

MAASTRICHTIAN SQUALOID SHARKS FROM SOUTHERN SWEDEN

by MIKAEL SIVERSON

ABSTRACT. The Maastrichtian of southern Sweden has yielded more than 2000 teeth of squaloid sharks. Seven species have been identified: *Microetmopterus wardi* gen. et sp. nov., *Proetmopterus hemmooriensis* gen. nov., *Eoetmopterus* cf. *E. supracretaceus*, *Centroscymnus schmidi*, *Squalus ballingsloevensis* sp. nov., *S. balsvikensis* sp. nov. and *S. gabrielsoni* sp. nov. Etmopterine sharks, now restricted to the cold bottom-waters of the outer continental and insular shelves and slopes, apparently thrived in the shallow coastal waters of the Kristianstad Basin during the earliest Maastrichtian. As indicated by its extremely small teeth, *Microetmopterus wardi* may have been the smallest known neoselachian. The Recent *Centroscyllium* could be an example of a restricted form of 'hopeful monster', by instantaneously having acquired a monognathic heterodonty in a single ancestral individual or litter. The type series of *Eoetmopterus supracretaceus* is a heterogeneous mix of *Eoetmopterus* and *Proetmopterus*. Similarly, the type series of *Centroscymnus schmidi* also includes *Proetmopterus hemmooriensis*.

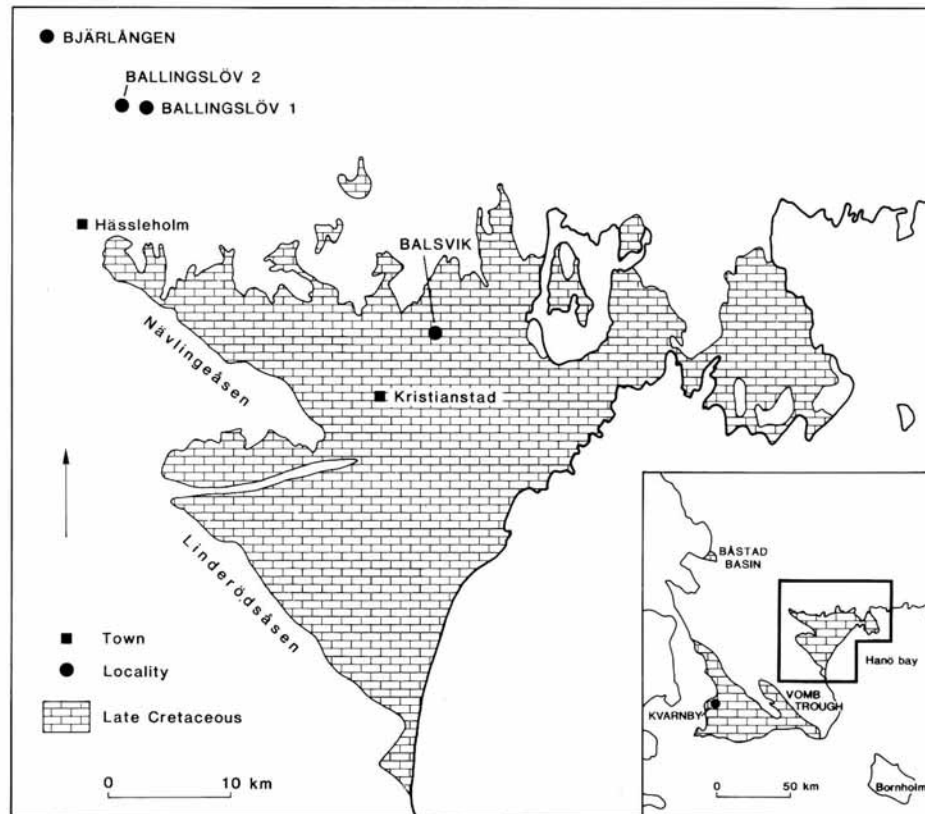
THE archipelago palaeoenvironment of the Kristianstad Basin with its rocky shorelines (see Lundgren 1934; Surlyk and Christensen 1974; Surlyk 1980) was the habitat for rich selachian faunas during the Campanian and earliest Maastrichtian (Davis 1890; Siverson 1992, in press). There were several breaks in sedimentation during this interval, interpreted by Christensen (1975) as evidence of regressions. The sea remained shallow during the transgressions with a maximum water depth probably generally not exceeding 30–40 m in the Campanian and about 100 m in the earliest Maastrichtian (Gabrielson, pers. comm.). Maastrichtian strata are currently accessible at four localities within the Kristianstad Basin (Text-fig. 1), i.e. Balsvik, Bjärlången, Ballingslöv 1, and Ballingslöv 2 (Siverson in press). Placed in the NW-European belemnite stratigraphy, these sites are referred to the earliest Maastrichtian *Belemnella lanceolata* Zone (Christensen 1975; Siverson in press).

In addition to those outcrops, large glacial rafts of Maastrichtian white pelagic chalk are quarried at Kvarnby village, situated about 65 km SW of the Kristianstad Basin's SW margin (Text-fig. 1). Brood (1972), in his study of cyclostomatous bryozoans, suggested a late Early Maastrichtian age for the Kvarnby chalk. Based on Foraminifera, Holland in Ringberg *et al.* (1984) referred the strata to the Late, but not latest, Maastrichtian. The composition of the Kvarnby off-shore selachian fauna corresponds well with that of the mid-Maastrichtian of Hemmoor, Germany (see Herman 1982a). A reduced faunistic similarity is found in a comparison with a Late Maastrichtian assemblage from the bryozoan chalk at Stevns Klint, Denmark.

SQUALOID SHARKS

The most conspicuous differential external features of Recent squaloids are their lack of an anal fin and presence of dorsal fin spines (lost in some species). Dentally they differ from other sharks mainly by their almost exclusively interlocked lower jaw teeth, with a single cusp bent towards the rear. In the *Squalus*-group genera, the lower and upper jaw dentitions are much alike. Others, in particular *Etmopterus* Rafinesque, 1810, show a very marked dignathic heterodonty with firmly interlocked cutting lower teeth and multicuspidate erect upper teeth.

The adults of Recent squaloid genera range in maximum size from about 0.25 m, e.g. *Squaliolus*



TEXT-FIG. 1. Map of the Kristianstad Basin, showing the location of the sites referred to in this work (based on SGU Ba43/Ah15, SGU Af167 and SGU Af168).

Smith and Radcliffe, in Smith, 1912, to more than 6 m, e.g. *Somniosus* LeSueur, 1818 (see Compagno 1984). Most species live near the bottom on the temperate to tropical outer shelves and slopes (Compagno 1984). Some species, like certain *Squalus* Linnaeus, 1758 may enter shallow coastal waters at higher latitudes.

The earliest known unquestionable squaloid is *Protosqualus albertsi* Thies, 1981 from the late Middle Barremian (Early Cretaceous) of Germany. The Late Triassic *Pseudodalatias barnstonensis* (Sykes, 1971) had a dentition superficially similar to that of some Recent squaloids, e.g. *Dalatias* Rafinesque, 1810. Reif (1978) and Cappetta (1987) declined to relate it to the Squalidae on the basis of its different enameloid structure.

PREVIOUS WORK ON CRETACEOUS SQUALOID FAUNAS

There are few records of Cretaceous squaloid faunas other than single-species occurrences of the *Squalus*-group. Dalinkevičius (1935) described (partly unaware) three squaloids from the Turonian

of Lithuania, i.e. *Centrophorus? balticus* Dalinkevičius, 1935, a *Squaliolus*-like species, and a species of the *Squalus*-group (see Cappetta 1987, p. 53).

Cappetta (1980) redescribed skeletons of three previously poorly known squaloids from the Late Santonian of Sahel Alma, Lebanon: *Cretascymnus adonis* (Signeux, 1950) and the two *Squalus*-group taxa *Centrophoroides latidens* Davis, 1887, and *Centrosqualus primaevus* (Pictet, 1850).

Herman (1982a), in a study based on 80 selachian teeth (33 belonging to squaloids) from the mid-Maastrichtian of Hemmoor, Niederelbe, Germany, illustrated teeth of *Centrosymnus schmidi*, *Proetmopterus hemmooriensis*, possibly *Eoetmopterus supracretaceus* (see below), two taxa possibly related to *Scymnodon* (pl. 1, fig. 7; pl. 2, fig. 1, not fig. 2), and a species referred by him to *Centrosqualus appendiculatus* (Agassiz, 1843).

Müller and Schöllmann (1989) recorded seven nominal species (based on 270 teeth) of Squalidae from the Late Campanian of Westfalen, Germany. They figured 5 *Squalus*-group teeth from juvenile individuals referred to *Centrophoroides appendiculatus* (Agassiz, 1843) and to their new species *Squalus wondermarcki*, the latter based on a heterogeneous type-series and with insufficiently documented dental ontogeny. Their holotype differs from the Swedish *Squalus* mainly by its large cusp and small distal heel. The rest of their Squalidae fauna included *Eoetmopterus supracretaceus* with its heterogeneous type-series also including *Proetmopterus* (see below), a *Deania*-like lower jaw tooth and a *Proetmopterus*-like upper jaw tooth, both figured as *Etmopterine*, g. indet., n. sp., their new *Centrosymnus praecursor* and *Cretascymnus westfalicus*, and finally a tooth figured as *Somniosinae?* g. et sp. indet., resembling the upper jaw teeth of *Deania* Jordan and Snyder, 1902.

Considering the wide distribution of Recent *Squalus*, it may seem strange that I have been unable positively to identify any of the Swedish *Squalus* in the German faunas. However, poor quality of the illustrations and lack of documented dental ontogeny of the German *Squalus*-like taxa makes a careful comparison difficult.

MATERIAL AND METHODS

The Kvarnby and the Kristianstad Basin samples were enriched in their content of phosphatic fossils by treatment with buffered acetic acid (see Jeppsson *et al.* 1985), heavy liquids (sodium polytungstate), and magnetic separation. Depending on the state of preservation of the sharks' teeth and the amount of non-selachian phosphatic material, the residues were sieved down to 500, 355, or 250 μm .

About 10 per cent of the teeth from Kvarnby are perfectly preserved (250 μm sieve). The corresponding figure for the more near-shore Kristianstad Basin strata is less than 1 per cent.

Relatively few *Squalus* teeth from the Kristianstad Basin sites could be identified to species level. This is a result of the generally, though not exclusively, poor state of preservation (mainly bioerosion, see Pl. 4, figs 9–12) and at least bispecific nature of the *Squalus* assemblage.

Beside their presence in the Maastrichtian, teeth of squaloid sharks occur also in the Campanian of the Kristianstad Basin, infrequently in the Early Campanian, abundantly in the Late Campanian. This material is, however, less well preserved. As far as can be determined, all of the teeth belong to species of the *Squalus*-group.

Systematics and terminology follow those of Compagno (1984) and Cappetta (1987) respectively. All illustrated teeth are deposited in the type collection of the Department of Historical Geology and Palaeontology, Lund University (LO).

LOCALITIES

KVARNBY. *Map sheet* Bara 2C:26, Ed. 1987 (economic map 'Gula Kartan' in Swedish; 1:20,000); coordinates 6165 1330 (The Swedish National Grid 2.5 gon V system). *References.* Brotzen 1960; Brood 1972; Ringberg *et al.* 1984. *Age.* Probably mid-Maastrichtian, see Brood 1972; Holland in Ringberg *et al.* (1984), and discussion above. *Remarks.* East of the village of Kvarnby, glacial rafts (Schollen) of a very pure white chalk are quarried by the Malmökrita AB company. The tilted

Schollen are several hundred metres long and up to 30 m thick and are interbedded in a till. The commercial processing of the microbrecciated chalk includes washing the sediment over a 200 μm mesh. The rejected > 200 μm fraction is dumped into two abandoned quarries (not marked on the map) situated just west of Ångdala Farm (see Ringberg *et al.* 1984, fig. 2). One sample (S91-5-1-MS; 179 kg) of the > 200 μm residue was collected from the northwestern corner of the southern quarry, located immediately south of the sieving station.

BJÄRLÄNGEN. *Map sheet.* Bjärnum 3D 8e, Ed. 1 – Nov. 1975 (Swedish economical maps, 1:10,000); coordinates 624262 137120 (southern quarry). *References.* Moberg 1884; Siverson in press. *Age.* *B. lanceolata* Zone, earliest Maastrichtian. *Remarks.* The sample (S89-4-2-MS, 96.7 kg) was collected about 0.5–1.0 m below ground level in the northwestern corner of the small overgrown quarry.

BALSVIK. *Map sheet.* Balsby 3E 3a, Ed. 1 – Mar. 1975 (Swedish economical maps, 1:10,000); coordinates 621830 140184. *References.* Christensen 1972, 1975; Siverson in press. *Age.* *B. lanceolata* Zone, earliest Maastrichtian. *Remarks.* About 3 m of earliest Maastrichtian mainly fine-grained calcarenite is currently exposed in the partly overgrown quarry. Perfectly preserved teeth are rare (< 10/100 kg, 250 μm sieve) and mainly confined to the uppermost metre of the strata.

BALLINGSLÖV 1 and 2. For details see Siverson (in press).

SYSTEMATIC PALAEOLOGY

Order SQUALIFORMES Goodrich, 1909

Family SQUALIDAE Blainville, 1816

Genus SQUALUS Linnaeus, 1758

Type species. *Squalus acanthias* Linnaeus, 1758. Recent, boreal to warm-temperate, intertidal down to at least 900 m of the upper continental and insular slopes. Occurs throughout the water column but is usually found near the bottom (Compagno 1984).

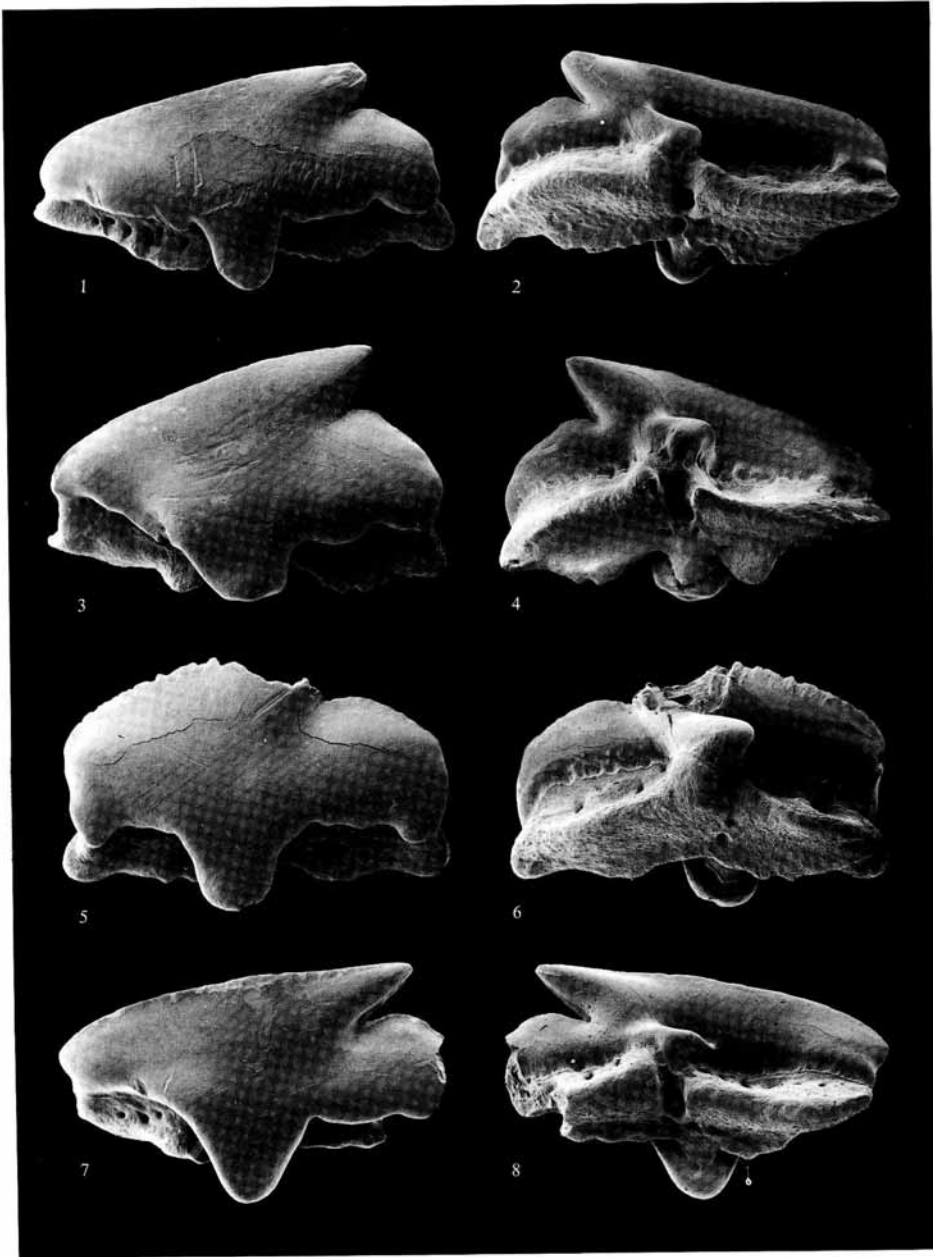
Remarks. The overall dental morphology has remained virtually unchanged within the genus since its appearance, probably some time during the Cenomanian to Campanian interval. Recognition of palaeospecies of dentally broadly static genera like *Squalus* is no easy task. Intraspecific variation in tooth morphology for a given tooth file is to a large extent governed by ontogeny (see below) and, after maturity, also by sex. Furthermore, schools of Recent *Squalus* are commonly segregated by size and sometimes by sex (Compagno 1984, p. 112).

Much of the dental interspecific variation in the *Squalus*-group is concentrated on the basal face of the root. Unfortunately, it does not take much corrosion of the root for vital information to be lost. Descriptions of new nominal species of *Squalus* and closely related genera based on teeth of the same size which are not of the best preservation, do not help the understanding of squaloid taxonomy.

The great similarities in general tooth morphology between species of *Squalus* result in descriptions of the dentition of each species differing only slightly. Therefore, separate descriptions have been omitted here. Herman *et al.* (1989) gave a detailed description of the type species, *S. acanthias*.

EXPLANATION OF PLATE I

Figs 1–8. *Squalus ballingsloevensis* sp. nov. 1–2, holotype, LO 5061 T, 5.2 mm long posterior lower jaw tooth from a mature male; labial and lingual views; Ballingslöv 1, sample S89-9-1-MS, 399.2 kg, $\times 13$. 3–4, paratype, LO 5062 t, 4.7 mm long antero-lateral tooth from a mature female; labial and lingual views; Ballingslöv 1, sample S89-9-1-MS, 399.2 kg, $\times 13.5$. 5–6, paratype, LO 5063 t, 3.8 mm long symphyseal tooth, cusp broken off; labial and lingual views; Ballingslöv 2, sample S89-4-8-MS, 10.9 kg, $\times 16$. 7–8, paratype, LO 5064 t, 2.62 mm long incomplete lower? jaw tooth from an immature individual, distal part of tooth broken off; labial and lingual views; Bjärlängen, sample S89-4-2-MS, 96.7 kg, $\times 23.5$.



SIVERSON, *Squalus*

Squalus ballingsloevensis sp. nov.

Plate 1, figs 1–8

Type stratum. Sample S89-9-1-MS, Ballingslöv 1 quarry (*Belemnella lanceolata* Zone, earliest Maastrichtian; for details see Siverson in press).

Derivation of name. After the type locality.

Holotype. LO 5061 T; Pl. 1, figs 1–2.

Paratypes. LO 5062 t–LO 5064 t; Pl. 1, figs 3–8.

Additional material. More than 100 poorly preserved teeth, most of them from Ballingslöv 1. The species has been found in all samples from the Swedish *B. lanceolata*-beds.

Diagnosis. A large, dentally primitive *Squalus*. Centrally situated apron: triangular in juveniles, but often well demarcated with parallel edges in adults. Lingual side of apron not covered by basal edge of root. Mesial expansion of basal edge of tooth root very poorly developed, particularly in juveniles. Basal face of root flat or slightly concave in profile. Axial foramina fused into large subcircular infundibulum. Teeth only moderately labio-lingually compressed.

Comparison. Teeth of *S. ballingsloevensis* most closely resemble those of '*Centrophoroides*' *worlandensis* Case, 1987 (Late Campanian of Wyoming). Teeth of the American species have a larger infundibulum and are slightly larger (up to at least 6.9 mm). Moreover, the lower part of the basal face of the root is incompletely mineralized in '*C.*' *worlandensis*, explaining the presence of a row of irregularly shaped foramina below the infundibulum. Normally, this area is covered by a cap of dentine. In *S. ballingsloevensis*, the mesial cutting edge is gently convex in mature females (Pl. 1, figs 3–4), and straight in mature males (Pl. 1, figs 1–2). In '*C.*' *worlandensis*, the cutting edge is straight in mature females and concave in mature males. Unfortunately, juvenile teeth of the latter species have never been illustrated.

Some teeth of mature females of the early Palaeogene *S. minor* (Leriche, 1902) and its possible ancestor *S. balsvikensis* sp. nov. have a short and poorly demarcated apron with its lingual side not covered by the basal edge of the root. Except for being more labio-lingually compressed and having a more convex mesial cutting edge, these teeth are fairly similar to the female tooth of *S. ballingsloevensis* figured herein (Pl. 1, figs 3–4). However, the development of the apron and the basal face of the root through ontogeny easily separates the latter from the former two species.

Squalus balsvikensis sp. nov.

Text-fig. 2A–F

Type stratum. About 0–0.3 m above the upper level of white-spotted flint nodules (see Christensen 1972, fig. 5), Balsvik quarry; *Belemnella lanceolata* Zone, earliest Maastrichtian.

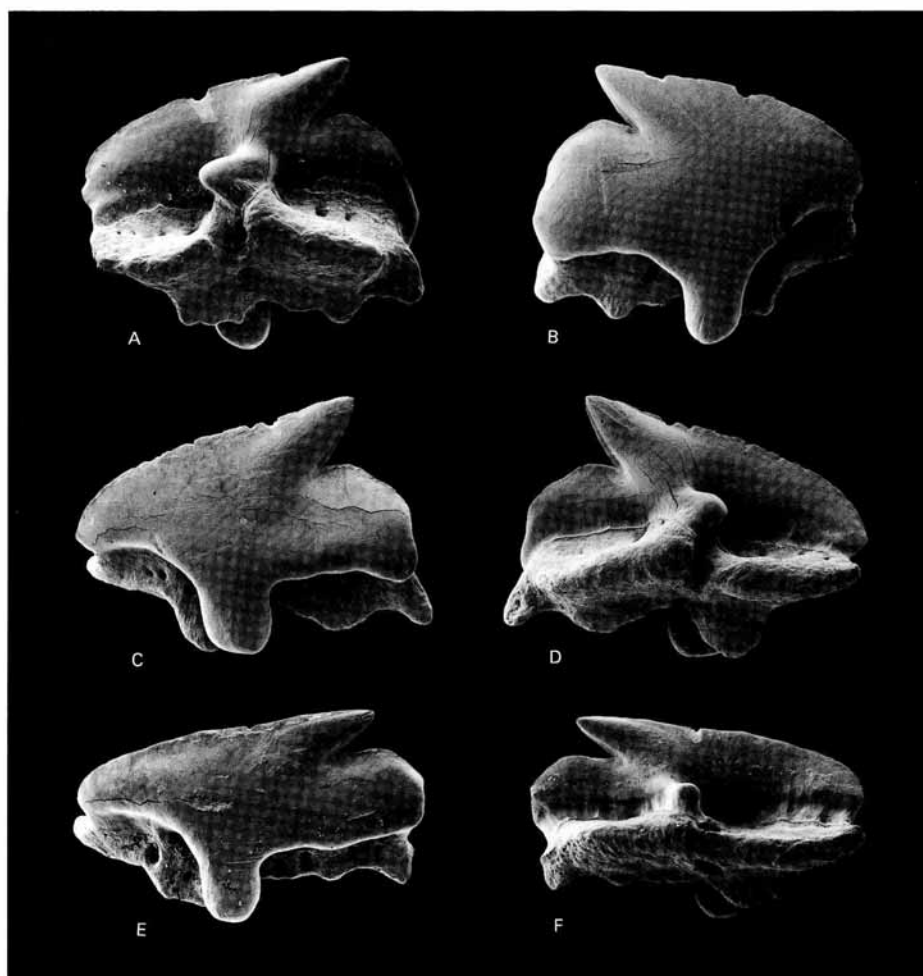
Derivation of name. After the type locality.

Holotype. LO 5065 T; Text-fig. 2C–D.

Paratypes. LO 5066 t–LO 5067 t; Text-fig. 2A–B, E–F.

Additional material. Several hundred teeth, most of them poorly preserved. The species has been found in all samples from the *B. lanceolata*-beds.

Diagnosis. Uvula very small and symmetrical in teeth from very young individuals; mesially twisted in teeth larger than about 1.1 mm. Axial foramina separated in teeth of very young individuals, otherwise fused into oblique infundibulum. Apron long and narrow with parallel edges in juveniles and mature males; relatively broad and short in large females. Basal face of root concave in profile.



TEXT-FIG. 2. *Squalus balsvikensis* sp. nov. A–B, paratype, LO 5066 t, 2.53 mm long anterior tooth from a female; lingual and labial views; Balsvik quarry, sample S90-4-1-MS, 21.35 kg, the cemented bed between the two levels of white-spotted flint nodules, $\times 21$. C–D, holotype, LO 5065 T, 2.35 mm long upper jaw tooth from a mature male; labial and lingual views; Balsvik quarry, sample S92-2-2-MS, 47.5 kg, 0–0.3 m above the upper flint level, $\times 24$. E–F, paratype, LO 5067 t, 1.01 mm long posterior lower jaw tooth from a very young individual; labial and lingual views; Balsvik quarry, sample S90-5-1-MS, 10.85 kg, 0.2–0.4 m above the upper flint level, $\times 54$.

Mesial expansion of basal edge of root well developed but mostly not reaching apex of apron. Distal part of basal edge of root markedly bilobate.

Comparison. Teeth of *S. balsvikensis* most closely resemble those of the Palaeocene to Eocene *S. minor*

(Leriche, 1902) and the very similar Oligocene *S. alsaticus* (Andreae, 1892). Judging from illustrations (Herman 1982b) and specimens of *S. minor* examined, teeth from adult *S. balsvikensis* differ from those of *S. minor* by their narrower and more inclined cusp, more concave basal face of the root, generally more prominent distal lobe of the basal edge of the root, and weaker sexual heterodonty. I am not convinced that the Eocene teeth figured as *S. smithi* sp. nov. by Herman (1982b) belong to a species other than *S. minor*.

Remarks. Females of *S. acanthias*, a Recent species probably close in size to *S. balsvikensis*, reach at least 1.24 m in body length, whereas newborn offspring from presumably smaller females are sometimes no larger than 0.22 m (Compagno 1984, p. 113). Based on the illustrations and data of *S. acanthias* teeth/body length, presented by Ledoux (1970) and Herman *et al.* (1989), the relationship between body length and tooth size in that species seems to be roughly isometric. In *Squalus*, the lower jaw teeth are about 20–30 per cent larger than the otherwise similar upper ones. Using the latter figure and assuming an isometric body length/tooth size ratio, the size ratio between upper teeth of the smallest newborn and corresponding lower teeth of the largest females of *S. acanthias* would be about 7.3:1. In my collection of *S. balsvikensis*, the size range for lateral teeth is 0.94–4.11 mm, giving a 4.4:1 ratio. It thus seems reasonably likely that the greater part of the ontogeny is covered.

Squalus gabrielsoni sp. nov.

Plate 2, figs 1–8

Type stratum. Kvarnby chalk Schollen (probably mid-Maastrichtian).

Derivation of name. After Jan Gabrielson, Lund, in recognition of field assistance and stimulating discussions on the Cretaceous geology of Sweden.

Holotype. LO 5068 T; Pl. 2, figs 3–4.

Paratypes. LO 5069 t–LO 5071 t; Pl. 2, figs 1–2, 5–8.

Additional material. About 50 teeth from Kvarnby, most of them poorly preserved.

Diagnosis. Axial foramina separated or fused. Apron very elongated and narrow, particularly in juveniles. Mesial expansion of basal edge of root well developed reaching apex of apron. Lingual side of mesial expansion of basal edge of root generally meeting root protuberance almost at right angle. Basal edge of root nearly straight.

Comparison. This species is a good example of a *Squalus* in the process of losing the thin bridge of dentine separating the two axial foramina. The species has otherwise a remarkably modern tooth morphology close to that of the Recent *S. acanthias*, a species which it resembles more than it does any fossil attributed to *Squalus*. The sexual dimorphism is, however, less marked in *S. gabrielsoni*. Further, in the latter, the apron is narrower and the distal part of the basal edge of the root does not reach the end of the apron. In contrast to *S. balsvikensis* and *S. minor*, the mesial expansion of the root commonly reaches beyond the apex of the apron

EXPLANATION OF PLATE 2

Figs 1–8. *Squalus gabrielsoni* sp. nov. 1–2, paratype, LO 5069 t, 3.08 mm long posterior lower jaw tooth from a mature male; lingual and labial views; Kvarnby, $\times 22$. 3–4, holotype, LO 5068 T, 2.55 mm long antero-lateral lower jaw tooth; lingual and labial views; Kvarnby, $\times 23$. 5–6, paratype, LO 5070 t, 2.31 mm long upper jaw tooth from a mature? male, basal face of root unusually flat; labial and lingual views; Kvarnby, $\times 27$. 7–8, paratype, LO 5071 t, 1.26 mm long tooth from an immature individual; labial and lingual views, Kvarnby, $\times 45$.



SIVERSON, *Squalus*

in *S. gabrielsoni* and *S. acanthias*. The bilobated distal part of the basal edge of the root is very similar in the former two taxa. In *S. gabrielsoni* and *S. acanthias* the basal edge is more or less straight with a poorly demarcated terminal lobe. The almost straight basal root edge, often fused axial foramina in adults, and weak mesial labial interlocking hollow of the crown in *S. gabrielsoni*, easily separate it from the contemporaneous *Centrophoroides? appendiculatus*.

In both *S. balsvikensis* and *S. gabrielsoni*, the uvula is very small and symmetrical in teeth (about 0.94–1.1 mm long) presumably of newborn individuals. In teeth larger than about 1.1 mm, the uvula rapidly increases in size and inclination towards the symphysis.

Genus MICROETMOPTERUS gen. nov.

Type species. Microetmopterus wardi gen. et sp. nov.

Derivation of name. Combination of 'mikros' (Greek, small) and *Etmopterus* (lanternsharks).

Diagnosis. Upper jaw teeth with very large lateral cusplets, reaching half the height or more of cusp. Labial face of crown very flat, without ornamentation. Flat, V-shaped basal face of root with two axial foramina or with infundibulum. Rectangular lower jaw teeth longer than high. Separate axial foramina; occasionally forming infundibulum. No disto-lingual foramen. Interlocking hollows poorly developed, especially in juveniles.

Comparison. The combination of mesio-distally elongated, poorly interlocked, lower jaw teeth, and advanced, smooth upper jaw teeth with very large cusplets, separates *Microetmopterus* from *Proetmopterus* and *Etmopterus*. The upper jaw teeth of *Microetmopterus* are very close in morphology to those of *Etmopterus*, whereas the lower teeth are quite different in the two genera. In *Etmopterus*, the lower teeth are roughly quadrangular with large interlocking hollow areas.

Microetmopterus wardi sp. nov.

Plate 3, figs 1–12

Type stratum. Kvarnby chalk Schollen (probably mid-Maastrichtian).

Deviation of name. After David J. Ward, Orpington, UK, in recognition of his publications on Tertiary selachians and his assistance in building me a clay-washing machine of the type described by him (Ward 1981).

Holotype. LO 5072 T; Pl. 3, figs 3–4.

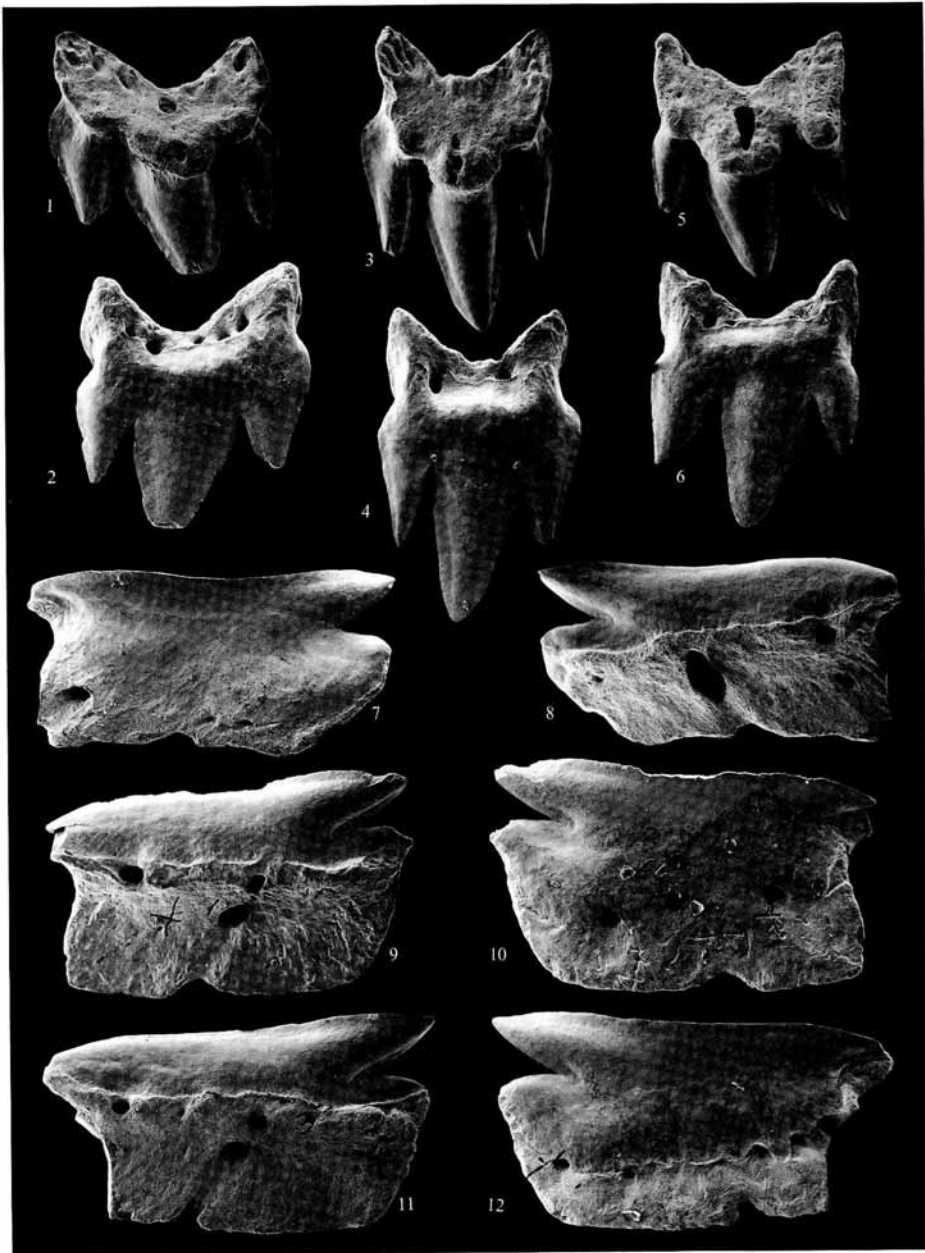
Paratypes. LO 5073 t–LO 5077 t; Pl. 3, figs 1–2, 5–12.

Additional material. 18 less well-preserved teeth; 9 upper jaw teeth and 9 lower jaw teeth, all from Kvarnby.

Diagnosis. As for the genus.

EXPLANATION OF PLATE 3

Figs 1–12. *Microetmopterus wardi* gen. et sp. nov. 1–2, paratype, LO 5073 t, 0.50 mm high upper lateral tooth; lingual and labial views; Kvarnby. 3–4, holotype, LO 5072 T, 0.57 mm high upper anterior tooth; lingual and labial views; Kvarnby. 5–6, paratype, LO 5074 t, 0.49 mm high upper lateral tooth; lingual and labial views; Kvarnby. 7–8, paratype, LO 5075 t, 0.71 mm long lower jaw tooth; labial and lingual views; Kvarnby. 9–10, paratype, LO 5076 t, 0.72 mm long lower jaw tooth; lingual and labial views; Kvarnby. 11–12, paratype, LO 5077 t, 0.75 mm long incomplete lower jaw tooth, mesial corner of root broken off; lingual and labial views. All specimens from Kvarnby, and $\times 80$.



SIVERSON, *Microetmopterus*

Description. Upper jaw teeth up to 0.62 mm high with one, or rarely two, pairs of erect, robust lateral cusplets, reaching two-thirds of height of main cusp. Labial face of crown smooth, very flat; lingual face convex. Crown overhangs root labially. Two or more foramina open along labial base of crown. Basal face of root flat with two axial foramina or infundibulum.

Lower jaw teeth, about 50 per cent longer than high, up to 1.1 mm long. Mesial cutting edge weakly sigmoidal; four to six times longer than distal convex cutting edge. Two separate axial foramina, rarely forming infundibulum. Mesio-lingual foramen present but no disto-lingual one. Interlocking hollows poorly developed, especially in juveniles. Two or more foramina open along labial base of crown. Basal edge of root straight.

Remarks. The upper jaw teeth, remarkably similar to those of *Etmopterus spinax* (Linnaeus, 1758), range in size from 0.45 to 0.62 mm in height. The variability in size is much greater for the lower jaw teeth, i.e. 0.57–1.1 mm in length. A sieve finer than 250 μm is probably needed in order to obtain upper jaw teeth of juveniles. The height of the smallest lower jaw tooth coincides with the diagonal of the aperture in a 250 μm sieve. Thus, obtaining lower jaw teeth of very young individuals may also require a sieve finer than 250 μm . The teeth of 0.30 m long individuals of the extant *E. spinax* appear gigantic if placed next to those of *M. wardi* figured herein. The latter may well be the smallest known neoselachian.

Genus PROETMOPTERUS gen. nov.

Type species. *Etmopterus? hemmooriensis* Herman, 1982a (p. 137, pl. 1, fig. 6; pl. 3, fig. 1).

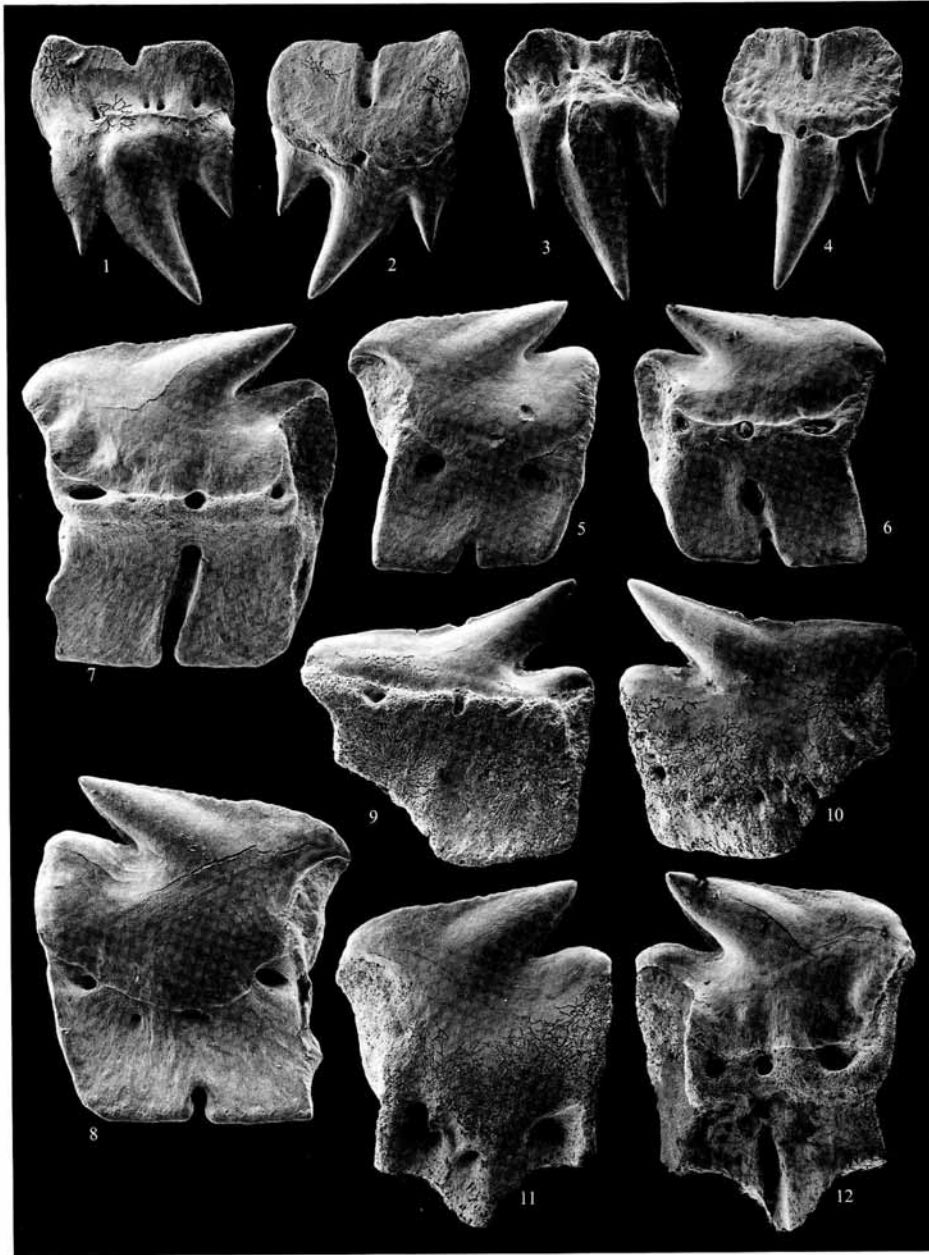
Derivation of name. Combination of 'pro' (Greek, before in time) and *Etmopterus* (lantern sharks).

Diagnosis. Lower jaw teeth with mesio-labial interlocking hollow not extending below mesio-labial main foramen. Disto-lingual interlocking hollow poorly developed below lingual bulge of root. Upper jaw teeth with rectangular root, one or two pairs of cusplets, and weakly to well-developed apron.

Comparison. *Proetmopterus hemmooriensis* is a good candidate for the species ancestral to *Etmopterus*. The lower jaw teeth of the two taxa are almost identical, except for the smaller interlocking area and open median lingual duct ('sillon' of Casier 1961) of the root in the former taxon. The upper jaw teeth of *P. hemmooriensis* have a primitive morphology, retaining a rectangular root unlike the advanced scyliorhinid-like roots of *Etmopterus* and *Microetmopterus*. Passing from *Proetmopterus* to *Etmopterus*, there is an increase in the interlocking area of the lower jaw teeth coupled with a development towards scyliorhinid-like upper jaw teeth. If *P. hemmooriensis*, or a later descendant, gave rise to *Etmopterus*, scyliorhinid-like upper jaw teeth with V-shaped roots evolved at least twice in Squalidae: in the mid-Maastrichtian *Microetmopterus* and in the Early Miocene to Recent *Etmopterus*.

EXPLANATION OF PLATE 4

- Figs 1–8. *Proetmopterus hemmooriensis* (Herman, 1982a) gen. nov. 1–2, LO 5078 t, 1.09 mm high upper latero-posterior tooth; labial and lingual views; Kvarnby. 3–4, LO 5079 t, 1.08 mm high upper anterior tooth, basal bulge of labial side of cusp worn, presumably during feeding; labial and lingual views; Ballingslöv 1, sample S89-9-1-MS, 399.2 kg. 5–6, LO 5080 t, 1.01 mm high lower jaw tooth; labial and lingual views; Bjärlången, sample S89-4-2-MS, 96.7 kg. 7–8, LO 5081 t, 1.34 mm high lower jaw tooth, mesial corner of root broken off; lingual and labial views; Ballingslöv 1, sample S89-9-1-MS, 399.2 kg. All specimens $\times 40$.
- Figs 9–10. *Etmopterus* cf. *E. supracretaceus* Müller and Schöllmann, 1989. LO 6332 t, 1.57 mm high lower jaw tooth, large portion of mesial side of root broken off, note bioerosion; lingual and labial views; Kvarnby, $\times 30$.
- Figs 11–12. *Centroscyrnus schmidi* Herman, 1982a. LO 6333 t, 1.4 mm high incomplete lower jaw anterior tooth, distal part of root missing, note bioerosion; labial and lingual views; Balsvik quarry, sample S90-6-1-MS, 8.4 kg, 20–30 cm below the lower flint level, $\times 40$.



SIVERSON, *Proetmopterus*, *Eoetmopterus*, *Centroscymus*

Proetmopterus hemmooriensis (Herman, 1982a)

Plate 4, figs 1-8

- ?1982a *Centroscymnus schmidi* Herman [partim], p. 135, pl. 1, fig. 5a, non figs 5b-c
 1982a cf. *Centroscymnus schmidi* Herman, p. 135, pl. 1, fig. 5d; pl. 3, fig. 6.
 1982a *Etmopterus? hemmooriensis* Herman, p. 137, pl. 1, fig. 6; pl. 3, fig. 1.
 ?1989 *Eoetmopterus supracretaceus* Müller and Schöllmann [partim], p. 11, figs 4·3a-b; ?4·5a-b; 4·6a-b;
 4·7a-c; 5·1a-c; 5·2a-c; 5·93a-c; non figs 4·4a-c (holotype of *E. supracretaceus*).
 ?1990 *Eoetmopterus supracretaceus* Müller [partim], pl. 2, figs 5-8, pl. 3, figs 1-3; non pl. 2, figs 3-4.

Type stratum. 0·5 m above bed T100; *Belemnella junior* Zone (early Late Maastrichtian) of Hemmoor, Niederelbe, Germany (Herman 1982a).

Material. More than 1000 teeth, most of them poorly preserved. All samples from the *B. lanceolata* beds yielded *P. hemmooriensis*.

Description. Upper jaw teeth up to 1·27 mm high with one or two pairs of erect cusplets; inner pair reaching half or less of height of main cusp. Labial basal border of crown straight or forming median apron. Several foramina open along labial base of crown. Cutting edges sharp. Labial face of cusp mildly convex, lingual face strongly convex. Basal face of root flat or labio-lingually concave. Single median foramen opens on lingual bulge of root. Lower half of basal face of root divided by median groove. Outline of root's basal face roughly rectangular. Anterior teeth erect; laterals bent towards commissure.

Lower jaw teeth up to 1·4 mm high. Overall tooth shape quadrangular (except for commissural teeth). Cusp strongly bent towards rear. Cutting edges with irregular, weak serrations. Mesial cutting edge occasionally convex in, presumably, adult females, otherwise straight. Large mesio-lingual foramen; smaller disto-lingual one. Median lingual foramen connecting with open median lingual duct. Disto-lingual interlocking hollow apico-basally elongated; poorly developed below lingual bulge of root. Mesial labial interlocking hollow not extending below mesio-labial main foramen. Basal border of labial face of crown broadly convex. Basal edge of root straight.

Remarks. Herman (1982a) based his new species *Etmopterus? hemmooriensis* on an upper jaw tooth lacking the distal part of the distal root branch. In the same paper, he also described the new species *Centroscymnus schmidi* with its type series comprising three fairly well-preserved lower jaw teeth along with an incomplete upper jaw tooth. By comparison with the Swedish collection of *Proetmopterus*, it is evident that the upper jaw tooth referred to *C. schmidi* by Herman (1982a, pl. 1, fig. 5d; pl. 3, fig. 6), is a poorly preserved tooth of *P. hemmooriensis* with broken cusplets. Unlike the holotype of *E.? hemmooriensis*, the specimen has a relatively well demarcated apron. This is, however, a highly variable character within the species. Most imaginable intermediate forms are present in the Swedish collection. Some have a labial side like the holotype, others show a more or less well-defined apron. One of the three lower jaw teeth referred to *C. schmidi* by Herman (1982a, pl. 1, fig. 5a) probably also belongs to *P. hemmooriensis*. Unfortunately, this tooth was not illustrated by scanning electron micrographs.

Genus EOETMOPTERUS Müller and Schöllmann, 1989

Type species. *Eoetmopterus supracretaceus* Müller and Schöllmann, 1989 (p. 11, figs 4·4a-c; non figs 4·3, 4·5-4·7, 5·1-5·3).

Remarks. The lower jaw tooth morphology alone does not justify a generic separation of *Eoetmopterus* from the Recent *Centroscymnus* (*Scymnodon?*) *crepidater* (Bocage and Capello, 1864). If my suggested recombination below of the lower jaw teeth of *E. supracretaceus* with the upper ones of Herman's Scymnorhinidae indet. n. sp. 2 is correct, then *E. supracretaceus* is a taxon generically difficult to separate from *Centroscymnus* (*Scymnodon?*) *crepidater*. The putative upper jaw teeth of

E. supracretaceus differ from those of other scymnorhinid squaloids by their lack of a basal constriction of the crown.

Eoetmopterus cf. *E. supracretaceus* Müller and Schöllmann, 1989

Plate 4, figs 9–10

- ?1982a Scymnorhinidae indet. n. sp. 2 Herman, p. 139, pl. 1, fig. 5e, and pl. 3, fig. 7.
 *1989 *Eoetmopterus supracretaceus* Müller and Schöllmann [*partim*], p. 11, fig. 4·4a–c; non figs 4·3, 4·5–4·7, 5·1–5·3.
 .1990 *Eoetmopterus supracretaceus* Müller [*partim*], pl. 2, fig. 4; non pl. 2, figs 3, 5–8, pl. 3, figs 1–3.

Type stratum. Upper Coesfelder Schichten (Late Campanian), Westfalen, Germany.

Material. One lower jaw tooth from Kvarnby.

Description. Tooth 1·57 mm high; 1·55 mm long. Mesial corner of root broken off, otherwise fairly well preserved. Cusp narrow. Mesial cutting edge concave, distal one convex. Several foramina open along diffuse basal labial edge of enameloid. Interlocking hollows poorly developed, affecting upper half of root only. Single mesio-lingual foramen, no disto-lingual one. Median lingual duct roofed over. Basal edge of root rectilinear.

Remarks. The figured material originally included in *Eoetmopterus supracretaceus* Müller and Schöllmann, 1989, comprises 5 upper jaw teeth (figs 4·6–4·7 and 5·1–5·3) and 3 lower jaw teeth (figs 4·3–4·5). As far as can be determined from the drawings of the imperfectly preserved upper jaw teeth, they do not differ generically from those of *Proetmopterus hemmooriensis*. Three of them have two pairs of cusplets whereas most Swedish specimens have one pair only. This difference may be significant but could also result from sexual segregation. Females of extant *Etmopterus* were reported to have fewer cusplets than males (Ledoux 1972). Judging from Müller and Schöllmann's drawings, one of the three lower jaw teeth (1989, figs 4·3a–b) also belongs to a species of *Proetmopterus*. The relatively large lower jaw tooth chosen as holotype of *E. supracretaceus* by Müller and Schöllmann (1989, fig. 4·4a–c), has a convex mesial cutting edge, elongated cusp, and diffuse labial borderline of the crown. No such teeth have been found in the *Proetmopterus*-yielding strata of the Kristianstad Basin. Consequently, the suggested combination of the 5 etmopterine upper jaw teeth with the holotype of *E. supracretaceus* is rejected. The remaining lower jaw commissural tooth (1989, figs 4·5a–b) has a distinct labial crown/root boundary, and thus differs significantly from the holotype of *E. supracretaceus*. It also differs from commissural teeth of *P. hemmooriensis* by its concave rather than straight mesial cutting edge and less mesio-distally elongated overall shape. Müller (1990, pl. 2, figs 5–6) figured two additional well preserved teeth as *E. supracretaceus* which undoubtedly belong to *Proetmopterus* and possibly to *P. hemmooriensis*. From the discussion above, it follows that of the eight specimens originally figured as *E. supracretaceus*, the holotype alone remains as representative of the taxon in the Westfalen Late Campanian selachian fauna. The early Late Maastrichtian specimen figured as Scymnorhinidae indet. n. sp. 2 by Herman (1982a, pl. 3, fig. 7), fits much better as upper jaw tooth of *E. supracretaceus*, both in size, labial root/crown boundary, distribution of labial foramina, and overall root shape.

The holotype of *E. supracretaceus* has double marginal foramina on the lingual face of the root, whereas the Swedish specimen has a single mesio-lingual foramen but no disto-lingual one. Other than that, the two teeth are almost identical in morphology.

Genus CENTROSCYMNUS Bocage and Capello, 1864

Type species. *Centroscymnus coelolepis* Bocage and Capello, 1864, Recent, on or near the bottom on the continental slopes (Compagno 1984).

Centroscymnus schmidi Herman, 1982a

Plate 4, figs 11–12

*1982a *Centroscymnus schmidi* Herman, p. 135, pl. 1, fig. 5b–c, and pl. 3, fig. 5; non pl. 1, fig. 5a, d, and pl. 3, fig. 6.

Type stratum. 0.6 m above bed F104, *Belemnella junior* Zone (early Late Maastrichtian) of Hemmoor, Niederelbe, Germany.

Material. Kvarnby; 5 specifically determinable lower jaw teeth. There are probably a few dozen additional, poorly preserved, upper and lower jaw teeth in my Kvarnby collection. Balsvik; sample S90-6-1-MS, 8.4 kg, one lower jaw tooth.

Description. Narrow lower jaw teeth reaching more than 1.65 mm in height. Crown relatively thick; root very compressed below lingual bulge. Mesial cutting edge generally straight with weak irregular serrations; distal cutting edge mildly convex. Mesial/distal cutting edge length ratio about 3.5–4:1. Large mesio-lingual foramen; smaller median and disto-lingual ones. One mesio-labial foramen; two or less disto-labial ones. Enameloid covered apron not extending below disto-labial foramen/foramina. Unroofed median duct. Mesio-labial interlocking hollow not reaching below mesio-labial foramen; disto-lingual one extending below lingual bulge of root.

Remarks. *C. schmidi* was the first described Cretaceous *Centroscymnus*, followed by the Late Campanian *C. praecursor* Müller and Schöllmann, 1989, from Westfalen, Germany. The lower jaw teeth of the latter are only moderately apico-basally elongated and lack a disto-lingual foramen.

CENTROSCYLLIUM, A RESTRICTED FORM OF 'HOPEFUL MONSTER'?

In the view of Compagno (1984), the subfamily Etmopterinae comprises the three Recent genera *Aculeola* de Buen, 1959 (monospecific), *Centroscyllium* Müller and Henle, 1841 and *Etmopterus*. In particular the latter two are very similar in overall body shape, whereas their lower jaw dentitions are fundamentally different (see Herman *et al.* 1989, pls 5–6). In *Centroscyllium* the upper and lower jaw teeth are very much alike, superficially resembling those of some scyliorhinids (see Herman *et al.* 1990). In complete contrast, *Etmopterus* shows a very marked dignathic heterodonty with firmly interlocked lower jaw cutting teeth with a single commissurally bent cusp, and multicuspitate erect upper jaw clutching teeth of scyliorhinid design.

Considering the observed rate of dental evolution in neoselachians, one may have to take a restricted form of 'hopeful monster' (see Goldschmidt 1940) into consideration in order to defend a close genetic relationship (e.g. a Tertiary splitting point) between *Centroscyllium* and *Etmopterus*. Let us assume a phenotypic transformation, in a mutant individual or litter, from a cutting/clutching dentition to a monognathic heterodonty with multicuspitate *Etmopterus*-like upper jaw teeth in the lower jaw as well. Instantly equipped with a basic scyliorhinid-like clutching dentition, *Centroscyllium*-phenotypes would then have been able, and certainly forced, to explore new food sources. They would simply no longer be able to cut pieces of flesh from larger prey the way their *Etmopterus*-phenotypic conspecifics could. Considering the opportunistic feeding behaviour of most Recent sharks, it is likely that *Centroscyllium*-phenotypes could change their choice of prey, if facing starvation. A resultant ecological barrier, maintained by way of different prey preference, could in time result in genotypical irreversible isolation. The otherwise typical scyliorhinid trademarks of *Centroscyllium*, such as longer jaws, strong labial folds on the tooth crowns, and divergent but rounded root lobes, may then have evolved rapidly as a response to the altered function of the food-gathering apparatus. Although undeniably speculative, this might be a possible explanation for the *Centroscyllium*/*Etmopterus* body shape/lower jaw teeth paradox. *Centroscyllium* has yet no fossil record. This is probably because very little work has been done on Tertiary small-toothed deep-water selachians. A Miocene species, probably belonging to a new squaloid genus, was erroneously referred to *Centroscyllium* by Ledoux (1972).

PALAEOECOLOGY

As would be expected, based on the deep-water habitat of most Recent squaloids, the pelagic white chalk at Kvarnby yielded a more diverse squaloid fauna than the slightly older Kristianstad Basin shallow-water strata. Five squaloids have been identified from Kvarnby: two etmopterines (*M. wardi* and *P. hemmooriensis*), two scymnorhinids (*C. schmidi* and *E. supracretaceus*), and one *Squalus* (*S. gabrielsoni*). Fragmentary material indicates that the Kvarnby squaloid fauna may include yet another *Squalus* along with a possible *Scymnodon*. The earliest Maastrichtian Kristianstad Basin strata have yielded four squaloids, i.e. *Squalus ballingsloevensis*, *S. balsvikensis*, *C. schmidi* and *P. hemmooriensis*.

Recent species of *Etmopterus* are all small (< 1 m) deep-water sharks, mostly occurring on or near the bottom on tropical and temperate continental and insular slopes (Compagno 1984). It is therefore surprising to find an abundance of *Proetmopterus hemmooriensis* teeth in the shallow coastal water facies strata of the Kristianstad Basin. Of the four sampled localities, the species is most common at Balsvik, where planktonic foraminifera constitute no more than 0.8–1.6 per cent of the total foraminiferal fauna (J. Gabrielson pers. comm.). The species is less common at Ballingslöv 1, Ballingslöv 2, and Bjärlängen, where up to about 40 per cent of the foraminiferal fauna consists of planktonic forms, indicating somewhat deeper water. The great abundance of orectoloboid teeth at these three localities indicates also warmer water. In the Balsvik *B. lanceolata*-beds, orectolobids comprise only a few per cent of the selachian fauna, whereas the squaloids make up more than 50 per cent.

Newborn individuals of *Etmopterus spinax* are 0.12–0.14 m long compared to 0.33–0.45 m for most of the mature females (see Compagno 1984, p. 85). The 3:1 size ratio between the largest and smallest teeth for a given tooth position for the Balsvik material indicates that most ontogenetic stages are present. It thus seems likely that *P. hemmooriensis* not only entered the shallow basin to feed, seasonally or more permanently, but also used it as a breeding area. Extant *Etmopterus* feed mainly on small bony fishes, squid and crustaceans (Compagno 1984). Schools of at least one species, i.e. *E. virens* Bigelow *et al.*, 1953, seem to attack and kill fairly large squid (Compagno 1984, p. 88). One can easily imagine individual belemnites being attacked by a school of *Proetmopterus hemmooriensis*. The shallow, temperate waters of the Kristianstad Basin archipelago, with its abundance of belemnites, may have constituted such a temptation to etmopterine sharks that they were willing to sacrifice the relative safety of deeper waters. Although belemnite rostra are very common fossils in the Campanian of the Kristianstad Basin as well, warmer water (inferred from e.g. *Squalus*-group/rhinobatid teeth ratios) combined with an abundance of large lamnoid sharks (Siverson 1992) probably provided an unhealthy environment for tiny squaloids like *P. hemmooriensis*.

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