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Barremian and Aptian (Cretaceous) sharks and rays from Speeton, Yorkshire, north-east England.

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SUMMARY: Bulk sampling of a number of horizons within the upper part of the Speeton Clay Type section has produced teeth and other remains of sharks and rays from several poorly studied horizons. At least 10 shark and two ray species were recorded, with two sharks, *Pteroscyllium speetonensis* and *Palaeobrachaelurus mitchelli*, being described as new. The oldest occurrences of the family Anacoracadae and the genus *Pteroscyllium*, as well as the youngest occurrence of the genus *Palaeobrachaelurus*, were recorded. The palaeoenvironmental significance of the faunas is briefly discussed.

The Speeton Clay Type section in north-east England exposes a condensed section of marine mudstones ranging from Late Berriasian to Middle Albian in age. Although the succession contains several stratigraphical gaps, and the upper part of the unit is often poorly exposed, the Speeton section contains the most complete exposed succession of the marine Lower Cretaceous of the North Sea Basin.

The sharks and rays (selachians) of the Early Cretaceous are currently poorly known, with published faunas from the Barremian and Aptian being largely represented by assemblages from shallow water (e.g. Biddle & Landemaine 1988; Batchelor & Ward 1990; Schmitz 2003) or from Tethyan (Cappetta 1975; Kriwet 1999) settings. The Early Cretaceous section at Speeton represent one of the most productive sites for the study of Boreal Early Cretaceous selachians, having previously produced diverse faunas from the Hauterivian (Underwood *et al.* 1999a) and Albian (Underwood & Mitchell 1999).

1. SHARKS AND RAYS OF THE SPEETON CLAY

Although the palaeontology of macroscopic invertebrates of the Speeton Clay, even the poorly exposed upper parts of the unit, has been studied for many years (with Aptian species recorded in Phillips, 1829), the smaller vertebrates have received little attention. Although 'fish bones and teeth' were recorded from various horizons by Lamplugh (1889) and Neale (1960), fish remains have rarely been identified. Otoliths of a single species of actinopterygian were figured by Stinton (1973), and two species of hexanchid sharks were recorded by Ward and Thies (1987), with all specimens probably originating from the lower part of the Hauterivian. More recently, Underwood *et al.* (1999a) described shark and ray faunas from the Hauterivian and basal Barremian and Underwood & Mitchell (1999a) described a number of additional species from the Albian.

No selachian material from the Berriasian or Valanginian of Speeton has been published, most likely because these horizons have never been systematically sampled for microvertebrates. The lower part of the Hauterivian section has produced the sharks *Notidanodon lanceolatus* (Ward & Thies 1987), *Notorynchus aptiensis*, *Synechodus dubrisiensis*, ?*Sphenodus* sp., *Cretorectolobus doylei*, and ?triakidae indet, along with the rays *Spathobatis rugosus* and *Dasyatis speetonensis* (Underwood *et al*. 1999a). A specimen of *Squatina* sp. has also been recorded in a private collection (pers. obs.). *Notorynchus aptiensis*, *Synechodus dubrisiensis*, and *Cretorectolobus doylei* have also been recorded from the basal Barremian (Underwood *et al*. 1999a), whilst a specimen of *Sphenodus* sp. is present in the British Geological Survey collections, supposedly also from the Barremian. A fragment of a gracile pointed tooth from Speeton is present in the Natural History Museum collection and appears to suggest the presence of a lamniform shark.

Samples from the Albian part of the Speeton Clay, as part of a more extensive study of faunas from the 'mid' Cretaceous, yielded a number of species described by Underwood & Mitchell (1999). Lower Albian samples yielded *Notorynchus aptiensis*, *Synechodus dubrisiensis*, *Protosqualus sigei*, *Squatina* cf. *cranei*, *Orectoloboides parvulus*?, *Cretorectolobus gracilis* and *Cretoscyliorhinus destombesi*. A Middle Albian sample contained *Notorynchus aptiensis*, *Protosqualus sigei*, *Squatina* cf. *cranei*, *Squatina* sp., *Chiloscyllium* cf. *greeni*, *Cretoscyliorhinus destombesi* and *Squatirhina thiesi*. Subsequent sampling of the top Lower or Middle Albian has added *Carcharias striatula* and *Pseudospinax heterodon* to the list. A study of the faunas of the uppermost Barremian and Aptian parts of the succession (Mitchell & Underwood 1999) indicated the presence of several selachians that are described in more detail here.

2. SAMPLING

Samples were collected from a number of horizons in the Barremian and Aptian parts of the Speeton Clay. The horizons under study are commonly obscured below landslip and beach deposits, and most of the material was collected during 1996 to 1998, when the Aptian part of the Speeton Clay was uncharacteristically well exposed. Condensed levels were preferentially sampled as these typically contain far higher numbers of microvertebrate remains (see Fig. 1).

The samples from the Middle B Beds were collected from two hiatal horizons exposed in a small cliff section close to the mouth of Speeton Beck comprising alternating pale and dark mudstones, the former containing very large septarian concretions. All of the selachian remains were collected from a level of pale mudstone with many belemnites below a level of large concretions, within one of which a large heteromorph ammonite was seen. Additional samples from a concentration of small aragonitic bivalves yielded no vertebrate material. The stratigraphical context of these samples could not be ascertained due to numerous slip planes cutting the exposure. Samples from the uppermost Barremian and Aptian were stratigraphically far more accurately constrained (Mitchell & Underwood 1999).

Clays and softer marls were oven dried before being soaked and wet sieved. Harder marls were dried and soaked in a saturated solution of sodium sulphate before being subjected to several freeze-thaw cycles and hand sieved. Residues were not concentrated in acid, as invertebrate fossils were also wanted, and all teeth, tooth fragments and scales of selachians were picked from residues down to 355µm. In total, about 130kg was sampled from the Aptian part of the Speeton Clay and 30kg from the Middle to Upper Barremian parts of the B Beds.

Many of the selachian remains had evidence of considerable bioerosion by endolithic micro-organisms (see Underwood *et al.* 1999b), and large numbers of the teeth are represented by isolated cusps. The highly incomplete nature of much of the selachian material makes assessment of numbers of specimens almost impossible, and so relative frequencies of taxa have had to be used instead. There was no sign of abrasion or indication that any of the remains represented parts of associated dentitions.

A number of invertebrate taxa were recorded associated with the microvertebrate remains, many representing taxa previously unknown from Speeton (Mitchell & Underwood 1999). Remains of actinopterygian fish were typically present in the samples, but commonly subordinate to those of selachians. Isolated teeth and jaw fragments suggested the presence of a number of taxa. A small number of well preserved otoliths were recovered from one horizon in the Middle B Beds (Barremian). These suggest the presence of at least two taxa, and are currently under study.

Type and most figured material is deposited in the Natural History Museum, London; some figured material is currently under study and has yet to be catalogued.

3. SYSTEMATIC PALAEONTOLOGY

An attempt has been made to figure and describe examples of each taxon recorded during this study, even those that are taxonomically indeterminate, as these are considered important if any faunal study is to be carried out. Descriptive terminology generally follows that of Cappetta (1987) (see Fig. 2). Higher level classification generally follows cladistic analysis of Shirai (1996).

Subcohort **NEOSELACHII** Compagno 1977 (Modern-type sharks and rays)
Superorder **GALEA** Shirai 1996
Order **CARCHARHINIFORMES** Compagno 1977 (Ground sharks)
Family **SCYLIORHINIDAE** Gill 1862 (Catsharks, spotted dogfish)
Genus **PTEROSCYLLIUM** Cappetta 1980

Pteroscyllium speetonensis sp. nov.
Fig. 3, 1-11.
Holotype. P. 66265, Basal Aptian, Speeton, Bed UB1B (Fig. 3, 1-3).
Etymology. After the type locality of Speeton, N. Yorkshire.
Other material. Numerous incomplete to fragmentary teeth, Aptian, Beds UB1B to LA6.
Diagnosis. Teeth bilaterally symmetrical except for posteriormost files. High main cusp at least as high as root with one pair of short and robust cusplets, cusps strongly united basally. Labial face of cusps ornamented with strong, sharp edged, longitudinal ridges, with up to ten ridges on larger teeth, fewer on smaller. Labial ridges subparallel and reach the base of the crown. Ridges rarely bifurcate in larger anterior teeth but do so more commonly in smaller, more posterior ones. Ridges reach the apex of lateral cusplets but not on the main cusp. Lingual face of cusps strongly convex with fine, somewhat sinuous ridges. Root bulky and thick with well separated lobes.
Description. Teeth, which are up to 3.5mm high, have an overall ‘odontaspid’ form with an erect main cusp flanked by a pair of well developed lateral cusplets and a

strongly “V” shaped root. The teeth show a moderate amount of heterodonty, with smaller teeth having fewer labial ridges and posterior teeth having asymmetrical root lobes and a short main cusp. The main cusp is straight in all teeth and is flanked by a single pair of equally sized lateral cusplets, which are either parallel to the main cusp or faintly divergent. All cusps are strongly joined basally, with the base of the crown extending at least half way down the labial face of the root lobes. Lateral cusplets are less than half the length of the main cusp, being closer to a quarter of its length in larger teeth. All cusps are similarly ornamented. The flat to faintly convex labial faces of all cusps are ornamented with well developed longitudinal ridges. These ridges reach the base of the crown and the apex of the lateral cusplets, but not the apex of the main cusp. Up to ten ridges are present on the main cusp and up to four ridges are present on the lateral cuspletsof the largest teeth, but on smaller teeth far fewer are present. On larger teeth, there is relatively little bifurcation of the labial ridges, but on smaller teeth all ridges bifurcate at least once. The lingual face of all cusps is strongly convex, and is separated from the labial face by a continuous and well developed cutting edge. The lingual face of all cusps is ornamented by numerous fine longitudinal ridges. These are somewhat sinuous and bifurcate irregularly. These lingual ridges reach the apex of all cusps but do not reach the base of the crown. The root is bulky and, when viewed lingually, of a similar height to the main cusp. Two root lobes are widely separated and, where seen, of equal size in all but the posteriormost teeth. Root lobes are parallel sided and slightly labio-basally flattened but with a convex basal face. The root lobes are separated lingually by a very well developed nutritive groove, which contains at least one large foramen. Several small foramina are present on the labial edge of the root on each side of the main cusp and near the junction of the root lobes on the root lingual edge. Broken teeth reveal a well-developed pulp cavity.
Remarks. This is a relatively abundant shark tooth in the Aptian at Speeton, although unbroken teeth are very rare. This may be the same species as a single, abraded tooth of *Pteroscyllium* from the Aptian of southern England (Batchelor & Ward 1990). Teeth of *P. speetonensis* sp. nov. differ from those of *P. ornatum* Underwood & Mitchell 1999, from the Albian of Speeton, in having a finer labial ornament and a consistent bilateral symmetry. It differs from *P. nolfi* Müller & Diedrich 1991, from the Cenomanian of Germany, in having a bifurcating labial ornament and straight cusps in lateral teeth. The relationship between *Pteroscyllium* and other scyliorhinids is uncertain, with *Pteroscyllium* having teeth with a pulp cavity (pers obs.) and sharing a body form and general dentition pattern with other scyliorhinids (Cappetta 1980), but having a tooth morphology more like that of lamniforms (Maisey 1984).

Order **LAMNIFORMES** Berg 1958 (Mackeral sharks and relatives)

Family **CRETOXYRHINIDAE s.l**. Glickman 1958 (Extinct family)

Cretoxyrhinidae indet.

Fig. 3, 12-13

Material. Several fragmentary teeth, Aptian, Beds LA6 to LA5.
Description. These isolated cusps may represent more than one species, but are not sufficiently well preserved to allow differentiation. Cusps are straight and considerably higher than wide, all apparently erect and bilaterally symmetrical. All have a faintly convex labial face and more strongly convex lingual face. A well developed and apparently continuous cutting edge is present on all cusps. Labial ornament was not observed. Ornament of the lingual face is variable. On some cusps,

ornament is almost absent and is represented by faint irregular ridges near the base of the cusp. Other cusps show a stronger ornament, with fine, rather discontinuous, longitudinal ridges being present on the lower half of the cusp. The root and any lateral cusplets are unknown.
Remarks. It is likely that more than one genus is represented within these indeterminate tooth fragments. Although the identities of the genera are far from certain, comparisons with similarly aged assemblages elsewhere suggest that it is possible that the smoother cusps belong the *Cretalamna* and the more ornamented ones to *Cretodus*.

Family ?**ODONTASPIDAE** Müller & Henle 1839 (Sand tiger sharks)

Genus **JOHNLONGIA** Siverson 1996

?*Johnlongia* sp.
Fig. 4, 1-3.

Material. One incomplete tooth, Aptian, Bed LA6.
Description. The single imperfect tooth of this species has a preserved height of about 1cm, but is missing the root lobes. A very elongate main cusp is inclined slightly to the posterior and has a very small lateral cusplet on the anterior side, but none on the posterior. The labial face of both main cusp and preserved cusplet are very flat and smooth, with no ornament other than a few very small and faint ridges near the base of the main cusp. The lingual face of both cusps is very convex and unornamented. The sharply angled edges of the labial face do not have a differentiated cutting edge. The base of the crown abuts a flat labial face of the root. The root is compressed linguo-labially with any root lobes fused together to some distance below the base of the crown. The basal face of the root is flat and bisected by a well developed nutritive groove. There is a distinct swelling of the lingual edge of the root below the base of the crown.
Remarks. The only specimen of this taxon is currently under study by Mikael Siverson. This tooth more closely resembles anterior teeth of the rather heterodont genus *Johnlongia* (Siverson 1996) than the teeth of any other Early or 'mid' Cretaceous lamniformes. It does, however, differ from teeth of other species of *Johnlongia* in having a compressed root with a flat basal face. More material would be needed to be certain of the identity of this specimen.

Family **ANACORACIDAE** Casier 1947 (Extinct family)

Anacoracidae indet.
Fig. 3, 14, Fig. 4, 4-11.

Material. Numerous complete to fragmentary teeth, Aptian, Beds UB1B to LA5.
Description. Teeth small, up to 3.5mm high, show a high degree of heterodonty. High, narrow teeth are interpreted as anterior and lower, broad teeth as lateral. In all teeth the crown is rather compressed, with a flat labial face and somewhat convex lingual face, the faces separated by a continuous and well developed cutting edge. There is a single cusp, which is inclined posteriorly in all teeth. This comprises at least two thirds of the width of the crown. The lower part of the cusp has a straight to convex anterior edge, becoming concave in anterior teeth to give an overall faintly sigmoidal profile. Behind the cusp is a distal heel, which is horizontal or slopes gently to the posterior. There is no ornament on either face of the crown, other than a faint oblique ridge on the labial face of a posterior tooth. The crown is narrower than the

root in all teeth, with a variably concave basal crown edge on both sides of all teeth. The crown base weakly overhangs the root labially. The root is relatively low in all teeth and little linguo-labially compressed. The basal edge of the root is variably concave in all teeth, with two distinct root lobes developed in some anterior teeth. The root is divided basally by a very well developed nutritive groove containing a large foramen. A row of small foramina are present on the labial face of the root below the centre of the cusp. Although no teeth were sectioned for histological study, broken teeth show no pulp cavity within the crown; a small cavity within the upper part of the root appears to be a very well developed horizontal root canal.
Remarks. All of the fairly complete teeth of this frequent species are currently under study by Mikael Siverson as part of work on anacoracid evolution. These specimens represent the earliest record of the Anacoracidae, which are otherwise only known from the Albian to Maastrichtian, becoming one of the most important groups of large predatory sharks in the Late Cretaceous.

These teeth are similar, in both crown and root morphology, to species of *Pseudocorax*, to which this species was referred by Mitchell & Underwood (1999). They, however, considerably predate any occurrences of *Pseudocorax*, which is unknown prior to the Turonian (Cappetta 1987). All other pre-Turonian anacoracids differ in lacking a nutritive groove and having a lower degree of heterodonty. Although it is possible that this taxon represents *Pseudocorax*, the lack of intervening records of this easily recognizable and widespread genus seems to make this unlikely. It is therefore considered more likely that this species represents a previously unknown taxon within the Anacoracidae, possibly close to the ancestry of the group. The general morphology of the teeth is similar to that of some members of the Triakidae, but the lack of a pulp cavity makes an assignment to the Triakidae unlikely unless there has been a change in tooth structure early in the evolution of the group. A single small tooth from the Hauterivian of Speeton, referred to as a triakid by Underwood *et al.* (1999a), is morphologically similar to some of these anacoracid teeth, and it is possible that they are related.

Order **ORECTOLOBIFORMES** Applegate 1972 (Nurse sharks)

Family ?**HEMISCYLLIIDAE** Gill 1862 (Bamboo sharks)

Genus **PALAEOBRACHAELURUS** Thies 1983

Palaeobrachaelurus mitchelli sp. nov.
Fig. 3, 15-21.
Holotype. P. 66273, Middle Barremian, Speeton, Middle B Beds, exact horizon unknown (Fig. 3, 15-17).
Etymology. After Simon Mitchell, who helped collect much of material described here.
Other material. One complete tooth, P. 66274, Middle Barremian, Speeton, Middle B Beds, exact horizon unknown.
Diagnosis. Crown wider than high with flat and unornamented labial face. Base of main cusp about one third of width of crown. Main cusp triangular and about as high as wide being either erect or inclined to posterior. Height of main cusp about equal to height of crown below cusp. One pair of weak to incipient lateral cusplets present, being better developed on posterior side of lateral teeth. Labial protuberance wide and only weakly differentiated from rest of crown basal edge. Weak uvula of similar width to main cusp. Root low and root lobes narrow forming gently curvature.

Description. These teeth are very small, about 1mm wide. One of these small teeth is bilaterally symmetrical and is likely to represent an anterior tooth, the other is asymmetrical and is probably from a lateral position. Both teeth have the same general form, with a broad, unornamented crown with a single main cusp and weakly cuspate lateral expansions. The labial face of the crown is flat, but with a slight concavity at the base of the main cusp of the anterior tooth. The triangular main cusp is robust and is flanked by a pair of short, rounded cusplets in the anterior tooth, with the angled main cusp of the lateral tooth having a small, triangular posterior cusplet but no anterior cusplet. A continuous cutting edge is present along the entire occlusal edge of the crown. The basal edge of the crown is generally convex and strongly overhangs the root. A labial protuberance is present, being at least as wide as the base of the main cusp, but short and poorly differentiated with a straight or gently convex labial edge. A poorly developed uvula is present at the base of the main cusp in the lingual side. This is as wide as the base of the cusp and triangular with a thin enameloid covering. The root is low and the same width as the crown. The basal face of the root is narrow and parallel sided, being somewhat curved with a slightly swollen lingual edge. A pair of well developed foramina are present at the labial apex of the root and on the basal face directly behind. Foramina are also present on the lateral faces of the root, with one larger and up to two smaller foramen being present on each side.
Remarks. Small orectolobiform teeth assignable to *Palaeobrachaelurus* are common in Jurassic and Lower Cretaceous rocks, with this representing the latest known occurrence of the genus. The systematic position of this genus, and similar genera, is poorly understood (Underwood & Ward 2004). Despite this, the general morphology of *Palaeobrachaelurus* teeth is similar to that of extant hemiscylliids, although this resemblance may be superficial. *Palaeobrachaelurus mitchelli* can be differentiated from *P. rocklumensis* (Thies 1981) in being wider and having less well developed lateral cusplets and labial protuberance. It is also similar to some species of *Cretorectolobus* such as *C. doylei* Underwood *et al.* 1999a and *C. gracilis* Underwood & Mitchell 1999, but can be recognised by the lack of a well developed labial protuberance and a generally broader labial face.
Hemiscylliidae indet.
Fig. 5,2.
Material. One partial tooth, Aptian, A/B Beds contact horizon.
Description. This small tooth crown is considerably longer than wide. About half of the crown length is the straight main cusp. This is flanked on the one preserved side by a very short, rounded lateral cusplet. The labial surface of the crown is slightly convex and unornamented. The labial edge of the crown is smoothly convex with no differentiated labial protuberance. The lingual face of the cusps is convex and unornamented. There are remains of a small but well defined uvula. The root is unknown but was apparently small and overhung by the crown.
Remarks. Similar to teeth from the Albian of Speeton assigned to *Chiloscyllium* cf. *greeni* by Underwood & Mitchell (1999), this tooth differs in lacking a concavity of the labial edge of the crown below the cusplet. This may be conspecific with a specimen from the Aptian of southern England referred to *Chiloscyllium* sp. by Batchelor & Ward (1990). Many Cretaceous teeth assigned to *Chiloscyllium* are more elongate and with more clearly differentiated lateral cusplets than those of any extant species (see Herman *et al.* 1992), and may represent other genera.

Order **HETERODONTIFORMES** Berg 1940 (Bullhead sharks)
Family **HETERODONTIDAE** Gray 1851
Genus **HETERODONTUS** de Blainville 1816 (Extant bullhead sharks)

?***Heterodontus*** sp.
Fig. 5, 1.
Material. One partial tooth, Aptian, A/B Beds contact horizon.
Description. This tooth is poorly preserved. The crown is higher than wide, with a flat labial face. A triangular main cusp has two small lateral cusplets on one side. The labial edge of the crown appears to be smoothly convex, but is badly damaged. The inner lateral cusplet is fused to the basal part of the main cusp, and is smaller than the outer cusplet. The only ornament on the tooth is a couple of fine longitudinal ridges below the base of the outer cusplet. The lingual face and root are not preserved.
Remarks. Due to poor preservation, this tooth cannot be identified to any degree of confidence. The general crown morphology is very much like that of the anterior teeth of *Heterodontus*, but it is possible that this represents an orectolobiform.

Superorder **SQUALEA** Shirai 1996
Order **HEXANCHIFORMES** Compagno 1973 (Six and seven-gill sharks)
Family **HEXANCHIDAE** Gray 1851
Genus **NOTORYNCHUS** Ayres 1855 (Bluntnose seven-gill sharks)

Notorynchus aptiensis (Pictet 1865)
Fig. 5, 3-4.
Material. Several incomplete to fragmentary teeth, Aptian, Beds UB1B to LA6.
Description. Most of the teeth of this species comprise isolated cusps, and add nothing to previous descriptions of specimens of the species (Cappetta 1975; Smart 1995; Siverson 1997). The most complete tooth is the posterior portion of a tooth possessing two posteriorly inclined cusps overlying a deep root (P. 66278). The cusps are distally inclined, with the more anterior of them being the larger. Below the more distal cusp is a small distal blade. The crown is compressed and unornamented, with a straight basal edge on both sides. The root is as deep as the crown, and gets shallower to the posterior. It is compressed with a faint ridge on the lingual side parallel with the base. A number of small and irregular foramina are present on the lingual face. Isolated anteriormost cusps are of similar general shape to posterior cusps, but all except the smallest have serrations on the lower third of the anterior edge. These serrations are usually irregular. A small tooth, considered here to be a commissural tooth of *N. aptiensis*, is also known (P. 66277). This is compressed and considerably wider than high. The crown is elongate and low, with no clearly defined cusps. A central ridge is flanked by a pair of lateral transverse ridges, which show faint crenulations. The root is considerably higher than the crown, with foramina on the lingual face, but is poorly preserved.
Remarks. Specimens assigned to *N. aptiensis* have been recorded from rocks ranging from Hauterivian to Cenomanian in age. Despite this, few assemblages have been studied in detail and it is possible that more than one species is present. The commissural tooth is the first to be recorded from this species. It closely resembles the commissural teeth of extant *Notorynchus* (Herman *et al.* 1987; pers. obs), differing largely in the possession of more clearly defined lateral ridges.

Order **SYNECHODONTIFORMES** Duffin & Ward 1993 (Extinct stem group squalean sharks)
Family **PALAEOSPINACIDAE** Regan 1906
Genus **SYNECHODUS** Woodward 1888

Synechodus dubrisiensis (Mackie 1863)
Fig. 5, 5-6.
Material. Many teeth, mostly highly fragmentary, Barremian and Aptian, Middle B Beds to LA6.
Description. Teeth of this taxon have been extensively described before (Biddle 1993; Underwood *et al.* 1999a), and the current material does not differ in any major way to material already described.
Remarks. Partial teeth of *S. dubrisiensis* are the commonest selachian remains in the Aptian of Speeton, making this an important part of the faunas throughout the Lower Cretaceous at the site (Underwood *et al.* 1999a; Underwood & Mitchell 1999).
Order **SQUALIFORMES** Goodrich 1909 (Dogfish)
Family **SQUALIDAE** Bonaparte 1834 (Spurdogs)
Genus **PROTOSQUALUS** Cappetta 1977

Protosqualus sp.
Fig. 5, 7.
Material. Two partial teeth, Barremian, Middle B Beds and Bed UB3.
Description. The better preserved of these incomplete teeth has a single, triangular, cusp which is strongly distally directed but does not extend as far distally as the end of the crown. Behind this is a low but well defined distal heel. A very well developed cutting edge is continuous along the occlusal edge. The labial face of the crown is somewhat convex. The labial basal edge is poorly preserved, but a well developed and wide labial protuberance is present. The lingual face of the cusp and distal heel is similar to the labial face; the rest of the tooth lingual face being missing.
Remarks. The general form of the tooth with the broad labial protuberance identify it as *Protosqualus*. It is uncertain whether this is *P. albertsi* Thies 1981, known from the Barremian of Germany, but the general robust nature of the tooth makes this a more likely assignment than the more gracile *P. sigei* Cappetta 1977, which is known from several European Albian and Cenomanian sites.
Order **SQUATINIFORMES** Compagno 1973 (Angel sharks)
Family **SQUATINIDAE** Bonaparte 1838
Genus **SQUATINA** Duméril 1806

Squatina sp.
Fig. 5, 8.
Material. Three partial teeth, Barremian, Middle B Beds to Aptian, Bed LA5.
Description. The single cusp is erect and straight, with no curvature either lingually or posteriorly. The cusp is longer than wide with a continuous and well developed cutting edge. Both labial and lingual faces are convex, and there is little difference between them. Basally, there is a smooth curve where the base of the cusp expands into the crown shoulders. The distal parts of the crown, root and any uvula or labial protuberance are missing.

Remarks. Despite the incompleteness of the specimen, it is very similar to well preserved teeth of *Squatina* from other Lower Cretaceous sites.

Order **BATIFORMES** Berg 1940 (Rays)

Family **RHINOBATIDAE** Müller & Henle 1838 s.l.(Guitarfish)

Genus **BELEMNOBATIS** Thiolliere 1854

Belemnobatis cf**. *picteti*** (Cappetta 1975).

Fig. 5, 9-12.

Material. Three incomplete teeth, Aptian, Bed LA6 and A/B beds contact horizon.

Description. These small teeth have a faintly cruciform shape in occlusal view. The crown is wider than high or deep. A central cusp is present on an occlusal ridge that runs across the full width of the crown. This takes up about the central third of the tooth and varies from incipient to well developed, well developed cusps being triangular with a blunt tip. The labial face of the crown is slightly convex and unornamented. The lateral parts of the crown taper and have an irregularly crenulated labial edge. A labial protuberance is present, being narrower than the cusp and poorly developed. The lingual face of the crown makes an angle of about ninety degree to the labial face, and is smooth. There is some concavity where lateral parts of the crown curve gently lingually. Below the cusp, the uvula is large and swollen, being rather larger than the labial protuberance. Only one tooth has a partial root. This is low and gracile, being of a similar width the crown, which strongly overhangs it.

Remarks. Two of the specimens of the species correspond very closely with the descriptions of specimens from the Aptian of southern France (Cappetta 1975), with a third differing in having a larger cusp. It is, however, known that some batoids show considerable heterodonty (Underwood & Rees 2002; Underwood 2002), with variations due to ontogeny, position within the jaw and sex, with more cuspate teeth belonging to males. It is therefore considered that this variation can be accommodated within the normal range of species of *Belemnobatis.*

INCERTAE FAMILAE

Genus ?**SQUATIRHINA** Casier 1947

? ***Squatirhina*** sp.

Fig. 5, 13.

Material. One fragmentary tooth, Aptian, Bed LA6.

Description. The tooth comprises a partial crown, showing part of a cusp, a lateral expansion and a labial protuberance. A well developed cusp was present, although only the base now exists, the broken edge showing the cusp to be almost round in cross section. A well developed, rounded labial protuberance is present opposite the cusp, being of a similar width to the base of the cusp. The preserved lateral part of the crown is narrow and curved lingually. A small ridge on the lingual side of the lateral expansion is the only sign of an occlusal ridge.

Remarks. The single tooth fragment is very similar in general form to the anterior teeth of the Albian *Squatirhina thiesi* Biddle 1993, although the quality of the specimen prevents further comparison. This is the earliest probable record of *Squatirhina*.

Placoid scales

Fig. 5, 14-17.

Material. A number of whole and partial scales from Bed LA6 and A/B Beds contact horizon.
Description. Four distinctly different morphologies of placoid scales were recovered, although there is some degree of variation within each morphotype.
Type 1. Several specimens of this scale type were recovered, but all lacked the root and stem of the scale. The crown of the scale is widest anteriorly, tapering to the posterior. It has an elongate central posterior point, with one or two pairs of smaller lateral points. A prominent ridge runs from the tip of the central point to a boss at the anterior end. A single pair of additional longitudinal ridges are also present, but these do not necessarily coincide with the lateral posterior points.
Type 2. Several partial and complete specimens of the scale type were recorded. The crown is oval and tapers both to the posterior and anterior, and is typically rather asymmetrical. The outer surface is smoothly convex, and has up to six faint longitudinal ridges that originate at the anterior end but do not reach the posterior. The surface, especially towards the posterior end, is typically worn smooth, and has a number of fine scratch marks. The stem is short and robust and only expands slightly at the base to form a diamond-shaped root.
Type 3. Only represented by one example, this scale has an almost round crown. This has a very prominent boss and the anterior end, which forms part of a short ridge. A second, sharper, ridge originates on the anterior edge and forms an unbroken loop around the scale parallel to the edge. The stem is short and constricted, expanding basally into a diamond-shaped root.
Type 4. These scales, rather larger than any of the others, are represented by two specimens. One of the specimens is bilaterally symmetrical, the other not, with the asymmetry especially well developed in the root. The crown is smaller than the root and rises directly from it, without a clearly differentiated stem. This is roughly ‘arrowhead’ shaped, with a posterior point, a pair of lateral extensions directed slightly to the anterior and a paired anterior projection. Fine but well developed ridges arise from the anterior ends of each of the four projections, extending towards the tip. These ridges divide at their anterior end. The tips of both specimens are worn and show clear scratch marks. The root is wide and flat, having a similar profile to the cusp.
Remarks. Placoid scale morphology is difficult to relate to taxonomy (e.g. Campbell 2003), with many selachian taxa having very different scales on different parts of the body, and some scale forms being found within a number of unrelated groups. Scales of Type 1 closely resemble those recorded on fossil hexanchids (Cappetta 1980) and palaeospinacids (Duffin & Ward 1993), and it is possible that they belong to *Notorynchus* or *Synechodus*. This scale morphotype was recorded from the Albian of Speeton (Underwood & Mitchell 1999), rocks which also contain common teeth of *Notorynchus* and *Synechodus*. Type 2 scales are relatively unspecialised, and similar forms are known from a range of taxa. The presence of extensive wear suggests that the shark was a benthic form where rubbing against the substrate was normal. Scales of this form are especially well developed in Orectolobiformes, and almost identical scales are present on extant taxa such as *Orectolobus* and *Sutorectus* (pers. obs). Scales of Type 3 are of a relatively uncommon design. Very similar forms have been figured from various positions on the skull of Jurassic *Synechodus* (Duffin & Ward 1993), but are also present on the dorsal surface of the rhinobatid *Trygonorrhina* (pers. obs.) and it is therefore possible that either *Synechodus* or a batiod were the

source. Although very characteristic, scales similar to Type 4 are present on several unrelated benthic taxa. The closest resemblance amongst modern taxa is the scales of *Heterodontus* (Reif 1974), although the dorsal scales of some species of *Squatina* are also very similar (pers. obs).

4. INTERPRETATION OF THE FAUNAS

Although very few selachian remains were recorded from the Middle B Beds, the fauna of *Synechodus*, small Orectolobiformes and *Squatina* is similar to that from other Jurassic to Early Cretaceous offshore mudstone sites (e.g. Underwood *et al.* 1999a; Underwood 2002; 2004). The addition of *Protosqualus* may suggest the first appearance of this taxon during the Barremian, with squalids commonly being present in Boreal deeper water assemblages from the Barremian onwards (Thies 1981; Siverson 1993; Biddle 1993). Although this study failed to recover any lamniform remains, tooth fragments in the natural History Museum collections suggest that at least one lamniform taxon was present in the Hauterivian or Barremian of Speeton. Lamniform sharks are known from a number of Valanginian to Barremian sites elsewhere (Rees *in press*).

Aptian faunas are somewhat different within the top B Beds and the Lower A Beds. Although represented by relatively few specimens, the selachian fauna of the top B Beds differs from later Aptian assemblages in comprising only two species. There is an apparent absence of presumed benthic taxa such as *Synechodus* and *Belemnobatis*. It is possible that hostile seafloor environments, as indicated by impoverished invertebrate assemblages (Mitchell & Underwood 1999) also adversely affected the selachian faunas. More diverse selachian assemblages are present within the Lower A Beds (Ewaldi Marl). Many of the taxa within the assemblage are of groups common throughout the latter parts of the Jurassic and Early Cretaceous (*Synechodus*, hexanchids, scyliorhinids, small orectolobids, *Heterodontus*, *Squatina* and *Belemnobatis*), but these are associated with several species of lamniforms. Although lamniform teeth are known from the Valanginian (Rees *in press*), and Barremian (e.g Biddle & Landemaine 1988; Kriwet 1999), it is typically within the Aptian that they become diverse (Cappetta 1975). This radiation continues throughout the ‘mid’ Cretaceous, and teeth of lamniforms are commonly a dominant element of Albian assemblages (Biddle 1993; Cappetta & Case 1999). Although members of the Cretoxyrhinidae s.l., Odontaspidae and Mitsukurinidae have previously been recorded from the Aptian (Cappetta 1987), this is the first time that members of the Anacoracidae have been recorded prior to the Albian. Previous study of the selachian faunas at Speeton have likewise revealed the presence of groups long predating their first occurrence elsewhere (Underwood *et. al* 1999a). It is therefore possible that the North Sea basin represented a rather different faunal realm to sites that have been studied elsewhere, and a number of taxa were appearing within this area long before colonizing other, less boreally influenced, regions.

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FIGURE CAPTIONS

Fig. 1.
Occurrences of selachian material from the Middle Barremian to Aptian of Speeton with (inset) maps showing the outcrop of Lower Cretaceous rocks in eastern England and the position of Speeton.

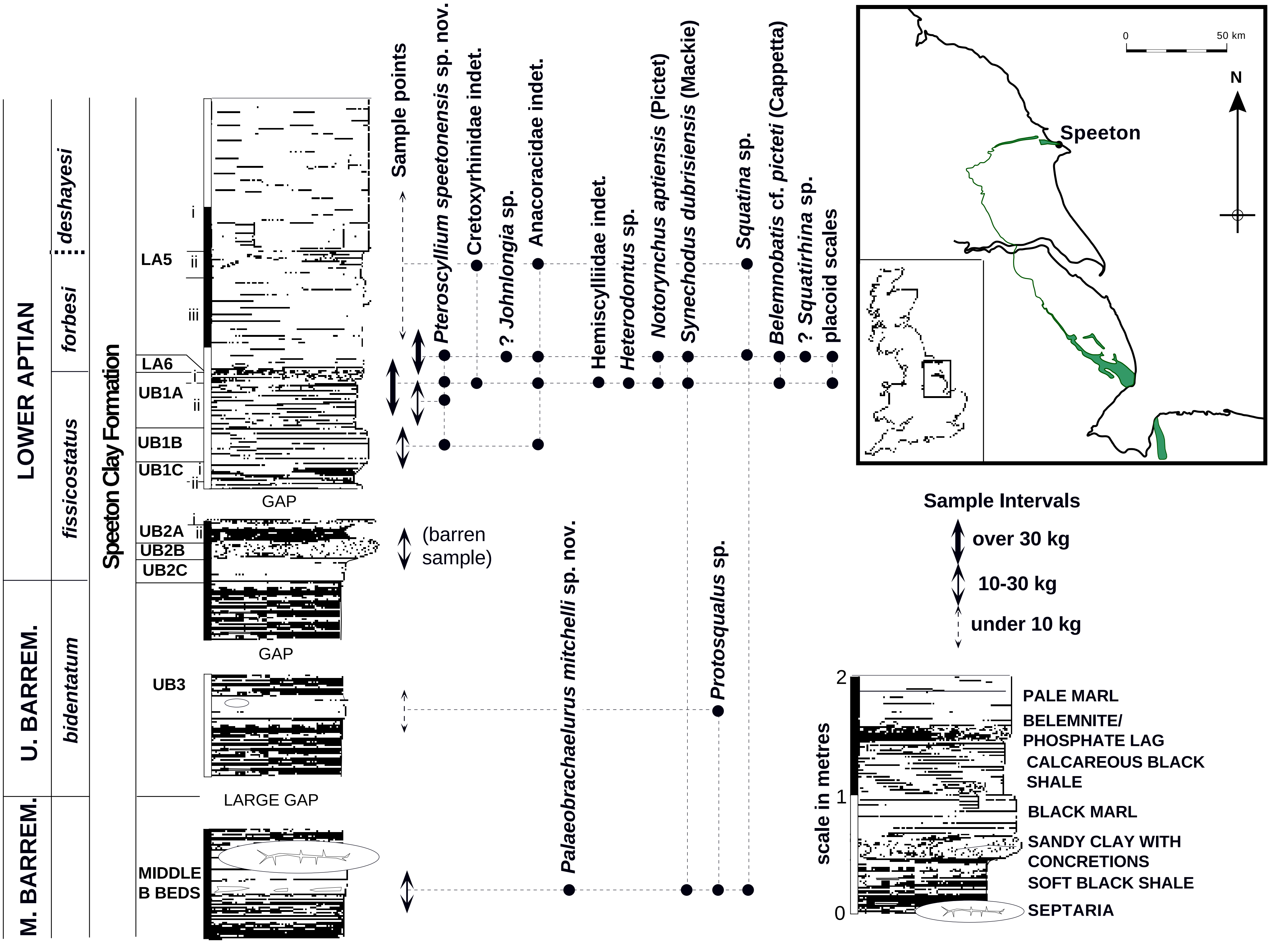
Fig. 2.
Diagram of a hypothetical shark tooth showing the morphological features mentioned in the text.

Fig. 3.
1-11. *Pteroscyllium speetonensis* sp. nov. 1-3. Holotype, P. 66265, X24, Bed UB1B, anterior tooth, 1 lingual, 2 labial, 3 oblique lateral views; 4-6. P. 66266, X24, A/B Beds contact horizon, 4 lingual, 5 labial, 6 oblique lateral views; 7-8. P. 66267, X24, LA6, 7 lingual, 8 labial views; 9. P. 66268, X24, LA6, labial view; 10-11. P. 66269, X48, LA6, posterolateral tooth,10 labial, 11 lingual views.
12-13. Cretoxyrhinidae indet.. 12. P. 66270, X16, LA6, lingual view; 13. P. 66271, X16, lingual view.
14. Anacoracidae indet. P. 66272, X15, LA6, anterior tooth, labial view.
15-21. *Palaeobrachaelurus mitchelli* sp. nov. 15-17. Holotype, P. 66273, X32, Middle B, lateral tooth, 15 labial, 16 lingual, 17 oblique lateral views; 18-21. P. 66274, X32, Middle B, anterior tooth, 18 labial, 19 lingual, 20 occlusal, 21 oblique lateral views.

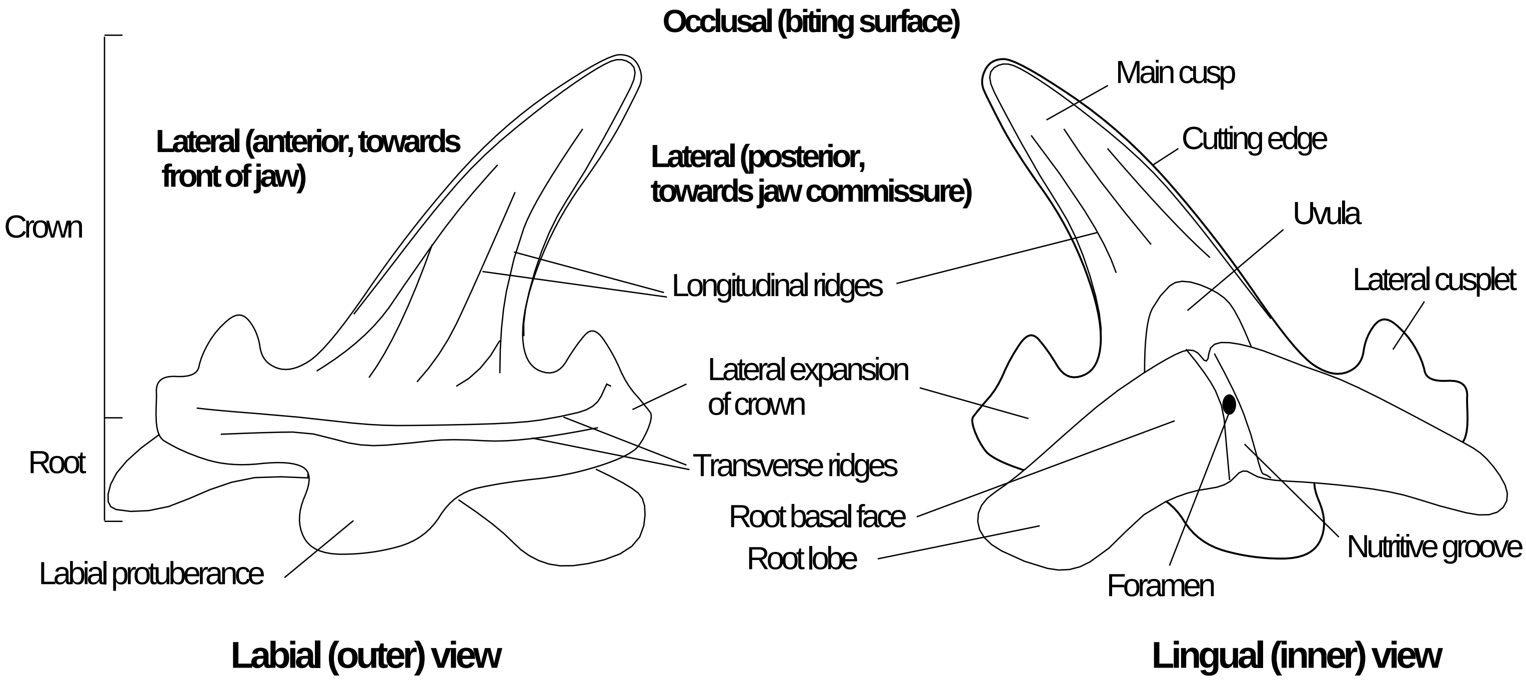
Fig. 4. Camera lucida drawings of lamniforme teeth under study by Mikael Siverson. All from various horizons within the Lower Aptian.
1-3. ?*Johnlongia* sp. Scale bar in mm, anterior tooth, 1 lingual, 2 labial, 3 lateral views.
4-11. Anacoracidae indet. Scale bar in mm, 4-5 lateral tooth, 4 lingual, 5 labial views; 6-7, commissural tooth, 6 lingual, 7 labial views; 8-9, anterior tooth, 8 lingual, 9 labial views; 10-11, lateral tooth, 10 labial. 11 lingual views.

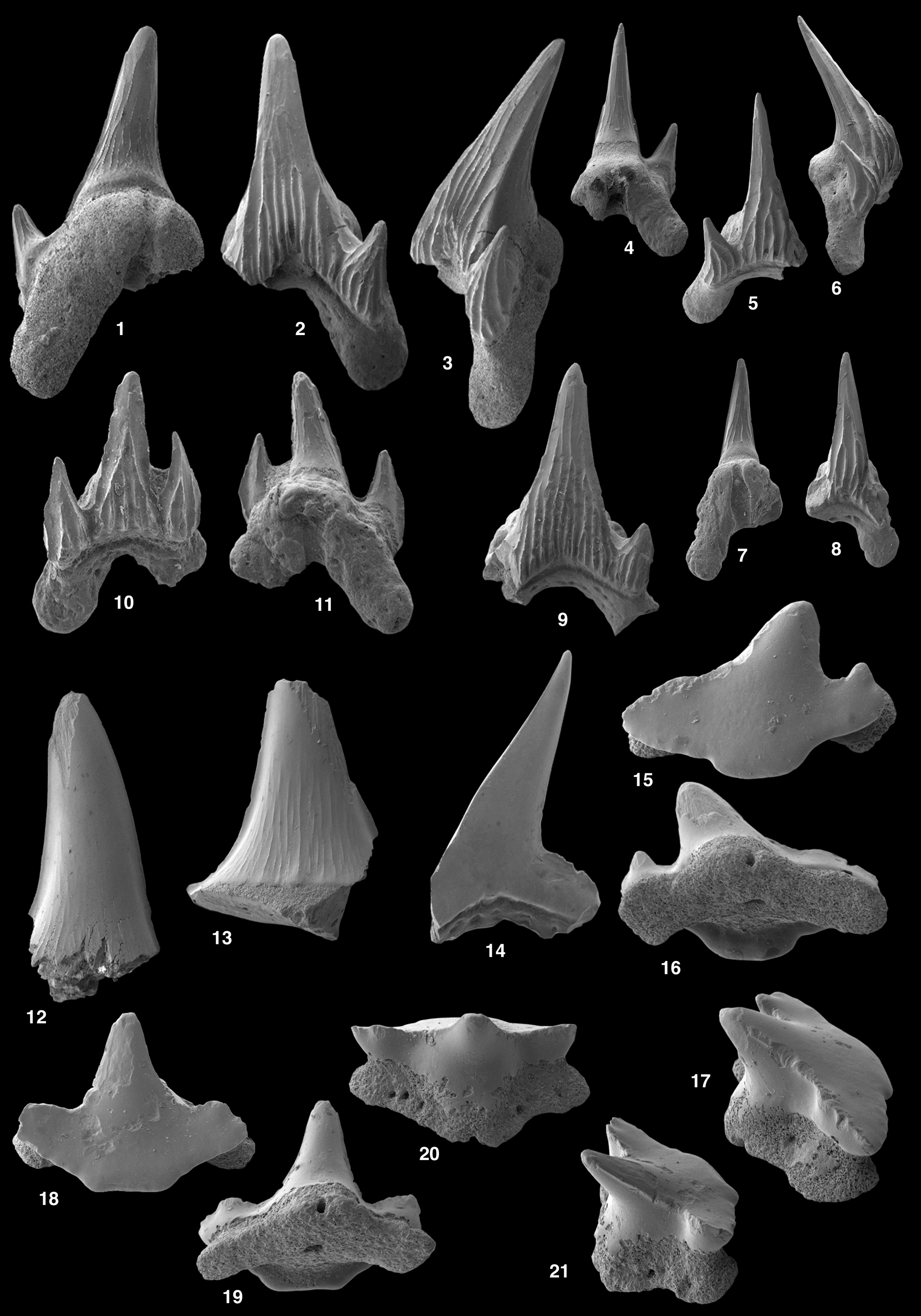
Fig. 5.
1. ? *Heterodontus* sp. P. 66275, X24, A/B Beds contact horizon, anterior tooth, labial view.
2. Hemiscylliidae indet. P. 66276, X48, A/B Beds contact horizon, labial view.
3-4. *Notorynchus aptiensis* (Pictet 1865). 3. P. 66277, X22, A/B contact, commissural tooth, linguo-occlusal view; 4. P. 66278, X22, LA6, lateral tooth, labial view.

5-6. *Synechodus dubrisiensis* (Mackie 1863). 5. P. 66279, X20, A/B A/B Beds contact horizon, posterolateral tooth, labio-occlusal view; 6. P. 66280, X20, LA6, anterior tooth of juvenile, labial view.
7. *Protosqualus* sp. P. 66281, X28, UB3, labial view.
8. *Squatina* sp. P. 66282, X13, Middle B, labial view.
9-12. *Belemnobatis* cf. *picteti* (Cappetta 1975). 9. P. 66283, X55, LA6, occlusal view; 10. P. 66284, X55, LA6, occlusal view; 11-12. P. 66285, X55, A/B Beds contact horizon, 11 labial, 12 oblique lateral views.
13. ? *Squatirhina* sp. P. 66286, X40, LA6, labial view.
14. Placoid scale type 1. P. 66287, X75, A/B Beds contact horizon.
15. Placoid scale type 2. P. 66288, X60, A/B Beds contact horizon.
16. Placoid scale type 3. P. 66289, X60, A/B Beds contact horizon.
17. Placoid scale type 4. P. 66290, X40, A/B Beds contact horizon.



LOWER APTIAN
U. BARREM.
M. BARREM.
deshayesi
forbesi
fissicostatus
bidentatum
Speeton Clay Formation
LA5
LA6
UB1A
UB1B
UB1C
UB2A
UB2B
UB2C
UB3
MIDDLE B BEDS
i
ii
iii
GAP
LARGE GAP
Sample points
Pteroscyllium speetonensis sp. nov.
Cretoxyrhinidae indet.
? Johnlongia sp.
Anacoracidae indet.
Hemiscylliidae indet.
Heterodontus sp.
Notorynchus aptiensis (Pictet)
Synechodus dubrisiensis (Mackie)
Squatina sp.
Belemnobatis cf. picteti (Cappetta)
? Squatirhina sp.
placoid scales
(barren sample)
Palaeobrachaelurus mitchelli sp. nov.
Protosqualus sp.
0
50 km
N
Speeton
Sample Intervals
over 30 kg
10-30 kg
under 10 kg
scale in metres
0
1
2
PALE MARL
BELEMNITE/ PHOSPHATE LAG
CALCAREOUS BLACK SHALE
BLACK MARL
SANDY CLAY WITH CONCRETIONS
SOFT BLACK SHALE
SEPTARIA


Occlusal (biting surface)
Lateral (anterior, towards front of jaw)
Lateral (posterior, towards jaw commissure)
Crown
Root
Longitudinal ridges
Lateral expansion of crown
Transverse ridges
Labial protuberance
Main cusp
Cutting edge
Uvula
Lateral cusplet
Root basal face
Root lobe
Foramen
Nutritive groove
Labial (outer) view
Lingual (inner) view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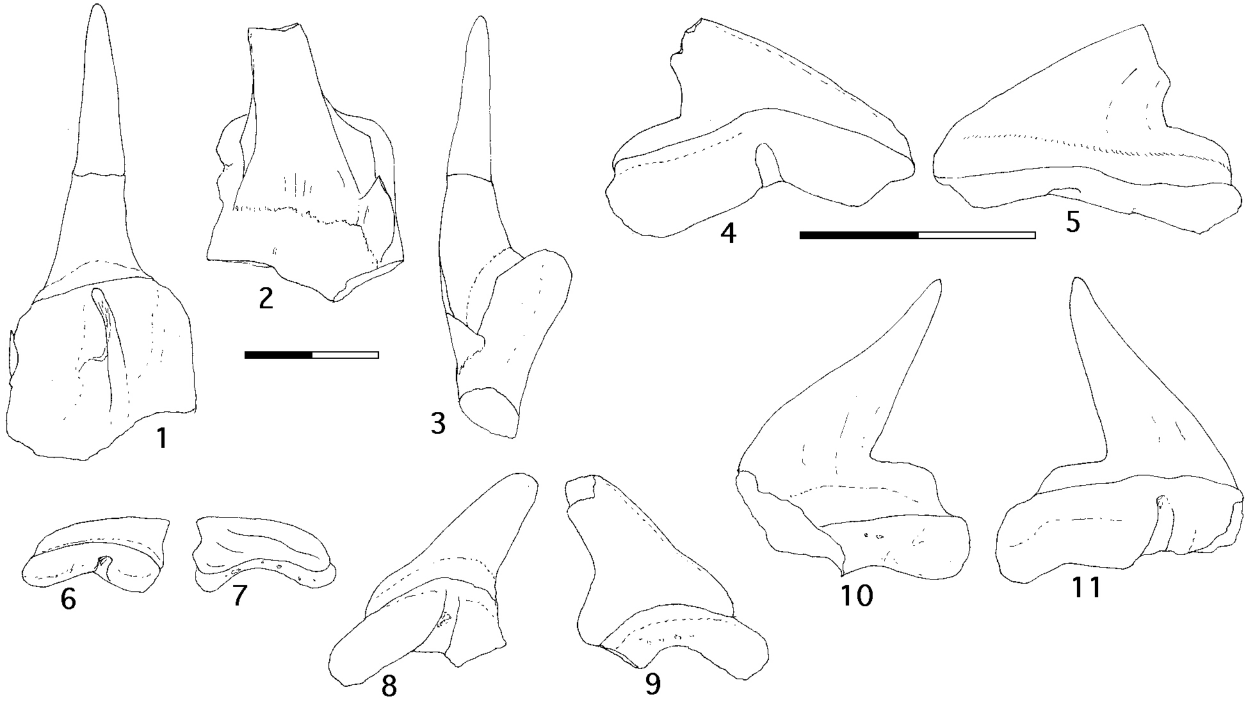
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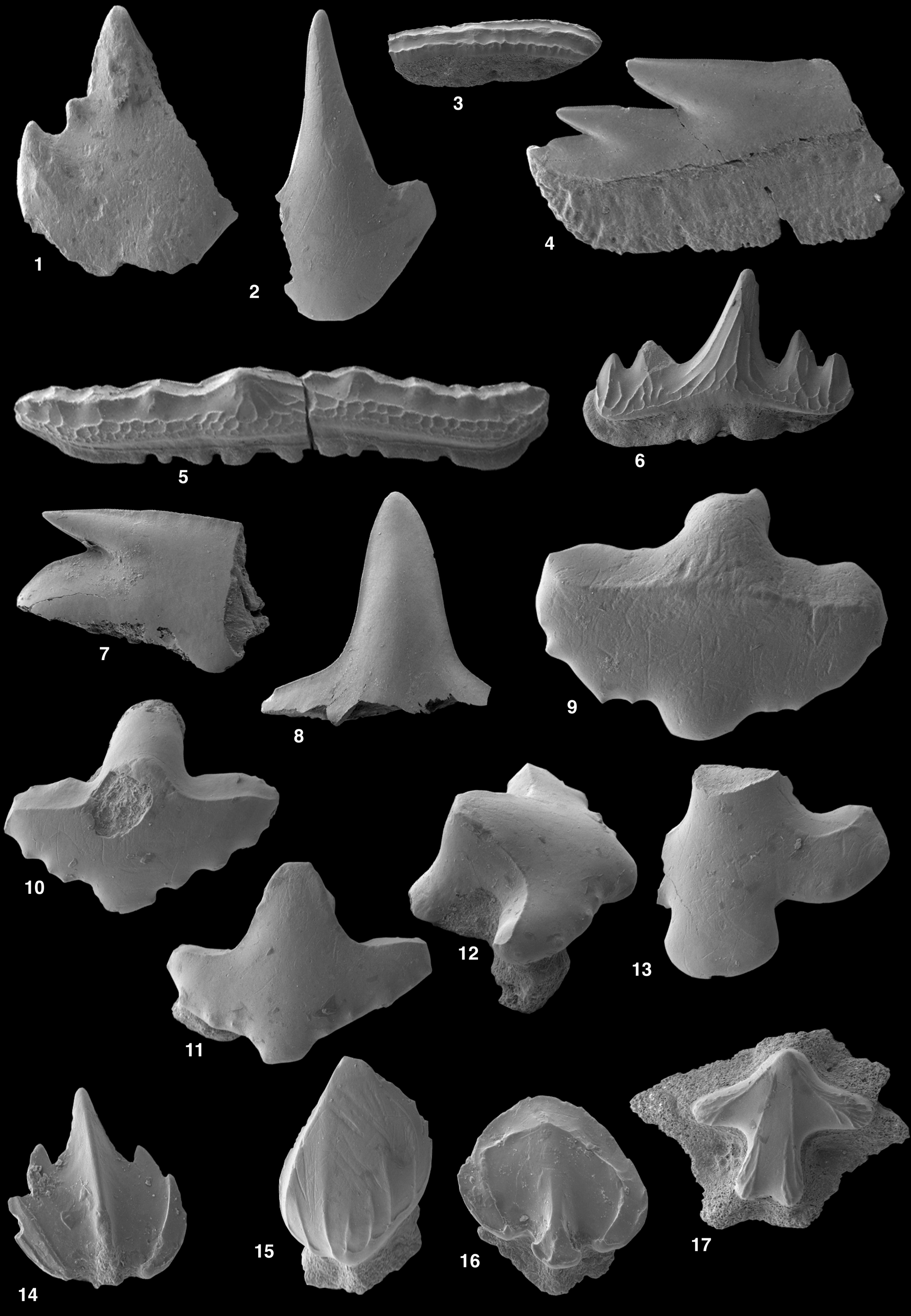
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