NEOSELACHIAN SHARKS AND RAYS FROM THE BRITISH BATHONIAN (MIDDLE JURASSIC)

by CHARLIE J. UNDERWOOD *and* DAVID J. WARD

ABSTRACT. Extensive sampling of Bathonian sediments from localities across southern and central England has produced over 8000 neoselachian teeth. These comprise diverse faunas, with over 25 species being represented in total, most of them previously undescribed. Seventeen new species and seven new genera are named: *Palaeoscyllium tenuidens* sp. nov., *Praeproscyllium oxoniensis* gen. et sp. nov., *Eypea leesi* gen. et sp. nov., *Proheterodontus sylvestris* gen. et sp. nov., *Paracestracion bellis* sp. nov., *Palaeobrachaelurus mussetti* sp. nov., *Heterophorcynus microdon* gen. et sp. nov., *Dorsetoscyllium terraefullonicum* gen. et sp. nov., *Ornatoscyllium freemani* gen. et sp. nov., *Pseudonotidanus semirugosus* gen. et sp. nov., *Synechodus duffini* sp. nov., *Protospinax magnus* sp. nov., *P. bilobatus* sp. nov., *P. carvalhoi* sp. nov., *Belemnobatis kermacki* sp. nov., *B. stahli* sp. nov. and *Spathobatis delsatei* sp. nov. In addition, a new family, the Pseudonotidanidae fam. nov., is defined and the status of *Paranotidanus* Ward and Thies, 1987, *Hybodus levis* Woodward, 1889 and *Breviacanthus brevis* (Phillips, 1871) are discussed. These taxa show strong facies specificity, with different species being restricted to different palaeoenvironments.

KEY WORDS: Bathonian, Cotswolds, Dorset, England, Jurassic, ray, shark.

THE Bathonian of southern England was one of the first geological intervals in the world to be systematically examined palaeontologically (e.g. Phillips 1871), but from the earliest studies onwards there has been a lack of study of non-macroscopic fossil material. Although many shark remains have been described from these rocks, these have invariably been in the form of large isolated teeth and fin spines of hybodonts, with the fossil record of neoselachians, which are largely represented by minute isolated teeth, remaining almost unknown. Elsewhere in the Jurassic, most work on neoselachian sharks and rays has concentrated on material preserved as entire skeletons in lithographic limestones. Few studies have concentrated on the isolated teeth, exceptions including the work of Thies (1983), Candoni (1995), Rees (2000) and Underwood (2002). Despite this poor systematic coverage, it is evident that the Jurassic represented a major period of radiation of the Neoselachii Compagno, 1977, with many extant groups being present by the end of the period.

GEOLOGICAL SETTING

Across northern Europe, the Bathonian represented a time of generally low sea levels and high carbonate production. These factors allowed a diverse suite of depositional environments to form across what is now Britain. Although the facies are highly variable, most of the southern British Bathonian is included in the Great Oolite Group, even though oolites are commonly subordinate to other lithologies.

The development of extensive oolitic and bioclastic shoal and barrier island systems, centred in the region of the present Cotswold Hills, separated marine and non-marine lagoon systems to the north-east from open marine conditions to the south. Throughout most of the Bathonian, these facies belts prograded to the south (Text-fig. 1). Within the Late Bathonian, the facies belts started to break down, with strongly channelised systems developing both in the lagoons and open sea. The latest Bathonian saw the development of a more stable and continuous carbonate shelf across much of southern Britain. The diversity of facies present within the Great Oolite Group allows samples to be collected from deposits representing a wide diversity of palaeoenvironments and thus the facies control on selachian faunas to be assessed.

MATERIAL AND METHODS

Samples were collected from a large number of horizons at localities across southern and south-central England. The majority of the neoselachian material studied was obtained by sieving bulk samples of mudstones and marls, with some additional material extracted from limestones by acid digestion. Bulk samples for sieving were typically 20–100 kg dry weight. These were oven dried and sieved through a 320 μm mesh in an automated sieve as described by Ward (1981). Carbonate material was removed from the residue by dissolution in 15 per cent acetic acid. Limestones were dissolved in 10 per cent formic or 20 per cent acetic acid (the former being faster in dissolution of compact lithologies). The insoluble residue was removed regularly to prevent possible acid damage to specimens. At some localities, the lithologies were suitable for *in situ* sieving to remove very coarse and fine material. In this case the 500 μm to 4 mm fraction was retained and processed as above.

Acid-insoluble residues were picked under a binocular microscope. There were few neoselachian teeth in the 1 mm sieve fraction. The 500 μm fraction yielded the greatest number of neoselachian teeth, but numerous small teeth were also present in the 355 μm fraction. Some limestones with very little insoluble material were sieved at 250 μm, producing some additional very small posterior and juvenile teeth.

The yields of neoselachian teeth were highly variable between samples, even those of similar lithology. Mudstones yielded between 0·1 and 11 teeth per kilo (2–4 teeth per kilo being typical). Limestone samples typically yielded between four and ten teeth per kilo. In total over 8000 neoselachian teeth were studied. In addition to neoselachian teeth, neoselachian scales, a partial neoselachian finspine, hybodont teeth and scales, several partial chimaeroid plates, actinopterygian material and rare tetrapod material were recovered. Additional neoselachian material was studied within museum collections, notably at The Natural History Museum, London.

The preservation of neoselachian teeth was very variable between samples. The majority of teeth from lagoonal facies are well preserved, having undergone little or no abrasion or bioerosion. Teeth from shallow marine and transported carbonates vary greatly in their quality of preservation. Many teeth, generally at least half, have a root that is either missing or severely damaged by bioerosion, with borings clearly visible at high magnifications (as in Underwood *et al.* 1999*a*). Furthermore, many teeth are abraded, with the degree of abrasion varying from very slight to extreme. This is readily differentiated from functional wear, where damage is largely restricted to the occlusal region of the tooth and produces discrete wear facets. Teeth from offshore mudstones and marls typically show the highest degrees of bioerosion, with over three-quarters of teeth lacking roots in many samples. Abrasion is generally absent. None of the samples contained what could be interpreted as associated dentitions or material that appeared to be derived from older rocks.

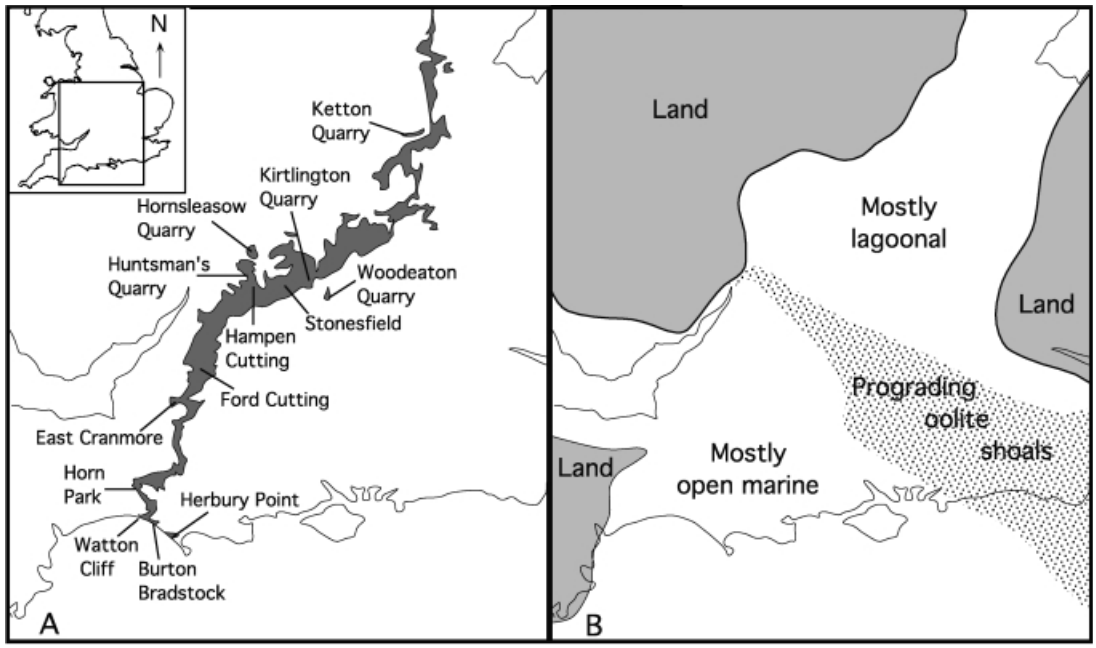
Smaller figured specimens were coated with gold-palladium alloy and observed with a scanning electron microscope. Larger specimens were uncoated and figured by standard optical photography. All figured specimens are deposited in the Department of Palaeontology at The Natural History Museum, London (NHM) prefixed BMNH P.

SAMPLE SITES

Samples yielding neoselachian material were collected at several main localities (Text-fig. 1).

Burton Cliff, Dorset (SY465901). About 30 kg of silty clay was collected from fallen material originating from the basal 4 m of the Fullers Earth Formation. Only four neoselachian teeth were recovered. See Arkell (1947) for details.

Watton Cliff, Dorset (SY449909). Several horizons were collected from this locality, well known for its vertebrate material (Evans and Milner 1994). Three samples totalling about 140 kg were collected from the brachiopod-rich shelly marls of the Wattonensis Beds. These yielded small numbers of generally poorly preserved neoselachian teeth. Faulted against the Wattonensis Beds is a thin unit of black, laminated mudstone containing a 5–10-cm oyster-belemnite bed. By comparison with the Winterbourne Kingston Borehole (Penn, 1982), this is considered to overly the Wattonensis Beds. This shell bed produced large numbers of selachian remains, 250 kg yielding about 2600 neoselachian teeth. Two horizons were also sampled from the Forest Marble Formation within the upper part of



TEXT-FIG. 1. A, outcrop of Bathonian rocks in southern Britain showing sample localities. B, generalised Middle Bathonian palaeogeography of southern Britain.

the cliff. Thirty kg of the rubbly brachiopod limestone of the Boueti Bed (see Arkell 1947 for details) yielded few neoselachian teeth. A unit of bioclastic limestone higher in the succession has yielded diverse vertebrate faunas (e.g. Evans and Milner 1994; Ward *in* Dineley and Metcalf 1999). Sampling of over 400 kg of unlithified lenses of shell gravel within the limestone produced over 3000 neoselachian teeth of variable preservation.

Herbury Point, Dorset (SY613808). About 15 kg of Boueti Bed (see above; Arkell 1947 for details) was sampled after being part sieved *in situ*. This yielded 75 neoselachian teeth. Samples from a brachiopod-rich biosparite at the southern end of the headland, differing in both lithology and fauna from the main limestone at Watton Cliff, yielded very few vertebrate remains.

Horn Park Quarry, Dorset (ST463020). About 40 kg of clay was sampled from the base of the Fullers Earth Formation, yielding only fragmentary teeth.

East Cranmore, Somerset (ST687435). A temporary exposure in the excavation for a lake showed about 2 m of nodular brachiopod limestones of the upper Fullers Earth Rock Formation; 50 kg of shelly marl lenses yielded about 150 neoselachian teeth. See Savage (1977) for regional details.

Ford Road Cutting, Wiltshire (ST854747). A partly overgrown road cutting contains two brachiopod-rich marls within the Upper Rags Member of the Forest Marble Formation. About 20 kg produced 11 teeth. See Wyatt and Cave (2002) for regional details.

Hampen Railway Cutting, Gloucestershire (SP057202). This disused railway cutting, although rather overgrown, exposes much of the lower part of the Great Oolite Group, from which several horizons were sampled. The section is most recently described by Sumbler and Barron (1996). Several small samples of limestones of the Eyford Member were sampled. These included both laminated silty limestones typical of the unit and concretions containing a shell concentration of *Praeexogyra acuminata* from the base of the unit. About 15 kg of samples were taken from a thin seam of marl rich in *Meleagrinella* from near the base of the Taynton Limestone Formation yielding 13 neoselachian

teeth, many abraded. Two levels within the Hampen Formation (beds 43 and 50 of Sumbler and Barron 1996) were also sampled, with about 120 kg of shelly and oolitic clay yielding about 300 neoselachian teeth.

Huntsman's Quarry, Gloucestershire (SP122255). Working faces in this quarry show the Eyford Member overlain by the Taynton Limestone Formation. Limestones totalling about 20 kg were sampled from the Eyford Member and yielded 150 neoselachian teeth, many very small, whilst about 15 kg of the Taynton Limestone yielded only ten teeth. It should be noted that the working facies of the Eyford Member show a somewhat different facies from those exposed in the older parts of the quarry described in earlier reports (e.g. Benton and Spencer 1995). The new faces show more obvious cross stratification, a higher fine biodetrital content and an apparent lower frequency of macroscopic vertebrate material.

Hornsleasow Quarry, Gloucestershire (SP131322). This quarry exposes the lowermost parts of the Great Oolite Group. The vertebrate-bearing Hornsleasow Clay (Metcalf *et al*. 1992) within the Chipping Norton Limestone Formation apparently contains little or no neoselachian material. An overlying coral-bearing mudstone within facies transitional between the Sharps Hill Formation and Lower Fullers Earth Formation yielded about 80 neoselachian teeth from 60 kg of samples.

Kirtlington Quarry, Oxfordshire (SP494199). Several horizons were sampled from this quarry, which exposes the upper part of the Great Oolite Group. Small quantities of a thin marl within the White Limestone Formation (bed 6f of McKerrow *et al.* 1969) yielded neoselachian teeth, whilst only two neoselachian teeth were recovered from 40 kg of the Fimbriatus-Waltoni Clay near the top of the formation (bed 3n of McKerrow *et al*. 1969). Samples of about 20 kg each were also taken from a lens of oolitic clay within the mid part of the Forest Marble Formation and from a brown shelly marl at the base of the Cornbrash Formation, yielding 20 and 30 neoselachian teeth respectively. The mammal bed at the base of the Forest Marble Formation (see Freeman 1979) was not sampled.

Woodeaton Quarry, Oxfordshire (SP534122). Exposing much of the Great Oolite Group, a number of samples were collected from this site. From the Rutland Formation, about 80 kg was sampled from beds 3, 5, 6, and 7 of Horton *et al*. (1995), yielding about 200 neoselachian teeth. A total of about 270 kg was sampled from horizons within the White Limestone Formation, with beds 1, 4, 8, 17 and 23 producing a total of about 1100 neoselachian teeth. About 15 kg of bioclastic limestones from within the Forest Marble Formation yielded about 120 teeth.

Ketton Quarry, Rutland (SK973058). The upper part of the south face of this large quarry exposes much of the Great Oolite Group. About 180 kg of shelly mudstone was sampled from the basal parts of five of the shallowing-upwards cycles of the upper part of the Rutland Formation, yielding 38 neoselachian teeth. A further sample of 30 kg of oyster-rich clay from the top of the Blisworth Limestone Formation produced over 100 teeth.

A number of other sites yielded no well preserved neoselachian material. These samples include marine limestones from within the Forest Marble and Cornbrash formations of southern England and non-marine limestones and mudstones from central England and from the Isle of Eigg, Scotland.

SYSTEMATIC PALAEONTOLOGY

The terminology used here for parts of the selachian teeth largely follows that of Cappetta (1987).

Cohort EUSELACHII Hay, 1902
Subcohort NEOSELACHII Compagno, 1977
Superorder GALEA Shirai, 1996
Order *incertae sedis*
Family *incertae sedis*

Gen. et sp. indet.

Plate 1, figures 1–5

In press *Paracestracion* sp. 2, Underwood and Ward, fig. 4Q.

Material. One incomplete tooth and three crowns including BMNH P. 66042, 66043, 66044.

Description. The teeth of this taxon are robust and relatively large, up to 3·5 mm wide. The crown is wider than high with an elongate main cusp and two pairs of smaller cusps. The main cusp is wide (at least one-third of the width of the crown) and slightly flattened in cross section, with a prominent cutting edge. The inner pair of lateral cusplets is far smaller than the main cusp. The outer pair of cusplets is very small and projects slightly laterally. The labial face of the crown has faint convex ridges at the base of the cusps, with the apron being either somewhat convex or faintly concave (in the largest tooth). The lingual margin of the enameloid crown is flared, with a longitudinal ridge (of Duffin and Ward 1983) that continues along the linguo-basal crown edge to a position just labial of the lateral cusplets. On the largest tooth, faint irregular vertical ridges are present on this lingual border. There is no sign of an enameloid-covered uvula. The labial edge of the crown is smoothly curved in the two narrower teeth, but is somewhat concave on the widest tooth. The root is not well preserved on any tooth, but in the widest tooth can be seen to comprise two low root lobes with a clear nutritive groove.

Remarks. Although incomplete, these teeth show similarities in their general morphology to members of the Orectolobiformes and Heterodontiformes. Despite this, the presence of a flared lingual edge with a longitudinal ridge is unknown within any neoselachian other than the enigmatic Late Triassic genus *Vallisia* Duffin, 1982 and the Early Jurassic supposed Orectolobiforme *Agaleus* Duffin and Ward, 1983. The lack of an enameloid-covered uvula is again an unusual feature within the Orectolobiformes and Heterodontiformes and is also a characteristic of *Vallisia* and *Agaleus*. The general form of the teeth described here is similar to that of *Agaleus*, but differs in lacking a swollen labial apron and probably a labial root buttress and possessing additional lateral cusplets. It is, therefore, considered here that these teeth represent an undescribed genus allied to *Agaleus*. Although the root of some specimens of *Agaleus dorsetenses* Duffin and Ward, 1983, including that of the holotype, are clearly hemiaulacorhize, other teeth have between one and three nutritive grooves on the basal face (e.g. Duffin and Ward 1983, text-fig. 3; Rees 1998, fig. 6). A root of two distinct root lobes with a clear central nutritive groove, as present on the supposed lateral tooth described here, has been recognised in posterolateral teeth of *Agaleus* (Delsate and Duffin 1993, pl. 9). The root vascularisation of *Vallisia coppi* Duffin, 1982 appears similar to that seen in most specimens of *Agaleus*, although the position of the main foramen in the latter is poorly documented and the resemblances cannot be confirmed. Additional differences exist between the enameloid microstructure of *Vallisia* and *Agaleus* (e.g. Cuny and Benton 1999) suggesting that although there are many morphological similarities between the teeth of these taxa, they may not be closely related.

The presence of shared characters of both the crown and root in *Agaleus* and the teeth described here suggest that these genera represent an unnamed taxonomic group with a known range from Hettangian/Sinemurian to Bathonian. The taxonomic position of this group is uncertain, as many of the diagnostic characters are autapomorphic. Despite this, the general form of the crown and, in some specimens of *Agaleus*, the root is similar to that of Orectolobiformes and Heterodontiformes. As all characters shared with either the Orectolobiformes or Heterodontiformes may be primitive, it is likely that this group of taxa represents stem group galeids, possibly being paraphyletic or a sister group to all other members of the Galea.

Occurrence. All four teeth of this taxon are known from deposits reflecting open marine palaeoenvironments at Watton Cliff, Dorset; two from open marine mudstones and two from a redeposited shell bed.

Order CARCHARHINIFORMES Compagno, 1977
Family SCYLIORHINIDAE Gill, 1862

Genus PALAEOSCYLLIUM Wagner, 1857, *non* Marck, 1863

Type species. *Palaeoscyllium formosum* Wagner, 1857, from the Upper Jurassic of Germany.

Palaeoscyllium tenuidens sp. nov.

Plate 1, figures 6–14

In press *Palaeoscyllium* sp., Underwood and Ward, fig. 5A–B.

Derivation of name. From the small and delicate nature of the teeth.

Holotype. BMNH P. 66045.

Material. About 420 teeth representing a range of jaw positions and ontogenetic stages including BMNH P. 66046–66049.

Diagnosis. Small teeth showing moderate heterodonty, with crown being higher than wide in all teeth. Main cusp high and either vertical or somewhat inclined to posterior. Up to three pairs of small but generally well-defined pairs of lateral cusplets; in some teeth lateral cusplets are reduced to bulbous cutting edge. Labial face of the crown ornamented by up to ten well-developed and faintly sinuous, vertical ridges which reach over two-thirds of the way to the cusp apex and occasionally bifurcate towards crown base. Hemiaulacorhize root distinctly V-shaped, root lobes flared and wider than crown. Root basal face flat. Lingual edge of the root swollen with large foramen.

Description. A large main cusp has a relatively flat labial and strongly convex lingual face. This is weakly inclined to the posterior in most teeth, only being completely erect in anteriormost files. The main cusp is flanked by paired lateral cusplets which are small, typically less than one-quarter of the length of the main cusp, but well defined. The lateral cusplets are slightly curved towards the main cusp in some teeth. Two pairs of lateral cusplets are typically present, although a third small cusplet is sometimes seen, especially in the anterior edge of the tooth. In some teeth anterior, or more rarely all, cusplets are partially or completely fused to form a strong cutting edge. The labial face of the crown has a number of well-developed longitudinal ridges. Up to ten ridges are seen on large lateral teeth, fewer being present on anterior or juvenile teeth. These typically extend from the base of the crown to a point close to the apex. The ridges are straight to slightly sinuous, with uncommon and irregular bifurcation being present towards the base of the crown. A sharp-edged swelling is occasionally present at the base of the ridges. Lingual ornament consists of weak and rather irregular longitudinal ridges, on many teeth being confined to the main cusp.

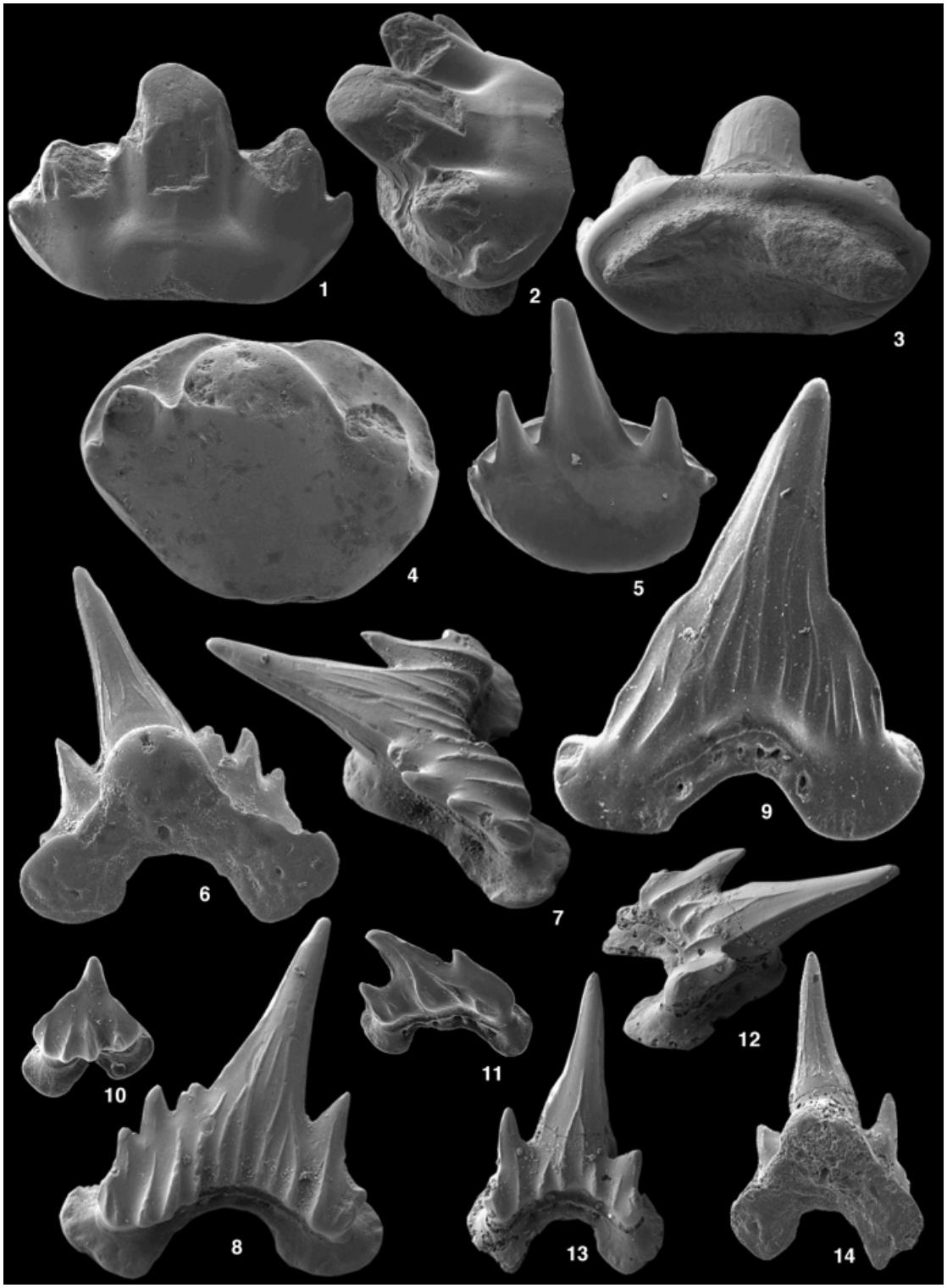
The root is fairly low and has an extremely flat base. This is wider than the crown in all teeth. Root lobes are well developed and typically form an angle of 60–120 degrees. The root lobes are flared at the base and in many teeth the lateral extremities of the root are faintly directed lingually. A series of well-developed foramina are present at the labial junction of the root lobes. The lingual face of the root is swollen, and has a well-developed foramen. A row of small foramina are present near the linguo-lateral crown-root junction.

Remarks. The degree of variation between the teeth of *P. tenuidens* sp. nov. suggests an ontogenetic heterodonty, with the addition of lateral cusplets during growth. By comparison with the dentition of *Scyliorhinus canicula* (Linnaeus, 1758), a similar if rather more extreme monognathic heterodonty is present. Small, narrow, erect teeth are likely to be parasymphyseal, with wider teeth lacking well-developed cusplets being very similar to some anterior teeth of *S. canicula*, especially resembling upper anterior file two. Asymmetrical teeth with more cusplets are from lateral positions. Dignathic heterodonty, represented in many extant scyliorhinids by different intensities of ornamentation (Herman *et al.* 1990), is not obvious.

EXPLANATION OF PLATE 1

Figs 1–5. Galeid gen. et sp. indet. 1–3, P. 66042, oyster-belemnite bed, Frome Clay Formation, Watton Cliff, lateral tooth. 1, labial view. 2, lateral view. 3, lingual view; all ×15. 4, P. 66043, bioclastic limestone, Forest Marble Formation, Watton Cliff, worn anterior tooth, labial view; ×30. 5, P. 66044, oyster-belemnite bed, Frome Clay Formation, Watton Cliff, small anterior tooth, labial view; ×30.

Figs 6–14. *Palaeoscyllium tenuidens* sp. nov. 6–8, P. 66045, holotype, concretions at base of Eyford Member, Hampen Cutting, anterolateral tooth. 6, lingual view. 7, lateral view. 8, labial view. 9, P. 66046, bioclastic limestone, Forest Marble Formation, Watton Cliff, anterior tooth lacking lateral cusplets, labial view. 10, P. 66047, Eyford Member, Huntsman's Quarry; commissural tooth, labial view. 11, P. 66048, Eyford Member, Huntsman's Quarry, posterolateral tooth, labial view. 12–14, P. 66049, concretions at base of Eyford Member, Hampen Cutting, anterior tooth. 12, lateral view. 13, labial view. 14, lingual view; all ×52.



UNDERWOOD and WARD, galeid, *Palaeoscyllium*

Teeth of *P. tenuidens* sp. nov. differ from those of the Late Jurassic *P. formosum* Wagner, 1857 in having variably developed lateral cusplets, a finer ornament and a more obtuse angle between the root lobes. The presence of *P. tenuidens* suggests that the known range of the genus *Palaeoscyllium* can now be recorded as Bathonian–Albian (Underwood and Mitchell 1999). This further extends the known range of the Family Scyliorhinidae, and probably Pentanchinae *sensu* Compagno (1984) (Candoni 1993), suggesting their first appearance in the Bathonian.

Occurrence and palaeoecology. *Palaeoscyllium tenuidens* sp. nov. is recorded from a number of samples representing a range of different palaeoenvironments (Underwood and Ward in press). It forms an uncommon part of the fauna within outer lagoon facies containing much shelly material and matrix-supported ooids washed over from the oolite barrier. Teeth of *P. tenuidens* are common in the nearshore limestones of the Eyford Member, where they dominate some samples, and are also present within shoal oolites. *P. tenuidens* is also present in open marine shelf carbonates (Boueti Bed and Cornbrash Formation) and forms a frequent component of the offshore transported carbonates of the Dorset Forest Marble Formation. In general it appears that *P. tenuidens* represents a taxon that occurred almost exclusively in shallow, clear, agitated water, not venturing far into lagoon systems or out onto the deep muddy shelf. As with modern scyliorhinids with a similar dentition, it is likely that *P. tenuidens* was a benthic generalist, feeding largely on small food items.

Scyliorhinidae? gen. indet.

Plate 2, figures 1–4

Material. Five teeth of variable preservation including BMNH P. 66050 and 66051.

Description. The best preserved tooth is almost symmetrical and about as wide as high. An elongate main cusp is flanked by two pairs of small lateral cusplets. The labial face of the crown is faintly convex and unornamented other than by a single ridge on one of the lateral cusplets. The lingual face of the cusps is ornamented with very fine longitudinal ridges. A faint but continuous cutting edge is present. The root is low and strongly V-shaped with a flat basal face, which is slightly flared. Vascularisation is hemiaulacorhize. Small foramina are rare, with only a single pair of foramina present on the lateral faces of the root. Other, less well-preserved teeth are from more anterior positions. These are symmetrical and at least twice as high as wide. An elongate main cusp is flanked by a single pair of very short but well-differentiated lateral cusplets. Labial ornament comprises widely spaced, faint, longitudinal ridges which reach neither the apex nor labio-basal margin. The root is low with short, rounded root lobes.

Remarks. The teeth of this taxon can be differentiated from those of *Palaeoscyllium tenuidens* sp. nov. in the absence of strong ornament, greater degree of symmetry, narrower anterior teeth, less flared basal face of the root and lower numbers of small linguo-lateral foramina. These differences are probably significant enough to suggest that this taxon belongs to a separate genus. It does not closely resemble any extant scyliorhinid or proscylliid genus and, although crown morphology of the anterior tooth is very similar to that of *Foumtizia* Noubhani and Cappetta, 1997, it differs in having a different vascularisation. These teeth therefore probably represent an as yet undescribed genus of scyliorhinid or possibly proscylliid.

Occurrence and palaeoecology. All the teeth of this taxon were found within shelf carbonate facies, both within the Boueti Bed and within the Lower Cornbrash. It therefore appears that the distribution of species was very strongly environmentally controlled.

Family? PROSCYLLIIDAE Fowler, 1941

Genus PRAEPROSCYLLIUM gen. nov.

Derivation of name. From the resemblance to the extant genus *Proscyllium* Hilgendorf, 1904, which it considerably predates.

Type species. *Praeproscyllium oxoniensis* gen. et sp. nov., from the Bathonian of southern England (by monotypy).

Diagnosis. Small teeth showing moderate heterodonty. Single main cusp is moderately high and erect or slightly angled to posterior. Little or no crown shoulder at base of cusp and lateral cusplets absent or incipient. Labial face flat and unornamented in anterior teeth, with short and strong vertical ridges in lateral teeth, never extending onto main cusp. Hemiaulacorhize root low and V-shaped, with root lobes forming an angle of 60–90 degrees. Root lobes parallel sided and basal face of root largely flat. Small foramina are very well developed at junction of root lobes; foramina also present along linguo-lateral side of root. Lingual extremity of root sharply angled and with large foramina.

Remarks. The dentition of *Praeproscyllium* gen. nov. is very similar to that of *Proscyllium habereri* Hilgendorf, 1904, differing largely in the lack of lateral cusplets in anterior teeth, the lack of a root nutritive groove and the greater degree of monognathic heterodonty (see Herman *et al.* 1991). The high degree of heterodonty of *Praeproscyllium* is almost unknown amongst other scyliorhinid and proscylliid genera, only some species of *Halaelurus* Gill 1862 having similarly high degrees of heterodonty (Herman *et al.* 1990).

The assignment of *Praeproscyllium* to the Proscylliidae is tentative, the teeth of members of the Proscylliidae and Scyliorhinidae being generally similar (Herman *et al.* 1991). Despite this, the teeth of *Praeproscyllium* are far more similar to those of *Proscyllium* than to any extant scyliorhinid genus. There is little recorded fossil record for the Proscylliidae, although teeth of *Proscyllium* appear to be present within the Miocene and Pliocene of eastern North America (J. Bourdon, pers. comm. 2002). It is also possible that taxa previously referred to the Scyliorhinidae and Triakidae should be referred to the Proscylliidae. Tooth morphology suggests that *Foumtizia* Noubhani and Cappetta, 1997 from the Palaeocene of North Africa and *Protoscyliorhinus* Herman, 1977 from the Cretaceous of Europe may belong within the Proscylliidae.

An additional species of *Praeproscyllium* appears to be present within the Kimmeridgian of northern France, being figured by Candoni (1995) as ?Proscylliidae (Candoni 1995, pl. 1). This would suggest a range of at least Bathonian to Kimmeridgian for the genus.

Praeproscyllium oxoniensis gen. et sp. nov.

Plate 2, figures 5–15

1982	Type 1 teeth, Young, fig. 1A–G
In press	'Scyliorhinid' sp. 1, Underwood and Ward, fig. 5E–F.

Derivation of name. From the common occurrence of this taxon at sites in Oxfordshire.

Holotype. BMNH P. 66052.

Material. Over 640 teeth from many samples including P BMNH. 66053–66057.

Diagnosis. As for genus.

Description. The crown of anterior teeth is distinctly Y-shaped, with a well-developed main cusp and lateral parts of crown extending along the upper part of the root lobes with little or no crown shoulder at the base of the cusp. The labial face of the crown is flat, or even faintly concave in some teeth. This is separated from the strongly convex lingual face of the cusp by a continuous but not especially sharp cutting edge. The crown of anterior teeth is essentially unornamented. In anterolateral teeth the crown shows some degree of asymmetry, with a shortening of the posterior part of the crown and the development of a posteriorly angled cusp. A weak crown shoulder is also developed, with incipient lateral cusplets, generally little more than expansions of the cutting edge being present. The labio-basal edge of the crown possesses a weak pectination, with associated short labial ridges. The crown of lateral teeth shows a moderate degree of asymmetry with a pair of small and irregular cusplets at the base of the main cusp. The labial ornament is moderate to strong but short, with up to eight short, straight ridges not reaching the base of the main cusp.

The roots of all teeth are similar, but become more asymmetrical in lateral teeth. The root is low and has a flat basal face with no sign of a nutritive groove. Viewed basally, the root is strongly V-shaped, with a sharp angle where the root lobes meet. The root lobes are longer than the labio-lateral lobes of the crown, but remain parallel-sided without obvious flaring at their labial end. Numerous foramina is present near the root-crown contact, as well as small foramina

on the basal face of the root lobes in some teeth. A cluster of small foramina is present where the root lobes join, and a row of foramina are present just below the crown-root junction along much of the linguo-lateral face of the root. The main lingual foramen is centrally placed on the root lingual protuberance.

Occurrence and palaeoecology. *Praeproscyllium oxoniensis* gen. et sp. nov. is present as a minor part of the fauna in many samples representing a wide range of palaeoenvironments (Underwood and Ward in press) from carbonate shelf to inner lagoon, only being absent in outer shelf mudstone facies. Despite this, *P. oxoniensis* is only common within samples representing largely to fully marine lagoons, where it is commonly the dominant taxon. The distribution of this species would, therefore, be highly analogous with that of *Triakis semifasciata* Girard, 1855 (Compagno 1984), and was probably likewise a nectobenthic predator of small fish and invertebrates.

Genus EYPEA gen. nov.

Derivation of name. From the occurrence of this genus near the village of Eype, Dorset.

Type species. *Eypea leesi* gen. et sp. nov., from the Bathonian of southern England (by monotypy).

Diagnosis. Teeth showing moderate to strong heterodonty. Single main cusp is robust and conical, being erect or slightly angled to posterior, and very reduced in posterior teeth. Little or no crown shoulder at base of cusp, which is thus poorly differentiated with no lateral cusplets. Labial face convex. In anterior teeth, labial face unornamented or with a single angled ridge running along the labial face of the basal crown lobes. Weak longitudinal ridges on the labial face of lateral teeth connect this ridge to the basal edge of the crown. Fine longitudinal ridges may be present on lower part of cusp. Ornament increasingly stronger towards posterior, commissural teeth being ornamented with a fine labial reticulation. A cutting edge is largely absent in anterior teeth, but is weak and continuous in lateral teeth. Hemiaulacorhize root low and V-shaped. Root lobes somewhat parallel-sided and basal face of root convex. Lingual apex of root swollen.

Discussion. Teeth of *Eypea* gen. nov. have a number of features in common with those of *Praeproscyllium* gen. nov., with the shape of the crown of anterior teeth, form of the root and high degree of heterodonty all being similar. There are, however, important differences that are here considered to warrant the erection of a separate genus. *Eypea* gen. nov. shows a higher degree of heterodonty, possessing low-crowned posterior teeth absent in *Praeproscyllium* or any other proscylliid. The weak lateral cusplets of lateral teeth of *Praeproscyllium* are absent in *Eypea*, as is the well-developed cutting edge on anterior teeth and the flat basal face of the root. The assignment of *Eypea* to the Proscylliidae is tentative, but the teeth are more similar to those of extant proscylliids than scyliorhinids.

Eypea leesi gen. et sp. nov.

Plate 3, figures 1–13

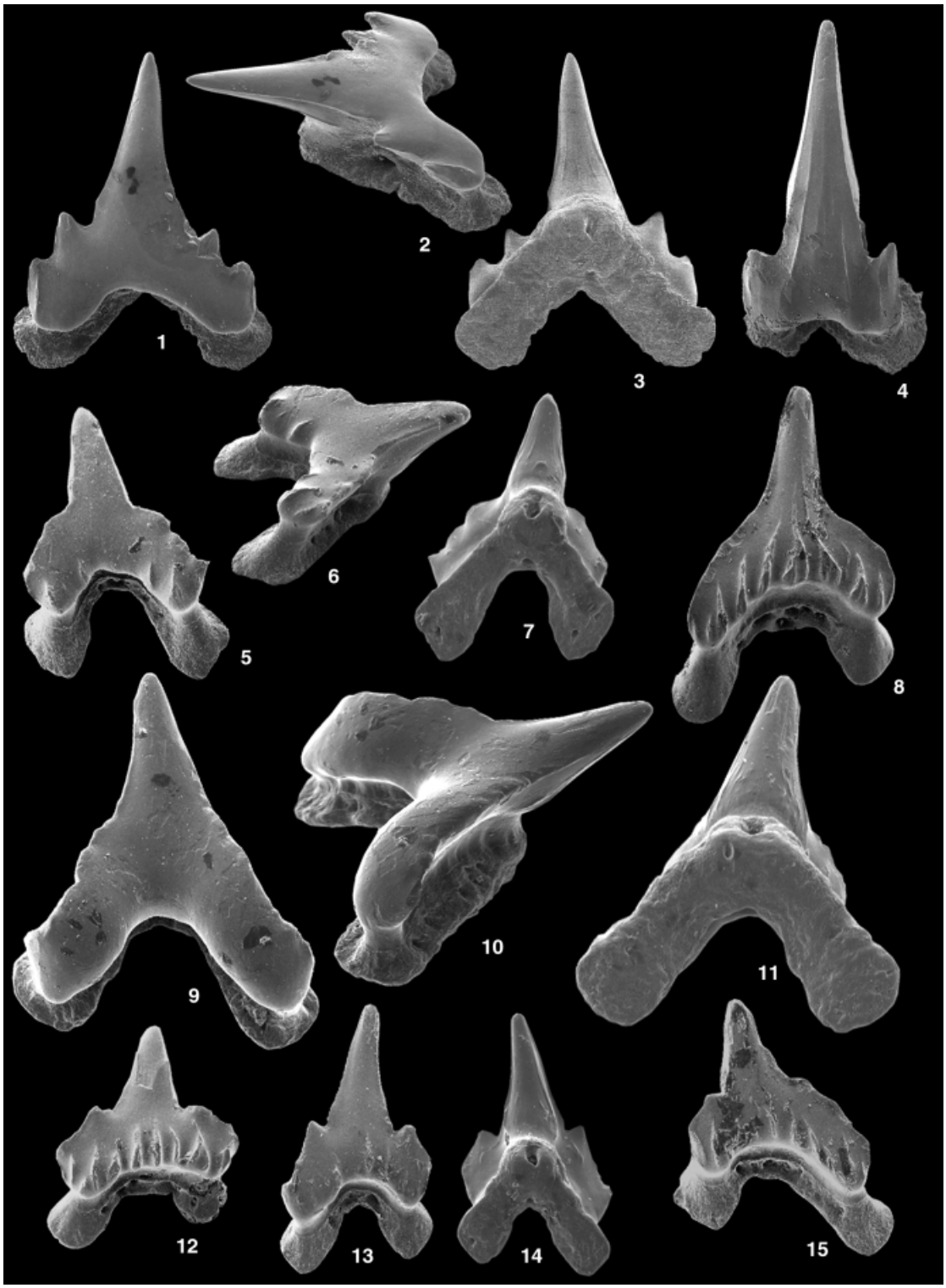
In press 'Scyliorhinid' sp. 2, Underwood and Ward, fig. 5C–D.

Derivation of name. After Patricia Lees, part of the University College London (UCL) team who first investigated the vertebrate fauna of the Bathonian at Watton Cliff.

EXPLANATION OF PLATE 2

Figs 1–4. *Scyliorhinidae*? gen. indet., all from Boueti Bed, Herbury Point. 1–3, P. 66050, lateral tooth. 1, labial view. 2, lateral view. 3, lingual view. 4, P. 66051, anterior tooth, labial view; all ×52.

Figs 5–15. *Praeproscyllium oxoniensis* gen. et sp. nov., all from Rutland Formation, Bed 7, Woodeaton Quarry. P. 66052, holotype. 5, labial view. 6, lateral view. 7, lingual view. 8, P. 66053, labial view. 9–11, P. 66054, 9, labial view. 10, lateral view. 11, lingual view. 12, P. 66055, labial view. 13–14, P. 66056. 13, labial view. 14, lingual view. 15, P. 66057, labial view; all ×52.



UNDERWOOD and WARD, *Praeproscyllium*, scyliorhinid

Holotype. BMNH P. 66058.

Material. About 875 teeth from all parts of jaw and from juveniles, many lacking root or variably abraded including BMNH P. 66059–66065.

Diagnosis. As for genus.

Description. The teeth are up to 2·7 mm high, and are overall more robust than those of any other Jurassic or Early Cretaceous carcharhiniform. Anterior teeth have a conical cusp with no cutting edge close to the apex. This cusp extends labio-basally into a pair of well-developed crown lobes which extend nearly to the end of the underlying root lobes and have weak to moderate cutting edges. There is no crown shoulder or lateral cusplets. The labial face of the crown is largely smooth and gently convex, although at least some sign of a ridge or angled edge along the labial face of the crown lobes is usually present. Very fine longitudinal striae may be present on the lingual side of the cusp. The crown of lateral teeth is similar, although the cusp is somewhat angled posteriorly. This may give a slight crown shoulder on the posterior side of some teeth. A continuous, if weak, cutting edge is present on these angled cusps. The ridge on the labial face of the crown lobes is typically well developed on lateral teeth, in many cases the ridges coming close to meeting at the base of the cusp, giving a nearly continuous ridge parallel to the labio-basal edge of the crown. Weak and widely spaced longitudinal ridges extend from the labio-basal edge of the crown to this ridge, giving a weakly reticulate pattern. Near the central part of the crown, these longitudinal ridges are more continuous and somewhat irregular, reaching up to half-way up the cusp. The very low and asymmetrical posterior teeth have a more diffuse reticulate ornament, although a ridge parallel to the basal edge of the crown is still present on the labial face.

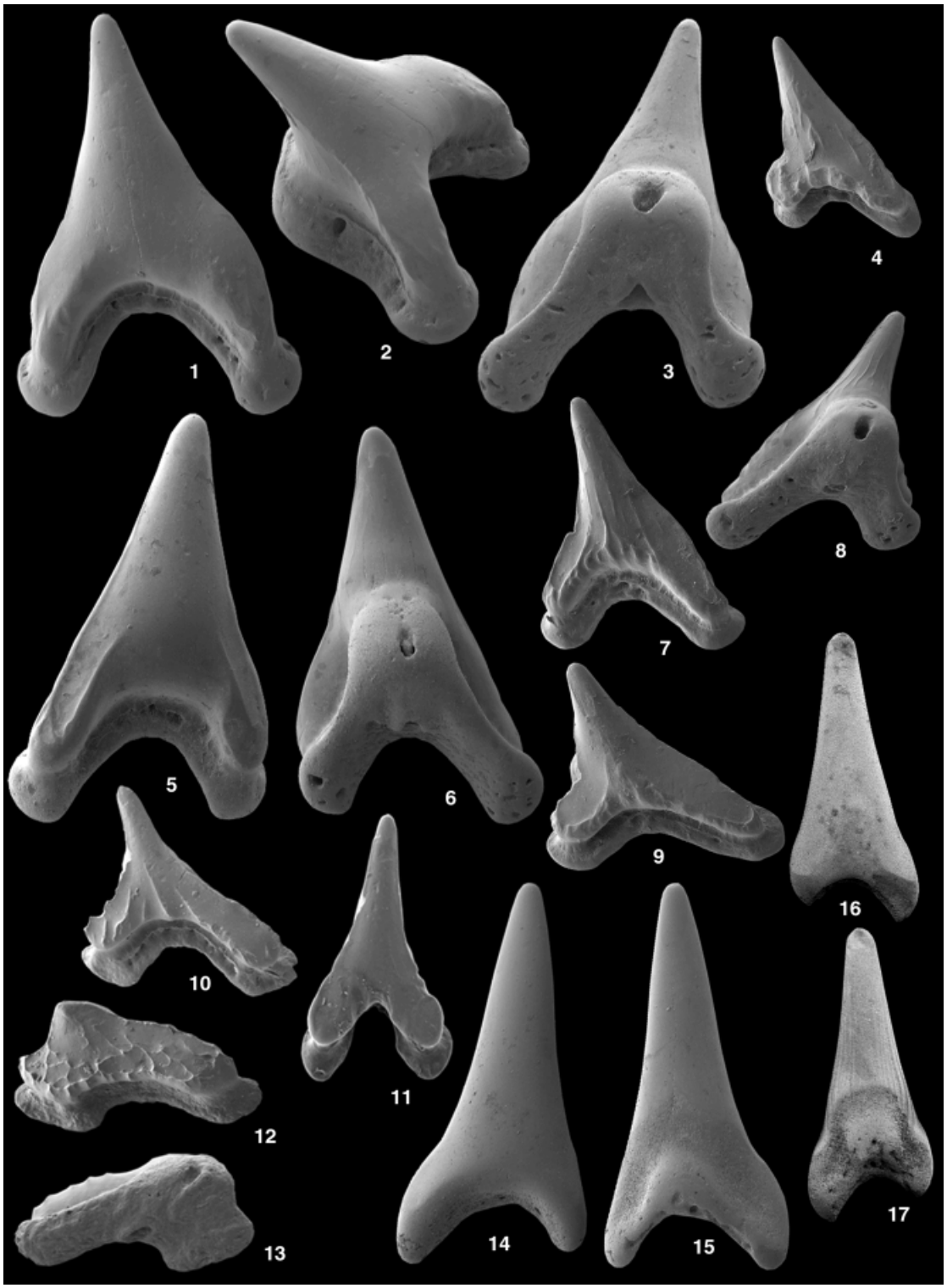
The root is low and lacks a nutritive groove. The basal face is convex, although a flatter basal face is present on posterior and juvenile teeth. The two root lobes are relatively narrow, especially in larger teeth, and somewhat bulbous at the labial ends as well as being somewhat swollen at the lingual apex. A row of well-developed foramina is present just below the crown-root junction along much of both sides of both root lobes. In addition, a major foramen is present at the junction of the root lobes and within the lingual protuberance of the root. Small and irregular foramina are sometimes present on the basal face of the root lobes.

Occurrence and palaeoecology. *Eypea leesi* gen. et sp. nov. is present as an uncommon element within both laminated mudstone and shelly marl facies at Watton Cliff and East Cranmore, both representing offshore neritic facies. Small teeth of this taxon, possibly juveniles, are also present within open marine shelf carbonates (Boueti Bed and Cornbrash Formation). It is also a frequent component of transported carbonates of the Dorset Forest Marble Formation. No teeth of the taxon were recorded in any sample from shoreface or lagoonal settings. It therefore appears that *E. leesi* was present within both moderately shallow carbonate and deeper marine muddy environments, but avoided very shallow water and lagoons. The dentition suggests a generalistic feeder possibly consuming both small fish and invertebrates. In general it is probably comparable to some modern scyliorhinids, especially the moderate-sized *Scyliorhinus stellaris* (Linnaeus, 1758), which occupies a range of inner to mid shelf settings.

EXPLANATION OF PLATE 3

Figs 1–13. *Eypea leesi* gen. et sp. nov. 1–9, 11 from bioclastic limestone, Forest Marble Formation, Watton Cliff; 1–9, ×25; 10–13, ×40. 1–3, P. 66058, holotype, anterior tooth. 1, labial view. 2, lateral view. 3, lingual view. 4, P. 66059, anterolateral tooth, labial view. 5–6, P. 66060, anterior tooth. 5, labial view. 6, lingual view. 7–8, P. 66061, lateral tooth. 7, labial view. 8, lingual view. 9, P. 66062, lateral tooth, labial view. 10, P. 66063, Fullers Earth Rock Formation, East Cranmore, juvenile lateral tooth, labial view. 11, P. 66065, juvenile anterior tooth, labial view. 12–13, P. 66064, oyster-belemnite bed, Frome Clay Formation, Watton Cliff, posterior tooth. 12, labial view. 13, lingual view.

Figs 14–17. Carcharhiniform gen. et sp. indet. 14–15, P. 66066, bioclastic limestone, Forest Marble Formation, Watton Cliff. 14, labial view. 15, lingual view. 16–17, P. 66067. Taynton Limestone Formation, Huntsman's Quarry. 16, labial view. 17, lingual view; all ×10.



UNDERWOOD and WARD, *Eypea*, carcharhiniform

Order Indeterminate
Family Indeterminate

Gen. et sp. indet.

Plate 3, figures 16–19

In press ?*Palaeocarcharias* sp., Underwood and Ward, fig. 4U.

Material. Three incomplete and abraded teeth including BMNH P66066–66067.

Description. These teeth are moderately large, with a preserved size of up to 7 mm high. A single cusp is high and slender, being convex on both faces, but more so on the lingual face. There is no well-defined cutting edge preserved. Two short and narrow crown lobes diverge from the base of the cusp. No ornament is present on two of the teeth, whilst the third has numerous straight, fine ridges on the lingual face and a ridge on the labial face of the crown lobes. Very little root is preserved, but it appears that the root was narrow and with clearly divergent root lobes. Where the root has broken away, no pulp cavity can be seen, and therefore appears to be absent.

Remarks. All teeth are indeterminate, but the large size and general shape of the crown differentiate these from any co-occurring carcharhiniforms. These teeth may have an affinity with *Palaeocarcharias* de Beaumont 1960, a genus showing both lamniform and orectolobiform features (Duffin 1988), but differ in the presence of a lingual ornament. The true affinities of this species cannot be resolved until more complete teeth are recovered.

Occurrence. Present only as a very rare element within high energy open marine carbonates of the Forest Marble Formation at Watton Cliff and the Taynton Limestone at Huntsman's Quarry.

Order HETERODONTIFORMES Berg, 1940
Family HETERODONTIDAE Gray, 1851

Genus PROHETERODONTUS gen. nov.

Derivation of name. From the resemblance to *Heterodontus* de Blainville, 1816, which it predates.

Type species. *Proheterodontus sylvestris* gen. et sp. nov., from the Bathonian of southern England (by monotypy).

Diagnosis. Moderate heterodonty of anterior and lateral teeth with specialised commissural teeth. Crown of anterior and anterolateral teeth higher than wide and fairly triangular in shape, being symmetrical or slightly asymmetrical with cusps inclined posteriorly. Crown of lateral teeth wider than high with cusps strongly inclined posteriorly. Anterior and anterolateral teeth with elongate and robust main cusp flanked by one to three pairs of smaller lateral cusplets. Lateral cusplets project laterally to some extent. All cusps flattened and have a continuous cutting edge. The labial face of crown flat and apron is slightly to very strongly concave in all teeth. Small lingual protuberance present. Hemiaulacorhize root relatively low, and very strongly V-shaped in basal view with root lobes extending beyond labio-basal margin of crown. Lingual and labio-basal foramina are very well developed, with other small foramina on basal face of root. Commissural teeth wider than high with crescent-shaped crown bearing numerous small cusps to form serrated occlusal edge. Hemiaulacorhize root shallow and similarly crescent shaped, being narrower than the crown.

Discussion. Anterior and anterolateral teeth of *Proheterodontus* gen. nov. have morphologies very similar to that of extant species of *Heterodontus* (e.g. Herman *et al.* 1993) and the two genera are presumably closely related. Despite this general similarity there are a number of distinct differences. The most significant of these is the apparent lack of molariform lateral teeth, despite the large sample sizes including both adult and juvenile teeth studied. In addition, the root is more gracile with more elongate root lobes

than is present within anterior teeth of *Heterodontus*. The form of the root and the crown of anterior teeth distinguish these teeth from those of *Paracestracion* (see Underwood 2002).

Proheterodontus sylvestris gen. et sp. nov.

Plate 4, figures 1–12

In press *Heterodontus* sp., Underwood and Ward, fig. 4R–T.

Derivation of name. From woodland or forest, after the occurrence in the Forest Marble; also after Alison Ward, formally Wood, the wife of DJW.

Holotype. P. 66068.

Material. About 800 teeth of a variety of morphologies and sizes including P. 66069–66074.

Diagnosis. As for genus.

Description. The anterior teeth have a high crown, which is strongly triangular in labial view. Small, paired lateral cusplets are present about half way along the sides of the crown. In symmetrical anterior teeth there are one or two pairs of lateral cusps, two or three pairs on slightly asymmetrical anterolateral teeth. The flat labial face of the crown has an apron that is slightly concave in anterior teeth, but progressively more concave in more lateral teeth. Lateral teeth are more semicircular in shape, being lower and wider with the main cusp being smaller in comparison to the others. All cusps are strongly inclined posteriorly, with cusps on the anterior side of the tooth typically being larger than on the posterior side. Commissural teeth are smaller than anterior or lateral teeth, and have a wide, curved crown with numerous small cusps forming a serrated occlusal edge. The crowns of some very small, asymmetrical teeth, presumably lateral teeth of juveniles, are more rounded and lack a clear concave apron. On these small teeth, a single pair of small or incipient lateral cusps flanks a low main cusp. Cusps of all teeth are flattened and commonly slightly curved lingually, especially in larger teeth. A well-developed, continuous, cutting edge is present along the entire occlusal edge of all teeth. The roots of all teeth are relatively low and hemiaulacorhize, but vary somewhat in shape between different teeth. The roots of anterior and anterolateral teeth are very strongly V-shaped in basal view, typically with a slightly swollen region at the junction of the root lobes. The narrow root lobes extend beyond the labio-basal edge of the crown. The roots of lateral teeth have a more obtuse angle between the root lobes, which are shorter and do not extend beyond the edge of the crown. The roots of commissural teeth are thin and arcuate. The roots of all teeth have well-developed lingual and labio-basal foramina. Small foramina are present on the root basal face and along the upper edge of the root. No molariform teeth were recorded.

Occurrence and palaeoecology. Teeth of this taxon are common within the redeposited shell bed within the Forest Marble Formation of Watton Cliff. Rare teeth, commonly small and presumably largely from juveniles, were also recorded from shallow marine oolitic, and fully marine lagoonal deposits. The distribution of this taxon suggests a species typically occurring in shallow marine conditions over a shelly or oolitic substrate, with juveniles also venturing into lagoon systems. Teeth rarely show wear, and it seems unlikely that this species was as durophagous as the co-occurring species of *Paracestracion*.

Genus PARACESTRACION Koken, *in* Zittel 1911

Type species. *Cestracion falcifer* Wagner, 1857.

?*Paracestracion* sp.

Plate 4, figure 13

Material. Two incomplete crowns including BMNH P. 66075.

Description. The crown has a flat, oval labial face with one prominent cusp and two or three pairs of small lateral cusplets. The main cusp is gracile and flattened, and flanked by short, rounded, lateral cusplets. The different pairs of lateral cusplets are all of similar size. The root is unknown.

Remarks. Although indeterminate, the teeth of this taxon are smilar to the anterior teeth of mature specimens of *P. falcifer* (Schweizer, 1964), differing largely in the more robust central cusp.

Occurrence. Teeth of this taxon are only known from the redeposited shell bed within the Forest Marble Formation at Watton Cliff.

Paracestracion bellis sp. nov.

Plate 5, figures 1–9

1982. Type 2(d) teeth, Young, fig. 2G–H, J–K, M–N.
In press *Paracestracion* sp. 1, Underwood and Ward, fig. 4N–P.

Derivation of name. From the generic name for the common daisy (*Bellis*), after the daisy-like shape of the teeth; also after Daisy Williamson, the wife of CJU.

Holotype. BMNH P. 66076.

Material. About 250 teeth, none of them molariform, including BMNH P. 66077–66080.

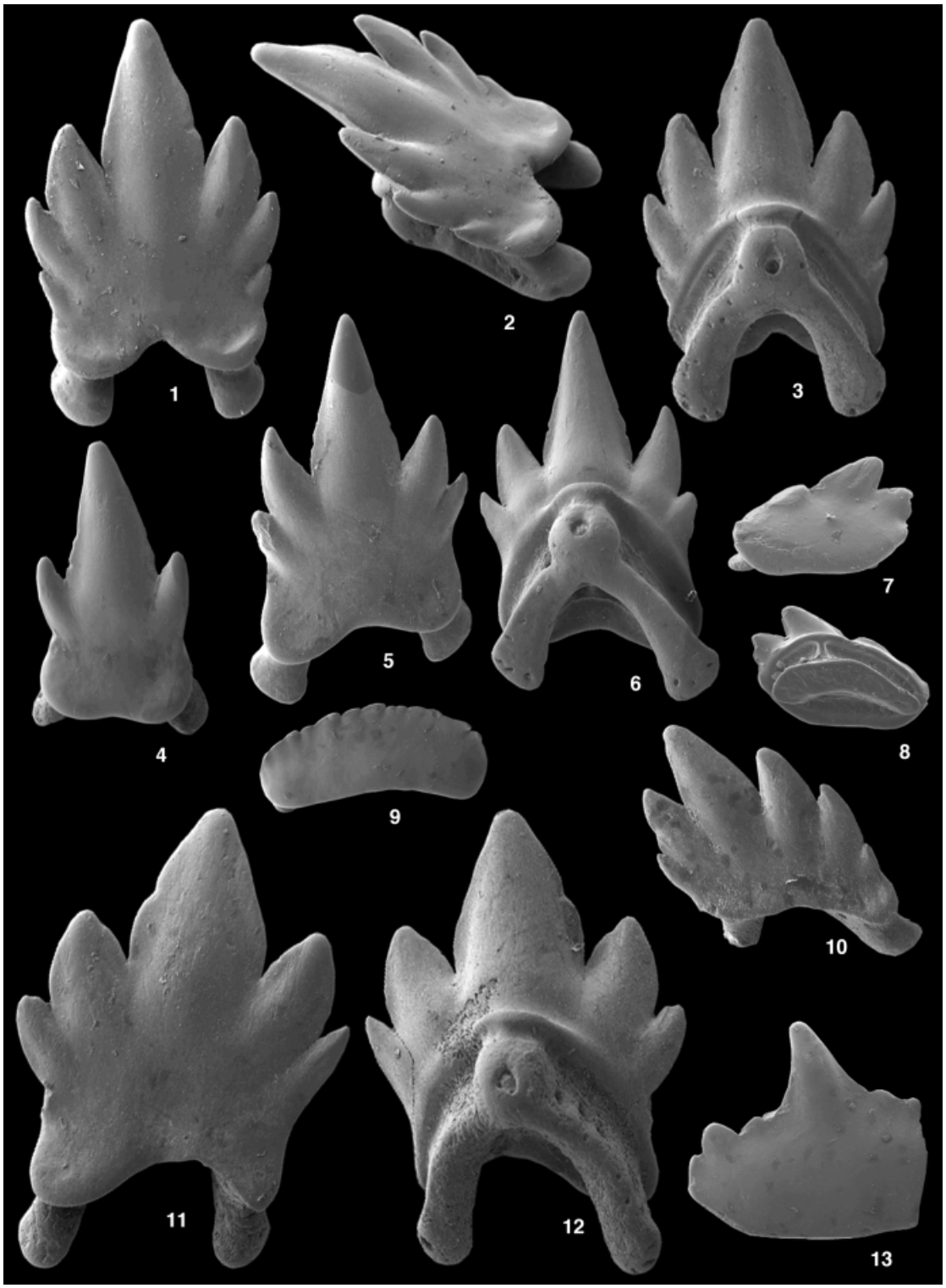
Diagnosis. Teeth moderately heterodont. Crown wider than high with six to eight cusps along occlusal edge. Cusps short, comprising less than one-third of total height of crown, with well-developed cutting edge and inclined to posterior in most teeth. Labial face of crown flat to faintly convex with smooth, convex, curved apron. Root low, narrower than crown with very well-developed nutritive groove and large central foramen. Root lobes narrow, curved and with flat basal face.

Description. All of the teeth recorded of this taxon are pectinate and typical of *Paracestracion* (*sensu* Underwood 2002). Relatively symmetrical teeth are rare and may represent only anteriormost files. The majority of teeth are asymmetrical with cusps inclined to the posterior and typically with one more cusplet anterior to the largest cusp than posterior to it. The crown is oval, usually one and a half to two times as wide as high. The flat to faintly convex labial face is unornamented and has a smooth convexly curved apron. Cusps occur along the entire occlusal edge of the crown, becoming progressively larger towards the central cusp. The cusps are flattened and short, comprising less than one-third of the total height of the crown. A continuous cutting edge is present along the occlusal edge of all cusps. A large proportion of the teeth show some degree of wear of the cusps, and in some teeth these are almost completely worn away. A small swelling on the lingual face of the tooth at the base of the main cusp represents an incipient uvula. The root is low and small, comprising about half of the area of the lingual side of the tooth. Two oval or elongate root lobes are separated by a well-developed nutritive groove. The basal face of the root is flat, and overall the root forms an arc, which is convex towards the cusps. A large foramen is present within the nutritive groove, whilst one or more pairs of foramina may be present on the basal face of the root.

EXPLANATION OF PLATE 4

Figs 1–12. *Proheterodontus sylvestris* gen. et sp. nov. 1–6, 9–12 from bioclastic limestone, Forest Marble Formation, Watton Cliff. 1–3, P. 66068, holotype, anterior tooth. 1, labial view. 2, lateral view. 3, lingual view. 4, P. 66069, ?parasymphyseal tooth, labial view. 5–6, P. 66070, anterior tooth. 5, labial view. 6, lingual view. 7–8, P. 66071, White Limestone Formation, Bed 17, Woodeaton Quarry, juvenile lateral tooth. 7, labial view. 8, lingual view. 9, P. 66072, posterior tooth, labial view. 10, P. 66073, anterolateral tooth, labial view. 11–12, P. 66074, anterolateral tooth. 11, labial view. 12, lingual view; all ×30.

Fig. 13. *Paracestracion* sp., P. 66075, bioclastic limestone, Forest Marble Formation, Watton Cliff, labial view; ×30.



UNDERWOOD and WARD, *Paracestracion, Proheterodontus*

Remarks. These small teeth differ from anterior and juvenile lateral teeth of *P. falcifer* (Wagner, 1857) from the Upper Jurassic in being more gracile and having greater numbers of well-differentiated and shorter cusps. *P. sarstedtensis* (Thies, 1983) from the Lower and Middle Jurassic differs in possessing longer cusps and a narrower crown. A species of *Paracestracion* figured from the British Callovian (Thies 1983, pl. 8, fig. 2a–c) is similar to *P. bellis* sp. nov. but differs in possessing a proportionately larger main cusp and smaller lateral cusps.

The lack of molariform lateral teeth may be due to the complete absence of teeth of that morphology within this species. Alternatively *P. bellis* could have shown age segregation, whereby different age classes lived within different palaeoenvironments, with only immature individuals being present at the sites sampled. It seems unlikely that age segregation was the cause for the lack of recorded molariform teeth, as pectinate teeth of a wide variety of sizes were collected from a range of beds reflecting a variety of palaeoenvironments. It has been noted that molariform teeth are only present within the largest specimens of *P. falcifer* (Schweizer, 1964), and that isolated molariform teeth are rare in tooth assemblages (Underwood 2002). It is, therefore, possible that molariform teeth first appeared in mature individuals of *Paracestracion* (possibly within later species such as *P. falcifer*), becoming progressively present within younger individuals by a process of peramorphosis until molariform teeth were present within juvenile or immature individuals (as in extant species of *Heterodontus*).

Occurrence and palaeoecology. Teeth of *P. bellis* sp. nov. were recorded, albeit typically in rather low numbers, within many of the palaeoenvironments represented, from open marine shelf to lagoon (Underwood and Ward in press). It is, however, only within fully marine lagoonal facies that this taxon is relatively common.

It is likely that *P. bellis* represented a small benthic generalist which, although lacking a specialised crushing dentition, probably consumed large proportions of shelled food, as evidenced by the high degree of wear on many teeth.

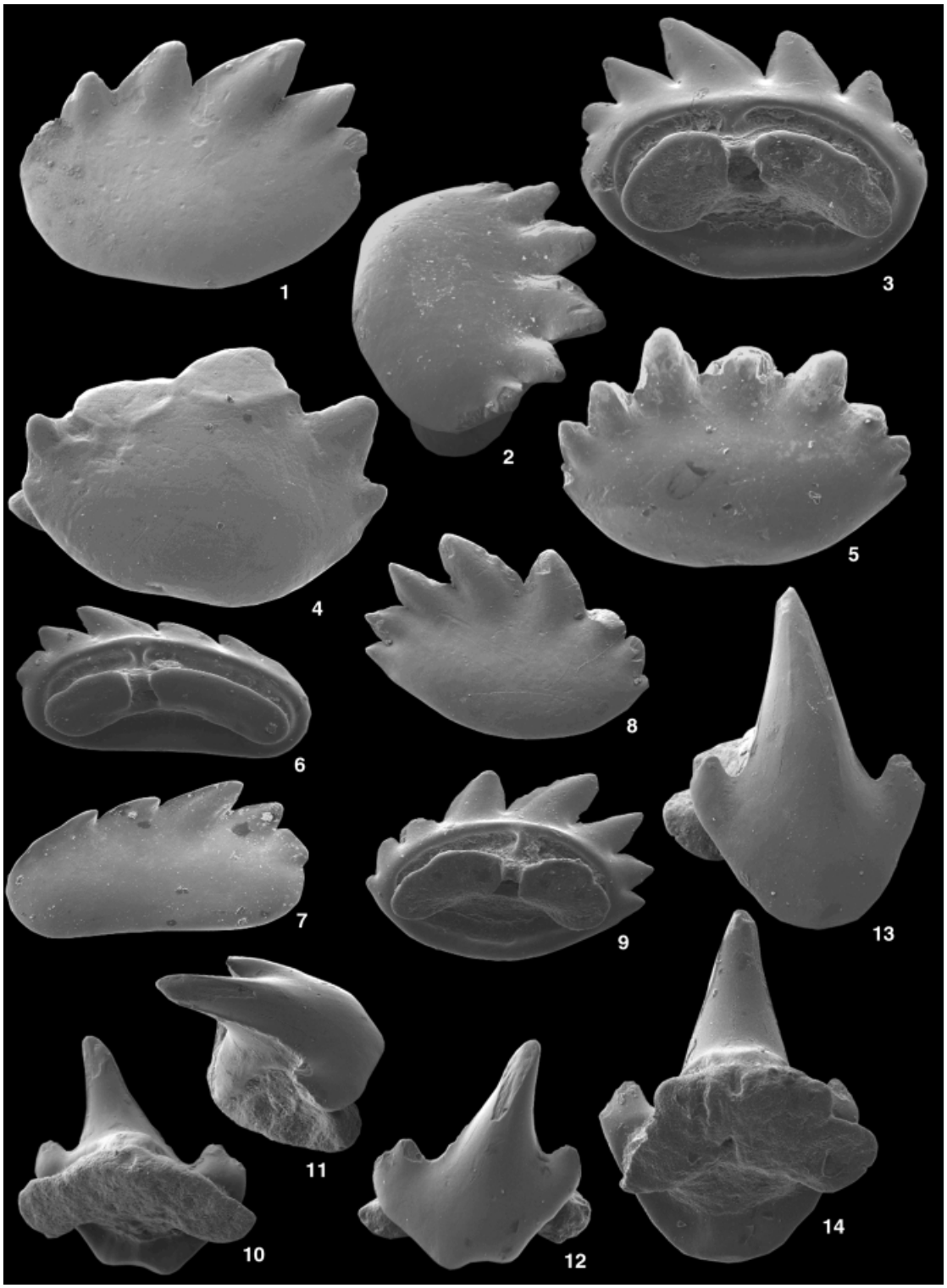
Order ORECTOLOBIFORMES Applegate, 1972
Incertae familiae

Remarks. Many of the orectolobiform genera encountered in the Jurassic and Cretaceous have relatively conservative tooth morphologies, which are not clearly assignable to any extant family. Furthermore, it is common for Mesozoic orectolobiforms to show degrees of ornamentation (Cappetta 1987) and heterodonty rare or unknown amongst extant taxa. Very few orectolobiform taxa are known from complete skeletons, one exception being *Phorcynus* Thiolliere, 1854, which is known from several extremely well-preserved specimens. *Phorcynus catulina* Thiolliere, 1854 shows a range of morphological characters not seen in any single extant orectolobid family (for example, a body shape and facial flanges similar to the modern *Orectolobus* Bonaparte, 1834, but a tooth morphology more similar to members of the Hemiscylliidae Gill, 1862). *Phorcynus* therefore cannot readily be included in any extant orectolobid family, suggesting that at least one extinct orectolobid family was present within the Jurassic. Although it is possible to distinguish several distinct tooth morphotypes of Jurassic orectolobids, which probably relate to families, it is here considered that designating these to specific families is premature until more complete skeletal material is discovered.

EXPLANATION OF PLATE 5

Figs 1–9. *Paracestracion bellis* sp. nov., all from White Limestone Formation, Bed 1, Woodeaton Quarry. 1–3, P. 66076, holotype, anterolateral tooth. 1, labial view. 2, lateral view. 3, lingual view. 4, P. 66077, worn anterior tooth, labial view. 5, P. 66078, anterior tooth, labial view. 6–7, P. 66079, lateral tooth. 6, lingual view. 7, labial view. 8–9, P. 66080, anterolateral tooth. 8, labial view. 9, lingual view; all ×60.

Figs 10–14. *Palaeobrachaelurus mussetti* sp. nov., 10–12, P. 66081, holotype, oyster-belemnite bed, Frome, Clay Formation, Watton Cliff, lateral tooth. 10, lingual view. 11, lateral view. 12, labial view. 13–14, P. 66082, Cranmore, anterior tooth. 13, labial view. 14, lingual view; all ×60.



UNDERWOOD and WARD, *Palaeobrachaelurus, Paracestracion*

Genus PALAEOBRACHAELURUS Thies, 1983

Type species. *Palaeobrachaelurus bedfordensis* Thies, 1983, from the Callovian of central England.

Palaeobrachaelurus mussetti sp. nov.

Plate 5, figures 10–14

In press *Palaeobrachaelurus* sp., Underwood and Ward, fig. 4D.

Derivation of name. After Frances Mussett, part of the UCL team who first investigated the vertebrate fauna of the Bathonian at Watton Cliff.

Holotype. BMNH P. 66081.

Material. Eleven moderately- to well-preserved teeth including BMNH P. 66082.

Diagnosis. Little apparent heterodonty. Crown higher than wide with a main cusp at least half the height of the crown. Single pair of short and rounded lateral cusps at base of main cusp project slightly laterally. Cusps and labial face of crown unornamented and somewhat convex. Labio-basal edge of crown smoothly convex or with concave indentation but no defined labial protuberance. Uvula present at the base of the main cusp, being wide but flat and poorly differentiated. Hemiaulacorhize root moderately high and as wide as crown. Basal face of root flat and arcuate. Lingual and labio-basal foramina well developed, with pair of large and several small foramina on root lingual face.

Description. These small teeth are less than 1 mm high. The crown is considerably higher than wide within both presumed anterior and lateral teeth. The upper half of the crown comprises a conical main cusp, which is round to slightly flattened in cross section. This is typically unornamented, although a single, very weak longitudinal ridge was seen on one tooth. The main cusp is slightly curved lingually in anterior teeth, and angled slightly to the posterior in lateral teeth. The main cusp is flanked by a single pair of small lateral cusps, which lack a pointed apex. A weak but continuous cutting edge is present over all cusps. The labial face of the crown is faintly convex and unornamented. The labio-basal edge of the crown tapers from the base of the lateral cusps and has either a smooth, near-semicircular profile or a small concave indentation. The crown overhangs the root labially, with the lateral cusps not being directly attached to the upper edge of the root lobes. A wide but flat area of enameloid below the main cusp marks the position of a poorly differentiated uvula. The root is moderately high and of a similar width to the crown. The basal face of the root is flat and gently curved. Well-developed foramina are present at the lingual apex of the root and at the junction of the root lobes. Other foramina are not clear, although at least one pair of large foramina is present on the lingual face of the root.

Remarks. These teeth somewhat resemble those of *P. aperizostus* Thies, 1983 from the Early Jurassic, but differ in having a narrower crown, considerably better developed lower region of the crown and a wider uvula. Teeth of *P. bedfordensis* Thies, 1983 from the Callovian and *P. roklumensis* (Thies, 1981) from the Barremian differ in having well-developed lateral blades housing the lateral cusps and a clearly differentiated labial protuberance.

Occurrence. Teeth of this species are rare and only known from open marine mudstone facies, being present both at Watton Cliff and Burton Bradstock, Dorset.

Genus HETEROPHORCYNUS gen. nov.

Derivation of name. From the general resemblance to the teeth of *Phorcynus* Thiolliere, 1854, but with a far more heterodont dentition.

Type species. *Heterophorcynus microdon* gen. et sp. nov., from the Bathonian of southern England (by monotypy).

Diagnosis. Strongly heterodont. Anterior teeth greatly elongated, moderately high and almost symmetrical. Prominent main cusp with minute or incipient lateral cusplets. Hemiaulacorhize root as narrow as crown with short root lobes, basal face flat with somewhat 'heart-shaped' profile. Lateral teeth smaller and nearly symmetrical to somewhat asymmetrical. Relatively short main cusp flanked by one pair of prominent but short cusplets. A second pair of cusplets may be present. Root moderately high with U-shaped basal face. Intermediate tooth morphologies present. Crown of all teeth has flat or slightly convex labial face with no ornament. Crown has no differentiated labial protuberance and overhangs the root labially and laterally. Uvula of all teeth narrow and poorly differentiated. Main lingual and labial foramina very well developed, with at least one pair of obvious foramina on lateral faces of root.

Discussion. The teeth of *Heterophorcynus microdon* gen. et sp. nov. show a diversity of morphologies suggesting a degree of heterodonty unknown within other orectolobids. It is evident, however, that all teeth are derived from a single taxon as intermediate forms are present and similar ratios of the different tooth morphologies are present within all samples where these teeth are present. The different tooth morphologies are reminiscent of several different orectolobid families. Anterior teeth are not dissimilar to teeth of members of the Parascylliidae Gill, 1862 (see Herman *et al.* 1992), differing largely in the greater degree of labial overhang of the crown. Anterolateral teeth are very similar to those extracted from *Phorcynus* Thiolliere, 1854 (see Cappetta 1987; Leidner and Thies 1999). Lateral teeth appear typical of members of the Hemiscylliidae Gill, 1862. The taxonomic position of *Heterophorcynus* gen. nov. is, therefore, uncertain, but it may be closely related to *Phorcynus*, probably within an as yet undescribed family.

Heterophorcynus microdon gen. et sp. nov.

Plate 6, figures 1–11

1982 Type 2(a) teeth, Young, fig. 2A–D.
In press Orectolobid sp. 1, Underwood and Ward, fig. 4G–I.

Derivation of name. From the very small size of the teeth.

Holotype. BMNH P. 66083.

Material. Two hundred and forty teeth, the majority lateral teeth with lesser numbers of anterior teeth including BMNH P. 66084–66087.

Diagnosis. As for genus.

Description. Teeth small, typically less than 1 mm high. Narrower anterior teeth far less common than lower lateral teeth suggesting only a small number of files of narrow teeth were present. Anterior teeth have a high crown, up to two and a half times as high as wide. About half of this is composed of a triangular main cusp. At the base of this is a single pair of very small to incipient lateral cusplets, typically forming little more than a slight swelling on the side of the tooth. A faint cutting edge is present, but does not extent to the tip of the main cusp. The crown apron may be smoothly curved or have a small central indent. The labial face of the crown is unornamented and slightly convex. The crown overhangs the root, which is somewhat displaced lingually. A narrow and low enameloid covered uvula is present at the base of the main cusp. The root is relatively high, massive, and a similar width to the crown. The basal face of the root is flat but not flared, with the root lobes being short and diverging at an acute angle. Large foramina are present at the lingual apex of the root and at the junction of the root lobes. At least one major and several minor pairs of foramina are present on the lateral faces of root. Anterolateral teeth are similarly high and fairly symmetrical, being somewhat wider than anterior teeth. One or two pairs of well-developed but short lateral cusplets are present. Lateral teeth are typically smaller than teeth from more anterior files. The crown is slightly higher than wide, with the main cusp being less than one-third of the total height of the crown and somewhat inclined posteriorly. One or two pairs of lateral cusplets are present; where two pairs are present these are typically sharply pointed but are usually blunt where only one pair is present. The root is higher and more gracile than in anterior teeth, with a curved basal face.

Occurrence and palaeoecology. Teeth of *Heterophorcynus microdon* gen. et sp. nov are present in many Bathonian facies, being recorded from many samples. It is generally present as only a very minor element of faunas, but from fully marine lagoonal facies it is frequently moderately common, although never the dominant selachian taxon. The generally clutching dentition (*sensu* Cappetta 1986) suggests that this species was a generalistic or opportunistic feeder consuming small food items. The lack of wear on most teeth suggests that shelled prey was rarely consumed.

Gen. et sp. indet.

Plate 6, figures 12–15

In press Orectolobid sp. 3, Underwood and Ward, fig. 4M.

Material. Two incomplete teeth; BMNH P 66088–66089.

Description. Both teeth of this taxon are nearly symmetrical, with an oval crown, slightly wider than high. A slender cusp is up to a similar length to the height of the rest of the crown. A single pair of very small lateral cusplets are present. The labial face of the crown is slightly concave. On the larger teeth this is ornamented with several short, sinuous longitudinal ridges. A single, very weak ridge is present on the smaller tooth. A very poorly developed uvula is little more than a slight swelling on the lingual face of the crown. The crown overhangs the root on all sides. The root is low and about as wide as the crown. The basal face is flat and somewhat flared. A narrow nutritive groove is present.

Remarks. Although the crown morphology is not unlike that of members of the Hemiscylliidae, the oval crown and poor uvula differentiate this taxon from any described genus. A holoaulacorhize root is rare within orectolobids, but present with several unrelated genera. Although this root vascularisation is a character more typical of *Paracestracion* and '*Agaleus*-like galeids', the crown morphology suggests that an orectolobid affinity is more likely.

Occurrence. This rare taxon was only recorded within open marine mudstones at Watton Cliff.

Genus DORSETOSCYLLIUM gen. nov.

Derivation of name. From the occurrence of the genus in Dorset.

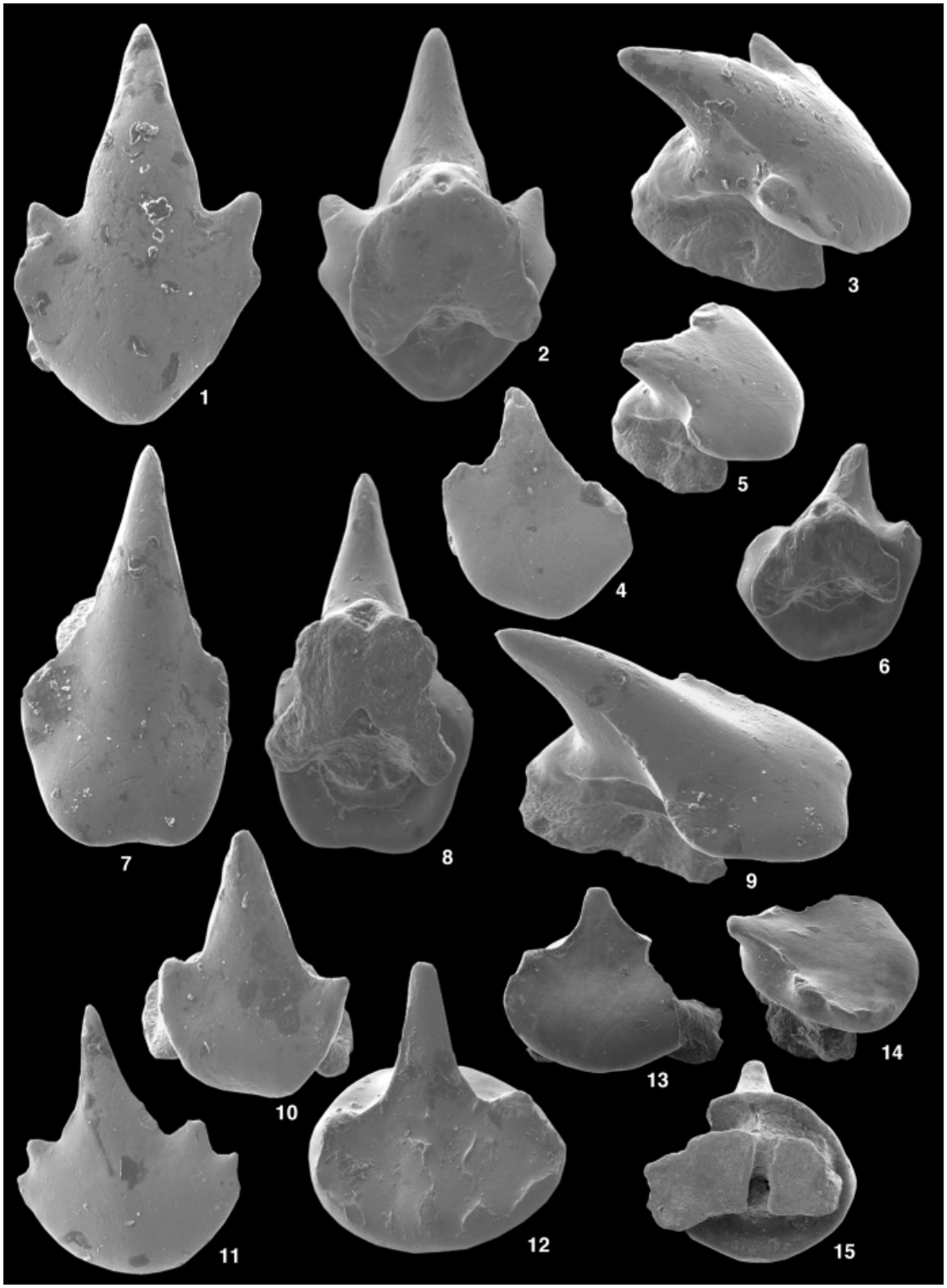
Type species. *Dorsetoscyllium terreafullonicum* gen. et sp. nov., from the Bathonian of southern England (by monotypy).

Diagnosis. Moderately heterodont. Crown of anterior teeth symmetrical, at least one and a half times as high as wide. Main cusp about half total height of tooth, with base at least half total width of crown. Distinct crown shoulders not differentiated into cusplets. Labial face unornamented with concavity at base of cusp. Crown apron semicircular without labial protuberance. Crown of anterolateral teeth narrower and asymmetrical, with cusp inclined posteriorly. The crown shoulder only well developed on the posterior side of tooth and concavity on labial face faint or absent. Crown of posterolateral teeth similar to anterolateral but wider and shorter. Root of all teeth hemiaulacorhize and similar width to crown. Root lobes meet at obtuse angle. Narrow but well-defined uvula present.

EXPLANATION OF PLATE 6

Figs 1–11. *Heterophorcynus microdon* gen. et sp. nov., all from Rutland Formation, Bed 7, Woodeaton Quarry. 1–3, P. 66083, holotype, anterolateral tooth. 1, labial view. 2, lingual view. 3, lateral view. 4–6, P. 66084, lateral tooth. 4, labial view. 5, lateral view. 6, lingual view. 7–9, P. 66085, parasymphyseal tooth. 7, labial view. 8, lingual view. 9, lateral view. 10, P. 66086, anterior tooth, labial view. 11, P. 66087, lateral tooth, labial view; all ×60.

Figs 12–15. Orectolobid gen. et sp. indet. 1, all from oyster-belemnite bed, Frome Clay Formation, Watton Cliff. 12, P. 66088, ?anterior tooth, labial view. 13–15, P. 66089, ?lateral tooth. 13, labial view. 14, lateral view. 15, lingual view; all ×60.



UNDERWOOD and WARD, *Heterophorcynus*, orectolobid

Remarks. These relatively robust teeth have an asymmetrical crown lacking well-defined lateral cusplets and a concave labial face, and do not closely resemble any described orectolobid. Anterior teeth have a strong superficial resemblance to teeth of the Cretaceous batoid *Squatirhina* Casier, 1947, but differ in possessing a hemiaulacorhize root.

Dorsetoscyllium terraefullonicum gen. et sp. nov.

Plate 7, figures 1–13

In press Orectolobid sp. 2, Underwood and Ward, fig. 4J–L.

Derivation of name. From the exclusive recorded occurrence of the taxon in the Fullers Earth.

Holotype. BMNH P. 66090.

Material. About 120 teeth, many broken or lacking root including BMNH P. 66091–66095.

Diagnosis. As for genus.

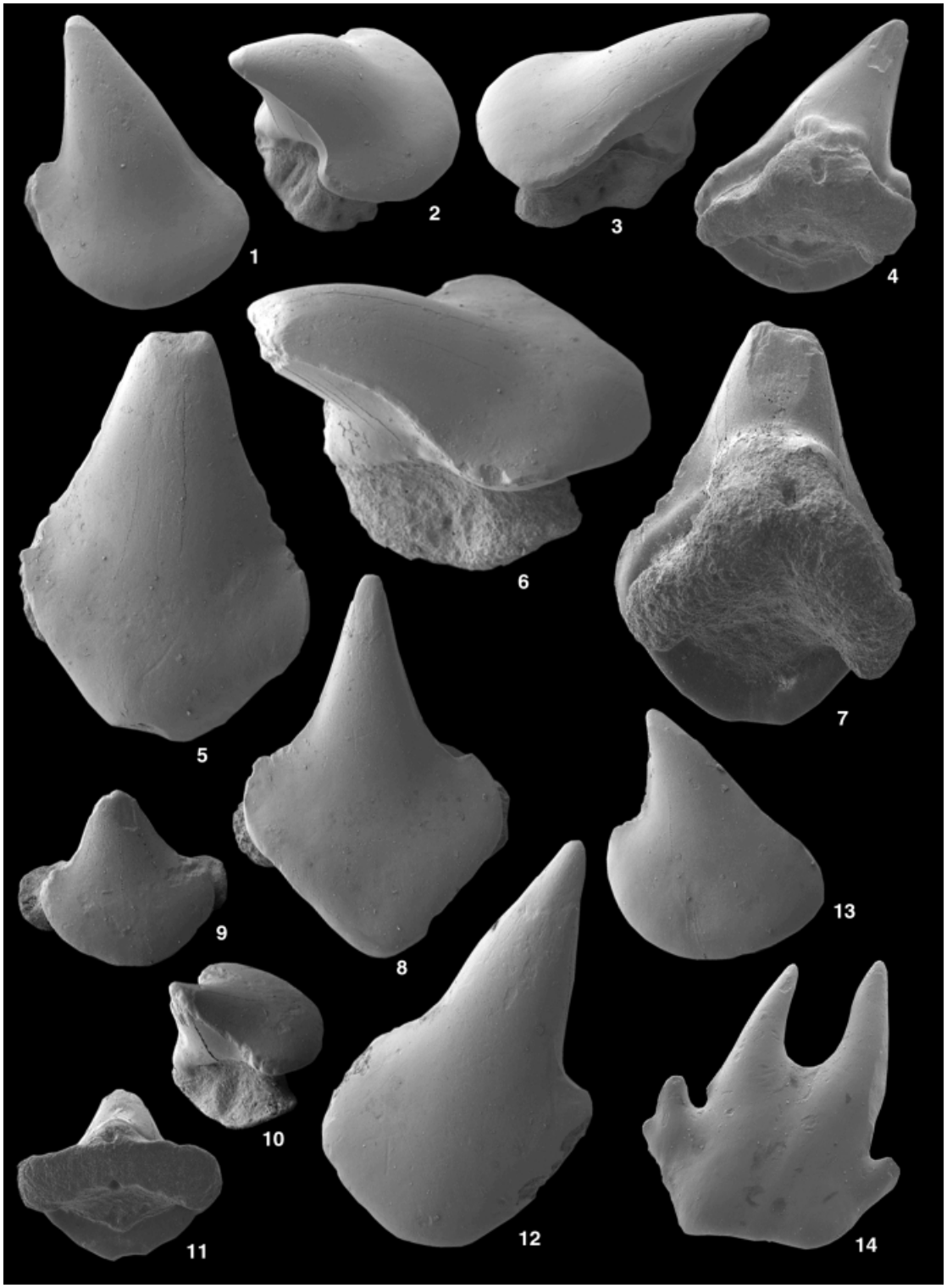
Description. These relatively robust teeth are up to 2·5 mm high. Anterior teeth are symmetrical, with an erect main cusp that is only slightly compressed in cross section. At the base of the cusp are prominent crown shoulders marking the position of incipient lateral cusplets. A faint but continuous cutting edge is present along the occlusal edge of the tooth. From the crown shoulders, the crown tapers to a smoothly rounded labio-basal edge with no labial protuberance. The labial face is unornamented and variably concave at the base of the cusp. A small swelling at the base of the lingual face of the cusp has an enameloid coating, forming a small but distinct uvula. The root is moderately high and bulky. Two faintly tapering root lobes meet at an angle of about 90 degrees. Anterolateral and lateral teeth are asymmetrical and narrower, with an elongate cusp inclined to the posterior. The crown shoulders are smaller than in anterior teeth, with the anterior crown shoulder greatly reduced, and the posterior forming a rounded incipient cusplet. The concavity on the labial face is less well developed than in anterior teeth. The roots of lateral teeth are essentially the same as in anterior teeth, if somewhat asymmetrical. The crowns of posterolateral teeth are shorter and wider than in other files, with a short but robust cusp flanked by well-developed crown shoulders. The root is rather lower than in other teeth, with the root lobes meeting at a very obtuse angle. Foramina are present at the lingual apex of the root and at the junction of the root lobes but are not particularly large. At least one major and several minor pairs of foramina are present on the lateral faces of root.

Occurrence and palaeoecology. *Dorsetoscyllium terraefullonicum* gen. et sp. nov. is a relatively abundant taxon in samples of offshore marine mudstones, with some smaller teeth also being recorded from open shelf carbonates. No teeth were recovered from shallow marine oolitic carbonates or lagoonal facies. It is thus evident that this orectolobid was restricted to offshore environments. Some anterior teeth show considerable wear, although wear is typically absent from other teeth, suggesting that although some shelled food items were taken, *D. terraefullonicum* did not feed by frequent crushing of shelled prey.

EXPLANATION OF PLATE 7

Figs 1–13. *Dorsetoscyllium terraefullonicum* gen. et sp. nov., all from oyster-belemnite bed, Frome Clay Formation, Watton Cliff. 1–4, P. 66090, holotype, anterolateral tooth. 1, labial view. 2, posterior view. 3, anterior view. 4, lingual view. 5–7, P. 66091, anterior tooth. 5, labial view. 6, lateral view. 7, lingual view. 8, P. 66092, anterior tooth, labial view. 9–11, P. 66094, posterolateral tooth. 9, labial view. 10, lateral view. 11, lingual view. 12, P. 66095, anterolateral tooth, labial view. 13, P. 66093, lateral tooth, labial view; all ×30.

Fig. 14. Orectolobid gen. et sp. indet. 2, P. 66096, oyster-belemnite bed, Frome Clay Formation, Watton Cliff, labial view; ×42.



UNDERWOOD and WARD, *Dorsetoscyllium*, orectolobid

Gen. et sp. indet.

Plate 7, figure 14

Material. One tooth crown; BMNH P. 66096.

Description. The single crown is asymmetrical and higher than wide. There are two similar-sized main cusps, which are somewhat inclined posteriorly. A pair of small lateral cusplets is present, with an additional incipient cusplet on the anterior edge. The labial face is unornamented and slightly convex. The crown apron is straight.

Remarks. The single tooth may well be pathological, with twin main cusps. It is, however, unclear to what taxon it may be aligned. It somewhat resembles *Palaeobrachaelurus burtonensis* but differs in being at least half again as large. It differs from the anterior teeth of *Dorsetoscyllium terraefullonicum* gen. et sp. nov. in possessing well-developed lateral cusplets and lacking the concave labial crown face. It therefore appears that although the tooth is probably pathological, its affinities are uncertain.

Occurrence. Only recorded from open marine mudstones at Watton Cliff.

Genus ORNATOSCYLLIUM gen. nov.

Derivation of name. From the highly ornate ornamentation of the teeth.

Type species. *Orectoloboides pattersoni* Thies, 1983, from the Callovian of southern England.

Diagnosis. Small heterodont teeth. Crown of anterior teeth about as high as wide, lateral teeth wider than high. Main cusp flanked by one or two pairs of lateral cusps, with all cusps pointed in anterior teeth, becoming lower and more rounded in lateral teeth; main cusp little more than a projection of the crown with no recognisable lateral cusplets in extreme posterolateral teeth. Crown ornamented with one or more longitudinal ridges, usually strong, on each cusp, becoming less prominent in more posterior teeth. Labial protuberance well developed in all but posterolateral teeth. Uvula well developed. Crown overhangs root labially and laterally. Root hemiaulacorhize with clearly separated large, lingual and labial foramina. Root massive, high, and wider than crown. Root lobes flared labially, with clearly angular termination.

Discussion. Teeth assigned here to *Ornatoscyllium* gen. nov. have been previously included in *Orectoloboides* Cappetta, 1977. There are, however a number of major differences between *Ornatoscyllium* and *Orectoloboides*. The crown of *Orectoloboides* does not overhang the root labially in either anterior or lateral teeth. The vascularisation on the basal face of the root of *Orectoloboides* is only partly covered over, resulting in the labio-basal foramen being within a distinct groove on the base of the root. In some teeth the vascularisation is completely unroofed, resulting in a holoaulacorhize state being present (see Cappetta 1977, pl. 1, fig. 2; Biddle 1993, pl. 1, fig. 7 and Werner 1989, pl. 9, fig. 2).

There are two species that should be referred to *Ornatoscyllium*: *Orectoloboides pattersoni* (Thies, 1983) from the English Callovian and *O. glashoffi* (Thies, 1981) from the German Barremian/Aptian, in addition to *Ornatoscyllium freemani* gen. et sp. nov. from the English Bathonian. An indeterminate species possibly referable to *Ornatoscyllium* has been figured from the German Aalenian by Thies (1989, fig. 4).

Two species are retained in *Orectoloboides*: *O. parvulus* (Dalinkevicius, 1935) from the north European Albian and *O. multistriatus* Werner, 1989 from the Cenomanian of Egypt.

Anterior teeth of *Ornatoscyllium* resemble teeth of *Annea* Thies, 1983, but differ in showing far greater degrees of heterodonty and a far more swollen labial protuberance.

Ornatoscyllium freemani gen. et sp. nov.

Plate 8, figures 1–11

In press aff. *Orectoloboides* sp., Underwood and Ward, fig. 4E–F.

Derivation of name. After Eric Freeman, who discovered several Bathonian microvertebrate sites.

Holotype. BMNH P. 66097.

Material. About 520 teeth, with both anterior and lateral teeth being abundant including BMNH P. 66098–66104.

Diagnosis. Crown about as wide as high in anterior teeth, wider than high in lateral teeth. Main cusp sharply pointed and makes up half of crown height in anterior teeth; rounded, compressed and proportionately smaller in lateral teeth. One relatively small pair of lateral cusplets present, with second pair of incipient cusplets in many teeth. Lateral cusplets low or absent in lateral teeth. Labial protuberance short and rounded, but as wide as base of main cusp. Single sharp-edged longitudinal ridge on labial face of main cusp of anterior teeth reaching neither apex nor labial protuberance. Ridge shorter in lateral teeth, but additional ridges may be present adjacent to lateral cusplets, with triangular swelling occasionally present on labial protuberance. Complete cutting edge present on occlusal edge. Uvula well developed, reaching almost to base of root. Root high and wider than crown, with strongly divergent root lobes. Ends of root lobes flared and sharply angled. Basal face of root flat. Large foramina at lingual apex of the root and at junction of the root lobes. Several pairs of foramina present on the lateral faces of root.

Description. These very small teeth are less than 1 mm high and form a heterodont assemblage, with relatively similar numbers of anterior and lateral tooth morphologies. The crown of anterior teeth comprises a robust main cusp making up at least half of the height and one-third of the width of the crown, flanked by one or two pairs of small lateral cusplets. The sharply pointed main cusp is only slightly compressed, whilst the lateral cusplets are more strongly compressed and less sharply pointed. A small but continuous cutting edge is present along the entire occlusal edge of the tooth. A rounded labial protuberance, almost equal in width to the base of the main cusp, is present but does not project far labio-basally. The labial face of the crown is gently convex and ornamented by one or more strong, sharp-edged, longitudinal ridges. A ridge bisecting the main cusp typically reaches neither the cusp apex nor labio-basal margin. Other, weaker, ridges may be present on the lateral cusplets. The lingual faces of the cusps are unornamented. The crown of lateral teeth differs from that of anterior teeth in being far lower and wider. The main cusp is proportionately lower, more compressed and with a rounded profile. Lateral cusplets are likewise lower, becoming incipient or absent in posterolateral teeth. Labial ornament comprises a strong longitudinal ridge below the main cusp, which passes into a triangular raised region on the labial protuberance on some teeth. One or more pairs of ridges below the lateral cusplets are common. The root of all teeth is similar. It is high and relatively massive for the size of the tooth. It is wider than the crown in all teeth, with the ends of the root lobes extending further labially than the crown. The root lobes meet at an angle of over 90 degrees, giving a wide V-shape to the root when viewed basally. The ends of the root lobes are flared and commonly have a sharply angled labial termination. A very prominent enameloid-covered uvula is present at the base of the main cusp, being about as wide as the cusp and extending nearly to the base of the root. Very well-developed circular foramina are present at the lingual apex of the root and at the junction of the root lobes. At least one well-developed pair of foramina are present on the lateral faces of the root immediately below the base of the crown enameloid. Small irregularly spaced foramina are typically present on the basal face of the root.

Remarks. Lateral teeth of this taxon resemble teeth of *O. pattersoni* (Thies, 1983), differing in the possession of a weaker and more widely spaced ornament and a wider and smoother labial protuberance.

Occurrence and palaeoecology. Teeth of *Ornatoscyllium freemani* gen. et sp. nov. are abundant in a black, laminated offshore mudstone at Watton Cliff, Dorset, with rare teeth also being recovered from open marine shelly marls. No remains of this taxon were found in shallow marine or lagoonal facies. It therefore appears to have been restricted to offshore muddy substrates, facies almost identical to those from which *O. pattersoni* has been collected (Martill 1991). The very small teeth rarely show significant wear and suggest that they formed a clutching dentition, presumably within a very small shark.

Superorder SQUALEA Shirai, 1996
Order HEXANCHIFORMES *sensu* Compagno 1973
Incertae familiae

Genus PARANOTIDANUS Ward and Thies, 1987

Type species. *Notidanus serratus* Fraas, 1885

Remarks. This genus was erected to include two species differing from teeth of *Notidanoides* in the possession of mesial cusplets attached to the main cusp. No type species was designated, and so the genus was rejected by *Cappetta* (1990). As this situation leaves two species unassigned to genera, it is here considered that the type species should be considered the first listed by Ward and Thies (1987) (*Notidanus serratus* Fraas, 1885). It has also been argued by Cappetta (1990) that no generic diagnosis exists. It is here considered that the phrase in Ward and Thies (1987, p. 93) 'species differ from *Notidanoides* in having serrations on the base of the mesial cutting edge of the principal cusp' constitutes a (brief) generic diagnosis.

?*Paranotidanus* sp.

Plate 8, figures 12–13

In press aff. *Notidanoides* sp., Underwood and Ward, fig. 4C.

Material. Five fragmentary teeth lacking root including BMNH P.66105.

Description. Incomplete teeth are up to about 4 mm wide. The largest and most complete tooth has a moderately compressed main cusp that is somewhat inclined to the posterior. This is more than twice as high as wide, and has a faintly convex anterior edge and concave posterior edge. At least three smaller posterior cusplets are present, all being much smaller than the main cusp and becoming progressively smaller posteriorly. A notch at the anterior end of one tooth suggests that at least one anterior cusplet is present as a large serration near the base of the main cusp. Both faces of the crown are convex, the convexity being greater on the lingual face. No ornament is present. The root is unknown.

Order SYNECHODONTIFORMES Duffin and Ward, 1993
Family PSEUDONOTIDANIDAE fam. nov.

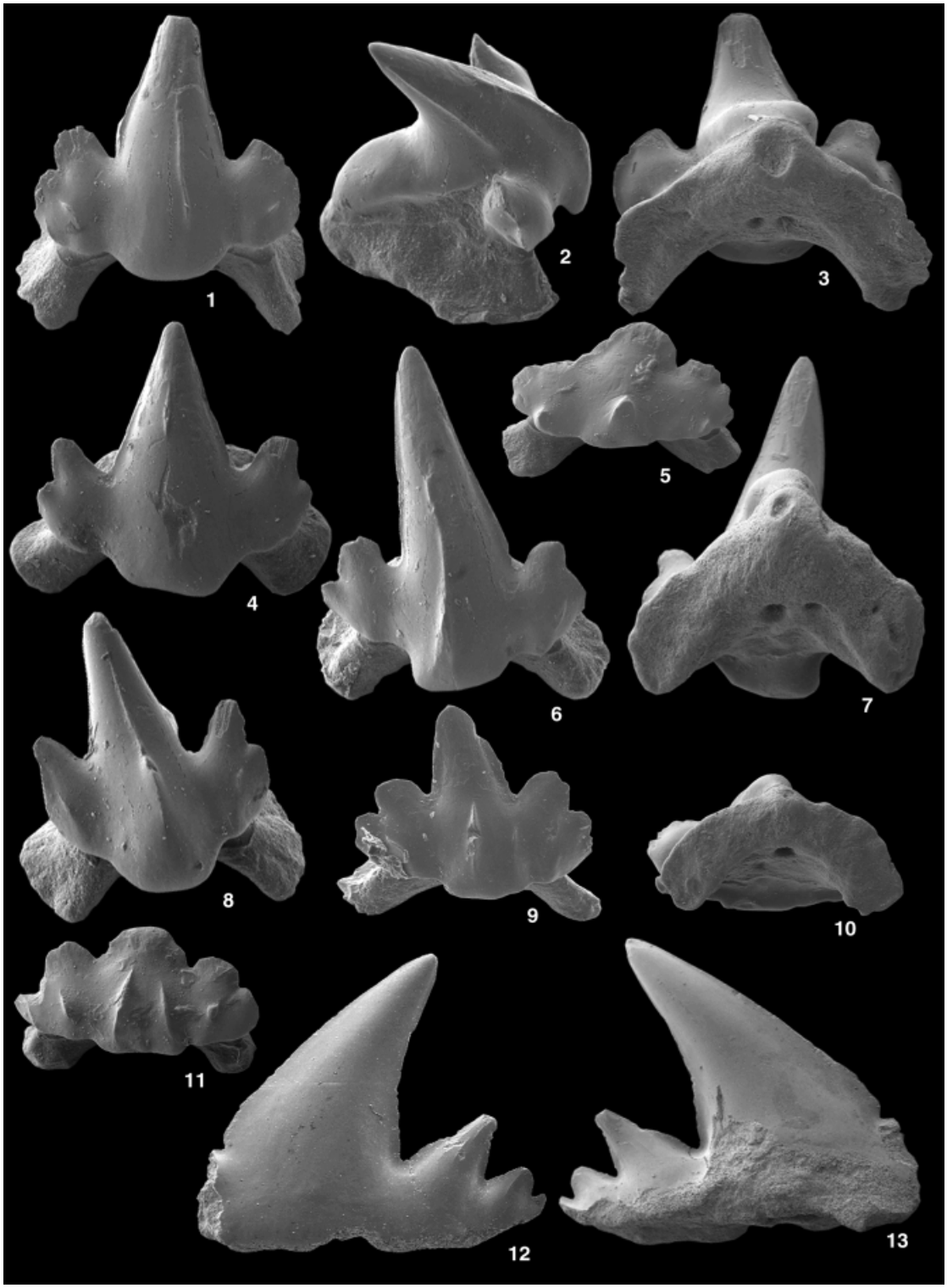
Derivation of name. From the superficial resemblance of teeth to those of '*Notidanus*', a genus to which many hexanchids have historically been referred.

Diagnosis. [Based largely on *Pseudonotidanus politus* (Thies, 1992)]. Vertebral column of about 130 amphicoelous, asterospondylous vertebrae. A small, curved, smooth fin spine is present at about the position of the eightieth vertebra. Meckel's cartilage relatively narrow and blade-like, with smoothly rounded symphyseal region. Little dignathic heterodonty but strong monognathic heterodonty. Cusps compressed, not curved lingually and with little or no ornamentation. Crown does not overhang root.

EXPLANATION OF PLATE 8

Figs 1–11. *Ornatoscyllium freemani* gen. et sp. nov., all from oyster-belemnite bed, Frome Clay Formation, Watton Cliff. 1–3, P. 66097, holotype, anterior tooth. 1, labial view. 2, lateral view. 3, lingual view. 4, P. 66098, anterior tooth, labial view. 5, 66099, posterolateral tooth, labial view. 6–7, P. 66100, ?parasymphyseal tooth. 6, labial view. 7, lingual view. 8, P. 66101, anterolateral tooth, labial view. 9, P. 66102, lateral tooth, labial view. 10, P. 66103, posterolateral tooth, lingual view. 11, P. 66104, posterolateral tooth, labial view; all ×60.

Figs 12–13. ?*Paranotidanus* sp., P. 66105, oyster-belemnite bed, Frome Clay Formation, Watton Cliff. 12, labial view. 13, lingual view; ×15.



UNDERWOOD and WARD, *Ornatoscyllium,* ?*Paranotidanus*

Lower symphyseal tooth large and symmetrical. Anterior and anterolateral teeth strongly asymmetrical, with main cusp and several posterior cusplets inclined to posterior. Crowns of posterior teeth low, long, without cusps but with occlusal ridge. Root anaulacorhize with foramina on labial face within irregular vertical folds. Root expanded lingually, with basal face normal to cusps.

Included taxa. Two genera may currently be referred to the Pseudonotidanidae: (1) *Welcommia* Cappetta, 1990, containing two named taxa, *W. terencei* Delsate and Godefroit, 1994 from the Toarcian of Belgium and *W. bodeuri* Cappetta, 1990 from the Valanginian of southern France. An unnamed species is present in the Oxfordian of southern France (Cappetta 1990). (2) *Pseudonotidanus* gen. nov., containing two species, *P. politus* (Thies, 1992) from the Toarcian of Germany and *P. semirugosus* gen. et sp. nov. from the Bathonian and Callovian of southern England.

Remarks. Teeth of this family contain features of both hexanchids (shape of the crown) and palaespinacids (lingually expanded, flat-based root). This combination of features was first recognised within W. *bodeuri*, which, although included within the suborder Hexanchoidea Garman 1913 by Cappetta (1990), was considered by Duffin and Ward (1993) to be close to the Palaeospinacidae. This combination of dental characters was also recognised within *P. politus* (Thies, 1992). This was originally described as a species of *Palaeospinax*, with it being subsequently recognised that the teeth are very similar to those of *Welcommia* (Delsate and Godefroit, 1994). Teeth differ significantly from the type material of *Welcommia* only in the possession of numerous anterior cusplets. Although possessing hexanchid-like teeth, the skeleton of *P. politus* differs from that of hexanchids in the possession of at least one fin spine. This skeleton therefore links *Welcommia*-like teeth with a palaeospinacid (spinose) posterior dorsal fin. It is unknown whether the anterior dorsal fin was absent, as in hexanchids, whether an anterior dorsal fin was present but bore no fin spine or whether the anterior dorsal fin spine has been lost through taphonomic processes. The presence of species containing features intermediate between these hexanchids and palaeospinacids appears to show a close relationship between these groups (as in Ward and Thies 1987). The Pseudonotidanidae is here provisionally included within the Synechodontiformes due to the possession of a greater number of typical 'palaeospinacid' features. It is, however, acknowledged that this position may well change if cladistic analysis is undertaken, where the Pseudonotidanidae (and Synechodontiformes) may prove to be paraphyletic.

Genus PSEUDONOTIDANUS gen. nov.

Derivation of name. As for family.

Type species. *Palaeospinax politus* Thies, 1992, from the Toarcian of Germany.

Diagnosis (based on dental material). Strong monognathic heterodonty. Cusps compressed, not curved lingually and with little or no ornamentation. Crown does not overhang root. Anterior and anterolateral teeth strongly asymmetrical. Lower symphyseal tooth large and symmetrical. Main cusp triangular to faintly sigmoidal and inclined posteriorly. Numerous anterior and posterior cusplets, all considerably shorter than main cusp, with anterior cusplets not fused to main cusp to form mesial serrations. Well-developed cutting edge is continuous along the occlusal edge. Root anaulacorhize and moderately high. Labial face of root with numerous irregularly spaced, vertical folds containing foramina, verging on the pseudopolyaulacorhize state of Cappetta (1987). Root expanded lingually to form robust shelf. Basal face of root flat, at right angles to crown and of similar width to root height.

Pseudonotidanus semirugosus gen. et sp. nov.

Plate 9, figures 1–7; Plate 10, figures 1–2

1991 *Notidanus muensteri* Agassiz; Martill, pl. 38, fig. 4.
In press aff. *Welcommia* sp., Underwood and Ward, fig. 3B–D.

Derivation of name. From the restricted rugose ornament at the base of the crown.

Holotype. BMNH P. 66106.

Material. One complete adult lateral tooth and four fragmentary juvenile teeth including BMNH P. 66108. Two additional teeth in NHM collection, BMNH P. 12524a, b.

Diagnosis. Teeth large, up to 20 mm in width. Crown with high main cusp, at least one and a half times as high as wide, inclined posteriorly with convex mesial edge. Numerous small cusplets anterior and posterior of main cusp, which is centrally placed in most teeth. Cusplets increase in size towards main cusp, the posterior cusplets larger than anterior ones. Enameloid covering of upper part of labial root face as high as cusplets. Basal edge of enameloid straight. Ornament of numerous, short vertical folds along base of enameloid on both lingual and labial faces. Labial face of root rectangular with numerous pseudopolyaulacorhize folds. Lingual face of root swollen, especially in mid region, with several large foramina. Basal face at right angle to cusps, flat and with numerous fine grooves.

Description. The teeth of this taxon are robust and wider than high. The small number of complete teeth (three) does not allow heterodonty to be clearly assessed, although it appears to be largely monognathic. The main cusp is somewhat inclined to the posterior, even in anterior teeth. This is at least twice as high as wide and moderately compressed. The anterior edge of the main cusp is convex to subtly sigmoidal; the distal edge is straight to convex. In lateral teeth, the main cusp is close to the centre of the tooth, with small cusplets both anterior and posterior of the main cusp. Both smaller anterior and larger posterior cusplets become progressively larger towards the main cusp, but all remain less than half of its height. All cusplets have a weakly convex labial face and a more strongly convex lingual face, the faces being separated by a well-defined cutting edge. Cusps are somewhat fused basally, with an enameloid apron extending over at least one-third of the root labially, and a similar amount lingually except immediately below the main cusp. The crown does not overhang the root lingually or labially. A narrow band of ornament is present along the base of the enameloid on both labial and lingual faces except immediately below the main cups on the lingual face. This ornament comprises many fine vertical ridges, which are somewhat irregular. The root is massive and rectangular, with the base of the root on the labial face being parallel with the base of the enameloid. Pseudopolyaulacorhize folds are irregularly spaced on the labial root face. These are narrow and concentrated in the central part of the tooth. The basal face of the root is flat and covered with fine labio-lingual striations, but no large foramina. The lingual face of the root is swollen, especially in the central part of the teeth, to form a convex shelf, the top of which lies below the base of the enameloid. Several large and irregularly spaced foramina are present along the most lingually expanded part of the root.

Remarks. The teeth of *Pseudonotidanus semirugosus* gen. et sp. nov. differ from those of *P. politus* in having a more robust main cusp, fewer anterior cusplets and a well-defined band of ornament at the base of the enameloid apron.

Occurrence and palaeoecology. This rare species was recovered both from the shelly offshore marls of the Wattonensis Beds (holotype) and shelly black mudstone (juveniles) at Watton Cliff. Offshore mudstone facies are also present within the Oxford Clay Formation from which additional specimens have been recovered. The teeth of *P. semirugosus* are the largest from any known Bathonian neoselachian, and are of similar dimensions to those of the largest known Middle Jurassic hybodonts (with which it co-occurs). The form of the teeth suggest a predatory lifestyle, possibly not dissimilar to that of extant hexanchids such as *Notorynchus* Ayres, 1855, and *P. semirugosus* may have similarly been a slow moving generalist predator.

Family PALAEOSPINACIDAE Regan, 1906

Genus SYNECHODUS Woodward, 1888

Type species. *Hybodus dubrisiensis* Mackie, 1863, from the Upper Cretaceous of southern England.

Remarks. The recognition of the genera *Palaeospinax* Egerton, 1872 and *Synechodus* Woodward, 1888 on dental remains has been the subject of some confusion (e.g. Cappetta 1987, 1992), with most teeth from the Jurassic being referred to *Palaeospinax* and those from the Cretaceous and Palaeogene to *Synechodus*. Duffin and Ward (1993) demonstrated that the dentition of these genera was inseparable, and the paratype

material of *Palaeospinax* was referred to *Synechodus* (the holotype being considered *nomen dubium*). However, it has been stated that *Palaeospinax* has cyclospondylic vertebrae, in contrast to asterospondylic vertebrae in *Synechodus* (Woodward 1889; Cappetta 1987). The vertebrae of most specimens assigned to *Palaeospinax* are partly concealed by sediment and consolidant, and are thus not clear; clearly asterospondylic vertebrae are, however, visible on both of the palaeospinacid taxa known from the type locality of the genus (see Duffin and Ward 1993, pls 2, 12). It has also been stated that fin spines are absent in *Synechodus* (e.g. Maisey 1985). Although no figured specimens of *Synechodus dubrisiensis* (Mackie 1863) have associated fine spines, only one (BM49032) possesses just enough vertebral material to reach the attachment point of a fin spine if one were present. An as yet unfigured specimen of *S. dubrisiensis* in the collection of the British Geological Survey (BGS 1480) does, however, appear to preserve a partial smooth fin spine, although as the specimen is preserved in three parts it is unclear whether this represents an anterior or posterior spine. There appear, therefore, to be no generic-scale differences between taxa referred to *Palaeospinax* and *Synechodus* and the synonymy is supported.

Synechodus levis (Woodward, 1889)

Plate 9, figures 9–11

1889 *Hybodus levis* Woodward, pl. 11, figs 5–7.

Material. A number of specimens in the NHM collection including BMNH P. 33474 (holotype).

Description. The teeth of this species are robust and relatively large, to over 1 cm in width. All teeth are almost symmetrical, with a central main cusp. The crown of anterior teeth has a robust and erect main cusp, which is about one and a half times as high as wide. One or more pairs of squat lateral cusplets are present, with the second and subsequent pairs, if present, being very small. The cusps have a somewhat flat labial face and a strongly convex lingual face with a weak cutting edge. Ornament may be absent or restricted to faint wrinkles near the base of the lateral parts of the crown. The crown strongly overhangs the root labially. The labial face of the root has very strong pseudopolyaulacorhize folding, which is quite evenly spaced. Anterolateral teeth have a lower main cusp, which is somewhat swollen at the base and faintly inclined to the posterior, and up to two pairs of squat lateral cusplets. An ornament of fine longitudinal ridges is present along the base of the labial face of the crown. The lingual face of the crown is bulbous and swollen with several prominent foramina. Lateral teeth are lower, with a short conical main cusp, and up to three pairs of short to incipient lateral cusplets. A closely spaced ornament of fine longitudinal ridges covers the labial face of the crown with the exception of the main cusp. Folding on the labial face of the root appears to be irregular. The occlusal face is wide and narrow, with a faint sigmoidal curvature. A strong ridge bisects the occlusal face, separating a moderately coarse reticulate ornament on the labial side from a similar but much finer ornament on the lingual side.

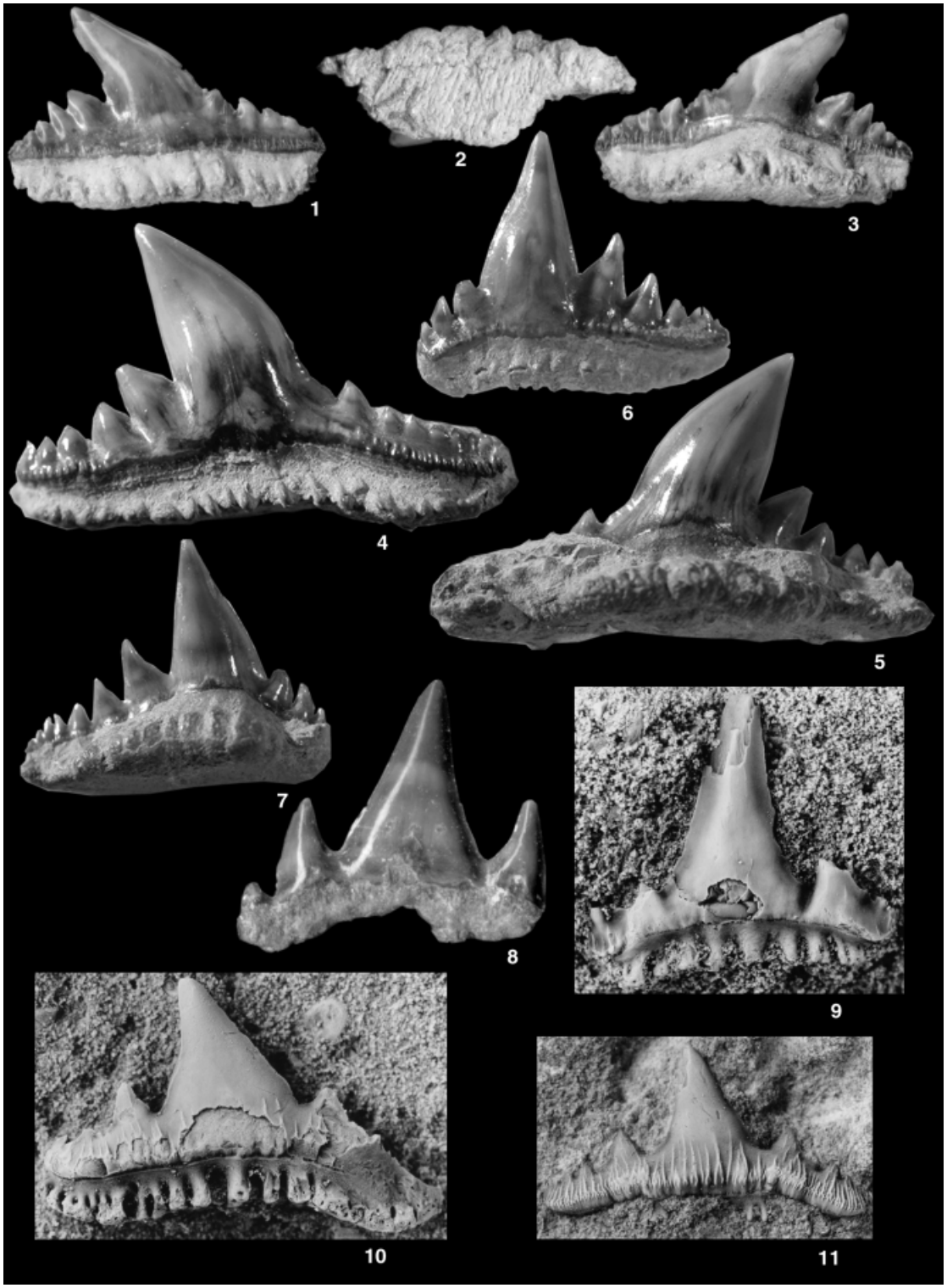
Remarks. When *Hybodus levis* was first described, its palaeospinacid affinities were not recognised, despite the fact that all of the specimens figured by Woodward (1889), including the holotype, clearly show at least part of the characteristic root.

EXPLANATION OF PLATE 9

Figs 1–7. *Pseudonotidanus semirugosus* gen. et sp. nov. 1–3, P. 66106, holotype, Wattonensis Beds, Watton Cliff, lateral tooth. 1, labial view. 2, basal view. 3, lingual view. 4–5, P. 12524a, Oxford Clay Formation, Peterborough, lateral tooth. 4, labial view. 5, lingual view. 6–7, P. 12524b, Oxford Clay Formation, Peterborough, anterior tooth. 6, labial view. 7, lingual view; all ×4.

Fig. 8. *Synechodus* cf. *levis* (Woodward 1889), P. 66107, oyster-belemnite bed, Frome Clay Formation, Watton Cliff, partial anterior tooth, labial view; ×5.

Figs 9–11. *Synechodus levis* (Woodward 1889), all from Stonesfield Slate, Stonesfield. 9, P. 2182b, anterior tooth, labial view. 10, P. 2845d, lateral tooth, labial view. 11, P. 33474, holotype, lateral tooth, labial view; all ×5.



UNDERWOOD and WARD, *Pseudonotidanus, Synechodus*

Occurrence. All specimens of *S. levis* were collected from the shallow marine laminated limestones of the Stonesfield Slate Formation. It appears unlikely that this was a common species as no specimens were recovered from the same facies during this study. The large number of specimens represented merely reflects the large size of the teeth (allowing field collection) and the high degree of collection from the Stonesfield Slate during the latter part of the nineteenth century.

Synechodus cf. *levis* (Woodward, 1889)

Plate 9, figure 8; Plate 10, figure 3

In press *Synechodus levis* (Woodward, 1889); Underwood and Ward, fig. 3A.

Material. One crown collected during this study (BMNH P. 66107). A commissural tooth is also tentatively referred to this taxon (BMNH P. 66109).

Description. The tooth crown comprises a triangular and somewhat compressed main cusp with a pair of large lateral cusplets and at least one further anterior cusplet. No ornament is evident. The root is absent. A commissural tooth referred to this species has a high and compressed root with a low crown. The occlusal face is wide and narrow, with a faint sigmoidal curvature. A strong ridge bisects the occlusal face, separating a moderately coarse reticulate ornament on the labial side from a similar but much finer ornament on the lingual side.

Remarks. The single partial tooth collected during this study compares well to anterior teeth of *S. levis*. It differs, however, from any previously figured specimens in having larger lateral cusplets and no ornament. Similar unornamented teeth are present within other species of *Synechodus* such as *S. plicatus* Underwood, 2002, and so this tooth could fall within the morphological range of *S. levis*. This single tooth is, therefore, here referred to as *S.* cf. *levis.* An imperfect commissural tooth is also referred to *S. levis* despite that fact that there are few diagnostic features present on palaeospinacid commissural teeth. This referral is largely on the grounds of size, as the tooth is, when compared to other species, far too large to be a commissural tooth of *S. duffini* sp. nov., and *S. levis* is the only large palaeospinacid recorded from the Bathonian.

Occurrence. The partial anterior tooth was collected from open marine laminated mudstones, whereas the commissural tooth was collected from offshore shelly marls.

Synechodus duffini sp. nov.

Plate 10, figures 3–14

In press *Synechodus* sp., Underwood and Ward, fig. 4A–B.

Derivation of name. After Chris Duffin, for his work on Mesozoic elasmobranchs.

Holotype. BMNH P. 66110.

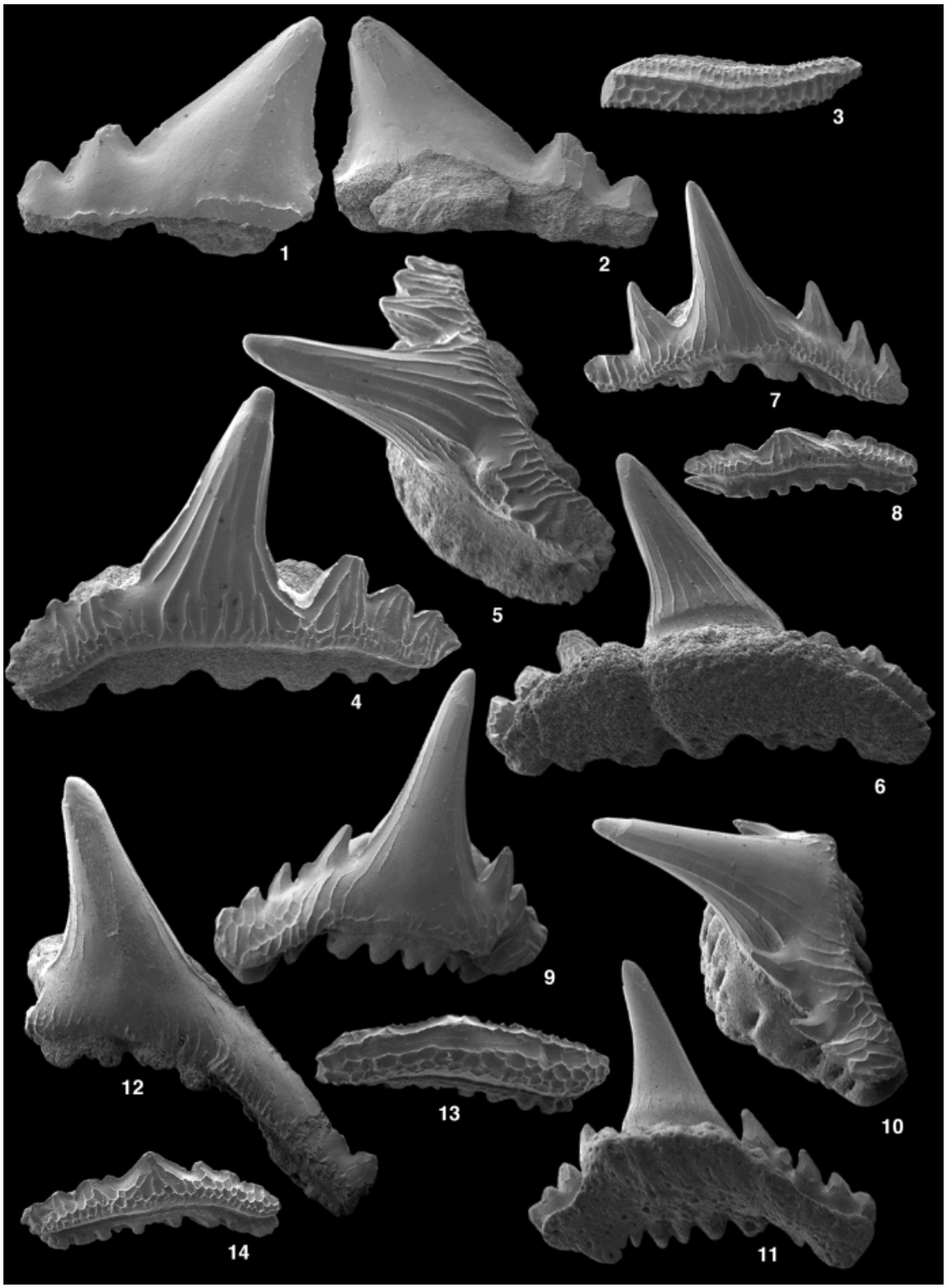
Material. About 290 entire and partial teeth, with anterior and lateral teeth being represented including BMNH P. 66111–66116.

EXPLANATION OF PLATE 10

Figs 1–2. *Pseudonotidanus semirugosus* gen. et sp. nov., P. 66108, oyster-belemnite bed, Frome Clay Formation, Watton Cliff, partial tooth of juvenile. 1, labial view. 2, lingual view; all ×17.

Fig. 3. *Synechodus* cf. *levis* (Woodward, 1889), P. 66109, Cranmore, commissural tooth, occlusal view; ×12.

Figs 4–14. *Synechodus duffini* sp. nov., all from oyster-belemnite bed, Frome Clay Formation, Watton Cliff. 4–12, 14, ×12; 13, ×24. 4–6, P. 66110, holotype, anterolateral tooth. 4, labial view. 5, lateral view. 6, lingual view. 7, P. 66111, anterior tooth, labial view. 8, P. 66112, posterolateral tooth, labial view. 9–11, P. 66113, anterior tooth. 9, labial view. 10, lateral view. 11, lingual view. 12, P. 66114, anterior tooth lacking lateral cusplets, labial view. 13, P. 66115, commissural tooth, labio-occlusal view. 14, P. 66115, posterolateral tooth, labial view.



UNDERWOOD and WARD, *Pseudonotidanus, Synechodus*

Diagnosis. Strongly heterodont. Crown overhangs root labially on all teeth. Crown of anterior and anterolateral teeth about as high as wide, with all cusps slightly inclined posteriorly. Main cusp elongate and slightly flared at base. Up to four pairs of lateral cusplets less than half height of main cusp. Crown of anterior teeth curved, being concave labially, with lateral cusplets being smaller, more irregular and almost absent in largest teeth. Labial ornament of fine, rather irregular, striations present, extending from labio-basal margin of crown to lower part of lateral cusplets, bifurcating and becoming somewhat reticulate basally. Striate ornament weak below main cusp. Some fine longitudinal striations present on lateral parts of main cusp in addition to very fine striations on lingual face. Anterolateral teeth moderately to strongly ornamented, with strong longitudinal ridges on labial face reaching apex of lateral cusplets and close of apex of main cusp. Ridges irregularly bifurcate basally to form loose reticulation. Lingual ornament of fine, parallel striations. Crown of posterolateral teeth low, with low conical main cusp flanked by several weak to incipient lateral cusplets. Ornament strongly reticulate labially, with lingual ornament of moderately strong longitudinal ridges. Labial face of root of all teeth low with irregularly spaced, very prominent pseudopolyaulacorhize folding. Basal face of root flat, rectangular in lateral teeth but expanded lingually in anterior teeth to give semicircular profile. Lingual face of root swollen, especially in anterior tooth, with several relatively evenly spaced foramina along mid part of face.

Description. Anterior teeth are about as high as wide. The crown is asymmetrical and has a rather 'twisted' appearance due to its vaguely S-shaped profile in labial view. The main cusp is elongate, at least twice as long as wide, and faintly compressed. The main cusp is closer to the anterior side of the crown than to the posterior. The anterior end of the crown is slightly curved lingually, whereas the posterior part is more strongly curved labially. Up to four pairs of short, pointed, lateral cusplets are present. Lateral cusplets are less well developed in larger teeth, and may be almost lacking. A poorly developed but continuous cutting edge is present. Labial ornament is typically faint. Fine, somewhat irregular, longitudinal ridges extend from the base of the crown to the lower part of the lateral cusplets. These become stronger and more irregular towards the base, where they form a reticulate pattern. Finer ridges are present at the base of the main cusp, whilst very fine ridges may extend much of the way up the sides of the main cusp. Lingual ornament comprises relatively long, regularly spaced, very fine ridges over much of the lingual crown face. The crown strongly overhangs the root labially. The labial face of the root has a number of very prominent, rather irregularly spaced, vertical folds. These folds overhang the flat basal face of the root. The mid part of the root is expanded lingually, giving it a rather D-shaped profile when viewed basally. The lingual face of the root is expanded lingually, but without a prominent shelf. A number of large foramina are present on the lower part of the lingual face. Lateral teeth differ from anterior teeth in being straight and having the main cusp fairly centrally positioned and slightly inclined to the posterior. Lateral cusplets are larger, up to half of the height of the main cusp, and more robust, typically having a rather blunt apex. Lingual ornament is strong, comprising closely spaced longitudinal ridges that reach the apex of the lateral cusplets and reach close to the apex of the main cusp. These ridges show some branching near the base, where they join to form a weak reticulation. The root shows relatively little lingual expansion. Posterolateral teeth are small and far wider than high. The crown has a low, conical main cusp with several pairs of low to incipient lateral cusplets. Only the upper part of the main cusp, which is ornamented by longitudinal ridges, is not covered by reticulate ornament. The root is straight and narrow, with both labial folds and lingual foramina being clearly evident.

Remarks. Teeth of this taxon differ somewhat from those of any other Jurassic species of *Synechodus*. *S. duffini* sp. nov. differs from *S. occultidens* Duffin and Ward, 1993 in lacking an extensive labial crown expansion. It differs from *S. enniskilleni* Duffin and Ward, 1993 and *S. riegrafi* (Thies, 1983) in possessing asymmetrical anterior teeth with multiple pairs of lateral cusplets and reduced labial ornament. Teeth of *S. duffini* show a similar range of morphologies and crown ornament as *S. dubrisiensis* (Mackie, 1863) from the Cretaceous. They may, however, be separated by the smaller number of lateral cusplets, greater degree of asymmetry of anterolateral teeth and more robust folds on the labial face of the root.

Occurrence and palaeoecology. Teeth of *Synechodus duffini* sp. nov. are a relatively abundant component of faunas collected from offshore mudstone facies. They are, in contrast, completely absent within shallower marine carbonate and lagoonal facies. This offshore distribution appears to be typical of palaeospinacids (e.g. Underwood 2002). The dentition and general body form of *Synechodus* suggest that it was predominantly a benthic ambush predator (e.g. Duffin and Ward 1993; Underwood 2002).

Superorder HYPNOSQUALEA Carvalho and Maisey, 1996
Family PROTOSPINACIDAE Woodward, 1918

Genus PROTOSPINAX Woodward, 1918

Type species. *Protospinax anectans* Woodward, 1918, from the Late Jurassic of Germany.

Remarks. Teeth of *Protospinax* are common within many Jurassic neoselachian tooth assemblages. The teeth are rather conservative in general form, but when populations of teeth are studied, a number of diagnostic features become apparent. Major differences between species occur in the form of root vascularisation; in some taxa hemiaulacorhize roots are present in all teeth, whereas in others variable proportions of teeth possess a nutritive groove. Major differences also occur in the degree of heterodonty. It is possible that further studies on the *in situ* dentitions of protospinacids will allow the differentiation of several genera or subgenera.

Protospinax magnus sp. nov.

Plate 11, figures 1–15

In press *Protospinax* sp. 1. Underwood and Ward, fig. 5H–J.

Derivation of name. From the large size of the anterior teeth.

Holotype. P. 66116.

Material. At least 1680 complete and partial teeth including P. 66117–66122.

Diagnosis. Dentition heterodont. Large anterior teeth with large main cusp about as high as wide, all other teeth considerably wider than high. Labial face of crown oval, becoming wider with straighter apron in posterolateral teeth. Main cusp triangular and prominent on all but posterolateral teeth or where removed by wear, and displaced towards posterior side of teeth. Two pairs of very short and rounded lateral cusplets present on anterior teeth, otherwise incipient or absent. Entire labial face of crown flat except for faint convexity at base of main cusp on anterior teeth. Crown strongly overhangs root labially and laterally. Continuous cutting edge present along occlusal edge, with a somewhat acute angle being present between labial and lingual faces of crown. Relatively short, triangular, but prominent uvula present at base of main cusp. Root moderately high and robust, and of similar width to crown. Root lobes meet at obtuse angle, with junction rather swollen in larger teeth. Basal face of root convex, becoming flat in posterolateral teeth. Vascularisation hemiaulacorhize with nutritive groove never being present. Lingual and labio-basal foramina very prominent. One large pair of foramina present within indents on lateral faces of root, with several smaller foramina also being present on most teeth.

Description. Teeth show a high degree of heterodonty, with larger, higher anterior teeth and lower, smaller posterior teeth. Anterior teeth, which may be over 2 mm wide, comprise a relatively small part of the assemblage, suggesting that they comprise only a relatively small number of files. The labial face of the crown of anterior teeth has a large main cusp, which can be up to one-third of the width of the crown, with one or two pairs of far smaller lateral cusplets. A pair of additional incipient cusplets may be present at the lateral edge of the crown. The crown apron is smoothly curved. No crown ornament is present, and the labial face is nearly flat, with faint convex ridges at the base of the cusps. A weak but continuous cutting edge separates the labial and lingual faces of the crown, forming a slightly acute angle between them. A triangular uvula is present, reaching a little more than half-way to the base of the root. A concave wear facet is commonly present. The root is the same width as the crown, which strongly overhangs it. The hemiaulacorhize root is bulky and has a somewhat swollen appearance lingually. The root lobes are gently tapering with rounded ends, meeting at an obtuse angle. The basal face of the root is convex. Four large foramina are present, one at the lingual apex of the root, one at the junction of the root lobes and one centrally placed on each lateral face of the root. Several smaller foramina are present on the lateral faces of the root and along the lingual and labial edges of

the root basal face. Anterolateral teeth differ in possessing a poorly developed main cusp, although some degree of wear commonly makes it difficult to assess its original form. The main cusp is somewhat displaced posteriorly. Lateral cusplets are reduced, and comprise little more than raised portions of the occlusal edge. The crown of posterolateral teeth is at least twice as wide as high. The main cusp is relatively small but elongate, being displaced to the posterior side of the tooth and being angled posteriorly. Lateral cusplets are essentially absent. The root is similar to that of anterior teeth, but rather more gracile with a flatter basal face and with the root lobes meeting at a very obtuse angle. Smaller teeth of juveniles are essentially similar to those of adults, but tend to have less well-developed cusps and a more gracile root with a flat basal face.

Remarks. Teeth of *Protospinax magnus* sp. nov. show a far higher degree of heterodonty than any other known species of *Protospinax*, and it is only the presence of a large population of teeth that allows all morphologies to be confidently placed within a single taxon. The combination of heterodonty, well-developed cusps and bulky hemiaulacorhize root separate this taxon from any other described species of *Protospinax*. Teeth of an unnamed species erroneously assigned to *P. anectans* Woodward, 1918 by Thies (1983) (Underwood 2002) have a crown morphology very similar to that of juvenile *P. magnus* but differ in having a more gracile root which is flared lingually and a concave crown labial face.

Occurrence and palaeoecology. The occurrence of teeth of *Protospinax magnus* sp. nov is extremely strongly facies controlled. They are very common within offshore mudstone facies, where they typically comprise over half of the neoselachian assemblage and occur to the exclusion of other species of *Protospinax*. Uncommon teeth, probably assignable to juveniles, are present within the offshore carbonate shelf facies of the Boueti Bed. The taxon appears to have been completely absent within inshore carbonate and lagoonal environments.

The general body form of *Protospinax* (Carvalho and Maisey 1996) suggests that it was a slow moving benthic form, whilst the low-crowned teeth suggest that fast moving prey were not a major part of the diet. There is generally a low degree of wear of the type expected from a strictly durophagous diet on the teeth of *P. magnus*, and so it seems unlikely that shelled organisms comprised a major part of the diet. It is, therefore, likely that this species was a benthic generalist, taking a wide variety of food items.

Protospinax bilobatus sp. nov.

Plate 12, figures 1–11

In press *Protospinax* sp. 2 Underwood and Ward, fig. 5K–M.

Derivation of name. From the distinctly bilobed form of the root.

Holotype. BMNH P. 66124.

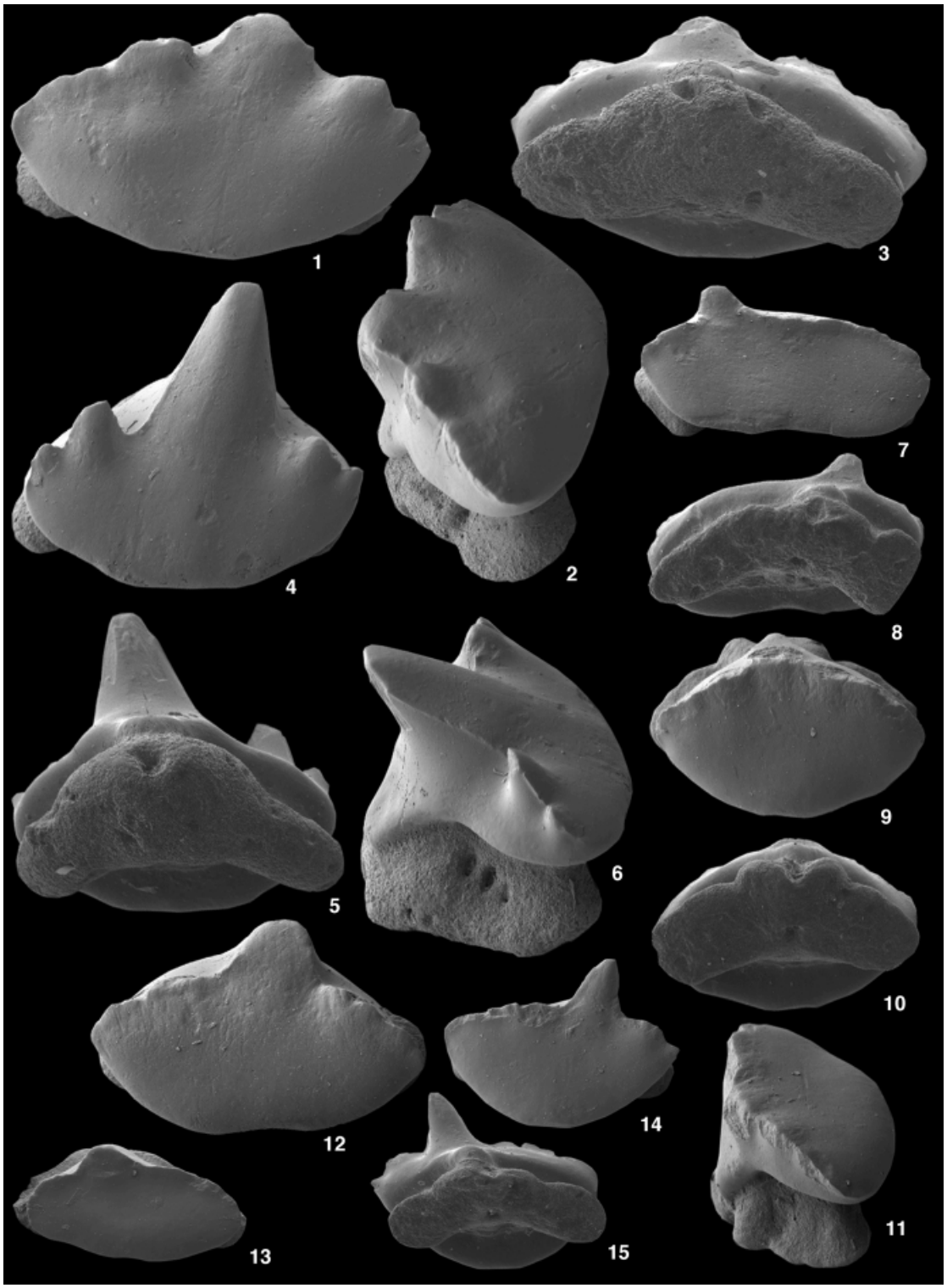
Material. About 1650 complete and partial teeth including BMNH P. 66125–66129.

Diagnosis. Dentition moderately heterodont. Crown wider than high in all teeth, being oval to somewhat diamond shaped. Most teeth symmetrical, although some more cuspate teeth have main cusp offset to posterior and slightly posteriorly inclined. Main cusp well differentiated but short and robust where present, although commonly removed by wear. Up to two pairs of very low to incipient lateral cusplets

---

EXPLANATION OF PLATE 11

Figs 1–15. *Protospinax magnus* sp. nov., all from oyster-belemnite bed, Frome Clay Formation, Watton Cliff; 1–12, ×30; 13–15, ×40. 1–3, P. 66116, holotype. 1, labial view. 2, lateral view. 3, basal view. 4–6, P. 66117, cuspate tooth. 4, labial view. 5, lateral view. 6, basal view. 7–8, P. 66118. lateral tooth. 7, labial view. 8, basal view. 9–11, P. 66119. 9, labial view. 10, basal view. 11, lateral view. 12, P. 66120, labial view. 13, P. 66122, posterior tooth, labial view. 14–15, P. 66121, posterolateral tooth. 14, labial view. 15, basal view.



UNDERWOOD and WARD, *Protospinax*

may be on teeth with defined main cusp. Labial face of crown flat to faintly concave. Apron of crown smoothly convex, with small concave wear facet. Continuous cutting edge along occlusal edge separates labial face from short lingual face of crown. Uvula small and triangular. Crown strongly overhangs root on all sides. Root relatively low and similar width to crown, with root basal face at about a 45 degree angle to labial face of crown. Root clearly divided into two lobes separated by strong nutritive groove, with uncommon examples of nutritive groove being partly closed over at its lingual end. Root lobes oval to rectangular in basal view, with flat basal face, which is somewhat flared. Large foramen present within nutritive groove, with pair of smaller foramina on lateral faces of root.

Description. The form of heterodonty of the teeth is not clear, as the most strongly cuspate teeth (usually a sign of anterior teeth) are also the most asymmetrical (usually a feature of lateral teeth). A very large proportion of the teeth show strong to intense wear, with the cusps and much of the occlusal edge often removed to give a flat wear facet. Strongly cuspate teeth, which comprise a minority of the collection, have a robust main cusp which is somewhat offset towards the posterior side of the tooth, and are commonly slightly angled to the posterior. The cusp is compressed and has a rounded apex. There is usually one pair of short lateral cusplets, and commonly a second pair of incipient cusplets close to the ends of the crown. The labial face of the crown is flat, with a smoothly curved labio-basal margin, although this is commonly interrupted by a wear facet. The lingual face of the crown has a short and triangular uvula, which does not project lingually of the rest of the lingual face. The crown very strongly overhangs the root labially and laterally; the linguo-basal edge of the crown also overhangs the root to some extent. The root is relatively low and gracile and is of similar width to the crown. The root flares somewhat towards the flat base, with a single pair of large foramina being present within major indentations on the lateral faces of the root. The basal face of the root is divided into two lobes by a prominent nutritive groove, although within some of the more strongly cuspate teeth, this is partly roofed over at its lingual end. A large foramen is present within the more lingual part of the nutritive groove. Less cuspate teeth differ in being essentially symmetrical and having a small, triangular, main cusp. Lateral cusplets are incipient or absent and labial face of the crown is generally faintly concave. Smaller teeth, presumably from posterolateral positions, have a labial face of the crown which forms an elongate oval, interrupted only by a very small triangular main cusp.

Remarks. The shape of the teeth, and the presence of similarly sized teeth in all jaw positions, suggests that the heterodonty of *Protospinax bilobatus* sp. nov. is rather unlike that of *P. magnus* sp. nov. The unusual heterodonty of this taxon may indicate a dentition composed largely of symmetrical, poorly cuspate teeth with a small number of cuspate files. The asymmetrical form of the cuspate teeth suggests that they are unlikely to be from anterior positions, and instead it is possible that they form specialised files in anterolateral positions.

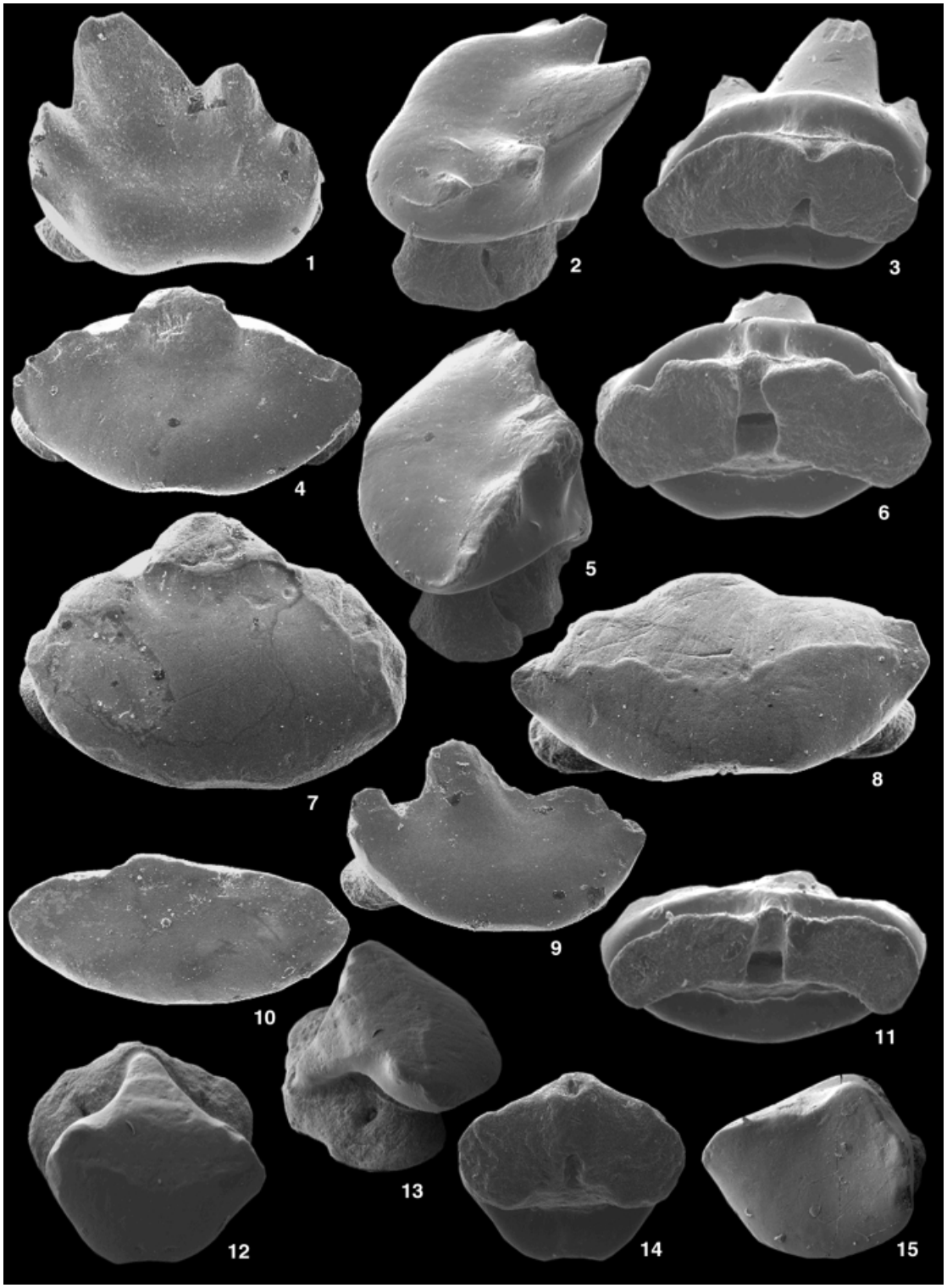
The low roots and nutritive groove of *P. bilobatus* are similar to what has been recorded in some teeth of *P. anectans* (Cappetta 1987, fig. 55; Thies 1983, fig. 5). Despite this, the presence of this root morphology within almost all teeth differs from *P. anectans*, where teeth with high, hemiaulacorhize roots are present within adults and in anterior teeth of juveniles (Cappetta 1987, fig. 62), a complete nutritive groove apparently only being present within lateral teeth of juveniles. Roots of this morphology are unknown within any other species of *Protospinax*.

Occurrence and palaeoecology. The distribution of *Protospinax bilobatus* sp. nov. is rather restricted, being largely limited to outermost lagoon facies, where shell beds contain abundant ooids swept in from nearby shoals, with some teeth also being recorded from shallow marine carbonate facies. Despite this limited occurrence, where *P. bilobatus*

EXPLANATION OF PLATE 12

Figs 1–11. *Protospinax bilobatus* sp. nov., all from White Limestone Formation, Bed 17, Woodeaton Quarry. 1–3, P. 66124, holotype, cuspate tooth. 1, labial view. 2, lateral view. 3, basal view. 4–6, P. 66125. 4, labial view. 5, lateral view. 6, basal view. 7, P. 66126, labial view. 8, P. 66127, worn tooth, labial view. 9, P. 66128, labial view. 10–11, P. 66129, lateral tooth. 10, labial view. 11, basal view; all ×60.

Figs 12–15. *Protospinax carvalhoi* sp. nov. 12–14, P. 66130, holotype, White Limestone Formation, Bed 1, Woodeaton Quarry, anterior tooth. 12, labial view. 13, lateral view. 14, basal view. 15, P. 66131, concretions at base of Eyford Member, Hampen Cutting, anterior tooth, labial view; all ×60.



UNDERWOOD and WARD, *Protospinax*

teeth are present, they are generally the dominant selachian element, comprising well over half of the neoselachian assemblage. The high degree of wear on the majority of teeth of *P. bilobatus* suggests a specialist durophagous diet. It is, therefore, unclear whether this species was restricted to specific physical environments, or whether it was a specialist requiring the presence of shell banks for its (presumably molluscan) diet.

Protospinax carvalhoi sp. nov.

Plate 12, figures 12–15; Plate 13, figures 1–6

1982 Type 2(d) teeth, Young, fig. 2E–F.
In press *Protospinax* sp. 3. Underwood and Ward, fig. 5N–P.

Derivation of name. After Marcelo de Carvalho, for his work on the systematic position of *Protospinax*.

Holotype. BMNH P. 66130.

Material. One hundred and twenty-eight complete and partial teeth including BMNH P. 66131–66134.

Diagnosis. Fairly low degree of heterodonty. Crown wider than high and rather rhombic in labial view. Crown symmetrical in most teeth, with main cusp slightly offset to posterior in some lateral teeth. Single small cusp triangular and wider than high, although often removed by wear. Single pair of incipient lateral cusplets is present on some wider teeth. Lateral ends of crown fairly sharply angled, with the crown tapering labio-basally. Apron of crown straight or slightly concave. Labial and lingual crown faces meet at an acute angle. Labial face of crown flat and unornamented. Crown overhangs root labially and laterally. Uvula well developed and bulbous. Root moderately high and rather displaced lingually. Hemiaulacorhize root large, at least three-quarters the size of the crown when viewed basally, with root lobes flared and poorly differentiated. Basal face of root flat and sloping labially. Large foramina present at root lingual apex, at junction of root lobes, and as single pair on lateral faces of root.

Description. These small teeth, up to about 1 mm wide, show a lower degree of heterodonty than other Bathonian *Protospinax*. The crown typically shows wear, and teeth with no wear to the occlusal region are very rare. Narrower and higher teeth, presumably from anterior files, have a crown labial face that is almost as high as wide as well as a high root. A very short, blunt main cusp is centrally positioned, with lateral cusplets being absent other than as the lateral extremities of the crown being very slightly occlusally directed. The crown tapers labio-basally with relatively straight edges, meeting at a short concave apron. A well-developed and parallel-sided uvula is present. The crown strongly overhangs the root laterally and labially. The root is relatively high and somewhat displaced lingually. From its attachment point on the underside of the crown, the root flares basally, covering much of the crown when viewed basally. A wide, flat basal face of the root lacks well-differentiated root lobes. Foramina are well developed on the labio-basal part of the root and at the lingual root apex immediately below the base of the uvula. A single pair of well-developed foramina are present on the lateral faces of the root, being set into shallow vertical grooves.

Remarks. *Protospinax carvalhoi* sp. nov. more closely resembles *Protospinax planus* Underwood, 2002 than other described species. It differs from *P. planus* in being smaller, having a more gracile crown with larger uvula and more flared root with flatter basal face.

Occurrence and palaeoecology. *Protospinax carvalhoi* sp. nov. is a frequent and widespread member of lagoonal shark assemblages, although unlike the other *Protospinax* species, it rarely dominates. It is also present within shallow marine carbonates but absent within offshore mudstones. Occurrences of more than one species of *Protospinax* within a single sample are very rare, and the three species tend to occur in almost complete exclusion of each other. This is especially evident within lagoonal facies, where *P. bilobatus* sp. nov. dominates in oolitic and shell bed facies, whilst *P. carvalhoi* is present within less shelly mudstone facies and amongst more restricted inner lagoon faunas.

As with *P. bilobatus*, *P. carvalhoi* teeth invariably show intense wear from consuming shelled-food items. It is possible that these species avoided direct competition for food by favouring different substrates, with *P. bilobatus* favouring a coarse or shelly seafloor and *P. carvalhoi* favouring finer substrates.

Genus BREVIACANTHUS Maisey, 1976

Type species. *Nemacanthus brevis* Phillips, 1871, from the Bathonian of Stonesfield.

Breviacanthus brevis (Phillips, 1871)

Plate 13, figure 7

1871 *Nemacanthus brevis*, Phillips, *in* Woodward 1890, pl. 2, figs 3–5.
1890 *Nemacanthus brevis*, Phillips; Woodward 1890, pl. 3, fig. 1.
1976 *Breviacanthus brevis* (Phillips, 1871); Maisey 1976*a*, figs 1A–C, 3.

Material. One spine tip (BMNH P. 66135), also numerous spines in museum collections.

Remarks. New material does not add anything to the descriptions of Maisey (1976*a*). The structure of the spines of *B. brevis* does not differ greatly from that of *Protospinax* (Maisey 1976*a*), differing largely in the greater extent of the enamelled covering, which is ornamented rather than smooth. Although *Protospinax* was at the time considered to be a batoid synonymous with *Belemnobatis* (Maisey 1976*b*), this has subsequently been shown not to be the case (Carvalho and Maisey 1996). The shallow marine carbonate facies yielding *B. brevis* contain two species of *Protospinax* (*P. bilobatus* sp. nov. and *P. carvalhoi* sp. nov.); it is, therefore, likely to be synonymous with one of these. It is at present not possible to synonymise one of the *Protospinax* species with *B. brevis*; indeed, it is not impossible that *B. brevis* encompasses fin spines of more than one species, a situation probably common among fin spine taxa of hybodonts. Due to the uncertainties in the taxonomic position of *B. brevis*, it is here considered that it should be regarded as a parataxon of uncertain affinities until associated dental and fin spine material is discovered.

Order RAJIFORMES Berg, 1940
Family RHINOBATIDAE Müller and Henle, 1838 *s.l.*

Remarks. Several species of Late Jurassic batoid are known from complete skeletons, although teeth of these taxa have only recently been figured in detail (Cavin *et al*. 1995; Leidner and Thies 1999). Of the three genera named from these skeletal remains, *Belemnobatis* Thiolliere, 1854 and *Spathobatis* Thiolliere, 1854 may be recognised from both skeletal and dental characteristics. A further batoid genus, *Asterodermus* Agassiz, 1843, is present in Upper Jurassic rocks of Germany associated with the other genera. Leidner and Thies (1999) considered the overall skeletal morphology and placoid scales of *Spathobatis* and *Asterodermus* to be identical. They considered, however, that some specimens assigned to *Asterodermus* contained teeth more similar to those of *Belemnobatis* than *Spathobatis*, an observation confirmed by Jürgen Kriwet (pers. comm. 2002). It has been recognised, however, that the degree of heterodonty of *Spathobatis* is poorly understood and greater than usually recognised (Underwood 2002). It is, therefore, possible that the different tooth morphologies recorded within *Spathobatis* and *Asterodermus* are end members within the morphological range of *Spathobatis* teeth. Hence, it is considered here that the genus *Asterodermus* should be restricted to the type material until a more complete study of the dentition of specimens referred to it is carried out.

The degree of heterodonty of early batoids is rather poorly known, with studies of collections of isolated teeth suggesting that many species possessed high degrees of heterodonty (see Underwood *et al*. 1999*b*; Underwood 2002; Underwood and Rees 2002). This is also suggested by the variations in tooth morphology of teeth extracted from skeletons (Cavin *et al*. 1995). It is likely that further study of the heterodonty patterns among early batoids will allow additional genera to be recognised within the taxa currently referred to *Belemnobatis* and *Spathobatis*.

Genus BELEMNOBATIS Thiolliere, 1854

Type species. *Belemnobatis sismondae* Thiolliere, 1854, from the Upper Jurassic of France.

Belemnobatis kermacki sp. nov.

Plate 13, figures 8–12; Plate 14, figures 1–5

Derivation of name. After Kenneth Kermack, part of the UCL team who first investigated the vertebrate fauna of the Bathonian at Watton Cliff.

Holotype. BMNH P. 66136.

Material. About 65 teeth, many lacking roots, including BMNH P. 66137–66140.

Diagnosis. Low heterodonty. Teeth small, up to about 1 mm wide. Crown wider than deep when viewed occlusally, typically close to twice as wide as deep. Crown low with well-developed straight transverse keel. Cusp absent. Keel divides flat labial face from lingual face with included angle about 90 degrees. Labial protuberance poorly developed as slight swelling of apron. Well-developed uvula narrow and longer than wide. Occlusal keel and labial edge of crown subparallel. Root low and slightly deflected lingually. Root as wide as crown and similarly compressed labio-lingually. Nutritive groove typically partly covered over. Basal face of root lobes somewhat angled away from lingual edge, with base somewhat swollen close to position of nutritive canal.

Description. These small teeth show a relatively homodont dentition, with all teeth being considerably wider than deep and symmetrical. The crown is low and has a continuous, straight crest reaching the lateral extremities of the tooth. There is no cusp, although a raised central portion of the keel may form an incipient cusp. The lateral ends of the crown are smoothly rounded, with the keel and labial edge of the crown being close to parallel, other than at the central part of the tooth where a poorly developed labial protuberance is present. The labial face of the crown is flat and unornamented. The lingual face of the crown is flat and separated from the labial face by an angle of about 90 degrees. A well-developed enameloid-covered uvula is present with a somewhat swollen region of the lingual crown face above. The uvula is longer than wide in all teeth. The root is relatively low and slightly displaced lingually, being overhung by the crown on all sides except for close to the uvula. The root is of similar size to the crown. The root lobes are partly separated by an incomplete nutritive groove, which is variably covered in all teeth. The root lobes have a convex labial edge and concave lingual edge, and taper distally to a point. A flat basal face is generally somewhat swollen close to the nutritive canal. Foramina at either end of the nutritive canal are large as are a pair of foramina either side of the uvula.

Remarks. Teeth of *B. kermacki* sp. nov. are similar in general morphology and probable lack of heterodonty to those of *B. moorbergensis* (Thies, 1983), *B. werneri* (Thies, 1983) and *B. noviodunumensis* Delsate and Candoni, 2001, but differ from them in lacking a well-developed labial protuberance and an obvious, if small, cusp. Other described Jurassic species of *Belemnobatis* have, among other differences, a greater degree of heterodonty.

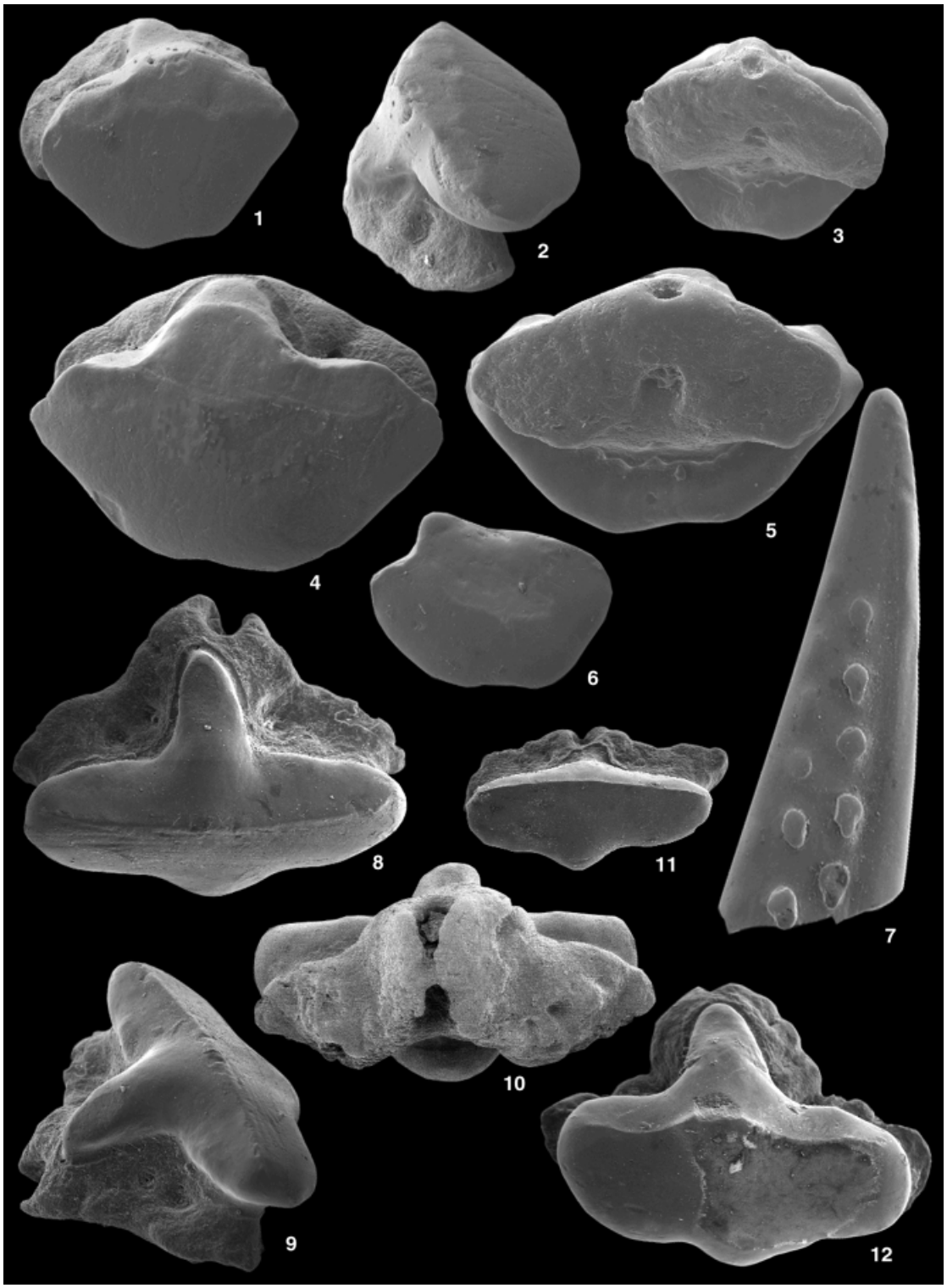
Occurrence. Well-preserved specimens of *Belemnobatis kermacki* sp. nov. have only been recognised from offshore mudstone facies. In addition, some fragmentary teeth from the carbonate shelf facies of the Cornbrash Formation may also be referable to this species.

EXPLANATION OF PLATE 13

Figs 1–6. *Protospinax carvalhoi* sp. nov. 1–3, P. 66132, White Limestone Formation, Bed 1, Woodeaton Quarry. 1, labial view. 2, lateral view. 3, basal view. 4–5, P. 66133, concretions at base of Eyford Member, Hampen Cutting, lateral tooth. 4, labial view. 5, basal view. 6, P. 66134, White Limestone Formation, Bed 1, Woodeaton Quarry, labial view; all ×60.

Fig. 7. *Breviacanthus brevis* (Phillips, 1871), P. 66135, bioclastic limestone, Forest Marble Formation, Watton Cliff, fin spine tip, lateral view; ×25.

Figs 8–12. *Belemnobatis kermacki* sp. nov., all from oyster-belemnite bed, Frome Clay Formation, Watton Cliff. 8–10, P. 66136, holotype. 8, occlusal view. 9, lateral view. 10, basal view. 11, P. 66137, commissural tooth, occlusal view. 12, P. 66138, anterior tooth, occlusal view; all ×60.



UNDERWOOD and WARD, neoselachian teeth

Belemnobatis stahli sp. nov.

Plate 14, figures 5–16

1982	Type 2(c) teeth, Young, fig. 2O–Q.
?1983	*Spathobatis werneri* Thies, pl. 12, fig. 4.
In press	*Belemnobatis* cf. *moorbergensis* (Thies 1983); Underwood and Ward, fig. 5R–S.

Derivation of name. After Barbara Stahl, for her work on fossil chimaeroids.

Holotype. BMNH P. 66141.

Material. At least 350 complete and partial teeth including BMNH P. 66123–66146.

Diagnosis. Moderate heterodonty. Teeth small, up to 1 mm wide. Crown up to as wide as deep in anterior teeth when viewed occlusally, up to twice as wide as deep in lateral teeth. Crown low with well-developed straight transverse keel. Cusp absent or incipient. Keel divides flat labial face from lingual face with included angle about 90 degrees. Labial protuberance moderately to well developed, where not removed by wear, and as wide as uvula. Faint pectination commonly present on apron. Uvula very well developed and parallel-sided to gently tapering. Lingual face of crown somewhat swollen between cusp and uvula where cusp is present. Root low and slightly deflected lingually. Root as wide as crown but more compressed labio-lingually. Nutritive groove typically partly or fully roofed over. Basal face of root lobes somewhat angled away from nutritive groove. One or more pairs of moderate-sized foramina on either side of uvula.

Description. Teeth of this taxon show a moderate degree of heterodonty, with teeth varying from about one to two times as wide as deep. Most teeth are symmetrical, although lateral teeth with an anteriorly angled lingual face are also present. The crown is low and has a continuous, straight crest reaching the lateral extremities of the tooth, with an incipient cusp typically being present. The lateral ends of the crown are somewhat angular, with the labial edge being angled towards the moderately well-developed labial protuberance. There is weak pectination on the lingual edge of the crown of most teeth. Both lingual and labial face of the crown are flat and unornamented, although many teeth have a slightly swollen region of the crown lingual face above the uvula. An uvula is well developed and prominent, commonly with a small wear facet on its lower part. The root is relatively low in anterior teeth, but somewhat higher on posterior teeth and is of a similar width to the crown. This is slightly displaced lingually, being overhung by the crown on all sides except for close to the uvula. The root lobes are partly separated by a shallow trough marking the position of the fully covered nutritive groove in most teeth, although an open nutritive groove with large central foramen is present on some lateral teeth. The root lobes have a convex labial edge and concave lingual edge, and taper distally to a rounded extremity. The basal face of the root is relatively flat and slopes away from the position of the nutritive groove. One or two pairs of well-developed foramina are present on either side of the uvula.

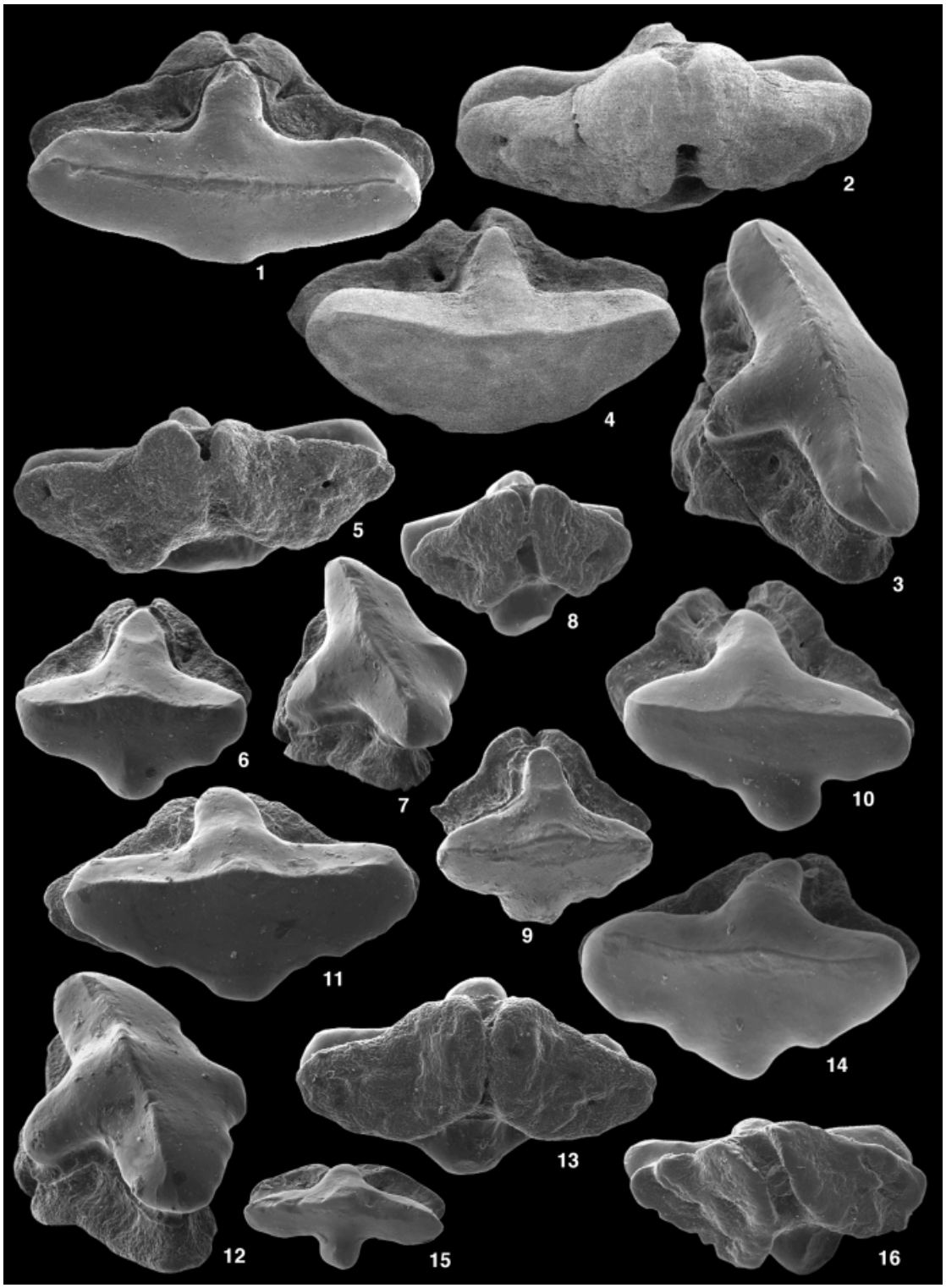
Remarks. More elongate teeth of *B. stahli* sp. nov. are superficially similar to those of *B. kermacki* sp. nov. and several other Early and Middle Jurassic species of *Belemnobatis*. Teeth of *B. stahli*, however, differ from all other species in having a somewhat pectinate labial edge of the crown that is not parallel to the

---

EXPLANATION OF PLATE 14

Figs 1–5. *Belemnobatis kermacki* sp. nov., all from oyster-belemnite bed, Frome Clay Formation, Watton Cliff. 1–3, P. 66139. 1, occlusal view. 2, basal view. 3, lateral view. 4–5, P. 66140. 4, occlusal view. 5, basal view; all ×60.

Figs 6–16. *Belemnobatis stahli* sp. nov. 6–9, 11–13, 16, Rutland Formation, Bed 7, Woodeaton Quarry; 10, 14, Lower Fullers Earth Formation, Hornsleasow Quarry. 6–8, P. 66141, holotype, anterior tooth. 6, occlusal view. 7, lateral view. 8, basal view. 9, P. 66123, anterior tooth, occlusal view; 10, P. 66143, anterolateral tooth, occlusal view. 11–13, P. 66142, lateral tooth. 11, occlusal view. 12, lateral view. 13, basal view. 14, P. 66144, anterolateral tooth, occlusal view. 15, P. 66145, Eyford Member, Huntsman's Quarry, tooth of juvenile, occlusal view. 16, P. 66146, ?posterolateral tooth, basal view; all ×60.



UNDERWOOD and WARD, *Belemnobatis*

occlusal keel. A similar situation is present on the paratype of *B. werneri*, but not the holotype. As only two specimens assigned to *B. werneri* have been well figured, it is unclear whether the type assemblage contains two species, one being *B. stahli*, or whether the morphological range within the heterodonty of *B. werneri* comes close to overlapping with that of *B. stahli*. In addition, teeth of *B. stahli* show a greater degree of heterodonty than *B. kermacki* (and possibly other, less well-figured, taxa) with the majority of teeth narrower for their width than any recorded for *B. kermacki*, *B. moorbergensis*, *B. werneri* or *B. noviodunumensis.*

Occurrence. Teeth of this species are present within almost all samples of lagoonal facies studied, as well as within shallow marine carbonates. Although generally a relatively minor part of the assemblages, within the muddy but shallow marine facies at Hornsleasow Quarry, *B. stahli* sp. nov. is the dominant selachian recorded.

Belemnobatis sp.

Text-figure 2A–C

Material. One well-preserved tooth, P.66154.

Description. This moderately robust tooth has a somewhat cruciform appearance in occlusal view. A flat labial face of the crown is expanded laterally. A large, rounded labial protuberance makes up about one-third of the length of the apron. A prominent, erect, triangular cusp is present. The labial crown face is separated from the lingual face by a transverse keel, which is continuous over the cusp. The lingual face of the crown is short and faintly concave. The region below the cusp is swollen to form a major convex ridge, which passes down into a short but obvious uvula. The root is relatively low and wider than the crown. The basal face is flat and expanded labio-laterally into large lobes. A nutritive groove is present but partly roofed over in the mid part. The lateral faces of the root are strongly flared basally. Large foramina are present on either side of the uvula. Smaller foramina are not seen.

Remarks. This tooth differs from other species of *Belemnobatis* in several respects. It is larger and bulkier than teeth of *B. werneri* and *B. stahli*, with a far more prominent cusp and larger root. It differs from teeth of *Belemnobatis delsatei* in being more gracile, and in having a wider and flatter root and a far more prominent cusp.

Occurrence. The single tooth of this species comes from a lagoonal marl within the White Limestone Formation of Woodeaton Quarry. It co-occurs with *B. stahli* sp. nov. and *S. delsatei* sp. nov., suggesting that a moderately diverse ray fauna was present.

Genus SPATHOBATIS Thiolliere, 1854

Type species. *Spathobatis bugesiacus* Thiolliere, 1854, from the Upper Jurassic of France.

Spathobatis delsatei sp. nov.

Plate 15, figures 1–13.

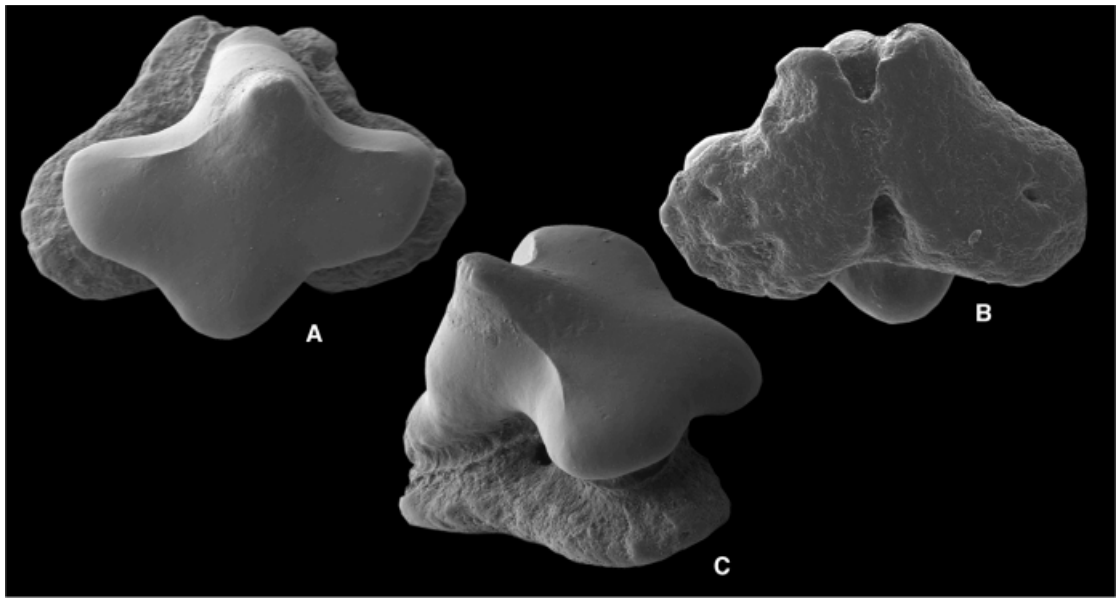
In press *Spathobatis* sp. Underwood and Ward, fig. 5T–U.
In press Rhinobatid sp. Underwood and Ward, fig. 5V.

Derivation of name. After Dominique Delsate, for his work on early batoids.

Holotype. BMNH P. 66147.

Material. At least 150 complete and partial teeth including BMNH P. 66148–66153.

Diagnosis. Dentition very heterodont, with intermediates between tooth morphologies. Teeth robust and up to over 1·5 mm wide. Crown varies from slightly narrower than deep when viewed occlusally to nearly



TEXT-FIG. 2. *Belemnobatis* sp. P. 66154, White Limestone Formation, Bed 1, Woodeaton; ×60. A, occlusal view. B, lateral view. C, basal view.

twice as wide. Crown low with weakly developed transverse keel not quite reaching ends of crown, being faint or absent in some larger anterior teeth. Small conical cusp present on some teeth, especially in narrower teeth where well-developed keel is absent. Labial protuberance very poorly developed or absent in wider teeth, narrow and triangular in narrower teeth. Lateral ends of crown rounded and slightly lingually projecting or swollen. Uvula very well developed and parallel-sided to gently tapering. Lingual face of root somewhat swollen between cusp and uvula where cusp is present. Moderate to high root as massive as crown and deflected lingually. Nutritive groove wide in most teeth, but may be fully or partly roofed over in larger teeth. Large foramina within nutritive groove and at least one pair beside uvula. Small foramina common on basal face of root.

Description. Teeth of this species have a generally robust appearance. Strong heterodonty is present, and it is only the presence of intermediate tooth morphologies that allows the nature of the heterodonty to be realised. The most obvious variations are in the width of teeth and presence or absence of a cusp and the relative height of the root. In general, teeth fall into three main morphologies; wide with an occlusal keel and low root, large and narrow with little or no occlusal keel and high root; small and narrow with keel and moderately high root. These supposedly represent lateral, adult anterior and juvenile anterior teeth respectively. The labial face of the crown is gently convex and relatively triangular in shape, becoming rather heart-shaped in anterior teeth. The labial apron is angled, lacking a well-differentiated labial protuberance in most teeth, with a small triangular protuberance in some anterior teeth. Labial and lingual faces are separated by a moderately- to well-developed transverse keel in all but the largest anterior teeth. This keel is straight or curved lingually on the lateral parts of the crown and does not reach the ends of the crown. A small conical cusp is present on all but the widest lateral teeth. The lingual face of the crown is at an obtuse angle to the labial face, and is either flat or slightly concave. The lateral ends of the crown are somewhat curved lingually, with a somewhat flared tip. Where a cusp is present, the lingual face below the cusp is swollen and continuous with the uvula. The uvula is prominent and long, being parallel-sided or slightly tapering, with a rounded termination immediately above the lingual end of the nutritive groove. A wear facet is commonly present near the end of the uvula. The root is bulky and deflected lingually, with the basal face of the root being of a similar size to the crown. This is especially high and strongly lingually deflected in large anterior teeth. The appearance of the root in basal view is highly dependent on the state of the nutritive groove, which is open and wide in some teeth, but partly to largely or completely closed over in

others. The basal faces of the root lobes are slightly concave and strongly angled away from the central part of the root. The lateral faces of the root are overhung by the crown, and have a distinct notch on either side of the uvula which contains a large foramen. A large basal foramen is present within the nutritive groove, with a clear tube being present where this is roofed over. Small foramina are abundant on the basal faces of the root, whilst several small foramina are commonly present on the lateral faces of the root.

Remarks. The heterodonty of *Spathobatis delsatei* sp. nov. appears to be not unlike that of *B. sismondae* Thiolliere, 1854 from which it differs in having a more robust crown, higher root and narrower nutritive groove. *S. delsatei* differs from *Belemnobatis morinicus* (Sauvage, 1873) (see Cavin *et al*. 1995), and *Spathobatis bugesiacus* Thiolliere, 1854 in having a longer uvula, curved and discontinuous crest and more lingually displaced root, and the absence of an occlusal crest in some teeth. It is also probable that a lower degree of heterodonty is present in *B. morinicus*.

Occurrence and palaeoecology. The relatively large teeth of this taxon are present within a wide range of facies, from lagoonal to open marine, but are consistently uncommon or rare. Largest teeth are typically limited to open marine mudstone facies, whereas some smaller teeth are present within lagoons that probably had a reduced salinity. It may therefore be that this represented a very cosmopolitan taxon with the juveniles living preferentially within lagoons, only moving into offshore environments later in life.

DIVERSITY OF JURASSIC NEOSELACHIANS

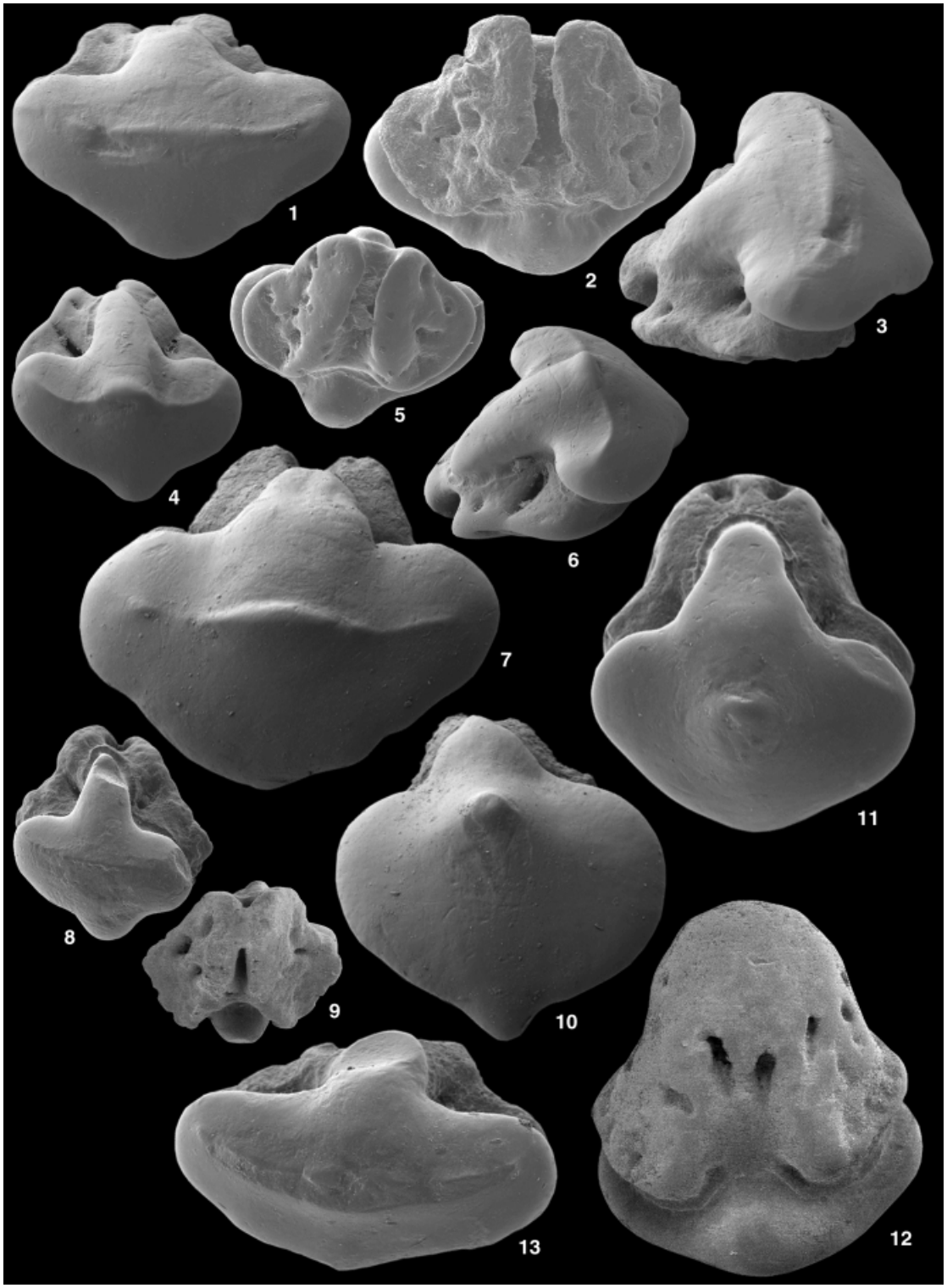
Despite the importance of the Jurassic and Early Cretaceous as a period of radiation within the neoselachians, no studies have attempted to assess the diversity of neoselachians at any point of time during this interval. The majority of studies of early neoselachian faunas have relied on analysis of the assemblage of a single locality (e.g. Candoni 1995; Underwood 2002) where selachian remains have been collected from a single facies, or have been piecemeal studies of remains collected from rocks of a wide range of ages and facies (Thies 1983). It has thus remained unclear whether these single locality studies are representative of the fauna as a whole, and whether any neoselachian taxa were facies specific (but see Underwood 2002). The study of neoselachian remains collected from a wide range of facies within a single stage and single geographical area has allowed these topics to be addressed.

The majority of the species of neoselachians recognised during the course of this study have proven to be extremely facies specific, with very few species being present within lagoonal, shallow carbonate shelf and open marine mudstone facies, with this environmental specificity being common to both rare and abundant taxa. Some entire taxonomic groups are present within specific settings, with the Synechodontiformes being entirely absent within lagoonal palaeoenvironments. In other cases specificity is apparent within different genera of the same major groups, such as is seen within the Orectolobiformes and Carcharhiniformes. In some cases, however, different species of the same genera are present in deposits reflecting different environments, this being especially evident within *Protospinax* and *Belemnobatis*. It is, therefore, obvious that a true idea of the diversity of neoselachians at a point in time is only possible if a range of facies is studied. The concentration of earlier studies on a single facies has, therefore, only allowed for the recognition of a single facies-specific fauna within each collection. It may, therefore, be

---

EXPLANATION OF PLATE 15

Figs 1–13. *Spathobatis delsatei* sp. nov. 1–3, P. 66147, holotype, White Limestone Formation, Bed 1, Woodeaton Quarry, lateral tooth. 1, occlusal view. 2, basal view. 3, lateral view. 4–6, P. 66148, White Limestone Formation, Bed 1, Woodeaton Quarry, small anterior tooth. 4, occlusal view. 5, basal view. 6, lateral view. 7, P. 66149, oyster-belemnite bed, Frome Clay Formation, Watton Cliff, lateral tooth, occlusal view. 8–9, P. 66151, Rutland Formation, Cycle 3, Ketton Quarry, small anterior tooth. 8, occlusal view. 9, basal view. 10, P. 66152, oyster-belemnite bed, Frome Clay Formation, Watton Cliff, large anterior tooth, occlusal view. 11–12, P. 66150, Bioclastic limestone, Forest Marble Formation, Watton Cliff, large anterior tooth. 11, occlusal view. 12, basal view. 13, P. 66153, Blisworth Limestone Formation, Ketton Quarry, lateral tooth, occlusal view; all ×40.



UNDERWOOD and WARD, *Spathobatis*

presumed that the actual diversity of neoselachians at any point in time through the Jurassic and Early Cretaceous was higher than has previously been recognised.

Acknowledgements. We thank a number of collaborators who helped with the sampling for this project, especially in its early stages. Eric Freeman, who first sampled some of the localities studied, the University College, London microvertebrate group and Alison Ward are thanked for their extensive help with sampling and sample processing. More recent studies have largely been carried out with the aid of a Birkbeck College Faculty of Science Research Grant, whilst Aaron Hunter and Andy Beard are thanked for their help in the field and on the SEM respectively. Alison Longbottom is thanked for her help at The Natural History Museum, London, whilst photographic staff at that museum are thanked for providing photographs of some specimens. The management of Huntsman's Quarries, Naunton, Woodeaton Quarry, Oxford and Castle Cement, Ketton are thanked for allowing access to sites. Jürgen Kriwet and a second referee are thanked for their input.

REFERENCES

APPLEGATE, S. P. 1972. A revision of the higher taxa of orectolobids. *Marine Biological Association of India Publication*, **14**, 743–751.

ARKELL, W. J. 1947. *The geology of the country around Weymouth, Swanage, Corfe and Lulworth.* Memoir of the Geological Survey, HMSO, London, 386 pp.

AYRES, W. O. 1855. A shark of a new generic type: *Notorynchus maculatus. Proceedings of the Californian Academy of Natural Sciences*, **1**, 72–73.

BEAUMONT, G. de 1960. Observations préliminaires sur trois sélaciens nouveaux du Calcaire lithographique d'Eichstät (Baviere). *Ecologae Geologicae Helvetiae*, **53**, 315–328.

BENTON, M. J. and SPENCER, P. J. 1995. *Fossil reptiles of Great Britain.* Joint Nature Conservation Committee, Chapman & Hall, London, 386 pp.

BERG, L. S. 1940. Classification of fishes, both recent and fossil. *Transactions of the Institute of Zoology, Academy of Sciences of the USSR*, **5**, 85–517. [In Russian].

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.

BLAINVILE, H. M. D. de 1816. Prodrome d'une distribution systématique du regne animal. *Bulletin de la Société Philomatique de Paris*, **8**, 105–124.

BLOCH, M. E. and SCHNEIDER, J. G. 1801. Systema Ichthyologiae iconibus cx illustratum. Post obitum auctoris opus inchoatum absolvit, correxit, interpolavit Jo. *Sumtibus Austoris Impressum et Bibliopolio Sanderiano Commissum. Systema Ichthyologica*. i–lx + 1–584.

BONAPARTE, C. L. J. L. 1832–38. Selachorum tabula analytica. *Nuovi Annali delle Scienze Naturali*, **1**, 195–214.

CANDONI, L. 1993. Découverte de *Parasymbolus* gen. et sp. nov. (Scyliorhinidae-Elasmobranchii) dans le Kimméridgien de Normandie, France. *Professional Paper of the Belgian Geological Survey*, **264**, 147–156.

—— 1995. Deux faunes inédites se sélaciens dans le Jurassique terminal Francais – premiers résultats stratigraphiques. *Bulletin de la Société Géologique Normandie et Amis Muséum de Havre*, **82**, 29–49.

CAPPETTA, H. 1977. Observations sur quelques selaciens du Crétacé Supérieur d'Angleterre avec la description d'un genre nouveau. *Geobios*, **10**, 479–485.

—— 1986. Types dentaires adaptatifs chez les sélaciens actuels et post-Paléozoiques. *Palaeovertebrata*, **16**, 57–76.

—— 1987. Mesozoic and Cenozoic elasmobranchii. Chondrichthyes II. *In* SCHULTZE, H. P. (ed.). *Handbook of Paleoichthyology*, **3B**. Gustav Fischer Verlag, Stuttgart, 193 pp.

—— 1990. Hexanchiforme nouveau (Neoselachii) du Cretace Inférieur du Sud de la France. *Palaeovertebrata*, **20**, 33–54.

—— 1992. New observations on the palaeospinacid dentition (Neoselachii, Palaeospinacidae). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1992**, 565–570.

CARVALHO, M. R. de and MAISEY, J. G. 1996. Phylogenetic relationships of the Late Jurassic shark *Protospinax* Woodward 1919 (Chondrichthyes: Elasmobranchii). 9–49. *In* ARRATIA, G. and VIOHL, G. (eds). *Mesozoic fishes – systematics and paleoecology.* Verlag Friedrich Pfeil, München, 576 pp.

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. Révision 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), 563 pp.

—— 1977. Phyletic relationships of living sharks and rays. *American Zoologist*, **17**, 303–322.

—— 1984. FAO species catalogue. Sharks of the world. *An annotated and illustrated catalogue of shark species known to date, part 2 (Carcharhiniformes)*. FAO, Roma, 251–655

CUNY, G. and BENTON, M. J. 1999. Early radiation of the neoselachian sharks in western Europe. *Geobios*, **32**, 193–204.

DALINKEVICIUS, J. A. 1935. On the fossil fishes of the Lithuanian Chalk. I. Selachii. *Mémoires de la Faculté des Sciences de l'Université de Vytautas le Grand*, **9**, 247–305.

DELSATE, D. and CANDONI, L. 2001. Description de nouveaux morphotypes dentaires de Batomorphii toarciens (Jurassique inférieur) de Bassin de Paris: Archaeobatidae nov. fam. *Bulletin de la Société Naturelle du Luxembourg*, **102**, 131–143.

—— and DUFFIN, C. 1993. Chondrichthians du Sinémurien de Belgique. *Professional Paper of the Belgian Geological Survey*, **264**, 103–136.

—— and GODEFROIT, P. 1994. Chrondrichthyens du Toarcien inférieur d'Aubagne (Lorraine belge). *Professional Paper of the Belgian Geological Survey*, **278**, 23–43.

DINELEY, D. L. and METCALF, S. J. 1999. *Fossil fishes of Great Britain*. Joint Nature Conservation Committee. Chapman & Hall, London, 675 pp.

DUFFIN, C. J. 1982. Teeth of a new selachian from the Upper Triassic of England. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1982**, 156–166.

—— 1988. The Upper Jurassic selachian *Palaeocarcharias* de Beaumont (1960). *Zoological Journal of the Linnean Society*, **94**, 271–286.

—— and WARD, D. J. 1983. Teeth of a new neoselachian shark from the British Lower Jurassic. *Palaeontology*, **26**, 839–844.

—— —— 1993. The Early Jurassic palaeospinacid sharks of Lyme Regis, southern England. *Professional Paper of the Belgian Geological Survey*, **264**, 53–102.

EGERTON, P. G. 1872. *Palaeospinax priscus*. Figures and descriptions illustrative of British organic remains. *Memoirs of the Geological Survey of the United Kingdom*, *Decade 13*. HMSO, London, 1–3, pl. 7.

EVANS, S. E. and MILNER, A. R. 1994. Microvertebrate faunas from the Middle Jurassic of Britain. 303–321. *In* FRASER, N. and SUES, H. D. (eds). *In the shadow of the dinosaurs: early Mesozoic tetrapods*. Cambridge University Press, Cambridge, 435 pp.

FRAAS, O. 1885. Beiträge zum obersten Weissen Jura in Schwaben. *Wuttenberg Jahrbuch*, **11**, 77–107.

FOWLER, H. W. 1941. The fishes of the groups Elasmobranchii, Holocephali, Isospondyli, and Ostariophysi obtained by US Bureau of Fishing Steamer *Albertross* in 1907 to 1910, chiefly in the Philippine Islands and adjacent seas. *Bulletin of the United States Natural History Museum*, **100** (13), 1–879.

FREEMAN, E. F. 1979. A Middle Jurassic mammal bed from Oxfordshire. *Palaeontology*, **22**, 135–166.

GARMAN, S. 1913. The Plagiostomia (sharks, skates and rays). *Memoirs of the Museum of Comparative Zoology, Harvard College, Cambridge*, **36**, 1–515.

GILL, T. 1862. Analytical analysis of the order of Squali and revision and nomenclature of genera. *Annals of the Society of Natural History of New York*, **7**, 367–408.

GIRARD, C. F. 1855. Characteristics of some cartilaginous fishes of the Pacific coast of North America. *Proceedings of the Academy of Natural Sciences, Philadelphia*, **7**, 196–197.

GRAY, J. E. 1851. *List of specimens of fish in the collection of the British Museum*, *Part 1*. British Museum (Natural History), London, 160 pp.

HAY, O. P. 1902. Bibliography and catalogue of the fossil vertebrata of North America. *Bulletin of the United States Geological Survey*, **179**, 1–868.

HERMAN, J. 1977. Les Sélachians néocrétacés et paléocènes de Belgique et des contrées limitrophes eléments d'une biostratigraphie intercontinentale. *Mémoires pour Server à l'Explication des Cartes Géologiques et Minières de la Belgique*, **15**, 1–450.

—— HOVESTADT-EULER, M. and HOVESTADT, D. C. 1990. Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living supraspecific taxa of chondrichthyan fishes. STEHMANN, M. (ed.). Part A: Selachii. No. 2b: Order: Carcharhiniformes – Family: Scyliorhinidae. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique*, *Biologie*, **60**, 181–230.

—— —— —— 1991. Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living supraspecific taxa of chondrichthyan fishes. STEHMANN, M. (ed.). Part A: Selachii. No. 2c: Order: Carcharhiniformes – Families: Proscylliidae, Hemigaleidae, Pseudotriakidae, Leptochariidae and Carcharhinidae. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique*, *Biologie*, **61**, 73–120.

—— —— —— 1992. Contributions to the study of the comparative morphology of teeth and other relevant

ichthyodorulites in living supraspecific taxa of chondrichthyan fishes. STEHMANN, M. (ed.). Part A: Selachii. No. 4: Order: Orectolobiformes – Families: Brachaeluridae, Ginglymostomatidae, Hemiscylliidae, Orectolobidae, Parascylliidae, Rhynchodontidae, Stegostomatidae. Order: Pristiophorifirmes – Family: Pristiophoridae. Order: Squatiniformes – Family Squatinidae. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique*, *Biologie*, **62**, 193–254.

—— —— —— 1993. Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living supraspecific taxa of chondrichthyan fishes. STEHMANN, M. (ed.). Part A: Selachii. No. 1b: Order: Hexanchiformes – Family: Chlamydoselachidae; No. 5: Order: Heterodontiformes – Family: Heterodontidae; No. 6: Order: Lamniformes – Families: Cetorhinidae, Megachasmidae; Addendum 1 to No. 3: Order Squaliformes; Appendum 1 to No. 4: Order: Orectolobiformes; General glossary; Summary Part A. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique*, *Biologie*, **63**, 185–256.

HILGENDORF, F. M. 1904. Ein neuer *Scyllium*-artiger Haifisch, *Proscyllium habereri*, nov. subgen., n. spec. von Formosa. *Sitzungsberichte der Gesellshaft Naturforschender Freunde zu Berlin*, **2**, 39–41.

HORTON, A., SUMBLER, M. G., COX, B. M. and AMBROSE, K. 1995. *Geology of the country around Thame*. Memoir of the British Geological Survey. HMSO, London. 168 pp.

KOKEN, E. 1911. Pisces. *In* ZITTEL, K. A. von, *Grundzüge der Paläontologie, Zweite Abteilung, Vertebrata*. Second edition. München and Berlin, 3–142.

LEIDNER, A. and THIES, D. 1999. Placoid scales and oral teeth of Late Jurassic elasmobranchs from Europe. 29–40. *In* ARRATIA, G. and SCHULTZE, H.-P., (eds). *Mesozoic fishes 2 – systematics and fossil record.* Verlag Friedrich Pfeil, München.

LINNAEUS, C. 1758. *Systema naturae.* Tenth edition, vol. 1. Salvi, Stockholm, 824 pp.

MACKIE, S. J. 1863. On a new species from the Lower Chalk. *The Geologist*, **6**, 241–246.

MAISEY, J. G. 1976*a*. The Middle Jurassic selachian fish *Breviacanthus* n.g. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1976**, 432–438.

—— 1976*b*. The Jurassic selachian fish *Protospinax* Woodward. *Palaeontology*, **19**, 733–747.

—— 1985. Cranial morphology of the fossil elasmobranch *Synechodus dubrisiensis*. *American Museum Novitates*, **2804**, 1–28.

MARCK, W. von der 1863. Fische der Oberen Kreide Westfalens. *Paleontographica, Cassel*, **11**, 233–267.

MARTILL, D. M. 1991. Fish. 197–225. *In* MARTILL, D. M. and HUDSON, J. D. (eds). *Fossils of the Oxford Clay*. The Palaeontological Association, Field Guides to Fossils, **4**, 286 pp.

METCALF, S. J., VAUGHAN, R. F., BENTON, M. J., COLE, J., SIMMS, M. J. and DARTNELL, D. L. 1992. A new Bathonian (Middle Jurassic) microvertebrate site, within the Chipping Norton Limestone Formation at Hornsleasow Quarry, Gloucestershire. *Proceedings of the Geologists' Association*, **103**, 321–342.

MCKERROW, W. S., JOHNSON, R. T. and JAKOBSON, M. E. 1969. Palaeoecological studies in the Great Oolite at Kirtlington, Oxfordshire. *Palaeontology*, **12**, 56–83.

MÜLLER, J. and HENLE, J. 1838–41. *Systematische beschreibung der Plagiostomen*. Veit and Co., Berlin, 200 pp.

NOUBHANI, A. and CAPPETTA, H. 1997. Les Orectolobiformes, Carchariniformes, et Myliobatiformes (Elasmobranchii, Neoselachii) des Bassins à phosphate du Maroc (Maastrichtian–Lutétien basal). *Palaeo Ichthyologica*, **8**, 1–327.

PENN, I. E. 1982. Middle Jurassic stratigraphy and correlation of the Winterborne Kingston borehole, Dorset. 53–76. *In* RHYS, G. H., LOTT, G. K. and CALVER, M. A. (eds). *The Winterborne Kingston borehole, Dorset, England.* Institute of Geological Sciences Report **81/3**. HMSO, London, 196 pp.

PHILLIPS, J. 1871. *Geology of Oxford and the valley of the Thames.* Clarendon, Oxford, 529 pp.

PLIENINGER, T. 1847. Die Wirbeltierreste im Korallenkalk von Schnaitheim. *Wuttenberg Jahrbuch*, **3**, 227.

REES, J. 1998. Early Jurassic selachians from the Hasle Formation on Bornholm, Denmark. *Acta Palaeontologica Polonica*, **43**, 439–452.

—— 2000. A new Pliensbachian (Early Jurassic) neoselachian shark fauna from southern Sweden. *Acta Palaeontologica Polonica*, **45**, 407–424.

REGAN, C. T. 1906. A classification of selachian fishes. *Proceedings of the Zoological Society of London*, **1906**, 722–758.

SAUVAGE, H.-E. 1873. Notice sur un spathobate du terrain portlandien de Boulogne-sur-Mer. *Bulletin de la Société Académique de Boulogne-sur-Mer*, **2**, 94–103.

SAVAGE, R. 1977. The Mesozoic strata of the Mendip Hills. 85–100. *In* SAVAGE, R. (ed.). *Geological Excursions in the Bristol District.* University of Bristol Press, 196 pp.

SCHWEIZER, R. 1964. Die elasmobranchier und holocephalen aus den Nusplinger plattenkalken. *Palaeontographica Abteilung A*, **123**, 58–110.

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, xiii + 496 pp.

SUMBLER, M. G. and BARRON, A. J. M. 1996. The type section of the Hampen Formation (Middle Jurassic, Great Oolite Group) at Hampen Cutting, Gloucestershire. *Proceedings of the Cotteswold Naturalists Field Club*, **151**, 118–128.

THIES, D. 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.

—— 1989. Some problematical sharks teeth (Chondrichthyes, Neoselachii) from the Early and Middle Jurassic of Germany. *Palaeontologische Zeitschrift*, **63**, 103–117.

—— 1992. A new species of *Palaeospinax* (Chondrichthyes, Neoselachii) from the Lower Jurassic *Posidonia* Shale of southern Germany. *Palaeontologische Zeitschrift*, **66**, 137–146.

THIOLLIERE, V. J. 1854. Descriptions des poissons fossiles provenant des gisements coralliens du Jura dans le Bugey. *Annales des Sciences Physiques et Naturelles, 2ième Série*, **4**, 1–27.

UNDERWOOD, C. J. 2002. Sharks, rays and a chimaeroid from the Kimmeridgian (Late Jurassic) of Ringstead, southern England. *Palaeontology*, **45**, 297–325.

—— and MITCHELL, S. H. 1999. Albian and Cenomanian selachian assemblages from North East England. 9–59. *Special Papers in Palaeontology*, **60**, 220 pp.

—— —— and VELTKAMP, C. J. 1999*a*. Microborings in mid Cretaceous fish teeth. *Proceedings of the Yorkshire Geological Society*, **52**, 269–274.

—— —— —— 1999*b*. Shark and ray teeth from the Hauterivian (Lower Cretaceous) of north-east England. *Palaeontology*, **42**, 287–302.

—— and REES, J. 2002. Selachian faunas from the earliest Cretaceous Purbeck Group of Dorset, southern England. *Special Papers in Palaeontology*, **68**, 83–101.

—— and WARD, D. J. in press. Environmental distribution of Bathonian (Middle Jurassic) neoselachians in southern England. *In* ARRATIA, G. (ed.). *Mesozoic fishes 3 – systematics and palaeoecology.* Verlag Friedrich Pfeil, München.

WAGNER, J. A. 1857. Charakteristik neuer Arten von Knorpelfischen aus den lithographischen Schiefern der Umgegend von Solnhofen. *Gelehrte Anzeiger Bayer Akademie Wissenschaft*, **44**, 288–293.

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 Research*, **1**, 89–106.

WERNER, C. 1989. Die elasmobranchier-fauna des Gebel Dist Member der Bahariya Formation (Obercenoman) der Oase Bahariya, Ägypten. *Palaeo Ichthyologica*, **5**, 1–111.

WOODWARD, A. S. 1888. On the Cretaceous selachian genus *Synechodus*. *Geological Magazine*, **3**, 496–499.

—— 1889. *Catalogue of the fossil fishes in the British Museum. Part 1*. British Museum (Natural History), London, 474 pp.

—— 1890. A synopsis of the fossil fishes of the English Lower Oolites. *Proceedings of the Geologists' Association*, **11**, 285–306.

—— 1918. On two new elasmobranch fishes (*Crossorhinus jurassicus* sp. nov. and *Protospinax anectans* sp. nov.) from the Upper Jurassic lithographic stone of Bavaria. *Proceedings of the Zoological Society of London*, **1918**, 231–235.

WYATT, R. J. and CAVE, R. 2002. The Chalfield Oolite Formation (Bathonian, Middle Jurassic) and the Forest Marble overstep in the South Cotswolds, and the stratigraphical position of the Fairford Coral Bed. *Proceedings of the Geologists' Association*, **113**, 139–152.

YOUNG, T. 1982. Neoselachian sharks from the Middle Jurassic of England. *The Sheffield University Geological Society Journal*, **8**, 24–31.

C. J. UNDERWOOD

School of Earth Sciences, Birkbeck College
Malet Street
London WC1E 7HX, UK
e-mail c.underwood@bbk.ac.uk

D. J. WARD

Crofton Court
81 Crofton Lane,
Orpington, Kent BR5 1HB, UK
e-mail david@fossil.ws

Typescript received 13 August 2002
Revised typescript received 5 February 2003