

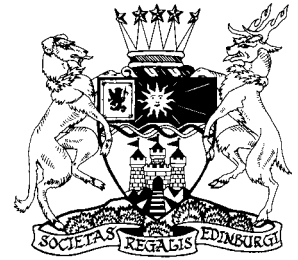
# Shark fauna and depositional environment of the earliest Cretaceous Vitabäck Clays at Eriksdal, southern Sweden

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**ABSTRACT:** A section of the Vitabäck Clays at Eriksdal in southern Sweden was sampled for vertebrate fossils. Large bulk samples were collected from three horizons, including two coquina beds, VC3 and VC11, and a silty clay bed, VC7. Shark teeth are very common and constitute the main portion of the vertebrate material discussed herein. The selachian tooth faunas are almost exclusively represented by hybodonts, although a single tooth from a neoselachian shark, Squatinidae indet., was recorded from one horizon (VC3). Hybodont species identified from the Vitabäck Clay samples include *Egertonodus basanus*, *Hybodus parvidens* and *Parvodus rugianus*. Hybodont remains, other than teeth, include five morphotypes of placoid scales, incomplete cephalic spines and fragmentary fin spines.

Other fossil groups represented in the sieved residues from the bulk samples include bivalves, gastropods and bony fish. Together with the selachians, they indicate fluctuating palaeosalinities in the area. The lower coquina bed, VC3, includes taxa indicating mesohaline conditions while the composition of the fauna in the other coquina bed, VC11, suggests oligohaline settings. In bed VC7, the presence of amphibian remains and the rarity of selachian fossils indicate an even lower salinity. Palynomorphs from the basal part of the section, immediately below bed VC3, indicate an earliest Cretaceous (Berriasian) age.

**KEY WORDS:** Berriasian, Elasmobranchii, Hybodontoida, Neoselachii, non-marine, palaeoecology, palaeosalinity, teeth.



During the Middle and Late Jurassic, the selachian faunas in European coastal marine environments shifted from being hybodont-dominated, or at least having a substantial hybodont component, to being characterised more by the diversifying neoselachians. In marine selachian assemblages of Early Jurassic age, neoselachians are usually outnumbered, both in terms of species and specimens, by the hybodonts (e.g. Duffin 1993; Rees 1998). Middle Jurassic faunas are not as well known, but there appears to be a fair mixture of both groups (Young 1982; Duffin 1985), while marine faunas from the Late Jurassic are rich in neoselachians, particularly smaller species (e.g. Schweizer 1964; Martill & Hudson 1991). Hybodonts only constitute a minor portion of Cretaceous marine selachian faunas, although they can still be found as late as the late Maastrichtian (Case & Cappetta 1997).

Non-marine selachian faunas were dominated by hybodonts throughout the Mesozoic, perhaps with the exception of the Early Triassic, and these non-marine selachians were particularly common and diverse in the Early Cretaceous (Patterson 1966; Underwood & Rees 2002). Non-marine hybodonts are known from many parts of the world and they inhabited a wide range of ecological niches. Neoselachians have always been rare in non-marine environments and only a few groups are represented. In the Early Cretaceous, non-marine batoids (Rhinobatoidei) have been found in Brazil (Martill 1993) and England (Underwood & Rees in press) in association with hybodonts. Today, non-marine batoids are found in South American and African lakes (Cappetta 1987), and a few species of nearshore living carcharhinids are known to frequent rivers and even lakes (Compagno 1984).

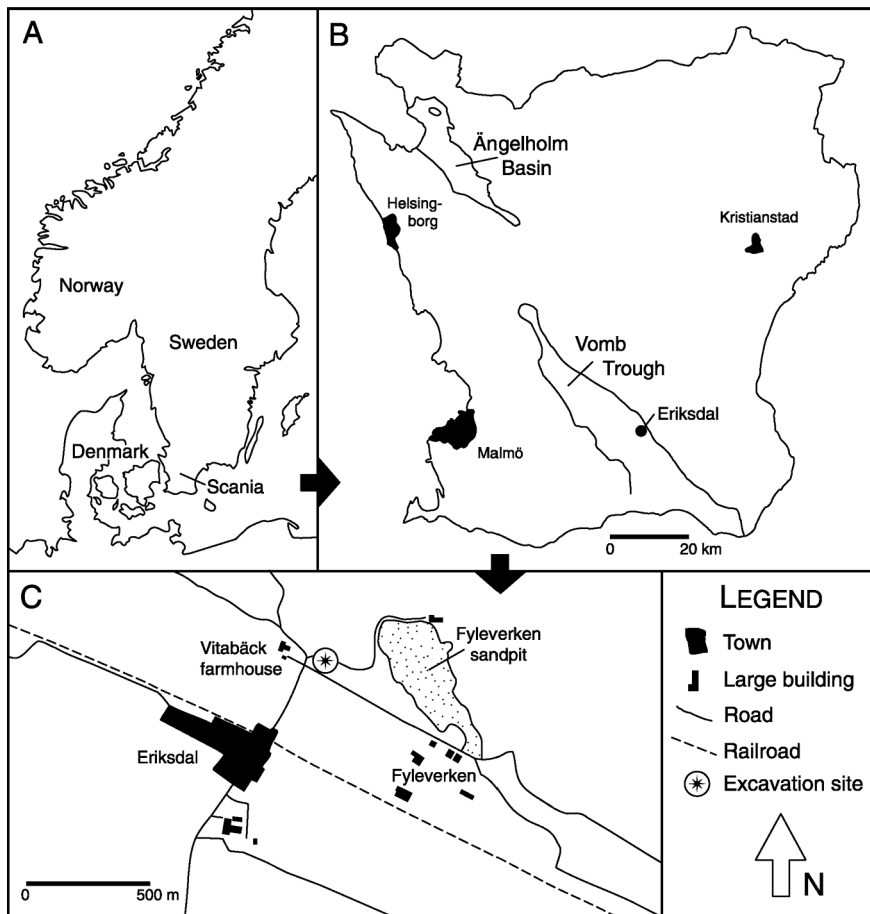
Shed teeth and other isolated remains from hybodont sharks are commonly recorded from Mesozoic coastal, estuarine and

freshwater sediments, while articulated skeletons are extremely rare finds. These sharks possessed large fin spines, situated in front of both dorsal fins. The spines were ornamented with ribs or granulae on the anterior side and with denticles on the posterior side. Male hybodonts were equipped with one or two pairs of cephalic spines, a character exclusive to these sharks. The degree of calcification of the cartilage in different parts of the skeleton of hybodonts differs markedly from that in neoselachians (see Cappetta 1987).

## 1. Geology

### 1.1. Geological setting

Late Jurassic and Early Cretaceous sediments in Sweden can only be found in Scania (Skåne), the southernmost province (Fig. 1). These strata cannot be found in natural outcrops as they are covered by Quaternary deposits and our knowledge of the sediments is derived from studying quarries, drillcores and temporary excavations. The main portion of Scania is situated within the Fennoscandian Border Zone and the geological setting is characterised by several phases of large-scale block faulting (Norling & Bergström 1987). Sediments from the Late Jurassic and Early Cretaceous can be found as surface bedrock beneath the Quaternary in two areas (Fig. 1), the Vomb Trough and the Ängelholm Basin (Norling 1981). The Vomb Trough is an asymmetric graben and the tectonics of the area are rather complex (Norling *et al.* 1993). The Jurassic and Berriasian strata in the area (NE of the Fyledalen Fault Zone) are tilted and slightly overturned by tectonic movements later in the Cretaceous (Norling & Bergström 1987). Strati-



**Figure 1** Composite map of the location of Scania in Scandinavia (A), showing the Vomb Trough and the Ängelholm Basin (B); detail map of the Eriksdal area (C) with the excavation site (Swedish National Grid coordinates [616377 137285]) and the Fyleverken sand pit.

graphically, Late Jurassic to earliest Cretaceous strata are included in the Annero Formation (Fig. 2), ranging from the mid-Oxfordian to the Berriasian in the area. The sediments of this formation are mainly alternating clay, silt and sand deposits, often poorly lithified. The three units present in the area, the Fyledal Clay, the Nytorp Sand and the Vitabäck Clay members, were all deposited in marginal facies (Guy-Ohlson & Norling 1994). Sediments of the Fyledal Clay are exposed in the Fyleverken sand pit (Fig. 1) and have been sampled at two separate horizons, although no vertebrate remains were found. The Vitabäck Clays primarily include alternating clay and silt deposits (Erlström *et al.* 1991). Layers of sand occur less frequently, often as thinner beds. The faunal and floral composition was studied by Erlström *et al.* (1991), who suggested brackish and freshwater environments with occasional marine influence. Alternating palaeosalinities within the member were also discussed by Christensen (1968), who discovered that ostracods in different parts of the Vitabäck Clays indicated fluctuating salinity levels. The sediments were probably deposited in an area of low gradient where lagoons and shallow lakes could develop (Erlström *et al.* 1991).

**1.2. The age of the Vitabäck Clays**

Throughout northern and western Europe, the precise age determination of Late Jurassic and Early Cretaceous non-marine strata has been, and still is, complicated. The biostratigraphy in the Jurassic and Cretaceous is often based on marine invertebrates such as ammonites and foraminifera, naturally lacking in the non-marine environments prevailing in many areas of northwestern Europe during this period. Regarding

the Vitabäck Clays, Hägg (1940) studied the molluscs from a collection of Vitabäck Clay fossils, attempting to determine the age. He found species previously known from the English Purbeck and Wealden deposits, but he was not able to make a closer age determination. Ostracods from the same collection were studied by Christensen (1968), who considered the Vitabäck Clays to be contemporary with the Lower ‘Purbeckian’, at that time placed in the Late Jurassic. The greater part of the sediments of the Purbeck Group in southern England are now considered to have been deposited above the Jurassic–Cretaceous boundary and the group ranges from the Tithonian to the Valanginian. Erlström *et al.* (1991) attempted to determine the age of the Vitabäck Clays by means of palynomorphs.

CRET.	BERRIASIAN	?	ANNERO FORMATION
		VITABÄCK CLAYS	
JURASSIC	TITHONIAN	NYTORP SAND	
	KIMMERIDGIAN	FYLEDAL CLAY	
	OXFORDIAN		

**Figure 2** Stratigraphic position of the members within the Annero Formation at Eriksdal (based on Norling *et al.* 1993).

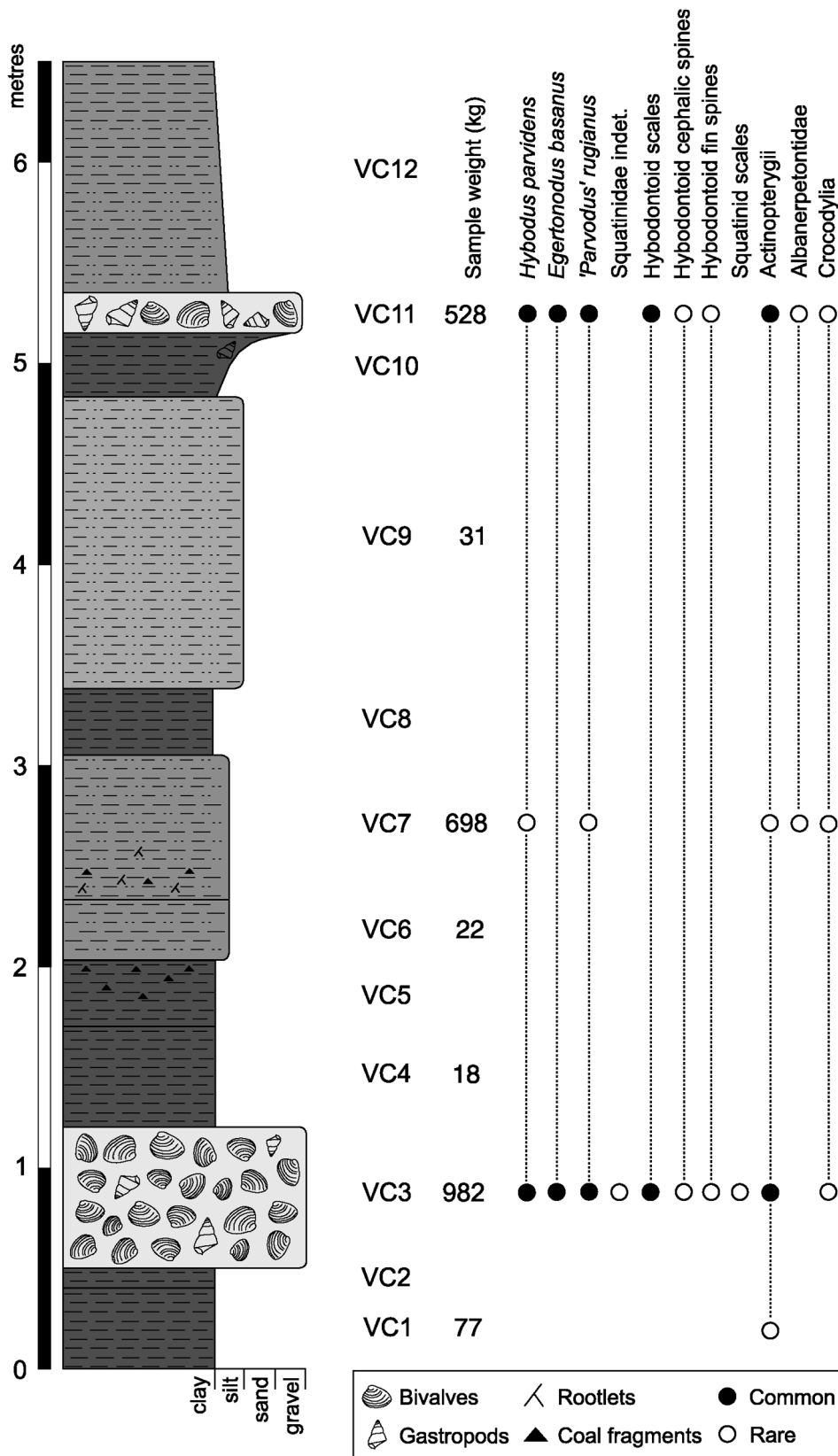


Figure 3 Distribution of vertebrate fossils in the Vitabäck Clay section excavated and sampled at Eriksdal.

The upper part of their section is most likely Berriasian, as the palynoflora from the mid-part included *Cicatricosisporites australiensis* and *Trilobosporites obsitus*, previously only recorded from Early Cretaceous deposits (Erlström *et al.* 1991). The lower parts of their section did not include any stratigraphically diagnostic palynomorphs and were consequently not dated.

While sampling the section described herein, a number of smaller samples were collected for palynological investigation. The lowermost parts of the section (beds VC1 and VC2) contained spores of the genus *Cicatricosisporites*, previously known only from the Early Cretaceous (V. Vajda pers. comm.). Thus, the whole section described in this work is considered to be Berriasian or possibly younger, although the lower parts of the Vitabäck Clays, not treated here, are likely to be Tithonian (Erlström *et al.* 1991). Berriasian age is further indicated by the composition of the shark fauna, which is very similar to that of Berriasian sediments within the Purbeck Group in southern England (Underwood & Rees 2002).

In the Ängelholm Basin, the Vitabäck Clays occur beneath a thick Quaternary cover. Guy-Ohlsøn & Norling (1988) examined core material and found foraminifera indicative of an Early Cretaceous age in the upper parts of the Vitabäck Clays. The foraminifera also imply that the marine influence was higher in northwestern Scania than in the Vomb Trough.

## 2. Associated fauna

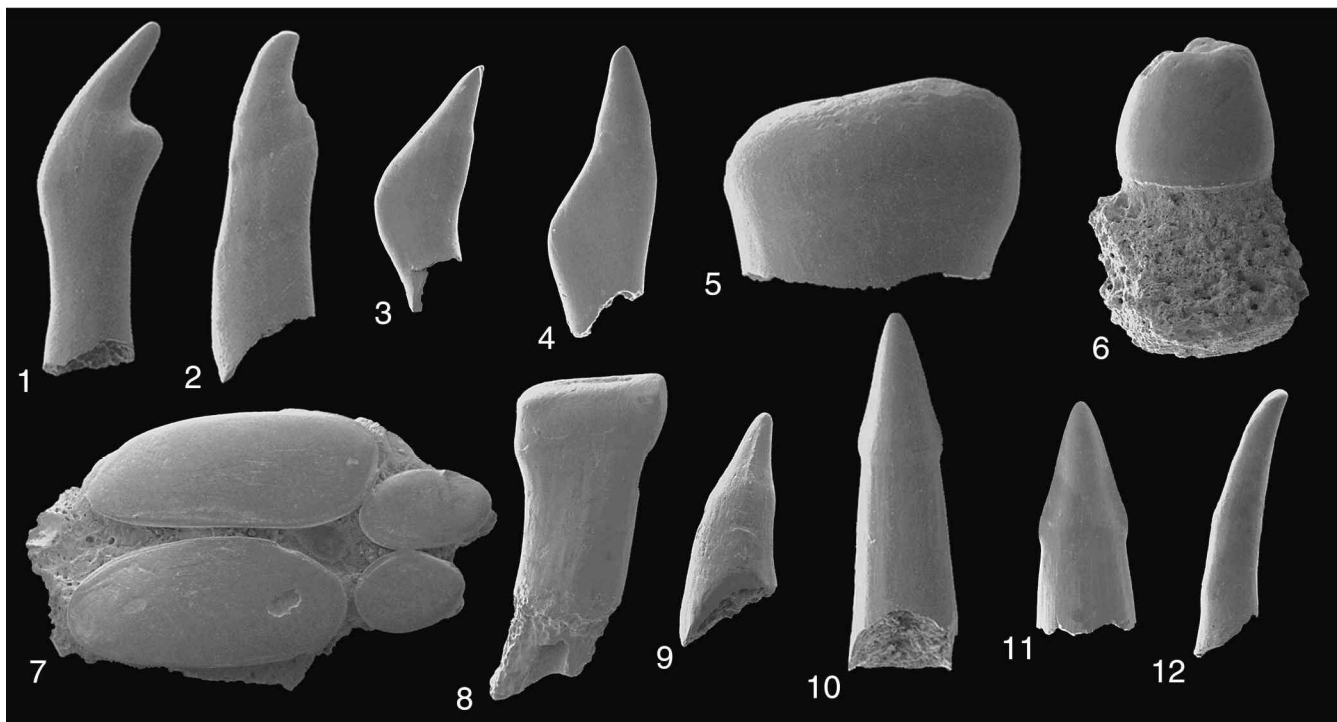
### 2.1. Molluscs

Macrofossils of bivalves and gastropods occur in large numbers only in the two coquina beds, VC3 and VC11. Although the molluscs are quite fragile, they are well preserved with rare specimens still possessing the original shell pattern. Bivalves are primarily represented by three taxa within three genera:

*Neomiodon*, *Isognomon* and an indeterminate ostreid. The vast majority of the gastropods are referred to two common species of the two genera *Viviparus* and *Ptychostylus*. Other gastropod species are rare. The composition of the mollusc fauna is slightly different in the two coquina beds (see also 3.1). Both faunas are characterised by low diversity. The most common mollusc is *Neomiodon*, which is frequent in both coquina beds. The other two common bivalve taxa, *Isognomon* and the ostreid, are abundant in VC3 but the latter is missing in the VC11 fauna. Gastropods are rare in VC3, with only a few *Ptychostylus* recorded. The gastropod fauna in VC11 comprises primarily numerous *Viviparus*, although a few other taxa are present, including *Ptychostylus* and *Neritoplica*. In VC7, only fragmented shells of *Neomiodon* have been found.

### 2.2. Actinopterygians

No articulated actinopterygian skeletons have been found in the Vitabäck Clays but isolated remains, including teeth, scales and bones, are very common in the two coquina beds, VC3 and VC11, and less so in VC1 and VC7. Traditionally, isolated remains of bony fishes have largely been considered more or less taxonomically useless. However, Mudroch & Thies (1996) were able to identify isolated actinopterygian teeth from Kimmeridgian deposits to the generic level by comparing them to teeth on articulated skeletons from the Tithonian lithographic limestones of southern Germany. The most common actinopterygian remains are included in *Lepidotes* (Fig. 4. 1–5), a widespread semionotiform genus. The material includes both oral and branchial teeth. The variable morphology of the oral, and in particular the branchial, teeth suggests that more than one species is present in the Vitabäck Clay material. Species of *Lepidotes* are believed to have been euryhaline (Thies & Mudroch 1996) and cannot be used as reliable indicators of palaeosalinity. Other, less common, teeth can be referred to



**Figure 4** Actinopterygian teeth from the Vitabäck Clay section, 1–5, 9–10, 12 from VC3; 6–8, 11 from VC11: (1–4) branchial teeth of *Lepidotes* sp., LO8385t–LO8388t, showing different morphologies,  $\times 20$ ; (5) oral tooth of *Lepidotes* sp., LO8389t,  $\times 20$ ; (6) tooth of ?*Macromesodon* sp., LO8390t,  $\times 20$ ; (7) partial dentary of *Proscinetes* sp., LO8391t,  $\times 8$ ; (8) tooth of ?*Macromesodon* sp., LO8392t,  $\times 20$ ; (9) tooth of *Ionoscopus* sp., LO8393t,  $\times 20$ ; (10–11) teeth of *Caturus* sp., LO8394t, LO8395t,  $\times 20$ ; (12) tooth of ?*Thrissops* sp., LO8396t,  $\times 20$ .

different halecomorphs, including *Caturus* (Fig. 4. 10–11) and *Ionoscopus* (Fig. 4. 9). All three taxa mentioned above are present in both VC3 and VC11 and only *Caturus* is lacking in the VC7 sample. A few teeth and partial dentaries of pycnodontiforms are also recorded (only in VC11) and some of these can be referred to *Proscinetes* (Fig. 4. 7), a genus that also occurs in the German Kimmeridgian and is considered marine and stenohaline (Thies & Mudroch 1996). This does not agree well with other indicators of palaeosalinity in VC11, which imply oligohaline conditions (see 3. 1). Other actinopterygian teeth can possibly be included in *Macromesodon* (Fig. 4. 6, 8) and *Thrissops* (Fig. 4. 12) although these identifications are only tentative. Both the latter taxa are recorded in VC3 and VC11. Some additional actinopterygian remains could not be identified.

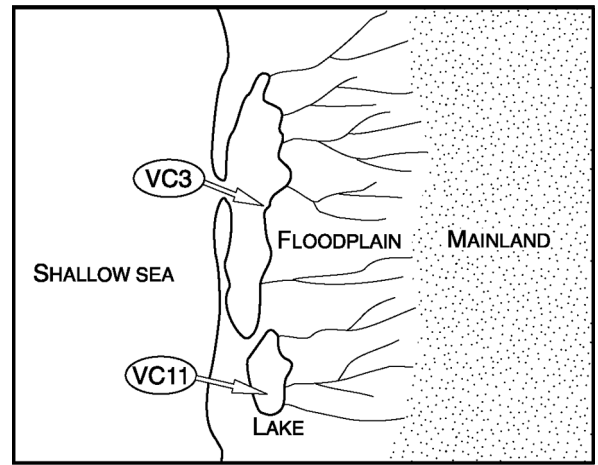
### 2.3. Tetrapods

Tetrapod remains are extremely rare and had previously not been recorded in the Vitabäck Clays. Amphibians are represented by isolated skeletal remains of the Albanerpetontidae, present primarily in VC7, although two incomplete dentaries and one articular bone were extracted from VC11. The bones are not complete enough to allow a closer determination, but are fully described by Rees & Evans (2002). Crocodile remains have been recorded in VC3, VC7 and VC11. A total of eight teeth and a single scute have been found. The remains probably belong to two species, one of which is possibly referable to *Theriosuchus*.

## 3. Palaeoecology

### 3.1. Depositional environment

The faunas from the Vitabäck Clays clearly indicate fluctuating palaeosalinity levels previously noted in other parts of the member by Christensen (1968). The molluscs extracted from VC3 appear to have lived in a brackish-marine environment (Erlström *et al.* 1991). The bivalves *Isognomon* and the ostreid indicate at least mesohaline (5–18‰) conditions (Fürsich 1993). The gastropod *Ptychostylus*, also found in VC3, is a typical element in mesohaline environments (Fürsich 1993). The presence of serpulid tubes on the ostreid shells also suggests marine influence (Fürsich 1993). The mollusc fauna of the other coquina bed, VC11, primarily includes the bivalve *Neomiodon*, typical of freshwater to mesohaline conditions (Hudson *et al.* 1995), and the gastropod *Viviparus*. In combination with *Neomiodon*, this gastropod forms a typical oligohaline (0.5–5‰) association (Hudson 1963). The vertebrate faunas also indicate a higher palaeosalinity in VC3. A few remains of Squatinidae indet. and a single chimeroid tooth plate fragment were found in VC3. Both indicate marine conditions. However, as these occurrences are very rare, they may represent allochthonous elements in the fauna. The amphibian remains occurring in VC11 suggest that this bed may have been deposited in a floodplain lake (Fig. 5). The coquina bed VC3 was deposited closer to the shallow sea (Fig. 5), probably in a lagoonal environment. The erosional boundary at the bottom of VC3 may indicate that the bed is a storm concentration. The enrichment of shells in VC11 is more gradual and there is no erosional boundary at the bottom of the bed, perhaps indicating an environment such as a floodplain lake or pond. The molluscs have possibly been concentrated by migration when the water in the pond evaporated (cf. Noe-Nygaard *et al.* 1987). The presence of amphibian remains, in combination with the rarity of shark teeth in VC7, may indicate that this bed was deposited in a freshwater environment. The actinopterygian remains



**Figure 5** Proposed depositional environment of the two coquina beds (VC3 and VC11), partly based on Erlström *et al.* (1991, fig 26).

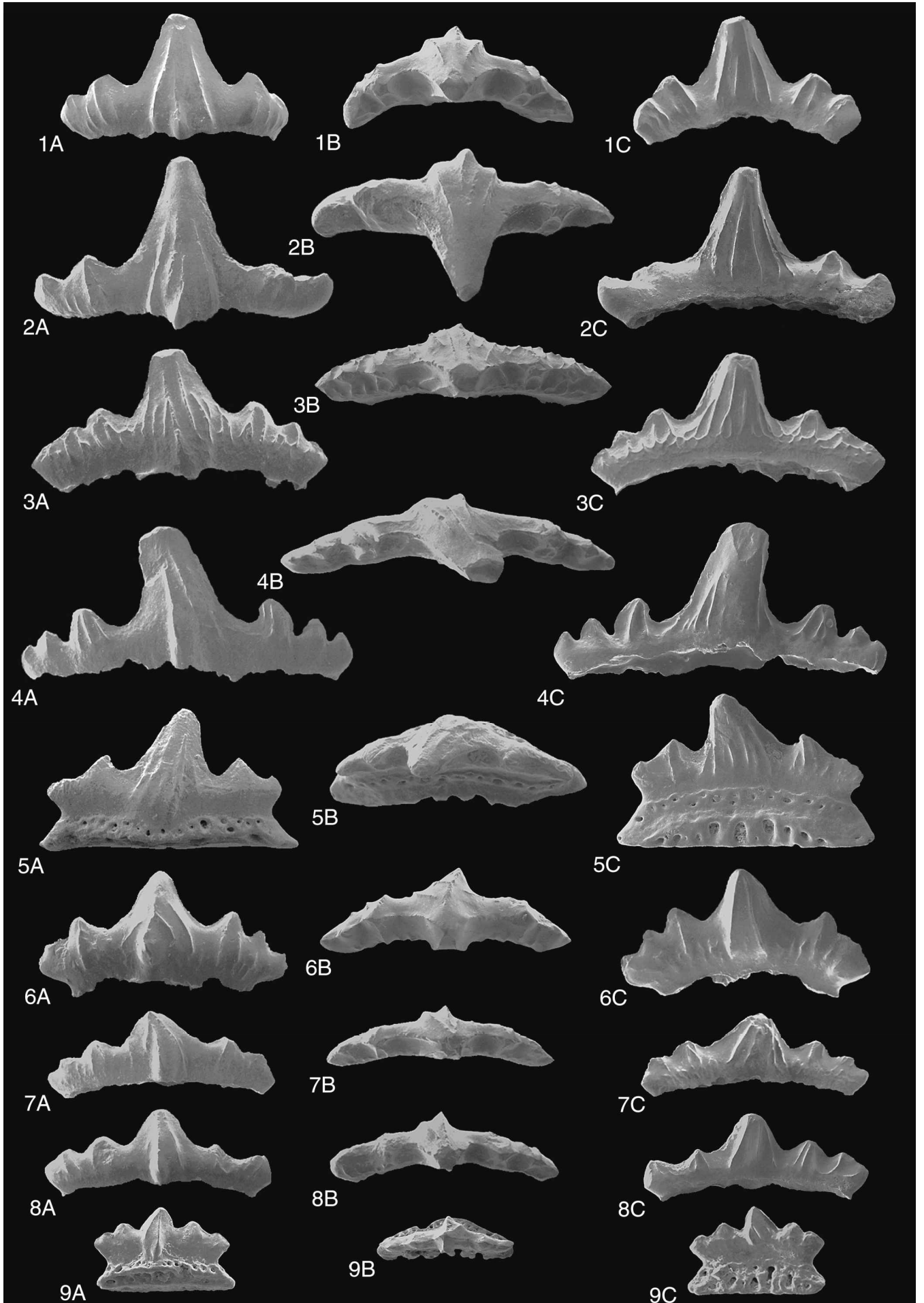
include only *Lepidotes* and *Ionoscopus*, two genera that are considered brackish by Thies & Mudroch (1996).

### 3.2. Shark autecology

As complete fossil sharks with preserved stomach contents are extremely rare, their diet has to be inferred by studying their dentition. Teeth with a high and slender central cusp are most likely used to pierce through the soft skin of non-shelled invertebrates, such as cephalopods, or the thin scales of smaller actinopterygians or other sharks. Species with piercing teeth in the Vitabäck Clay material include *Egertonodus basanus* and, to a lesser extent, *Hybodus parvidens*, where only the anterior teeth are piercing. The dentition of *E. basanus* is a more pronounced tearing type dentition where all teeth, including the laterals, have a high central cusp. These sharks were probably at the top of the food web, accompanied by the occasional crocodile in the lagoonal environment. Small hybodont sharks with lower multicuspidate teeth, including *Parvodus rugianus* from the Vitabäck Clays, probably had a number of functional teeth in each file. The teeth in the anterior files would form a clutching-type dentition (of Cappetta 1987). Lateral files, with lower, often less cuspidate teeth, form a crushing surface in the back of the jaw. These sharks probably fed on various invertebrates with fairly thin shells. Thin-shelled molluscs, like *Viviparus*, were probably part of the diet of *P. rugianus* in the Vitabäck Clay fauna.

## 4. Palaeobiogeography

Selachian faunas from non-marine Late Jurassic and Early Cretaceous strata are primarily known from Europe and adjacent areas, including England (Patterson 1966; Underwood & Rees in press), Germany (Ansorge 1990) and Sweden (herein), with scattered remains known from France (Cuny *et al.* 1991; Hervat & Hervat 1993) and Morocco (Duffin & Sigogneau-Russell 1993). The selachian assemblages from southern England, including both the Purbeck (Tithonian–Valanginian) and the Wealden (Valanginian–Barremian) faunas, are by far the most thoroughly investigated (Woodward 1916, 1919; Patterson 1966; Underwood & Rees 2002). The Purbeck fauna includes eight species, of which six are hybodonts. The other two species are rhinobatoid rays, only present in a narrow stratigraphic interval where the molluscs are indicative of a higher palaeosalinity. Among the hybodonts, three species



appear to be endemic to England. The other three Purbeck species, *Egertonodus basanus*, *Hybodus parvidens* and *Parvodus rugianus* are also recorded from the Vitabäck Clays. The slightly younger Wealden fauna, spanning a larger time interval, is more diverse, comprising ten hybodont species. Only *E. basanus* and *H. parvidens* are present in both the Wealden and the Vitabäck Clay faunas.

In Germany, a small assemblage from the Early Cretaceous on the island of Rügen was described by Ansgore (1990). The shark teeth occur in a glacial raft of 'Wealden Clay' transported to its present location during the Quaternary. The hybodont fauna described by Ansgore (1990) have the same composition as the Vitabäck Clay fauna including *E. basanus* (recorded as *Hybodus* sp.), *H. parvidens* (recorded as '*Lissodus*' *rugianus*) and *P. rugianus*. In France, *H. parvidens* has been recorded in Tithonian non-marine sediments both in the SW (Hervat & Hervat 1993) and in the N (Cuny *et al.* 1991, recorded as *Hybodus* sp.) of the country. Duffin & Sigogneau-Russell (1993) described Early Cretaceous (?Berriasian) shark teeth of two species from Morocco, including the seemingly endemic '*Lissodus*' *marocensis*, and *E. basanus*, the latter also found in southern Sweden.

## 5. Material and methods

Since the Vitabäck Clays are covered by at least 1 m of Quaternary deposits, large bulk samples can only be obtained from temporary excavations. The material dealt with in this work was collected during three excavations, carried out in 1995, 1998 and 1999. The excavation site is situated in a field, NE of the road crossing at the Vitabäck farmhouse (Fig. 1). The locality is now inaccessible due to agricultural activities. During the 1998 excavation, a section of 6.5 m was measured (Fig. 3) and the beds were assigned numbers prefixed VC (Vitabäck Clays). The lower coquina bed, VC3, was used as a reference bed, as it was used for the same purpose in the excavation carried out by the Swedish Geological Survey in 1989 (Bed E: 1 in Erlström *et al.* 1991). This horizon is the only bed that can be correlated between the two excavations as the large section in Erlström *et al.* (1991) is not detailed enough. The bed thick-

nesses in Figure 3 are not reliable, but represent the conditions observed in the field. The true bed thicknesses are difficult to determine (Erlström *et al.* 1991), as the Quaternary overburden has distorted the unconsolidated Mesozoic sediments. Bulk samples were primarily collected from three horizons, VC3, VC7 and VC11. The sediment was dried and washed in a clay washing machine (as described in Ward (1981)), using a sieve with a 355 µm aperture. The washed residue of the coquina beds, which included many carbonate shell fragments, was dissolved in buffered acetic acid. The poorly consolidated siltstones present in VC11 were frozen in several cycles to break down the sediment. After being dried, the fraction below 1.0 mm was fed through a magnetic separator in order to remove iron-cemented pieces of siltstone. All residues were picked to the 500 µm fraction and the residues of VC3 and VC11 were also picked to the 355 µm fraction. The quartz grains of the latter fraction were removed by means of density separation using sodium polytungstate. Hybodont teeth are very abundant in VC3 and VC11 and fairly well preserved, particularly in VC3. Endolithic borings are rare but occur occasionally on smaller teeth. Apart from shark teeth, actinopterygian remains and molluscs are the most common fossils in VC3 and VC11.

The descriptive terminology of the shark teeth follows that of Cappetta (1987), while the placoid scale terminology is largely from Thies (1995). All illustrated specimens are deposited in the type collection of the Division of Historical Geology and Palaeontology at Lund University, Sweden, and prefixed LO (Lund Original). Photographed specimens were coated with gold and photographed using a SEM.

## 6. Systematic palaeontology

Cohort Euselachii Hay, 1902  
 Superfamily Hybodontoida Owen, 1846  
 Family Hybodontidae Owen, 1846  
 Genus *Hybodus* Agassiz, 1837

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

*Hybodus parvidens* Woodward, 1916  
 (Fig. 6)

- 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.  
 1982 *Hybodus parvidens* Woodward; Estes & Sanchiz, p. 22, fig. 1A–B.  
 1987 *Polyacrodus parvidens* (Woodward); Cappetta, p. 37.  
 1989 *Lissodus* sp.; Buffetaut *et al.*, p. 1065, pl. 1, fig. I.  
 1990 *Lissodus rugianus* n. sp. [*partim*]; Ansgore, p. 136, figs 10–11 non 4–9, 12–15.

**Table 1** Number of teeth and scales of the different taxa in beds VC3, VC7 and VC11.

Species	Bed:	VC3	VC7	VC11
<i>Hybodus parvidens</i>		163	3	144
<i>Egertonodus basanus</i>		319	–	257
<i>Parvodus rugianus</i>		1712	3	332
Squatinae indet.		1	–	–
Hybodontoid scales		363	–	292
Squatinae scales		10	–	–
Total		2568	6	1025

**Figure 6** Teeth of *Hybodus parvidens* Woodward, 1916, ×20, all teeth from VC3 except 1, 3, and 6 from VC11: (1) anterior tooth-crown, LO8397t, in labial (A), occlusal (B) and lingual (C) views; (2) anterior tooth-crown, LO8398t, in labial (A), occlusal (B) and lingual (C) views; (3) antero-lateral tooth-crown, LO8399t, in labial (A), occlusal (B) and lingual (C) views; (4) antero-lateral tooth-crown, LO8400t, in labial (A), occlusal (B) and lingual (C) views; (5) lateral tooth (possibly ingested), LO8401t, in labial (A), occlusal (B) and lingual (C) views; (6) lateral tooth-crown, LO8402t, in labial (A), occlusal (B) and lingual (C) views; (7) posterior tooth-crown, LO8403t, in labial (A), occlusal (B) and lingual (C) views; (8) posterior tooth-crown, LO8404t, in labial (A), occlusal (B) and lingual (C) views; (9) juvenile tooth, LO8405t, in labial (A), occlusal (B) and lingual (C) views.

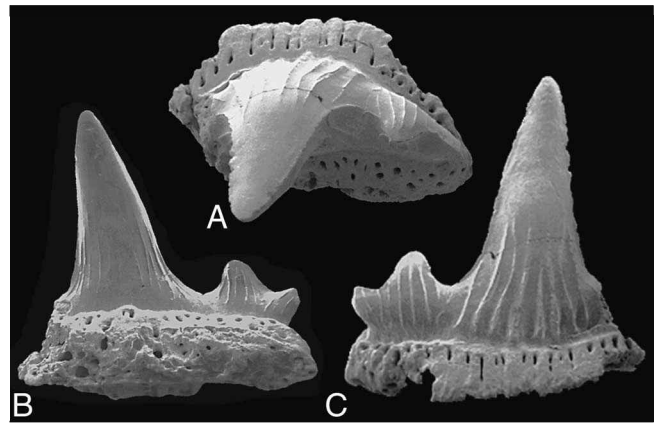
- 1991 *Hybodus* sp.; Cuny *et al.*, p. 326, fig. 1T.  
 1993 *Polyacrodus parvidens* (Woodward); Hervat & Hervat, pp. 43–8, figs 1–8.  
 2002 *Polyacrodus parvidens* (Woodward); Underwood & Rees, p. xx, pl. 1, fig. 1, 4, 8–9.

**Material.** Five complete and 305 incomplete teeth, LO8397t–LO8405t and unnumbered.

**Occurrence.** This species was widespread in northwestern Europe where its remains are found exclusively in non-marine sediments. Apart from the English Purbeck and Wealden (Berriasian to Barremian) occurrences (Patterson 1966; Underwood & Rees 2002), *H. parvidens* also occurs in latest Jurassic and Early Cretaceous deposits in France (Cuny *et al.* 1991 as *Hybodus* sp.; Hervat & Hervat 1993), northern Germany (Ansorge 1990 as '*Lissodus*' *rugianus*) and Spain (Estes & Sanchíz 1982). The presence of *H. parvidens* in the Vitabäck Clays extends its palaeogeographical range to the N.

**Description.** The dentition of this species is characterised by gradient monognathic heterodonty. The piercing anterior teeth (Fig. 6. 1–2) have a high and slender central cusp flanked by two or, less commonly, three pairs of lateral cusplets. A keel is present on the labial side of the cusp. Ornamentation consists of a small number of coarse folds covering large parts of the crown. The cutting edges are well developed, particularly on anterior teeth. In occlusal view, anterior teeth may be curved, with the lateral tips lingually inclined. Antero-lateral teeth (Fig. 6. 3–4) are as high as anteriors but the whole crown is distally inclined. Lateral teeth (Fig. 6. 5–6) have a slightly lower cusp that is usually also distally inclined. The lateral cusplets are of the same size as in the anterior teeth. Latero-posterior and posterior teeth (Fig. 6. 7–8) are low-crowned with a cusp that is only twice the height of the cusplets. Juvenile teeth (Fig. 6. 9) are low and less ornamented than larger specimens and the foramina on the root are more irregularly placed. The labial crown–root junction is slightly incised but flat on the lingual side. The root is characterised by a low labial side and a much higher lingual side. The labial side of the root displays an irregular row of small circular foramina, close to the crown–root junction. On the lingual side, there is a similar row and additionally a number of larger foramina on the lower part of the root. The largest tooth (Fig. 6.4) measures 3.1 mm in total width.

**Discussion.** This species was reassigned to *Polyacrodus* Jaekel, 1889 by Cappetta (1987), a view followed by Underwood & Rees (2002). A closer study of the type species of *Polyacrodus*, *P. polycyphus* (Agassiz, 1837) from the Middle Triassic of northern France, reveals that *H. parvidens* is very different from this species, both in general tooth morphology and in heterodonty pattern. The high and slender central cusp of *H. parvidens* is clearly different from the low and blunt cusp of *P. polycyphus*. The ornamentation on teeth of *H. parvidens* comprises a few coarse folds, while numerous weak folds cover the entire crown in *P. polycyphus*. Lateral teeth of *P. polycyphus* are mesio-distally more expanded than anterior teeth, while the proportions between anteriors and laterals are the opposite in *H. parvidens*. Consequently, *H. parvidens* cannot be included in *Polyacrodus*. The heterodonty pattern of *H. parvidens* is more similar to that of *H. reticulatus* and *Egertonodus basanus* (see Maisey 1983, fig. 18). Isolated teeth of the latter genus are at present not possible to distinguish from those of the dentally similar *Hybodus* (Underwood & Rees 2002) and *Egertonodus* is at present best considered monotypic until more skeletal material of nominal *Hybodus* species is investigated. As originally described, *H. parvidens* is at present best retained in the genus *Hybodus*.



**Figure 7** Incomplete anterior tooth of *Egertonodus basanus* (Egerton, 1845), LO8406t, in occlusal (A), lingual (B) and labial (C) views,  $\times 10$ , from VC11.

#### Genus *Egertonodus* Maisey, 1987

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

#### *Egertonodus basanus* (Egerton, 1845) (Fig. 7)

- 1845 *Hybodus basanus* sp. nov.; Egerton, p. 197, pl. 4.  
 1916 *Hybodus basanus* Egerton; Woodward, p. 5, pl. 1, figs 1–3, pl. 2, fig. 1.  
 1966 *Hybodus basanus* Egerton; Patterson, pp. 288–92, pl. 1, fig. 1, text-figs 1–3.  
 1983 *Hybodus basanus* Egerton; Maisey, pp. 1–64, figs 1–26.  
 1987 *Hybodus basanus* Egerton; Cappetta, p. 31, fig. 38.  
 1987 *Egertonodus basanus* (Egerton); Maisey, p. 27.  
 1990 *Egertonodus basanus* (Egerton); Batchelor & Ward, p. 184–5, pl. 1, fig. 1.  
 1993 *Egertonodus basanus* (Egerton); Duffin & Sigogneau-Russell, pp. 181–4, fig. 5.  
 2002 *Egertonodus basanus* (Egerton); Underwood & Rees, p. xx, text-figs 4–5.

**Material.** One almost complete tooth, LO8406t, and 575 incomplete tooth-crowns.

**Occurrence.** Remains of this shark were originally described from the Early Cretaceous of southern England, but it has also been encountered in Germany (Ansorge 1990, as *Hybodus* sp.) and Morocco (Duffin & Sigogneau-Russell 1993).

**Description.** The dentition of *E. basanus* is of the tearing type with a low degree of monognathic heterodonty. The teeth have a high and slender cusp, usually flanked by two pairs of moderately high lateral cusplets. The cusp has a sigmoidal curvature in lateral view, as the crown is inclined lingually but the apex of the cusp is bent labially. The cusp is oval to circular in cross-section with strongly developed cutting edges. Vertical folds cover the entire crown, except for the upper half of the cusp. The folds are generally weaker but more numerous on the lingual side. Lateral and posterior teeth become gradually lower and the cusp and cusplets more posteriorly inclined towards the back of the jaw. The largest teeth are up to 6 mm in width and 5 mm in height.

**Discussion.** The sigmoidal curvature of the cusp in this species is unique among hybodonts and may be a character that can be used to separate teeth of *Egertonodus* from teeth of *Hybodus*, although more characters would certainly be preferable.



The assemblage of *E. basanus* teeth from the Vitabäck Clays only includes fairly small teeth with a maximum cusp height of 5 mm as opposed to at least 8 mm in the material from southern England. The difference can possibly be explained by the lagoonal or floodplain lake environments that prevailed when the Vitabäck Clays were deposited and larger sharks may have lived in deeper water. The Purbeck and Wealden deposits in southern England were exposed to more marine influence during deposition.

#### Family Lonchidiidae Herman, 1977

**Remarks.** In contrast to the opinion of Duffin (1985), Rees & Underwood (2002) consider the genus *Lonchidion* Estes, 1964 as justified and not a junior synonym of *Lissodus* Brough, 1935. The author also agrees with Batchelor & Ward (1990) in treating the family Lonchidiidae as a justified taxon as the synonymy above is rejected. Among the species included in *Lissodus* by Duffin (1985), there are three species ('*L.*' *curvidens* Duffin & Thies, 1997; '*L.*' *pattersoni* Duffin, 1985 and '*L.*' *rugianus* Ansorge, 1990) forming a distinct group. These species are included in the new genus *Parvodus* Rees & Underwood, 2002, of which *P. rugianus*, being the most well-known species, is the type species.

#### Genus *Parvodus* Rees & Underwood, 2002

**Type species.** *Lissodus rugianus* Ansorge, 1990 from the Early Cretaceous of the island of Rügen, northern Germany.

#### *Parvodus rugianus* (Ansorge, 1990) (Fig. 8)

- 1966 *Lonchidion heterodon* sp. nov. [*partim*]; Patterson, pp. 326–8, text-fig. 25B non text-fig. 25A, C–D.  
 1990 *Lissodus rugianus* sp. nov. [*partim*]; Ansorge, pp. 136–7, figs 4–8 non figs 9–11.  
 2002 *Polyacrodus rugianus* (Ansorge); Underwood & Rees, p. xx, plate 1, figs 7, 10–12.  
 2002 *Parvodus rugianus* (Ansorge); Rees & Underwood, p. xx, fig. 3S–X.

**Material.** 20 complete and 207 incomplete teeth, LO8407t–LO8420t and unnumbered.

**Occurrence.** This species was originally described from the island of Rügen in northern Germany and has since been recorded in the Purbeck of southern England (Underwood & Rees 2002) and is so far restricted to a fairly small area in northern Europe.

**Description.** The dentition of this species is characterised by a low degree of monognathic heterodonty where anterior teeth have a moderately high cusp and up to three pairs of cusplets. The number of vertical folds is highly variable within the species, particularly on anterior teeth. Folds are always present on the cusp and the cusplets except on a few teeth where weaker, undulating striations comprise the ornamentation (Fig. 8. 8). The labial protuberance is moderately strong and so is the occlusal crest. The most proximal pair of cusplets is situated far away from the cusp but the cusplets themselves are all closely spaced. In this species, lateral teeth are mesiodistally as wide as anteriors but have a lower cusp. Posterior teeth may lack demarcated cusplets and only possess a minute cusp. These are also less ornamented than anteriors. Extreme posterior teeth (Fig. 8. 14) have a mesiodistally narrow crown with a clearly wider root. The root is preserved on 20 teeth and the lingual side displays a very porous structure with large irregular foramina. The labial side is low and has a number of small, circular foramina arranged in an irregular

row above a shelf on the root. The largest teeth in the Vitabäck Clays collection measure 3.7 mm in width.

**Discussion.** This species was first described by Ansorge (1990) on the basis of eight teeth, although three of these actually belong to *Hybodus parvidens*. There has been some confusion as to the generic affinity of the species. Originally, it was included in *Lissodus* but the tooth morphology is only distantly similar to that of *L. africanus* (Broom, 1909), the type species of *Lissodus*. Because of a superficial resemblance to *H. parvidens*, previously included in *Polyacrodus* (Cappetta 1987), this species will also be assigned to the latter genus by Underwood & Rees (2002), awaiting a revision of *Polyacrodus*. However, when examining the type species of *Polyacrodus*, it became obvious that *Parvodus rugianus* could not be referred to this genus either. It has to be separated and is now the type species of *Parvodus* Rees & Underwood, 2002.

#### Hybodontoida gen. et sp. indet.

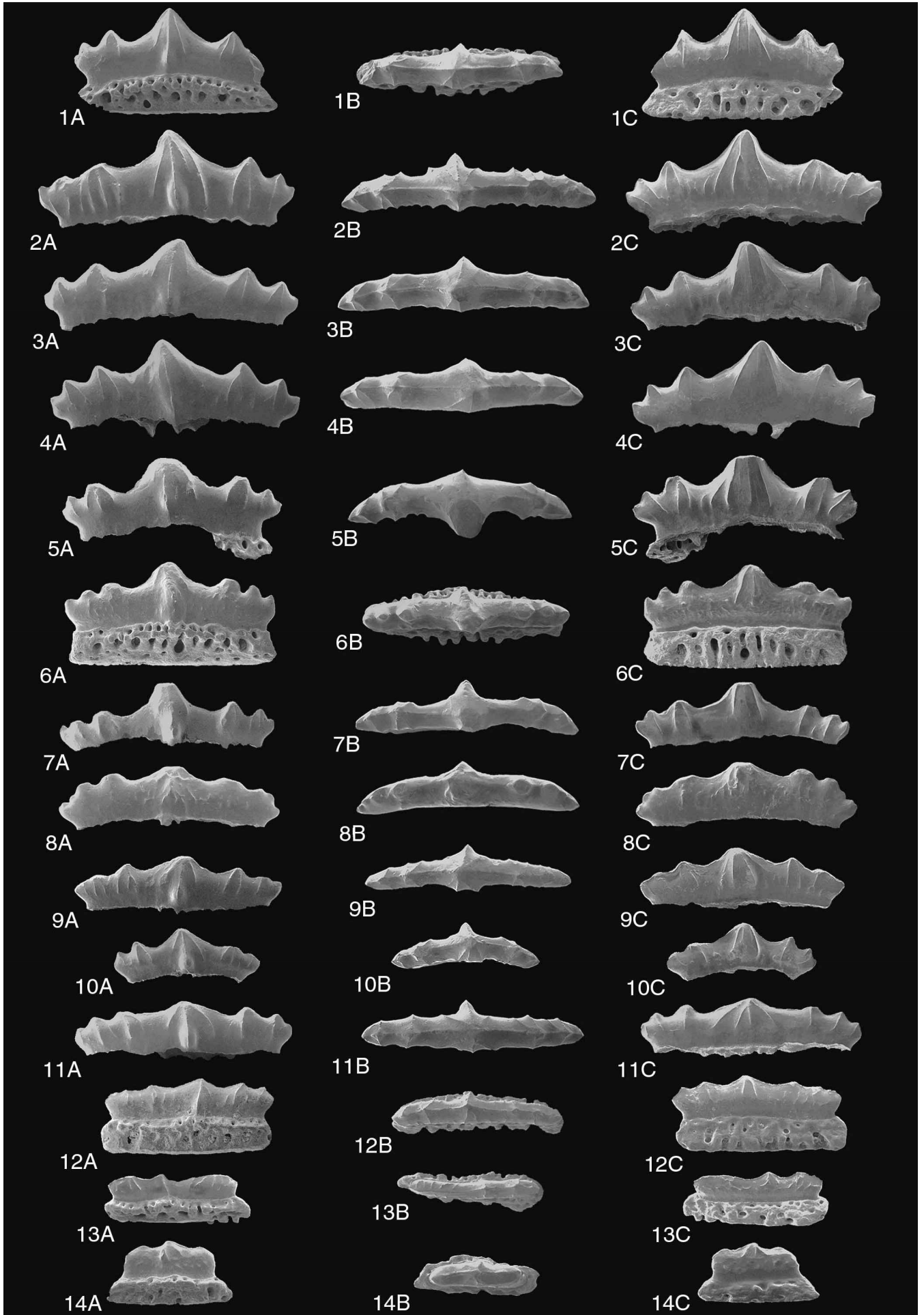
**Remarks.** Common remains of hybodont sharks include isolated placoid scales, fin spines and cephalic spines. All three types of remains share an obvious affinity problem if they occur associated with oral teeth of more than one hybodont species. Both fin spines and cephalic spines have previously been given species names of their own (e.g. Agassiz 1843; Woodward 1919), but unless they can be matched to a particular species by association with teeth, they are likely to remain as *nomina dubia* in the view of most authors.

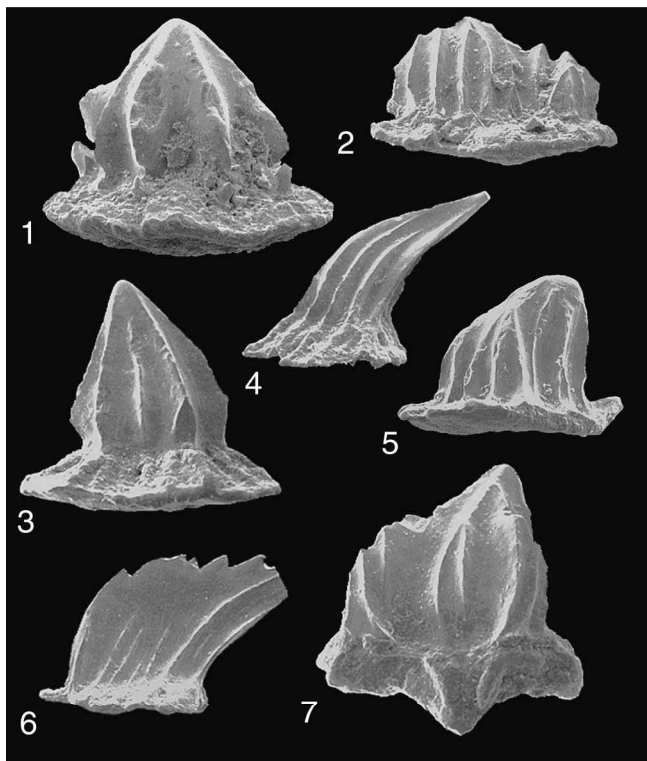
**Placoid scales.** The mineralised placoid scales or dermal denticles of selachians are often overlooked because of their small size and problematic systematic position. After studying scale morphogenesis, Reif (1978) assigned placoid scales from different groups of sharks to three different morphological types, including the Hybodontoid type. More recently, Thies (1995) split up the latter group into five morphotypes within the superfamily Hybodontoida. He concluded that even though isolated scales cannot at present be assigned to a single species or even genus, they can have stratigraphical significance as they may have in the Palaeozoic. The classification of Hybodontoid scales below follows that of Thies (1995) with the addition of a new morphotype.

Five different morphotypes of hybodontoid scales have been recorded in the Vitabäck Clays. The most common scales belong to morphotype 1 (Fig. 9. 1–3), which are large, up to 2.6 mm in basal width, and knob-like. These scales are ornamented with coarse ridges, usually continuing to a lesser degree on the base. All ridges merge at the apex, situated in the centre of the scale, and the scales are almost symmetrical. The basal face is slightly convex or flat and displays a few nutritive foramina. On a few smaller scales the ridges are frequently branching. Two scales included in morphotype 1 have two tips and appear to have been formed by two fused scales (Fig. 9. 2) while other scales in the collection are clearly higher and more slender (Fig. 9. 3) than the scales figured by Thies (1995). These are at present retained in morphotype 1.

Scales of morphotype 2 (Fig. 9. 5) are similar to those of morphotype 1, but differ in that the apex is not situated above the centre of the base and most scales are slightly inclined to the posterior. Variation occurs in the number of ridges and in that all ridges may not reach the apex. The morphology of the base is similar to that of morphotype 1. These scales measure up to 0.8 mm in basal width.

Scales of morphotype 3 (Fig. 9. 4) are pointed and strongly posteriorly inclined. All ridges may merge at the apex even though this is not the case in the scales of this morphotype figured by Thies (1995). The base is small and basally concave. These scales measure up to 1.0 mm in length.

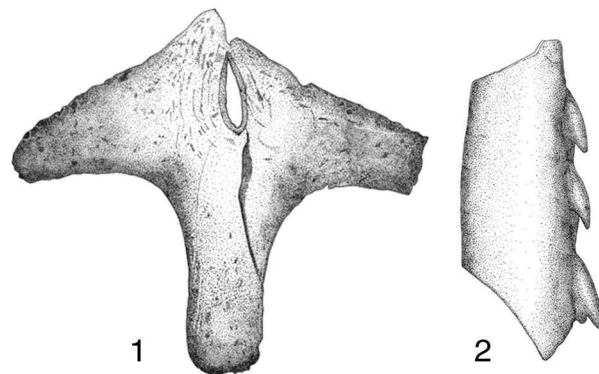




**Figure 9** Hybodontoid placoid scales, all from VC3: (1) morphotype 1, LO8421t, in lateral view,  $\times 30$ ; (2) morphotype 1, LO8422t, in lateral view,  $\times 35$ ; (3) morphotype 1, LO8423t, in lateral view,  $\times 35$ ; (4) morphotype 3, LO8424t, in lateral view,  $\times 35$ ; (5) morphotype 2, LO8425t, in lateral view,  $\times 60$ ; (6) morphotype 6, LO8426t, in lateral view,  $\times 35$ ; (7) morphotype 4, LO8427t, in anterior view,  $\times 60$ .

Morphotype 4 (Fig. 9. 7) include scales with a blade-like appearance in anterior view, where one or two ridges end half-way towards the apex. The ridges are not as closely spaced as in the other morphotypes discussed above. The morphology of the base is irregular, often having two lateral lobes. The largest scale of this morphotype measures 0.7 mm in width.

In the Vitabäck Clay material, there is another type of hybodontoid scale not described from the Kimmeridgian sediments of northern Germany studied by Thies (1995). This type is a very thin blade, oriented parallel to the long axis of the shark and inclined posteriorly. The scales are ornamented with a few weak ridges, primarily close to the base, and have an irregular upper edge. The base is small and non-ornamented. The scales measure up to 1.8 mm in length. This is a new type of hybodontoid scale that appears to be derived from scales of morphotype 3. It is here referred to the new morphotype 6 (Fig. 9. 6).



**Figure 10** Hybodontoid cephalic spine, tentatively referred to *Egertonodus basanus* (Egerton, 1845), and indeterminate fin spine: (1) cephalic spine from VC11 lacking the cusp, LO8428t, in dorsal view,  $\times 6$ ; (2) fragmentary fin spine from VC3, LO8429t, in lateral view,  $\times 7$ .

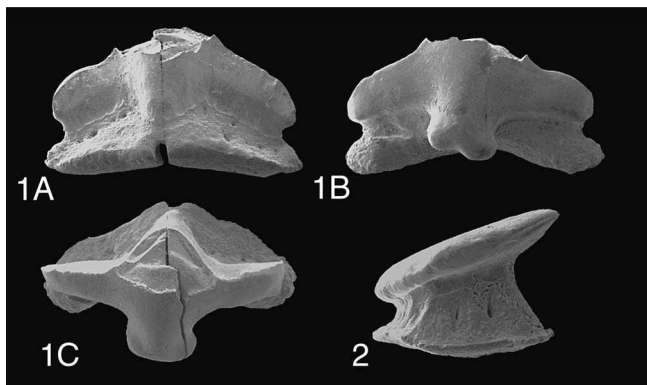
**Cephalic spines.** Two incomplete cephalic spines, both lacking the cusp, are present in the Vitabäck Clays collection, found in VC3 and VC11 (Fig. 10. 1) respectively. The basal plate is 'T-shaped' with two anterior and one posterior lobe. The anterior lobes are terminally rounded while the posterior lobe is parallel-sided and only rounded towards the very end. Among the hybodont species recorded by teeth in the Vitabäck Clays, the cephalic spine morphology is known from *Hybodus parvidens* and *Egertonodus basanus*. The former species was recorded by both teeth and spines as the only hybodont in a latest Jurassic non-marine deposit in France (Hervat & Hervat 1993). Hence, the cephalic spine morphology could be determined. The basal plate of cephalic spines of *H. parvidens* has a 'convict-arrow' shape with posteriorly inclined anterior lobes, quite unlike that of the spines from the Vitabäck Clays. The cephalic spine morphology of *E. basanus* is well known from several complete and partial skulls from the Early Cretaceous of southern England. The basal plate is 'T-shaped' and similar to that of the spines from the Vitabäck Clays. However, since the morphology of the spines in *Parvodus rugianus* is not known, the referral of the spines to *E. basanus* has to be tentative.

**Fin spines.** Only a few fragmentary fin spines were recorded in the Vitabäck Clay samples (Fig. 10. 2). Even the largest of them only comprises a small portion of the spine, so assigning it to a particular species proved impossible.

Subcohort Neoselachii Compagno, 1977  
Order Squatiniformes Buen, 1926  
Family Squatinidae Bonaparte, 1838

Squatinidae indet.  
(Fig. 11)

**Figure 8** Teeth of *Parvodus rugianus* (Ansorge, 1990),  $\times 15$ , all teeth from VC3 except 1 from VC11: (1) anterior tooth, LO8407t, in labial (A), occlusal (B) and lingual (C) views; (2) anterior tooth-crown, LO8408t, in labial (A), occlusal (B) and lingual (C) views; (3) anterior tooth-crown, LO8409t, in labial (A), occlusal (B) and lingual (C) views; (4) anterior tooth-crown, LO8410t, in labial (A), occlusal (B) and lingual (C) views; (5) antero-lateral tooth-crown, LO8411t, in labial (A), occlusal (B) and lingual (C) views; (6) antero-lateral tooth, LO8412t, in labial (A), occlusal (B) and lingual (C) views; (7) antero-lateral tooth-crown, LO8413t, in labial (A), occlusal (B) and lingual (C) views; (8) lateral tooth-crown, LO8414t, in labial (A), occlusal (B) and lingual (C) views; (9) lateral tooth-crown, LO8415t, in labial (A), occlusal (B) and lingual (C) views; (10) lateral tooth-crown, LO8416t, in labial (A), occlusal (B) and lingual (C) views; (11) latero-posterior tooth-crown, LO8417t, in labial (A), occlusal (B) and lingual (C) views; (12) posterior tooth, LO8418t, in labial (A), occlusal (B) and lingual (C) views; (13) juvenile posterior tooth, LO8419t, in labial (A), occlusal (B) and lingual (C) views; (14) extreme posterior tooth, LO8420t, in labial (A), occlusal (B) and lingual (C) views.



**Figure 11** Tooth and placoid scale of *Squatinidae* indet: (1) tooth, LO8430t, in lingual (A), labial (B) and occlusal (C) views,  $\times 15$ ; (2) placoid scale, LO8431t, in lateral view,  $\times 50$ ; both from VC3.

**Material.** A single tooth, LO8430t, lacking the apex of the cusp and ten placoid scales, LO8431t, and unnumbered.

**Description.** The tooth has a relatively high crown lacking cusplets. There is a strong labial protuberance, divided distally into two smaller lobes. This protuberance is not supported by the root. A tapering median uvula is present on the lingual side and fully supported by the root. A few extremely small folds are present on the cutting edges. There is a single large foramen in the basal surface of the root and a groove is present on the lingual side. A number of small, circular foramina open on the lingual side of the root, close to the crown–root junction. The tooth measures 2.2 mm in mesio-distal width.

Ten squatinid scales (Fig. 11. 2) have been encountered in VC3. These have a flat crown situated on a fairly high base. The crown is tilted towards the anterior edge and lacks ornamentation. The base is of the same size as the crown and there are a few foramina on the lateral sides. A single, large foramen is also present in the centre of the slightly convex basal plate. Similar scales were also recorded by Thies (1995) in Kimmeridgian sediments from northern Germany and referred to the *Squatinomorphii*.

**Discussion.** This tooth is fairly similar to Oxfordian teeth from southern Germany referred to *Squatina* sp. by Thies (1983) and to undescribed teeth from the Kimmeridgian of southern England, but can be separated from these two as the labial protuberance is subdivided into two lobes.

Jurassic teeth referred to *Squatina* are somewhat different from the Late Cretaceous teeth of this genus. The labial protuberance is often larger and not supported by the root. The protuberance in Late Cretaceous taxa is also more vertical and less projected labially and the development of lateral cusplets and ornamentation on the cutting edges appear to be less frequent. It is not clear whether the tooth from the Vitabäck Clays, or the Jurassic '*Squatina*' records, really belong in that genus.

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sieved some of the sediment and sorted numerous vertebrate remains from VC3 and VC11. Mikael Siverson and Anita Löfgren, Lund, commented upon the manuscript and provided constructive criticism. Steve Tracey, London, contributed with his knowledge on fossil molluscs and Vivi Vajda, Lund, shared the results of her palynomorph investigation of the section. The Department of Geology, Lund University, the Royal Swedish Academy of Sciences and Lund Geological Fieldclub sponsored the fieldwork of 1995, 1998 and 1999 respectively. David Ward and Franco Cigala-Fulgosì acted as referees and provided useful comments. My sincere thanks to all.

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