth (Fig. 7A, B), there is a horizontal fold slightly above the crown-root junction on both sides of the tooth. This is most likely the lowest part of the tooth in use, as several teeth in each row formed a crushing surface, like in *S. dubrisiensis* (see Woodward 1889).

Synechodus enniskilleni Duffin & Ward, 1993

Fig. 7G–J.

Palaeospinax priscus (Agassiz, 1843); Maisey 1977: pp. 261–269 (in part), figs. 1a, c, e, 2, 3a–c, pl. 1a.

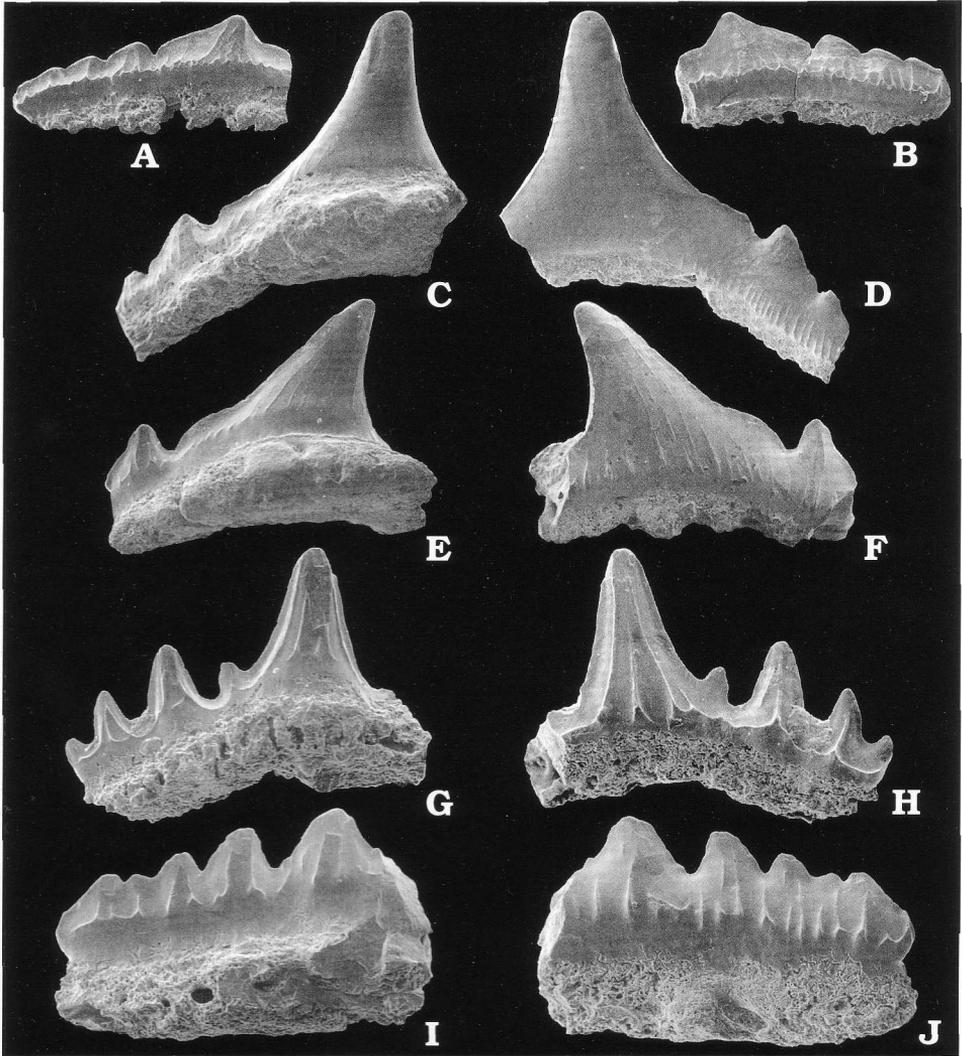


Fig. 7. *Synechodus* teeth, SEM micrographs. A–F. *S. occultidens* Duffin & Ward, 1993. A, B. LO8259t, posterior tooth in lingual (A) and labial (B) views $\times 20$. C, D. LO8260t, anterior tooth in lingual (C) and labial (D) views $\times 14$. E, F. LO8261t, anterolateral tooth in lingual (E) and labial (F) views $\times 20$. G–J. *S. enniskilleni* Duffin & Ward, 1993 $\times 20$. G, H. LO8262t, anterior tooth in lingual (G) and labial (H) views. I, J. LO8263t, lateral tooth in lingual (I) and labial (J) views.

Synechodus enniskilleni sp. nov.; Duffin & Ward 1993: pp. 63–72, pls. 2–7, 8b, 10a, text-figs. 4, 5, 9.
Synechodus enniskilleni Duffin & Ward, 1993; Delsate & Duffin 1993: p. 118, pls. 7: 1, 2, 10: 6.

Material.— Two incomplete teeth, one anterior (LO8262t) and one lateral tooth (LO8263t), both lacking cusplets on one side.

Description.— The anterior teeth have a high cusp and three cusplets on the complete side. The most proximal cusplet reaches half the height of the central cusp while the second and third

cusplets are lower. At the base of the cusp, there is a small accessory cusplet. A few, quite coarse vertical folds cover most of the crown. There is only a slight labial overhang by the crown at the crown-root junction and the root extends lingually more than the crown. The anterior tooth measures 1.2 mm in width. The lateral tooth is lower and the cusplets are more densely spaced. The crown is also slightly labio-lingually compressed. The root is less extended lingually in the lateral tooth and there is no overhang at the crown-root junction. This incomplete tooth also measures 1.2 mm in width.

Discussion.— The teeth described above differs slightly from the teeth of *S. enniskilleni* in the articulated specimens of Lyme Regis, southern England, figured by Maisey (1977: fig. 2) and Duffin & Ward (1993: text-fig. 4). The anterior tooth has three pairs of cusplets compared to two pairs on anterior teeth in the English specimens. The lateral tooth have a slightly higher crown than the posterolateral tooth figured by Duffin & Ward (1993: text-fig. 4c) and the crown is not posteriorly inclined.

'*Synechodus*' sp.

Fig. 8A–D.

Material.— One complete tooth, LO8264t.

Description.— This well preserved tooth is extremely small and measures only 0.7 mm in width and 0.3 mm in height. The low cusp is flanked by two pairs of minute cusplets, which are inclined lingually. The cutting edges are prominent. There is a well developed horizontal ridge slightly above the crown-root junction on both the labial and the lingual side. The root is convex on the lingual side below the incised crown-root junction. Here, a few irregular foramina are present. Below the crown-root junction on the labial side, the root is concave and a number of small foramina open here.

Discussion.— Extremely small palaeospinacid teeth, with a morphology quite different from the type species of *Synechodus*, *S. dubrisiensis*, have previously been described from the Late Triassic of Canada by Johns *et al.* (1997) and denominated *S. incrementum* Johns, Barnes & Orchard, 1997. Although undoubtedly palaeospinacids, these teeth may not belong to *Synechodus* (Cuny & Benton 1999). The tooth described above may represent a new species as it differs from '*S.*' *incrementum* in having a prominent horizontal ridge on the crown and in lacking folds in the enameloid.

Synechodontiform scales

Remarks.— These scales are included in the placoid morphotype *sensu* Reif (1978). Thorough descriptions of synechodontiform scales have been given by Duffin & Ward (1993), in their study of the well-preserved *Synechodus*-remains from the Early Jurassic of Lyme Regis, southern England. Their conclusion was that, although the scale morphology of the two species, *S. occultidens* and *S. enniskilleni*, appear to be distinct from each other, assigning specimens without teeth to a particular species proved impossible. In a study on Kimmeridgian placoid scales from Germany, Thies (1995) assigned the scales to different morphotypes. He was able to correlate some of these morphotypes with different neoselachian genera by comparing with articulated specimens from the Tithonian Solnhofen limestones. More work may result in an extended taxonomic utility, but so far, the systematic position of scales can at best be determined to the generic level. A different approach was used by Johns *et al.* (1997), in their work on Middle and Late Triassic shark remains from Canada. Scales were given form species names using binominal nomenclature and even though it was clearly stated that these were form species names, it may add to taxonomic confusion. Nevertheless, Johns *et al.* (1997) were able to show that placoid scales may be stratigraphically useful, although further studies are needed.

Synechodus? sp.

Fig. 8E–I.

Material.— One complete scale (LO8265t) and three crowns (LO8266t and unnumbered).

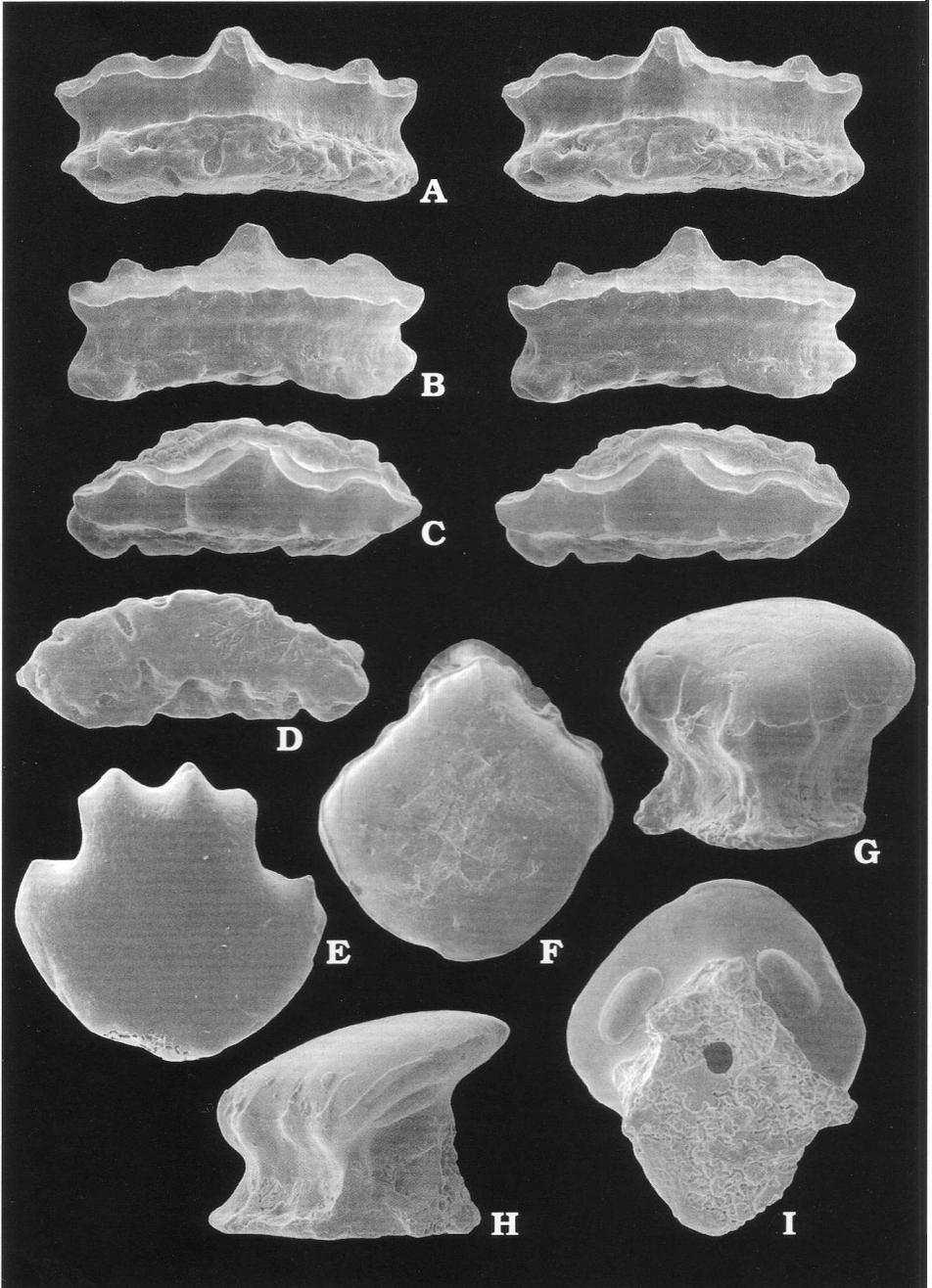


Fig. 8. '*Synechodus*' sp. and synechodontiform scales, SEM micrographs. A–D. '*Synechodus*' sp., LO8264t in lingual (A), labial (B), occlusal (C) views (all stereo pairs) and in basal (D) view $\times 50$. E–I. Synechodontiform scales. E. LO8266t in surface view $\times 60$. F–I. LO8265t in surface (F), anterior (G), lateral (H) and basal (I) views $\times 100$. Note bioerosion.

Description.— The complete scale is composed of a base and a crown of approximately equal size. The neck connecting them is comparably thick. The crown tilts slightly towards the anterior side. Five ridges are present on the anterior edge of the crown and two of them reach towards the apex on the lateral edges. On the crown shoulder, there is a single horizontal ridge. In surface view, the crown lacks ornamentation. On the basal surface of the crown, there are two oval shaped elevations. The base is rhomboid in basal view and a single rounded nutritive foramen is present. One of the broken scales have a more irregular anterior side where large folds form two inward bends one third the distance from the anterior side to the apex.

Discussion.— The complete scale described above most closely resembles scales from *Synechodus pinnai* (Duffin, 1987) from the Sinemurian of northern Italy. All scales figured by Duffin & Ward (1993) from *S. occultidens* and most scales from *S. enniskilleni* possess ridges on the surface of the crown. A few scales from *S. enniskilleni* lack ridges but the surface outline of these scales is not particularly close to the complete scale described above. Placoid scales are currently not possible to assign to any particular species.

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Nowe wczesnojurajskie (pliensbach) zespoły nowożarłaczy z południowej Szwecji

JAN REES

Streszczenie

W pracy omówiono zespoły zębów wczesnojurajskich nowożarłaczy (Neoselachii) z Europy Północnej. W zespołach z osadów morskich najwcześniejszych pięter wczesnej jury (hetang–pliensbach) przeważają paleospinacydy, jednak różnorodność gatunkowa jest niska. W toarku, fauny spoustych różnicują się bardziej, w tym po raz pierwszy pojawiają się rodziny rekinów rogatych (różnozębnych; Heterodontidae), Brachaeluridae i rochowatych (Rhinobatidae).

Z osadów pliensbachu formacji Rya w południowej Szwecji pochodzi mały, lecz zaskakująco zróżnicowany zespół zębów nowożarłaczy, liczący siedem gatunków. Fauna ta obejmuje pięć gatunków synechodontokształtnych: *Synechodus occulti-dens*, *S. enniskilleni*, '*Synechodus*' sp., *Paraorthacodus* sp. and *Sphenodus* sp. Pozostałe dwie formy to *Agaleus dorsetensis* i bliżej nieoznaczony przedstawiciel sześcioszczparowatych (Hexanchidae). Wyłącznie wczesnojurajski *A. dorsetensis* różni się od wszystkich pozostałych nowożarłaczy morfologią zębów, toteż został zaliczony do nowej, jednogatunkowej rodziny Agaleidae. Do cech odróżniających Agaleidae od innych nowożarłaczy należą: poziomy grzbiecik u podstawy korony zęba oraz wysoki korzeń z centralnym zgrubieniem od strony wargowej.

Zespół z formacji Rya jest pierwszą fauną rekinów z jury Szwecji i różni się składem gatunkowym od ówczesnych zespołów z innych regionów Europy. Nowożarłacze z formacji Rya są bardziej różnorodne gatunkowo, zaś hybodonty reprezentuje pojedynczy gatunek *Hybodus reticulatus*. Synemurskie fauny z Anglii i Belgii zawierają natomiast kilka gatunków hybodontów zaliczanych do dwóch rodzajów: *Hybodus* i *Acrodus*, a tylko trzy gatunki nowożarłaczy. *Acrodus* wymarł zapewne przed pliensbachem i nie występuje w żadnej ze znanych faun tego wieku. Zespół synechodontokształtnych z formacji Rya jest najbogatszy z dotąd opisanych. Synechodontokształtne mogły przeżyć rozkwit we wczesnej jurze, gdyż prawie nie było wówczas innych nowożarłaczy.