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Environmental controls on the distribution of neoselachian sharks and rays within the British Bathonian (Middle Jurassic)

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Abstract

Extensive sampling from a range of facies within the Bathonian (Middle Jurassic) of southern England has allowed the palaeoenvironmental distribution of a number of taxa of neoselachian sharks and rays to be assessed. Faunas were collected from a number of recurrent facies, with different assemblages being characteristic of particular palaeoenvironments. Palaeoenvironmental specificity occurred at both ordinal and specific level. Samples from offshore facies contain high diversity faunas containing members of all neoselachian groups known to have been present in the Middle Jurassic. Shallower water assemblages contain lower diversity faunas lacking *Synechodontiformes* and *Hexanchiformes*. Samples from lagoonal facies contain low diversity faunas typically comprising different species from open marine settings. The presence of different taxa within different palaeoenvironments suggests that by the Bathonian neoselachians had differentiated into a wide range of niches and ecologically more diverse than has previously been recognised. Implications for early neoselachian palaeoecology, salinity tolerance and diversification are discussed.

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1. Introduction

Neoselachians, including all extant sharks and rays, represent an extremely important and diverse group within modern marine environments, with a smaller number of taxa present in restricted marine and non-marine settings. Despite their importance within modern and ancient marine eco-

systems, very little is known about the ecology and evolution of early neoselachians. Although there are a number of localities that have yielded exceptionally preserved skeletons (e.g. Cappetta, 1980; Schweizer, 1964), the vast majority of neoselachian fossils are represented by isolated teeth. Although teeth with an enameloid microstructure characteristic of neoselachians first appear in rocks of Triassic age, the relationships of these early forms to each other and to later neoselachians is poorly understood (e.g. Cuny and Benton, 1999). Within the Early Jurassic, radiation of the neoselachians saw the appearance of new

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groups, with several orders being present by the end of the Toarcian (e.g. Rees, 2000). Further radiations within the Middle Jurassic resulted in diverse neoselachian faunas by the Bathonian.

Despite the development of diverse neoselachian faunas within the Jurassic, the palaeoenvironmental specificity of the taxa has generally been ignored. This is in part due to the largely open marine settings from which isolated tooth assemblages have been collected (Underwood, 2002) and the dominantly allochthonous nature of exceptionally preserved specimens. It is therefore unclear if early neoselachian taxa were restricted to particular palaeoenvironments or whether early neoselachian radiation events occurred largely within open marine, nearshore or lagoonal environments. Initial investigation into the relationships between Bathonian neoselachian faunas and facies (Underwood and Ward, in press a) showed a strong correlation between the distribution of species and palaeoenvironment. Taxonomy of the Bathonian neoselachians was at the time poorly understood. Subsequent work and additional sampling has allowed the affinities of all but a few rare and poorly preserved forms to be studied (see Underwood and Ward, in press b for a full taxonomic summary; see caption to Fig.

4 for taxonomic authorship) and increased the number of facies available for study.

2. Geological setting

Middle Jurassic sedimentary rocks are well represented in southern Britain. Units of Bathonian age are well developed and present in a diversity of facies (Fig. 1). Although most of these Bathonian formations are included within the Great Oolite Group, oolite barrier systems were largely restricted to south central England. To the south of these barriers, open marine palaeoenvironments predominated, with both mud and carbonate-rich sea floors. To the north of the oolites, lagoonal complexes contained a mosaic of fully marine, freshwater and coastal plain palaeoenvironments. These palaeoenvironments persisted throughout much of the Bathonian, with only minor changes in the suite of facies deposited over time, and a gradual progradation towards the south. Breakdown of the oolite barriers within the Upper Bathonian led to a change in depositional style, with a rise to predominance of allochthonous bioclastic limestones.

Within this complex sedimentological frame-

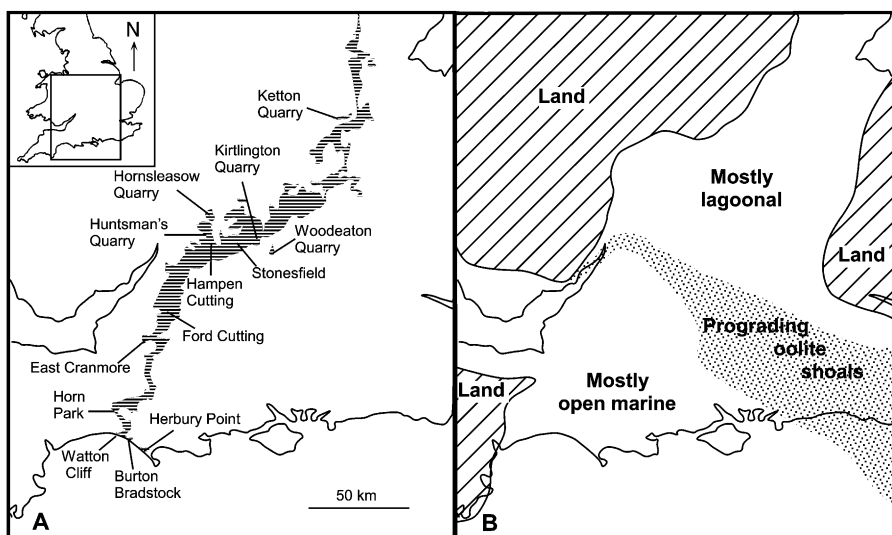


Fig. 1. (A) Outcrop of Bathonian rocks in southern Britain showing sample localities. (B) Generalised Middle Bathonian palaeogeography of southern Britain.

work, it has been possible to differentiate a number of recurrent facies from which neoselachian material could be collected. Although it must be noted that boundaries between these facies may be somewhat subjective, a number of distinct facies can be readily recognised:

2.1. *Neritic mudstones*

Homogeneous silty mudstones are present across much of the southern part of the Bathonian outcrop. These are typically very poorly fossiliferous, although rare neoselachian teeth were recorded in two samples. At one locality, however, diverse neoselachian remains were recorded from a unit of dark, poorly laminated and very shelly mudstone. A relatively diverse assemblage of marine invertebrates is dominated by two taxa of oysters, along with thin-shelled epifaunal and infaunal bivalves, belemnites and frequent pyritised ammonite nuclei. The only ichnofauna recognised comprised fine pyrite-filled meandering burrows. A rich and diverse selachian fauna was predominantly obtained from a 5 cm oyster and belemnite shell lag. In addition to selachian material, diverse actinopterygian teeth, several fragmentary chimaeroid toothplates and a plesiosaur tooth were recovered.

2.2. *Brachiopod-rich limestones*

Closely associated with the neritic mudstones, this facies consists of nodular micrite with seams or thicker interbeds of homogeneous marl. A rich and diverse invertebrate fauna is dominated by several taxa of brachiopod, along with common oysters, pectinids, belemnites and bryozoa. Ammonites, gastropods and large infaunal bivalves are uncommon. Intense bioturbation has obliterated most trace fossils, but *Chondrites* and *Planolites* can be recognised. In addition to neoselachian teeth, relatively diverse actinopterygian remains and a mandibular plate of *Ischyodus* were recorded. A relatively minor component of the neritic association, the lithology and faunas suggest a reduction in sedimentation rates and development of a moderately firm substrate.

2.3. *Shelly carbonate shelf*

Thin but very laterally extensive units of biomicrite packstones are present at two levels within the Upper Bathonian. These are generally nodular and variable lithified. Shelly fossils are diverse and commonly close to life position in a shell detrital matrix. Brachiopods and epifaunal bivalves dominate, with echinoids often being present. Shell material is commonly encrusted by oysters, serpulids and bryozoa. This facies occurs as erosively based horizons associated with transgressive surfaces. Severe reduction in clastic input allowed the development of hiatal shell detrital lags, sometimes with secondary colonisation of shell debris by brachiopod colonies.

2.4. *Marine forest marble facies*

Within the essentially open marine facies of the English South coast, a channelised unit of cross-stratified shell detrital limestone contains a mixed and transported fossil assemblage. Such Bathonian detrital limestones have historically been referred to as 'forest marble', although they vary considerably in detail. Uncemented lenses within the limestone were extensively sampled. Many of the fossils are broken and abraded, being dominated by diverse bivalves and echinoderms, the latter including abundant *Apiocrinites*. Brachiopods are patchily distributed and cephalopods are very rare. The vertebrate assemblage is likewise mixed, containing abundant neoselachian and hybodont sharks, actinopterygian remains and tetrapods including marine, freshwater and terrestrial forms (e.g. [Evans and Milner, 1994](#)).

2.5. *Tilestones*

Typified by the well-known Stonesfield Slate, this facies comprises laminated and very low angle cross-stratified silty and micro-oolitic limestones. Beds containing abundant *Skolithos*, ooids or plant debris are present at some localities. The invertebrate fauna is of low diversity, with the bivalves *Praeexogyra*, *Vaugonia* and *Placunopsis* dominating; cephalopods, echinoderms and brachiopods are all very rare. Actinopterygian and

hybodont teeth are common and diverse, whilst chimaeroid and reptile remains are frequent and well-known. This facies is interpreted as being inner shelf to lower shoreface and is largely confined to several horizons within the lower part of the Middle Bathonian.

2.6. *Muddy embayment*

Only sampled at a single locality, this facies comprises bioturbated silty mudstones with scattered ooids. The invertebrate fauna is diverse and abundant, with brachiopods, corals and gastropods being especially well represented. Cephalopods are absent as are characteristic lagoonal invertebrates. Actinopterygian and hybodont material is subordinate to neoselachian teeth. The facies and faunas suggest a shallow but protected open marine setting rather than within a lagoon, with the unit sampled having been mapped in continuity with open shelf mudstones (Wyatt, 1996).

2.7. *Oolite shoal*

Oolitic grainstones and packstones typically contain variable quantities of comminuted shell debris, becoming bioclastic in places. Channelised and tabular cross-stratification is usually prominent and there is generally little evidence for autochthonous faunas. Vertebrate remains are typically rare and highly abraded; much of that recorded here coming from two shelly channel lags.

2.8. *Lagoonal forest marble facies*

Superficially similar to the open marine forest marble facies, channelised bioclastic limestones are present within the Upper Bathonian of the lagoonal facies belt. Invertebrate faunas are more restricted than in the open marine forest marble, being dominated by oysters, *Camptonectes* and *Isocrinus*, whilst lacking *Apiocrinites* and other open marine forms. The vertebrate fauna is diverse, with neoselachians, hybodonts, actinopterygian and aquatic and terrestrial tetrapods. Open marine forms such as *Asteracanthus*, chi-

maeroids and teleosaurian crocodiles appear to be absent.

2.9. *Shelly-oolitic lagoon*

Characterised by abundant matrix supported ooids within a mudstone matrix, this facies also contains variable quantities of shelly material. Within most occurrences of this facies, bivalves, either diverse or oyster-dominated, form clast-supported shell beds. The brachiopod *Epithyris* is commonly present, whilst echinoderms are diverse with abundant asteroid material. Actinopterygian and hybodont material is typically subordinate to neoselachian teeth. The fully marine fauna and presence of ooids within an obviously low energy setting indicate the deposition within the outer part of a lagoon complex, close to the oolite barrier from which washovers of ooids originate.

2.10. *Fully marine lagoon*

These marls and calcareous mudstones occur as partings within massive micrites. Both marls and micrites are generally completely bioturbated and contain rich invertebrate faunas. Diverse bivalves are accompanied by common but low diversity echinoderm assemblages (especially *Hemicidaris* and a small isocrinid), with gastropods and *Epithyris* frequently being present. Actinopterygian and hybodont material is typically far less common than neoselachian, with rare crocodylian teeth also frequently being present. Faunally and sedimentologically, this facies is almost identical to the surrounding micrites, differing only in being less indurated, probably due to a slightly elevated clastic mud content. Sedimentological and faunal features suggest deposition within a lagoon of close to fully marine salinity.

2.11. *Calcareous restricted lagoon*

Bioclastic material forms a minor component of these, typically pale coloured, mudstones which typically interbed with massive micrites. Plant rootlets and lenses of silt are commonly present, the sediments otherwise being homogeneous.

Shelly fossils are restricted in diversity and dominated by oysters, ‘*Corbula*’ and *Placunopsis*, with rare echinoderm remains. Neoselachian teeth are rare, with semionotid and crocodilian remains usually being relatively common; remains of amphibians, terrestrial reptiles and mammals are frequently present. Invertebrate faunas indicate reduced palaeosalinities, whilst the bivalves and echinoderms indicate conditions were not fully freshwater.

2.12. Muddy restricted lagoon

Sampled levels represent shell beds at the base of shallowing-upwards cycles, which typically terminate in rootlet beds. Unlike lagoonal facies further south, limestones are restricted to a single major marine transgressive horizon, otherwise the sequence is totally within mudstones and siltstones. The shell beds contain typical lagoonal bivalve taxa, with *Lingula* and rare rhynchonellids present at one level. Echinoderms are absent in some shell beds and restricted to monospecific assemblages of ophioroid or echinoid fragments in others. Although the shell beds at the base of each cycle represent the most marine conditions, the faunas suggest that salinity was still restricted.

3. Sampling strategy and methodology

Sampling was carried out to include examples of all the main facies present and to attempt to obtain significant numbers of neoselachian teeth from each. Due to the mobility of Bathonian facies belts, it was possible to collect samples from a range of facies within the same sections. For this reason, the bulk of samples were collected from a relatively small number of sites. Several samples were collected from different horizons at Ketton Quarry, Rutland, Kirtlington and Woodeaton Quarries, Oxfordshire, Hampen Railway Cutting and nearby quarries, Gloucestershire and Watton Cliff, Dorset. Additional sites were used for examples of facies poorly represented here.

The majority of the material studied was extracted from bulk samples of mudstones and marls, with some additional material extracted

from limestones by acid digestion. Bulk sieving and acid preparation techniques are given in [Underwood and Ward \(in press b\)](#). During this study, about 2000 kg of samples were processed and sorted for selachian material, yielding a total of about 8500 neoselachian teeth.

4. Taphonomy

As would be expected within the wide range of palaeoenvironments studies, the state of preservation of vertebrate material is highly variable. There was no evidence for any of the teeth recovered being part of associated dentitions, and it is therefore evident that all represent either shed teeth or teeth from a disarticulated cadaver. Post-mortem damage to teeth is common (see below), and readily separated from functional wear ([Underwood and Ward, in press b](#)). Many of the neoselachian teeth recovered show signs of damage to the root by endolithic organisms ([Underwood et al., 1999](#)). The degree of this bioerosion was seen to vary considerably between samples. Teeth from neritic settings show the highest degree of bioerosion, with roots being missing from 50–80% of teeth. There is a relationship between tooth size and preservation, with the smallest teeth generally having a lower degree of endolith damage. There is typically a low rate of root destruction in teeth collected from lagoonal sediments, destruction of roots being highest in samples from hiatal horizons.

5. Biostratigraphy

A high diversity of neoselachians was recorded during this study ([Underwood and Ward, in press b](#)), with over 25 taxa being represented in total. Despite this, the faunas present within different samples contain radically different assemblages. This could be due to either palaeoenvironmental or biostratigraphic control on species distribution. Although the general rarity of ammonites hinders the detailed correlation of the Bathonian of southern Britain, a reasonable correlation scheme has been constructed ([Cope et al., 1980](#); [Wyatt,](#)

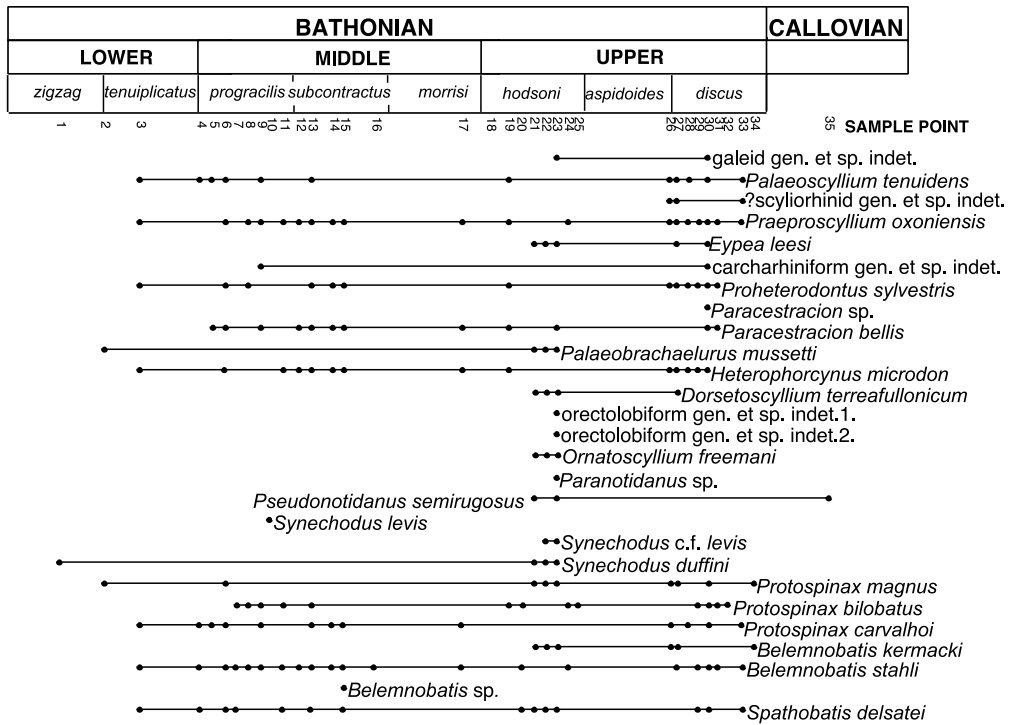


Fig. 2. Approximate biostratigraphical distribution of neoselachians within the British Bathonian. Sample numbers refer to sites in Appendix A.

1996). When occurrences of taxa are plotted against their approximate stratigraphical position (Fig. 2), there are little or no obvious biostratigraphical differences within the neoselachian faunas throughout the Bathonian. Although a number of taxa seem to first appear within the lower part of the Upper Bathonian, this is almost certainly a result of the almost total restriction of fossiliferous open marine facies to this level. This lack of biostratigraphical control on the faunas therefore strongly suggests that variations were almost exclusively due to palaeoenvironmental differences.

6. Faunas (see Fig. 3)

Many of the faunas studied comprise well preserved or bioeroded teeth and other remains showing no signs of abrasion, and these are here considered to be largely autochthonous. It is probable that whereas some of the facies yielding

abraded teeth contain mixed and partly allochthonous assemblages, others represent parautochthonous faunas with only intra-facies transport. Examples of the species covered here are seen in Fig. 4.

6.1. Neritic mudstones

Large numbers of neoselachian teeth were collected from this facies, giving the highest diversity recorded during this study. The most abundant element within this fauna is *Protospinax magnus*, which makes up over 57% of the neoselachian fauna. Although the teeth of this taxon are very variable in size, smaller teeth dominate, although it is uncertain whether this is due to the nature of heterodonty shown by this species or a predominance of small individuals. The second most abundant neoselachian remains are the small teeth of the Orectolobiforme *Ornatoscyllium freemani*, which comprise about 20% of the assemblage. Nearly 10% of the assemblage is composed of

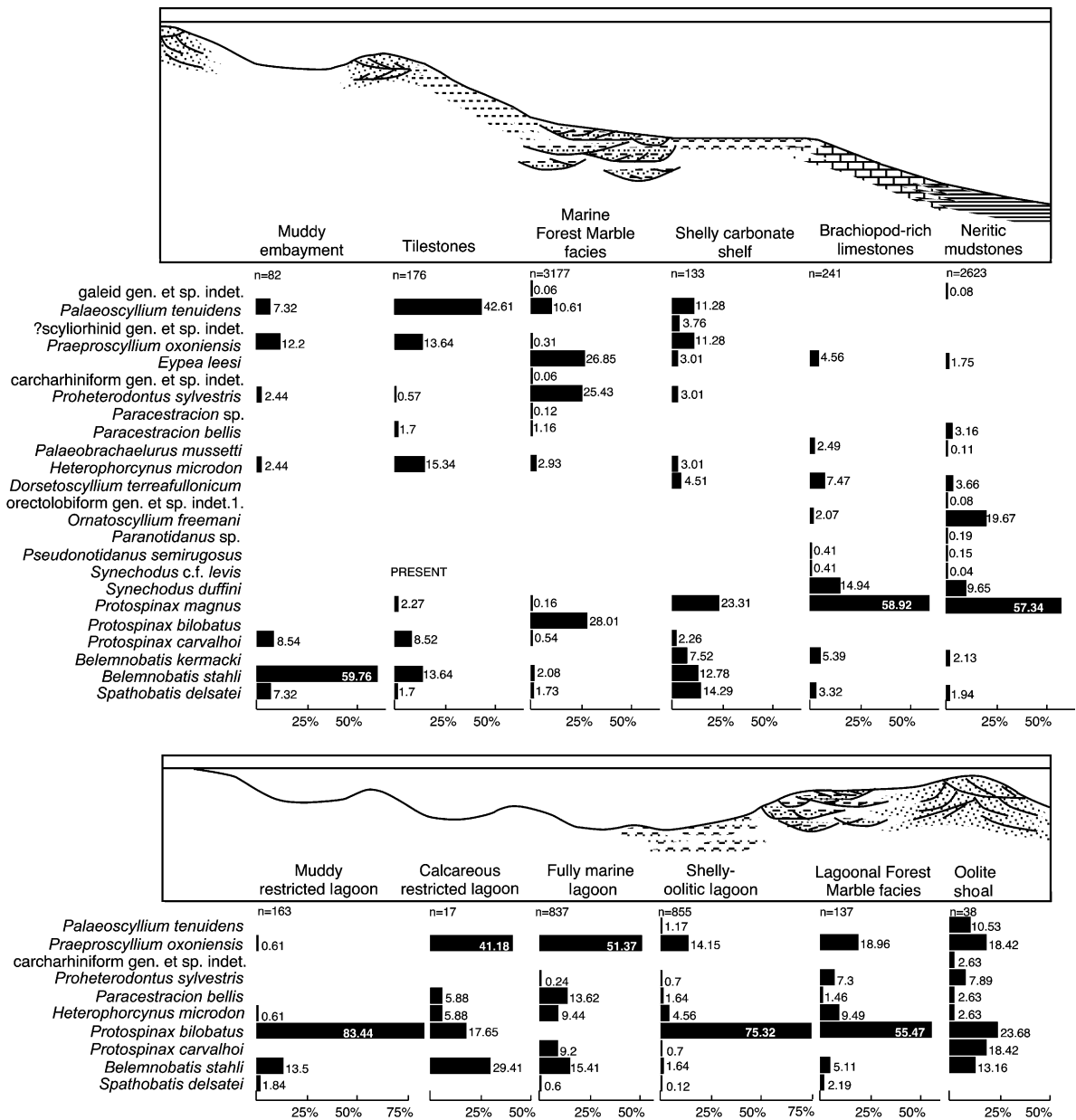
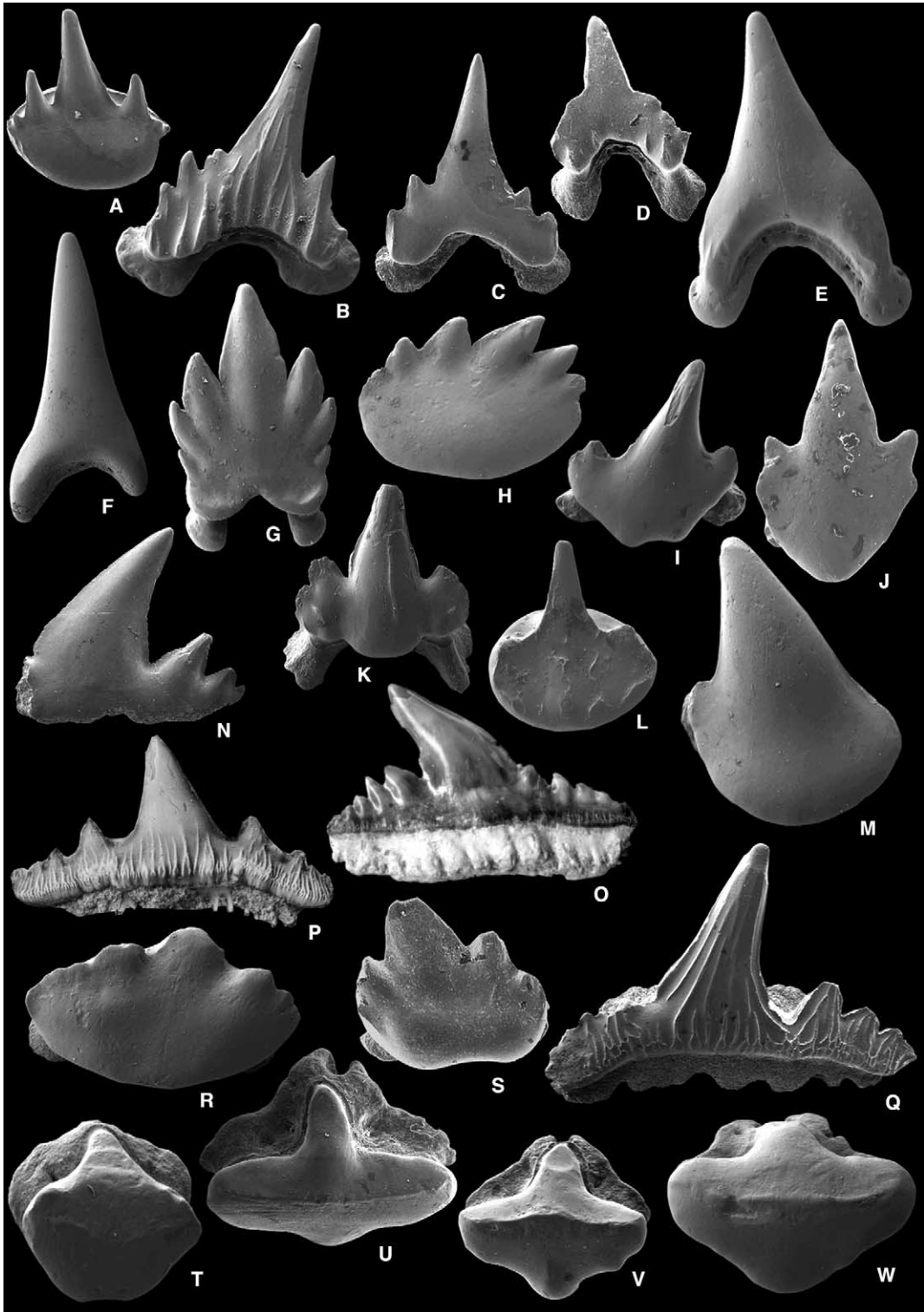


Fig. 3. Percentages of neoselachian teeth within the 12 facies recognised in this study.

teeth of the *Synechodontiforme* *Synechodus duffini*. Teeth of the sharks *Eypea leesi*, *Paracestracion bellis*, *Dorsetoscyllium terraefullonicum* and the rays *Belemnobatis kermacki* and *Spathobatis delstaei* each comprise over 1% of the assemblage. Several other, rarer, species were also recorded.

6.2. Brachiopod-rich limestones

The assemblage of neoselachian teeth recorded from this facies is very similar to that recorded from the neritic mudstones, being likewise dominated by specimens of *Protospinax magnus*, com-



prising 60% of the assemblage. The lower total diversity is probably a function of the lower sample size from this facies. The only significant difference between the neoselachian faunas of the neritic mudstones and brachiopod-rich limestones appears to be the rarity of *Ornatoscyllium freemani* in the latter, where it comprises only 2% of the assemblage. As in the neritic mudstones, two taxa of rays are present, with small gracile teeth of *Belemnobatis kermacki* and more robust teeth of *Spathobatis delsatei*. The teeth of *S. delsatei* from these open marine facies are consistently large, if invariably poorly preserved, with smaller teeth of the same species known from more inshore facies apparently being absent.

6.3. Shelly carbonate shelf

Faunas from this facies show no strong dominance of any particular species. The most abundant teeth are of *Protospinax magnus*, with only small teeth being present. Rare teeth of a second species of *Protospinax*, *P. carvalhoi*, are also present. Several species of Carcharhiniformes are present, with uncommon *Eypea leesi* being outnumbered by *Palaeoscyllium tenuidens*, *Prae-*

proscyllium oxoniensis and an unidentified scyliorhinid. As with the Carcharhiniformes, Orectolobiformes include both a species present within neritic facies (*Dorsetoscyllium terraefullonicum*) and *Heterophorcynus microdon*, a species not recorded in deeper water. Uncommon teeth of *Proheterodontus sylvestris* are the only remains recorded of a heterodontid. Three species of rays are present, with *Belemnobatis stahli* being present alongside *B. kermacki* and *Spathobatis delsatei*. Specimens of *S. delsatei*, *D. terraefullonicum* and *E. leesi* are typically smaller than in more offshore facies. Teeth of Synechodontiformes and Hexanchiformes are absent.

Although many of the neoselachian teeth collected from this facies show some degree of abrasion, it is here considered that there was little if any mixing of faunas from different palaeoenvironments. Both of the formations sampled are extremely laterally continuous in comparison to most other units within the British Bathonian, and very considerable transport would have been required to bring selachian material into these depositional settings from elsewhere. Most of this abrasion was probably due to hiatal reworking within these highly condensed units,

Fig. 4. Photographs of Bathonian Neoselachians. All images show labial view except T–W, which show occlusal view. All specimens in The Natural History Museum, London (prefix BMNHP). (A) (66044): Galeid gen. et sp. indet. Frome Clay Formation, Watton Cliff, $\times 20$. (B) (P. 66045): *Palaeoscyllium tenuidens* Underwood and Ward in press, holotype, Eyford Member, Hampen Cutting, anterolateral tooth, $\times 40$. (C) (66050): Scyliorhinidae? gen. indet., Boueti Bed, Herbury Point, $\times 40$. (D) (66052): *Praeproscyllium oxoniensis* Underwood and Ward in press, holotype, Rutland Formation, Bed 7, Woodeaton Quarry, $\times 40$. (E) (66058): *Eypea leesi* Underwood and Ward in press, holotype, forest marble Formation, Watton Cliff, $\times 20$. (F) (66066): Carcharhiniform gen. et sp. indet., forest marble Formation, Watton Cliff, $\times 7.5$. (G) (66068): *Proheterodontus sylvestris* Underwood and Ward in press, holotype, forest marble Formation, Watton Cliff, $\times 20$. (H) (66076): *Paracestracion bellis* Underwood and Ward in press, holotype, White Limestone Formation, Bed 1, Woodeaton Quarry, $\times 40$. (I) (66081): *Palaeobrachaelurus mussetti* Underwood and Ward in press, holotype, Frome Clay Formation, Watton Cliff, $\times 50$. (J) (66083): *Heterophorcynus microdon* Underwood and Ward in press, holotype, Rutland Formation, Bed 7, Woodeaton Quarry, $\times 40$. (K) (66097) *Ornatoscyllium freemani* Underwood and Ward in press, holotype, Frome Clay Formation, Watton Cliff, $\times 40$. (L) (66088): Orectolobid gen. et sp. indet., Frome Clay Formation, Watton Cliff, $\times 40$. (M) (66090): *Dorsetoscyllium terraefullonicum* Underwood and Ward in press, holotype, Frome Clay Formation, Watton Cliff $\times 30$. (N) (66105): ?*Paranoitidanus* sp., Frome Clay Formation, Watton Cliff, $\times 10$. (O) (66106): *Pseudonotidanus semirugosus* Underwood and Ward in press, holotype, Wattonensis Beds, Watton Cliff, $\times 4$. (P) (33474): *Synechodus levis* (Woodward 1889), Stonesfield Slate, Stonesfield, $\times 4$. (Q) (66110): *Synechodus duffini* Underwood and Ward in press, holotype, Frome Clay Formation, Watton Cliff, $\times 10$. (R) (66116): *Protospinax magnus* Underwood and Ward in press, holotype, Frome Clay Formation, Watton Cliff, $\times 20$. (S) (66124): *Protospinax bilobatus* Underwood and Ward in press, holotype, White Limestone Formation, Bed 17, Woodeaton Quarry, $\times 40$. (T) (66130): *Protospinax carvalhoi* Underwood and Ward in press, holotype, White Limestone Formation, Bed 1, Woodeaton Quarry, $\times 50$. (U) (66136): *Belemnobatis kermacki* Underwood and Ward in press, holotype, Frome Clay Formation, Watton Cliff, $\times 40$. (V) (66141): *Belemnobatis stahli* Underwood and Ward in press, holotype, Rutland Formation, Bed 7, Woodeaton Quarry, $\times 50$. (W) (66147): *Spathobatis delsatei* Underwood and Ward in press, holotype, White Limestone Formation, Bed 1, Woodeaton Quarry, $\times 30$.

and the fauna may be regarded as relatively autochthonous.

6.4. *Marine forest marble facies*

Although largely collected from a single site, a very large sample of neoselachian teeth has been collected from this facies, with a high total diversity. Although there is no dominant species, teeth of three taxa each comprise over 25% of the assemblage. Teeth of *Eypea leesi* are both common and large, as are teeth of *Proheterodontus sylvestris*. Small teeth of *Protospinax bilobatus* are also common, whereas teeth of *P. magnus* and *P. carvalhoi* are very rare. Teeth of *Palaeoscyllium tenuidens* are frequent. Teeth of several other species comprise over 1% of the assemblage; the sharks *Paracestracion bellis*, *Heterophorcynus microdon*, and the rays *Belemnobatis stahli* and *Spathobatis delsatei*. Several other rare taxa are present, although *Belemnobatis kermacki*, *Synechodontiformes* and *Hexanchiformes* are absent.

Varying degrees of abrasion are present on almost all material, both vertebrate and invertebrate, collected from this facies. Fossils include forms considered open marine (e.g. rare belemnites), marine hard substrate (e.g. *Apiocrinites*), freshwater (e.g. amphibians and non-marine ostracods) and terrestrial (e.g. mammals). It is therefore evident that considerable mixing of faunas has occurred, with considerable transport of material into an open marine setting. It is therefore likely that the selachian assemblages, as with other fossils, would include both parautochthonous open marine forms and allochthonous shallow marine and lagoonal taxa.

6.5. *Tilestones*

Teeth from this facies are typically very small. The commonest are of *Palaeoscyllium tenuidens*, which comprise over 40% of the assemblage. Teeth of *Praeproscyllium oxoniensis*, *Heterophorcynus microdon*, *Protospinax carvalhoi* and *Belemnobatis stahli* also each comprise about 10% or more of the fauna. Teeth of *Synechodus levis* are present in museum collections, but were not re-

corded during this study, whereas no other *Synechodontiformes* are known.

Moderate to high degrees of abrasion of some specimens suggests that transport and/or reworking of selachian material was common. Although it unclear to what degree the assemblage is transported, the very characteristic composition of the fauna suggests that it is likely to be parautochthonous, with relatively little mixing.

6.6. *Muddy embayment*

Relatively small samples of teeth were recovered from this facies, producing an assemblage dominated by teeth of *Belemnobatis stahli*, which comprise about 60% of the neoselachian remains recovered. Teeth of *Palaeoscyllium tenuidens*, *Praeproscyllium oxoniensis*, *Protospinax carvalhoi* and *Spathobatis delsatei* are also known from several specimens.

6.7. *Oolite shoal*

The general rarity of vertebrate remains within this facies resulted in relatively small samples of teeth, many showing strong abrasion. No strong dominance of one taxon was recognised, with *Palaeoscyllium tenuidens*, *Praeproscyllium oxoniensis*, *Protospinax bilobatus*, *P. carvalhoi* and *Belemnobatis stahli* all being represented by a number of specimens. Rare specimens of several other species were also recorded.

Almost all vertebrate material from this facies is highly abraded, with many specimens being indeterminate bone 'granules'. It is therefore probable that considerable reworking and possibly transport had occurred. The mixture of taxa otherwise largely limited to either lagoonal or open marine settings suggests that there may have been faunal mixing within this facies.

6.8. *Lagoonal forest marble facies*

Although lithologically superficially similar to the more open marine forest marble facies, the selachian fauna, as with the invertebrate fauna, is very different. Teeth of *Protospinax bilobatus* are the dominant selachian elements, comprising

over 55% of the assemblage. *Praeproscyllium oxoniensis* teeth comprise about 20% of the neoselachian teeth, whilst teeth of *Proheterodontus sylvestris*, *Heterophorcynus microdon* and *Belemnobatis stahli* all constitute over 5% of the assemblage. *Eypea leesi* and *Palaeoscyllium tenuidens*, both common elements of the open marine forest marble facies, are absent, whilst teeth of *P. sylvestris* are consistently smaller within the lagoonal facies. As with all of the lagoonal facies, Synchodontiformes, Hexanchiformes, *Protospinax magnus* and *Belemnobatis kermacki* are absent.

As with the marine forest marble facies, there is evidence of faunal mixing. There is no evidence of characteristically open marine or hard substrate forms, but there are taxa presumed to have required normal marine salinity (diverse echinoderms and bryozoans), along with remains of both freshwater (amphibians) and terrestrial taxa (mammals). Likewise, the selachian fauna probably represents a somewhat mixed assemblage of remains of species from a number of lagoonal settings in addition to the final environment of deposition.

6.9. Shelly-oolitic lagoon

The neoselachian tooth assemblage of this facies is strongly dominated by *Protospinax bilobatus*, which comprises 75% of the assemblage. The only other reasonably abundant neoselachian teeth are of *Praeproscyllium oxoniensis*, although uncommon or rare remains are present of several other taxa, including the only lagoonal occurrence of *Palaeoscyllium tenuidens*.

6.10. Fully marine lagoon

As with all of the lagoonal facies, a relatively low diversity of species was recovered from these samples. The dominant selachian remains are the teeth of *Praeproscyllium oxoniensis*, which comprise about half of the assemblage in all of the samples studied. Other typical and frequent species are *Paracestracion bellis*, *Heterophorcynus microdon*, *Protospinax carvalhoi* and *Belemnobatis stahli*. Teeth of *Proheterodontus sylvestris* and

Spathobatis delstatei are rare and smaller than in more open marine facies. In contrast to the shelly-oolitic lagoonal facies assemblages, *Protospinax bilobatus* was not recorded.

6.11. Calcareous restricted lagoon

The neoselachian fauna from this facies appears to be essentially the same as that from fully marine lagoonal facies, differing only in the extreme rarity of neoselachian teeth (typically about one tooth per 10 kg of sediment) resulting in a small sample size.

6.12. Muddy restricted lagoon

Neoselachian remains varied greatly in abundance between the different samples processed. In all samples, however, teeth of *Protospinax bilobatus* dominated, forming over 80% of the assemblage overall. The only other reasonably frequent neoselachian teeth were of *Belemnobatis stahli*, with rare teeth of three other taxa occurring in a single sample.

6.13. Non-marine lagoons

A number of additional samples were studied from lagoonal facies from both England and the Isle of Eigg, Scotland. Samples containing very restricted mollusc faunas, including *Neomiodon* and *Placunopsis* but lacking echinoderms and brachiopods, contained hybodont, actinopterygian and tetrapod remains but no neoselachians. Samples containing supposed freshwater fossils such as charophyte cysts and the bivalve *Praemytilus* similarly lacked neoselachian fossils.

7. Interpretation of faunas

7.1. Environmental specificity

The facies specific distribution of different neoselachians indicates a strong palaeoenvironmental specificity of shark and ray taxa during the Bathonian. Within some neoselachians, the specificity is at ordinal level, such as within the Synchodonti-

formes, which were absent from lagoonal settings. Within other taxonomic groups, however, this specificity was at the specific level, as within the genera *Protospinax* and *Belemnobatis*.

Within the Carcharhiniformes, *Eypea leesi* shows the greatest preference for offshore palaeoenvironments. This species is uncommon but present within both muddy offshore facies and in shelly carbonate shelf limestones, although no larger specimens were recorded in the latter. *Eypea leesi* is at its commonest within the transported forest marble facies, where large specimens are common. It is absent in shallower water and lagoonal settings. It therefore appears that although this species was limited to moderately deep water, the shelly substrate and high energy of the forest marble facies were especially suitable.

The relatively rare remains of ?scyliorhinid indet. are only known from the carbonate shelf facies and its absence from far larger samples from other facies suggests it was probably limited to that palaeoenvironment. A larger Carcharhiniforme, known from only three teeth, has only been recorded in high-energy carbonates of the oolitic and transported forest marble facies. A similar preference for shallower water carbonate settings is shown by *Palaeoscyllium tenuidens*. Reaching its acme in the tilestone facies, this species is present in all of the open marine detrital carbonate facies. It is also present, if less common, within mudstones deposited close enough to carbonate shoals to contain derived ooids (muddy embayment and shelly-oolitic lagoon facies). It is absent within both offshore mudstones and within all other lagoonal facies.

An additional Carcharhiniforme, *Praeprosyllum oxoniensis*, shows a distinct preference for shallower water facies. This is the commonest neoselachian in many lagoonal sediments, even where salinity appears to have been reduced. It is also present, if less commonly, in rocks deposited within shallower open marine carbonate settings. Despite this wide palaeoenvironmental distribution, it is absent within offshore mudstone facies.

The Heterodontiforme *Proheterodontus sylvestris* is widely distributed within lagoonal and carbonate shelf facies, but is rare within many of

these facies. Teeth of this species are common within the transported forest marble facies, whilst they are frequent within both oolitic and lagoonal forest marble facies. *Proheterodontus sylvestris* teeth are absent within both neritic mudstones and restricted lagoon facies. There therefore appears to be not only a preference for shallower water, but especially shallow water settings with fast currents and a carbonate sand substrate. Even within these facies, the lack of larger teeth from lagoonal and oolitic sediments suggests that these shallower water settings may only record teeth from juveniles. In contrast to many other taxa, remains of *Paracestracion bellis* are widespread, being present in low numbers within most lagoonal facies as well as within some of the open marine facies. It therefore appears that this represents one of the most cosmopolitan Bathonian neoselachian taxa.

Remains of Orectolobiformes are at their most diverse within neritic facies, with only a single species being present within lagoonal sediments. Teeth of *Palaeobrachaelurus mussetti* are never common, and appear to be restricted to the neritic facies. A similar restriction to these offshore facies is shown by *Ornatoscyllium freemani*, which is relatively abundant within the neritic mudstone facies but far less so within the brachiopod-rich limestones. *Dorsetoscyllium terraefullonicum* constitutes a third species of orectolobiform restricted to offshore palaeoenvironments. In addition to occurring in muddy neritic facies, small teeth of this taxon are also present within carbonate shelf sediments. It is therefore evident that *D. terraefullonicum* was less restricted to either deep water or muddy substrates than either *P. mussetti* or *O. freemani*.

In contrast to the more offshore distribution of other Orectolobiformes, teeth of *Heterophorcynus microdon* are widely distributed and present within rocks of many facies. Remains of this species are typical, although rarely common, in lagoonal facies, as well as within shallow open marine carbonates. *Heterophorcynus microdon* appears to have been absent within deeper marine neritic and brachiopod-rich limestone facies.

The palaeoenvironmental distribution of species of Hexanchiformes and Synechodontiformes, with

the possible exception of *Synechodus levis*, is similar. All specimens recorded during this study were recorded from either neritic mudstone or brachiopod-rich limestone facies. Although only rare teeth of *Paranotidanus* sp., *Pseudonotidanus semirugosus* and *Synechodus* cf. *levis* were recorded, remains of *Synechodus duffini* were relatively common within these offshore facies. Although a number of specimens of *S. levis* collected from tilestone facies are present in museum collections, none was collected during this study. It is therefore likely that *S. levis* is very rare in this facies, but has been collected at the intensely studied sites within the Stonesfield Slate Formation due to its large size and distinctive appearance. It is therefore evident that, with the exception of rare incursions into shallower water, these taxa were restricted to deeper water settings.

The three Bathonian species of *Protospinax* show very different palaeoenvironmental preferences. Teeth of *Protospinax magnus* are the dominant neoselachian remains in both the neritic and brachiopod-rich limestone facies, where they comprise over half of the assemblage. It is only within these facies that a full range of tooth sizes was recorded; other facies having only small teeth. Although less dominant, teeth are also common shelf carbonate facies. Rare specimens are also present in the other open marine carbonate facies, but are absent within all lagoonal facies.

Both *Protospinax carvalhoi* and *P. bilobatus* are present within lagoonal facies and within some samples of open marine shelf carbonates, but not in deeper water mudstones. Despite this general co-occurrence, teeth of both taxa are very rarely found within the same samples. *P. carvalhoi* typically occurs as a relatively minor part of the fauna, and is present within calcareous restricted and fully marine lagoonal facies, as well as in more open marine settings of the muddy embayment and the various shelf carbonate facies. *P. bilobatus*, by contrast, commonly dominates the neoselachian tooth assemblage, occurring in the near or total absence of *P. carvalhoi* in muddy restricted and shelly-oolitic lagoon facies, lagoonal forest marble facies and marine forest marble facies. Remains of the two taxa only co-occur without extreme dominance of one form within

the oolite shoal facies. The differential distribution of *P. carvalhoi* and *P. bilobatus* is clearly unlikely to be due to either salinity or water depth. The only consistent feature characterising all of the occurrences of *P. bilobatus* being the presence of a shelly substrate, as opposed to the mud or finer carbonate substrate characterising facies containing common *P. carvalhoi*, indicating a strong substrate control on species distribution.

Amongst the batoids, the two species of *Belemnobatis* show a strong palaeoenvironmental preference, in contrast to the more cosmopolitan distribution of *Spathobatis delstatei*. Teeth of *Belemnobatis kermacki* are persistent but uncommon within the neritic and brachiopod-rich limestone as well as shelly shelf carbonate facies. They are absent in shallower marine and lagoon facies. In contrast, remains of *Belemnobatis stahli* are frequent within most samples from lagoonal facies, as well as within open marine carbonate facies, co-occurring with *B. kermacki* only within the shelly carbonate shelf facies. *B. stahli* teeth are only dominant with one facies, comprising over half of the neoselachian remains in the muddy embayment facies. In contrast to the other rays, teeth of *Spathobatis delstatei* are widely distributed and present in low numbers in most facies. Despite this wide distribution, there are some palaeoenvironmental size differences, with practically all teeth of the taxon from offshore facies being large, whereas smaller teeth dominate within shallower water and lagoonal facies. This size differentiation led to the erroneous splitting of this taxon into two species by Underwood and Ward (in press a).

7.2. Autecology

Study of the palaeoenvironmental distribution, tooth morphology and wear and comparison with living taxa allows the autecology of extinct neoselachians to be assessed. Many of the neoselachians known from the Jurassic have living relatives, and Jurassic members of many of these taxonomic groups (Scyliorhinidae, Heterodontidae, Orectolobiformes, Hexanchiformes, Squatinidae, Rhinobatidae) are known from well preserved skeletons, demonstrating that overall

morphology has remained relatively unchanged. In addition, genera belonging to extinct groups (such as *Protospinax*, *Synechodus* and *Palaeocarcharias*) are also known from well preserved skeletons.

It is probable that the Bathonian Carcharhini-formes were, as with modern Scyliorhinidae and Proscylliidae, elongate, slow moving nectobenthic forms. The small, sharply pointed teeth (clutching dentition of Cappetta, 1986) are similar to those of related extant generalistic feeders. Although the lower-cusped posterior teeth of *Eypea leesi* may suggest that shelled prey could be consumed, no wear facets characteristic of a durophagous diet were recognised. The poorly known carcharhini-form indet. had larger, more elongate teeth and may represent a more active predator, but similar teeth are present in *Palaeocarcharias*, which is known to have had a poorly streamlined and probably flattened body (de Beaumont, 1960; Duffin, 1988). The teeth, possibly forming a tearing dentition of Cappetta (1986), suggest a diet of small, active prey.

A poorly streamlined, tapering body is known from all extant and well preserved fossil Heterodontiformes. It is therefore probable that Bathonian forms were, like extant species, sluggish and largely benthic. Although somewhat generalistic in their diet, extant *Heterodontus* possess large molariform teeth suitable for crushing shelled food (e.g. Compagno, 2001). None of the related Bathonian taxa is known to have possessed such teeth, and therefore lacked a dentition suitable for particularly robust prey. Despite this, wear is often evident on teeth of *Paracestracion bellis*, suggesting that some hard food items were consumed. The otherwise grasping dentition of both this taxon and *Proheterodontus sylvestris*, the teeth of which rarely show wear, suggests a more generalised diet of small prey items was typical.

Extant Orectolobiformes exist in three main morphologies; the streamlined filter feeder *Rhincodon*, strongly flattened Orectolobidae and a more elongate body form of most other taxa. Filter feeding amongst the order appears to be a post-Mesozoic adaptation (Cappetta, 1987). The only Jurassic Orectolobiforme known from well preserved skeletal material is *Phorcynus*, which

had a flattened body. The body form of other Jurassic taxa is uncertain due to uncertainty of their affinities. It is therefore likely that Bathonian taxa included some benthic taxa with a flattened body (*Heterophorcynus* appears to have affinities to *Phorcynus*), and possibly some nectobenthic taxa with more elongate bodies. All of the Bathonian Orectolobiformes had small, pointed teeth, presumably arranged into a clutching dentition. Although extant flattened orectolobid taxa, such as *Orectolobus*, are ambush predators, *Heterophorcynus* and *Phorcynus* lacked the tearing dentition of modern flattened forms, and are therefore unlikely to have had the same feeding strategy.

Extant Hexanchiformes are slow moving, if manoeuvrable, mid-water predators. The body form of Synechodontiformes appears to have been similar to that of Hexanchiformes (Duffin and Ward, 1993). Teeth of *Paranotidanus* and *Pseudonotidanus semirugosus* are similar to those of extant taxa such as *Notorhynchus*, if rather less compressed, and presumably likewise formed part of a cutting-clutching dentition (of Cappetta, 1986) and similarly took variously sized prey items. The dentition of *Synechodus* is well-known from a number of specimens (e.g. Mackie, 1863; Duffin and Ward, 1993), and comprises grasping teeth in the anterior part of the jaws and smaller crushing teeth further back. These grasping anterior teeth, in combination with a poorly streamlined body, probably suggest a benthic or nectobenthic ambush predator, taking relatively small prey. The presence of crushing posterior teeth may suggest some reliance on shelled food, although little wear was observed.

Skeletons of *Protospinax* show a flattened body, rather like that of extant species of *Squatina* (de Carvalho and Maisey, 1996), suggesting a benthic mode of life. Despite this resemblance, the pointed teeth of *Squatina* are lacking and *Protospinax* was unlikely to have been an ambush predator. Although the teeth of all three *Protospinax* species are reasonably similar, variations both in the development of cusps and degree of wear suggest rather different diets. Teeth of *P. magnus* are variously cusped and never appear to show significant wear. They therefore probably formed a

clutching dentition. Teeth of *P. bilobatus* are likewise cusped, but commonly show high degrees of wear, often resulting in the removal of the cusps altogether. It is therefore evident that although the teeth may have originally formed a clutching dentition, wear from the consumption of hard prey wore the teeth down into a crushing dentition similar to that of many batoids. It is possible that the restriction of this species to very shelly substrates was related to a specialised diet of shelled molluscs. Teeth of *P. carvalhoi* are non-cusped and invariably show severe wear. Although rather thinner than many batoid teeth, they presumably formed a very ray-like grinding dentition.

Skeletons are known of both *Belemnobatis* and *Spathobatis*, with both genera having a very similar body shape to extant rhinobatids, with a flattened but elongate body and muscular tail. Like modern taxa, the Bathonian batoids were presumably benthic, commonly partly buried for much of the time. The Bathonian batoid taxa possessed relatively similar teeth, which would have formed a crushing dentition. Despite this, degrees of wear are typically low, suggesting that none of the taxa fed largely on especially hard-shelled prey.

7.3. Perception of early neoselachian diversity

Relatively few studies have been carried out on Jurassic and Early Cretaceous neoselachians. The first assemblages of diverse neoselachians, including taxa such as Heterodontiformes, Orectolobiformes, *Protospinax* and batoids, are known from rocks of Toarcian age (e.g. [Delsate and Godefroit, 1994](#)). Despite this, the oldest rocks that have been systematically studied for neoselachian remains at numerous sites worldwide are Albian in age (e.g. [Biddle, 1993](#); [Cappetta and Case, 1999](#)). Of the studies of neoselachian assemblages of the intervening period, a large proportion have focussed on the spectacularly well preserved skeletons collected from plattenkalk limestones, especially those of southern Germany (e.g. [Schweizer, 1964](#)). The degree to which these assemblages represent living faunas is uncertain, and it is likely that they represent essentially allochthonous fau-

nas ([Viohl, 1996](#)) containing taxa from local reefal settings and possibly other shallow marine habitats. As a result, the recorded diversity is high, but deep-water species are likely to be absent. More recent study of early neoselachians has concentrated on disarticulated tooth assemblages. Many of these have been collected from either lagoonal or restricted marine facies (e.g. [Thies, 1995](#); [Underwood and Rees, 2002](#); [Arratia et al., 2002](#)) and typically reveal a low diversity, often batoid dominated, fauna. Other studies (e.g. [Martill, 1991](#); [Candoni, 1995](#); [Underwood, 2002](#)) have sampled neritic mudstones. Where these have been collected from Toarcian or younger rocks, they typically contain relatively higher diversity faunas than those from more restricted settings. The rather piecemeal sampling of this work has not allowed faunas from different palaeoenvironments of comparable age and faunal realm to be compared. Within the Kimmeridgian–Tithonian, where both neritic ([Candoni, 1995](#); [Underwood, 2002](#)) and shallower marine (e.g. [Thies, 1983](#); [Schweizer, 1964](#)) neoselachian faunas are known, selachians are associated with boreal and Tethyan invertebrate faunas respectively, suggesting that they are unlikely to represent elements of the same association. It is therefore evident that any previous estimates of early neoselachian diversity at a given point in time are likely to have been biased by the lack of investigation of a range of facies at any particular time interval. This study has shown that the degree of palaeoenvironmental specificity of neoselachians as early as the Middle Jurassic was such that only a relatively small part of the neoselachian assemblage of a particular region would be encountered if only a single facies was sampled. Within the British Bathonian, sampling of a range of palaeoenvironments resulted in the recording of a diversity of neoselachian taxa otherwise unknown prior to the mid-Cretaceous. If the faunas of the Bathonian are representative of those of the Toarcian to Albian period as a whole, it is evident that the current perception of the diversity of neoselachians during this interval is incorrect, and actual diversities were far higher than has previously been realised.

7.4. Limitations to early neoselachian distribution

Within the Bathonian, there appears to have been a strong water depth and salinity control on the distribution of neoselachians. The high diversity neoselachian assemblages of offshore marine facies include members of all of the orders known to have been in existence at the time. Within even fully marine lagoons, however, palaeospinacids and hexanchids are absent, whilst the majority of open marine species of other groups are replaced by other, lagoonal taxa. Within the lower salinity lagoons, many of the same taxa are present as in fully marine lagoons, although they appear to have been far less common. It therefore appears that members of a number of neoselachian orders were tolerant to some degree of salinity change. Despite this, no neoselachian remains were recovered from rocks containing mollusc faunas indicative of especially low salinity conditions (see Fürsich, 1994). Neoselachian remains were likewise absent from rocks deposited in supposed freshwater environments. Despite the lack of neoselachians from low salinity palaeoenvironments, remains of small hybodont sharks are often common and relatively diverse. Within the Bathonian, the salinity tolerance of neoselachians is very similar to that of echinoderms, with forms being most tolerant of low salinity, commonly *Acrosalenia* or ophioroids, present in almost all neoselachian-bearing samples.

Samples from low salinity lagoonal palaeoenvironments of the Late Jurassic and basal Cretaceous contain neoselachian assemblages composed almost entirely of batoids (Thies, 1995; Underwood and Rees, 2002). Invertebrate assemblages associated with one of these assemblages (Underwood and Rees, 2002) indicate some degree of marine influence, but probably a lower salinity than that associated with any Bathonian neoselachians. It therefore appears that by the end of the Jurassic, some batoids were more tolerant of low salinity conditions than during the Bathonian. Mid-Cretaceous marginal environments contained several taxa of sclerorhynchid batoids and lamniforms (Thurmond, 1971), with some possibly entering fluvial environments. This association, with the addition of batoids such as

Myledaphus, continues within marginal marine and possible fluvial settings until the end of the Cretaceous (e.g. Beavan and Russell, 1999). All of these taxa are also present in coastal marine facies, and there is therefore no direct evidence of any Mesozoic neoselachian taxa entirely restricted to freshwater habitats.

7.5. Implications for neoselachian diversification

The earliest neoselachians from the Triassic are commonly known from ‘Rhaetic’ facies, the depositional environment of which is poorly understood, but probably including both lagoonal and inshore marine settings. Early Jurassic neoselachians are known exclusively from open marine facies, although faunas are known from both offshore mudstones (e.g. Rees, 2000) and nearshore sandstones (Rees, 1998). Within these, palaeospinacids, hexanchids and the enigmatic genus *Agaleus* are typically present in pre-Toarcian assemblages (e.g. Rees, 1998, 2000). Higher diversity faunas are known from the Toarcian, with the addition of batoids, *Protospinax*, heterodontids and orectolobiforms (e.g. Delsate and Godefroit, 1994). All of these ‘crown group’ neoselachians, with the addition of carcharhiniforms, were present within both open marine and lagoonal palaeoenvironments by the Bathonian. It is possible that the sudden and seemingly simultaneous appearance of a number of clades is purely a function of the lack of extensive sampling for neoselachian material in Lower Jurassic rocks. Alternatively, it is possible that the lack of many of these forms within any Pliensbachian neoselachian assemblages is due to the lack of species from these groups within open marine conditions, or within northern Europe, all published faunas having been collected within this area. It would be possible that neoselachians radiated within lagoonal or marginal marine environments in the Early Jurassic, moving into open marine environments in the Toarcian.

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Appendix A. Sample localities

Numbers in brackets refer to sample sites on Fig. 2. For more details on sample sites see Underwood and Ward (in press b).

Neritic mudstones

(23) Watton Cliff (SY449909), above Wattonensis Beds, black shaly clay with very common *Praeexogyra acuminata* and other bivalves, common belemnites and ammonite nuclei.

Brachiopod-rich limestones

(21) Watton Cliff, Wattonensis Beds, upper part, shelly grey marl interbed within hard nodular biomicrite wackestone. Very rich and diverse shelly fauna.

(21) Watton Cliff, Wattonensis Beds, middle part, grey marl interbed within hard nodular biomicrite wackestone. Moderately rich and diverse shelly fauna.

(21) Watton Cliff, Wattonensis Beds, lower part, shelly grey marl interbed within hard nodular biomicrite wackestone. Rich and diverse shelly fauna.

(22) East Cranmore (ST687435) (excavation for lake), Fullers Earth Rock, Rugitela Beds, shelly tough grey marl interbeds within hard nodular biomicrite wackestone. Rich and diverse shelly fauna including ammonite nuclei.

Shelly carbonate shelf

(34) Shipton-on-Cherwell Quarry (SP480175), Lower Cornbrash, Bed 4, brown clay with fine

shell debris and rich and diverse invertebrate fauna fauna.

(33) Kirtlington Quarry (SP494199), Lower Cornbrash, basal marl, Orange-brown marl with fine shell debris and rich and diverse invertebrate fauna fauna, especially brachiopods.

(26) Watton Cliff, forest marble Formation, Boueti Bed, very shelly rubbly and partly indurated grey marl. Rich and diverse shelly fauna dominated by rhynchonellids and pectinids.

(27) Herbury Point (SY613808), forest marble Formation, Boueti Bed, extremely shelly rubbly and marl. Rich and diverse shelly fauna dominated by rhynchonellids and terebratulids.

Marine forest marble facies

(30) Watton Cliff, main Limestone, cross-stratified bioclastic limestone with unlithified lenses. Diverse invertebrate fauna, frequently broken and abraded.

(31) Herbury Point, Digona Bed, cross-stratified bioclastic limestone lacking *Apiocrinites* but with frequent brachiopods.

Tilestones

(5) Hampen cutting (SP057202) Eyford Member, 1–2 m below top; facies transitional to Fullers Earth, silty thinly bedded calcareous marl, with rare and small bivalves and gastropods.

(4) Hampen cutting, Eyford Member, near base, concretions around shell debris lags, silty biomicrite with diverse small bivalves and other fossils.

(6) Huntsmans Quarry (SP122255), Eyford Member, quasilaminated sandy limestones with restricted mollusc fauna.

(10) Stonesfield area, various localities, Stonesfield Slate, quasilaminated sandy and oolitic limestones with restricted mollusc fauna (observed in museum collections).

Muddy embayment

(3) Hornsleasow Quarry (SP131322), Fullers Earth Clay Formation, Coral Bed, top 30 cm, silty clay with scattered ooids and diverse faunas including brachiopods.

(3) Hornsleasow Quarry, Fullers Earth Clay Formation, Coral Bed, middle part, silty clay with diverse faunas including many brachiopods.

(3) Hornsleasow Quarry, Fullers Earth Clay

Formation, Coral Bed, lower part, silty and sandy clay with corals.

Oolite shoal

(8) Hampen cutting, ?Sevenhampton Rhynchonella Bed, very thin marl with intraclasts, with common and diverse shells (brachiopods, *Meleagrinnella*), very diverse echinoderms.

(9) Huntsmans Quarry, Taynton Limestone Formation, cross-stratified oolitic packstones and grainstones with fragmented and restricted mollusc fauna.

(28) Ford cutting (ST854747), Upper Rags, nodular marl parting with ooids and shell debris, especially diverse brachiopods.

Lagoonal forest marble facies

(29) Woodeaton Quarry (SP534122), forest marble Formation, various horizons within lowest 2 m of the formation. Cross-stratified bioclastic limestones with common ooids.

Shelly-oolitic lagoon

(30) Kirtlington Quarry, forest marble Formation, oolitic clay rich in bivalve and echinoderm material.

(19) Woodeaton Quarry, White Limestone Formation, Ardley Member, Bed 17, upper part, dark oolitic marl packed with oysters, diverse echinoderms and large *Epithyris*.

(19) Woodeaton Quarry, White Limestone Formation, Ardley Member, Bed 17, lower part, oolitic oyster-packed marl with diverse echinoderms and rare large *Epithyris*.

(13) Hampen Cutting, Hampen Formation, Bed 50, oolitic marl, with common oysters, some *Pinna*, *Modiolus*, *Trigonia*, and burrowers and low diversity echinoderms (?*Hemicidaris*, *Isocrinus*).

(13) Hampen Cutting, Hampen Formation, Bed 43, partly indurated oolitic marl with very common oysters, some *Modiolus*, and burrowers and low diversity echinoderms (?*Hemicidaris*, *Isocrinus*).

Fully marine lagoon

(17) Woodeaton Quarry, White Limestone Formation Shipton Member, Bed 8, marl with lithified nodules with varied molluscs and echinoderms.

(16) Woodeaton Quarry, White Limestone Formation Shipton Member Bed 4, grey to yellow silty clay with moderately diverse shelly fauna.

(15) Woodeaton Quarry, White Limestone Formation Shipton Member of BGS, Bed 1, uppermost part, grey clay with moderately diverse shelly fauna.

(15) Woodeaton Quarry, White Limestone Formation Shipton Member of BGS, Bed 1, Lower to mid-part, brown-grey gritty clay with moderately diverse shelly fauna (including ammonite nucleus).

(14) Woodeaton Quarry, Rutland Formation, Bed 7, grey clay with moderately diverse shelly fauna inc *Isognomon*, *Trigonia*, ?*Hemicidaris*, *Isocrinus*.

(14) Woodeaton Quarry, Rutland Formation Bed 6, finely shell detrital biomicrite with moderately diverse shelly fauna.

Calcareous restricted lagoon

(24) Woodeaton Quarry, White Limestone Formation, Bladon Member, Fimbriata-Waltoni Bed, Bed 24, Grey clay with scattered oysters and low diversity other bivalves; frequent tetrapod remains.

(25) Kirtlington Quarry, White Limestone Formation, Bladon Member, Fimbriata-Waltoni Bed, black-grey clay with scattered oysters and low diversity other bivalves; frequent tetrapod remains.

(12) Woodeaton Quarry, Rutland Formation, Bed 4–5, lenses of sandy grey clay and black clay with many small aragonitic bivalves and some crinoids (*Isocrinus*); frequent tetrapod remains.

Muddy restricted lagoon

(20) Ketton Quarry (SK973058), Clay immediately above Blisworth Limestone Formation, yellow silty clay with oysters.

(11) Ketton Quarry, shell bed at base of fifth cycle, aragonitic bivalves in grey clay penetrated by rootlets.

(11) Ketton Quarry, shell bed at base of fourth cycle, aragonitic bivalves and oysters in yellow sandy clay.

(11) Ketton Quarry, shell bed at base of third cycle, aragonitic bivalves in grey clay.

(11) Ketton Quarry, shell bed at base of second cycle, aragonitic bivalves in grey clay penetrated by rootlets.

(7) Ketton Quarry, shell bed at base of first

cycle, aragonitic bivalves, *Lingula* and rare rhynchonellids in grey clay.

Other Sites

(35) Oxford Clay Formation, various localities. Some specimens observed in museum collections.

(2) Burton Cliff (SY465901), basal Fullers Earth Formation, grey silty clay with small gastropods and belemnites. Not included in study.

(1) Horn Park Quarry (ST463020), basal Fullers Earth Formation, brown clay with ferruginous ooids. Terebratulids and ammonites present. Not included in study.

References

- Arratia, G., Kriwet, J., Heinrich, W.-D., 2002. Selachians and actinopterygians from the Upper Jurassic of Tendaguru, Tanzania. *Mitt. Mus. Nat.kd. Berlin Geowiss. Reihe* 5, 207–230.
- Beavan, N.R., Russell, A.R., 1999. An elasmobranch assemblage from the terrestrial-marine transitional Lethbridge coal zone (Dinosaur Park Formation: Upper Campanian), Alberta, Canada. *J. Paleontol.* 73, 494–503.
- Biddle, J.P., 1993. Les Elasmobranches de l'Albien inférieur et moyen (Crétacé inférieur) de la Marne et de la Haute-Marne (France). *Prof. Pap. Belg. Geol. Surv.* 264, 191–240.
- Candoni, L., 1995. Deux faunes inédites de séliaciens dans le Jurassique terminal Français - Premiers résultats stratigraphiques. *Bull. Soc. Géol. Normandie Amis Mus. Havre* 82, 29–49.
- Cappetta, H., 1980. Les séliaciens du Crétacé supérieur du Liban. *Palaeontogr. Abt. A* 168, 1–229.
- Cappetta, H., 1986. Types dentaires adaptatifs chez les séliaciens actuels et post-Paléozoïques. *Palaeovertebrata* 16, 57–76.
- Cappetta, H., 1987. Mesozoic and Cenozoic elasmobranchii. Chondrichthyes II. In: Schultze, H.P. (Ed.), *Handbook of Paleichthyology*, 3B. Gustav Fischer Verlag, Stuttgart, 193 pp.
- Cappetta, H., Case, G.R., 1999. Additions aux faunes de séliaciens du Crétacé du Texas (Albien supérieur - Campanien). *Palaeo Ichthyol.* 9, 1–112.
- Compagno, L.J.V., 2001. *Sharks of the world, an annotated and illustrated catalogue of shark species known to date. Volume 2. Bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes)*. FAO Species catalogue for fishery purposes No. 1, Vol. 2, Rome, 269 pp.
- Cope, J.C.W., Duff, K.L., Parsons, C.F., Torrens, H.S., Wimbleton, W.A., Wright, J.K., 1980. A correlation of Jurassic rocks of the British Isles. Part two: Middle and Upper Jurassic. *Geological Society of London Special Report* 15, 109 pp.
- Cuny, G., Benton, M.J., 1999. Early radiation of the neoselachian sharks in western Europe. *Geobios* 32, 193–204.
- de Beaumont, G., 1960. Observations préliminaires sur trois séliaciens nouveaux du Calcaire lithographique d'Eichstätt (Bavière). *Ecol. Geol. Helv.* 53, 315–328.
- de Carvalho, M.R., Maisey, J.G., 1996. Phylogenetic relationships of the Late Jurassic shark *Protospinax* Woodward 1919 (Chondrichthyes: Elasmobranchii), 9–49. In: Arratia, G., Viohl, G. (Eds.), *Mesozoic Fishes – Systematics and Paleocology*. Verlag Friedrich Pfeil, Munich, 576 pp.
- Delsate, D., Godefroit, P., 1994. Chondrichthyens du Toarcien inférieur d'Aubagne (Lorraine belge). *Prof. Pap. Belg. Geol. Surv.* 278, 23–43.
- Duffin, C.J., 1988. The Upper Jurassic selachian *Palaeocarcharias* de Beaumont (1960). *Zool. J. Linn. Soc.* 94, 271–286.
- Duffin, C.J., Ward, D.J., 1993. The Early Jurassic palaeospinacid sharks of Lyme Regis, southern England. *Prof. Pap. Belg. Geol. Surv.* 264, 53–102.
- Evans, S.E., Milner, A.R., 1994. Microvertebrate faunas from the Middle Jurassic of Britain. In: Fraser, N., Sues, H.D. (Eds.), *In the Shadow of the Dinosaurs: early Mesozoic Tetrapods*. Cambridge University Press, 303–321, 435 pp.
- Fürsich, F.T., 1994. Palaeoecology and evolution of Mesozoic salinity-controlled benthic macroinvertebrate associations. *Lethaia* 26, 327–346.
- Mackie, S.J., 1863. On a new species of *Hybodus* from the Lower Chalk. *Geologist* 6, 241–246.
- Martill, D.M., 1991. Fish. In: Martill, D.M., Hudson, J.D. (Eds.), *Fossils of the Oxford Clay*, 197–225. The Palaeontological Association, Field Guides to Fossils, 4.
- Rees, J., 1998. Early Jurassic selachians from the Hasle Formation on Bornholm, Denmark. *Acta Palaeontol. Pol.* 43, 439–452.
- Rees, J., 2000. A new Pleinsbachian (Early Jurassic) neoselachian shark fauna from southern Sweden. *Acta Palaeontol. Pol.* 45, 407–424.
- Schweizer, R., 1964. Die elasmobranchier und holocephalen aus den Nusplinger plattenkalcken. *Palaeontogr. Abt. A* 123, 58–110.
- Thies, D., 1983. Jurazeitliche Neoselachier aus Deutschland und S-England. *Cour. Forsch.inst. Senckenb.* 58, 1–117.
- Thies, D., 1995. Placoid scales (Chondrichthyes: Elasmobranchii) from the Late Jurassic (Kimmeridgian) of Northern Germany. *J. Vertebr. Palaeontol.* 15, 463–481.
- Thurmond, J.T., 1971. Cartilaginous fishes of the Trinity Group and related rocks (Lower Cretaceous) of North Central Texas. *Southeast. Geol.* 13, 207–227.
- Underwood, C.J., 2002. Sharks, rays and chimaeroid from the Kimmeridgian (Late Jurassic) of Ringstead, southern England. *Palaeontology* 45, 297–325.
- Underwood, C.J., Mitchell, S., Veltkamp, C.J., 1999. Microborings in mid Cretaceous fish teeth. *Proc. Yorks. Geol. Soc.* 52, 269–274.
- Underwood, C.J., Rees, J., 2002. Selachian faunas from the earliest Cretaceous Purbeck Group of Dorset, southern England. *Special Papers in Palaeontology* 68, 83–102.

- Underwood, C.J., Ward, D.J., in press a. Environmental distribution of Bathonian (Middle Jurassic) neoselachians in southern England. In: Tintori, A., Arratia, G. (Eds.), *Mesozoic Fishes 3 – Systematics, Palaeoenvironments and Biodiversity*. Verlag Dr. Friedrich Pfeil, Munich.
- Underwood, C.J., Ward, D.J., in press b. Neoselachian sharks and rays from the British Bathonian (Middle Jurassic). *Palaeontology*.
- Viohl, G., 1996. The palaeoenvironment of the Late Jurassic fishes from the southern Franconian Alb (Bavaria, Germany), 513–528. In: Arratia, G., Viohl, G. (Eds.), *Mesozoic Fishes – Systematics and Paleocology*. Verlag Friedrich Pfeil, Munich, 576 pp.
- Wyatt, R.J., 1996. A correlation of the Bathonian (Middle Jurassic) succession between Bath and Burford, and its relation to that near Oxford. *Proc. Geol. Assoc.* 107, 299–322.