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HYBODONT SHARKS OF THE ENGLISH BATHONIAN AND CALLOVIAN (MIDDLE JURASSIC)

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Abstract: Recent bulk sampling and study of museum collections has revealed a high diversity of hybodont sharks from the English Bathonian, with 15 species being recognised. In addition, study of dental and skeletal material from the English Callovian has allowed the diagnosis of a new genus and species, *Planohybodus peterboroughensis* gen. et sp. nov., allowing the Bathonian species *Hybodus grossiconus* Agassiz to be referred to *Planohybodus*. Two additional new genera, *Secarodus* and *Frangerodus*, are erected for the Bathonian taxa *Hybodus polyprion* Agassiz and *Strophodus lingualis* Woodward, respectively. *Egertonodus duffini* sp. nov. is described

and the diagnosis of *Egertonodus* based on dental material is discussed. The previously unrecorded *Hybodus* sp., *Parvodus* sp., and *Lonchidion* sp. are recognised but left in open nomenclature. *Asteracanthus medius* (Owen) is recorded in the British Bathonian for the first time, and the status of Bathonian nominal species of *Asteracanthus* are assessed. Bathonian hybodonts showed great diversity in trophic ecology and many of the species are specific to particular palaeoenvironments.

Key words: Bathonian, England, hybodont, Jurassic, palaeoecology, shark, taxonomy.

TEETH and fin spines of hybodont sharks have been recorded from rocks of the British Bathonian (Middle Jurassic) since the earliest days of geology. Despite numerous specimens being figured and named in publications dating from the nineteenth century (e.g. Agassiz 1833–44; Phillips 1871; Woodward 1889), there has been very little subsequent work. In addition, almost all of the studies have dealt only with material from inshore carbonate facies, the vast majority having originated from the Stonesfield Slate. Our recent work on hybodonts from other areas (Rees and Underwood 2006) and time intervals (Rees 2002; Rees and Underwood 2002; Underwood and Rees 2002) has shown that the taxonomy of hybodonts is in urgent need of revision.

The Middle Jurassic marks an important period in the history of the hybodonts, representing a transition interval between the very different assemblages of the Triassic–Early Jurassic and the Late Jurassic–Cretaceous. During much of the Triassic and Early Jurassic, hybodonts were the dominant group of selachians within the majority of both marine and non-marine environments. By the Late Jurassic, however, hybodonts had become relatively minor components of open marine selachian assemblages, having been largely replaced by the neoselachians, and only remained diverse within restricted marine and fluvial settings, a situation that continued throughout the Cretaceous Period.

GEOLOGICAL SETTING

The majority of the Bathonian of southern and central England is included in the Great Oolite Group. Despite this name, oolitic limestones are just one of many facies present, and the group contains rocks representing a wide range of depositional environments, many of which contain abundant selachian remains (see Underwood 2004). There is a general trend from restricted marine and lagoonal facies in east-central England, through a carbonate, commonly oolitic, barrier or shelf in south-central England, to open marine facies near the south coast. There is a general southerly progradation of the carbonate shelf during much of the Bathonian, and numerous periods of minor relative sea-level change causing rapid facies changes at many localities. During the late Bathonian, the carbonate barriers largely broke down, and the superficially more homogeneous Forest Marble Formation was deposited, comprising channel fills of bioclastic limestone within either lagoonal or open marine mudstones. For a more detailed account of the geology of the English Middle Jurassic and the correlation of lithostratigraphic names used below, see Cope *et al.* (1980).

Bathonian sedimentary rocks are also present elsewhere in Britain. The fluvial facies of the English North East are at least partly Bathonian in age, but have not yielded

identifiable selachian material. In the Hebridean region of Scotland, Bathonian strata representing mainly freshwater and lagoonal environments are well represented and some horizons contain abundant hybodont faunas (e.g. Rees and Underwood 2006).

MATERIAL AND METHODS

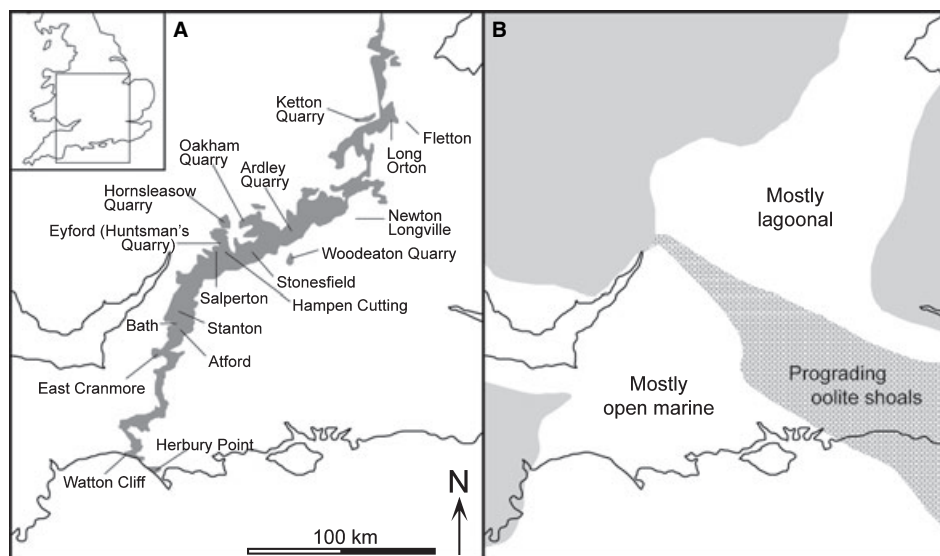
This study made use of both the large collections available within museums, especially the Natural History Museum, London, and large numbers of specimens collected from sites across southern and central England (Text-fig. 1), largely by bulk sampling. Soft mudstones and marls were broken down in water before being wet sieved. The residue was then treated with 10% buffered acetic acid to remove shell and other carbonate material. Samples of limestones were dissolved in buffered acetic or formic acid. All sieve fractions above 355 μm were picked for selachian remains and some samples were searched at fractions down to 250 μm . For more details on sampling methods, see Underwood and Ward (2004).

SAMPLE SITES

A large number of samples were collected and processed for selachian remains during the course of this study. Many of the hybodonts were recovered from neosela-

chian-bearing samples described in Underwood and Ward (2004), with additional material having been subsequently collected from several sites (Text-fig. 1). A number of samples are not included here as they yielded no hybodont material, being either barren of selachian material altogether, or yielding only remains of neoselachians.

Watton Cliff, Dorset (SY449909). Several horizons were collected from this locality. All of these contained neoselachian remains (Underwood and Ward 2004), and three yielded teeth of hybodonts. Large samples from the *Wattonensis* Beds yielded only three teeth of two taxa. A fault bounded unit of black, laminated mudstone containing a 5–10-cm oyster-belemnite bed was considered by Underwood and Ward (2004) to overly the *Wattonensis* Beds. A sample of 250 kg from this shell bed produced large numbers of selachian remains, including numerous hybodont teeth, but of only three species. Two horizons were sampled from the overlying Forest Marble Formation. Samples of the brachiopod-rich Boueti Bed (see Arkell 1947 for details) yielded few hybodont teeth, but in contrast, a unit of bioclastic limestone higher in the succession has yielded the most diverse hybodont assemblage recorded during this study. Samples totaling of over 400 kg of unlithified lenses of bioclastic material were sampled, the majority by David Ward, with additional sampling by us. In addition to tetrapod and neoselachian material previously described (e.g. Evans and Milner 1994; Ward in Dineley and Metcalf 1999; Underwood and Ward 2004), large numbers of hybodont teeth of variable preservation were recovered including the only tooth of *Secarodus polyprion* (Agassiz, 1843) discovered in our samples.



TEXT-FIG. 1. Maps of southern England showing, A, areas of Bathonian outcrop and the field sites mentioned in the text and, B, generalised palaeogeographical reconstruction of the Middle Bathonian; grey shading indicates Bathonian land areas. Note that locality names are those used on museum labels and some may differ from place names as currently in use (see text).

Herbury Point, Dorset (SY613808). Samples of the Boueti Bed (see Arkell 1947 for details) were collected after being partly sieved in the field. Only very rare hybodont remains were found.

East Cranmore, Somerset (ST687435). A sample of 50 kg of shelly marl was collected from a temporary exposure of about 2 m of nodular brachiopod limestones of the upper Fullers Earth Rock Formation. Very rare hybodont remains were recovered in a total of four teeth, but these included the only two specimens of *Frangerodus lingualis* (Woodward, 1889) collected during this study. See Savage (1977) for regional details.

Hampen Railway Cutting, Gloucestershire (SP057202). Several horizons were sampled within this disused railway cutting (see Sumbler and Barron 1996), but only two yielded rare hybodont teeth, one from near the base of the exposed section within the limestones of the Eyford Member, and the other from Bed 50 (of Sumbler and Barron 1996) of the Hampen Formation. Other samples yielded neoselachian remains but no hybodonts.

Hornsleasow Quarry, Gloucestershire (SP131322). Although rare hybodont teeth have been recorded from the Hornsleasow Clay (see Metcalf *et al.* 1992) within the Chipping Norton Limestone Formation, this horizon was not re-sampled owing to its extremely low yield of selachian material. Over 100 kg of samples were collected from the middle and upper parts of an overlying coral-bearing mudstone, which is within a facies transition between the Sharps Hill Formation and lower Fullers Earth Formation. These yielded rather low diversity assemblages of hybodont teeth, mostly of small taxa, but also included the only large *Asteracanthus* tooth collected during this study.

Woodeaton Quarry, Oxfordshire (SP534122). Exposing much of the Great Oolite Group (see Horton *et al.* 1995, although more of the lower part of the succession has been exposed since this publication), a number of samples were collected from this site (see Underwood and Ward 2004), but only a few yielded hybodont remains. Nine teeth were recorded from samples close to the contact between the Rutland Formation and the White Limestone Formation. The oyster-rich Bed 17 (of Horton *et al.* 1995) was the only other level of the White Limestone that yielded hybodont teeth, although these were scarce. More abundant hybodont remains were recovered from bioclastic limestones within the Forest Marble Formation at this quarry.

Oakham Quarry, Warwickshire (SP282307). This quarry exposes about 0.9 m of a *Placunopsis* shell bed at the base of the Sharps Hill Formation. A sample of 30 kg from this bed yielded 35 hybodont teeth, primarily of *Lissodus* spp. This was the only English locality that yielded hybodonts but no neoselachian teeth.

Ketton Quarry, Rutland (SK973058). Much of the local Great Oolite Group is exposed within the south face of this large quarry. Samples of shelly mudstone from the basal parts of five of the shallowing-upwards cycles of the upper part of the Rutland Formation produced rare hybodont teeth of three taxa. Additional hybodont material was collected from an

oyster-rich clay bed at the top of the Blisworth Limestone Formation.

MUSEUM MATERIAL

In addition to hybodont material collected during this study, numerous specimens in the collections of the Natural History Museum, London (NHM) and the British Geological Survey, Keyworth, were also studied. Much of the locality information on this material is vague, but the following sites are given as the provenance for specimens figured herein (see Text-fig. 1).

Stanton, Wiltshire. Of the two villages in Wiltshire sharing this name, the locality is certain to be close to Stanton Saint Quintin, which is a very short distance from the vertebrate site at Leigh Delamere (Evans and Milner 1994). Matrix on some of the specimens from Stanton confirms that these are likely to have originated from bioclastic limestones within the Forest Marble Formation.

Atford, Wiltshire. The area around Atworth, known as Atford in the past, once had several quarries working irregularly fissile bioclastic limestones of the Forest Marble Formation. Large numbers of hybodont and other vertebrate remains are present in museum collections from this area, but the majority of specimens are heavily abraded.

Bath, Somerset. There are numerous quarries and underground workings in oolitic and bioclastic limestones in the area around Bath. As the specimen from the Bath area has clearly been acid prepared from carbonate matrix, it is not possible to assign it to formation other than that it was from one of the limestone units that are, in this region, largely confined to the Upper Bathonian.

Eyford, Gloucestershire. Numerous quarries, most now infilled, have worked the Eyford Member of the Charlbury Formation around the village of Eyford for fissile silty and micro-oolitic limestones. The largest extant quarry is Huntsman's Quarry (SP122255), which exposes the Eyford Member overlain by Taynton Limestone Formation. Recent sampling at this locality yielded no hybodont remains, although one of us (CJU) has previously seen numerous specimens of several hybodont taxa here. It should be noted that the currently exposed Eyford Member shows a somewhat different facies from those exposed in the past (e.g. Benton and Spencer 1995), with the currently active quarry face being several hundred metres from that worked ten years ago. The Eyford Member as presently exposed shows more obvious cross stratification, higher fine biotrital content and an apparent lower frequency of macroscopic vertebrate material than previously recorded.

Salperton, Gloucestershire. There were formally a number of small quarries near the village of Salperton working the Eyford Member. The specimen figured from this locality is on the

surface of a worked roofing slate of a lithology clearly from the Eyford Member.

Stonesfield, Oxfordshire. By far the most abundant Bathonian hybodont remains in the museum collections studied are from the Stonesfield Slate around Stonesfield. The lithology is a locally developed laminated limestone facies of the Taynton Limestone Formation (see Boneham and Wyatt 1993). It was formerly mined from numerous underground workings around the village of Stonesfield, but no exposures are currently suitable for collection of new material.

Ardley Quarry, Oxfordshire. This large quarry exposes a number of units within the Great Oolite Group (e.g. Palmer and Jenkyns 1975), but it is likely that the teeth figured from this locality originated from one of the clay seams within the White Limestone Formation.

Long Orton, Huntingdonshire. This site probably refers to Orton Longueville, now a suburb of Peterborough. There is some matrix of pale limestone on some specimens, but it is not clear from which part of the Great Oolite Group these specimens are likely to have originated. As there are few limestone units in this area, and it is geographically very close to outcrops of Callovian Clays, it is possible that the fossils originate from the top Bathonian–basal Callovian Cornbrash Formation.

Newton Longville, Huntingdonshire. A single hybodont skull from the Callovian Oxford Clay was studied for comparison with Bathonian material. It was collected from the London Brick Company quarry.

Fletton, Peterborough, Huntingdonshire. Associated hybodont jaw and skull elements and fin spines from the Callovian Oxford Clay were studied for comparison with Bathonian material. Fletton Quarry, now infilled, has been well known for vertebrate fossils (e.g. Benton and Spencer 1995).

Normandy. A single articulated dentition of *Asteracanthus* is labelled as 'Great Oolite, Normandy, France' without further information. The matrix of pale, finely bioclastic limestone compares favourably with several horizons within the Normandy Bathonian, and as a result it is not possible to locate the provenance of this specimen with more precision. Woodward (1889) gives the locality information as close to Caen.

SYSTEMATIC PALAEOLOGY

Descriptive tooth terminology largely follows that of Cappetta (1987) whereas higher systematic relationships are a mixture of Maisey (1989) and Rees and Underwood (2002). All figured specimens are housed at the NHM.

Cohort EUSELACHII Hay, 1902
Superfamily HYBODONTOIDEA Owen, 1846

sensu Zangerl 1981

Family HYBODONTIDAE Owen, 1846
Subfamily HYBODONTINAE Owen, 1846

Genus HYBODUS Agassiz, 1837

Type species. *Hybodus reticulatus* Agassiz, 1837 from the Sinemurian, Lower Jurassic of Lyme Regis, southern England.

Hybodus obtusus Agassiz, 1843

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

- 1843 *Hybodus obtusus* Agassiz, p. 186, pl. 23, figs 43–44.
1889 *Hybodus obtusus* Agassiz; Woodward, p. 272, pl. 11, figs 8–3.
1991 *Hybodus obtusus* Agassiz; Martill, p. 197, pl. 36, fig. 8.

Material. Three complete adult tooth-crowns (P. 2182a, P. 2845c, P. 52522), one juvenile specimen (P. 66487), and a few fragmentary teeth (P. 66488–66489).

Description. The teeth are robust with a low, conical central cusp and two pairs of rather well developed cusplets. A minute outer, third pair may occur. One fragmentary tooth shows four lateral cusplets. The base of the crown is ornamented with frequent large nodes, primarily on the labial side. On the largest nodes, enameloid folds may form an incipient cusplet. Smaller nodes may also occur on the lingual side. The number and size of the nodes appear to be highly variable, and on some fragmentary teeth they may be so common that they almost create a horizontal ridge at the base of the crown. Nodes are commonly situated at the level of the lateral cusplets and on the central cusp. The presence of frequent nodes gives the base of the crown a wide appearance in occlusal view. Other ornamentation includes strong but rather widely spaced enameloid folds over large parts of the crown. These folds are equally well developed on labial and lingual sides of the tooth. Additionally, weak and short folds occur on the lowermost lingual part of the crown, slightly above the crown-root junction. The juvenile tooth-crown is less ornamented than the larger teeth, with both nodes and folds being relatively poorly developed. A rather strong occlusal crest runs across the entire long axis of the tooth. The variation within the Bathonian examples of this species primarily includes differences in height of the central cusp, where lateral teeth have a lower and wider cusp, and the number of nodes. The largest tooth-crown from the English Bathonian measures 11.5 mm but the size of the incomplete specimens implies that the teeth could have been somewhat larger.

Remarks. Although the original material upon which *Hybodus obtusus* was based is Bathonian in age (Agassiz 1843), the occurrences in England are commonly younger (Callovian, Oxfordian, and Kimmeridgian; e.g. Woodward 1889; Martill 1991; Underwood 2002). The frequent nodes and the blunt, conical cusp of the teeth from the

English Bathonian provide clear evidence of their specific affinity. The dentition of *H. obtusus* appears to have experienced little variation with time and is, furthermore, quite homodont with only minor variation in cusp height, number of lateral cusplets, and development of nodes at the labial base of the crown.

In general architecture, the teeth of *H. obtusus* are rather more similar to those of *H. hauffianus* Fraas, 1895 from the Toarcian of southern Germany and *H. delabechei* Charlesworth, 1839 from the Sinemurian of southern England than to those of the type species, *H. reticulatus*. As the skeletal morphologies of all three Early Jurassic species are similar, it is considered here that both *H. hauffianus* and *H. delabechei* should be retained in *Hybodus* (see Maisey 1987). The dental morphology within the genus would consequently include both the slender, high-cusped teeth of *H. reticulatus* and the more robust teeth of *H. delabechei*, *H. hauffianus* and *H. obtusus*, as the last species is dentally similar to *H. hauffianus* in particular. Nodes at the labial base of the crown appear to have developed at several occasions in different hybodont lineages and this character alone thus possesses limited systematic relevance. As a result, the genus *Polyacrodus* Jaekel, 1889 may have to be considered a *nomen dubium* because it is based on a species (*Hybodus polycyphus* Agassiz, 1837) with a dental morphology similar to that of *H. obtusus* and *H. hauffianus* (see also Rees and Underwood 2002). Contrary to conclusions of some previous studies (e.g. Jaekel 1889; Glikman 1964), the orthodont tooth histology of *H. polycyphus* cannot be used to diagnose the genus as variation in histology has proven on several occasions to be highly unreliable in the phylogenetic context (e.g. Patterson 1966; Maisey 1987; Błażejowski 2004). A closer investigation of the dental morphology and heterodonty pattern of *H. polycyphus* is needed, but is beyond the scope of this study.

Occurrence. This species occur as a rare faunal component in samples of the Forest Marble Formation and the Wattonensis Beds at Watton Cliff, whilst a specimen from Ardley Quarry was probably from the White Limestone Formation. This species is also recorded from the Callovian, Oxfordian and Kimmeridgian of southern England (Woodward 1889; Martill 1991; Underwood 2002).

Hybodus sp.

Plate 1, figures 4–12

Material. Four complete tooth-crowns from different parts of the jaw and numerous fragmentary teeth (P. 66490–66494).

Description. The teeth of this species are low and mesio-distally expanded with 1–4 pairs of very low, widely spaced cusplets.

Anterior teeth are less mesio-distally expanded than laterals with a slightly higher cusp and only a single pair of low cusplets. A small labial protuberance occurs in most teeth, being quite robust in anteriors and may be completely lacking in laterals. Posterior teeth possess only incipient cusps and cusplets and have an almost horizontal upper surface. The ornamentation comprises simple folds that are weaker but increasingly densely spaced in teeth situated closer to the commissure of the jaw. In anteriors and laterals, the folds originate mainly from the cusp and cusplets whereas posterior teeth are more evenly striated as folds originate from the occlusal crest. The lower lingual side of the teeth is usually smooth regardless of tooth position. Anterior teeth are curved in occlusal view with the lateral extremities being inclined to the lingual side. This curvature can also be observed in some laterals whereas posterior teeth appear to be close to straight. None of the recorded specimens has a root preserved. The largest tooth-crown is a lateral with a width of 10 mm.

Remarks. Although these teeth undoubtedly represent an undescribed species, we do not consider that the quantity and state of preservation of the specimens is sufficient for a specific diagnosis, and for this reason we prefer to keep the taxon in open nomenclature. The lack of nodes in combination with a very low cusp separates teeth of this species from those of *H. obtusus* (see above) while the strongly mesio-distally expanded crown in laterals and posteriors separates this species from all other Hybodontidae known from the English Bathonian. Apart from the marked size difference, the tooth morphology and heterodonty pattern of *Hybodus* sp. are quite similar to those of '*Polyacrodus*' *gramanni* Duffin and Thies, 1997 and '*Lissodus*' *multicuspidatus* Duffin and Thies, 1997, both from the Kimmeridgian of northern Germany. The teeth of both German species are more strongly ornamented with vertical folds, but nodes appear to be lacking in '*P.*' *gramanni* while they are more frequent and well developed in '*L.*' *multicuspidatus*. Teeth of '*P.*' *gramanni* further possess a wider, more pyramidal central cusp and are not curved in occlusal view. Teeth of '*L.*' *multicuspidatus* also differ from those of *Hybodus* sp. in possessing nodes on the lateral cusplets. As all three species appear to be closely related in sharing a dental morphology with a mesio-distally wide crown and a low cusp, we propose that the two Kimmeridgian species be referred to *Hybodus* rather than '*Polyacrodus*' or *Lissodus* in the future (see also Rees and Underwood 2002) as their teeth are very different from those of the type species, '*P.*' *polycyphus* and *L. africanus* (Broom, 1909) respectively. An additional dentally similar species occurs in marine Valanginian strata in central Poland (JR, pers. obs.).

Occurrence. *Hybodus* sp. is fairly common in the Forest Marble Formation at Watton Cliff and in the black mudstone above the

Wattonensis Beds at the same locality. It has not been recorded in lagoonal facies.

Genus EGERTONODUS Maisey, 1987

Type species. *Hybodus basanus* Egerton, 1845, apparently from the Lower Cretaceous of the Isle of Wight, southern England, although the preservation of the specimen suggests that it is more likely to have originated from near Hastings, Sussex, southern England.

Included species. When erected, *Egertonodus* only included the type species and tentatively *Hybodus fraasi* Brown, 1900 from the Tithonian of southern Germany, although several crucial characters were unknown in the latter species (Maisey 1987). What is preserved of the teeth however, suggest that the dental morphology is very different from that of the type species. It is likely that several other nominal species of *Hybodus* may be placed within *Egertonodus* in light of future research, but at this time, we prefer only to include *E. duffini* described below in addition to the type species. Isolated teeth from the Kimmeridgian of southern England (*Hybodus* sp. 1 of Underwood 2002) suggest the presence of an additional species of *Egertonodus*. The stratigraphical distribution of the genus, as currently identified, includes the Bathonian to the Barremian or Aptian.

Remarks. When originally diagnosed, the dental morphology of *Egertonodus* was not considered as the genus was based primarily on cranial characters (Maisey 1987). We have studied numerous teeth from the type species, *E. basanus*, originating from both southern England and southern Sweden, and this material has allowed us to identify a number of dental characters that separate isolated teeth of *E. basanus* from those of *Hybodus reticulatus*, the type species of *Hybodus*. These characters may be used to determine the generic affinity of species based only on isolated teeth, although they cannot, at

this stage, serve to enlarge the diagnosis of *Egertonodus*. The dental characters that separate the type species of *Egertonodus* and *Hybodus* are: (1) the sigmoidal curvature of the cusp in anterior teeth of *E. basanus* (Rees 2002) is rare or absent in teeth of *H. reticulatus*; (2) labially displaced and strong cutting edges resulting in a more flattened labial surface of the central cusp occur in *E. basanus* whereas the cusp in teeth of *H. reticulatus* is more circular in cross section or has cutting edges placed half-way between labial and lingual sides of the cusp; (3) there are high, slender lateral cusplets in teeth of *E. basanus* as opposed to slightly more stout cusplets in teeth of *H. reticulatus*; (4) there is moderate ornamentation on cusps of *E. basanus* with weak, often bifurcating, folds compared to a more extensive ornamentation with coarser folds in teeth of *H. reticulatus*. Despite these differences, it may still be difficult to separate isolated teeth from the two genera, especially as these characters are not discrete, but it should be possible in many cases if a sufficient number of teeth are at hand.

Egertonodus duffini sp. nov.

Plate 1, figures 13–17; Plate 2, figures 4–10

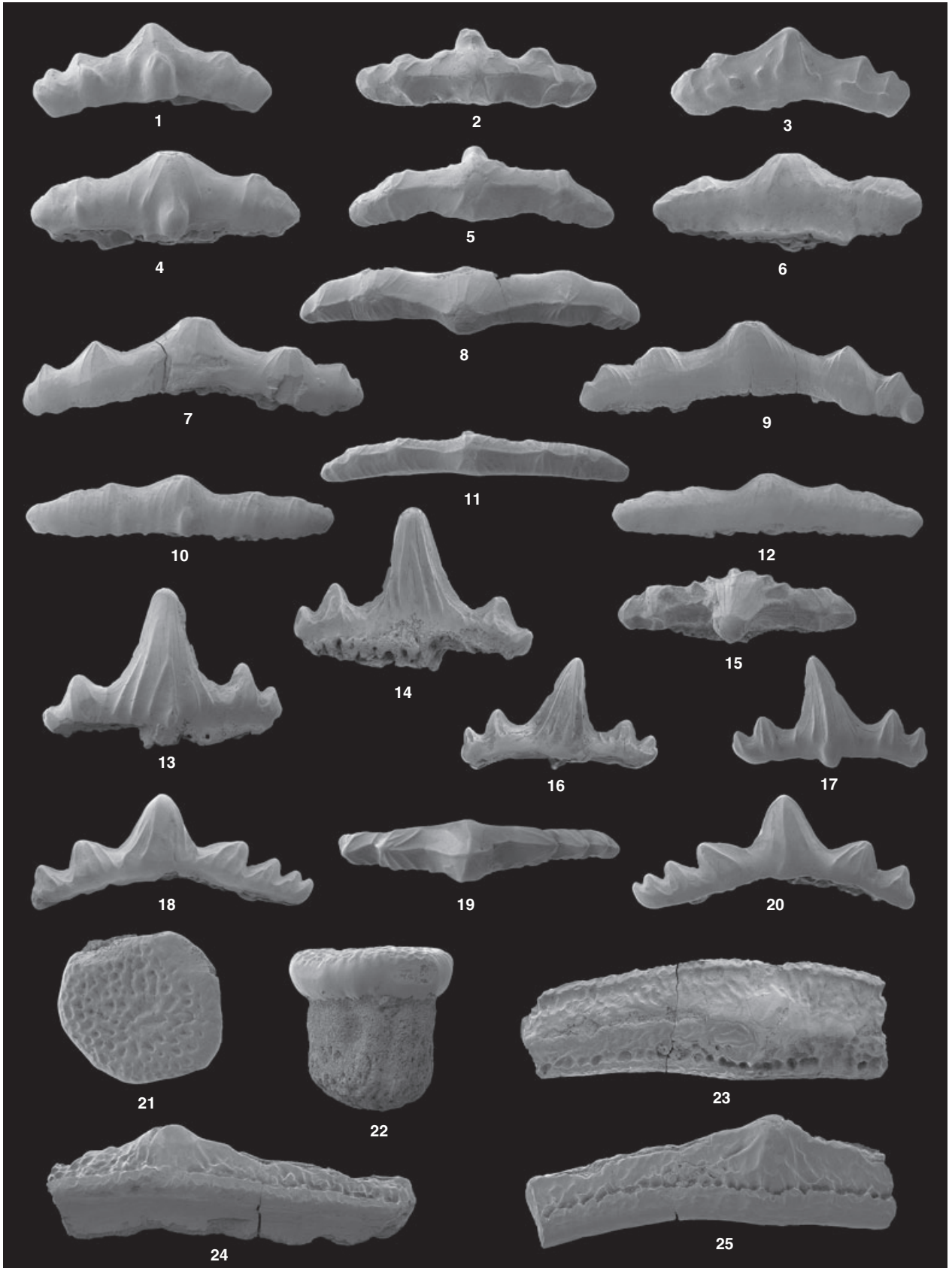
Derivation of name. After Dr Christopher J. Duffin in recognition of his immense work on Mesozoic hybodont sharks.

Type specimen. Holotype, P. 66479, Plate 2, figure 4, complete anterior tooth-crown; paratypes, P. 66480, Plate 2, figure 8, complete lateral tooth-crown and 35495, Plate 2, figure 7, complete anterior tooth-crown.

Type stratum. Stonesfield Slate (Taynton Limestone Formation), Middle Bathonian at Stonesfield, Oxfordshire. Exact horizon unknown.

EXPLANATION OF PLATE 1

- Figs 1–3. *Hybodus obtusus* Agassiz, 1843, P. 66487, juvenile tooth-crown, Forest Marble Formation, Watton Cliff, labial, occlusal, and lingual views; $\times 15$.
- Figs 4–12. *Hybodus* sp. 4–6, P. 66490, anterior tooth-crown, labial, occlusal, and lingual views; $\times 12$. 7–9, P. 66491, lateral tooth-crown, labial, occlusal, and lingual views; $\times 6$. 10–12, P. 66492, posterior tooth-crown, labial, occlusal, and lingual views; $\times 6$. All from Forest Marble Formation, Watton Cliff.
- Figs 13–17. *Egertonodus duffini* sp. nov. 13–15, P. 66495, juvenile tooth-crown, labial, lingual, and occlusal views; $\times 15$. 16–17, P. 66496, juvenile tooth-crown, lingual and labial views; $\times 20$. Both from Forest Marble Formation, Watton Cliff.
- Figs 18–20. *Secarodus polyprion* (Agassiz, 1843), P. 66501, juvenile tooth-crown, Forest Marble Formation, Watton Cliff, lingual, occlusal, and labial views; $\times 15$.
- Figs 21–22. *Asteracanthus* sp., P. 66505, posterior juvenile or embryonic tooth, Boueti Bed, Forest Marble Formation, Watton Cliff, occlusal and lateral views; $\times 15$.
- Figs 23–25. *Frangerodus lingualis* (Woodward, 1889), P. 66506, lateral tooth, Fullers Earth Rock Formation, East Cranmere, occlusal, labial, and lingual views; $\times 8$.



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Additional material. Numerous complete teeth, tooth-crowns and broken teeth including P. 2181, P. 5104, 28590a, 37750, P. 66495, and P. 66496. The teeth originate from all dental positions and represent several ontogenetic stages.

Diagnosis. Large hybodont shark separated from all *Hybodus* and other *Egertonodus* species possessing high, multi-cuspid teeth by the following combination of dental characters: (1) anterior teeth with a high, slender, sigmoidally curved central cusp; (2) strong, somewhat labially displaced cutting edges and a flattened labial surface; (3) three pairs of widely spaced, high, slender lateral cusplets in anterior teeth.

Description. The plentiful material of this species, representing the entire range of variation in ontogeny and jaw position allows a detailed description. Large anterior teeth have a high, relatively slender cusp that is sigmoidal in lateral view. The cutting edges are well developed and situated closer to the labial than to the lingual side of the tooth and occur on both cusp and cusplets. This leads to a somewhat more flattened labial surface of the cusp. In large anteriors, three pairs of high and slender cusplets are common but two pairs may occur on some teeth. Anterior teeth are slightly inclined to the posterior and no completely symmetrical teeth have been seen. The ornamentation of large anteriors is quite variable but always includes weak folds over the lower part of the crown and a smooth tip of the cusp, but folds may also cover the larger part of the cusp. Enameloid folds rarely branch but in some large teeth additional short folds occur on the lower labial rim of the crown. Anterior teeth from young individuals are very close to symmetrical, possess two pairs of cusplets and are more strongly ornamented with relatively coarser folds covering most of the crown. Cutting edges are not particularly well developed and do not seem to be labially displaced in juvenile teeth. In lateral and posterior teeth, the cusp and cusplet height decreases towards the back of the jaw and the cusp is increasingly inclined to the posterior. With decreasing cusp height, the shape becomes slightly stouter. Enameloid folds cover most of the crown in posteriors and distal laterals while mesial laterals possess a smooth upper half of the

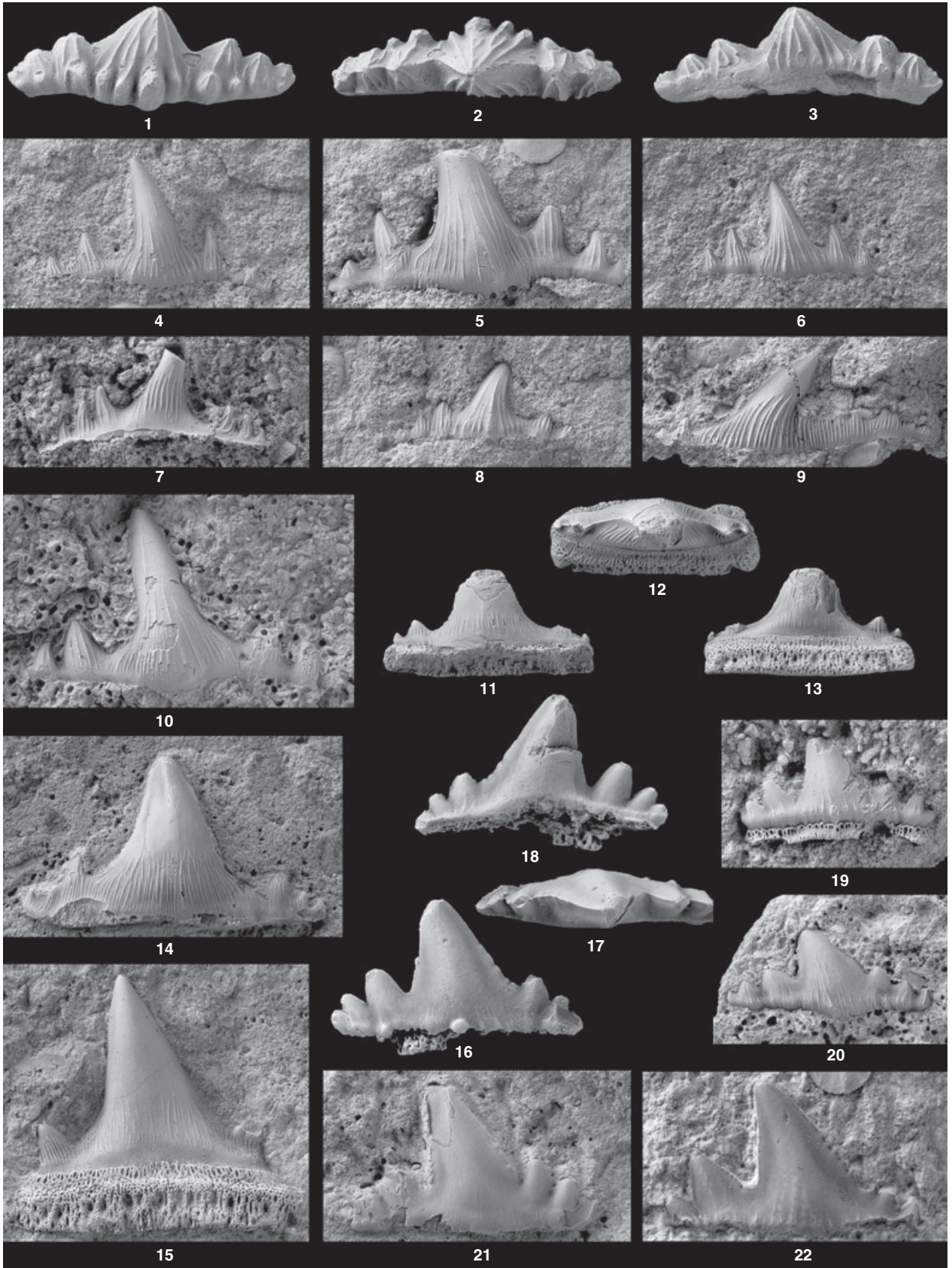
cusp. Posterior teeth are very low, covered by folds and possess up to three pairs of very low cusplets. Apart from the size difference, juvenile lateral and posterior teeth are similar to those of adults but may differ in the development of cusplets and in that the ornamentation is relatively coarser, as in anterior juvenile teeth. Only small parts of the root have been preserved in different specimens and these show a porous texture with numerous large foramina randomly placed all over the root. The size variation of this species is large and the mesio-distal width range from 1.3–15.3 mm.

Remarks. The general dental morphology and heterodonty pattern of *E. duffini* is very similar to that of *E. basanus* from Lower Cretaceous deposits of Europe and North Africa. All characters included above as typical for *Egertonodus* are shared by the two species and the generic affinity of the new species can be regarded as resolved. The differences between *E. basanus* and *E. duffini* are small and include a more slender cusp and higher lateral cusplets in antero-laterals of *E. duffini* (cf. Maisey 1983, fig. 18) occurring in three pairs as opposed to commonly two pairs in *E. basanus*. Large tooth-crowns of the former species are further more mesio-distally expanded and juveniles and laterals may possess an enlarged labial fold or even a small node at the base of the crown, a feature not seen in *E. basanus*. Juvenile teeth of *E. duffini* are strikingly similar to adult anterior teeth of *Hybodus parvidens* Woodward, 1916 from the Lower Cretaceous of north-west Europe, although teeth of intermediate morphology show that these are juvenile *E. duffini* and do not represent a separate taxon. Teeth of *H. parvidens* are more coarsely ornamented, with a strong central labial fold and have lingually inclined lateral extremities of the teeth causing a curved appearance in occlusal view (see Rees 2002).

Occurrence. This species is widespread in the English Bathonian and is frequent in most sampled horizons in addition to numerous localities that have yielded specimens in the collection at the

EXPLANATION OF PLATE 2

- Figs 1–3. *Hybodus obtusus* Agassiz, 1843, P. 52522, tooth-crown, ?White Limestone Formation, Ardley Quarry, labial, occlusal, and lingual views; $\times 3$.
- Figs 4–10. *Egertonodus duffini* sp. nov. 4, holotype, P. 66479, anterior tooth-crown, labial view. 5, 28590a, anterior tooth-crown, labial view. 6, P. 2181, antero-lateral tooth-crown, labial view. 7, paratype, 35495, anterior tooth-crown, lingual view. 8, paratype, P. 66480, antero-lateral tooth-crown, labial view. 9, P. 5104, lateral tooth-crown, labial view. 10, 37750, anterior tooth-crown, labial view. All from Stonesfield Slate, Stonesfield; $\times 3$.
- Figs 11–15. *Planohybodus grossiconus* (Agassiz, 1843). 11–13, P. 52523, upper anterior tooth, ?White Limestone Formation, Ardley Quarry, labial, occlusal, and lingual views. 14, P. 2841, upper anterior tooth-crown, Stonesfield Slate, Stonesfield, labial view. 15, P. 29994, lower anterior tooth, Eyford Member, Salperton, lingual view. All $\times 2$.
- Figs 16–22. *Secarodus polyprion* (Agassiz, 1843). 16–18, P. 66486, anterior tooth-crown, horizon unknown, Bath, labial, occlusal, and lingual views. 19, 38026, anterior tooth, Stonesfield Slate, Stonesfield, labial view. 20, 39778, lateral tooth-crown, Stonesfield Slate, Stonesfield, labial view. 21, P. 2845, anterior tooth-crown, Stonesfield, labial view. 22, P. 2186, anterior tooth-crown, horizon unknown, Bath, labial view. All $\times 3$.



REES and UNDERWOOD, hybodont sharks

NHM. This is one of few species recorded in offshore, inshore, and lagoonal facies.

Genus *PLANOHYBODUS* gen. nov.

Derivation of name. Latin *planus*, flat, and *Hybodus*, in reference to the labio-lingually flattened teeth of this genus and its close relationship to *Hybodus*.

Type species. *Planohybodus peterboroughensis* sp. nov. from the Callovian, Middle Jurassic of Peterborough, southern England.

Included species. Apart from the two Middle Jurassic species *P. peterboroughensis* (type species) and *P. grossiconus* (see below), we also include '*Hybodus*' *ensis* Woodward, 1916 from the Berriasian–Barremian of southern England. All three species display great dentitional similarity and together they provide a stratigraphical distribution of *Planohybodus* from the Bathonian to the Barremian. Another, undescribed species with strongly ornamented teeth occurs rarely in the Berriasian of Bornholm, Denmark (*Hybodus* sp. 4 of Rees 2001).

Diagnosis. Hybodont shark with a dentition that can be separated from all other hybodont genera by the following combination of dental characters: (1) high and wide, labio-lingually flattened cusp; (2) strongly developed cutting edges; (3) ornamentation with short, simple folds; (4) porous, lingually projected root lacking arranged differentiated foramina. Additionally, two spine characters are included: (5) two pairs of irregularly ornamented cephalic spines with a lower barb and T-shaped basal plate; (6) dorsal fin spines with lateral ribs diverting posteriorly on the lower half of the spine.

Remarks. Teeth of *Planohybodus* can be separated from those of *Hybodus* and *Egertonodus* on the wide and flat central cusp and the low degree of heterodonty. *Planohybodus* appears to be more closely related to *Hybodus* than to *Egertonodus* as it shares some characters with *H. reticulatus*, including the possession of two pairs of cephalic spines. Teeth of *Egertonodus* are somewhat similar to those of *Planohybodus* in having a slightly flattened labial side of the cusp but are always much more slender and have higher lateral cusplets.

Fin spines of *Planohybodus* seem to differ somewhat from those of the type species of *Hybodus* and *Egertonodus*. The combination of robust spines lacking a clear groove between the posterior hooks and having proximally discontinuous ribs that are slightly diverted towards the posterior appears to be diagnostic of *Planohybodus*. The presence of a similar ornamentation on both sides of both anterior and posterior fin spines suggests that it is unlikely to be a pathological character. Further studies of hybodont fin spine morphology

are needed to evaluate the systematic value, if any, of isolated spines.

Cephalic spines of *Hybodus*, *Egertonodus* and *Planohybodus* appear to have a similar architecture with a large, T-shaped basal plate and a crown displaying a barb below and slightly anterior to the apex. Minor differences include wider and more rounded lateral lobes in *Planohybodus* than in the other two genera and a crown that is more extensively ornamented in *Planohybodus* and *Egertonodus* (cf. Pl. 4; Maisey 1983, fig. 24, 1987, figs 12–13). Spines of both *Planohybodus* and *Egertonodus* lack accessory cusplets while these appear in spines of *Hybodus*, at least in *H. reticulatus* (Maisey 1987). Woodward (1889) noted accessory cusplets on the anterior pair of cephalic spines in *H. delabechei* but not on posterior spines.

Although both specimens of the type species of *Planohybodus* have some cranial material present, neither reveals many diagnostic features, and no cranial characters could be recognised that clearly differentiate this genus from other hybodont genera.

When the dermal skeleton is considered, this genus displays a unique combination of characters that differentiate it from *Egertonodus* and *Hybodus*, but also a number of features that link it to both of those genera, and it is consequently placed in the same subfamily, Hybodontinae.

The labio-lingually compressed teeth and low degree of heterodonty of *Planohybodus* are similar to features present in *Priohybodus* d'Erasmus, 1960 and may suggest a close relationship between these genera. This close affinity of *Planohybodus* and *Priohybodus* is also suggested by the presence of incipient serrations on some teeth of *Planohybodus ensis* (see Underwood and Rees 2002).

Planohybodus peterboroughensis sp. nov.

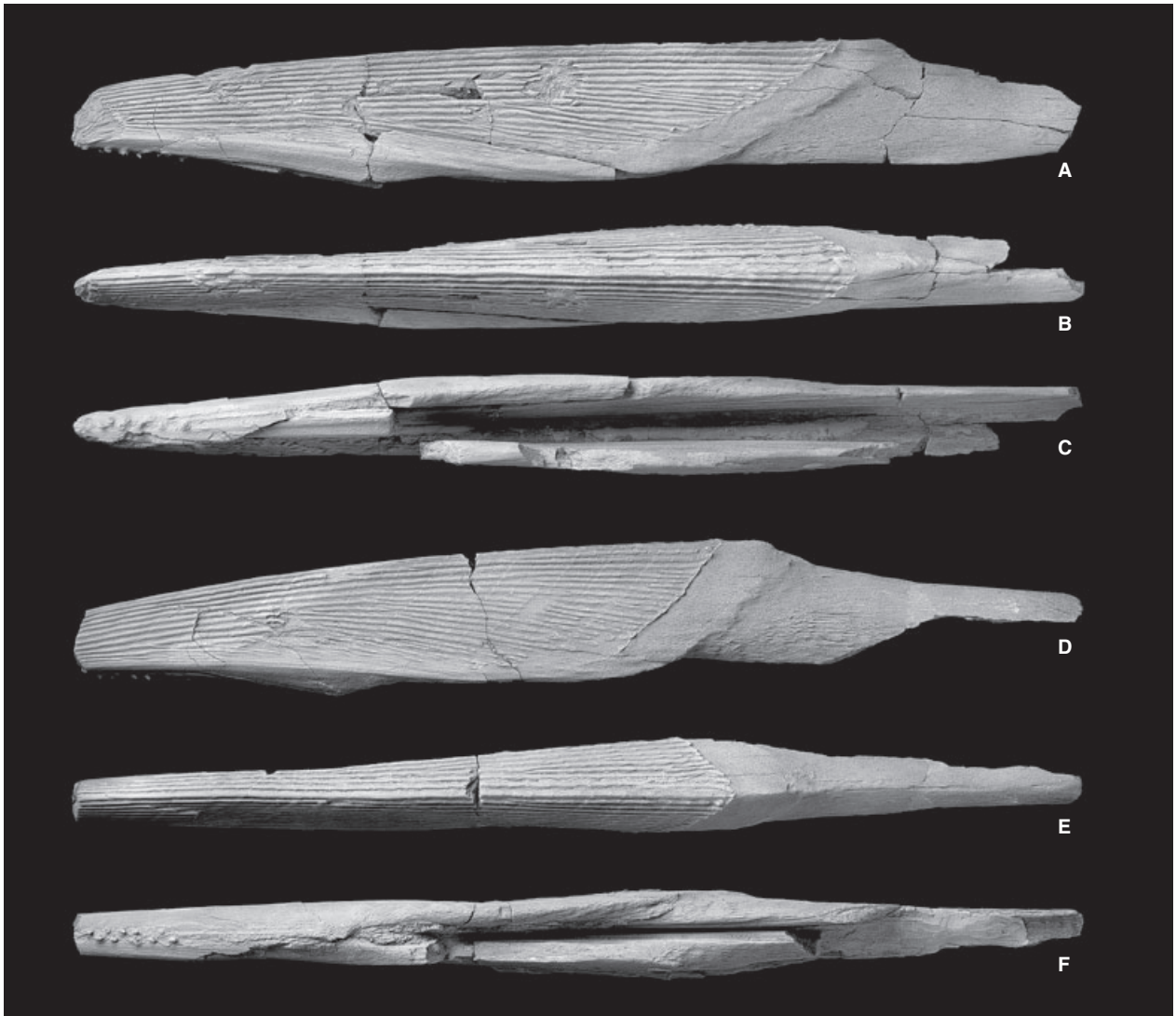
Plates 3–4; Text-figure 2

Derivation of name. From the county of Peterborough where the type material was discovered and collected.

Type specimen. Holotype, P. 8386, Plate 3, Text-figure 2, associated remains comprising jaws with teeth and fin spines; paratype P. 62254, Plate 4, pyritized skull of male shark within concretion displaying cephalic spines, dermal denticles, and broken teeth on the surface.

Type stratum. Lower or Middle Oxford Clay, Middle or Upper Callovian at Fletton Quarry, Peterborough. Exact horizon unknown.

Additional material. Six incomplete isolated teeth (35670–35673, 39205) from the Oxfordian of Yorkshire, northern England.



TEXT-FIG. 2. Fin spines of *Planohybodus peterboroughensis* sp. nov., holotype, P. 8386. A–C, anterior spine in right lateral, anterior, and posterior views; D–F, posterior spine in right lateral, anterior, and posterior views. Oxford Clay, Fletton Quarry; $\times 0.5$.

Diagnosis. Hybodont shark with a dental morphology separated from that of other members of *Planohybodus* by the combination of the following characters: (1) wide and robust, labio-lingually flattened cusp; (2) three pairs of well-developed lateral cusplets in upper jaw teeth; (3) ornamentation comprising non-branching folds reaching half the height of the central cusp.

Description. Teeth of this species are large, with a wide and flattened central cusp flanked by two or three pairs of lateral cusplets. In the upper jaw, teeth have three well-developed cusplets and are ornamented with slightly irregular or crenulated vertical folds, covering the larger part of the tooth-crown, except for the upper half of the cusp. In the lower jaw, the teeth are narrower, with a more slender central cusp, although the mid part of the cusp is slightly expanded. The lateral cusplets are markedly small-

er in lower jaw teeth and the third pair is rarely developed. Labial folds are less prominent and do not reach as high as in teeth from the upper jaw while lingual folds occur only close to the base of the crown. Cutting edges are well developed in both upper and lower teeth, particularly on the lateral cusplets, and the lower labial edge of the crown is somewhat swollen. The root is low, slightly lingually projected and porous, with larger foramina opening only on the lingual and basal surfaces. The dentition appears to be rather homodont along each jaw with only slight inclination towards the posterior in lateral teeth. No posterior teeth are visible on either specimen. The largest teeth measure 24 mm in mesio-distal width.

The associated fin spines are robust and of the typical hybodontoid architecture with longitudinal ribs on the anterior and lateral surfaces and two alternating rows of small hooks on the posterior side. No clear groove can be seen between the poster-

ior hooks. The tips of both spines are broken off but it is obvious that one of the spines (anterior) was slightly larger than the other. On the lower lateral surface, the ribs are slightly diverted posteriorly and are proximally discontinuous.

Two pairs of cephalic spines occur in males of this species. The spines have a wide and T-shaped basal plate with a smoothly rounded anterior edge. The entire posterior lobe is not visible but appears to be wide and dorso-ventrally rather thick. In the anterior pair, the lateral lobes are narrower and not as rounded terminally as in the posterior spines. The crown is strongly recurved with a small terminal barb on the ventral side. A strong ridge runs from the barb to the anterior edge on either side of the crown. The remaining ornamentation on the lower anterior parts of the crown includes rather strong, slightly crenulated folds and simple, weak folds close to the basal plate. Weaker ridges occur on the lateral sides of the crown. The posterior spine is slightly larger than the anterior one. The position of the cephalic spines seems to be similar to, or slightly more lateral than, that of *Hybodus delabechei* (see Maisey 1982), and unlike that of *H. hauffianus*.

The most common morphotype of dermal denticles, apparently covering large parts of the head, is the symmetrical, knob-like denticle (morphotype 1 in Thies 1995) with prominent ridges covering the crown and merging at the apex. Other denticles are similar but slightly inclined to the posterior. No strongly inclined or blade-like denticles were observed.

The fragments of palatoquadrate and Meckel's cartilage present in specimen P.8386 (Pl. 3) demonstrate that both cartilages were compressed and very deep posteriorly, with both having a very well developed internal mandibular ridge (of Maisey 1983). Although specimen P. 62254 (Pl. 4) preserves an entire articulated skull, this is thickly covered in pyrite and only very gross morphological features are visible. The mouth is subterminal with the palatoquadrates apparently reaching considerably further anteriorly than the neurocranium. The dorsal surface of the braincase is flat, with a hollow towards the posterior presumably marking the position of a rounded endolymphatic fossa. Laterally, the postorbital process is well developed, and appears to be the attachment site of the anterior cephalic spines. Behind this, a particularly robust lateral otic process appears to be anterior to the attachment site of the posterior cephalic spines. A ridge above and anterior to the orbit seems to be a thick and somewhat displaced ectethmoid process.

Remarks. Although the teeth of *P. peterboroughensis* are similar to those of *P. grossiconus* (see below), there are a few clearly visible differences, the most conspicuous being three pairs of cusplets in upper anterior teeth as opposed to two pairs in *P. grossiconus*. Furthermore, the ornamentation in teeth of *P. peterboroughensis* is more extensive in that the folds are more distinct and reach higher on the central cusp. Despite of these differences, the two species

are undoubtedly very closely related. Teeth of *P. ensis*, the third species assigned to the new genus, have commonly only a single pair of cusplets, although a minute distal pair may occur. Ornamentation is less prominent than in *P. peterboroughensis* and more similar to that in teeth of *P. grossiconus*.

The denticles displayed on the head of P. 62254 are of a type very common among several different hybodonts [e.g. *H. delabechei* (Reif 1978) and *E. basanus*] and cannot be used as a diagnostic character. No fin spines or cephalic spines have ever been documented as being found associated with teeth of *P. grossiconus* or *P. ensis*, making intrageneric comparisons of these structures impossible.

Occurrence. The distribution of *P. peterboroughensis* is so far restricted to the Callovian of Peterborough and the Oxfordian of Yorkshire.

Planohybodus grossiconus (Agassiz, 1843)

Plate 2, figures 11–15

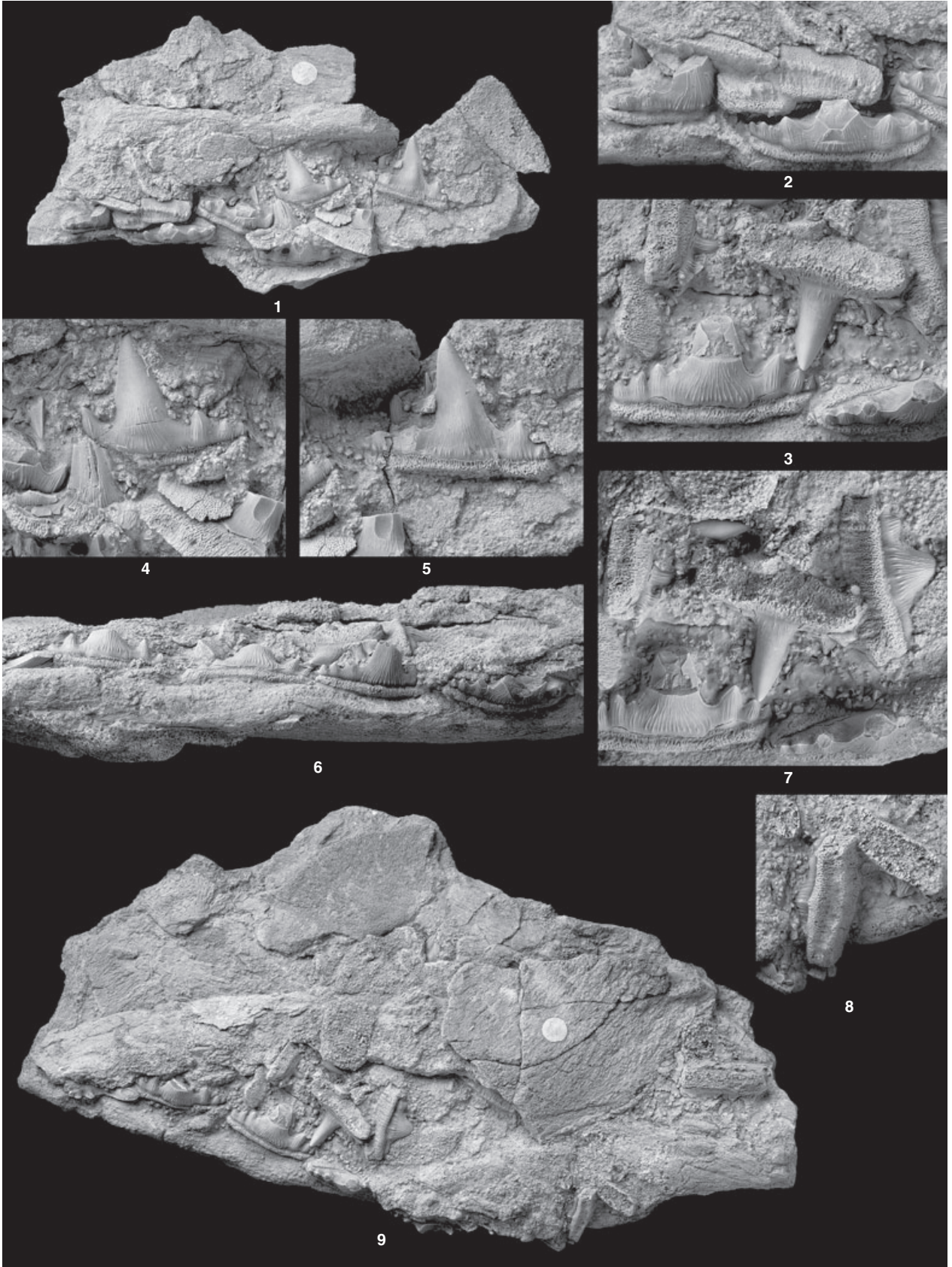
- 1843 *Hybodus grossiconus* Agassiz, p. 184, pl. 23, figs 25–41.
- 1889 *Hybodus grossiconus* Agassiz; Woodward, p. 270, pl. 11, fig. 4.
- 1890 *Hybodus grossiconus* Agassiz; Woodward, p. 287, fig. 1.4–1.6.
- 2006 *Hybodus grossiconus* Agassiz; Rees and Underwood, p. 355, fig. 3.

Material. Numerous complete teeth, tooth-crowns, and incomplete teeth including P. 2841, P. 29994, P. 52523, and P. 66500.

Description. These teeth have a high and triangular central cusp that is flanked by one or two pairs of lateral cusplets. The width of the cusp is somewhat variable, and it is likely that the dentition was characterised by dognathic heterodonty, with teeth from the lower jaw being more slender. The cusplets are small to minute and widely separated both from the cusp and from each other. Cutting edges are prominent and ornamentation comprises simple folds on the lower part of the crown, reaching approximately one-quarter to half of the cusp height, although this is somewhat variable. On the lingual side, the folds are weaker and more widely spaced. The root is low, porous and lingually projected. It is completely perforated by small irregular foramina while larger foramina are restricted to the lingual side, where they are randomly placed on the lower root face. Most teeth are symmetrical and the heterodonty seems to be limited

EXPLANATION OF PLATE 3

Figs 1–9. *Planohybodus peterboroughensis* sp. nov., holotype, P. 8386, Oxford Clay, Fletton Quarry. 1, Meckel's cartilage with associated teeth; $\times 0.7$. 2–3, 7–8, details of teeth from the upper jaw in occlusal and labial views; $\times 1.5$. 4–5, detail of teeth from the lower jaw in labial views; $\times 1.5$. 6, palatoquadrate from lateral side; $\times 1$. 9, palatoquadrate with associated teeth; $\times 0.7$.



REES and UNDERWOOD, *Planohyodus*

to variations in cusp width and size of the cusplets. The largest teeth of this species are 27 mm in mesio-distal width.

Remarks. The dentitional pattern of *P. grossiconus* can be assessed by direct comparison with *P. peterboroughensis*. The teeth fall into two groups, where the cusp is either wide and stout (Pl. 2, fig. 14) or rather more slender (Pl. 2, fig. 15); the former are regarded here as teeth from the upper jaw. A similar pattern can also be recognised in teeth of *P. ensis* (see Underwood and Rees 2002, fig. 4), which are quite similar to those of *P. grossiconus* but can be separated in possessing slightly weaker vertical folds and lacking a second pair of lateral cusplets. Large teeth of *P. ensis* occasionally develop irregular serrations on the cutting edges (see Underwood and Rees 2002, fig. 5), a character so far not recorded in either *P. grossiconus* or *P. peterboroughensis*.

Occurrence. *Planohybodus grossiconus* is the most widely distributed hybodont encountered during this study. In addition to the occurrences of the English Bathonian, where *P. grossiconus* has been recorded in several of the sampled horizons and is numerous in the NHM collection, the species has been found in the Bathonian of Scotland (Rees and Underwood 2006) and France (Woodward 1889) and has been reported from the Toarcian of Luxembourg (Delsate 1995), although this last record cannot be confirmed at present as it is based on a single incomplete tooth.

Genus SECARODUS gen. nov.

Derivation of name. Latin, *secare*, cut or slice and Greek, *odous*, tooth, in reference to the cutting dentition of the genus.

Type species. *Hybodus polyprion* Agassiz, 1843 from the Bathonian, Middle Jurassic of southern England (by monotypy).

Diagnosis. Hybodont shark with a well-developed cutting dentition that can be separated from those of all other hybodont genera by the following combination of dental characters: (1) strong labio-lingual flattening of the crown; (2) well-developed, partly serrated cutting edges; (3) a simple, knob-like labial protuberance at the base of the crown; (4) distally recurved crown in lateral teeth; (5) complete lack of ornamentation in antero-lateral teeth; (6) cusplets diverging from the central cusp in anterior teeth.

Remarks. The teeth of *Secarodus* are very similar to those of some species of the neoselachian hexanchiforms. Despite this close resemblance, its root morphology (as displayed in 38026), in combination with the crown structure of the juvenile tooth (*P.* 66501), demonstrates that, despite the highly different crown architecture in adults, *Secarodus* is related to *Hybodus*; consequently, it is placed in the subfamily Hybodontinae. The teeth of *Secarodus* are morphologically similar to those of *Planohybodus* and *Priohybodus* in being labio-lingually compressed and possessing serrations. Teeth of *Secarodus* also resemble those of *Priohybodus* in possessing divergent lateral cusplets, a character not recorded in other hybodont genera. It is therefore likely that *Secarodus*, *Planohybodus* and *Priohybodus* comprise a closely related group. Although cutting dentitions are rare among the hybodont clade, they are developed in several species but none of the other taxa (*Priohybodus arambourgi* d'Erasmus, 1960; *Porrhiza molimbaensis* Casier, 1969; *Thaiodus rucha* Cappetta *et al.*, 1990; *Planohybodus* spp.) has developed teeth as remarkably close in general morphology to the neoselachian hexanchiforms as *Secarodus*.

Secarodus polyprion (Agassiz, 1843)

Plate 1, figures 18–20; Plate 2, figures 16–22

1843 *Hybodus polyprion* Agassiz, p. 185, pl. 23, figs 1–15.

1889 *Hybodus polyprion* Agassiz; Woodward, p. 268, pl. 11, figs 1–3.

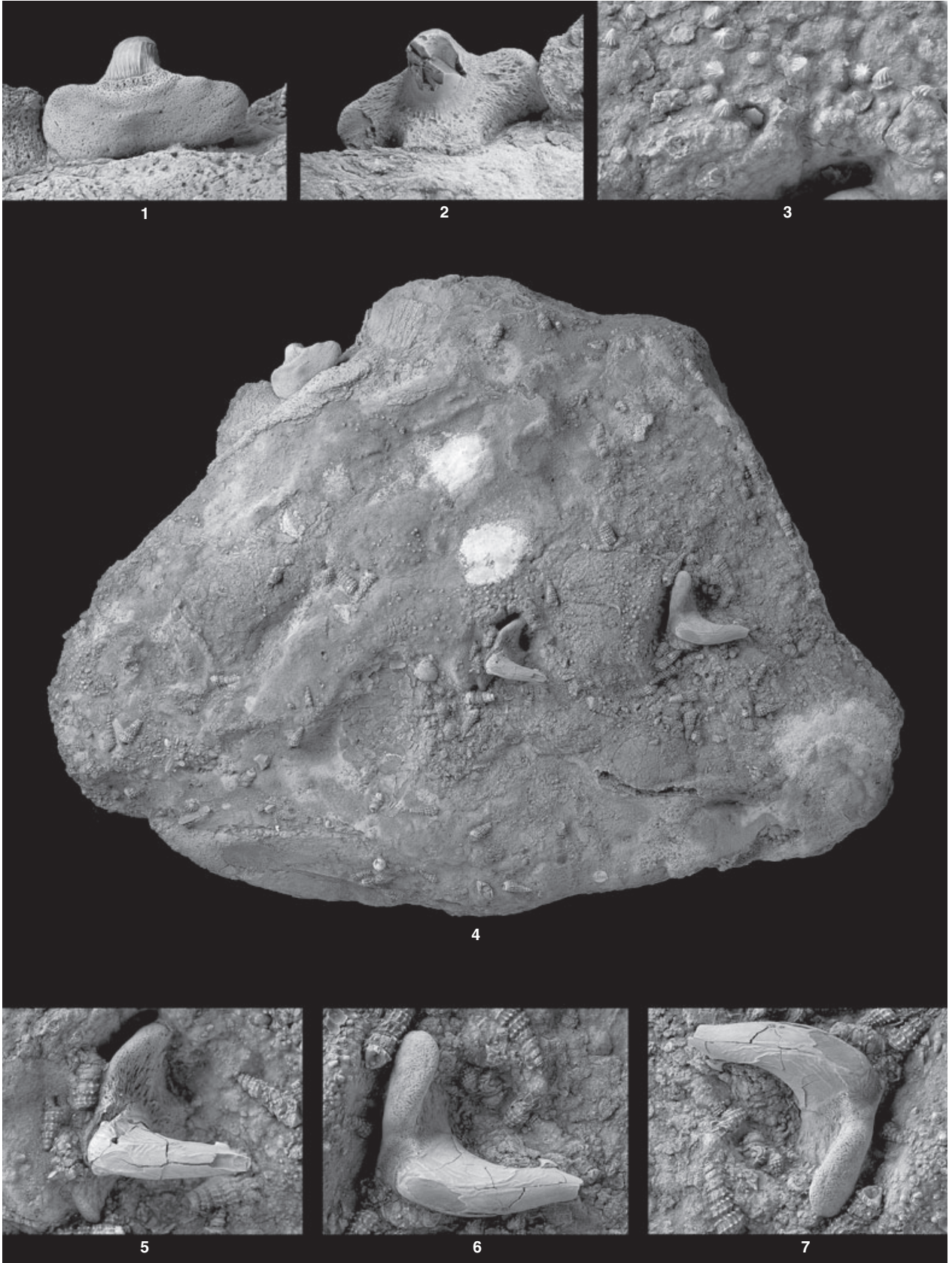
1890 *Hybodus polyprion* Agassiz; Woodward, p. 287, fig. 1.1–1.3.

Material. Twelve teeth and tooth-crowns representing several dental positions and including P. 2186, P. 2845, 38026, 39778, P. 66486, and P. 66501.

Description. These teeth are strongly labio-lingually flattened with two or three pairs of lateral cusplets. Anterior teeth are close to symmetrical, while in laterals and posteriors the entire crown is increasingly distally inclined towards the commissure of the jaw. Cutting edges are prominent on both cusp and cusplets and are occasionally serrated, primarily close to the base of the mesial edge. A few teeth display a small, centrally placed knob at the labial base of the crown. Other ornamentation is largely non-existent in large anteriors and laterals but may occur as weak folds on the lowermost part of the crown. In posterior teeth, vertical folds may be more prominent but the amount of

EXPLANATION OF PLATE 4

Figs 1–7. *Planohybodus peterboroughensis* sp. nov., paratype, P. 62254, Oxford Clay, Newton Longville. 1–2, anterior right cephalic spine in basal and dorsal views; × 1. 3, dermal denticles situated on the dorsal side of the head; × 2. 4, overview of entire specimen; × 0.4. 5, anterior left cephalic spine in oblique anterior view; × 1. 6–7, posterior left cephalic spine in oblique anterior and lateral views; × 1.



REES and UNDERWOOD, *Planohyodus*

ornamentation seems highly variable. A single juvenile tooth-crown has been recovered. It is rather low, with characteristically diverging lateral cusplets and weak folds occurring over the entire crown. The root is low and perforated by numerous small foramina on the labial side. The lingual and basal surfaces of the root are not displayed on any specimen. This species appear to have a dentition with a fair degree of monognathic heterodonty, where the variations occur mainly in the height and inclination of the cusp, the presence or absence of a labial knob and the distribution of vertical folds and cutting edge serrations. The largest teeth measure 14.3 mm in width and the juvenile tooth-crown is 3.3 mm wide.

Remarks. Some tooth-crowns of this species are more reminiscent of those of neoselachian hexanchiforms than of any other hybodont. Teeth interpreted as laterals are likely to have been used in a similar fashion as in hexanchiforms, indicating that *S. polyprion* was feeding on larger prey and carrion. As only a single, juvenile tooth of this species has been recorded during the systematic sampling undertaken by us, we believe that *S. polyprion* was a rare faunal component in the hybodont faunas of southern England during the Middle Jurassic. The larger number of specimens in museum collections derived from the Stonesfield Slate is probably a result of the intensive collecting from this unit in the past. It is not certain whether this species was a rare inhabitant of near-shore carbonate environments (in which all of the teeth have been found) or represented a deep-water shark that rarely ventured into the environments represented by the facies sampled during this study.

A few teeth of a possibly related species referred to as *Polyacrodus* sp. were recorded in the Bathonian of southern France (Kriwet *et al.* 1997). Apart from being minute, these teeth share several characters with those of *S. polyprion*, including a wide, flattened crown that is weakly ornamented and a small labial protuberance. Other close relatives to this taxon are unknown.

Occurrence. In addition to the single juvenile tooth-crown found in the Forest Marble Formation at Watton Cliff, *S. polyprion* is known only from the Stonesfield Slate (Woodward 1889).

Subfamily ACRODONTINAE Casier, 1959 *sensu* Maisey 1989

Remarks. This subfamily, first used by Maisey (1989), can be roughly diagnosed as hybodontid sharks with a crushing dentition; only two genera, *Acrodus* Agassiz, 1837 and *Asteracanthus* Agassiz, 1837, were included. As we regard *Acrodus* (the type genus) as closely related to traditional Hybodontidae such as *Hybodus* as well as to new genera described herein, these are all included in the family Hybodontidae, following Maisey (1989). It is acknowledged that the overall resemblance of the dentitions of *Aster-*

acanthus and *Acrodus* may be superficial, and that the taxonomic position of the former genus may need to be re-evaluated in future. The morphology of the jaws of *Asteracanthus* is rather different from that of *Acrodus* (J. Maisey, pers. comm. 2006), suggesting that a close relationship is unlikely.

Genus ASTERACANTHUS Agassiz, 1837

Type species. *Asteracanthus ornatissimus* Agassiz 1837, from the Middle and Late Jurassic of southern England.

Remarks. Although the stratigraphically oldest representative of this genus is Middle Triassic in age (Rieppel 1981), it is only during a geologically short interval in the Middle and Late Jurassic that species of *Asteracanthus* were diverse and probably represented the dominant sharks with a crushing dentition. A number of species referred to *Asteracanthus*, or previously to *Strophodus* Agassiz, 1838, are based solely on isolated fin spines (e.g. *A. acutus* Agassiz, 1837; *A. semisulcatus* Agassiz, 1837; *A. granulatus* Egerton, 1854; *A. semiverrucosus* Egerton, 1854; *A. verrucosus* Egerton, 1854; *A. aegyptiacus* Stromer, 1927) or teeth that are poorly preserved or too few to allow an analysis of the dentitional pattern (e.g. *A. biformatus* Kriwet, 1995). These taxa complicate a revision of the genus and are not included in the discussion below. Dorsal fin spines ornamented with granulae as opposed to ribs on the anterior and lateral sides are traditionally referred to *Asteracanthus* (e.g. Egerton 1854; Woodward 1916) but this interpretation is not well supported (Underwood and Rees 2002). Until the specific significance, if any, of isolated hybodont dorsal fin spines has been thoroughly investigated, nominal species based solely on fin spines will have to be considered *nomina dubia*.

Teeth of *Asteracanthus* are most often found isolated; only very rarely are associated dentitions discovered. The single most complete articulated dentition of *Asteracanthus* is the holotype (41378) of *A. medius* (Owen, 1869) recovered from Bathonian strata near Caen in northern France. A revised description of this specimen is included below for comparative reasons and as a reference in reconstructing dentitional patterns of other Bathonian species. Associated dentitions of *A. ornatissimus* from the Callovian of southern England (P. 10908, P. 6831) were also compared to the isolated Bathonian teeth. The material of *A. medius* and *A. ornatissimus* indicates that the dentitional pattern of *Asteracanthus* is rather stable and includes two rows of relatively high anterior teeth, two rows of enlarged laterals and two posterior rows of small and rounded teeth. It is at present not clear whether this dental formula applies to both upper and lower jaws but the associated material of *A. ornatissimus* does imply that

a symphyseal row may have been present in either the lower or the upper jaw. It has proven possible to place isolated teeth of other species within the dental pattern seen in *A. medius* and *A. ornatissimus*. Geologically older species, such as the Middle Triassic *Asteracanthus* cf. *A. reticulatus* (Rieppel 1981) appear to be less restricted in the development of anterior teeth and display a number of small teeth in front of the enlarged laterals. In the Middle Jurassic species, anterior teeth are usually higher than laterals with a well-developed occlusal crest and tapering lateral extremities. Laterals are commonly larger, more rectangular teeth without an occlusal crest, and strongly adapted for crushing. Posterior teeth are small and rounded, and the surface is flat to slightly domed.

Asteracanthus magnus (Agassiz, 1838)

Plate 5, figures 1–11

1838 *Strophodus magnus* Agassiz, p. 126, pl. 18, figs 11–15.

1889 *Strophodus magnus* Agassiz; Woodward, p. 314, pl. 15, figs 4–8.

1890 *Asteracanthus magnus* (Agassiz); Woodward, p. 288, fig. 1.7.

Material. Numerous teeth in the collections of the NHM including P. 5882, P. 48529, P. 66481–66483, and additionally, three teeth from the sampled horizons (P. 66502–66503).

Description. Teeth from the first anterior row are short mesio-distally and domed with a subtriangular outline and lack a clear occlusal crest. In teeth from the second row, the mesial side is lingually projected and narrower than the more angular distal side. These teeth are more elongate and subrhomboidal. The ornamentation in anteriors comprises only reticulate folds forming a regular, finely pitted surface. Lateral teeth are close to rectangular in occlusal outline and have a flat or weakly domed occlusal surface. The ornamentation is finely reticulate without any trace of an occlusal crest. On the vertical sides of the teeth, the enameloid is smooth to weakly folded. The lateral teeth from the mesial row differ from those of the distal row in being more elongated and in having an expanded mesial extremity projected labially, while laterals from the distal row are close to rectangular. Teeth from the posteriormost tooth-rows are small and ovoid in occlusal outline and the ornamentation is similar to that in laterals in being finely reticulate on the surface and smooth on the lateral sides. No anterior teeth with preserved root have been recognised but several lateral teeth display a low, massive root with a single, irregular row of larger foramina on the labial and lingual sides. In posterior teeth, the root appears to lack larger foramina and is very strongly directed lingually. Anterior teeth are up to 24 mm wide and the largest laterals are 45 mm in width.

Remarks. Anterior teeth of *A. magnus* are surprisingly rare in the collections at the NHM compared to lateral teeth, which could be a collecting bias or perhaps an indi-

cation that this species only possessed a single row of anterior teeth.

Occurrence. During this study we recorded *A. magnus* from the coral-bearing mudstone at Hornsleasow, the Forest Marble Formation at Watton Cliff and in the Boueti Bed at Herbury Point. The species also occurs at many other sites in the English Bathonian and in contemporaneous strata in northern France (Woodward 1889). All of the specimens recorded were recovered from shelf to shore-face carbonate facies, with the exception of the single tooth from Hornsleasow which is from a palaeoenvironment interpreted as a muddy marine embayment. No examples of this species were recorded from lagoonal facies.

Asteracanthus tenuis (Agassiz, 1838)

Plate 5, figures 12–16

1838 *Strophodus tenuis* Agassiz, p. 127, pl. 18, figs 16–25.

1889 *Strophodus tenuis* Agassiz; Woodward, p. 317, pl. 15, figs 2–3.

1890 *Asteracanthus tenuis* (Agassiz); Woodward, p. 288, fig. 1.9.

Material. Numerous teeth and tooth-crowns including P. 5884, P. 66484, and 11046.

Description. Anterior teeth are strongly arched in labial and lingual views, particularly in the first row where teeth are almost symmetrical. The occlusal crest is well developed although frequently removed by wear, and the crown is somewhat projected lingually. Teeth from the second row are more elongate and slightly less arched but similar to those of the first row. Lateral teeth of the third row have extremities that are curved lingually (distal) and labially (mesial) to give the occlusal crest a sigmoidal curvature. Crowns of these teeth are more elongate than in anteriors, and the centre of the tooth is domed. Lateral teeth from the fourth row are more strongly elongate, with a domed area in the anterior third of the tooth. The ornamentation of anterior teeth comprises rather strong folds originating from the centre of the tooth, and in laterals the folds form a more reticulate pattern with smooth areas on the lateral sides. No posterior teeth have been found that can confidently be assigned to this species. The root in anteriors is high and shaped as two lobes separated by a shallow central groove. Lateral teeth have a much lower root, and in all teeth it is perforated by a few, randomly placed, larger foramina. In mesio-distal width, the anterior teeth measure up to 21 mm and the largest lateral teeth are 35 mm wide.

Remarks. Among previously described species of *Asteracanthus*, *A. tenuis* is very similar only to *A. longidens* (Agassiz, 1838) from the Bathonian of northern France. Unfortunately, the holotype of the latter species, originally in the collection of Eude Deslongchamps and deposited in the Caen Museum, France, was destroyed during the Second World War (Bigot 1945). Comparisons with plate

16 in Agassiz (1838) suggest that *A. longidens* might have slightly more elongate teeth than *A. tenuis*, but without direct comparison it is very difficult to establish whether the two nominal species are conspecific.

Occurrence. This species is known from several localities in the English Bathonian but was not encountered in the recently collected samples. It has also been reported from the Aalenian of southern Germany (Woodward 1889). As with *A. magnus*, teeth of *A. tenuis* were only recorded from carbonate facies, and none was found to originate from lagoonal palaeoenvironments.

Asteracanthus ornatissimus Agassiz, 1837

Plate 5, figures 17–20

- 1837 *Asteracanthus ornatissimus* Agassiz, p. 31, pl. 8.
 1838 *Strophodus reticulatus* Agassiz, p. 123, pl. 17.
 1889 *Asteracanthus ornatissimus* Agassiz; Woodward, p. 307, pl. 15, fig. 14, *non* fig. 11.
 1889 *Strophodus* sp., Woodward, pl. 15, fig. 13.
 1991 *Asteracanthus ornatissimus* Agassiz; Martill, p. 198, pl. 36, fig. 9.

Material. Two teeth, both from the lateral part of the dentition (P. 5886, 47134).

Description. The mesial side of the crown is narrower than the distal, more acute part and curved towards the labial side. The domed area in the centre of the tooth is almost pyramidal and the originating point for a complex ornamentation pattern including prominent, frequently branching folds. In P. 5886, additional folds originate at the highly irregular occlusal crest and from both the folds and the crest, minor striations branch off. On the lower parts of the tooth, the crown surface is reticulate. In 47134, the ornamentation is less complex with folds, but no striations, on the upper part of the tooth, and a clear occlusal crest is lacking. The tooth displays a partial root that is massive and seems to lack larger foramina. The teeth are 33.8 mm (P. 5886) and 36.7 mm (47134) in width.

Remarks. By comparison with associated material of *A. ornatissimus* from the Callovian of England (P. 10908) these teeth both appear to originate from the third tooth row as they have a high domed area and a mesial part that is labially inclined. The ornamentation pattern in P. 5886 is rather more complex than commonly observed in Callovian teeth of *A. ornatissimus*, but this is nevertheless regarded as being within the normal range of variation for any given species of *Asteracanthus*.

Occurrence. This is a widespread species both geographically and stratigraphically. Apart from the Bathonian material from the NHM and a few fragmentary teeth in the samples from the Forest Marble Formation at Watton Cliff, teeth of *A. ornatissimus* are known from Bathonian–Kimmeridgian strata in England, France, Switzerland and Germany (Woodward 1889; Martill 1991). This species is common within the neritic mudstones of the Callovian Oxford Clay Formation, where it appears to be the sole species of *Asteracanthus*; it is possible that this was a generally deep water taxon that rarely ventured onto shallow carbonate shelves. The lack of teeth of this species in the large collections from Eyford and Stonesfield may suggest that it only appeared in the Upper Bathonian.

Asteracanthus medius (Owen, 1869)

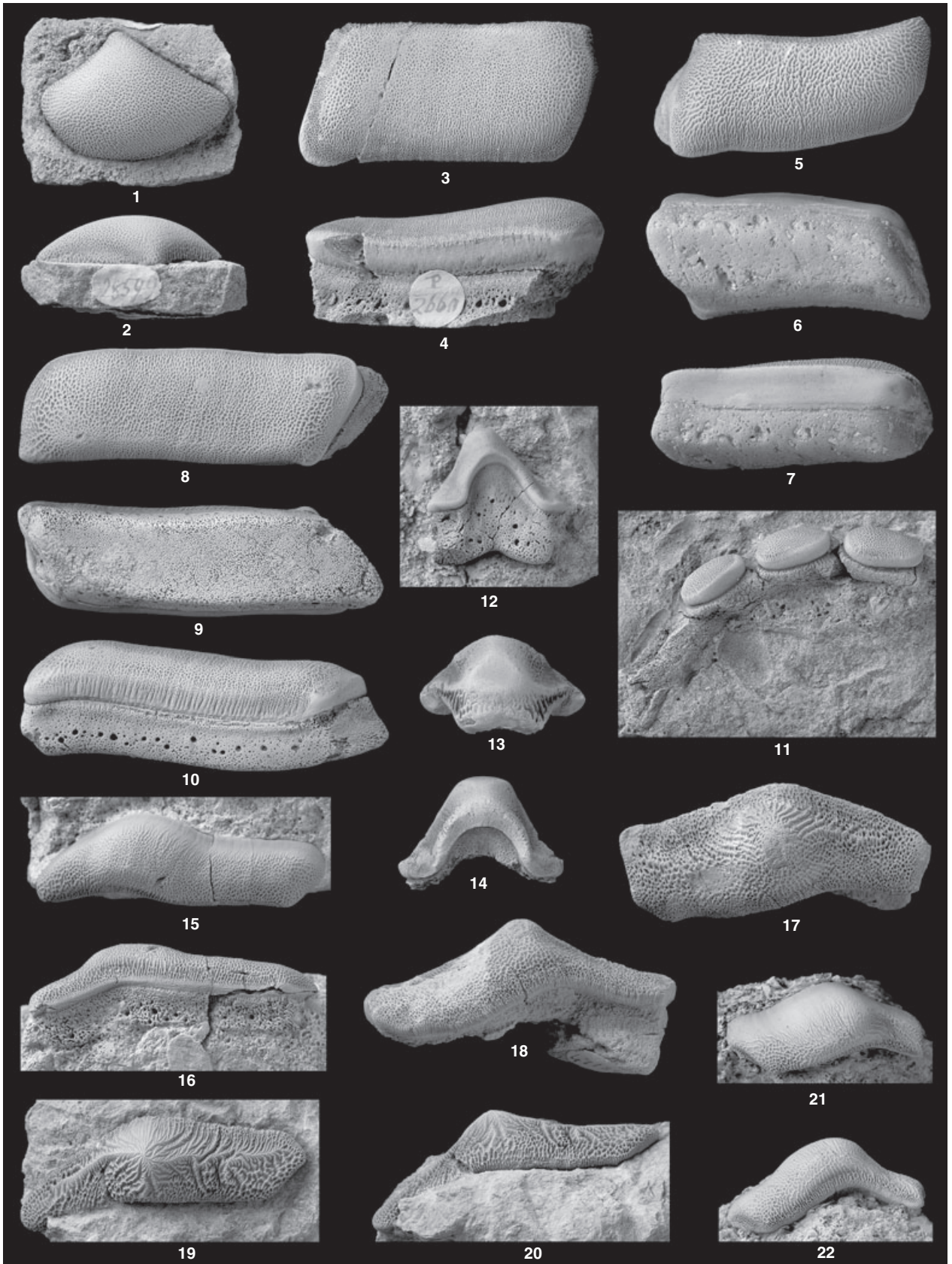
Plate 5, figures 21–22; Text-figure 3

- 1869 *Strophodus medius* Owen, p. 193, pl. 7, fig. 1.
 1889 *Asteracanthus ornatissimus* Agassiz; Woodward, p. 307, fig. 12.
 1890 *Asteracanthus medicus* [sic] Owen; Woodward, p. 288, fig. 3.

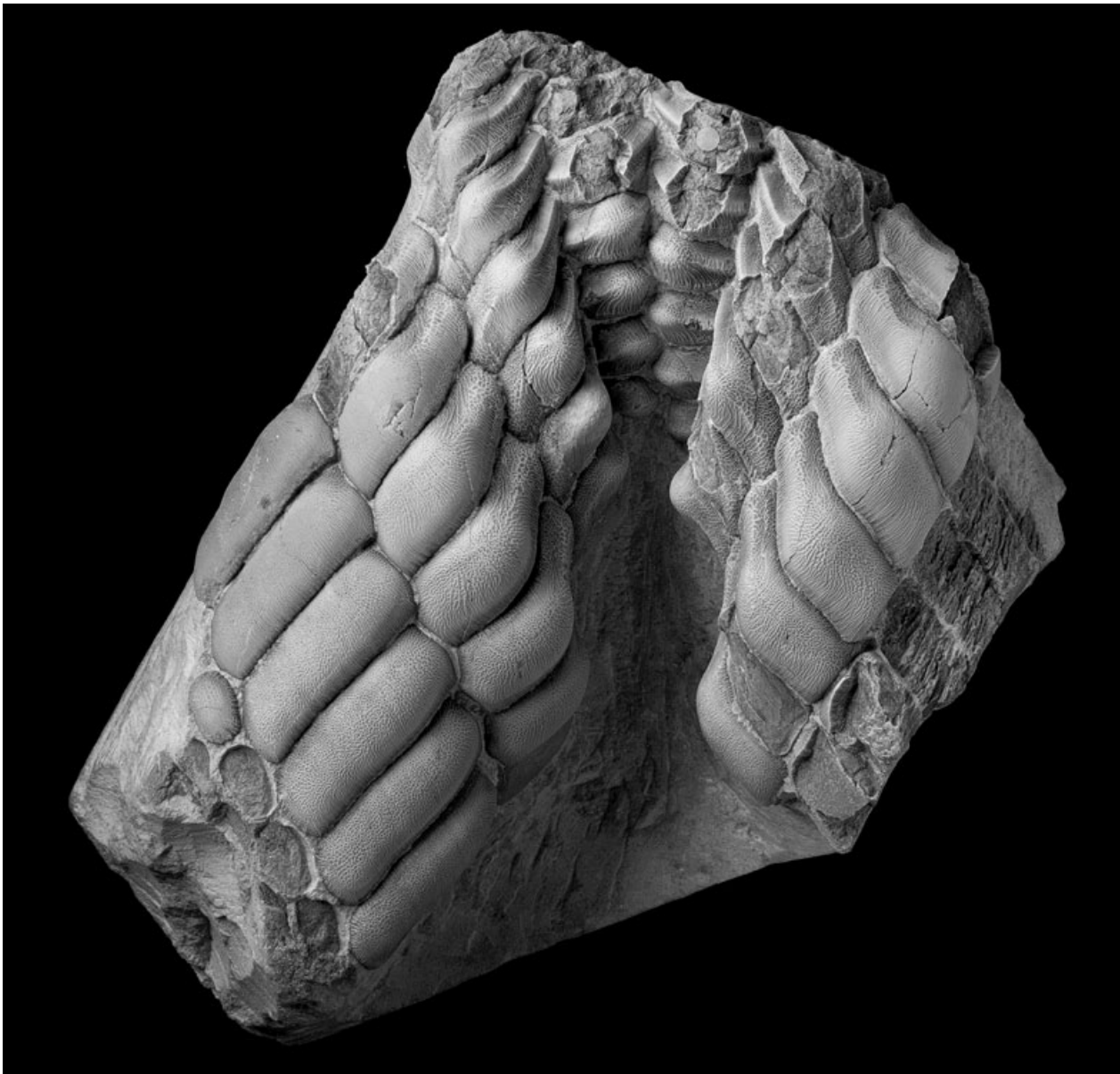
Material. A single articulated dentition, with preserved teeth in all rows except the second posterior (41378), and a single isolated tooth (P. 66485).

EXPLANATION OF PLATE 5

- Figs 1–11. *Asteracanthus magnus* (Agassiz, 1838). 1–2, P. 66481, anterior tooth-crown, Stonesfield Slate, Stonesfield, occlusal and lingual views. 3–4, P. 66482, lateral tooth, ?Cornbrash Formation, Long Orton, occlusal and labial views. 5–7, P. 66483, antero-lateral tooth, Stonesfield Slate, Stonesfield, occlusal, basal, and labial views. 8–10, P. 48529, lateral tooth, ?Forest Marble Formation, Stanton, occlusal, basal, and labial views. 11, P. 5882, three articulated posterior teeth, Stonesfield Slate, Stonesfield, oblique anterior view.
- Figs 12–16. *Asteracanthus tenuis* (Agassiz, 1838). 12, P. 5884, anterior tooth, Forest Marble Formation, Atford, lingual view. 13–14, P. 66484, anterior tooth-crown, ?Forest Marble Formation, Stanton, occlusal and lingual views. 15–16, 11046, lateral tooth, Stonesfield Slate, Stonesfield, occlusal and lingual views.
- Figs 17–20. *Asteracanthus ornatissimus* Agassiz, 1837. 17–18, 47134, antero-lateral tooth, ?Cornbrash Formation, Long Orton, occlusal and lingual views. 19–20, P. 5886, antero-lateral tooth-crown, ?Forest Marble Formation, Stanton, occlusal and labial or lingual views.
- Figs 21–22. *Asteracanthus medius* (Owen, 1869), P. 66485, lateral tooth-crown, ?Forest Marble Formation, Box, occlusal and labial views. All $\times 1.5$.



REES and UNDERWOOD, *Asteracanthus*



TEXT-FIG. 3. Articulated dentition (holotype) of *Asteracanthus medius* (Owen, 1869), 41378, occlusal view. Normandy; $\times 1$.

Description. The first row of anteriors comprises teeth with a highly domed crown and prominent occlusal crests. In occlusal view, the teeth are close to hexagonal but the labial edge is slightly longer than the lingual one. Ornamentation mainly comprises a reticulate pattern, although parallel ridges, originating from the domed centre of the tooth, occur primarily on the lingual side. Teeth of the second row are similar but differ in that the more expanded mesial and distal extremities of the teeth are curved labially and lingually, respectively. On the mesial part, the occlusal crest is particularly strong. The ornamentation is furthermore uniformly reticulate except for the highest parts of the teeth. In the two rows of laterals, the teeth are only slightly domed. Teeth of the fourth row are rectangular while the mesial parts in teeth from the third row are narrow and slightly curved to the labial side. Reticulate ornamentation completely covers

the occlusal surface of these teeth. A single tooth from the first posterior row is preserved and it is ovoid in occlusal outline with a somewhat elevated crown and weak reticulate ornamentation. No teeth from the second row of posteriors are preserved and the root is not visible in any teeth. The largest lateral tooth measures 39.5 mm in mesio-distal width and the entire length of a single jaw (as preserved) is approximately 120 mm.

Remarks. Woodward (1889) regarded *A. medius* as a junior synonym of *A. ornatissimus* but this view is not supported here. Both species are known from associated dentitions and it is clear that there are major differences regarding both the heterodonty pattern and characters on isolated teeth. Teeth from the third and fourth rows in

A. medius are very low, lacking any traces of cusp and occlusal crest, and have a reticulate ornamentation. Corresponding teeth of *A. ornatissimus* have a domed area in the centre of the tooth (third row) or on the mesial part (fourth row). The ornamentation comprises folds radiating from this area and a well-developed occlusal crest in contrast to teeth of *A. medius*. The dentition of *A. medius* is similar to that of *A. magnus* in having large and only slightly domed lateral teeth, but is different in that the anterior teeth have prominent occlusal crests and are hexagonal rather than subtriangular (see also below).

Occurrence. This species was previously restricted to a single specimen from the Bathonian near Caen in northern France, but the recognition of P. 66485 as a tooth of *A. medius* expands the distribution to include southern England. As the exact horizon of the holotype is unknown (with carbonates being present through much of the Upper Bathonian and into the basal Callovian in Normandy) and the English specimen is likely to have originated from the uppermost Bathonian–Callovian Cornbrash Formation, it is possible that the extreme rarity of this taxon is because it is restricted to the very top of the Great Oolite Group.

Asteracanthus sp.

Plate 1, figures 21–22

Material. A single, juvenile or embryonic tooth, NHM P. 66505.

Description. The tooth is minute with an almost circular occlusal outline and a flat upper surface ornamented with a reticulate pattern. The high root is twice the height of the crown and seems to have been poorly mineralised as no structures can be observed. The specimen is 1.9 mm wide.

Remarks. This tooth almost certainly belongs to one of the species of *Asteracanthus* recognised in the English Bathonian, perhaps to *A. magnus* on the basis of similar ornamentation. We prefer, however, to keep it in open nomenclature as juvenile and embryonic teeth of this genus are virtually unknown.

Distinction of Middle Jurassic Asteracanthus species

By reconstructing the entire dentition in different species of *Asteracanthus*, it has been possible to provide characters that separate the Middle Jurassic taxa, of which we recognise *A. magnus*, *A. tenuis*, *A. ornatissimus*, *A. medius*, and tentatively *A. longidens* (see above). These species fall into three groups when both tooth morphology and dentitional pattern are considered: (1) *A. magnus* and *A. medius* possess teeth with a weak reticulate ornamentation and a dentition with wide, rectangular lateral teeth and weakly arched anterior teeth; (2) *A. tenuis* and *A. longidens*

possess much elongated lateral teeth with asymmetrically situated domed areas and anteriors that are highly arched; (3) the dentition of *A. ornatissimus* is unique, primarily in the type of ornamentation where all teeth, regardless of position, are covered in a complex pattern of enameloid folds.

Anterior teeth of *A. medius* apparently differ from those of *A. magnus* in having a prominent occlusal crest, at least on the lateral parts of the crown, and in being hexagonal rather than subtriangular. Lateral teeth are more domed in *A. medius* than in *A. magnus* while posterior teeth seem to be more ornamented with weak folds on the sides of the teeth in the former species. It is possible that the two nominal species *A. tenuis* and *A. longidens* are conspecific but because the holotype of the latter was destroyed (see above), direct comparisons are impossible. The figures of *A. longidens* in Agassiz (1838, pl. 16) display a possible associated dentition, including what can be expected in heterodonty compared to the range of morphologies found in isolated teeth of *A. tenuis*. Minor differences between the two taxa have been identified but may be the result of intraspecific variation. Lateral teeth in the figured specimen of *A. longidens* seem to be less domed than those of *A. tenuis* and the anterior teeth of the former are slightly more elongate. Apart from the unique ornamentation pattern, teeth of *A. ornatissimus* can also be separated from those of all other Middle Jurassic *Asteracanthus* by the prominent occlusal crest in all teeth regardless of position. Another species known from well-preserved associated material is *A. smithwoodwardi* Peyer, 1946 from the Toarcian of Switzerland. The dentitional reconstruction of this species (Peyer 1946, fig. 13) shows strongly enlarged teeth in the second lateral row while those of the first lateral row are less than half their size. The rectangular teeth of the second lateral row are finely ornamented with a reticulate pattern and are quite similar to those of *A. magnus*. Anterior teeth of *A. smithwoodwardi* are also reminiscent of *A. magnus* in being low-domed but are rhomboidal in occlusal view, in contrast to the subtriangular shape of anteriors in *A. magnus*. Compared to *A. medius*, the anterior teeth of *A. smithwoodwardi* are much more rounded in occlusal view and both anteriors and laterals are much shorter mesio-distally. Other material figured by Peyer (1946, fig. 11, pl. 5, figs 5–8; pl. 6, fig. 1) and originating from the Upper Jurassic of Switzerland probably represents an undescribed species dentally similar to *A. ornatissimus*. The reconstructed dentition can be separated from the latter species by the smaller width of the lateral teeth, in particular those from the second row of laterals. The ornamentation and occlusal crests of the teeth are also less developed in the Swiss material, and folds on the anterior teeth are more reticulate than in *A. ornatissimus*.

Genus FRANGERODUS gen. nov.

Derivation of name. Latin, *frangere*, to crush, and Greek, *odous*, tooth, in reference to the crushing function of the dentition of this hybodont shark.

Type species. *Strophodus lingualis* Woodward, 1889 from the Bathonian of southern England (by monotypy).

Diagnosis. Hybodont shark with a crushing dentition that can be separated from those of all other hybodont genera by the following combination of dental characters: (1) strong occlusal crest; (2) prominent crest around the outer rim of the crown; (3) elongated lateral teeth with asymmetrical domed area; (4) a single lateral cusplet on the mesial side in lateral teeth; (5) smooth enameloid surface beneath the labial longitudinal shelf of the crown; (6) deep reticulate ornamentation covering the lower parts of the crown.

Remarks. The ornamentation of the teeth and, in particular, the outer longitudinal ridge on the rim of the crown, is quite different from that in teeth of *Asteracanthus* spp. Further differences between *Frangerodus* and *Asteracanthus* include the presence of a more cusp-like domed structure and a single lateral cusplet in lateral teeth of the new genus and minute cusplets also in anteriors. Anterior teeth are also mesio-distally wider and *Frangerodus* appear to be less heterodont than *Asteracanthus*. On the other hand, the two genera display somewhat similar dentitional patterns and are regarded as closely related. Compared to other hybodonts with a crushing dentition (e.g. *Acrodus*, *Palaeobates* Meyer, 1849 and *Bdellodus* Quenstedt, 1882), *Frangerodus* is clearly distinguishable by the combination of characters constituting the diagnosis.

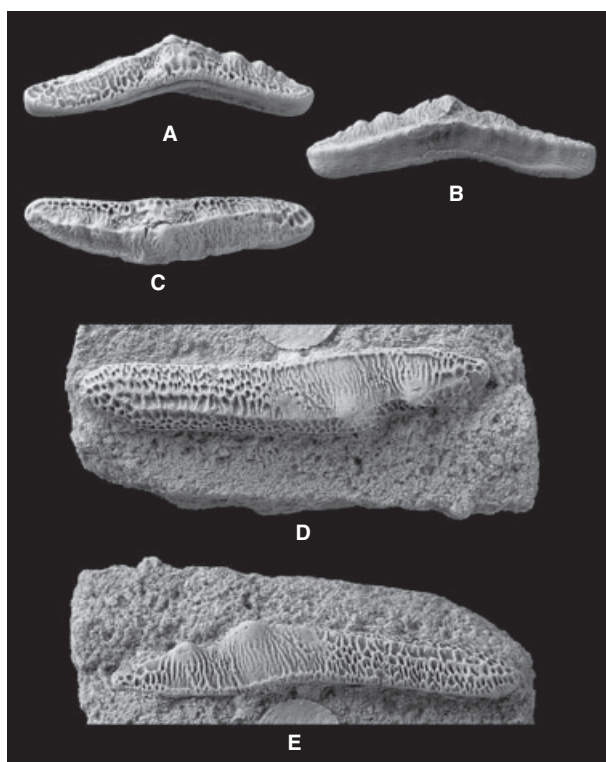
Frangerodus lingualis (Woodward, 1889)

Plate 1, figures 23–25; Text-figure 4

- 1871 *Strophodus lingualis* Phillips, p. 177, fig. 8 (figure and name only).
 1889 *Strophodus lingualis* Woodward, p. 319, pl. 15, figs 9–12.
 1890 *Strophodus lingualis* Woodward; Woodward, p. 289, fig. 1.8.

Material. Seven incomplete teeth including P. 10497, 28600, and P. 66506–66507.

Description. Anterior teeth of this species have a symmetrical crown with smoothly rounded extremities. The ornamentation is coarsely reticulate and occurs primarily on the lower lingual parts of the crown. A strong and somewhat irregular occlusal crest runs along the long axis of the tooth, and at the outer rim



TEXT-FIG. 4. Teeth of *Frangerodus lingualis* (Woodward, 1889). A–C, P. 10497, antero-lateral tooth-crown, Exford Member, Exford, lingual, labial, and occlusal views. D–E, 28600, lateral tooth-crown, Exford Member, Exford, occlusal and lingual views. Both $\times 3$.

of the crown there is a horizontal ridge, often ornamented with small crenulations. Teeth from what is interpreted as the second anterior or first lateral tooth row are more elongate with strong ornamentation, reticulate on the lower parts and irregular, but parallel, folds branching from the occlusal crest and domed cusp on the upper part of the crown. On the labial side, there is a high enameloid-covered, smooth area beneath the horizontal ridge that seems to be lacking on the lingual side. Small elevations of the occlusal crest occur, primarily on the mesial side, and represent incipient lateral cusplets. Lateral teeth are more elongate with a domed cusp that is mesially displaced. A single lateral cusplet may occur on the mesial side. The distal half of the tooth is ornamented with coarse reticulate folds and on the mesial half the folds form an irregular pattern. Lateral teeth also possess a horizontal ridge on the rim of the crown but it is less developed than in more anterior teeth. None of the specimens displays the root. The largest tooth measures 19 mm in width.

Remarks. The relatively narrow, cusped teeth of *F. lingualis* and the low degree of wear seen on the teeth studied may suggest a less durophagous diet than *Asteracanthus* spp.

Occurrence. This species was recorded from the upper part of the Fullers Earth Rock Formation (two juvenile teeth), with

museum material being from the Eyford Member at Eyford and a single specimen from the Forest Marble Formation (Woodward 1889). It is likely that this species favoured more offshore, muddy, habitats. This is suggested by its occurrence within the small sample of material from the Fullers Earth Rock, and its presence at Eyford and not Stonesfield, as the Eyford Member rapidly passes southwards into the deeper water Fullers Earth Clay Formation, whereas the lithologically similar Stonesfield Slate is surrounded by shallow water oolites of the Taynton Limestone Formation. There is no record of *F. lingualis* within lagoonal facies.

Family LONCHIDIIDAE Herman, 1977

Genus LONCHIDION Estes, 1964

Type species. *Lonchidion selachos* Estes, 1964, from the Maastriechian, Upper Cretaceous of eastern Wyoming, USA.

Lonchidion sp. Plate 6, figures 1–15

Material. One complete tooth and ten isolated tooth-crowns numbered P. 66508–66514.

Description. Symphyseal teeth are small and highly angular, completely lacking ornamentation. The cusp is worn off on the only recorded symphyseal but it appears to have been rather high and is flanked by a single pair of minute cusplets. Teeth from all other positions share a quite similar morphology, although anterior teeth are somewhat narrower and possess a more robust labial protuberance. In unworn teeth, the occlusal crest is sharp and elevated to form a minute cusp and remnants of cusplets. An occlusal crest may also be present on the labial protuberance. Some teeth are slightly ornamented with faint irregular ridges, while others lack ornamentation altogether. The lateral extremities of the crown are extended and the crown is wider than the root. The labial protuberance is quite variably developed and comparatively larger in smaller teeth. The root is lower than the crown but slightly larger than the incised crown base. It is somewhat lingually projected and perforated by large foramina on the lower part while smaller, more circular foramina open on the upper parts of the root. The largest tooth is 2.3 mm wide.

Remarks. The occurrence of *Lonchidion* in the Bathonian of southern England is only the second undoubted record from Jurassic strata. Two incomplete teeth from the Lower Toarcian of France, described as *Lissodus del-satei* by Guennegues and Biddle (1989) are typical of *Lonchidion* (Rees and Underwood 2002), but no characters on the holotype specimen or in the diagnosis can serve to separate confidently this species from others of the genus. Consequently, *L. del-satei* must be considered

a *nomen dubium*, at least until better preserved material is found. The dental morphology of *Lonchidion* is very conservative and dentitions of many species are extremely similar so a large number of well-preserved teeth are necessary when erecting a new species. The material described here probably represents an undescribed taxon but, as a result of the scarcity of specimens, we refrain from erecting a new species. The presence of specimens of *Lonchidion* in the Bathonian demonstrates that the large gap in the stratigraphical distribution of the genus from the Toarcian to the Berriasian (see Rees and Underwood 2002) is probably a sampling artefact caused by the paucity of studies of small shark teeth from Jurassic marginal facies.

Occurrence. Rare teeth of *Lonchidion* sp. have been found in four of the sampled horizons, namely the upper part of the Rutland Formation at Ketton Quarry, Bed 17 of the White Limestone Formation at Woodeaton, the upper part of the coral-bearing mudstone at Hornsleasow and the Forest Marble Formation at Watton Cliff. Three of these sites represent lagoonal or protected embayment palaeoenvironments, while the material from Watton Cliff could easily represent allochthonous elements within this mixed assemblage. There are no Bathonian records of *Lonchidion* from open marine or carbonate shelf palaeoenvironments.

Genus LISSODUS Brough, 1935

Type species. *Hybodus africanus* Broom, 1909, from the Scythian, Lower Triassic of Bekkerskraal, South Africa.

Lissodus leiopleurus (Agassiz, 1839) Plate 6, figures 16–18

- 1839 *Acrodus leiopleurus* Agassiz, p. 145, pl. 22, fig. 5.
- 1887 *Acrodus leiopleurus* Agassiz; Woodward, p. 102.
- 1889 *Acrodus leiopleurus* Agassiz; Woodward, p. 295, pl. 13, fig. 8.
- 1890 *Acrodus leiopleurus* Agassiz; Woodward, p. 302.
- 2002 *Lissodus leiopleurus* (Woodward) [*sic*]; Rees and Underwood, p. 472.
- 2006 *Lissodus leiopleurus* (Agassiz); Rees and Underwood, p. 359, fig. 6.3–6.6.

Material. Six complete tooth-crowns and five fragmentary teeth including P. 5875 and P. 66515–66516.

Description. Anterior teeth have a well-developed cusp and up to three pairs of minute cusplets. Ornamentation is commonly extensive but often removed by wear. The form of the ornamentation is somewhat variable, as is exemplified by P. 5875, a tooth-crown displaying folds over the entire crown except for

the lowermost parts. Folds are slightly undulating in this specimen and originate primarily from the cusp and cusplets but also from a single, central fold on the labial protuberance. Other teeth possess weaker and fewer folds. Small nodes occur frequently on the lower labial side, and the labial protuberance is supported by a root buttress. Juvenile teeth also have a marked cusp but are not as highly ornamented as those of adults. Nodes occur less frequently and cusplets are fewer and lower. The largest tooth-crown is 4.1 mm wide but most juvenile teeth are c. 2 mm in width.

Remarks. The distinction between adult teeth of the two Bathonian species *L. leiodus* and *L. leiopleurus* have been thoroughly discussed by Rees and Underwood (2006) and no new information is provided by this study. Differentiation of teeth of juveniles of *Lissodus* is not as clear as with teeth of adults, but most teeth can be confidently assigned to either species unless heavily worn. Juvenile teeth of *L. leiodus* are lower, without a clear cusp or lateral cusplets and are ornamented with more densely spaced vertical folds. In *L. leiopleurus*, corresponding teeth have a higher crown with well-demarcated cusp and cusplets, a strong occlusal crest and only a few strong vertical folds. Furthermore, juveniles of the latter species are more robust with a larger labial protuberance.

Occurrence. This species occurs in the base of the Sharps Hill Formation at Oakham Quarry, the upper part of the coral-bearing mudstone at Hornsleasow, and rarely in the Forest Marble Formation at Watton Cliff. The holotype is from the oolitic limestones of Minchinhampton, Gloucestershire, and was the only specimen of this taxon recorded from England prior to this study. *Lissodus leiopleurus* is common at some horizons within the Great Estuarine Group of the Hebrides, Scotland (Rees and Underwood 2006) and appears to be almost entirely limited to

lagoonal or similar facies, with only a single specimen, the holotype, probably being recorded as an autochthonous element within open marine facies.

Lissodus leiodus (Woodward, 1887)

Plate 6, figures 19–26

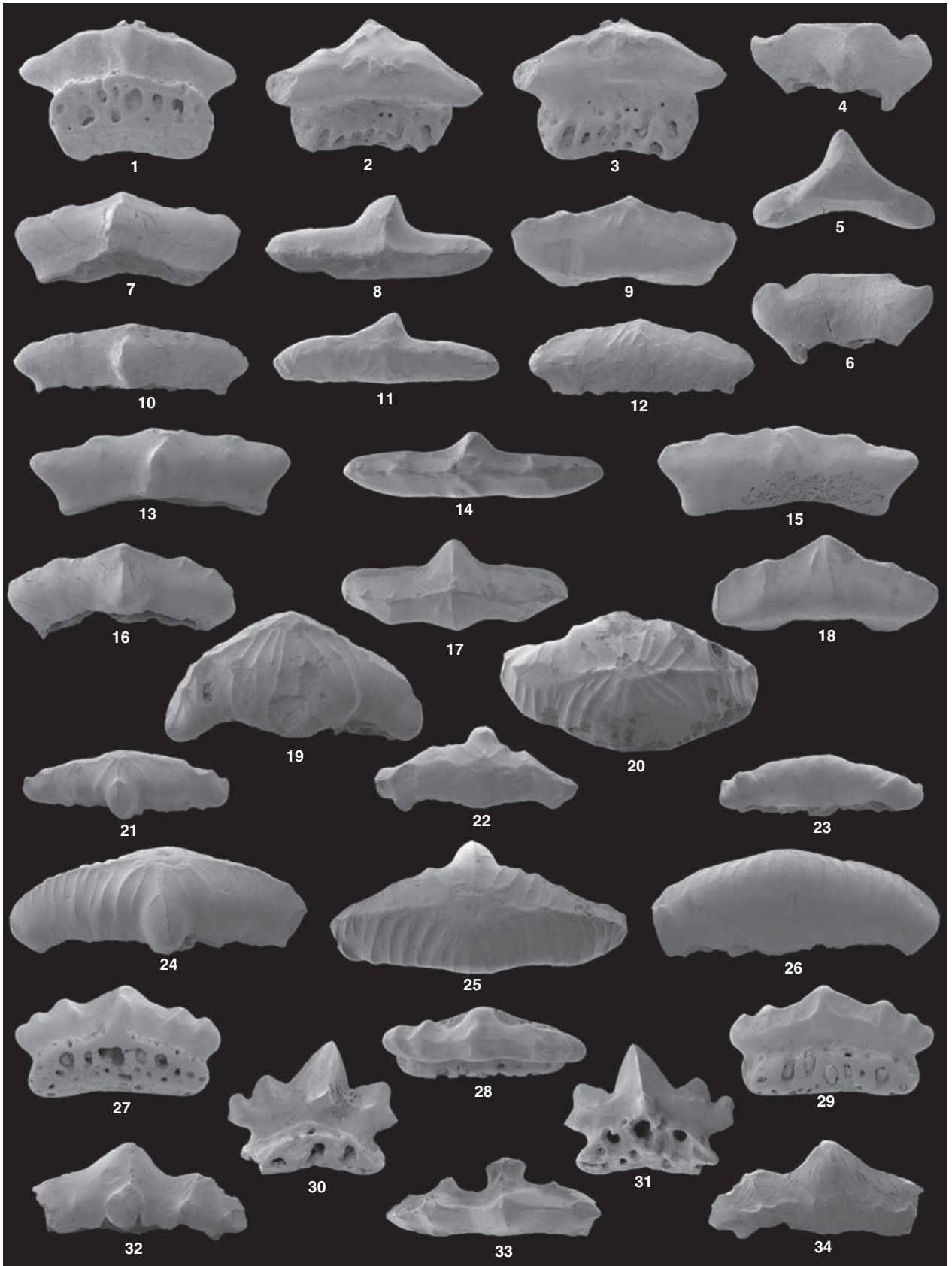
- 1844 *Acrodus leiodus* Agassiz, p. 38 (name only).
 1887 *Acrodus leiodus* Agassiz; Woodward, p. 101, fig. 1.
 1889 *Acrodus leiodus* Woodward; Woodward, p. 295, pl. 13, figs 5–7.
 1890 *Acrodus leiodus* Woodward; Woodward, p. 288, fig. 1.10.
 1985 *Lissodus leiodus* (Woodward); Duffin, p. 125, fig. 15, pl. 4, figs 3–4.
 1985 *Lissodus wardi* Duffin, p. 134, fig. 23, pl. 6, fig. 3.
 1991 *Lissodus leiodus* (Woodward); Brown and Keen, p. 92.
 2001 *Lissodus leiodus* (Woodward); Duffin, p. 179, fig. 20.
 2001 *Lissodus wardi* Duffin; Duffin, p. 178, fig. 19.
 2002 *Lissodus leiodus* (Woodward); Rees and Underwood, p. 472.
 2002 *Lissodus wardi* Duffin; Rees and Underwood, p. 472.
 2006 *Lissodus leiodus* (Woodward); Rees and Underwood, p. 359, fig. 6.1–6.2.

Material. 17 tooth-crowns and numerous tooth fragments including P. 66517–66523 in addition to numerous previously collected teeth in the NHM.

Description. This species is characterised by teeth with a rounded appearance, lacking a pronounced cusp or cusplets. Anterior teeth are high-crowned and almost triangular in labial and lingual views while laterals are much lower with a smoothly rounded shape, although the occlusal surface of both anterior and lateral teeth is often modified by wear. The lingual side of

EXPLANATION OF PLATE 6

- Figs 1–15. *Lonchidion* sp. 1–3, P. 66508, anterior tooth, Rutland Formation, Ketton quarry, labial, occlusal, and lingual views; × 20. 4–6, P. 66509, symphyseal tooth-crown, Rutland Formation, Ketton quarry, labial, occlusal, and lingual views; × 40. 7–9, P. 66510, juvenile tooth-crown, upper coral-bearing mudstone, Hornsleasow quarry, labial, occlusal, and lingual views; × 40. 10–12, P. 66511, lateral tooth-crown, Rutland Formation, Ketton quarry, labial, occlusal, and lingual views; × 20. 13–15, P. 66512, lateral tooth-crown, Forest Marble Formation, Watton Cliff, labial, occlusal, and lingual views; × 20.
 Figs 16–18. *Lissodus leiopleurus* (Agassiz, 1839), P. 66515, juvenile tooth-crown, upper coral-bearing mudstone, Hornsleasow quarry, labial, occlusal, and lingual views; × 20.
 Figs 19–26. *Lissodus leiodus* (Woodward, 1887). 19–20, P. 66517, anterior tooth-crown, base of Sharps Hill Formation, Oakham quarry, labial and occlusal views. 21–23, P. 66518, juvenile tooth-crown, base of Sharps Hill Formation, Oakham quarry, labial, occlusal, and lingual views. 24–26, P. 66519, lateral tooth-crown, upper coral-bearing mudstone, Hornsleasow quarry, labial, occlusal, and lingual views. All × 12.
 Figs 27–31. *Parvodus pattersoni* (Duffin, 1985). 27–29, P. 66524, anterior tooth, labial, occlusal, and lingual views; × 40. 30–31, P. 66525, juvenile tooth, lingual and labial views; × 50. Both from Forest Marble Formation, Watton Cliff.
 Figs 32–34. *Parvodus* sp., P. 66527, anterior tooth-crown, upper coral-bearing mudstone, Hornsleasow quarry, labial, occlusal, and lingual views; × 20.



REES and UNDERWOOD, hybodont sharks

all teeth is heavily incised above the crown-root junction. The labial protuberance is clearly differentiated, particularly in lateral teeth, but is rather small and parallel-sided. Ornamentation is extensive and weak vertical folds cover most of the crown in both anterior and lateral teeth, although the lower lingual side is most often smooth. In anteriors, most folds originate at the highest point of the tooth whereas lateral teeth have folds branching off the occlusal crest. Nodes occur rarely, primarily on the lingual side in small and juvenile teeth. No teeth studied have an entire root, but from incomplete teeth it can be noted that the root in anterior teeth is high, with large irregular foramina on the lower parts. In laterals, the root is lower, lingually projected, and possesses a row of small circular foramina close to the crown-root junction. The largest lateral tooth is 7.3 mm in mesio-distal width.

Remarks. As noted by Rees and Underwood (2006), the nominal species *L. wardi* Duffin, 1985 is based on material that cannot be separated from teeth of juvenile *L. leiodus*; this species must therefore be regarded as a junior synonym of *L. leiodus*.

Occurrence. Teeth of *L. leiodus* were recorded in a large number of the samples from lagoonal and carbonate shelf facies collected for the present study. No specimens were recorded from offshore mudstone facies. Further occurrences include records from the Bathonian and possibly also the Bajocian of Scotland (Duffin 2001; Rees and Underwood 2006), and the species was listed as present in the Callovian of England by Brown and Keen (1991), but not figured. This species appears to be far more common than *L. leiopleurus* in the English Bathonian and is as common within carbonate shelf facies as in deposits representing more restricted environments. The opposite situation has been observed in contemporaneous strata of the Hebridean Basin in Scotland (Rees and Underwood 2006) where teeth of *L. leiopleurus* are more common than those of *L. leiodus* within the freshwater lagoon facies present there. It therefore appears that *L. leiodus* was the dominant species of *Lissodus* in open marine habitats and *L. leiopleurus* dominated restricted environments with reduced salinity.

Genus PARVODUS Rees and Underwood, 2002

Type species. *Lissodus rugianus* Ansoerge, 1990 from the Lower Cretaceous of Rügen, northern Germany.

Parvodus pattersoni (Duffin, 1985)

Plate 6, figures 27–31

- 1985 *Lissodus pattersoni* Duffin, p. 133, text-fig. 22, pl. 7, fig. 1.
 2001 *Lissodus pattersoni* Duffin; Duffin, p. 178, fig. 18.
 2002 *Parvodus pattersoni* (Duffin); Rees and Underwood, p. 476.
 2006 *Parvodus pattersoni* (Duffin); Rees and Underwood, p. 361, fig. 6.7–6.8.

Material. Four complete and several incomplete teeth including P. 66524–66526 in addition to 22 teeth in previous collections at the NHM (see Duffin 1985).

Description. This species has small to minute teeth with a well demarcated cusp and two to three pairs of lateral cusplets. A moderate labial protuberance occurs on the cusp and further ornamentation comprises a few folds on the upper half of the crown, originating from the cusp and cusplets. A root buttress often supports the labial protuberance. Anterior teeth have a higher cusp and cusplets than the lower and more mesio-distally expanded laterals and posteriors. Below the incised crown-root junction, the root displays an irregular row of small circular foramina on both lingual and labial root-faces. The lower parts of the root are perforated by large, irregularly placed foramina. Juvenile teeth are relatively higher with a smaller root perforated by larger irregular foramina. The largest complete tooth of this species measures 0.9 mm in mesio-distal width but incomplete specimens show that some teeth could be somewhat larger.

Remarks. So far, only three species have been confidently assigned to *Parvodus*. Apart from *P. pattersoni*, these are the type species *P. rugianus*, and *P. curvidens* (Duffin and Thies, 1997) from the Kimmeridgian of northern Germany. Teeth of *P. pattersoni* (see Duffin 1985) can be separated from *P. curvidens* by the lack of labio-lingual curvature in anterior teeth and the less well-developed lateral cusplets. Teeth of *P. rugianus* also possess higher lateral cusplets than those of *P. pattersoni*, and are more robust and wider mesio-distally.

Occurrence. Within the sampled strata, *P. pattersoni* was recorded from the coral-bearing mudstone at Hornsleasow and the Forest Marble Formation at Wood Eaton Quarry and Watton Cliff (see also Duffin 1985, 2001). Additionally, this species was encountered in the Bathonian of the Hebridean Basin in Scotland (Rees and Underwood 2006). No examples of this species, or indeed other species of *Parvodus*, have been recorded from autochthonous open marine assemblages. As with the Bathonian *Lissodus* species, *P. pattersoni* occurs in facies indicative of a range of salinity from fully marine to fresh water.

Parvodus sp.

Plate 6, figures 32–34

Material. Two incomplete teeth numbered P. 66527–66528.

Description. The teeth referred to *Parvodus* sp. are small but rather robust with a marked cusp and low cusplets, with at least two pairs of cusplets being present. The occlusal crest is prominent but vertical folds seem to be limited to the cusp and cusplets. A large, well-developed labial protuberance, which is almost square in occlusal view, is situated on the central cusp, and smaller labial nodes may occur on the lateral cusplets. On

the lingual side, there is an irregular horizontal shelf on the lower part of the crown. Nothing is preserved of the root in either specimen. Both teeth are preserved with the central cusp and one lateral side of the tooth, and are 2.0 mm (P. 66527) and 1.5 mm (P. 66528) wide, respectively.

Remarks. The morphology of the labial protuberance is identical in these two teeth but different from that in any other material referable to *Parvodus*. These specimens also differ from *P. pattersoni* in possessing a rather well developed, shelf-like horizontal ridge on the lingual side and more robust crown architecture. As only two incomplete teeth have been found, and as the heterodonty pattern of *P. pattersoni* is not fully understood, it is difficult to determine whether the differences observed fall within the natural range of variation of the latter species or whether they indicate another species. No teeth from the very numerous specimens of *P. rugianus* that we have studied have been found with this shape of labial protuberance. Until more material is discovered and the variation within *P. pattersoni* is investigated further, these teeth are kept in open nomenclature.

Occurrence. The two teeth referred to this taxon originate from the Sharps Hill Formation at Oakham Quarry and the upper coral-bearing mudstone at Hornsleasow.

PALAEOENVIRONMENTAL DISTRIBUTION

The wide range of facies present within the British Bathonian allows the palaeoenvironmental preferences of the hybodont sharks to be assessed. A study of the neoselachian sharks and rays (Underwood 2004) demonstrated that almost all species were restricted to a limited range of facies. A similar pattern appears to be present with the hybodonts, although the smaller sample sizes from many facies makes assessing palaeoenvironmental specificity rather less clear than with the neoselachians.

Offshore mudstone and shelly marl facies yielded a number of species, the majority being medium- to large-toothed taxa with sharply pointed teeth, with the assemblages dominated by *Egertonodus duffini* and *Planohybodus grossiconus*. Other taxa are rare and represented by single specimens or just a small number and include *Hybodus obtusus*, *Hybodus* sp. and *Frangerodus lingualis*.

Carbonate shelf palaeoenvironments are represented by grainstone shelves and shoal complexes and tilestone (Stonesfield Slate facies) shoreface carbonates. These have provided most of the specimens seen in museum collections (largely from Eyford and Stonesfield), with some additional material collected during this study. The domi-

nant taxa in museum collections are large teeth of *Egertonodus duffini*, *Planohybodus grossiconus*, *Asteracanthus magnus*, and *A. tenuis*. Field observations by one of us (CJU) of oolitic and tilestone facies around Eyford indicate that teeth of *Egertonodus* and *Planohybodus* appear to be far more common than those of *Asteracanthus*. Teeth of *Secarodus polyprion*, *Frangerodus lingualis* and other species of *Asteracanthus* all seem to be rare. Small teeth of *Lissodus leiodus* appear to be frequent, but are underrepresented in museum collections, with only a single tooth of *L. leiopleurus* being recorded.

Lagoonal and other enclosed or restricted facies studied were dominated by mudstones yielding a shelly fauna suggesting fully marine to moderate salinity but not open marine conditions. These yielded a fauna dominated by small taxa, with larger teeth being rare. Although teeth of *Hybodus obtusus*, *Egertonodus duffini*, *Planohybodus grossiconus* and *Asteracanthus magnus* were all recorded, it is only small specimens of *E. duffini* that were recorded from more than one site. Within lagoonal and muddy embayment facies where there was normal marine salinity these rare larger teeth are associated with *Lonchidion* sp., *Lissodus leiopleurus*, *L. leiodus*, *Parvodus pattersoni* and *Parvodus* sp. Samples from facies that represented palaeoenvironments with reduced salinity contained the same small taxa, but without larger teeth.

In addition to facies containing autochthonous and parautochthonous assemblages, bioclastic channel fills within the Forest Marble Formation contain mixed faunas including obvious allochthonous elements, such as terrestrial vertebrates. Channelised limestones in the Forest Marble from Oxfordshire, which occur within very shallow water or lagoonal settings, contain low diversity hybodont faunas with *Egertonodus duffini*, *Planohybodus grossiconus* and *Parvodus pattersoni* all being frequent. Superficially similar Forest Marble limestones from localities further to the south in Wiltshire and Dorset were deposited in more open marine settings. High diversity hybodont assemblages were recorded both during this study and from museum collections; the majority of the specimens show some degree of abrasion, with teeth so rounded as to be indeterminate being common. The museum collections are dominated by *Egertonodus duffini*, *Planohybodus grossiconus*, *Asteracanthus magnus* and *A. tenuis*, with rare specimens of *Secarodus polyprion*, *Frangerodus lingualis* and *Lissodus leiodus* also present in some collections. Sampling of the Forest Marble Formation at Watton Cliff yielded every hybodont taxon known from the English Bathonian except *Frangerodus lingualis*, with specimens of *Egertonodus duffini*, *Planohybodus grossiconus* and *Parvodus pattersoni* being especially abundant.

PALAEOBIOLOGY

Hybodont sharks were the dominant group of chondrichthyans in the Triassic and Early Jurassic, but are generally considered to have declined in diversity through the remainder of the Jurassic and Cretaceous until their extinction at, or very close to, the Cretaceous/Palaeogene boundary. The perceived decline of the hybodonts is coincident with the radiation of both the neoselachian sharks and rays and the teleost actinopterygians. The first phase of diversification of the neoselachians in the Late Triassic (Cuny and Benton 1999) apparently had little effect on the composition of Early Jurassic shark faunas, although this is not easy to gauge owing to the unusual facies of most latest Triassic shark-bearing deposits. Further neoselachian diversification in the latest Early and Middle Jurassic (Underwood 2006) coincided with a reduction in the importance of hybodonts within marine palaeoenvironments, a trend that appears to have continued until the Late Cretaceous. Despite this loss of diversity within the marine realm, various investigations (Patterson 1966; Underwood and Rees 2002; Cappetta *et al.* 2006; Cuny *et al.* 2004, 2006) have shown a great deal of specific and ecological diversity among hybodont sharks during the Early Cretaceous in non-marine and marginal marine settings. Although some Jurassic and Early Cretaceous neoselachians were present in areas of reduced salinity (Underwood and Rees 2002; Underwood 2004) very few entered fresh water (Sweetman and Underwood 2006). It is therefore possible that increased competition within marine environments led to a decline in hybodont diversity, but in lagoonal and freshwater environments Early Cretaceous hybodonts flourished in the near absence of neoselachians. The dentitions of these hybodonts imply that they inhabited a wide range of ecological niches with teeth adapted for cutting, clutching, and crushing. Few investigations have focused on non-marine selachian faunas from the Jurassic, but the present study in combination with previous investigations (Nessov and Kaznyshkin 1988; Rees and Underwood 2006) show that there was a high diversity of non-marine hybodonts in the Middle Jurassic. The variety of dental morphologies further suggests that these hybodonts adopted a wide range of different lifestyles.

During the Middle Jurassic, present-day England was inhabited by two groups of large hybodonts with very different dentitional patterns. The size of the fin spines and skull material of the Callovian *Planohybodus peterboroughensis* suggests that this species was 2–3 m long. The dentition was probably adapted for dealing with moderate-sized prey and tearing flesh from larger prey (Cappetta 1986). It is likely that the wider upper jaw teeth cut through flesh while the more slender lower jaw teeth held the prey in

place. Similar teeth of approximately the same size occur in *P. grossiconus*, and it is likely to have inhabited similar trophic niches during the Bathonian. In addition to these species, the somewhat smaller shark *Secarodus polyprion* developed a cutting dentition, a rare feature among non-neoselachian sharks. The dentition of this species is very similar to some species of the neoselachian hexanchiforms. It is possible that *S. polyprion* shared the deep water habitats of Recent and coexisting hexanchiforms (Underwood 2004) as appears to be suggested by its distribution (see above). Sharks that are referred to the large genus *Hybodus* occur in many different environments through a long period of time and species of it cannot be regarded as having any particular adaptation. Teeth of *H. obtusus* that occur rarely in the English Bathonian, but more frequently in younger Jurassic strata, have a wide base ornamented with prominent nodes and a blunt conical cusp. These sharks are likely to have been generalists but the nodes at the tooth bases could possibly have provided protection against spiny and sharp prey such as sea urchins. This species has mainly been recorded in open marine strata. The other, unnamed, species of *Hybodus* that occurs in the English Bathonian has much lower teeth that were probably arranged in a fashion where several tooth rows were functional at any given time. This arrangement would have formed a crushing surface in the lateral files while the anterior parts of the jaws were equipped with higher and mesio-distally narrower teeth used for grasping prey such as molluscs attached to the bottom or living within the substrate. The dentitional pattern of *Egertonodus duffini* suggests a diet of softer prey caught in the open water. The high, slender teeth could quite easily pierce through the softer skin of cephalopods or the thin scales of many actinopterygians or smaller selachians.

The other group of large hybodonts contained several species of *Asteracanthus* and *Frangerodus lingualis*. Fin spines and teeth of *A. magnus* and *A. ornatissimus* suggest that these sharks could well have matched the size of the largest Hybodontinae. With their extreme crushing dentitions, which often show high degrees of wear, they probably preyed upon bivalves and other shelly invertebrates on the sea-floor. The different dentitions of all species occurring in the English Bathonian suggest that they may have had particular specialisations but, like many recent selachians with these types of dentition, they are likely to have been opportunists to a greater or lesser degree. As teeth of *Asteracanthus* spp. are rare in the English Bathonian, it is likely that they were never particularly common within the facies sampled, the abundant specimens in museum collections being a result of the very obvious nature of *Asteracanthus* teeth in the field.

Teeth from five species of small-toothed Lonchidiidae have been recorded in the English Bathonian. Both spe-

cies of *Lissodus* have similar dentitions with low, enlarged lateral teeth adapted for crushing, with shed teeth often showing very well-developed wear facets. The anterior teeth are somewhat higher and could perhaps have grasped the shelled prey that these species probably fed upon. The other three smaller species, *Lonchidion* sp., *Parvodus pattersoni* and *Parvodus* sp., were more likely to have been generalists as they lack any pronounced type of dentition. It is possible that the low and mesio-distally wide lateral teeth formed some kind of crushing surface but it is uncertain as to what extent several lateral teeth were used at the same time.

In addition to the diverse English faunas, Middle Jurassic hybodont taxa have been recorded from other regions. Bathonian assemblages from Scotland include a species of *Acrodus*, *A. caledonicus* Rees and Underwood, 2006, with a pronounced crushing dentition, although of a different architecture than those of *Asteracanthus* spp. Well-developed crushing dentitions have also been recorded in the Callovian *Hylaeobatis verzilini* (Nessov and Kaznyshkin, 1988; Rees and Underwood 2006) from Kirghizia.

In conclusion, the ecological diversity of Middle Jurassic hybodont sharks is far greater than previously appreciated. Taxa were adapted for a number of feeding strategies, including cutting, clutching, piercing, and crushing, the last of which appears to have been particularly widespread with at least nine species of five genera equipped with well-developed crushing dentitions. In total, there are more than 20 species of 11 hybodont genera present in the Middle Jurassic, strong evidence that hybodonts flourished during this period as well as in the Early Cretaceous.

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