



BIROn - Birkbeck Institutional Research Online

Underwood, Charlie J. and Mitchell, S.F. and Veltkamp, K.J. (1999) Shark and ray teeth from the Hauterivian (Lower Cretaceous) of north-east England. *Palaeontology* 42 (2), pp. 287-302. ISSN 0031-0239.

Downloaded from: <https://eprints.bbk.ac.uk/id/eprint/73/>

Usage Guidelines:

Please refer to usage guidelines at <https://eprints.bbk.ac.uk/policies.html>
contact lib-eprints@bbk.ac.uk.

or alternatively

SHARK AND RAY TEETH FROM THE HAUTERIVIAN (LOWER CRETACEOUS) OF NORTH-EAST ENGLAND

by CHARLIE J. UNDERWOOD, SIMON F. MITCHELL *and* KEES J. VELTKAMP

ABSTRACT. Sampling of hiatal horizons within the Hauterivian part of the Speeton Clay Formation of north-east England has produced teeth of several species of sharks and rays, four of which are previously unnamed. One species of shark, *Cretorectolobus doylei* sp. nov., and two species of rays, *Spathobatis rugosus* sp. nov. and *Dasyatis speetonensis* sp. nov., are named, whilst the presence of an indeterminate triakid shark is also noted. *Synechodus dubrisiensis* (Mackie) is shown to be a senior synonym of *S. michaeli* Thies. Although the dasytid ray and triakid shark are by far the oldest representatives of their respective families, the overall composition of the fauna is considered to resemble more closely assemblages known from the Jurassic than those from upper parts of the Cretaceous.

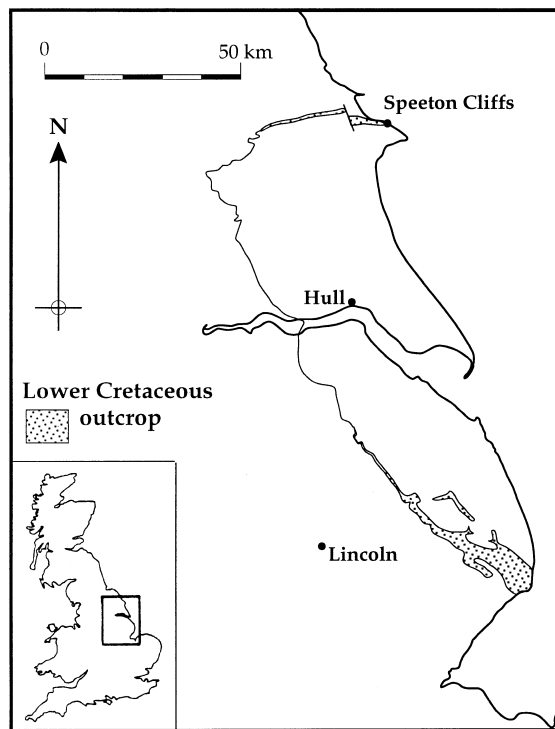
THE Early Cretaceous was a period of transition of shark and ray faunas between the unspecialized neoselachian faunas of the Mid and Late Jurassic (e.g. Thies 1983; Cappetta 1987) and the establishment of essentially modern faunas in the Albian and Cenomanian (e.g. Müller and Diedrich 1991; Biddle 1993; Underwood and Mitchell, 1999). Despite this, studies of Berriasian to Barremian selachian assemblages have been very limited, having largely concentrated on taxa from non-marine (e.g. Patterson 1966) or restricted marine (Biddle and Landemaine 1988) facies, studies of marine assemblages having been restricted to occasional descriptions of new species (e.g. Thies 1981; Ward and Thies 1987; Cappetta 1990). This lack of study is due largely to the lack of exposures of marine sediments suitable for sampling for microvertebrates. The marine clays of the Speeton Clay Formation represent one of the few examples of sediments well suited to bulk sampling for selachian remains.

GEOLOGICAL SETTING

The Speeton Clay Formation is exposed at Speeton on the north-east coast of England (Text-fig. 1). It consists of a condensed succession, about 130 m thick, spanning much of the Lower Cretaceous from the Upper Berriasian to Middle Albian. The sediments are dominantly bioturbated open marine clays, some levels being rich in diagenetic carbonate and phosphate concretions and many units being rich in glauconite. The formation has been divided into 'members' A, B, C and D by the characteristic belemnite fauna (see Lamplugh 1889), being further subdivided into numbered lithological units. Following Lamplugh (1889), beds are numbered from the top down. There are a number of distinct horizons of hiatal condensation and erosion at which phosphatic fish material is concentrated (Text-fig. 2). These are usually highly glauconitic and marked by concentrations of reworked phosphate nodules and/or bioeroded belemnites. Five such horizons within the Hauterivian and basal Barremian were sampled. Beds D2D, D1, C7H and C7E are from the Lower to Middle Hauterivian (for details see Lamplugh 1889; Neale 1960; Doyle 1989), whilst bed C2A is basal Barremian (for details see Mitchell 1992).

MATERIALS AND METHODS

Bulk samples of clay, 30–70 kg in dry weight, were sieved for fish material using a 125 μm or 250 μm mesh (see Ward 1981 for techniques). The residues were picked for fish remains at size fractions down to 355 μm where possible, but coarse glauconite in some samples meant that picking size fractions below 500 μm was impractical.



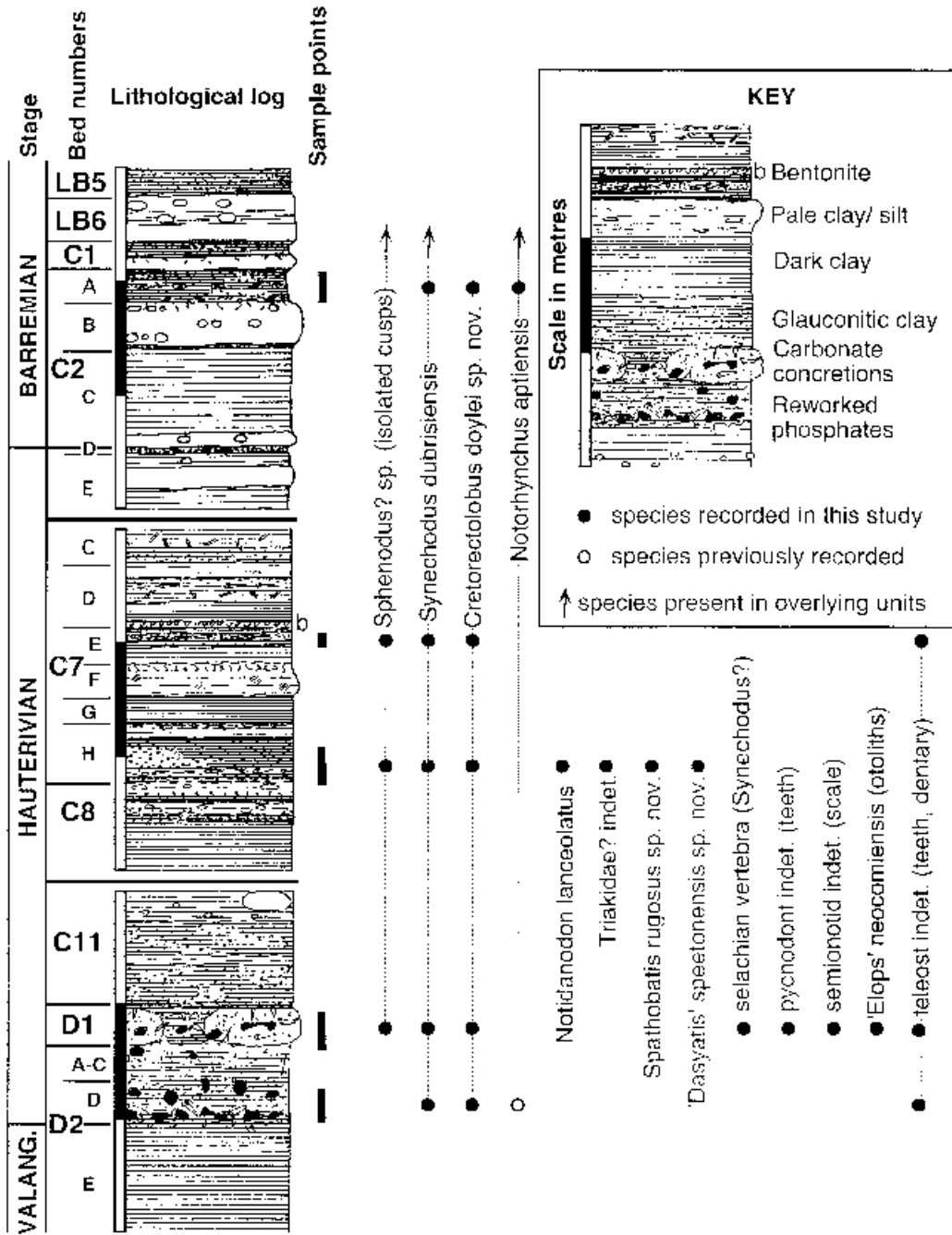
TEXT-FIG. 1. Locality map showing Speeton.

Figured specimens were coated with gold-palladium alloy and observed under a scanning electron microscope. All specimens figured and cited here are deposited in Liverpool Museum, National Museums and Galleries on Merseyside (LIVCM). Much of the cited material is deposited as multiple specimens with a single acquisition number.

FISH FAUNAS

Despite extensive documentation of the invertebrate faunas of the Speeton Clay, fish remains have remained very poorly studied. Relatively diverse selachian faunas are present in both the Aptian (Mitchell and Underwood 1999) and Albian (Underwood and Mitchell 1999) parts of the section, but little is known from the lower parts of the formation. Teeth of the hexanchiform sharks *Notorhynchus aptiensis* (Pictet, 1865) and *Notidanodon lanceolatus* (Woodward, 1886a) have been recorded from the Speeton Clay (Ward and Thies 1987). Although specimens were generally poorly located, *Notidanodon lanceolatus* is known from bed C7 (Ward and Thies 1987) and *Notorhynchus aptiensis* from bed D2D (J. Doyle, pers. comm. 1997), both within the Hauterivian. A tooth of *Sphenodus* sp. in the British Geological Survey museum (incorrectly labelled as *Lamna* sp.) is probably from the Barremian. Bony fish material has also been recorded only rarely, although the otolith taxon '*Elops*' *neocomiensis* (Priem, 1908) is known from bed D1 (Stinton 1973). Unidentified 'fish bones and teeth' have been reported from several horizons (Lamplugh 1889; Neale 1968).

The poor documentation of fish remains from the Speeton Clay Formation is probably in large part due to their rarity. Four of the horizons sampled in this study contained only rare selachian remains, and these often of poor preservation due to extensive bioerosion (Underwood *et al.* in press). Only the sample from bed C7H contained abundant, well-preserved selachian teeth. Only indeterminate bony fish material and '*Elops*' otoliths were found by surface collecting.



TEXT-FIG. 2. Distribution of selachian and bony fish remains recorded from the Hauterivian and basal Barremian at Speeton.

Bed D2D represents a major hiatus at the base of the Hauterivian. Although most of the remains are poorly preserved, *Cretorectolobus doylei* sp. nov. and *Synechodus dubrisiensis* (Mackie, 1863) were identified. Occasional conical bony fish teeth and vertebrae were also seen.

The selachian fauna of bed D1 produced a similar fauna, with *Cretorectolobus doylei* sp. nov., *Synechodus dubrisiensis* and an elongate cusp possibly referable to *Sphenodus* sp., as well as a selachian vertebra, possibly from *Synechodus*. Bony fish material is more abundant, with pycnodont and semionotid fragments, a small teleost dentary and common examples of the large otolith '*Elops*' *neocomiensis*.

In contrast with the underlying hiatus beds, bed C7H is rich in well preserved selachian teeth. The bulk of these are of *Synechodus dubrisiensis*, with well over 200 teeth collected. A number of specimens of *Cretorectolobus doylei* sp. nov. were also recorded, along with teeth of *Spathobatis rugosus* sp. nov. and broken elongate cusps of a 'lamniform' or *Sphenodus* sp. Three teeth of *Dasyatis speetonensis* sp. nov. were also found as well a single tooth of a possible triakid and a partial tooth of *Notidanodon lanceolatus*. Placoid scales of several morphotypes were also seen.

Smaller samples from bed C7E yielded material referable to *Cretorectolobus doylei* sp. nov., *Synechodus dubrisiensis* and probable *Sphenodus* cusps.

Bed C2A contained the least selachian material, with two fragmentary teeth of *Cretorectolobus doylei* sp. nov., a cusp probably assignable to *Synechodus dubrisiensis* and a tooth of *Notorhynchus aptiensis*.

SYSTEMATIC PALAEOLOGY

Subclass ELASMOBRANCHII Bonaparte, 1838

Order SYNECHODONTIFORMES Duffin and Ward, 1993

Genus SYNECHODUS Woodward, 1888a

Type species. Synechodus dubrisiensis (Mackie, 1863), from the Cenomanian of southern England.

Synechodus dubrisiensis (Mackie, 1863)

Plate 1, figures 1–5

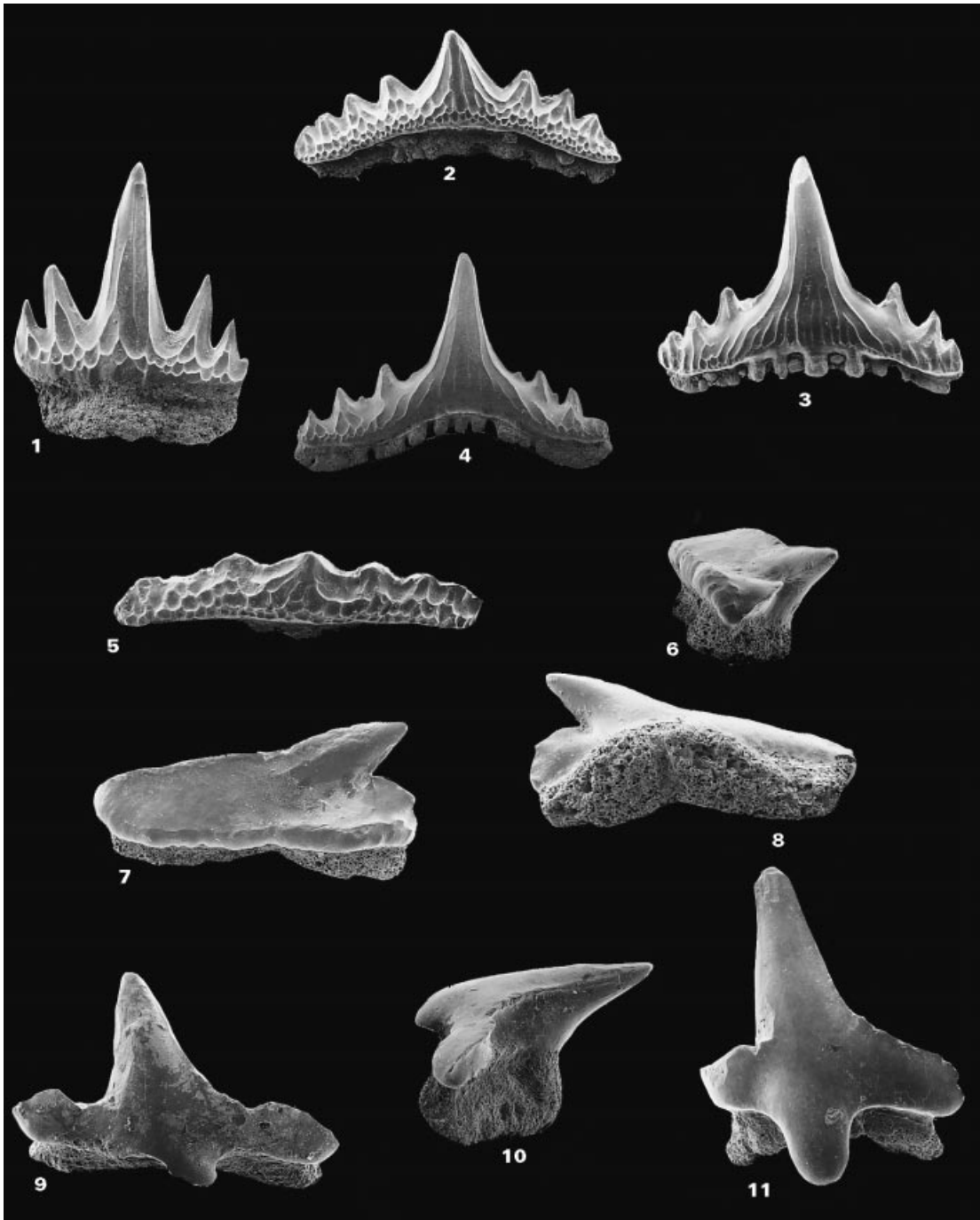
- 1863 *Hybodus dubrisiensis* Mackie, p. 241, pl. 13.
 1886b *Hybodus* (?) *dubrisiensis* Mackie; Woodward, p. 218, pl. 20.
 1888a *Synechodus dubrisiensis* (Mackie); Woodward, p. 496.
 1888b *Synechodus dubrisiensis* (Mackie); Woodward, p. 288.
 1889 *Synechodus dubrisiensis* (Mackie); Woodward, p. 327, text-fig. 12; pl. 11, figs 17–20; pl. 12, fig. 6.
 1894 *Synechodus dubrisiensis* (Mackie); Woodward, p. 193, text-fig. 1.
 1911 *Synechodus dubrisiensis* (Mackie); Woodward, p. 217, pl. 45, figs 6–7; pl. 46, figs 1–2.
 1977 *Synechodus dubrisiensis* (Mackie) Herman, p. 28.
 1978 *Synechodus* sp. Thies, p. 216, pl. 1, figs 1–6.
 1981 *Synechodus michaeli* sp. nov.; Thies, p. 476, figs 1–4.
 1985 *Synechodus dubrisiensis* (Mackie); Maisey, p. 1.

EXPLANATION OF PLATE 1

Figs 1–5. *Synechodus dubrisiensis* (Mackie, 1863). 1, LIVCM 1998.48.A; Bed C7H; 1.25 mm wide symphyseal tooth; labial view; $\times 38$. 2, LIVCM 1998.48.B; Bed C7H; 2.9 mm wide anterolateral tooth, file 4 or 5; labial view; $\times 23$. 3, LIVCM 1998.48.C; Bed C7H; 3.5 mm wide anterior tooth, file 2 or 3; labial view; $\times 18$. 4, LIVCM 1998.48.D; comparative specimen from Gault Clay Formation, Upper Albian, *cristatum* Subzone, Folkestone, Kent; 2.9 mm wide anterior tooth, file 2 or 3; labial view; $\times 23$. 5, LIVCM 1998.48.E; Bed C7H; 2 mm wide lateral tooth, file 8 or 9; labial view; $\times 38$.

Figs 6–8. Triakidae? indet. LIVCM 1998.48.F; Bed C7H; 1.3 mm wide tooth. 6, labial view. 7, lingual view. 8, lateral (posterior) view. All $\times 52$.

Figs 9–11. *Cretorectolobus doylei* sp. nov. 9–10, LIVCM 1998.48.G; Bed D2D; holotype; 1.4 mm wide lateral tooth. 9, labial view. 10, lateral view. Both $\times 49$. 11, LIVCM 1998.48.H; Bed C7H; 2 mm high anterior tooth; labial view; $\times 34$.



UNDERWOOD *et al.*, *Synechodus*, Triakidae?, *Cretorectolobus*

- 1987 *Synechodus dubrisiensis* (Mackie); Longbottom and Patterson, p. 240, pl. 54 fig. 9.
 ? non 1987 *Synechodus dubrisiensis* (Mackie); Longbottom and Patterson, text-fig. 11.2.f.
 1990 *Synechodus dubrisiensis* (Mackie); Batchelor and Ward, p. 191, pl. 1, figs 7–8.
 1991 *Synechodus dubrisiensis* (Mackie); Müller and Diedrich, p. 46, pl. 22, figs 8–10.
 1993 *Synechodus dubrisiensis* (Mackie); Biddle, p. 214, pl. 5, figs 1–3.
 1999 *Synechodus dubrisiensis* (Mackie); Underwood and Mitchell, pl. 1, figs 1–5.

Material. Very numerous (more than 200) teeth including well preserved specimens from all parts of the jaw: LIVCM 1998.48.A, B, C, E; LIVCM 1998.120.A, B, C, D.

Horizons. Most specimens from bed C7H, some other specimens from all other beds sampled (Lower Hauterivian to basal Barremian).

Description. The teeth of *Synechodus dubrisiensis* have been well described, both as regards the general tooth morphology and its relation to position within the jaw (Woodward 1911) and detailed description of surface ornament (Thies 1981; Müller and Diedrich 1991; Biddle 1993; Underwood and Mitchell in press). The larger (adult) teeth studied here do not differ from these previous descriptions. Weak dignathic heterodonty of the anterior teeth is suggested by the presence of either small or large lateral cusplets, a feature recognized by Woodward (1911). Smaller teeth, probably of juveniles, differ only in the rather stronger ornament on the labial face of anterior teeth.

Remarks. Specimens of *S. dubrisiensis* have been figured on numerous occasions, and include several specimens with preserved cranial and post-cranial skeletal elements (e.g. Woodward 1886b, 1911; Maisey 1985), as well as specimens showing *in situ* dentition (e.g. Woodward 1889, 1911). Despite this, it is only recently that well preserved teeth have been figured in detail so as to show the strong and characteristic ornamentation (e.g. Batchelor and Ward 1990; Müller and Diedrich 1991; Biddle 1993; Underwood and Mitchell 1999). This lack of figures showing the ornamentation of teeth of *S. dubrisiensis*, combined with the restricted stratigraphical range of material figured prior to 1980 (probably all Cenomanian) led Thies (1981) to erect a new species, *S. michaeli*, for specimens from the Hauterivian and Barremian of Germany. The holotype of *S. michaeli* is small and heavily ornamented, the presence of this heavy ornament being cited as the main defining characteristic of the species. Identical ornament is present in similar sized juvenile *S. dubrisiensis* teeth (Underwood and Mitchell 1999, pl. 1, figs 3–5). It is considered here that the type assemblage of *S. michaeli* is indistinguishable from material from Speeton, as well as from material figured from the Aptian (Batchelor and Ward 1990), Albian (Pl. 1, fig. 4; Biddle 1993; Underwood and Mitchell 1999) and Cenomanian (Müller and Diedrich 1991; Underwood and Mitchell 1999).

It is therefore evident that *S. dubrisiensis* represents a long lived taxon, ranging from at least the early Hauterivian to late Cenomanian, although it appears to be of limited geographical range, not having been recorded outside the North Sea and Anglo Paris basins.

Order CARCHARINIFORMES Compagno, 1973

Genus unknown

Triakidae? indet.

Plate 1, figures 6–8

Material. Single tooth, intact but with bioeroded root: LIVCM 1998.48.F.

Horizon. Bed C7H (Hauterivian, *inversum* Zone).

Description. This single tooth is small, only 1.3 mm wide, with a narrow crown overhanging a rather bulky root. The single cusp is strongly directed to the posterior, overhanging the small and unserrated distal heel. The labial face of the crown is flat, becoming slightly concave distally. The lower edge of this is straight and bulbous, strongly overhanging the root. The crown is generally unornamented, although small, irregular ridges are present along the labial edge. The holaulacorhize root is relatively bulky with a flat basal face. The nutritive groove is narrow and shallow. Further details of the root have been destroyed by bioerosion.

Remarks. The overall form of the tooth is similar to that of members of several families within the carchariniformes. The strong labial overhang and slight ornamentation, however, probably suggest an affinity with the Triakidae. Although several triakid genera are known from the uppermost Cretaceous, (e.g. Herman 1977; Cappetta 1987), the oldest previously recorded species is *Paratriakis bettrechianus* Herman, 1977 from the Turonian. Teeth of *Paratriakis* differ from the tooth described here by possessing a hemiaulacorhize root and more elongate cusp. It is therefore likely that this tooth represents an as yet undescribed genus.

Order ORECTOLOBIFORMES Applegate, 1972

Genus CRETIRECTOLOBUS Case, 1978

Type species. *Cretirectolobus olsoni* Case, 1978, from the Campanian of Montana, USA.

Cretirectolobus doylei sp. nov.

Plate 1, figures 9–11; Plate 2, figures 1–3

?1978 *Squatina* sp. Thies, p. 218, pl. 2, fig. 8.

Holotype. LIVCM 1998.48.G (Pl. 1, figs 9–10); Speeton Clay Formation, bed D2D basal belemnite/phosphate lag; Hauterivian, *amblygonium* Zone, Speeton, Yorkshire.

Paratypes. LIVCM 1998.48.H, J, K (Pl. 1, fig. 11; Pl. 2, figs 1–3); LIVCM 1998.120.H, J, K, L, M, N.

Material. Numerous (more than 30) poorly preserved and four moderately well preserved teeth.

Horizons. Specimens from all beds studied (Lower Hauterivian to basal Barremian); better preserved teeth from beds D2D and C7H (Lower Hauterivian).

Derivation of name. After J. C. Doyle, who has worked extensively on the Hauterivian at Speeton.

Diagnosis. Tooth small, with the crown up to 3 mm high. The crown is unornamented, and is strongly inclined lingually. The single cusp is narrow and straight and only slightly compressed, in some teeth being slightly angled posteriorly. Cutting edges are continuous around the crown and along the upper edge of the lateral blades. The lateral blades are narrow and overhang the root labially. These may be as long as the cusp in smaller teeth, although they are proportionally shorter in larger teeth. A single pair of incipient lateral cusplets may be present in small teeth, but is usually absent. The crown extends labially to form a labial bulge which strongly overhangs the root. This is short and flat in small teeth, more globose in larger ones. The root is hemiaulacorhize and relatively high but narrow with a well developed lingual bulge below the base of the cusp. Basal and lingual foramina are well developed. In large teeth, the distal extremities of the root are flared giving a broad basal surface.

Remarks. This species differs from *Cretirectolobus olsoni* Case, 1978, *sensu* Siverson 1995, by the less well developed labial bulge and a narrower and higher hemiaulacorhize root. It differs from *Cretirectolobus gracilis* Underwood and Mitchell, 1999 by possessing considerably better developed lateral blades and a larger overall size. Other figured specimens assigned to *Cretirectolobus* probably belong within the genera *Cederstroemia* Siverson, 1995 or *Cretascyllium* Müller and Diedrich, 1991.

Teeth of very similar morphology been recorded from the Oxfordian (Thies 1983) and Kimmeridgian (Batchelor and Ward 1990), and have been referred to *Squatina*. The presence of incipient lateral cusplets and a high and narrow root suggests that they almost certainly belong to *Cretirectolobus*. It is likely that *Cretirectolobus* is closely related to *Palaeobrachaelurus* Thies, 1983, a Jurassic to ?Lower Cretaceous genus (the Barremian species *Brachaelurus roklumensis* Thies, 1981 probably being a species of

Palaeobrachaelurus), which differs only in the possession of well developed lateral cusplets. Close similarities between many of the dentally rather simple orectolobiformes of the Jurassic and Cretaceous suggest that they probably form a single clade. The relationships between this group and Cenozoic orectolobiform families is unclear, but it is possible that the similar tooth morphology of the extant Orectolobidae was acquired independently (e.g. Siverson 1995).

Superorder BATOIDEA Cappetta 1980

Genus SPATHOBATIS Thiolliere, 1854

Type species. Spathobatis bugesiacus Thiolliere, 1854, from the Kimmeridgian of Cerin, France.

Spathobatis rugosus sp. nov.

Plate 2, figures 4–10

Derivation of name. After the characteristic rugosity of the teeth.

Holotype. LIVCM 1998.48.L (Pl. 2, figs 4–6); Speeton Clay Formation, bed C7H basal belemnite lag; Hauterivian, *inversum* Zone, Speeton, Yorkshire.

Paratypes. LIVCM 1998.48.M, N (Pl. 2, figs 7–10); LIVCM 1998.120.P, Q.

Material. Ten teeth, four with roots preserved.

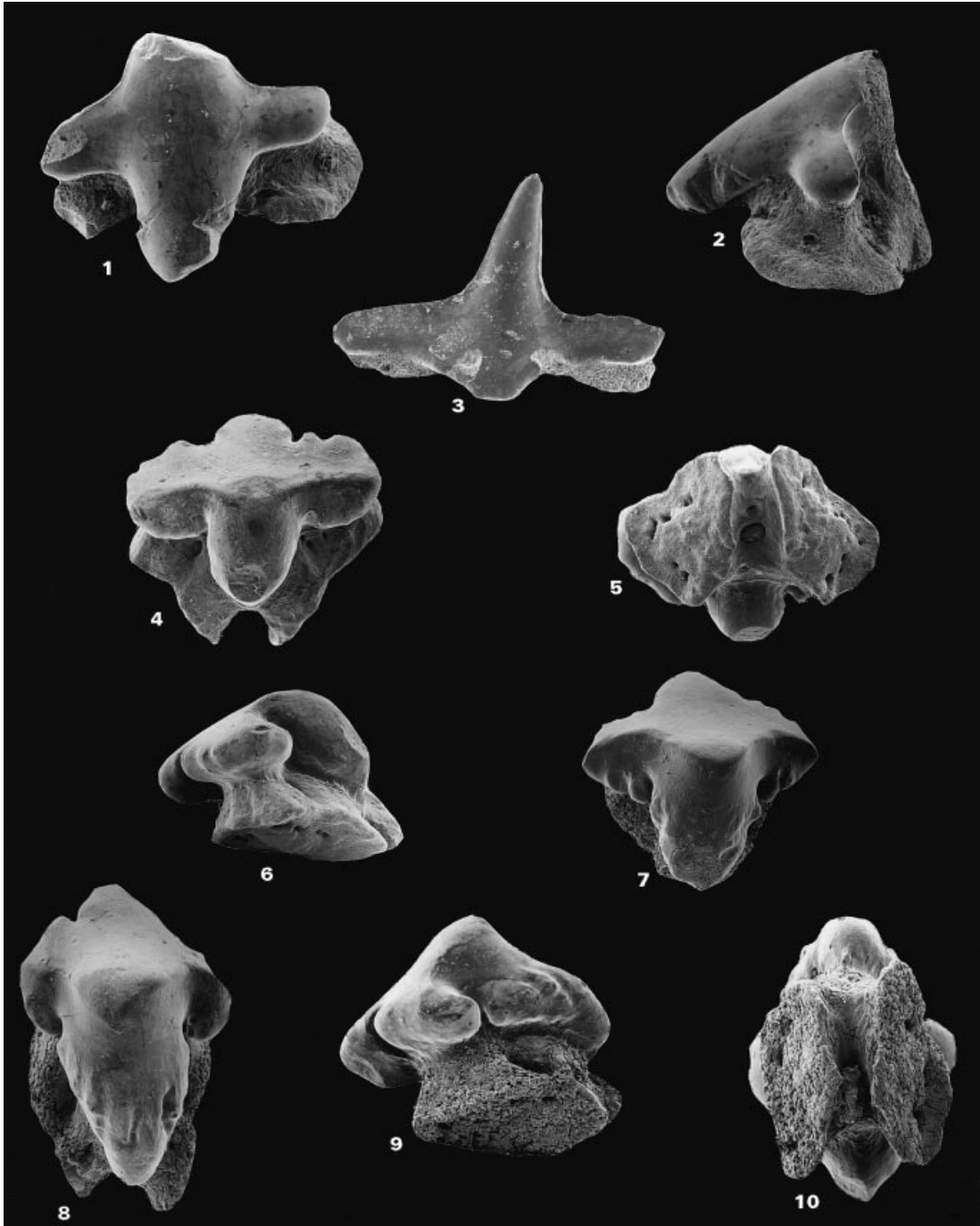
Horizon. Bed C7H (Hauterivian, *inversum* Zone).

Diagnosis. The teeth are somewhat heterodont, varying in both overall crown shape and in the presence or absence of a well defined central cusp, suggesting that both monognathic and sexual heterodonty is present. In occlusal view, the crown is faintly crusiform in outline, with the labial projection, lingual uluva and lateral expansions all being clearly differentiated. The labial face is flat or slightly concave terminating occlusally at a well defined and sharply angled transverse crest. The labial bulge is globular and often has a somewhat pectinate edge. The labial, and occasionally lingual, edges of the lateral expansions are generally rather irregular or pectinate, with a distinct notch usually present at the junction with both the lingual uluva and labial projection. The crown profile may be either fairly low (in females) or rise to a triangular cusp (in males). The lingual uluva is very well developed, being at least as wide as the labial projection. This extends for some distance down the lingual face of the root, and in many teeth has irregular vertical folds, giving it an overall globose and rugose appearance. The root is bulky, being about the same size as the crown, and projects somewhat lingually. The basal face is strongly bilobate with a large nutritive groove, the flat base of each side being slightly angled outwards. Lingual marginal foramina and basal foramina are well developed.

EXPLANATION OF PLATE 2

Figs 1–3. *Cretorectolobus doylei* sp. nov. 1–2, LIVCM 1998.48.J; Bed D1; 3 mm wide anterior (caniniform?) tooth. 1, labial view. 2, lateral view. Both $\times 20$. 3, LIVCM 1998.48.K; Bed C7H; 1.6 mm wide anterior tooth; labial view; $\times 42$.

Figs 4–10. *Spathobatis rugosus* sp. nov. 4–6, LIVCM 1998.48.L; Bed C7H; holotype; 1 mm wide lateral tooth of female. 4, occlusal view. 5, basal view. 6, lateral view. All $\times 53$. 7, LIVCM 1998.48.M; Bed C7H; 1.1 mm wide lateral tooth of male; occlusal view; $\times 44$. 8–10, LIVCM 1998.48.N; Bed C7H; 0.8 mm wide anterior tooth of male. 8, occlusal view. 9, lateral view. 10, basal view. All $\times 51$.



UNDERWOOD *et al.*, *Cretorectolobus*, *Spathobatis*

Remarks. *Spathobatis* is well known from the Upper Jurassic, with teeth assigned to a number of species being figured from the Kimmeridgian by Thies (1983), although it is possible that many or all of these are synonymous with *Spathobatis bugesiacus* Thiolliere, 1854. Teeth of *Spathobatis rugosus* sp. nov. differ from these in the possession of a well defined labial projection, a pectinate crown margin and a globose and folded lingual uluva. *Rhinobatos picteti* (Cappetta, 1975a) (probably assignable of *Spathobatis*) from the Aptian, and an undescribed species from the basal Cretaceous of southern England (CJU, pers. obs.) differ in possessing a far more gracile and smooth lingual uluva and a lower root. An isolated crown probably assignable to *Spathobatis* from the German Campanian (Müller 1989, pl. 16, fig. 5) has a small lingual uluva and a poorly differentiated labial projection. Teeth of Late Jurassic species of *Belemnobatis* Thiolliere, 1854 differ not only in lacking an ornamented crown, but also in possessing a stronger transverse crest, larger basal foramen and a poorly defined labial projection (Cavin *et al.* 1995). Other Lower Cretaceous 'rhinobatids', such as '*Spathobatis*' *halterii* (Biddle and Landemaine, 1988) from the Barremian and Albian, '*Rhinobatos*' *beurleni* Santos, 1968 from the Aptian or Albian and an undescribed species from the basal Cretaceous of southern England (CJU, pers. obs.) differ in having a far more rounded overall form.

The pectinate lingual crown edge and high crown gives this species an overall similarity to the enigmatic genus *Squatirhina* Casier, 1947, especially earlier species such as *Squatirhina thiesi* Biddle, 1993. It is therefore possible that this species lies close to the ancestry of *Squatirhina*, which developed by increased pectination of the crown margin and elongation of the cusp.

Order MYLIOBATIFORMES Compagno, 1973

Genus DASYATIS *sensu lato* Rafinesque, 1810

Type species. *Dasyatis ujo* Rafinesque, 1810, extant.

Dasyatis speetonensis sp. nov.

Plate 3, figures 1–9

Derivation of name. From the Speeton Clay Formation in which this material was found.

Holotype. LIVCM 1998.48.P (Pl. 3, figs 1–3); Speeton Clay Formation, bed C7H basal belemnite lag; Hauterivian, *inversum* Zone, Speeton, Yorkshire.

Paratypes. LIVCM 1998.48.Q, R (Pl. 3, figs 4–9).

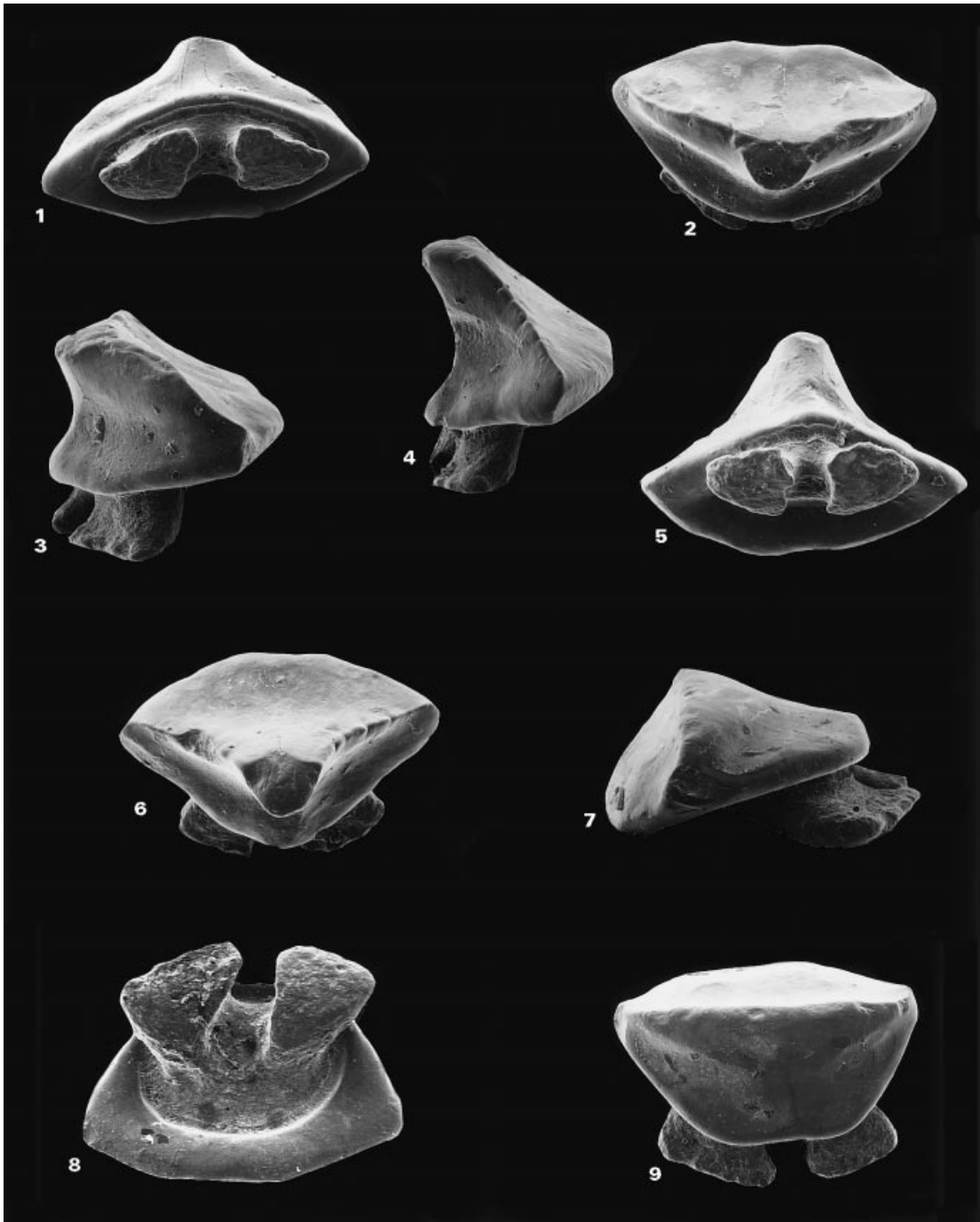
Material. Three teeth, two high crowned (male) and one low crowned (female), all well preserved.

Horizon. Bed C7H (Hauterivian, *inversum* Zone).

Diagnosis. These very small teeth, the largest only 0.9 mm wide, show extreme sexual heterodonty. In occlusal view, the crown of all teeth is rather lozenge-shaped with sharp marginal angles. The basal face of

EXPLANATION OF PLATE 3

Figs 1–9. *Dasyatis speetonensis* sp. nov. 1–3, LIVCM 1998.48.P; Bed C7H; holotype; 0.9 mm wide tooth of male. 1, basal view. 2, occlusal view. 3, lateral view. All $\times 74$. 4–6, LIVCM 1998.48.Q; Bed C7H; 0.8 mm wide tooth of male. 4, lateral view. 5, basal view. 6, occlusal view. All $\times 86$. 7–9, LIVCM 1998.48.R; Bed C7H; 0.8 mm wide tooth of female. 7, lateral view. 8, basal view. 9, occlusal view. All $\times 79$.



the crown is flat, and there are no lingual or labial projections of the crown edge. In the female tooth, a slightly curved transverse crest separates the smooth labial and lingual faces at an obtuse angle. The lingual face is gently curved; the labial face is flat with a slight concavity adjacent to the transverse crest. In the male teeth, the transverse crest rises to form a triangular cusp and has several faint notches along its length in one specimen. The somewhat flattened cusp has a blunt tip, probably as a result of wear in life, and is directed lingually. The labial face is almost flat, but the lingual face is curved giving the cusp a rather hooked appearance. The root of all specimens is small and directed lingually, especially in the female tooth. The two lobes of the root are separated by a wide and deep nutritive groove. The basal faces of the two lobes are flat with an oval or triangular profile.

Remarks. The dental morphology of different extant genera of dasyatid rays is poorly known (Cappetta 1987), and as such many fossil teeth are lumped into the extant genus *Dasyatis*. This is followed here, and it is acknowledged that, in future, further information may allow this species to be placed within another genus.

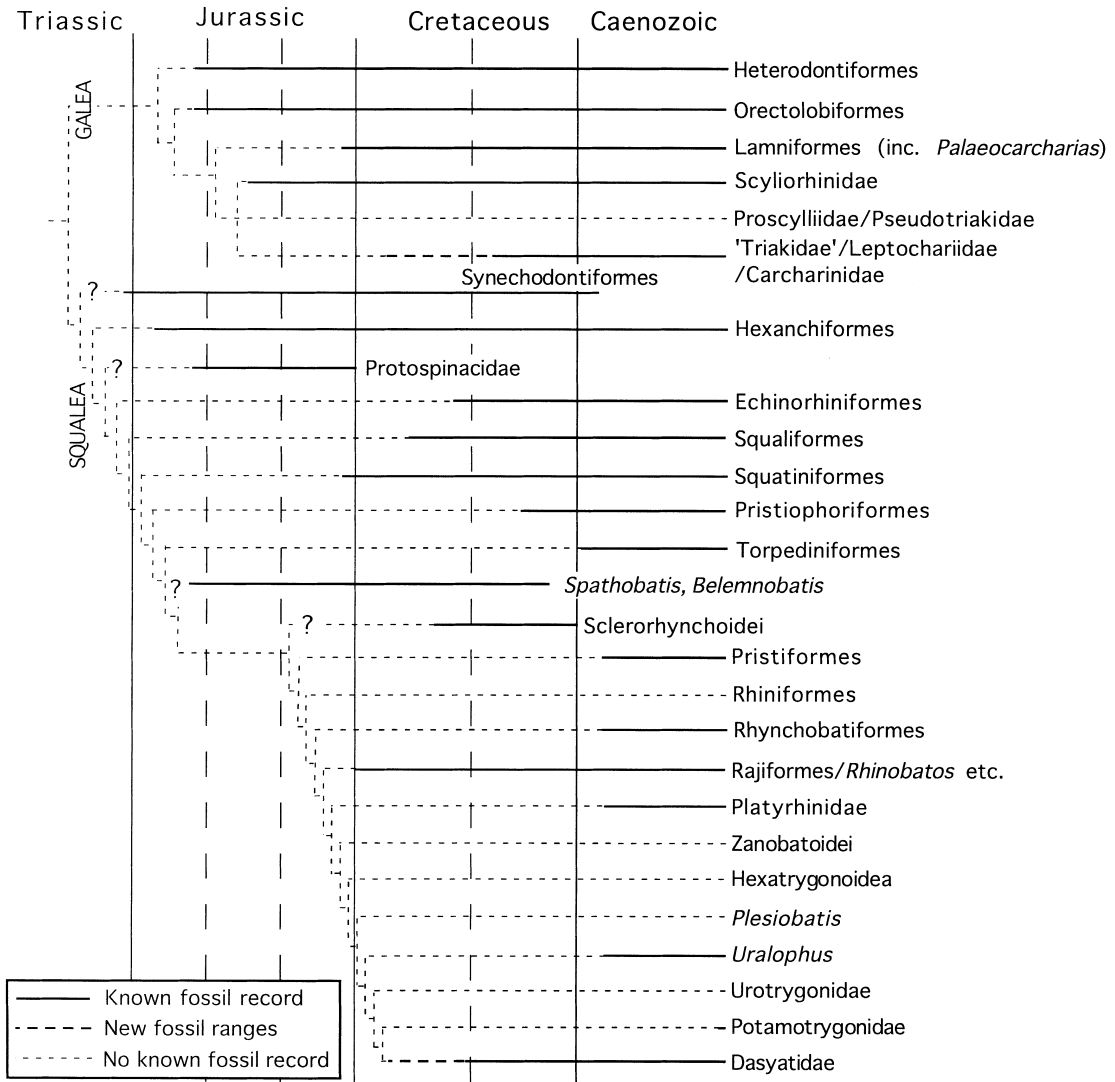
This species represents a considerable range extension both for Dasyatidae and for the Myliobatiformes. The oldest well recorded species assigned to *Dasyatis* are known from the uppermost Cretaceous (e.g. Cappetta 1975*b*; Herman 1977), although possible *Dasyatis* have been recorded from the Cenomanian (Landemaine 1991) along with other Myliobatiformes such as *Turoniabatis* Landemaine, 1991, which probably also occurs in the Albian (Welton and Farish 1993, p. 157). The presence of essentially modern dasyatid teeth from the Hauterivian suggests that Dasyatidae is a more ancient group than had previously been recognized.

IMPLICATIONS FOR THE NEOSELACHIAN FOSSIL RECORD

Recent cladistic analyses (e.g. de Carvalho 1996; McEachran *et al.* 1996; Shirai 1996) have provided detailed information on the interrelationships and phylogeny of neoselachians. This provides a framework of the relative order of clade origination with which the fossil record can be compared (Text-fig. 3). Considerable uncertainty exists in the relative positions of major extinct neoselachian groups within this phylogeny. For this study, the positions of extinct clades within the neoselachians are based largely on Maisey (1984), Cappetta (1987) and Duffin and Ward (1993), the detailed relationships between the extant and fossil taxa being beyond the scope of this work.

The recorded diversity of Jurassic and Early Cretaceous neoselachians is far less than the predicted diversity. This is probably in large part due to collection failure, as teeth of many neoselachians are too small to be found by surface collecting, and bulk sampling for selachian remains is rarely practised in pre-Late Cretaceous sediments. Within the Galea, the fossil record generally appears to correspond relatively well to the predicted divergence times, the main exception being the clade containing Proscylliidae and Pseudotriakidae, fossils of which have not been recognized. The early occurrence of a possible triakid would be expected from the predicted divergence time. The holaulacorhize root of the ?triakid tooth from Speeton suggests that it may be more highly derived than *Paratriakis*. This makes it unlikely that this species represents one of the earliest triakids, and it is therefore probable that other triakid taxa occur within older Cretaceous or late Jurassic sediments.

The fossil record of the Squalea appears to be far less complete. The presence of teeth referred to *Spathobatis* in the Toarcian (Thies 1983) suggests that the Mesozoic fossil record of many of the squalean sharks and the Torpediniformes is very poor, an observation supported by the highly derived appearance of the oldest known fossil taxa of clades such as Squaliformes and Pristiophoriformes (e.g. Cappetta 1987). The fossil record of the batoids also appears to be far from complete. *Dasyatis* represents a highly derived taxon (McEachran *et al.* 1996; Shirai 1996), and its presence within the Hauterivian suggests that a major period of radiation of the batoids, including the Myliobatiformes, must have occurred by the Late Jurassic or earliest Cretaceous. There is almost no Mesozoic fossil record of taxa originating within this radiation event, other than within the clade containing the Rajiformes and some of the 'rhinobatids'. It is possible, however, that some of the diverse batoid teeth from the Upper Cretaceous (e.g. Cappetta 1987) represent members of clades which originated during this Jurassic to Cretaceous period of radiation.



TEXT-FIG. 3. Phylogenetic relationships of neoselachians calibrated to the known fossil record. The phylogenetic tree is largely based on Shirai (1996), other than the relationships within the batoids which are taken from McEachran *et al.* (1996), with no re-analysis. The Hexanchiformes and Squaliformes are here treated as monophyletic (de Carvalho 1996). Major extinct neoselachian groups are placed within this phylogeny using data from Cappetta (1987), Duffin and Ward (1993) and Maisey (1984). Note that it is likely that clades that are monophyletic as regard living species may be paraphyletic if fossil species are included (Maisey 1984). Fossil occurrences from various sources, especially Cappetta (1987) and Cappetta *et al.* (1993).

PALAEOECOLOGY

The overall composition of the fish faunas of the Hauterivian at Speeton is in many ways more reminiscent of faunas from the Middle and Upper Jurassic than the middle to Upper Cretaceous, despite the presence of dasyatid and possible triakid teeth. As in many faunas from the Toarcian to Kimmeridgian of Britain and Germany (e.g. Thies 1983; Delsate and Thies 1994; David Ward, pers. comm. 1996; CJU, pers. obs.), the

Speeton Hauterivian contains very low diversity selachian faunas, dominated by *Synechodus*, *Spathobatis* and dentally simple orectolobids, with rarer, larger teeth represented by *Sphenodus* and hexanchiformes. This suggests a selachian fauna of dominantly benthic or nectobenthic habit. The rays were, by analogy with extant taxa, benthic durophagous forms. The 'squatoid' dentition of *Cretorectolobus* and general body form of orectolobids suggest a benthic ambush predator. The body form of *Synechodus* (Duffin and Ward 1993) suggests a weak swimmer, whilst the strongly heterodont dentition with clutching anterior files (*sensu* Cappetta 1987) suggests a varied diet of both soft-bodied and shelled organisms. The dentitions of the hexanchiformes and *Sphenodus* suggest that they probably hunted larger prey in mid-water, but it is unlikely that either were rapid pursuit hunters. This contrasts with faunas from similar facies in the Albian (e.g. Biddle 1993; David Ward, pers. comm. 1996) which contain high diversity selachian faunas including members of many modern groups. These faunas are dominated by lamniformes and carcharhinids, both nectic pursuit predators, whilst squalids represent small nectobenthic hunters with a cutting dentition. Within calcareous facies in the Albian (Underwood and Mitchell 1999) and Upper Cretaceous (e.g. Herman 1977; Müller and Diedrich 1991), neoselachian faunas are even more diverse. Aptian faunas (Cappetta 1975a; Mitchell and Underwood 1999) are also of moderate to high diversity and contain abundant lamniformes and carcharhinids. As with neoselachians, bony fish from the Speeton Hauterivian are of distinctly Jurassic affinities, with pycnodont and semionotid remains more common than those of teleosts. It therefore seems likely that the community structure of marine fish faunas remained fairly constant throughout much of the Jurassic and part of the Cretaceous, only developing into a more diverse, 'modern' type community once many of the modern neoselachian groups had appeared in the Aptian–Albian.

Acknowledgements. We thank especially David Ward for his help in the field and for much of the sieving of the samples, as well as Daisy Williamson for her help in the field. Jack Doyle is thanked for passing on his invaluable field knowledge of the Speeton section. We also thank two reviewers for their helpful comments.

REFERENCES

- APPLEGATE, S. P. 1972. A revision of the higher taxa of orectolobids. *Bulletin of the Marine Biological Association of India*, **14**, 743–751.
- BATCHELOR, T. J. and WARD, D. J. 1990. Fish remains from a temporary exposure of the Hythe Beds (Aptian–Lower Cretaceous) near Godstone, Surrey. *Mesozoic Researches*, **2**, 181–203.
- BIDDLE, J. P. 1993. Les Elasmobranches de l'Albien inférieur et moyen (Crétacé inférieur) de la Marne et de la Haute-marne (France). *Professional Paper of the Belgian Geological Survey*, **264**, 191–240.
- and LANDEMAINE, O. 1988. Contribution à l'étude des sélachiens du Crétacé du Bassin de Paris. Découverte des quelques nouvelles espèces associées à une faune de type Wealden dans le Barrémien supérieur (Crétacé inférieur) des environs de Troyes (Aube). *Publications Musée de Saint-Dizier*, **2**, 1–22.
- BONAPARTE, C. L. J. L. 1838. Selachorum tabula analytica. *Nuovi Annali della Scienze Naturali, Bologna*, (1), **2**, 195–214.
- CAPPETTA, H. 1975a. Sélaciens et holocéphale du Gargasien de la région de Gargas (Vaucluse). *Géologie Méditerranéenne*, **2**, 115–134.
- 1975b. Sur quelques sélaciens nouveaux du Crétacé supérieur de Bolivie (Amérique du Sud). *Géobios*, **8**, 5–24.
- 1980. Les selaciens du Cretace superieur du Liban 2: Batoides. *Palaeontographica, Abteilung A*, **168**, 149–229.
- 1987. Mesozoic and Cenozoic elasmobranchii. Chondrichthyes II. In SCHULTZE, H. P. (ed.). *Handbook of palaeoichthyology*, 3B. Gustav Fischer Verlag, Stuttgart, 193 pp.
- 1990. Hexanchiforme nouveau (Neoselachii) du Cretace Inferieur du Sud de la France. *Palaeovertebrata*, **20**, 33–54.
- DUFFIN, C. and ZIDEK, J. 1993. Chondrichthyes. 593–609. In BENTON, M. J. (ed.). *The fossil record 2*. Chapman and Hall, London.
- CARVALHO, M. R. de 1996. Higher-level elasmobranch phylogeny, basal squalians, and paraphyly. 35–62. In STIASSEY, M. L. J., PARENTI, L. R. and JOHNSON, G. D. (eds). *Interrelationships of fishes*. Academic Press, San Diego.
- CASE, G. R. 1978. A new selachian fauna from the Judith River Formation (Campanian) of Montana. *Palaeontographica, Abteilung A*, **160**, 176–205.
- CASIER, E. 1947. Constitution et évolution de la racine dentaire des Euselachii. *Bulletin du Musée Royal d'Histoire Naturelle de Belgique*, **23** (13) 1–15; (14) 1–32; (15) 1–45.
- CAVIN, L., CAPPETTA, H. and SÉRET, B. 1995. Revision de *Belemnobatis morinicus* (Sauvage, 1873) du Portlandien du

- Boulonnais (Pas-de-Calais, France). Comparison avec quelques Rhinobatidae Jurassiques. *Geologica et Palaeontologica*, **29**, 245–267.
- COMPAGNO, L. J. V. 1973. Interrelationships of living elasmobranchs. 15–16. In GREENWOOD, P. H., MILES, R. S. and PATTERSON, C. (eds). *Interrelationships of fishes*. *Zoological Journal of the Linnean Society*, **53** (supplement).
- DELSATE, D. and THIES, D. 1994. Teeth of the fossil shark *Annea Thies* 1983 (Elasmobranchii, Neoselachii) from the Toarcian of Belgium. *Professional Paper of the Belgian Geological Survey*, **278**, 45–64.
- DOYLE, J. C. 1989. The stratigraphy of a late Hauterivian horizon in the Speeton Clay Formation (Lower Cretaceous) of East Yorkshire. *Proceedings of the Geologists' Association*, **100**, 175–182.
- DUFFIN, C. J. and WARD, D. J. 1993. The Early Jurassic palaeospinacid sharks of Lyme Regis, southern England. *Professional Paper of the Belgian Geological Survey*, **264**, 53–102.
- HERMAN, J. 1977. Les Sélachiens néocrétacés et paléocènes de Belgique et des contrées limitrophes éléments d'une biostratigraphie intercontinentale. *Mémoires pour servir à l'Explication des Cartes Géologiques et Minières de la Belgique*, **15**, 1–450.
- LAMPLUGH, F. G. S. 1889. On the subdivisions of the Speeton Clay. *Quarterly Journal of the Geological Society, London*, **45**, 575–618.
- LANDEMAINE, O. 1991. Selaciens nouveaux du Cretace Supérieur du Sud-Ouest de la France; quelques apports à la systématique des elasmobranches. *Société Amicale des Géologues Amateurs*, **1**, 1–45.
- LONGBOTTOM, A. E. and PATTERSON, C. 1987. Fishes. 238–265. In OWEN, E. and SMITH, A. B. (eds). *Fossils of the Chalk*. Palaeontological Association, London, 306 pp.
- MACKIE, S. J. 1863. On a new species of the Lower Chalk. *The Geologist*, **6**, 241–246.
- MAISEY, J. G. 1984. Higher elasmobranch phylogeny and biostratigraphy. *Zoological Journal of the Linnean Society*, **82**, 33–52.
- 1985. Cranial morphology of the fossil elasmobranch *Synechodus dubrisiensis*. *American Museum Novitates*, **2804**, 1–28.
- McEACHRAN, J. D., DUNN, K. A. and MIYAKE, T. 1996. Interrelationships of the batoid fishes (Chondrichthyes: Batoidea). 63–84. In STIASSEY, M. L. J., PARENTI, L. R. and JOHNSON, G. D. (eds). *Interrelationships of fishes*. Academic Press, San Diego.
- MITCHELL, S. F. 1992. The belemnite faunal changes across the Hauterivian-Barremian boundary in north-east England. *Proceedings of the Yorkshire Geological Society*, **49**, 129–134.
- and UNDERWOOD, C. J. in press. Lithological and faunal stratigraphy of the Aptian and Albian (Lower Cretaceous) of the type Speeton Clay, Speeton, North East England. *Proceedings of the Yorkshire Geological Society*.
- MÜLLER, A. 1989. Selachier (Pisces, Chondrichthyes) aus dem höheren Campanium (Oberkreide) Westfalens (Nordrhein-Westfalen, NW-Deutschland). *Geologie und Paläontologie in Westfalen*, **14**, 1–161.
- and DIEDRICH, C. 1991. Selachier (Pisces, Chondrichthyes) aus dem Cenomanium von Ascheloh am Teutoberger Wald (Nordrhein-Westfalen, NW-Deutschland). *Geologie und Paläontologie in Westfalen*, **20**, 1–105.
- NEALE, J. W. 1960. The subdivision of the Upper D Beds of the Speeton Clay of Speeton, East Yorkshire. *Geological Magazine*, **97**, 351–362.
- 1968. Biofacies and Lithofacies of the Speeton Clay D Beds, E. Yorkshire. *Proceedings of the Yorkshire Geological Society*, **36**, 309–335.
- PATTERSON, C. 1966. British Wealden sharks. *Bulletin of the British Museum (Natural History), Geology Series*, **11**, 283–349.
- PICTET, F. J. 1865. Note sur une dent de l'étage aptien des environs d'Apt, appartenant à un *Notidanus* non décrit. *Annales de la Société Littéraire, Scientifique et Artistique d'Apt*, **1**, 67–70.
- PRIEM, F. 1908. Étude des poissons fossiles du Bassin Parisien. *Annales Paléontologique, Paris*, **1**, 1–114.
- RAFINESQUE, C. S. 1810. *Caratteri di alcuni nuovi generi e nuove specie di animale e piante della Sicilia*. Palermo, 105 pp.
- SANTOS, R. da S. 1968. Paleoictiofauna da Formacao Santana-Euselachii. *Anais, Acedemia Brasileira de Ciencias*, **40**, 493–496.
- SHIRAI, S. 1996. Phylogenetic interrelationships of neoselachians (Chondrichthyes: Euselachii). 9–34. In STIASSEY, M. L. J., PARENTI, L. R. and JOHNSON, G. D. (eds). *Interrelationships of fishes*. Academic Press, San Diego.
- SIVERTON, M. 1995. Revision of *Cretorectolobus* (Neoselachii) and description of *Cederstroemia* n. gen., a Cretaceous carpet shark (Orectolobiformes) with a cutting dentition. *Journal of Paleontology*, **69**, 974–979.
- STINTON, F. C. 1973. Fish otoliths from the English Cretaceous. *Palaeontology*, **16**, 293–305.
- THIES, D. 1978. Selachierzähne aus der nordwestdeutschen Unterkreide. *Aspekte der Kreide Europas, IUGS Series A*, **6**, 211–222.
- 1981. Vier neue Neoselachier-Haiarten aus der NW-deutschen Unterkreide. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1981**, 75–86.

- 1983. Jurazeitliche Neoselachier aus Deutschland und S-England. *Courier Forschungsinstitut Senckenberg*, **58**, 1–117.
- THIOLLIERE, V. J. 1854. *Descriptions des poissons fossiles provenant des gisements coralliens du Jura dans le Bugey*. J.-B. Baillière, Paris-Lyon, 37 pp.
- UNDERWOOD, C. J. and MITCHELL, S. F. 1999. Albian and Cenomanian (Cretaceous) selachian assemblages from north-east England. *Special Papers in Palaeontology*, **60**.
- — and VELTKAMP, C. J. in press. Microborings in Cretaceous fish teeth. *Proceedings of the Yorkshire Geological Society*.
- WARD, D. J. 1981. A simple machine for bulk processing of clays and silts. *Tertiary Research*, **3**, 121–124.
- and THIES, D. 1987. Hexanchid shark teeth (Neoselachii, Vertebrata) from the Lower Cretaceous of Germany and England. *Mesozoic Researches*, **1**, 89–106.
- WELTON, B. J. and FARISH, R. F. 1993. *The collector's guide to fossil sharks and rays from the Cretaceous of Texas*. Beforetime, Lewisville, Texas, 204 pp.
- WOODWARD, A. S. 1886a. On the palaeontology of the selachian genus *Notidanus* Cuvier. *Geological Magazine*, **3**, 205–217, 253–259.
- 1886b. On the relations of the mandibular and hyoid arches in a Cretaceous shark (*Hybodus dubrisiensis* Mackie). *Proceedings of the Zoological Society of London*, **1886**, 218–224.
- 1888a. On the Cretaceous selachian genus *Synechodus*. *Geological Magazine*, **3**, 496–499.
- 1888b. A synopsis of the Vertebrate Fossils of the English Chalk. *Proceedings of the Geologists' Association*, **10**, 273–338.
- 1889. *Catalogue of fossil fishes in the British Museum, London*. Trustees of the British Museum (Natural History), London, 474 pp.
- 1894. Notes on the sharks' teeth from the British Cretaceous formations. *Proceedings of the Geologists' Association*, **13**, 190–200.
- 1911. The Fossil fishes of the English Chalk. Part 6. *Monograph of the Palaeontographical Society*, **64** (313), 185–224, pls 42–53.

CHARLIE J. UNDERWOOD

Department of Earth Sciences
University of Liverpool
Brownlow Street
Liverpool L69 3BX, UK
e-mail cju@liv.ac.uk

SIMON F. MITCHELL

Department of Geography and Geology
University of The West Indies
Mona, Kingston, Jamaica

KEES J. VELTKAMP

Department of Environmental and Evolutionary Biology
University of Liverpool
Brownlow Street
Liverpool L69 3BX, UK

Typescript received 3 June 1998

Revised typescript received 20 October 1998