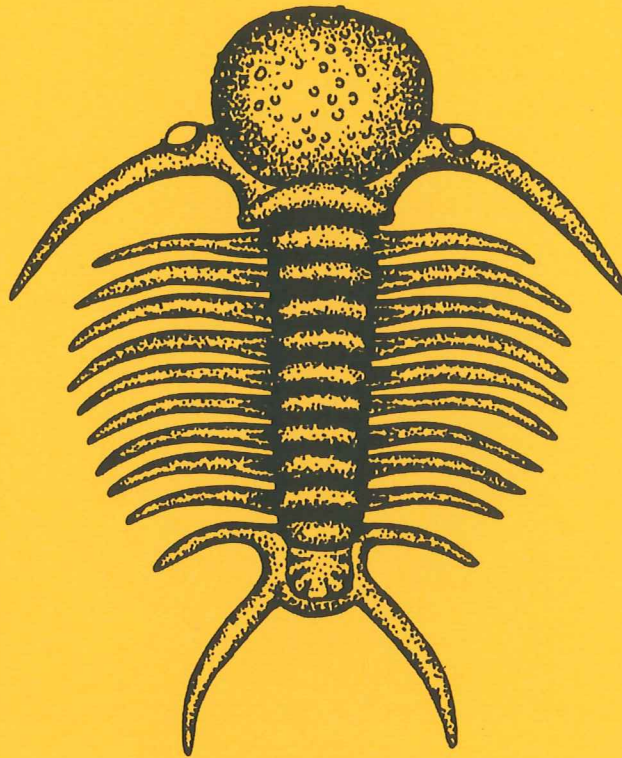


# EXAMENSARBETE I GEOLOGI VID LUNDS UNIVERSITET

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## Historisk geologi och paleontologi

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**A new hybodont shark fauna from the Upper Jurassic  
Vitabäck Clays at Eriksdal, Scania, southern Sweden**

**Jan Rees**

Lunds univ. Geobiblioteket



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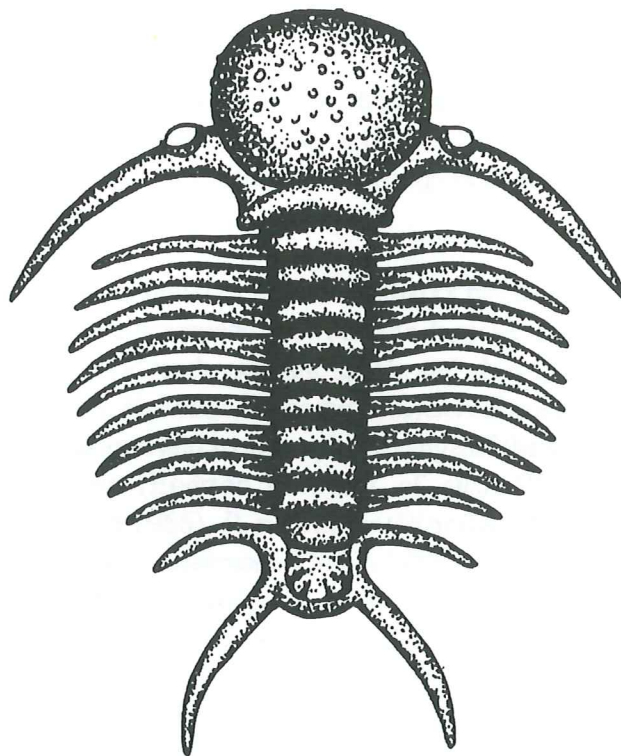
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Geologiska Institutionen, Lunds Universitet

Nr 74

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## A new hybodont shark fauna from the Upper Jurassic Vitabäck Clays at Eriksdal, Scania, southern Sweden

JAN REES

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A previously unknown fauna of hybodont sharks has been revealed from the Vitabäck Clays at the boundary between the Jurassic and Cretaceous. The material consists of oral teeth, cephalic spines and placoid scales from the five genera *Egertonodus*, *Hybodus*, *Lissodus*, *Polyacrodus* and *Hylaeobatis*. The palaeogeographical area and stratigraphical range of the six species found are extended: *E. basanus* (Egerton 1845), *H. cf. ensis* (Woodward 1916), *L. cremulatus* (Patterson 1966), *P. parvidens* (Woodward 1916), *P. heterodon* (Patterson 1966) and *P. pattersoni* (Duffin 1985). *Lissodus heterodon* and *L. pattersoni* are moved to *Polyacrodus* on the basis of tooth morphology and heterodonty. Two different cephalic spines are described and their systematic significance is discussed. Four morphotypes of placoid scales have been found and their affinity is discussed. The fauna is compared to other faunas of the same age and the hybodonts seem to have been repressed by neoselachians in Late Jurassic marine environments.

□ *Hybodontoida*, *Euselachii*, *Egertonodus*, *Hybodus*, *Lissodus*, *Polyacrodus*, *Hylaeobatis*, *oral teeth*, *cephalic spines*, *placoid scales*, *Vitabäck Clays*, *Eriksdal*, *Scania*, *Tithonian*, *Upper Jurassic*.

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Hybodont sharks are members of the superfamily Hybodontoidae, an extinct group of euselachians. They are characterized by calcified neurapophyses, haemapophyses and ribs (Cappetta 1987); their vertebrae are consequently cartilaginous. Dorsal fins are large with one fin spine each (Brough 1935). The spines can be ornamented with ribs, canals or denticles. Cephalic spines also seem to be characteristic and Maisey (1982) considered this feature to be the most reliable way to identify a hybodont.

Hybodont sharks are mainly present in the Mesozoic, where they dominated the shark

fauna completely. They could originate, however, as far back as the Mid Devonian (Zangerl 1981), but the fossil record of Palaeozoic hybodonts is so fragmental that it is not even possible to group them in families. Zangerl (1981) proposed that they are a sister-group of the ctenacanth, but he also considered the possibility that they have evolved from the ctenacanth one or several times, the evolutionary origin remains obscure. The earliest complete skeleton that shows clear hybodont relation is *Hamiltonichthys mapesi* Maisey and comes from the Upper Carboniferous of Kansas (Maisey 1989).

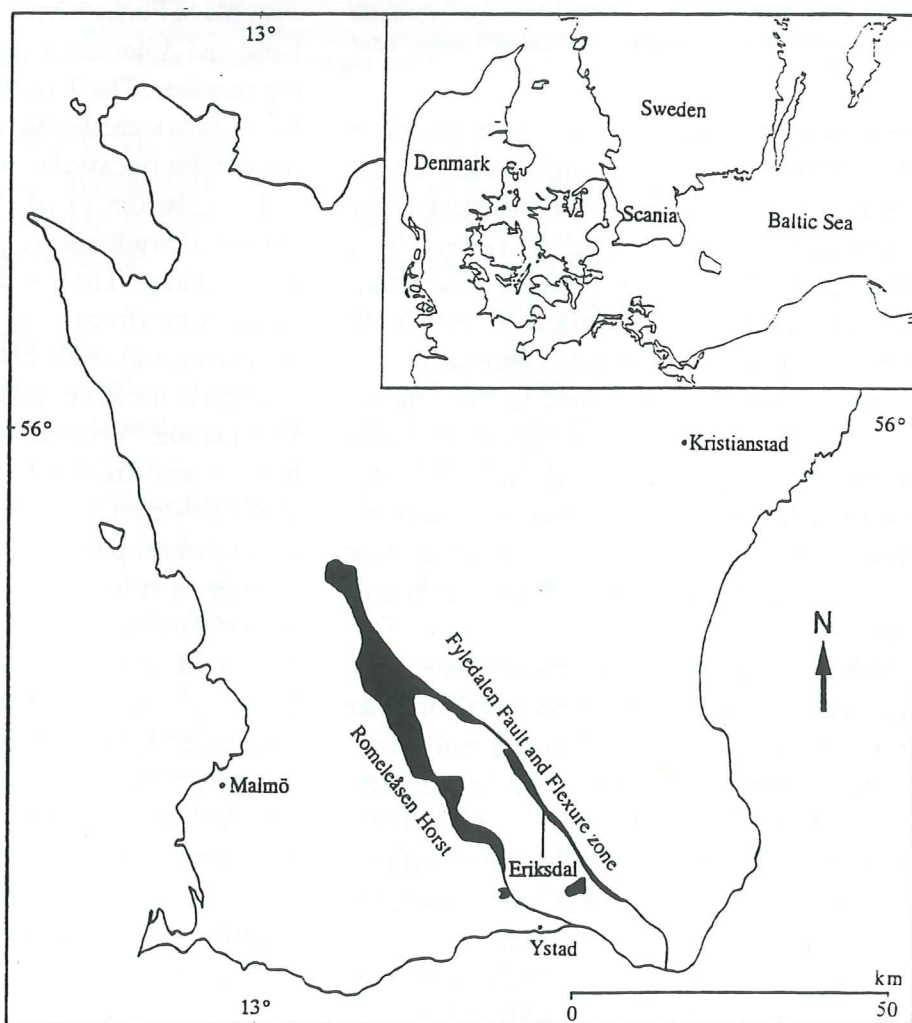


Fig. 1: Map over Scania with the boundaries of the Vomb Trough. Black colour shows Jurassic strata within the Trough (after Norling *et. al* 1993).

Chronostratigraphy		Formation	Member
C r e t a c e o u s	L o w e r	Albian	
		Aptian	
		Barremian	
		Hauterivian	
		Valanginian	
		Berriasian	
J u r a s s i c	U p p e r	Tithonian	Vitabäck Clays
		Kimmeridgian	Nytorp Sand
		Oxfordian	Fyledal Clays
	M i d d l e	Callovian	Fortuna Marl
		Bathonian	Glass Sand
		Bajocian	Fuglunda Marl
		Aalenian	Rödödinge Fm

Fig. 2: Chronostratigraphy of Middle-Upper Jurassic and Lower Cretaceous strata in the Vomb Trough (after Norling *et al.* 1993).

The characters are, however, more primitive than in Mesozoic forms. Brough (1935) did not consider hybodont sharks to be ancestral to any living selachian, a view shared by Maisey (1975, 1982). Thies & Reif (1985), on the other hand, believed that hybodonts probably were both ancestors and a sister-group to Neoselachii, the modern sharks that developed in the Triassic and dominate the recent fauna. Hybodont sharks decreased rapidly in numbers in the Late Cretaceous and the youngest hybodont, *Hybodus* sp., is found in the Maastrichtian, i. e. uppermost Cretaceous of New Jersey, USA (Cappetta & Case 1975).

Hybodont taxonomy is difficult since many species are known only from oral teeth or other pieces of dermal skeleton. It is still more complicated by the fact that many species are heterodont. According to Cappetta (1987), there are five Mesozoic families within the superfamily. The validity of these families will be discussed further under each family respectively.

Hybodont sharks are very rarely mentioned in the literature on the Swedish Mesozoic.

Lundgren (1878, fig. 43) illustrated a fragmental *Hybodus* tooth from the Lower Jurassic and Siverson (1992) encountered hybodont teeth in the Upper Cretaceous. In the Vitabäck Clays there is one earlier find of *Hybodus* sp. (Ekström 1985). The purpose of this paper is to shed some light on the Upper Jurassic shark fauna in Scania.

## Geology

The Vomb Trough in Scania, is limited in the southwest by the Romeleåsen Horst, and in the northeast by the Fyledalen Fault and Flexure zone (Fig. 1). About 200 m Jurassic sediments (Erlström 1994) ranging from the Sinemurian to the Tithonian in age (Norling *et al.* 1993) are recorded. The Jurassic and Lower Cretaceous strata were tilted and slightly overturned by tectonic movements in the Early Cretaceous (Erlström 1994). The Annero Formation (Fig. 2) ranges from the Oxfordian to the Berriasian (Norling *et al.* 1993; Erlström *et al.* 1991) and consists of Fortuna Marl, Fyledal Clays, Nytorp Sand and Vitabäck Clays, the latter being the top member. The Tithonian to Berriasian Vitabäck Clays were deposited in fresh and brackish water with occasional marine influx (Ekström 1985; Erlström *et al.* 1994). The sediments consist of argillaceous clays, varying in colour and bedding. The particular fauna described herein comes from a single coquina bed in which the marine influence has been strong. The bed belongs to the lower part of the Vitabäck Clays. The boundary between Jurassic and Cretaceous beds is not known for the present (Norling 1981; Erlström *et al.* 1991) but the lower parts are probably uppermost Jurassic in age. The bed represents storm sediments deposited in a lagoonal environment, which would mean that the fauna could comprise marine as well as brackwater species. The invertebrate fauna, is dominated by bivalves including *Ostrea*, which indicates a marine environment (Ekström 1985). The bed also contains several types of teeth from bony fishes.

During the Uppermost Jurassic, the palaeo-coastline had a northwest to southeast extension in Scania and formed the northeastern shore of a shallow shelf sea covering large parts of

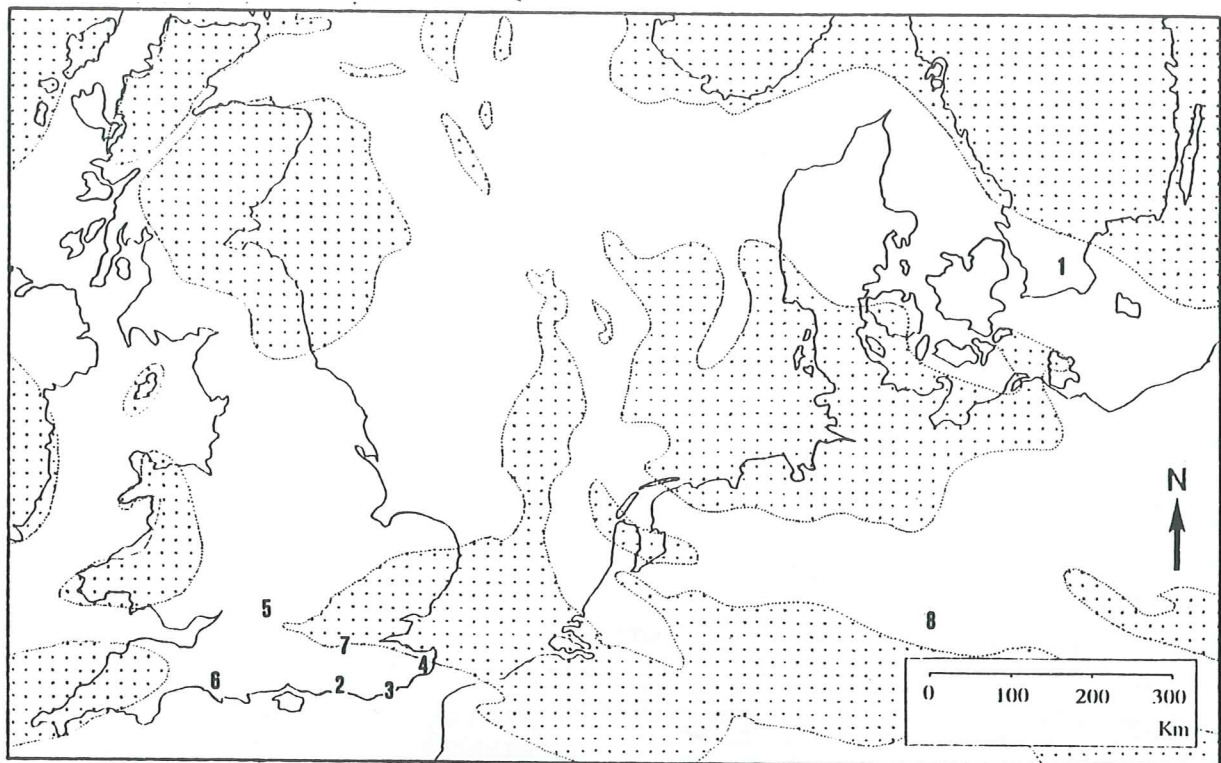


Fig. 3: Palaeogeography of northwestern Europe during the Kimmeridgian-Tithonian, showing the extension of the northwest European shelf sea. Dotted parts represent areas that were above the sea level during more than half of the time (after Ziegler 1990). Figures show localities discussed in the text; 1 Eriksdal, 2-4 localities with Wealden sharks (Patterson 1966), 5-6 localities where *Polyacrodus pattersoni* have been found (Duffin 1985), 7 locality for the fauna described by Batchelor & Ward (1990), 8 The placoid scale locality in Germany (Thies 1995).

northwestern Europe (Fig. 3). The climate was warm and seasonally wet (Hallam 1994). Sweden was at this time located at a latitude of approximately 30 degrees north.

### Material and Methods

The Vitabäck Clays are covered by at least one meter of Quaternary deposits and the sample was collected from a temporary excavation. The locality is now inaccessible due to agricultural activities and is situated in a field, 50 meters northwest of the road crossing at the Vitabäck farmhouse. A bulk sample of approximately 520 kg was collected and the clay was removed in a clay washing machine with a 350  $\mu\text{m}$  sieve (as described in Ward (1981)). The remaining material, including numerous carbonate shells, was dissolved in buffered acetic acid (see Jeppsson *et al.* (1985)). The material was then dried and treated in a magnetic separator in order to concentrate the phosphatic fossils. The non-magnetic material was simply sorted on a tray under a binocular microscope.

I follow the descriptive terms for the teeth used by Duffin (1985), simplified and shown in Fig. 4. Descriptive terms for placoid scales are modified from Thies (1995) and shown in Fig 5.

The general preservation is not very good; most teeth are found as fragments. Some are complete crowns and a very few are complete with roots. The material is housed in the Department of Geology, Lund University, Sweden.

### Palaeoecology

The largest hybodont sharks were smaller than the largest neoselachians and this means that they were probably not living in the open sea. Smaller sharks generally live near the bottom and some are found in lacustrine and brackish environments, especially in the Triassic and Cretaceous (Duffin 1985). This is probably due to new competitors such as actinopterygians and neoselachians. Some hybodont species are known to be euryhaline or even exclusively freshwater living (Patterson 1966, Murry 1981)

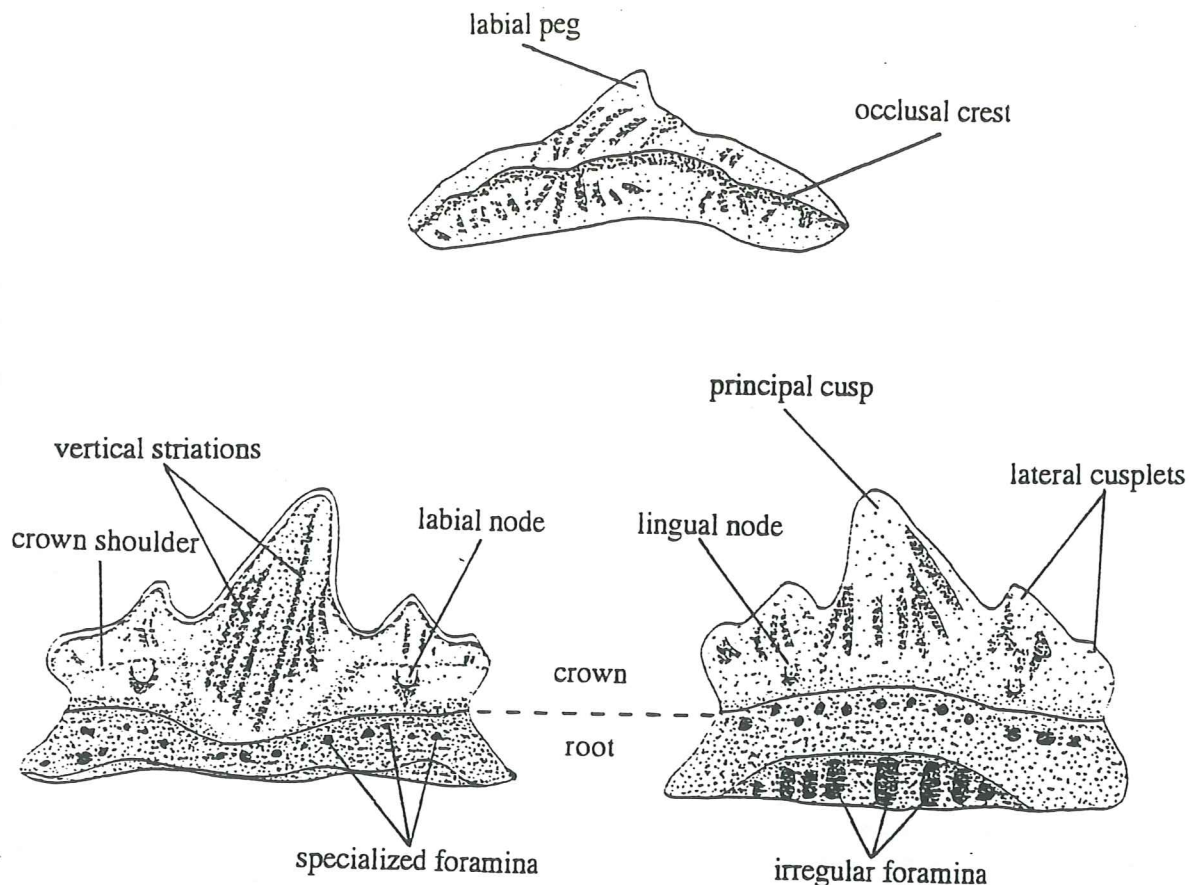


Fig. 4: Descriptive terms for a generalized hybodontoid shark's tooth (simplified from Duffin 1985).

while others lived in open marine environments. Smaller hybodont shark species seem to be more nearshore and lacustrine than larger sharks, that lived further out on the shelf (valid at least for *Hybodus* and *Lissodus*)

Smaller sharks (*Lissodus*, *Polyacrodus*) probably preyed on benthic shelly invertebrates, mostly molluscs, but also on smaller bony fishes. This diet appears to be confirmed as the investigated bed from the Vitabäck Clays is very rich in bivalves, up to five cm in length, and there are also teeth from small bony fishes. Larger species within the genera *Hybodus* and *Egertonodus* with more marked tearing-type dentition had a diet of bony fishes and smaller sharks as well as larger invertebrates, e. g. cephalopods (Pollard 1990, Fig. 2). Martill (1991) suggested that species of *Hybodus* were scavengers since isolated crowns of teeth often are found associated with remains of marine reptiles.

Hybodont sharks in Jurassic waters had few enemies as adults. Small species and juveniles were preyed on by larger hybodonts and neoselachians, e. g. *Synechodus* (Maisey 1985).

### Palaeobiogeography

There are few shark faunas described from the Late Jurassic and Early Cretaceous. However, the fauna from the Wealden of southern England described by Patterson (1966) shows major resemblance to the one in Scania. Four or possibly five species from Scania are also found in the Wealden, namely *Egertonodus basamus*, *Lissodus crenulatus*, *Polyacrodus parvidens*, *P. heterodon* and *Hybodus cf. ensis*. The only species not present in the Wealden is *P. pattersoni*, which was found in England, but only in the Bathonian. It is possible that *P. pattersoni* was extinct in England by the Early Cretaceous. The Wealden fauna is more diverse than the Scanian, when treated as one. This is due to more material from four major localities, each representing a particular environment. When comparing the faunas from each locality, the diversity is fairly equal. There are four species at one locality and six at the other three, while the fauna from Eriksdal includes seven species. The general environment is dominated by brackish conditions as in the Vitabäck Clays. The material of the Wealden sharks represents a

rather long period: from the Berriasian to the Barremian. Great Britain was at this time situated on the western margin of the shallow shelf sea in northwest Europe (Fig. 3), that was not very difficult to cross even for nearshore sharks. Batchelor & Ward (1990) described another fauna from the Aptian of England. In this fauna, found in open marine glauconitic sand, there is a much larger amount of neoselachians, compared with only one species that is found in the Eriksdal material. Among the hybodonts there are only one or possibly two species in common with Scania, *E. basanus* and *P. cf. parvidens*. This could be explained by the open marine environment. Especially *E. basanus* seems to have been able to live in highly variable salinity. The shark fauna from the Callovian-Oxfordian Oxford Clay in England, includes four hybodont shark species (Martill 1991) but none of these are present in this study. Duffin (1993b) described a marine shark fauna from the Oxfordian of southern Germany that only included neoselachians. These studies lead to the conclusion that hybodonts were very repressed or in decline in Late Jurassic and Early Cretaceous marine environments.

## Systematics

General systematics follow Cappetta (1987).

Class Chondrichthyes Huxley, 1880

Subclass Elasmobranchii Bonaparte, 1838

Cohort Euselachii Hay, 1902

Superfamily Hybodontoidae Zangerl, 1981

Family **Hybodontidae** Owen, 1846

Hybodontidae include five genera; *Hybodus* Agassiz 1837, *Egertonodus* Maisey 1987 and three monotypic genera only known from Asia and Africa. Many authors also include forms with grinding-type dentition, like *Acrodus*, but they are excluded by Cappetta (1987) to keep the family from being too heterogeneous. *Egertonodus* is separated from *Hybodus* on basis of cranial anatomy (Maisey 1987, p. 27) and it is possible that other species known only from teeth and referred to *Hybodus* could in fact belong here. The two genera are extremely closely related and Maisey (1989) even grouped them together in Hybodontinae. Teeth of

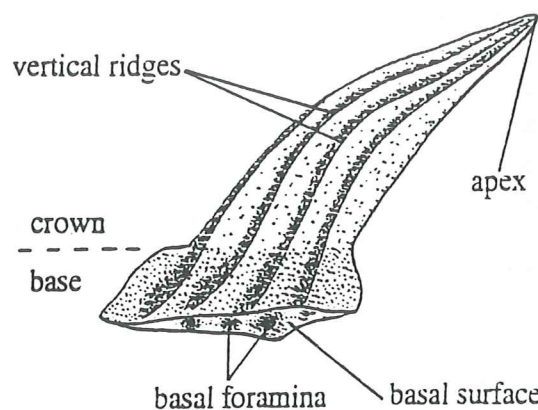


Fig. 5: Descriptive terms for a hybodontoid placoid scale (modified from Thies 1995). Anterior to the left.

*Hybodus* and *Egertonodus* are very typical and are characterized by a high principal cusp and two or three pairs of lateral cusplets (Maisey 1989). *Hybodus* is well represented in Jurassic and Lower Cretaceous strata in England (Patterson 1966; Martill 1991; Duffin 1993a), Belgium (Delsate & Duffin 1993), France (Biddle 1993) and Denmark (pers. obs.). It has also been reported from China (Wang 1977, cited not seen) and found in the United States (Schaeffer & Patterson 1984).

Genus *Hybodus* Agassiz, 1837

Type species.- *Hybodus reticulatus* Agassiz, 1837 from the Lower Jurassic of Lyme Regis in southern England.

*Hybodus cf. ensis* Woodward, 1916

Fig. 7A.

*Synonymy.* - ●cf. 1916 *Hybodus ensis* sp. nov. - Woodward, p. 11, pl. 2, figs. 2-6. ●cf. 1966 *Hybodus ensis* Woodward-Patterson, pp. 292-296, text-figs. 4-5.

*Material.* - 21 incomplete teeth, one with fragments of the root.

*Description.* - Dentition is of tearing-type and shows low grade of heterodonty. The teeth are around 5 mm wide. The crown is high and labiolingually flattened. The principal cusp is broad at the base and high. There is one pair of lateral cusplets bent towards the principal cusp. There are, however, rudimentary traces of one more pair. The ornamentation consists of rarely bifurcating strong vertical striations that reach as high as half the height of the principal cusp on



both lingual and labial sides. The occlusal crest is weak on the principal cusp but strong on the lateral cusplets. The small root fragment on one of the teeth shows one row of irregular foramina close to the crown/root junction on the labial side.

Discussion.- The teeth in this study are different from those figured by Patterson (1966, fig 4-5) in having vertical striations reaching higher on the principal cusp, generally covering one half compared to one fifth in the Wealden specimen. The teeth in this study are also much smaller, the most complete tooth is 4 mm wide while the Wealden specimen can reach a width of 20 mm. This could be explained by the fact that the environment was different and the material in this study comes from younger sharks living closer to the shoreline. Maisey (1983) considered *H. ensis* to be a synonym of *Egertonodus basanus* after having studied the complete dentition of that species. My material of *H. cf. ensis* is incomplete. The question whether differences between teeth are due to individual differences or that the teeth represent different parts of the jaw or even separate species will consequently have to be left open. However, some teeth figured by Maisey (1983) do show resemblance to *H. ensis* but there is in no case only one pair of lateral cusplets and when there are two pairs, both are fairly well developed. Compared to other *Hybodus*, teeth from *H. ensis* are rather typical in having a heavier principal cusp and never more than two pairs of lateral cusplets (Patterson 1966), while three or even four pairs are more common in *Hybodus*. The record of *H. ensis* is Berriasian to Valanginian, Lower Cretaceous.

#### Genus *Egertonodus* Maisey, 1987

Type species.- *Hybodus basanus* Egerton, 1845 from the Lower Cretaceous of the Isle of Wight, southern England.

#### *Egertonodus basanus* (Egerton, 1845)

Fig. 7B-C.

Synonymy.- •1845 *Hybodus basanus* sp. nov. - Egerton p. 197, pl. 4. •1966 *Hybodus basanus* Egerton - Patterson pp. 288-292, pl. 1, fig. 1,

text-figs. 1-3. •1983 *Hybodus basanus* Egerton - Maisey pp. 1-64, figs. 1-26. •1987 *Egertonodus basanus* (Egerton) - Maisey p. 27.

Material.- 2 crowns with lateral cusplets and several isolated principal cusps.

Description.- Tearing-type dentition as in most *Hybodus*. The grade of heterodonty is very low and there are almost only size differences. The most complete tooth in my collection would be 4.4 mm wide, had it been complete. The crown is high and the principal cusp would give a circular cross section. The principal cusp is high and slender. It is lingually curved at the base but the very top bends back labially to give the cusp a slight s-shape. In the lateral teeth the principal cusp is also slightly bent posteriorly. There are at least two pairs of well developed lateral cusplets. Vertical striations are strong without bifurcation. They reach about one half of the height of the principal cusp on the labial side and a little higher on the lingual side. The occlusal crest is moderately strong on both principal cusp and lateral cusplets. Nothing is preserved from the root of any of the specimens.

Discussion.- Teeth of *E. basanus* are distinguished from all *Hybodus* since they have an s-shaped principal cusp. The only *Hybodus* with the same stratigraphical range is *H. ensis* (see above). *E. basanus* resembles *H. cloacinus* and *H. reticulatis* from the Early Jurassic, but these both lack the s-shaped principal cusp and generally have larger lateral cusplets. Maisey (1983) showed that the stratigraphical range of *E. basanus* was Valanginian-Barremian but it has also been recorded in the Aptian by Batchelor & Ward (1990) making the range Tithonian-Aptian including this find.

#### Family **Polyacrodontidae** Glückman, 1964

This family comprises *Lissodus* and *Polyacrodus*, Cappetta (1987) also tentatively included *Palaeobates*. In my opinion *Palaeobates* is too different to belong to this family. Its teeth lack features that are characteristic for the two other genera. The inclusion was at first based on tooth histology (Glückman 1964, cited not seen). Maisey (1989) considered Polyacrodontidae to

be founded on plesiomorphic characters but if *Palaeobates* was to be excluded, derived features could characterize the family (see below). Both *Polyacrodus* and *Lissodus* are small sharks with low-crowned teeth and a typical feature in the two, is a well-developed labial peg (Stensiö 1921; Duffin 1985). *Polyacrodus* seems to have had a less developed one, more like a keel on the principal cusp (Stensiö 1921). Teeth of *Polyacrodus* are also more heterodont than those of *Lissodus* (cf. *P. claveringsensis*, Stensiö 1932). *Polyacrodus* was first described as a Triassic genus but recently other younger species (*P. brevicostatus*, *P. parvidens*) have been incorporated by Cappetta (1987). The two genera are closely related and some species are difficult to assign to one or the other. Two species, *Lissodus heterodon* and *L. pattersoni*, are here moved to *Polyacrodus* on basis of tooth morphology and heterodonty that show resemblance to *P. parvidens* among others. That *L. heterodon* should be moved was already suggested by Cappetta (1987). Both *Polyacrodus* and *Lissodus* have been found in Middle Jurassic to Lower Cretaceous strata in Britain (Duffin 1985; Cappetta 1987) and in France (Biddle 1993). *Lissodus* is in addition present in Lower Jurassic strata in Denmark.

#### Genus *Lissodus* Brough, 1935

Type species. - *Hybodus africanus* Broom, 1909 from the Lower Triassic of Bekker's Kraal, South Africa.

#### *Lissodus crenulatus* (Patterson, 1966)

Fig. 7D-E.

Synonymy. - •1966 *Lonchidion breve crenulatum* sp. et. ssp. nov. - Patterson, pp. 316-317, text-figs. 17-18. •1985 *Lissodus crenulatus* (Patterson) - Duffin, p. 110, text-fig. 3, pl. 1, fig. 2 a-b. •1985 *Lissodus pustulatus* (Patterson 1966) - Duffin, (in part), text-fig. 4.

Material. - 1 almost complete tooth and 4 crowns.

Description. - Dentition is a combination of tearing and crushing-type and the teeth described here show little sign of heterodonty. They range from 1.2 to 1.5 mm in width. The teeth are elongate with very low crowns. In the occlusal

view they are straight. The principal cusp is very low and bears a rather weak labial peg. There are small traces of one pair of lateral cusplets. The best preserved specimen shows a rather strong crown shoulder on the lingual side. Vertical striations are very weak and only present on the cusp and cusplets on both lingual and labial sides. An occlusal crest is present on four of the specimens, but is weak. The root is larger than the crown and the crown/root junction is slightly concave. There are irregular foramina all over the root placed in a random fashion. The basal face is concave.

Discussion. - Patterson originally described three subspecies of "*Lonchidion breve*", of which *L. crenulatus* was one. Duffin (1985) gave these subspecies the status of species and included them in *Lissodus*. The teeth described herein are very similar to one tooth figured by Patterson (1966, text-fig. 17B). However, the same tooth is also figured by Duffin (1985, text-fig. 4) under the name *Lissodus pustulatus*. Following the first author, *L. crenulatus* seems to be the correct name for this tooth. All specimens in this study lack accessory cusplets, there are, as mentioned above, vertical striations which would rule out an assignment to *L. breve*. According to Patterson (1966) no striations should be present on "*Lonchidion breve pustulatum*" but the ornamentation consists of accessory cusplets, which are lacking on the teeth in this study. *Lissodus crenulatus* was earlier known from the Valanginian, Lower Cretaceous and this investigation extends the stratigraphical distribution down into the Tithonian, Upper Jurassic.

#### Genus *Polyacrodus* Jaekel, 1889

Type species. - *Hybodus polycyphus* Agassiz, 1837 from the Middle Triassic of Lunéville, eastern France.

#### *Polyacrodus parvidens* (Woodward, 1916)

Fig. 7F-H.

Synonymy. - •1916 *Hybodus parvidens* sp. nov. - Woodward, p. 12, pl. 2, figs. 8-14. •1966 *Hybodus parvidens* Woodward - Patterson, pp. 296-300, text-figs. 6-9. •1987 *Polyacrodus parvidens* (Woodward) - Cappetta, p. 37.

Material.- 1 complete tooth and 9 crowns.

Description.- Teeth of this species are from a tearing-type dentition and show moderate heterodonty. The teeth range from 1.8 to 2.9 mm in width. The general shape is an elongate tooth with a principal cusp that is high and slender in anterior teeth and low and stout in posterior teeth. Lateral teeth have an intermediately high principal cusp that is slightly bent posteriorly. All types of teeth have two pairs of lateral cusplets, following the shape pattern of the principal cusp in the different teeth. A weak labial peg is formed from a vertical ridge that runs from two thirds of the height of the principal cusp and forms a slight overhang at the crown/root junction. Vertical striations are in general intermediate and are present as above on the labial side, while the lingual side is ornamented almost to the top. Vertical striations are present on both sides of the lateral cusplets. The striations are only rarely bifurcating and only on the lingual side. The occlusal crest is strong and forming cutting edges on both principal cusp and lateral cusplets. The root is perforated by a row of specialized foramina close to the crown/root junction on both lingual and labial sides. On the lingual root face there is, in addition, a wedge-shaped row of irregular foramina near the base. The basal face of the root is also perforated by a row of irregular foramina, situated near the labial margin.

Discussion.- The high principal cusp of *P. parvidens* is rather *Hybodus*-like and only lateral teeth show resemblance to other *Polyacrodus*, particularly *P. brevicostatus*. However, in *P. parvidens* the principal cusp is higher and lateral teeth of *P. brevicostatus* have a larger amount of lateral cusplets. Also, *P. parvidens* have weaker vertical striations. Maisey (1983) incorporated this species in *Egertonodus basamus*. Since some important features differ: in *P. parvidens* there is no s-shaped principal cusp but there is a strong vertical keel on the principal cusp, I do not believe that this is the same species. Furthermore, there are no specialized foramina on the basal plate of *E. basamus* (Maisey 1983) but as pointed out above, this is

the case in *P. parvidens*. The stratigraphical range of this species is from the Berriasian to the Barremian, Lower Cretaceous (Patterson 1966). This corresponds rather well with this find, which extends the stratigraphical range down into the Tithonian.

*Polyacrodus heterodon* (Patterson, 1966)  
Fig. 7I-K.

Synonymy.- •1966 *Lonchidion heterodon* sp. nov. - Patterson, pp. 326-328, text-fig. 25A-C, not 25D. •1985 *Lissodus heterodon* (Patterson) - Duffin, p. 112, text-fig. 6.

Material.- 2 complete teeth and 276 crowns.

Description.- The dentition is of tearing type and the species is strongly heterodont. The teeth range from 1.2 mm to 3.8 mm in width. Anterior and lateral teeth are very elongate while posterior teeth show a smaller width. All teeth are convex in labial view, most strikingly in some small teeth interpreted as symphysals. There is a quite high principal cusp in anterior teeth, a feature that is declining distally and is very weak in posterior teeth. The lateral cusplets are, like the principal cusp, stronger mesially. There are two pairs in symphyseal and some anterior teeth while lateral, posterior and other anterior teeth have three. All teeth show a moderately strong labial peg and rather strong vertical striations. The striations are present on the whole crown, from crown/root junction to cusp and cusplet apex, on both lingual and labial sides. There are no bifurcating striations. The occlusal crest is strong in anterior and lateral teeth and weak in symphyseal and posterior teeth. The labial face of the root has one row of specialized foramina near the crown/root junction. On the lingual face there is a similar row, but this one is not as symmetrical as on the other side. Closer to the base and on the basal face there is one row each of irregular foramina.

Discussion.- The lateral teeth show most resemblance to *Lissodus striatus* but the principal cusp is higher and the vertical striations are not as close to each other in *P. heterodon*. Both anterior and lateral teeth resemble those in *P. pattersoni*. The anterior teeth are different in

having larger lateral cusplets than in *P. pattersoni* and lacking labial nodes. The vertical striations are also stronger in *P. pattersoni*. Lateral teeth lack labial nodes and have weaker labial peg as well as weaker vertical striations. Teeth of *P. heterodon* are generally more curved in occlusal view. One tooth figured by Patterson (1966, fig 25 D) and tentatively included by him in the synonymy, does not belong to *P. heterodon*. It lacks striations and similar forms are not present in the large material in this study. Stratigraphically, *P. heterodon* was previously known from the Berriasian to the Valanginian, Lower Cretaceous, and the results of this study imply, that its known range is now from the Tithonian.

*Polyacrodus pattersoni* (Duffin, 1985)  
Fig. 8A-C.

Synonymy.- •1985 *Lissodus pattersoni* sp. nov.  
- Duffin, pp. 133-134, text-figs. 22, pl. 7, fig 1 a-i.

Material.- 1 complete tooth and 9 crowns.

Description.- Tearing-type dentition and strong heterodonty characterize this species. The width of the teeth range from 1.3 to 2.7 mm. Anterior teeth are higher and less wide compared to lateral teeth that are very elongate. The lateral teeth are not curved at all and the anterior ones only slightly in occlusal view. Anterior teeth are strikingly labio-lingually flattened. The principal cusp is moderately high in anteriors to low in laterals. All types of teeth bear two pairs of lateral cusplets, mostly developed in anterior teeth. The labial peg is strong in anterior teeth and weak in laterals. A distinct feature in this species is labial nodes that are strong in lateral teeth while weak and sometimes lacking in anterior teeth. Vertical striations are strong on the complete crown of lateral teeth and the upper part of the anterior crowns, while lacking on the lower part. Bifurcating striations are only present on one tooth. The striations sometimes form a small "lingual peg". The occlusal crest is overall rather strong. There are also two crowns with extremely convex crown/root junction included in this species. Since they share all the features described above, they are tentative-

ly considered to be symphyseal teeth. The lingual rootface is penetrated by a row of irregular foramina at the base and at least two specialised foramina close to the crown/root junction. On the labial side there is a complete row of specialised foramina near the crown/root junction. On the labial margin of the basal face there is a row of irregular foramina.

Discussion.- *P. pattersoni* is most closely resembling *P. heterodon* (see above). There is also resemblance to *L. striatus*, but *P. pattersoni* has much stronger vertical striations and labial nodes, that are missing in *L. striatus*. The stratigraphical record of *P. pattersoni* was previously limited to the Bathonian, Middle Jurassic and is now extended to the Tithonian, Upper Jurassic.

Family **Ptychodontidae** Jaekel, 1898

There are two genera in this family; *Hylaeobatis* and *Ptychodus*. Question has been raised whether these are hybodont sharks or not. One species from Kansas has calcified centra, but Cappetta (1987) does exclude that this could appear in specialized hybodonts. *Hylaeobatis* is known only from isolated teeth and only from the Wealden of England. Patterson (1966) suggests that they form a link between the Acrodontidae and the Ptychodontidae since they are much like *Acrodus* in appearance.

Genus *Hylaeobatis* Woodward, 1916

Type species: *Acrodus ornatus* Woodward, 1889 from the Lower Cretaceous of the Isle of Wight, England.

*Hylaeobatis* sp.

Fig. 8D-E.

Material.- 2 incomplete teeth.

Description.- The teeth come from a clutching-grinding type dentition. Two teeth are found, indicating a rather heterodont species. The crown width is 0.9 and 2.0 mm. The crown is oval to circular in occlusal view and it is flat. The only ornamentation present is weak striations on the side of the crown. There may also have been ornamentation on the top surface (as in *H. ornata*, Patterson 1966) but the occlusal surfa-

ce of the teeth is rather worn. The root is slightly smaller than the crown on the large tooth but much wider on the small tooth. In both teeth the root is at least twice as high as the crown. The large tooth has three more or less regular horizontal rows of specialised foramina while only one is present on the small tooth. No irregular foramina are present on either tooth.

Discussion.- The crown of the large tooth is much like that of specimens of *H. problematica* figured by Batchelor & Ward (1990, pl 1, figs. 4-5.). But these teeth lack root, which is the most characteristic part of the teeth in this study. Teeth of *H. ornata* (Patterson 1966, pp. 333-339, text-figs. 28-30, pl. 4, 5) are rather similar to those described here but the root is not as high. It is penetrated by specialised foramina, although only in one row. It is possible that the Scanian material represents a new species of *Hylaeobatis*.

### Cephalic spines

The cephalic spines of hybodont sharks are often well preserved but with isolated spines there is an obvious affinity problem. Maisey (1982) considered these spines to be the most reliable feature that distinguish hybodonts from other shark groups. The spines only occur on males and can be arranged in different ways on the skull (see Maisey 1982). The function of these spines is not known. Rieppel (1981) suggests two theories: either that they were used during copulation or used for defence/protection. Since the spines are rather small and sometimes placed in two pairs I consider the defence/protection theory to be the most likely. Some recent sharks are known to be territorial and the spines might have been used in defending an area. Cephalic spines have been recorded from *Egertonodus* (Maisey 1983), *Hybodus* (Maisey 1982), *Acrodus* (Rieppel 1981),

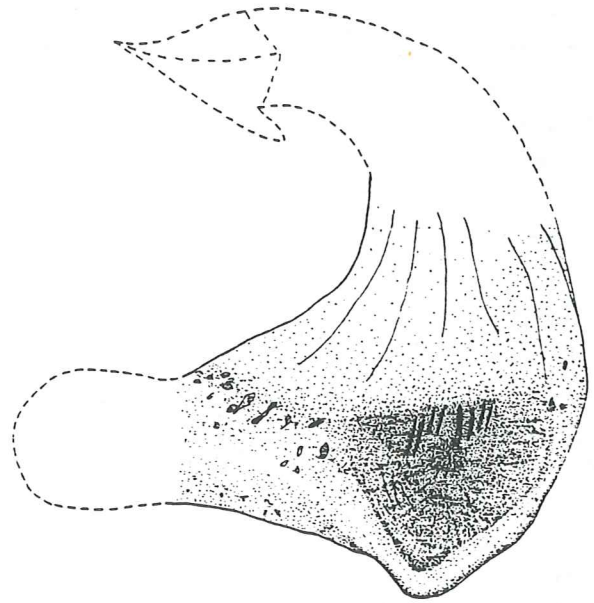


Fig. 6: Cephalic spine, tentatively assigned to *Egertonodus basanus*. Dashed lines show reconstructed parts.

*Lissodus* (Duffin 1985), *Palaeobates* (Rieppel 1981) and *Asteracanthus* (Martill 1991). So far, no cephalic spines have been found, that with certainty can be assigned to *Polyacrodus* (Maisey 1982).

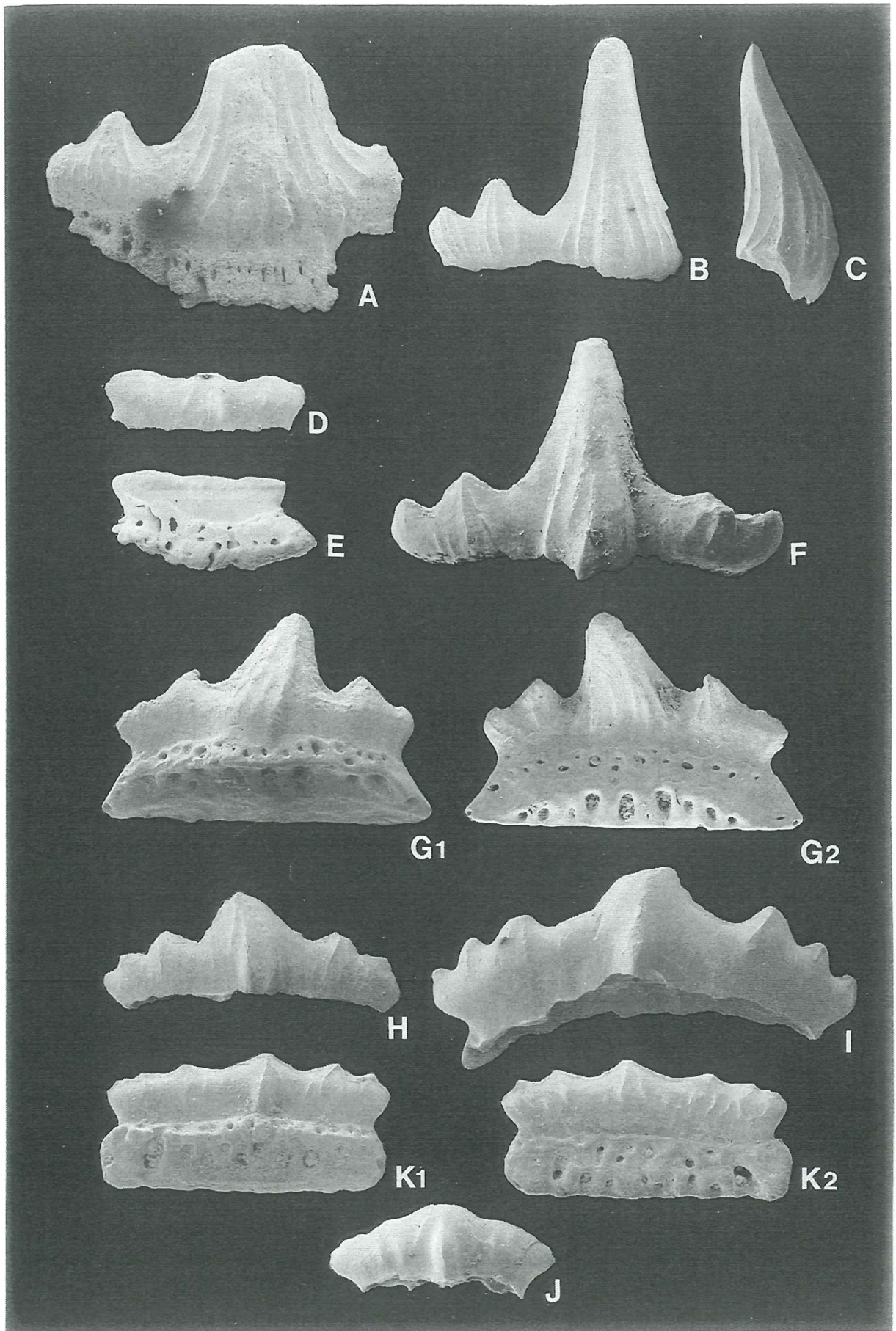
*Egertonodus basanus?* (Egerton 1845)  
Fig. 6.

Material.- 1 incomplete spine

Description.- This spine would be some 14 mm in basal length if it had been complete. The base is triradiate and it is almost symmetrical. The crown is broken off close to the base and the posterior lobe is also missing. On the base, near the junction to the spine, there are irregular foramina randomly placed. Weak striations are present on the lower part of the crown.

Discussion.- The spine is tentatively assigned to *E. basanus* because it is strongly resembling a spine of this species figured by Maisey (1983, fig 24) and since this is the largest species of which oral teeth are found in this study. No

Fig. 7 □A: *Hybodus* cf. *ensis* in labial view, x 20. □B-C. *Egertonodus basanus*: B. in labial view, x 20. C. principal cusp in lateral view, x 20. □D-E. *Lissodus crenulatus*: D. in labial view, x 30. E. in lingual view, x 30. □F-H. *Polyacrodus parvidens*: F. anterior tooth in labial view, x 30. G. lateral tooth in 1. labial view and 2. lingual view, x 30. H. posterior tooth in labial view, x 30. □I-K. *Polyacrodus heterodon*: I. anterior tooth in labial view, x 30. J. symphyseal tooth in labial view, x 30. K. lateral tooth in 1. labial view and 2. lingual view, x 30.



spines are described from the other large species, *H. ensis*.

*Lissodus/Polyacrodus* sp.?

Fig. 8F.

Material.- 1 incomplete spine.

Description.- This spine is 3.2 mm in basal length. The two anterior lobes are not preserved nor the tip of the crown. There is a distinct transition between crown and base. The surface of the crown is very smooth and there is no ornamentation on the crown or on the base.

Discussion.- Several species of *Lissodus* have been recorded to have cephalic spines, *L. africanus* (Brough 1935), *L. humblei* (Murry 1981) and *L. selachos* (Duffin 1985) among others. No *Polyacrodus* has with certainty been proven to bear cephalic spines. This spine shows most resemblance to spines of *L. selachos* with the base present in front of the crown (see Duffin 1985, text-fig. 27a). For these reasons the most obvious species assignment would be *L. crenulatus* but the possibility that the specimen belongs to a *Polyacrodus* species cannot be ruled out.

### Placoid scales

The mineralized placoid scales or dermal denticles of sharks are often overlooked because of their small size and doubtful affinity. Reif (1978) assigned placoid scales from all kinds of sharks to three different morphological types, of which the Hybodontoid type was one of them. Recently Thies (1995) split up this group into five morphotypes within the superfamily Hybodontoida and concluded that even though isolated scales can not be assigned to a single species or even genus they can have stratigraphical significance. It seems, however, that a lot of work needs to be done before the morphotypes can be split up and smaller stratigraphical extensions can be obtained. As will be shown below, one

species (*Hybodus delabechei*) has at least three types of scales.

In the following descriptions of placoid scales from the Vitabäck Clays, I will follow morphotype assignments made up by Thies (1995).

Morphotype 1

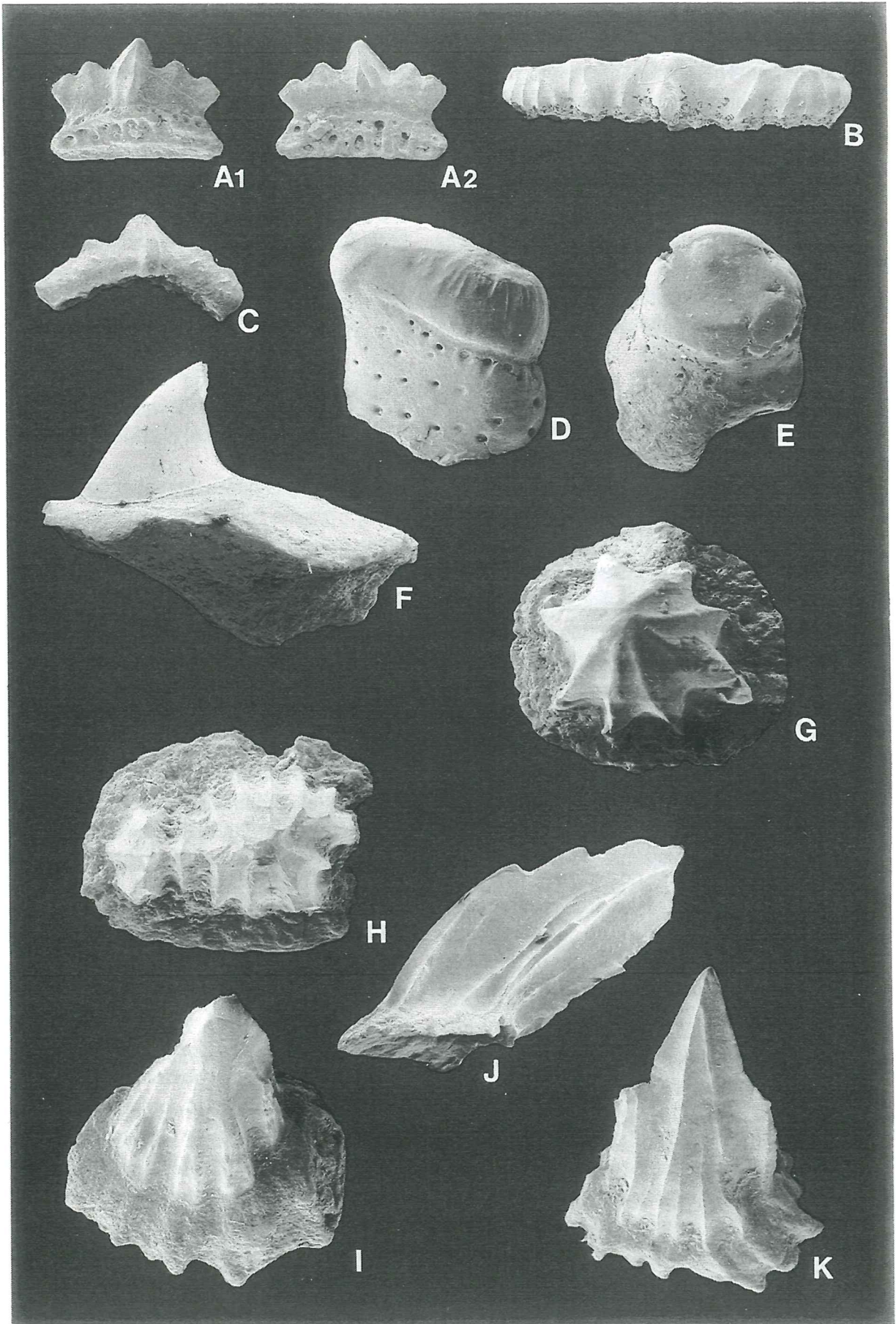
Fig. 8G-H.

Material.- 20 specimens. Material.- 20 specimens.

Description.- Scales ranging in basal width from 0.5 to 1.2 mm. The crown of these scales is generally low and rounded, lacking a sharp cusp. The scales are almost radial symmetrical in occlusal view. The ornamentation consists of strong vertical ridges which merge at the apex. In some specimens, the ridges branch close to the crown/base junction, while others lack branching. The base is wider than the crown and ornamented with ridges in continuation with those on the crown. The basal face is usually flat but it is slightly convex on three specimens. It is perforated by randomly placed foramina. Two scales included in this morphotype have two tips on the same base but they show all other characteristics of this morphotype and are consequently placed here.

Discussion.- According to Thies (1995) this morphotype is present in deposits from Late Triassic to Late Jurassic. This type of scale was probably common in hybodonts and this is also indicated by the size variation. Scales from this material show resemblance to one scale found in the Oxford Clay (Martill 1991) together with oral teeth from among others *Hybodus dawni* and *H. obtusus*. Scales of this type are also present on *H. delabechei* (Reif 1978, fig. 2A) and it is possible that this was a type of scale that was shared by all Hybodontidae. The scales in this study are probably from more than one species, but the size of the large ones makes it probable that they belong to *E. basamus* or *H. cf. ensis*.

Fig. 8 □A-C. *Polyacrodus pattersoni*: A. anterior tooth in 1. labial view and 2. lingual view, x 30. B. lateral tooth in labial view, x 30. C. symphyseal tooth? in labial view, x 30. □D-E. *Hylaeobatis* sp.: D. in labial view, x 25. E. in occlusal labial view, x 40. □F. Cephalic spine of *Lissodus/Polyacrodus*? in lateral view, x 25. □G. Placoid scale, morphotype 1 in occlusal view, x 45. □H. Placoid scale, morphotype 1? in occlusal view, x 70. □I. Placoid scale, morphotype 2 in anterior occlusal view, x 90. □J. Placoid scale, morphotype 3 in lateral view, x 70. □K. Placoid scale, morphotype 4 in anterior occlusal view, x 90.





#### Morphotype 2

Fig. 8I.

Material.- 13 specimens.

Description.- These scales are ranging from 0.5 to 0.8 mm in basal width. There is a moderately high, rather pointed crown, which is slightly to moderately curved posteriorly. The vertical ridges are strong and merge at the apex. They are bifurcating once or twice near the base. The base is larger than the crown and shows ridges corresponding to the vertical ridges on the crown. The basal face can be either concave, flat or convex and is only perforated by a few foramina.

Discussion.- Thies (1995) found this type of scale in the Kimmeridgian of Germany and it resembles scales from *E. basanus* (Maisey 1983, fig. 23C-E) as does the material in this study. So far, this is the only species known with this type of scales. The stratigraphic record would follow that of *E. basanus* if the hypothesis is correct, but no other remains of this species are found in the Kimmeridgian.

#### Morphotype 3

Fig. 8J.

Material.- 23 specimens.

Description.- The complete length from anterior part of the base to posterior apex range from 0.6 to 1.2 mm. The crown is high and moderately to strongly curved posteriorly. There is a sharp cusp and most scales are very flattened. Vertical ridges are weak and do not merge at the apex, but may form spines on top of the scale. The base is weak and the basal face is concave in all specimens.

Discussion.- This type of scale is present on three more or less complete specimens of *H. delabechei* (Reif 1978, fig. 8), *H. fraasi* (Maisey 1986, fig. 7C) and *E. basanus* (Maisey 1983, fig. 23A-B), respectively. The scales herein can probably be assigned to *E. basanus*.

#### Morphotype 4

Fig. 8K.

Material.- 7 specimens.

Description.- The scales range from 0.6 to 0.8 mm in total length. The crown is curved posteriorly and rather pointed. The vertical ridges are strong and one on each lateral side is much enlarged. This gives the scale a wing-like appearance in occlusal view. These ridges can sometimes form cusplets. Obviously, the ridges do not merge at the apex; some of them are bifurcating near the crown/base junction. The base is weak and there are only very small ridges. The basal face is concave in all specimens.

Discussion.- Scales of this type are present on *H. delabechei* (Reif 1978, fig. 2F). So, larger scales could be from either *E. basanus* or *H. cf. ensis*. The stratigraphical significance of this morphotype is low.

### Conclusions

The fauna described in this paper comprises oral teeth, cephalic spines and placoid scales from seven species of hybodont sharks. The teeth are described and modest attempts to reconstruct the jaws are made in three of the species. The affinity of the cephalic spines is discussed and the conclusion is that more articulated material is necessary for solving the affinity problem. It is concluded that placoid scales are not stratigraphical significant at the present time. No hybodonts are previously known from this area so the palaeogeographical areas are extended. The sharks lived in a shallow ocean close to the shore or even in a lagoonal environment. The water was brackish to marine. The sharks probably preyed on bivalves, gastropods and bony fishes, their remains are frequent in the bed. The fauna comes from the Tithonian, Upper Jurassic which extends the stratigraphical range of five of the found species. When comparing with other faunas from the Upper Jurassic and Lower Cretaceous it seems obvious that hybodonts were suffering from hard competition with neoselachians in marine environments while they were flourishing in brackish water at this time.

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