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 hennenrothi gen. nov., Eoetmopterus cf. E. supracrassaeus, Centrosynmus schmidii, Squalus ballingsloensis sp. nov., S. balvikenensis 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 Centrosynmus 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 supracrassaeus is a heterogeneous mix of Eoetmopterus and Proetmopterus. Similarly, the type series of Centrosynmus schmidii also includes Proetmopterus hennenrothi.

The archipelago palaeoenvironment of the Kristianstad Basin with its rocky shorelines (see Lundgren 1934; Suryl and Christensen 1974; Suryl 1980) was the habitat for rich selachian faunas during the Campanian and earliest Maastrichtian (Davis 1990; 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 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. Balviken, Bjærlången, Ballingslöv 1, and Ballingslöv 2 (Siverson in press). Placed in the NW-European belenite 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 denticular 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 A167 and SGU A168).

Smith and Radcliffe, in Smith, 1912, to more than 6 m, e.g. Somnious LeSueur, 1818 (see Compango 1984). Most species live near the bottom on the temperate to tropical outer shelves and slopes (Compango 1984). Some species, like certain Squallus Linnaeus, 1738 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 *Pseudodolatias barstonensis* (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 Squallidae 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 Dolinkevičius, 1935, a Squalliolus-like species, and a species of the Squallus-group (see Cappetta 1987, p. 53).

Cappetta (1980) redescribed skeletons of three previously poorly known squaloids from the Late Santonian of Sahel Alma, Lebanon: Cretasensymus adonis (Signeux, 1950) and the two Squallus-group taxa Centrophoridae latidens Davis, 1887, and Centrosquallus primaveus (Picet, 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 Centrosquallus schmidtii, Proctopterus hemmoorensis, possibly Eotemopterus supracrateraceus (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 Centrosquallus appendiculatus (Agassiz, 1843).

Müller and Schöflmann (1989) recorded seven nominal species (based on 270 teeth) of Squalidae from the Late Campanian of Westfalen, Germany. They figured 5 Squallus-group teeth from juvenile individuals referred to Centrophoridae appendiculatus (Agassiz, 1843) and to their new species Squallus wondemarki, the latter based on a heterogeneous type-series and with insufficiently documented dental ontogeny. Their holotype differs from the Swedish Squallus mainly by its large cusps and small distal heel. The rest of their Squalidae fauna included Eotemopterus supracrateraceus with its heterogeneous type-series also including Proctopterus (see below), a Deania-like lower jaw tooth and a Proctopterus-like upper jaw tooth, both figured as Eotemopterus, g. indet., n. sp., their new Centrosquallus praecursor and Cretasensymus 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 Squallus, it may seem strange that I have been unable positively to identify any of the Swedish Squallus in the German faunas. However, poor quality of the illustrations and lack of documented dental ontogeny of the German Squallus-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 Jeppson 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 Squallus 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 Squallus 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, and 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 Squallus-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 Varla 2C; 26, Ed. 1987 (economic map 'Gula Karte' in Swedish; 1:20,000); coordinates 6165 1330 (The Swedish National Grid 2-5 gon V system). References. Broód 1972; Ringberg et al. 1984. Age. Probably mid-Maastrichtian, see Broód 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 Angdala 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.

Björkåsen. Map sheet. Björkåsen 3D 8c, Ed. 1 – Nov. 1975 (Swedish economical maps, 1:10,000); coordinates 624262 137120 (southern quarry). References. Möberg 1884; Siverson in press. Age. B. lanceolata Zone, earliest Maastrichtian. Remarks. The sample (S89-4-2-MS, 96.7 kg) was collected about 05-1 m below ground level in the northwestern corner of the small overgrown quarry. Balslev, Map sheet. Balslev 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 PALAEONTOLOGY

Order SQUALIFORMES Goodrich, 1909
Family SQUILDAE Blainville, 1816
Genus Squalus Linnaeus, 1758

Type species. Squalus acanthias Linnaeus, 1758. Recent, boreal to warm-temperate, intertidal down to at least 500 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. Intraspesific 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 1

Figs 1–8. Squalus ballingslovenensis sp. nov. 1–2, holotype, LO 5061 T, 52 mm long posterior lower jaw tooth from a mature male; labial and lingual views; Ballingslöv 1, sample S89-9-1-MS, 399.2 kg, ×13. 3–4, paratype, LO 5062 T, 47.7 mm long anterior-lateral tooth from a mature female; labial and lingual views; Ballingslöv 1, sample S89-9-1-MS, 399.2 kg, ×13.5. 5–6, paratype, LO 5063 T, 38 mm long symphysial tooth, cusp broken off; labial and lingual views; Ballingslöv 2, sample S89-4-8-MS, 109 kg, ×16. 7–8, paratype, LO 5064 T, 262 mm long incomplete lower jaw tooth from an immature individual, distal part of tooth broken off; labial and lingual views; Bjärängen, sample S89-4-2-MS, 96.7 kg, ×23.5.
SIVERSON, Squitus
Squalus ballingsloensis sp. nov.

Plate 1, figs 1–8

Type stratum. Sample S89-9-1-MS, Ballingslöv 1 quarry (Belenula lanceolata Zone, earliest Maastrichtian; for details see Svenson 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. ballingsloensis 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. ballingsloensis, 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. balvikensis 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. ballingsloensis 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 balvikensis 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), Balsvika quarry; Belenula 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–G, 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 11 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, ×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, ×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, ×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. abaticus (Andreae, 1892). Judging from illustrations (Herman 1982a) and specimens of S. minor examined, teeth from adult S. baltvikensis 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. baltvikensis, reach at least 1.24 m in body length, whereas newborn offspring from presumably smaller females are sometimes no larger than 0.22 m (Compagnoni 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. baltvikensis, 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 gabrielii sp. nov.
Plate 2, figs 1–8

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

Derivation of name. After Jan Gabrielsson, 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 Kvarnbysk, 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. gabrielii. 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. baltvikensis 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 gabrielii sp. nov. 1–2, paratype, LO 5069 t, 3.08 mm long posterior lower jaw tooth from a mature male; lingual and labial views; Kvarnbysk, ×22. 3–4, holotype, LO 5068 T, 2.55 mm long anterolateral lower jaw tooth; lingual and labial views; Kvarnbysk, ×23. 5–6, paratype, LO 5070 t, 2.31 mm long upper jaw tooth from a mature male; basal face of root unusually flat; lingual and labial views; Kvarnbysk, ×27. 7–8, paratype, LO 5071 t, 1.26 mm long tooth from an immature individual; lingual and labial views, Kvarnbysk, ×45.
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
Centrophoridae's appendicularis.

In both S. balteolatus 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 Microetimopterus gen. nov.

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

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

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 Microetimopterus from Proetimopterus and
Etmopterus. The upper jaw teeth of Microetimopterus 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.

Microetimopterus wardi sp. nov.

Plate 3, figs 1–12

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

Designation 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. Microetimopterus wardi gen. et sp. nov. 1–2, paratype, LO 5073 t, 0.20 mm high upper lateral tooth;
labial 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 × 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. Lateral face of crowns 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 mm 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 PROEMOPTERUS gen. nov.

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

Derivation of name. Combination of 'pro' (Greek, before in time) and Etmopterus (lunart shark).

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. Proemopterus hemmoroiensis 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. hemmoroiensis have a primitive morphology, retaining a rectangular root unlike the advanced scyliorhinid-like roots of Etmopterus and Microthoarios. Passing from Proemopterus 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. hemmoroiensis, or a later descendant, gave rise to Etmopterus, scyliorhinid-like upper jaw teeth with V-shaped roots evolved at least twice in Squarcoela in the mid-Maastrichtian Microthoarios and in the Early Miocene to Recent Etmopterus.

EXPLANATION OF PLATE 4

Figs 1–8. Proemopterus hemmoroiensis (Herman, 1982a) gen. nov. 1–2, LO 5078 t, 149 mm high upper inter- posterior tooth; labial and lingual views; Kvarnby, 3–4, LO 5079 t, 168 mm high upper anterior tooth, basal bulge of labial side of cusp worn, presumably during feeding; labial and lingual views; Ballingslöv 1, sample S89-91-MS, 399-2 kg, 5–6, LO 5080 t, 151 mm high lower jaw tooth; labial and lingual views; Björldagen, sample S89-4-2-MS, 967 kg, 7–8, LO 5081 t, 134 mm high lower jaw tooth, mesial corner of root broken off; lingual and labial views; Ballingslöv 1, sample S89-91-MS, 399-2 kg. All specimens × 40.


Figs 11–12. Centroteleumas schmidt Herman, 1982a. LO 6333 t, 14 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, 84 kg, 20-30 cm below the lower flint level, × 40.
Proetopterus hemmoorienis (Herman, 1982a)

Plate 4, figs 1–8

?1982a  Centrostyles schmidei Herman [partim], p. 135, pl. 1, fig. 5a, non figs 5b–c

1982a  cf. Centrostyles schmidei Herman, p. 135, pl. 1, fig. 5d; pl. 3, fig. 6.

1982a  Eoetopterus hemmoorienis Herman, p. 137, pl. 1, fig. 6; pl. 3, fig. 1.

1989  Eoetopterus supraeraceus Müller and Schöllmann [partim], p. 11, figs 4a–h; 4a–b; 4c–d; 4e–f; 4g–h; 4i–j; 4k–l; 4m–n.

1990  Eoetopterus supraeraceus Müller [partim], pl. 2, figs 1–3; non pl. 2, figs 4–6.

Type stratum: 0.5 m above bed T100, Belumella junior Zone (early Late Maastrichtian) of Hemmoor, Niederloth, Germany (Herman 1982a).

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

Description. Upper jaw teeth up to 1.27 mm high with one or two pairs of erect cuspules; inner pair reaching half or less of height of main cusp. Labial basal border of crown straight or forming median aporn. 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. Distal-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 Eoetopterus? hemmoorienis on an upper jaw tooth lacking the distal part of the distal root branch. In the same paper, he also described the new species Centrostyles schmidei 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 Proetopterus, it is evident that the upper jaw tooth referred to C. schmidei by Herman (1982a, pl. 1, fig. 5d; pl. 3, fig. 6), is a poorly preserved tooth of P. hemmoorienis with broken cusptoms. Unlike the holotype of E. hemoorienis, the specimen has a relatively well-demarcated aporn. 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 aporn. One of the three lower jaw teeth referred to C. schmidei by Herman (1982a, pl. 1, fig. 5a) probably also belongs to P. hemmoorienis. Unfortunately, this tooth was not illustrated by scanning electron micrographs.

Genus Eoetopterus Müller and Schöllmann, 1989

Type species. Eoetopterus supraeraceus Müller and Schöllmann, 1989 (p. 11, figs 4–4a–c; non figs 4b, 4c–4–7, 5a, 5b, 5c).

Remarks. The lower jaw tooth morphology alone does not justify a generic separation of Eoetopterus from the Recent Centrostyles (Scymnodon?) crepidater (Bocage and Capello, 1864). If my suggested recombination below of the lower jaw teeth of E. supraeraceus with the upper ones of Herman’s Scymnorhinae indet. n. sp. 2 is correct, then E. supraeraceus is a taxon generically difficult to separate from Centrostyles (Scymnodon?) crepidater. The putative upper jaw teeth of
E. supracretaceus differ from those of other sceymrhnid squaloids by their lack of a basal constriction of the crown.

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

Plate 4, figs 9–10

7[1982a] Scymnorrhinidae indet. a. sp. 2 Herman, p. 139, pl. 1, fig. 5f, and pl. 3, fig. 7.

*1989* Eoetomopterus supracretaceus Müller and Schöllmann [partim], p. 11, fig. 4.4a–c; non figs 4.5, 4.5–4.7, 5.1–5.3.

1990 Eoetomopterus 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. Crown 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 rooted over. Basal edge of root rectilinear.

**Remarks.** The figured material originally included in *Eoetomopterus 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 *Proetoetomopterus hemmoortensis*. 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 *Etoetomopterus* were reported to have fewer cusplets than males (Leduc 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 *Proetoetomopterus*. 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 border-line of the crown. No such teeth have been found in the *Proetoetomopterus*-yielding strata of the Kristianstad Basin. Consequently, the suggested combination of the 3 etymology 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. hemmoortensis* 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 *Proetoetomopterus* and possibly to *P. hemmoortensis*. 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 Scymnorrhinidae 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 foramina but no disto-lingual one. Other than that, the two teeth are almost identical in morphology.

**Genus Centroscyamus** Bocage and Capello, 1864

**Type species.** Centroscyamus coeleoplis Bocage and Capello, 1864, Recent, on or near the bottom of on the continental slopes (Compagnon 1984).
Centrosyllum sp. 1982

Plate 4, figs 11-12

Type strain: 0.6 m above bed F104, Belummella junior Zone (early Late Maastrichtian) of Hemmoor, Niederohe, 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 S86-6-1-MS, 84 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/distal cutting edge ratio about 3:5-4:1. Large meso-labial foramen; smaller median and disto-labial ones. One meso-labial foramen; two or less disto-labial ones. Enameloid covered apex not extending disto-labial foramen foramina. Unroofed median duct. Meso-labial interlocking hollow not reaching below meso-labial foramen; disto-labial one extending below lingual bulge of root.

Remarks. C. schmidi was the first described Cretaceous Centrosyllum, 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-labial foramen.

CENTROSYLLIUM, A RESTRICTED FORM OF ‘HOPEFUL MONSTER’?

In the view of Compagno (1984), the subfamily Etmopterinae comprises the three Recent genera Aculeolida de Buen, 1959 (monospecific), Centrosyllum Müller and Heale, 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 Centrosyllum 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 denticulate heterodonty with firmly interlocked lower jaw cutting teeth with a single conically curved cusp, and multisulcate erect upper jaw clenching teeth of scyliorhinid design.

Considering the observed rate of dentinal 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 Centrosyllum and Etmopterus. Let us assume a phenotypic transformation, in a mutant individual or litter, from a cutting/clenching dentition to a monognathic heterodonty with multisulcate Etmopterus-like upper jaw teeth in the lower jaw as well. Instantly equipped with a basic scyliorhinid-like clenching dentition, Centrosyllum-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 Centrosyllum-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 Centrosyllum, 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 Centrosyllum/Etmopterus body shape/lower jaw teeth paradox. Centrosyllum has yet no fossil record. This is probably because very little work has been done on Tertiary small-toothed deepwater selachians. A Miocene species, probably belonging to a new squaloid genus, was erroneously referred to Centrosyllum 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. varutii and P. hemmooriensis), two scymnornithids (C. schmidtii and E. macroreticulatus), and one Squatius (S. gabrielssonii). Fragmentary material indicates that the Kvarnby squaloid fauna may include yet another Squatius along with a possible Scymnodon. The earliest Maastrichtian Kristianstad Basin strata have yielded four squaloids, i.e. Squatius ballingsloensis, S. balivikenensis, C. schmidtii and P. hemmooriensis.

Recent species of Etmopterus are all small (< 1 m) deep-water sharks, mostly occurring on or near the bottom in 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 0.8–16 per cent of the total foraminiferal fauna (J. Gabrielson pers. comm.). The species is less common at Ballingsløv 1, Ballingsløv 2, and Bjærlängen, 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, orectoloboids comprise only a few per cent of the selachian fauna, whereas the squaloids make up more than 30 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. virans Bigelow et al., 1953, seem to attack and kill fairly large squid (Compagno 1984, p. 88). One can easily imagine individual belemmites being attacked by a school of Proetmopterus hemmooriensis. The shallow, temperate waters of the Kristianstad Basin archipelago, with its abundance of belemmites, may have constituted such a temptation to etmopterine sharks that they were willing to sacrifice the relative safety of deeper waters. Although belemmite rostra are very common fossils in the Campanian of the Kristianstad Basin as well, warmer water (inferred from e.g. Squatius-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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