



# Geology and microvertebrate faunas of the Rhaetian Westbury Formation of Doniford Bay, Somerset

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## ABSTRACT

The Rhaetian (latest Triassic) succession of Doniford Bay, North Somerset has been noted as a site of fossils for over 200 years, and yet has never been described in detail despite its importance for palaeontology, for knowledge of a classic Triassic-to-Jurassic transition sequence, for structural geology, and as a venue for field trips. There are two bone beds, which differ substantially in sedimentary and palaeontological characteristics. Fossils include the usual teeth, denticles, and scales of small hybodont sharks, bony fishes, and marine reptiles. The lower (basal) bone bed is in many ways like those from other localities around Bristol and in South Wales, whereas the upper bone bed shows rich organic matter and an absence of calcite, suggesting a deeper location of deposition. Further, the lower bone bed contains abundant abraded silica grains, suggesting transport of sediment and bone debris from a beach or river. The two bone beds differ in faunal composition, and the upper bone bed lacks the locally derived clasts, larger silica grains, and calcite seen in the lower bone bed. Bones and teeth are equally abraded in both bone beds, confirming long-distance transport of fish and reptile fossils and that the upper bone bed cannot be interpreted as having derived from the lower.

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## 1. Introduction

The Rhaetian bone beds of the Westbury Formation are renowned for their content of teeth and scales of sharks and bony fishes. Exposures of these beds outcrop at multiple sites across the south-west of England and south Wales around the Bristol Channel and the Severn Estuary, and the faunas of many of these sites have been described in detail in recent years. However, less attention has been paid to Rhaetian bone bed geology and faunas of the North Somerset coast. This represents a gap in knowledge because the sedimentary succession here and in South Wales differs from contemporary deposits, given the presence of two sedimentary units that are absent elsewhere: the Williton Member ('Sully Beds') at the top of the Blue Anchor Formation, and the 'Watchet Beds' at the top of the Lilstock Formation.

The Triassic to Early Jurassic succession along the north Somerset coast has been studied by geologists for 200 years (Anstice, 1821; Buckland and Conybeare, 1824; Wright, 1860; Richardson, 1911; Hamilton and Whittaker, 1977; Mayall, 1981; Whittaker and Green, 1983; Warrington and Whittaker, 1984; Gallois, 2009), but the geology of Doniford Bay has been noted only rarely in these overviews. This lack

of detailed attention may be because the Doniford bone beds can only be reached at low tide, and the successions are interrupted by numerous faults. Further, many of the north Somerset sections, such as at neighbouring St Audrie's Bay, show only a meagre representation of the basal bone bed.

In this paper, we report the field geology and the context of the Rhaetian bone beds at Doniford Bay, then describe the faunas of the two bone beds, comparing and contrasting them, and offering some tentative hypotheses to explain the observed differences between the bone beds and with the bone beds at other sites in the general area.

## 2. Geological setting

### 2.1. Background

The first mention of the geology of the North Somerset coastal Mesozoic sections was by Robert Anstice (1821, p. 611), who noted, 'A fish, which appears to belong to the genus *Clupia*, and resembling *Clupia alosa*, has been found in lias at East Quantockhead, about 18 feet underground, above high water mark.' This was the report of a paper read at the meeting of the Geological Society of London on June 21st, 1816. East Quantockhead (now East Quantoxhead) lies 2 km east of Doniford, and the above fossil evidently came from the Early Jurassic strata exposed on the beach below the village, at the foot of the cliff.

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The same Robert Anstice made a further discovery, as reported three years later by [Buckland and Conybeare \(1824, pp. 301–302, footnote\)](#). These authors were describing the Lias around the Bristol Channel, including Aust ([Cross et al., 2018](#)), and the underlying strata, including 'black shales'—which we now term the Westbury Formation—and the underlying red beds of the Mercia Mudstone Formation. They described the occurrence of the Rhaetian bone bed at the base of the Westbury Formation at various localities on both banks of the Severn, in Gloucestershire, South Wales, and on the North Somerset coast, 'at the western extremity of Clevehill, near the town of Watchet'. Cleve Hill is the rising part of the main road west of Watchet, and so the discovery must have been on the foreshore between Watchet and Blue Anchor Bay, 3 km west of Doniford. They further describe the discovery:

This discovery of the bone-bed near Watchet has been made by Robert Anstice, Esq. of Bridgewater. It there forms a stratum from 2 to 9 in thick, chiefly composed of white quartzose sand, with small pebbles of quartz and a little mica sparingly interspersed, the whole being cemented together by carbonate of lime. The cement occasionally assumes the character of lias, and forms septaria in the bed of sandy breccia. It then is often full of small bivalve shells. The whole abounds with animal remains, which are often inseparably attached to one another by iron-pyrites. The bones are in few cases unbroken, and in one case only has Mr. A. found teeth or palatal bones attached to a jaw or palate, although they all occur abundantly throughout the stratum in a detached state. They are of a jet-black colour, and have a highly polished surface; but, from the brittleness of their substance and the hardness of the matrix, it is difficult to disengage without destroying them. Only a few fragments of large bones have been found; the rest seem generally to have belonged to small animals. The remains are as follows.

1. Fragments of spines of the same nature as those represented in plate iv. .figure 1. 2 and 3. vol. i. 2nd series, Geol. Trans. They belong to two varieties; both of which differ in some points from that in the plate referred to, and approach nearer to that described in Walcot's account of the petrifications near Bath. One of them is less deeply furrowed than that in the figure; the other is scarcely furrowed at all, and has tubercles on the sides towards the point. In neither of them are the dentiform processes so abundant, or so regularly disposed, as in the figure.
2. Many varieties of palates and teeth, some of the latter resembling those represented in .figures 5 to 10 of the plate above referred to.
3. Scales of several varieties of fish, many of them corresponding exactly with those of the *Dapedium politum*, plate vi. .figure 4. Geol. Trans., vol. i. 2nd series; there are also flat bony substances, studded with small tubercles such as belonging to the head of that fish.
4. Bones (or fragments of bones) for the most part small, black, and very compact; belonging apparently to some small reptile. Among these only one vertebra has been found.

There occur also many irregular bodies, varying much in form and substance, which are usually, however, cylindrical with rounded ends, some having a black and glossy surface and fracture, others being of a dull-brown colour. They are probably rolled palates, or rolled fragments of very solid bone.

Fish-bones are here of rare occurrence in comparison of spines, teeth and palates; which circumstance perhaps may be accounted for by reason of the soft and perishable nature of the bone of the cartilaginous fishes, to which the spines, teeth and palates belonged.

Robert Anstice (1757–1845) was a ship-owner and merchant, trading with Newfoundland, as well as being a civil engineer and Somerset's

first County Surveyor. As Commissioner of Sewers, he oversaw various projects to drain the Somerset Levels ([Dance, 2003](#); [Duffin, 2009](#), p. 106). He also held local office in Bridgwater, serving as mayor in 1804. He became a fellow of the Geological Society in 1818 and corresponded with various members. He was engaged as a surveyor for the building of the sea wall at Blue Anchor ([Skempton et al., 2002](#), pp. 17–18), and this might have prompted him to search up and down the foreshore, finding the Lias fishes and the Rhaetian bone beds; he was a regular correspondent of William Buckland during the 1820s ([Duffin, 2009](#), p. 106).

Further reference to the Rhaetian bone beds around Watchet was given by [Wright \(1860, p. 384\)](#), who reviewed the Rhaetian across the Midlands and southern England. At Watchet, he reported the Lower Lias ammonites, with their nacreous layer preserved, from Doniford Bay. He noted that: 'The Bone-bed here consists of a hard, bluish-grey, sandy limestone, about an inch in thickness, containing fragments of bone, with teeth and scales of Fishes. In the bands of sandstone small shells (*Pullastra arenicola*) are found in the state of moulds.'

[Dawkins \(1864\)](#) reported a mammal tooth, long since lost, from beds today recognised as part of the Blue Anchor Formation at Blue Anchor Point. He also described the geology of the area around Watchet, including a geological section 'about a quarter of a mile to the east of Watchet Harbour' in what can be recognised as Doniford Bay, and showing the succession of the Westbury and Lilstock formations as they were then understood in the cliff face and foreshore. He presented an incomplete log of the sequence above the Westbury Formation due to complex faulting and commented on the relatively unfossiliferous basal bone bed. [Etheridge \(1872\)](#) described the section at St Audrie's Bay and at a railway cutting south of Watchet in some detail, and associated sections were later published by [Bristow and Etheridge \(1873\)](#). The whole area was mapped by J.H. Blake of the Geological Survey between 1870 and 1876, and [Woodward and Ussher \(1908\)](#) presented sections at Doniford Bay and an associated railway cutting. [Richardson \(1911\)](#), in his overview of the Rhaetian of the region, noted about Doniford Bay that, 'so faulted are the beds, that their investigation is more interesting from the tectonic than from the stratigraphical point of view', and he described the more complete sections at Blue Anchor and St Audrie's Bay.

Parties of geologists have visited the area from time to time (e.g., [Evans et al., 1914](#)), but little research has been done there for 60 years. The bone beds of Blue Anchor and St Audrie's Bay were described in some detail by [Sykes \(1977\)](#) in his summary of British Rhaetian bone beds, but Doniford Bay is not mentioned. In the field guide to the Watchet area, [Hamilton and Whittaker \(1977\)](#) and [Whittaker and Green \(1983\)](#) mention Doniford Bay, but only briefly. Detailed stratigraphic and palaeontological work at Doniford Bay was undertaken by [Duffin \(1980b\)](#), and we use much of this information here. Further attention was paid to the North Somerset Rhaetian in revisions of stratigraphic nomenclature ([Warrington et al., 1980](#); [Gallois, 2009](#)) and especially the Williton Member ([Mayall, 1981](#); [Whittaker, 1978](#)).

Intense interest focused on the stratigraphy of St Audrie's Bay when it was proposed as the GSSP for the base of the Jurassic ([Warrington et al., 1994, 2008](#); [Hesselbo et al., 2004](#)). These proposals led to detailed work on magnetostratigraphy ([Briden and Daniels, 1999](#)), sedimentology ([Hesselbo et al., 2004](#); [Warrington et al., 2008](#)), dinoflagellate diversity ([Palliani and Buratti, 2006](#)), and the wider fauna ([Mander et al., 2008](#)) and flora ([Bonis et al., 2010](#)) of the area. The final GSSP proposal included the Doniford cliff and foreshore ([Warrington et al., 2008](#)).

Doniford Bay was also investigated as part of a study about the risk of reactivating faults in respect of the nearby Hinkley Point nuclear power station ([Gutmanis et al., 1991](#)). Studies of isotopes and microfossils across the Triassic–Jurassic boundary included materials from Doniford Bay ([Clémence et al., 2010](#); [Clémence and Hart, 2013](#)). Some marine reptiles were also reported from the area around Watchet ([Maisch and Kapitzke, 2010](#); [Lomax et al., 2018](#)).

## 2.2. Stratigraphy and sedimentology

The Westbury Formation at Doniford Bay is exposed along the foreshore (partially obscured by mud and sand), and is only visible at low tide, from ST 08393 43351 to ST 07041 43743, to the east of the small town of Watchet, Somerset, and northeast of Helwell Bay (Fig. 1). The rocks of the Doniford foreshore are folded and heavily faulted (Gutmanis et al., 1991), documenting a sequence spanning the Triassic–Jurassic boundary, with older Rhaetian deposits having later been faulted into contact, with the younger Hettangian strata exposed along the cliff faces at Doniford and Helwell bays.

The three lithological units of this sequence are the Mercia Mudstone Group, the Penarth Group, and the Lias Group. At the base is the uppermost unit of the Mercia Mudstone Group, the Blue Anchor Formation (Fig. 2), deposited during the Norian in an arid ephemeral terrestrial setting. The green to dark grey mudstones and siltstones of the Blue Anchor Formation (Tea Green Marls in older works) display characters of an ephemeral marine or coastal environment, with gypsum deposits, dolomitised siltstones and marine body and trace fossils. These all suggest deposition in a subtidal sabkha environment with the formation becoming increasingly marine higher in the sequence (Warrington and Whittaker, 1984; Warrington et al., 2008).

One unit of the Blue Anchor Formation, termed the ‘Sully Beds’ by Richardson (1905, 1911) and the ‘Williton Member’ by Mayall (1981), is unique to Glamorgan and the North Somerset coast (Fig. 2). Richardson (1911, p. 3) described it as ‘a thin band of impure limestone, practically made up of specimens of *Pteria (Rhaetavicula) contorta*, thus betokening slow formation.’ He noted that the Sully Beds, up to 14 ft (4.3 m) thick at some points along the coastline but much thinner at Doniford, lie immediately below the basal Rhaetian bone bed, and their contact shows evidence of erosion, and he mapped them as the top of the Blue Anchor Formation but listed them stratigraphically as forming the base of the Westbury Formation. Mayall (1981) classified these beds as the uppermost unit of the Blue Anchor Formation. Coupled with the restriction of the Williton Member geographically to South Wales and the North Somerset coast, it has been suggested that this unit represents the earliest beginnings of the Triassic marine transgression as it propagated from south to north across the country (Mayall, 1981; Swift, 1999). At St Audrie’s Bay, where it is better exposed, the unit is a 2-m-thick, well-bioturbated sequence of shale, with occasional lenticular beds of sandstone and siltstone, containing fish and bivalve remains and topped by a distinctive firmground (Hesselbo et al., 2004; Warrington et al., 2008). At Doniford Bay, we noted the Williton Member as a bed of muddy, calcite-cemented limestone containing abundant fossils of the bivalve *Rhaetavicula contorta* underlying the basal bone bed of the Westbury Formation.

The overlying Penarth Group is divided into the Westbury and Lilstock Formations, with the Lilstock Formation represented at Doniford Bay by both the Cotham and Langport members (Fig. 2). Both formations broadly represent shallow, intertidal facies. The Westbury Formation is an interbedded sequence of grey to black laminated pyritic shales, mudstones and fine sandstones, with occasional silty or muddy limestones, commonly occurring in association with fibrous ‘beef’, and rare highly fossiliferous conglomeratic bone beds. Ripple marks and trace fossils indicate deposition in a shallow-water restricted environment (Swift, 1999; Hesselbo et al., 2004). The depositional basin was marine, probably anoxic, and with rapid changes in salinity, water level, and oxygenation, all possibly brought about by storm events, contributed to a highly variable environment in which survival was difficult (Allington-Jones et al., 2010), as attested by the formation’s patchy fossil record (Swift, 1999).

The two bone beds, lower and the upper, occur towards the base of the Westbury Formation, and are separated by an interval of 50–60 cm (Fig. 2). The lower bone bed is a black sandy marl with an eroded top, roughly 5 cm thick, but varying in thickness and conglomeratic in places where marly limestone intraclasts from the underlying layers are

incorporated (Fig. 3D). The lower bone bed is generally a well-sorted coarse sandstone, dominated by >80% well rounded quartz grains, measuring 0.1–2 mm. Sedimentary structures are wavy lamination, suggesting current perturbation during deposition, and discriminating coarse sandstone with occasional wavy fine sandstone interleaved beds. Small bones and teeth, ranging in size from 0.5 to 5 mm, are common, representing c. 5% of grains, but most are abraded and black or brown. The grains are surrounded by a thin coating of white, calcite matrix. Some surfaces show brown crystalline siderite. The lower bone bed rests conformably on the Blue Anchor Formation, whose top forms a hardground marked by extensive burrowing or boring by invertebrates living on the seabed. It is presumably contemporaneous with the sea level rise associated with the influx of the initial Rhaetian transgression. The lower, or basal, bone bed has also been found to lie on an extensively bored/burrowed hardground at other sites along the North Somerset coast and on the margins of the Mendip palaeoisland at Hapsford Bridge (Ronan et al., 2020) and at Charton Bay, Devon, where *Thalassinoides* burrows are filled with packed bone bed debris (Korneisel et al., 2015).

The ‘upper bone bed’ occurs above 50–60 cm of black shales, laminated marly limestone and more massive limestone, as a 6.5 cm sandy bed with further vertebrate remains (Fig. 2). It is a black-coloured siltstone/fine sandstone with wavy bedding and lacks clasts. Fossils are isolated and rare, with one or two visible on the surface of a typical hand specimen. The matrix contains much less calcite than in the lower bone bed. Some larger fossils, such as an ichthyosaur tooth and scale imprint found in the bone bed, are pyritised. On processing, the low levels of calcite and abundant organic matter meant that we had to wash the crushed material to remove clay-sized particles and use paraffin to disaggregate grains.

Higher parts of the section include the Cotham and Lilstock members of the Lilstock Formation, the Watchet beds, and the Blue Lias Formation (Fig. 2). The Cotham Member at Doniford comprises a mix of greenish-grey calcareous mudstones and siltstones with occasional interbeds of argillaceous limestones, with a higher proportion further up in the sequence, all indicating deposition in very shallow brackish conditions (Hamilton and Whittaker, 1977; Gallois, 2009). The unit represents an extended period of lower sea levels, with desiccation cracks at one level suggesting a period of subaerial exposure (Hamilton and Whittaker, 1977; Swift, 1999; Hesselbo et al., 2004; Bonis et al., 2010). Cyclicity of deposition is observed, as in the Westbury Formation (Hesselbo et al., 2004). The base of the Cotham Member is marked by a unit displaying contorted bedding. This is a mappable unit which has been recorded as covering a total area of around 250,000 km<sup>2</sup>. It has been interpreted as a seismite (Simms, 2007).

The Langport Member at Doniford is well developed and extensive, unlike at Aust Cliff (Cross et al., 2018). At Watchet, the Langport Member is a relatively thin succession of light grey laminated micritic limestones and rare calcareous shales, probably representing a more oxic and clear-water environment than earlier, attested by the presence of corals that cannot survive in turbid environments, but still relatively hostile to life as seen in its low fossil diversity (Swift, 1999; Gallois, 2009). Despite these pervasive shallow conditions, it seems that the environment was occasionally subaerially exposed, as evidenced by desiccated erosional surfaces capping each limestone bed. Indeed, the highest bed of the Langport Member (and by extension the Penarth Group), has been termed the ‘sun bed’ for its marked dried and cracked appearance (Swift, 1999; Gallois, 2009).

Above the Lilstock Member are the problematic Watchet beds. First identified as a distinct unit by Richardson (1911), later authors tended to split it, with the base constituting the uppermost marly beds of the Langport Member and the top becoming the lowermost shaley beds of the Lias Group (Whittaker and Green, 1983). It has been resurrected as a distinct unit, whether as a member (Swift, 1999) or a formation (Watchet Mudstone Formation, with its type section in Doniford Bay; Gallois, 2009). The Watchet beds are unique to sequences from the North Somerset coast around Watchet and Glamorgan, matching the



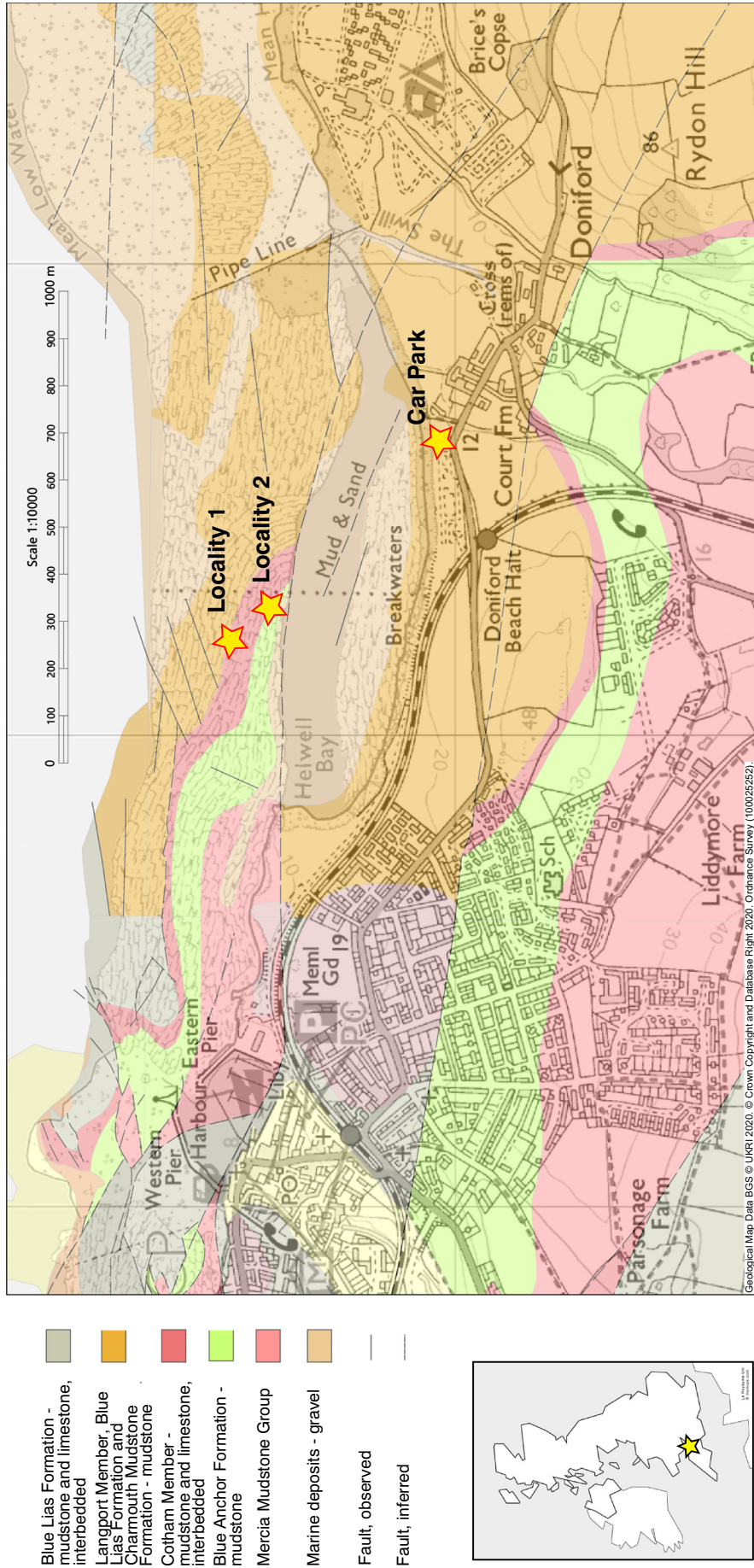


Fig. 1. Geological map of the Watchet and Doniford Bay area, showing the Triassic and Jurassic stratigraphy, and the two sampling locations. © Crown Copyright and Database Right 2017. Ordnance Survey (Digimap Licence).

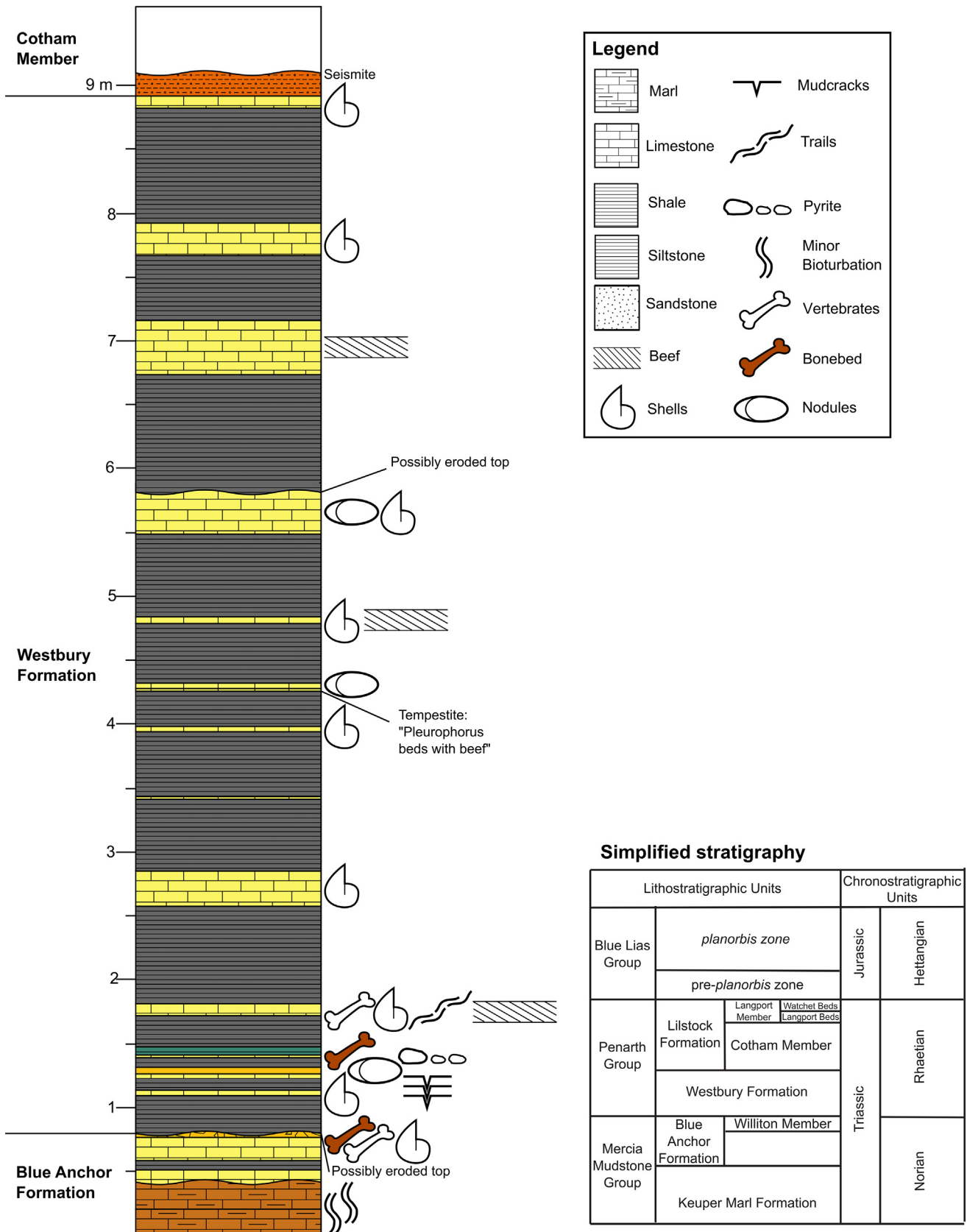


Fig. 2. Stratigraphic log through the lower Rhaetian (excluding Langport member) at Doniford Bay, Somerset, with lithologies, sedimentary structures, fossils, and key stratigraphic divisions, including bone beds, indicated, as well as a simplified log of the regional stratigraphic terminology.





**Fig. 3.** Field photographs of the Rhaetian at Doniford Bay, east of Watchet, North Somerset: (A) Perspective, looking west towards Watchet harbour, and showing gently northward-dipping Rhaetian sediments; (B) bedded unit of massive limestone overlain by the lower bone bed; (C) close-up of the surface of the upper bedding plane of the lower bone bed, showing rounded limestone pebble intraclasts.



area of deposition of the Sully Beds, being grey, marly, fissile, and occasionally bituminous shales and calcareous mudstones interbedded with occasional silty limestones, representing deepening marine facies and the possible onset of anoxia (Gallois, 2009). This unit is thin around Watchet (about 0.5 m), though thicker when exposed in South Wales (Gallois, 2009).

The marine limestones and calcareous mudstones of the Blue Lias Formation cap the sequence, representing the establishment of fully marine facies in the latest Rhaetian (Hamilton and Whittaker, 1977; Whittaker and Green, 1983). The Blue Lias Formation at Doniford comprises calcareous silty mudstones, often occurring as laminated 'paper shale', interbedded with thinner laminated argillaceous micritic limestones and the occasional shale, that lie unconformably above Penarth Group strata and indicate the return of deep marine conditions (Cox et al., 1999; Swift, 1999). Though the lowermost portions of this formation are latest Rhaetian, most of the unit is Hettangian in age, as evidenced by the rich abundance of ammonites, especially *Psiloceras planorbis* (Page and Bloos, 1995), the first appearance of which near the beginning of the formation marks the base of the Jurassic (Warrington et al., 1994), though more recent isotopic analyses place the boundary close to the base of the 'pre-planorbis beds' (Clémence et al., 2010). Due to post-depositional faulting at Doniford, the Blue Lias Formation is exposed both on the foreshore directly above the Cotham Member in sequence and extensively along the cliffs encircling the bay and immediate foreshore, where a great abundance of *Psiloceras* fossils may be collected.

### 3. Materials and methods

We studied samples collected from both bone beds at Doniford Bay by C. Duffin in 2017, and supplementary samples from the basal Rhaetian bone bed collected in June 2018 (Fig. 3). The standard method for isolating Rhaetian bone bed microfossils used in previous studies is digestion with dilute acetic acid (e.g., Cross et al., 2018).

The basal bone bed material was first treated with 5% acetic acid in aqueous solution with a buffer comprising 1 g calcium carbonate and 0.5 g tri-calcium di-orthophosphate in 2 l of water, then left to stand for 48 h. Following digestion, large undissolved blocks were removed for further processing, with the resulting solution of water and dissociated fragments sieved as described below.

This method did not work for samples from the upper bone bed because of the absence of calcium carbonate in the matrix. So, an alternative procedure using paraffin was used to further break down persistent clumps after the initial treatment (Ward, 1984). Dry samples were left to soak in paraffin for 24 h to disaggregate the matrix, after which excess material was poured away. To displace residual paraffin, samples were then covered in hot water, which caused the remaining paraffin to form a film on the water surface that was manually removed. Large blocks were removed for further processing after each run, with some notable macro-scale samples being set aside, including several specimens with pyrite veins, heavily abraded bone fragments (BRSUG 29953/36), and an ichthyosaur tooth (BRSUG 29953/34). One advantage of the paraffin process is that, unlike acid digestion, fragile structures containing calcium carbonate do not dissolve; however, as paraffin cannot entirely be removed, specimens carry a smell after processing. This smell could have been removed by detergent treatment, but we did not do this to avoid unwanted reactions that might have damaged specimens.

In both procedures, to partition the samples into different size categories, the mixture of undissociated matrix and water was washed through a series of sieves with gauges of 2 mm, 0.5 mm, and 0.18 mm respectively, using water flowing through filter paper in a funnel. This process was repeated multiple times, with successive runs of the disaggregation process, each sample being sieved and filtered in turn. Where possible, samples collected from coarser and finer material were kept separate. Some rare taxa were only found in one size of gauge: for

example, *Sargodon* teeth were picked from the coarse sediment residue and denticles from the fine.

Following sorting, the sediment was picked, with fossils removed and, where possible, sorted and identified. Unidentifiable fossil material was retained as evidence of the proportion of material that could be identified. Specimens were counted using methods outlined in previous studies (Korneisel et al., 2015; Cross et al., 2018). Figures showing the proportions of identifiable taxa from the lower and upper bone beds, as well as those from other Rhaetian localities in Britain, were compiled in R (v4.1.1) using the ggplot package. Taxonomic counts used to reconstruct faunal compositions at other localities were sourced from the supplementary materials of previous publications, as discrepancies were found between the supplementary and main documents of the Manor Farm and Aust Cliff publications (Allard et al., 2015; Cross et al., 2018).

Representative examples of each species and morphotype, along with more unusual specimens were put aside, catalogued appropriately, and photographed using an optical microscope fitted with a Leica DFC425 C camera possessing image-stacking capabilities. For each sample, a series of typically 40 digital photographs was taken at different magnifications, then concatenated and merged to produce an overall image, minimising the effects of depth-of-field and focusing artefacts. The resulting images were processed using Adobe Photoshop and Gimp (v2.10.25) to remove backgrounds, enhance the image by modifying hue, sharpness, and shade, and assemble figures. Fragments of an unidentified taxon were also imaged and spectroscopically analysed (EDS) using a Hitachi S-3500 scanning electron microscope. The only macro-scale specimen photographed was the ichthyosaur tooth (BRSUG 29953/34), which was too large to fit under the optical microscope. It was instead photographed using a Nikon D40 digital SLR camera with a Micro Nikon 60 mm lens and subsequently edited in Photoshop.

### 4. Systematic palaeontology

A total of 843 microfossils was identified in the upper Doniford bone bed and 444 in the lower one (see catalogue in Supplementary material). Descriptions of specimens are organised according to class and, where possible, genus or species. They include examples from Chondrichthyes, Osteichthyes, Reptilia, Crustacea, and Cephalopoda. Counts of individual taxa are presented in the text as well as in Table 1. Size ranges given for individual taxa are based on aggregate measurements of individual specimens.

#### 4.1. Chondrichthyans

Three distinct chondrichthyan tooth types have been assigned to named taxa, all of which were common during the British Rhaetian.

##### 4.1.1. *Lissodus minimus* (Agassiz, 1839)

The most abundant species, *Lissodus minimus* (Fig. 4A), is represented by dental remains from the upper ( $n = 158$ ) and basal bone beds ( $n = 88$ ). They consist mainly of tooth fragments, with the occasional largely complete crown. Specimens are between 1 mm and 3.5 mm in mesiodistal length and show moderate to heavy abrasion. Interestingly, teeth from the upper bed are black–grey, whilst those from the lower bed are a mix of brown, dark grey, and light grey. Central cusps appear low and flattened, featuring an occlusal crest extending the mesiodistal length of the crown. On both labial and lingual sides, crowns are either smooth or ornamented with basally diverging vertical ridges leading from the apex to crown base. One to three pairs of low-profile lateral cusplets flank the central cusp which extends forward into a low, bulging labial peg of varying sizes. Roots are entirely missing or highly abraded.

The low-profile teeth are triangular and would have been suitable for crushing benthic shelled invertebrates, like bivalves and crustaceans (Duffin, 1999, p. 201).

**Table 1**

Counts and proportions of taxa found in basal Rhaetian bone beds and bone beds of similar stratigraphic levels to the upper Doniford bone bed from in and around the Bristol area and deposited in deep-water or coastal environments.

	Basal bone bed							Upper bone bed				
	Offshore				Coastal			Offshore		Coastal		
	Doniford	Aust Cliff	M4–5 Motorway Junction	Manor Farm	Saltford	Charton Bay	Hampstead Quarry	Doniford	Westbury Gardens	Hampstead Quarry (HFQ17)	Hampstead Quarry (HFQ16)	Hampstead Quarry (HFQ1)
<i>Lissodus</i>	88	452	1099	202	1871	172	151	158	7	0	0	0
	51%	36%	45%	45%	55%	40%	35%	61%	4%	0%	0%	0%
<i>Rhomphaiodon</i>	36	357	721	173	547	37	40	24	16	0	0	1
	21%	28%	30%	38%	16%	9%	9%	9%	9%	0%	0%	3%
<i>Duffinselache</i>	0	0	1	0	0	4	0	2	41	0	0	0
	0%	0%	0%	0%	0%	1%	0%	1%	23%	0%	0%	0%
<i>Pseudocetorhinus</i>	0	6	1	0	0	1	0	0	0	7	7	8
	0%	0%	0%	0%	0%	0%	0%	0%	0%	26%	14%	25%
<i>Hybodius</i>	0	2	3	0	0	0	0	0	0	0	0	0
	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
<i>Parascylloides</i>	0	30	0	0	35	0	0	0	0	0	0	0
	0%	2%	0%	0%	1%	0%	0%	0%	0%	0%	0%	0%
<i>Pseudodalatias</i>	0	6	3	4	0	0	0	0	0	0	0	0
	0%	0%	0%	1%	0%	0%	0%	0%	0%	0%	0%	0%
<i>Nemacanthus</i>	0	0	1.5	0	0	0	0	0	0	0	0	0
	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
<i>Synechodus</i>	0	0	0	0	0	0	0	0	5	0	0	0
	0%	0%	0%	0%	0%	0%	0%	0%	3%	0%	0%	0%
<i>Vallisia</i>	0	0	0	0	0	0	1	0	2	0	0	0
	0%	0%	0%	0%	0%	0%	0%	0%	1%	0%	0%	0%
<i>Gyrolepis</i>	20	189	292	23	363	44	69	21	32	9	27	15
	12%	15%	12%	5%	11%	10%	16%	8%	18%	33%	55%	47%
<i>Severnichthys</i>	24	199	288	44	570	51	170	43	68	11	15	8
	14%	16%	12%	10%	17%	12%	39%	16%	39%	41%	31%	25%
<i>Sargodon</i>	4	13	7	4	25	58	2	11	4	0	0	0
	2%	1%	0%	1%	1%	13%	0%	4%	2%	0%	0%	0%
<i>Lepidotes</i>	0	9	1	1	0	60	0	2	0	0	0	0
	0%	1%	0%	0%	0%	14%	0%	1%	0%	0%	0%	0%
<i>Dapedium</i>	0	0	0	0	1	8	0	0	0	0	0	0
	0%	0%	0%	0%	0%	2%	0%	0%	0%	0%	0%	0%
<b>Total</b>	<b>172</b>	<b>1263</b>	<b>2417.5</b>	<b>451</b>	<b>3412</b>	<b>435</b>	<b>433</b>	<b>261</b>	<b>175</b>	<b>27</b>	<b>49</b>	<b>32</b>
	<b>100%</b>	<b>100%</b>	<b>100%</b>	<b>100%</b>	<b>100%</b>	<b>100%</b>	<b>100%</b>	<b>100%</b>	<b>100%</b>	<b>100%</b>	<b>100%</b>	<b>100%</b>

#### 4.1.2. *Rhomphaiodon minor* (Agassiz, 1837)

*Rhomphaiodon minor* is well-represented in both the upper ( $n = 24$ ) and basal bone beds ( $n = 36$ ). Though most specimens are moderately abraded, some are preserved almost entirely (Fig. 4B). They range from 0.5 mm to 4 mm in length. Crowns exhibit a prominent, flat central cusp, with a pair of lateral cusplets on either side. The first two cusplets are one third the height of the central cusp and are flanked by a smaller cusplet which protrudes laterally, curving lingually. These smaller cusplets are approximately half the size of the first cusplet. Both the central cusp and lateral cusplets present varying numbers of strong vertical striations. Where present, the upper labial root face is short relative to the crown. Vascular foramina are present on both faces. Teeth were found in multiple stages of development.

The lack of tooth serration and cusp orientation suggest that *Rhomphaiodon minor* was an opportunistic predator or a scavenger (Lakin et al., 2016).

#### 4.1.3. *Duffinselache holwellensis* (Duffin, 1998)

*Duffinselache holwellensis* is represented by a single tooth from the upper bone bed. The specimen is fragmented, roughly 1 mm in length (Fig. 4C). The crown is notably short and has a central, low-profile apical cusp which protrudes slightly forward on the lingual side and is distally inclined. No prominent cusplets are present. Both labial and lingual faces feature a vertical ridge ascending to a central cusp, and an occlusal crest spans the crown's length. A small incision exists at the crown/root boundary, with the root presenting prominent vascular foramina arranged in a longitudinal pattern.

#### 4.1.4. *Chondrichthyan scales*

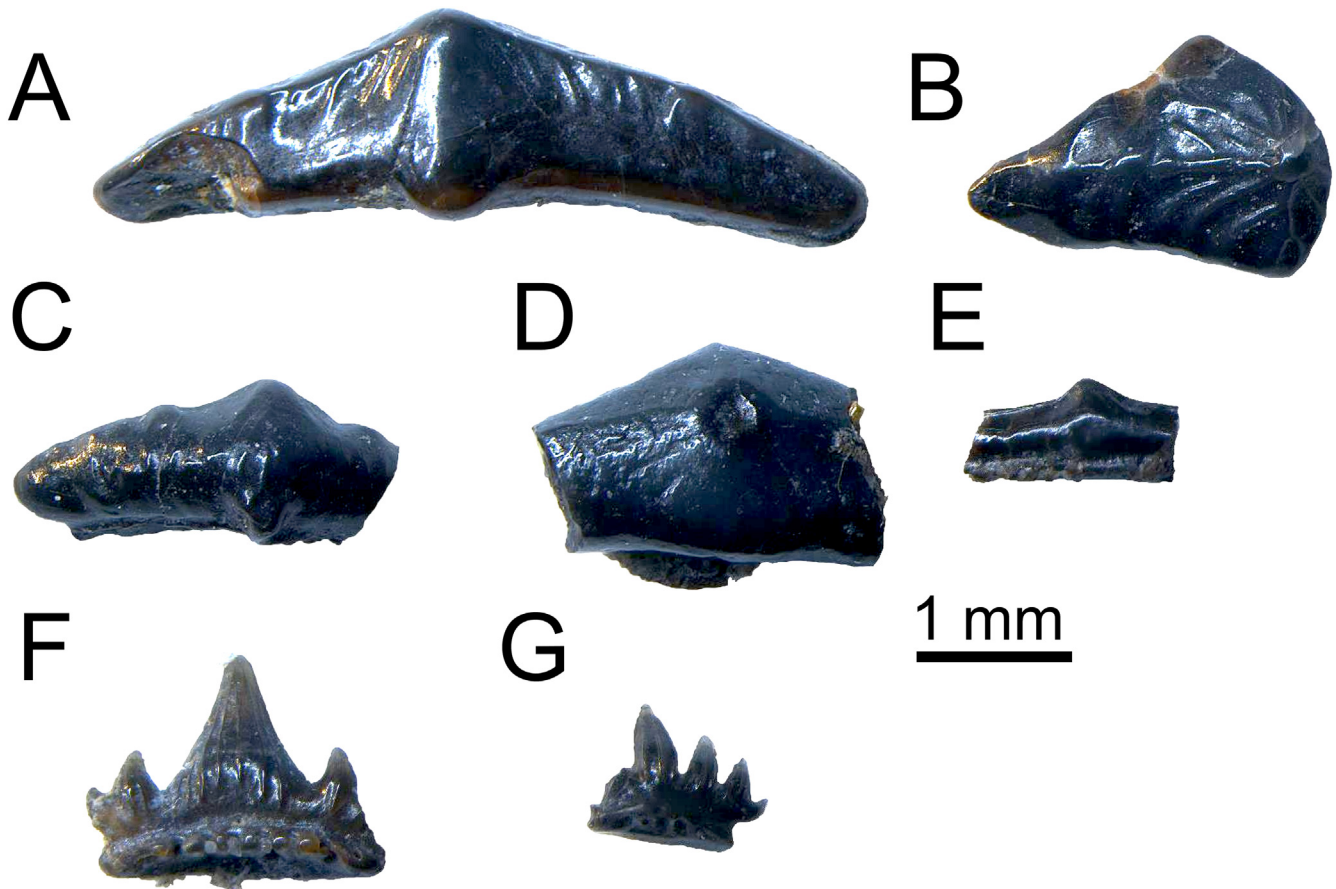
Few specimens were found in either bone bed, with some morphotypes being unique to one bed. Though some complete specimens were identified, most were partially abraded. Specimens have been described using terminology from Johns (1996). The scales have been divided into seven morphotypes. Morphs 1, 2, and 6 are placoid scales, whereas Morphs 3–5 are hybodontoid scales.

Morph 1 (Fig. 5A): The crown of this placoid scale features a prominent, central keel with four vertical ridges. Either side of the keel is a lateral wing. Each wing bears a central ridge that leads to a lateral cusp and is flanked by two vertical furrows. The wings curve posteriorly into a flattened, central apex. Overall, the scale is clam-shaped, approximately 0.5 mm in length, with a truncate pedicle. It resembles specimens from the Late Cretaceous *Synechodus dubrisiensis* (Mackie, 1863), as shown in Duffin and Ward (1993) and Cavicchini et al. (2018). This morphotype was only found in the upper bone bed ( $n = 3$ ).

Morph 2 (Fig. 5B): The crown is elliptical with a rounded apex and its underside is scalloped. The scale is ornamented with very fine, longitudinal ridges on the external surface, is smooth on the underside and is 1 mm in length. The pedicle is missing from both specimens found in the basal bone bed. Given its resemblance to specimens found by Landon et al. (2017, fig. 5D), a pedicle may have attached to one of the longitudinal sides.

Morph 3 (Fig. 5C): The base of the specimen is circular in surface view, with a stud-like central crown projecting perpendicular to it.



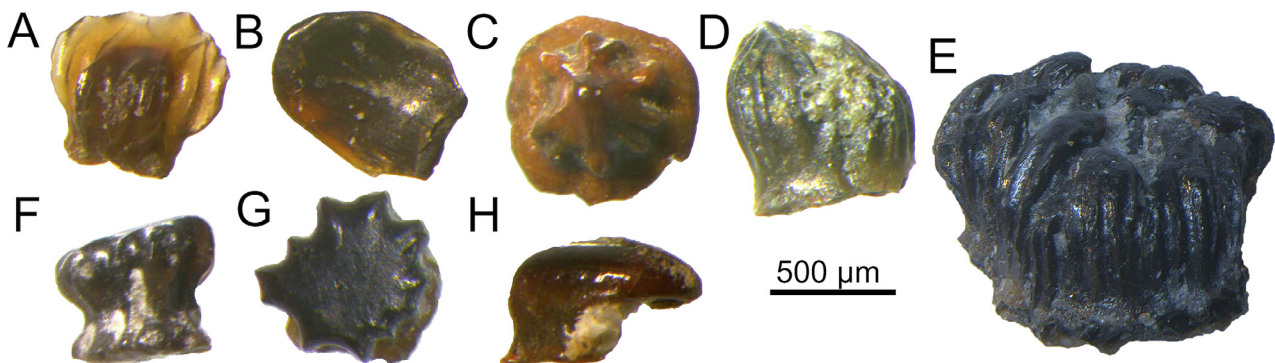


**Fig. 4.** Chondrichthyan teeth from the upper and lower Rhaetian bone beds at Doniford Bay: (A) *Lissodus minimus* tooth in labial view (BRSUG 29953/38); (B) *Lissodus minimus* tooth in occlusal view (BRSUG 29953/54); (C) *Lissodus minimus* tooth in labial view (BRSUG 29953/55); (D) *Lissodus minimus* tooth in oblique occlusal view (BRSUG 29953/56); (E) *Duffinselache holwellensis* tooth in labial view (BRSUG 29953/26); (F) *Rhomphaidon minor* in labial view (BRSUG 29953/19); (G) *Rhomphaidon minor* in labial view (BRSUG 29953/4).

The crown is conical and features a bulbous apex. Several very coarse, often bifurcating vertical ridges radiate from the crown apex towards the base of the scale, finishing in a slightly raised nodule. Altogether, the crown resembles a multi-pointed star. A single specimen was found in the basal bone bed and is between 0.8 and 1 mm in diameter. It resembles several specimens found by Cross et al. (2018, fig. 8E), and those described and figured by Reif (1978, figs. 2A, 6A–B) from *Hybodus delabechei* (Sinemurian, Early Jurassic

of Lyme Regis) and isolated scales from the Rhaetian of Gaisbrunnen (Germany).

Morph 4 (Fig. 5D, E): Specimens are notably elongate, roughly two and half times as long as they are wide. They range from being just under 1 mm in length to almost 2 mm. The pedicle is truncate and short. At the boundary between the pedicle and crown, the circumference narrows. It then broadens in the middle of the crown, tapering into an apex of grouped cusps. A series of prominent ridges runs



**Fig. 5.** Chondrichthyan denticles from the upper and lower Rhaetian bone beds at Doniford Bay: (A) Morph 1 placoid scale in anterior view (BRSUG 29953/74); (B) Morph 2 placoid scale in posterior view (BRSUG 29953/69); (C) Morph 3 simple hybodont scale in exterior view (BRSUG 29953/73); clusters of Morph 4 hybodont scales in lateral (D) and anterolateral (E) views (BRSUG 29953/72, BRSUG 29953/24); Morph 5 hybodont compound scales in lateral (F) and oblique lateral (G) views (BRSUG 29953/70); (H) Morph 6 placoid scale in lateral view (BRSUG 29953/71).

vertically along the circumference. Specimens feature a convex anterior and a concave posterior face. In hybodonts, the lateral ridges and furrows of the scales likely interlocked, as shown by several denticle masses found (Fig. 5E). A similar example is noted by Duffin (1999, pl. 27, fig. 6). Specimens belonging to this morphotype have only been identified in the upper bone bed (n = 3).

Morph 5 (Fig. 5F, G): Overall, specimens are short and dense, with a height of 0.2 to 0.4 mm. The complex of closely adjacent pedicles and crowns is prominent, and each has a similar width, although the compound crown is about three times taller than the pedicle. Between them, the crown/pedicle junction narrows. The surface of the crown is flat, roughly circular with jagged edges in surface view. Similarly, the pedicle is circular in cross section, though is much less jagged than the crown, and bears a central canal. The lateral surface of the crown and junction features a series of deep furrows and ridges around the circumference. These compound scales resemble those found by Cross et al. (2018, fig. 8C) and Duffin (1999, pl. 27, fig. 5), with the latter identifying such scales as hybodont. Specimens were found in both the basal (n = 1) and upper (n = 2) bone beds.

Morph 6 (Fig. 5H): At the anterior end of the crown is a thick pedicle bearing a series of vertical furrows. It extends dorsally into a smooth crown which elongates posteriorly. The specimen is 0.5 mm tall and 0.8 mm wide, with the pedicle comprising half the total height and width. Its base shows signs of abrasion, and may have extended to a wider base, somewhat like that shown in similar-looking specimens in Mears et al. (2016, fig. 9A–F). A single specimen was found in the upper bone bed.

## 4.2. Osteichthyes

Five osteichthyan taxa have been identified based on dental remains. Though several scale morphotypes were also found, these could not be assigned to specific taxa.

### 4.2.1. *Severnichthys acuminatus* (Agassiz, 1835)

*Severnichthys acuminatus* is known from teeth belonging to two morphotypes: *Birgeria acuminata* and *Saurichthys longidens*, once classified as separate taxa. Following Storrs (1994), both morphotypes have been categorised and counted together, but are described separately. *Severnichthys* teeth were found both in the upper (n = 43) and lower (n = 24) bone beds. Both beds contain moderately abraded to nearly unworn, complete specimens, though the upper bone bed has slightly more complete examples. Overall, specimens measure between 0.4 mm and 2.2 mm in length.

*Birgeria*-type teeth (Fig. 6A) bear a prominent ridge that separates the acrodin enamel cap from the basal shaft of the tooth. The cap is vertically ridged and semi-translucent, ending in a rounded apex. The cap comprises 60% of the tooth's total length. The tooth base is cylindrical, opaque, and is ornamented by a series of vertical ridges like those of the cap, though at more regular intervals. A large, root pulp cavity is present in the base.

*Saurichthys*-type teeth (Fig. 6B) are slightly more elongate than the *Birgeria*-type, with the tooth base comprising a larger portion (~60%) of the total tooth. The cusp lacks a ridge separating the acrodin cap from the cusp base, and the cap lacks ornamentation. The base is cylindrical and bears vertical ridges. Though no complete teeth were found, they would likely resemble specimens from Cross et al. (2018, fig. 10C).

Both tooth types would have been suitable for holding and tearing prey. This suggests that *Severnichthys* was a predator, probably feeding on small bony fish (Lombardo and Tintori, 2005) or sharks, like *Lissodus* or *Rhomphaiodon* (Lakin et al., 2016).

### 4.2.2. *Sargodon tomicus* (Plieninger, 1847)

*Sargodon tomicus* (Fig. 6C) was poorly represented in the basal bone bed, with few teeth being found (n = 4), though somewhat better represented in the upper bone bed (n = 11). The molariform cusp is low-profile, broad and dome-shaped, with a flat gingival face. Both the occlusal and circumferential surfaces are semi-translucent and khaki in colour. Crescent- or star-shaped markings can be seen at regular intervals underneath the transparent acrodin cap. These are large canals in the underlying dentine, which are distinctive for this genus (Andreev, 2011). A shallow indentation is often present at the centre of the occlusal surface which appears worn. Specimens range from 0.5 mm to 1.9 mm in height.

Short, broad, flat teeth are suitable for crushing prey. Their presence suggests that *Sargodon* was durophagous, feeding on hard shelled organisms, like echinoids, crustaceans or molluscs (Lombardo and Tintori, 2005).

### 4.2.3. *Gyrolepis albertii* (Agassiz, 1835)

Teeth of *Gyrolepis albertii* (Fig. 6D) consist of a short acrodin enamel cap atop a long, conical shaft. The cap is smooth and conical, leading to a translucent apex, and comprises 25–35% of the entire tooth. The shaft is curved lingually and opaque, occasionally bearing irregular wrinkles and a flared base. Specimens were well-represented in both the basal (n = 20) and upper bone beds (n = 21). Specimens range from being moderately abraded to complete and are between 0.4 mm and 1.7 mm long.

The conical shape and size of the teeth suggest a predatory diet of small fishes (Lombardo and Tintori, 2005).

### 4.2.4. *Lepidotes* sp.

A single tooth belonging to the genus *Lepidotes* (Fig. 6E) was identified in the upper bone bed. The specimen is oblong, curving inwards slightly at the top and bottom, and is 0.7 mm long. The occlusal surface features a short, bulbous peg that features multiple indents less than 2 µm in length. Starting just below the peg, a broad, medial indent runs much of the vertical length of the tooth. The specimen resembles a tooth presented in Korneisel et al. (2015, fig. 7F) whose species also could not be determined. *Lepidotes* was likely a durophage, given that the tooth is short and features a flat occlusal surface (Lombardo and Tintori, 2005).

A jaw fragment featuring two teeth (Fig. 6F) was also found in the upper bone bed. The jawbone itself is heavily abraded whilst the teeth are well-preserved. Two crowns, approximately 0.5 mm wide and 0.7 mm tall, protrude from sockets in the jawbone. The most pharyngeal crown is slightly larger than the other. Two-thirds up, the crown bulges, then tapers into a blunt, semi-translucent apex, with the pharyngeal surface being more steeply inclined than the proximal. The frontmost crown lacks a bulge and is instead a single, semi-translucent cone, with a flat proximal side and rounded labial surface. At the base of the first crown is a pit, which may be a tooth replacement pore, indicating ankylosis of the teeth.

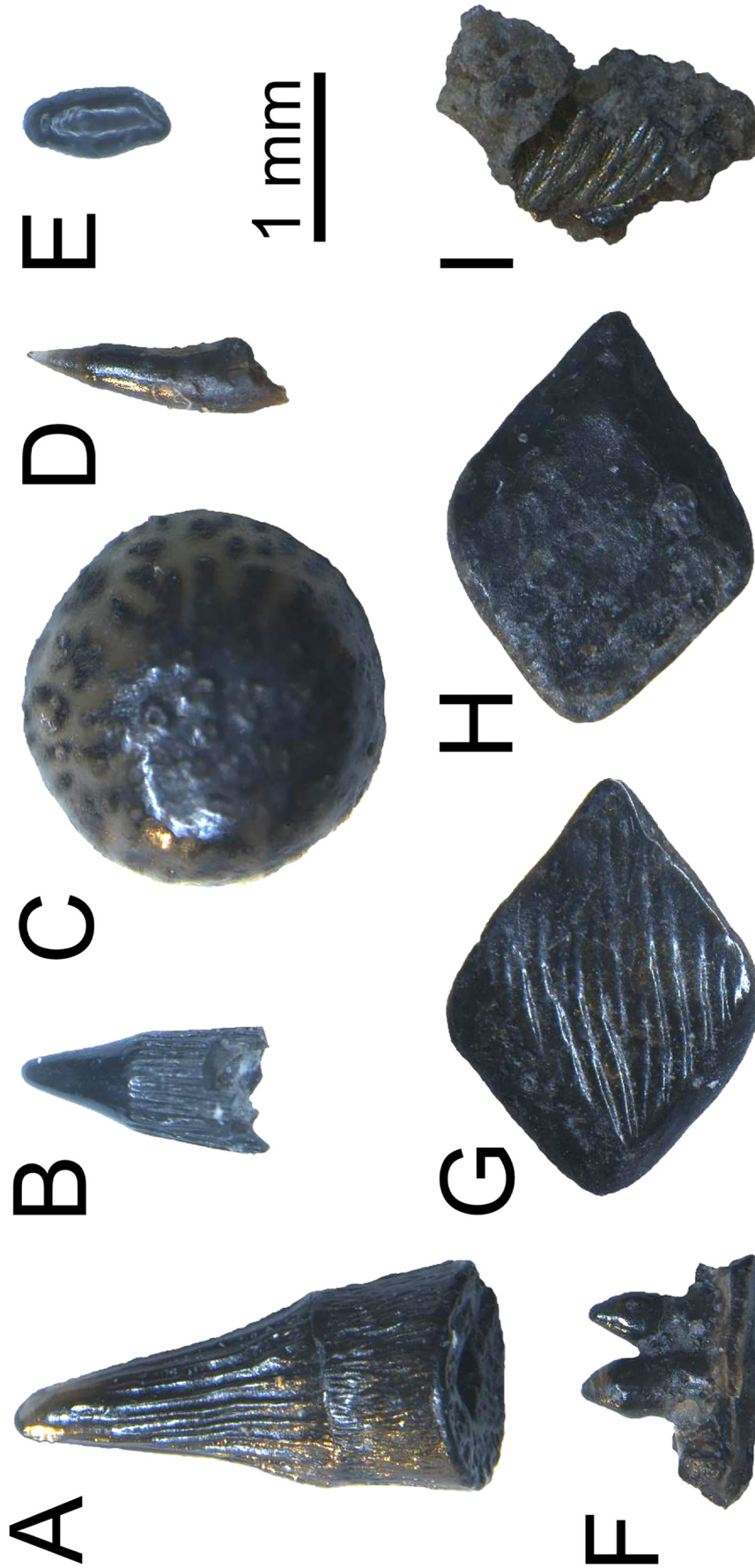
The teeth resemble those of *Lepidotes* (Mears et al., 2016, fig. 7i; Cross et al., 2018, fig. 10d). Tooth replacement and ankylosis have been shown to have occurred in a member of *Scheenstia* (Leuzinger et al., 2020), the sister group to *Lepidotes* (Lopez-Arbarello, 2012). If indeed the jaw fragment comes from *Lepidotes*, and the pit is a tooth replacement pore, it is possible that *Lepidotes* shared the ability to grow replacement teeth.

## 4.3. Other osteichthyan remains

### 4.3.1. Scales and gill rakers

Osteichthyan scales and scale fragments (n = 442), most of which are highly abraded, were identified in the upper bone bed. Fewer than 1% of scales are complete, with fragments being between 0.2 mm and 2 mm wide. Scales and scale fragments (n = 221) were also found in the basal bone bed. They are partially to moderately abraded, ranging





**Fig. 6.** Osteichthyan scales and teeth from the upper and lower Rhaetian bone beds at Domiford Bay: (A) *Birgeria acuminata*-type *Severnichthys acuminatus* tooth in lateral view (BRSUG 29953/58); (B) *Saurichthys longidens*-type *Severnichthys acuminatus* tooth in lateral view (BRSUG 29953/60); (C) *Sargodon tomicus* tooth in occlusal view (BRSUG 29953/62); (D) *Gyrolepis albertii* tooth in lateral view (BRSUG 29953/63); (E) *Lepidotes* sp. tooth in lateral view (BRSUG 29953/27) (F) osteichthyan tooth plate fragment in lateral view (BRSUG 29953/59); (G) Morph 1 scale in (G) external and (H) internal views (BRSUG 29953/57); (I) pyritised Morph 1 scale imprint in external view (BRSUG 29953/31).

from 0.4 mm to 3 mm wide. More than 20% of these scales are complete. One distinct morphotype was identified in both bone beds. Further morphotypes may be present in the collection; however, identification of such morphotypes was difficult, given the abrasion of the scales. Gill rakers like those figured by Landon et al. (2017, fig. 6H, I) and Mears et al. (2016, fig. 5N) were also found in both the upper (n = 81) and lower (n = 15) bone beds.

The scales have a rhomboidal shape (Fig. 6G–I) and extend in an anteroposterior direction. A ganoine layer is present on the external surface, bearing a series of vertical, ripple-like striations. The internal surface of the scale is smooth, providing much of the scale's thickness, and lacks notable features. The scale resembles specimens found by Cross et al. (2018, fig. 11A–B) and are assigned to *Gyrolepis albertii*. In less abraded specimens, the external face may have featured round, longitudinal ridges like those featured in Cross et al. (2018).

A pyritised, partial scale imprint was found in the upper bone bed (Fig. 6I). It features a series of ripple-like, vertical striations and appears rhomboid, given the presence of a slight elongation on either the dorsal or ventral side of the imprint. The impression was likely made by the ganoine layer of a scale and resembles the external surface of Morphotype 1 scale or a *Gyrolepis albertii* scale, as described in Mears et al. (2016, fig. 10a–b). The imprint is embedded in a small piece of sediment.

#### 4.4. Reptilia

##### 4.4.1. Ichthyosaurs

A single ichthyosaur tooth was identified in the upper bone bed (Fig. 7A–C). Much of the root has been preserved, though its crown is absent. With the labial surface in view, the partial tooth measures 1.21 cm high, 0.6 cm wide, and 0.5 cm deep at its thickest point. Overall, the specimen curves in a lingual direction, and its thickness decreases in direction of the cutting surface. On the lingual side, the root becomes convex, leading to a small, central replacement pit. Vertical ridges feature around the circumference of the root, most notably on the labial surface. As the crown is missing, a transverse section of the tooth can be seen when viewed inferiorly. It exhibits a thick layer of folded dentine surrounding a centre of dental pulp. Both the dentine and pulp appear to have been pyritised. The tooth is similar to specimens identified by Mears et al. (2016, fig. 12a–b).

##### 4.4.2. Undetermined taxon

Two fragments (Fig. 7E–F), 1 to 2 mm long and 0.4 to 0.6 mm thick, of an undetermined taxon were identified in the basal bone bed. One surface (here referred to as “external”) bears prominent, brown–red reticulate structures filled with a grey matrix. The other (the “internal” surface) is smooth and exhibits a mottle of orange–brown and grey. When magnified, tiny circular or reticulate structures appear dispersed along its surface, giving it a shimmering appearance. In lateral cross section, both fragments appear porous and spongy (Fig. 7G, H). Superficially, the reticulate structures on the external surface resemble the pitting of temnospondyl dermal armour from the late Triassic (Gruntmejer et al., 2016, fig. 1); however, as the fragments are much thinner than dermal armour and characterised by well-defined rather than rounded pits, we do not assign them to Temnospondyli. Instead, they may be fragments of cancellous bone, possibly from an ichthyosaur or plesiosaur (Wings, 2004, fig. 3), which have been found in other Rhaetian deposits of southwest England (Allard et al., 2015; Mears et al., 2016). The presence of calcium, phosphate, and fluorine in both specimens (Fig. S1A–C) further supports the conclusion that they are fossilised bone fragments and indicates that they underwent phosphatisation (Prévôt and Lucas, 2001; Wings, 2004). In addition to the above elements, iron, carbon, and silica were found in the matrix within the reticulate structures, suggesting that it is a mix of a carbonate, possibly calcite or siderite, and sand.

#### 4.5. Invertebrates

##### 4.5.1. Crustacea

Microcoprolites (n = 9) were present in the basal bone bed but absent from the upper. Each coprolite is approximately 1 mm in length and isopolar, featuring flattened short axes and straight long axes (Fig. 8A). This gives it an overall pellet-like appearance. The lateral surface features linear furrows extending the length of the microcoprolite in a rough zig–zag pattern. Each specimen is black.

Altogether, they externally resemble crustacean microcoprolites identified by Cueille et al. (2020), who identified such remains as decapod, based on the appearance of internal canals. Without analysis of thin sections or CT scans, the nature of internal canals within our specimens cannot be determined. Therefore, we hypothesise our specimens to be decapod based solely on external similarity to specimens found by Cueille et al. (2020, fig. 11A, B) and their assertion that internal canals resemble those in decapod coprolites (Brönnimann et al., 1972; Kietzmann et al., 2010).

##### 4.5.2. Cephalopoda

A single cephalopod hooklet was found in the upper bone bed (Fig. 8B). Terminology used to describe the specimen follows that of Engeser and Clarke (1988, fig. 1). The hooklet consists of an ellipsoidal base, roughly 0.2 mm in length, inclined at a 45° angle to the shaft, which is overall about 0.5 mm long. The shaft is of similar length, from the top of the base to the breadth below the uncinus. The uncinus curves laterally at a 75° angle, in the direction of the top end of the base. The hooklet appears smooth and free from spurs. An orbicular scar is not clearly present. The specimen is much thinner and differently shaped to hooklets found by Landon et al. (2017, fig. 8A, B). Our specimen resembles that found by Cross et al. (2018, fig. 12) in terms of size, angle of curvature, and the slight compression towards the tip.

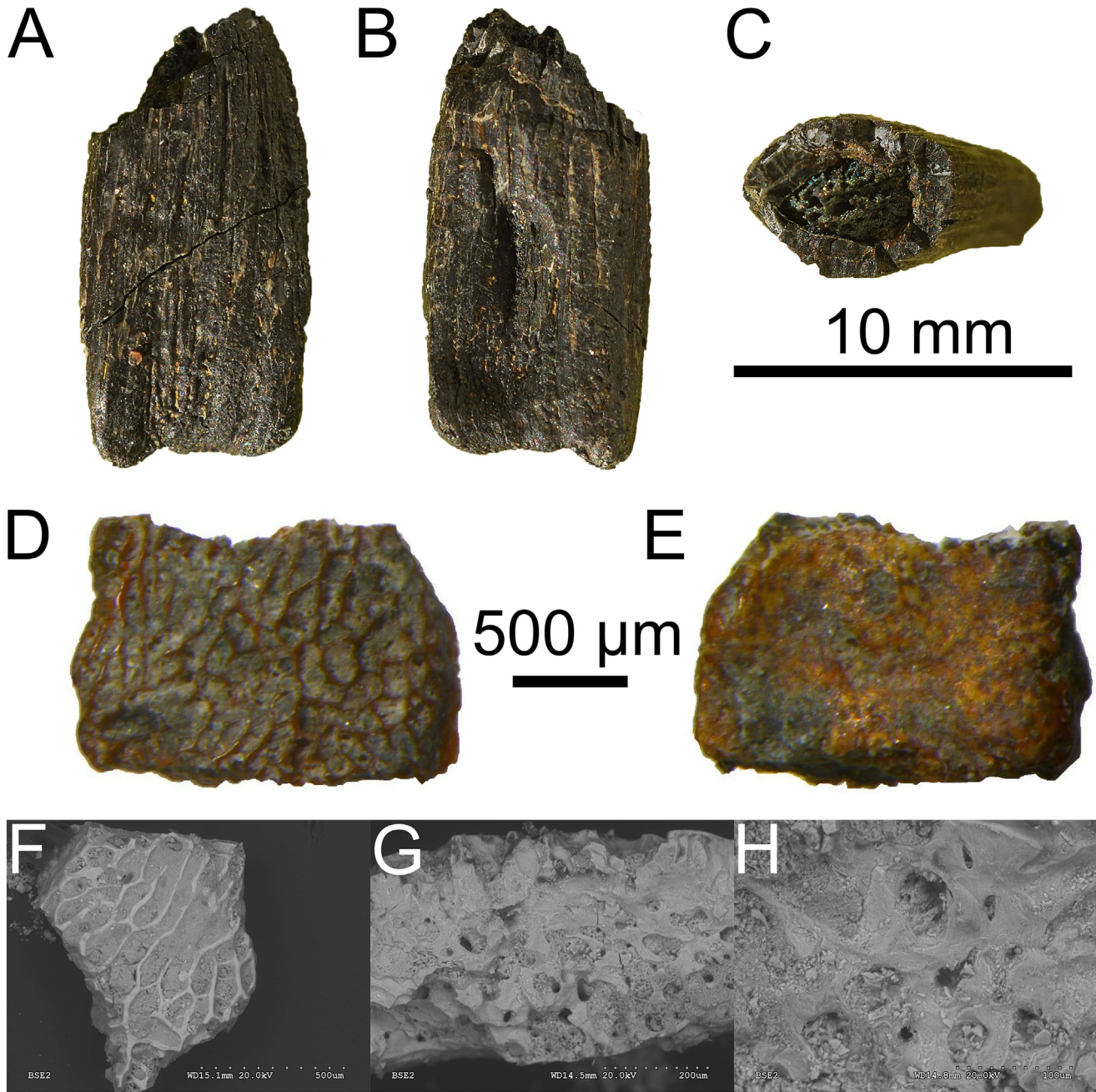
During the Triassic, four coleoid orders existed: Aulacoceratida, Belemnitida, Hematitida and Phragmoteuthida (Engeser and Clarke, 1988, fig. 3; Doguzhaeva et al., 2002; Fuchs and Hoffmann, 2017). Belemnitid and phragmoteuthid hooklets are spurless (Engeser and Clarke, 1988, fig. 2), so it is possible that our specimen belongs to one of these orders, as Cross et al. (2018, p. 648) suggested for their specimen. Equally, our specimen may belong to Aulacoceratida or Hematitida. Aulacoceratid and hematitid specimens bearing *in-situ* hooklets have not yet been discovered; however, spurless hooklets are sometimes found alongside aulacoceratid remains, meaning that our hooklet may derive from this taxon (Fuchs and Hoffmann, 2017; Fuchs et al., 2021). Either way, this, like the two other reports of Rhaetian cephalopod hooklets (Landon et al., 2017; Cross et al., 2018), is an important record, showing the occurrence of belemnoid micro-hooks (<5 mm) in Rhaetian seas. Micro-hooks generally occur in pairs along the ten tentacles (arms) of the living belemnoid and assist in grasping prey (Fuchs et al., 2021).

## 5. Discussion

### 5.1. Depositional environment

The upper and lower Rhaetian bone beds at Doniford were likely deposited in an anoxic environment, given their dark sediments and black fossils. This is supported by the presence of pyrite in both beds and phosphatised material in the lower bed (Evans et al., 1914; Martill, 1999), as pyrite and phosphorus require slightly alkaline (pH > 7.8), low-oxygen conditions to precipitate (Krumbein and Garrels, 1952; Wings, 2004). Such conditions are known to occur in the intermediate and benthic zones of marine–freshwater basins when circulation is restricted, organic input is high, and the rate of freshwater flow into the basin exceeds that of evaporation (Krumbein and Garrels, 1952). This suggests the Doniford bone beds were deposited in a basin with similar characteristics, which is consistent with reconstructions of bone bed





**Fig. 7.** Osmian remains of marine reptiles found at Doniford Bay: Ichthyosaurus tooth root from the upper Rhaetian bone bed in labial (A), lingual (B), and basal (C) views (BRSUG 29953/34); fragment of unknown taxon from the lower Rhaetian bone bed in external (D) and internal (E) views (BRSUG 29953/76); SEM images of the fragment (BRSUG 29953/7) in external (F) and lateral views (G) and a (H) close-up of a lateral cavity.

depositional environments at several sites in the Bristol district (Storrs, 1994; Swift, 1999; Suan et al., 2012; Williams et al., 2022) as well as other lines of evidence.

When the bone beds were deposited, Doniford was situated in the Western Gate of the Central European Basin (Fischer et al., 2012) and was probably several kilometres from the nearest shore, like nearby St. Audrie's Bay (Whiteside et al., 2016, fig. 4). Supporting this is the presence of sand (quartz grains) in both bone beds, a material which has only been found in shallow marine and coastal localities of the Bristol Basin (Mears et al., 2016; Cross et al., 2018; Lovegrove et al., 2021; Williams et al., 2022). The finding of sub-angular quartz pebbles in the lower bed further supports this as it suggests beach or riverine input. At St. Audrie's Bay, signals for positive  $\delta^{13}\text{C}$  excursions have been

found in strata roughly corresponding to the Doniford bone beds, in conjunction with marine palynomorphs, microplankton, and terrestrial plant pollen, signalling a productive, shallow marine environment (Warrington and Whittaker, 1984; Suan et al., 2012). Given its proximity to St. Audrie's Bay, Doniford may also have had substantial organic matter in its waters at this time, which would have produced suitable conditions for creating the pyrite and phosphorous found in the bone beds. Alternatively, bone bed material may have been produced at St. Audrie's Bay and then pushed eastwards into Doniford by water entering the Rhaetian Sea from the Western Gate (Fischer et al., 2012). As the top of the Williton Member at St. Audrie's Bay is eroded (Duffin, 1980b; Hesselbo et al., 2004), it is not possible to determine whether it once featured the basal Rhaetian bone as at Doniford, nor whether the

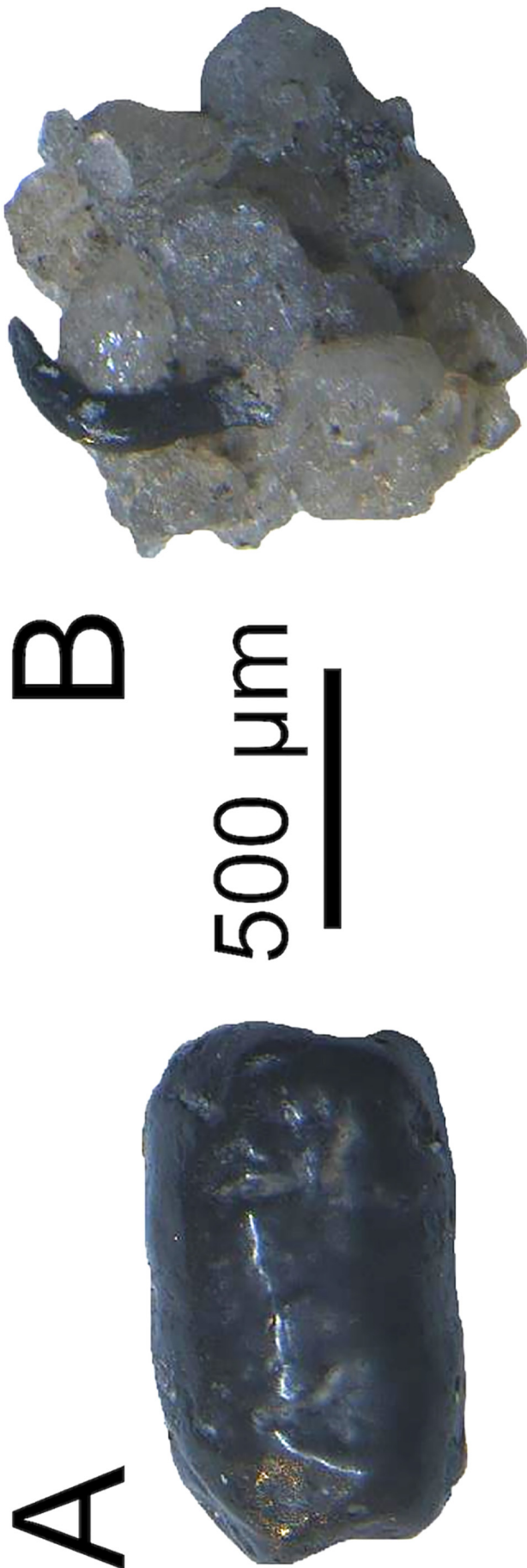


Fig. 8. Invertebrate remains from the lower and upper Rhaetian bone beds at Doniford Bay: (A) crustacean microcoprolite in lateral view (BRSUG 29953/61); (B) cephalopod hooklet in anterolateral view (BRSUG 29953/23).

material at Doniford was produced *in situ* or at a nearby site. Moderate to high levels of abrasion to specimens in both beds suggest some level of transport in a moderate- to high-energy environment.

### 5.2. Differences in deposition of the two bone beds

The basal Rhaetian bone bed at Doniford shares many similarities with such units from elsewhere in the Bristol district. It comprises a phosphatic conglomerate or sandstone containing a high frequency of broken vertebrate remains (Evans et al., 1914; Martill, 1999). As elsewhere (e.g., Korneisel et al., 2015), the basal bone bed has an erosive base and is laterally continuous over a large area. It should be noted that the sequence at St Audrie's Bay does not preserve a basal bone bed (Hesselbo et al., 2004). Multiple bone beds are found throughout the Westbury Formation (Mears et al., 2016), and sometimes even in the lower parts of the Cotham Member (e.g., Allard et al., 2015), so the occurrence of a second bone bed at Doniford is not unexpected.

There have been many hypotheses for the formation of the Rhaetian bone beds (Martill, 1999). They have generally been interpreted as cyclical basal transgressive lag deposits (Duffin, 1980a; MacQuaker, 1999), perhaps involving the erosion, reprocessing and subsequent redeposition of prior deposits (Sykes, 1977), or some combination of the above. For example, MacQuaker (1994) suggested that fossil material, derived from a previously deposited unit now exposed to the elements at the lowest ebb of a transgression, accumulated as lag deposits at parasequence boundaries and was subsequently eroded away or washed into the basin from an external source by exceptional storm events (Suan et al., 2012). The idea (Sykes, 1977; Duffin, 1980a; Martill, 1999) that the higher Westbury Formation bone beds were reworked from a basal one has now been rejected (Allard et al., 2015; Mears et al., 2016; Slater et al., 2016; Cavicchini et al., 2018) because the higher bone beds show different faunal compositions to the lower ones and the state of abrasion in them is variable. Further, isotopic and trace element analyses (Trueman and Benton, 1997; Suan et al., 2012) show that even the basal bone beds show different regimes of transport and deposition depending on the location and nature of the fossils within them. As specimens from both beds show moderate to high levels of abrasion, they may have been transported and deposited during storm events, as at other sites in the Bristol Basin (Ronan et al., 2020).

The lower and upper bone beds at Doniford differ substantially in terms of composition and faunal content. The two main differences are the absence of locally derived clasts, larger silica grains, and calcite in the upper bone bed. These features of the lower (basal) bone bed indicate active erosion ripping up locally derived clasts coupled with long-distance transport of the heavily abraded, land-derived silica grains. The abundant calcite matrix suggests a more alkaline, perhaps shallower site of deposition. In the lower bone bed, the abundant organic matter and absence of calcite suggest deposition at greater depth. Absence of calcite can indicate more acidic ( $\text{pH} < 7.8$ ) conditions (Krumbein and Garrels, 1952). In modern restricted basins, pH is a function of depth (Zhang and Millero, 1993; Yao and Millero, 1995), with the deepest waters being the most acidic. Therefore, the lack of carbonate material in the upper bone bed may indicate that it was deposited in deeper water than the lower bed.

This is consistent with lithofacies analysis of St. Audrie's Bay, which shows a substantial rise in sea-level between the top of the Williton Member and the middle of the Westbury Formation (Hesselbo et al., 2004). Acidification of the depositional environment may also have been induced by a rise in temperature, causing increased mineralisation and the release of carbon dioxide from the water (Omstedt et al., 2012).

### 5.3. Faunal composition of the Doniford bone beds and comparison with other localities

We identified 843 specimens in the upper Doniford bone bed and 444 specimens in the lower one (see catalogue in Supplementary



material). The difference in proportion is largely attributable to the high number of scales, gill rakers, and *Lissodus* teeth found in the upper bone bed. When these categories are removed, the number of identifiable specimens in the upper bone bed is 162 and 120 in the lower bone bed. *Lissodus* was found to dominate both beds, with the second-most prominent taxon in the lower bed being *Rhomphaidon* and *Severnichthys* in the upper bed (Fig. 9; Table 1). Counts of *Gyrolepis* were similar between beds but more specimens of *Sargodon* were discovered in the upper bed. Evidence for *Duffinselache*, *Lepidotes*, and cephalopods was also present in the upper bed but absent from the lower one.

The higher number of taxa and individuals in the upper bone bed may reflect increased productivity. Lithofacies and palynological analysis of St. Audrie's Bay indicate that sea levels and marine primary production were relatively low during Williton Member times, rising sharply at the start of the Westbury Formation (Warrington and Whittaker, 1984; Hesselbo et al., 2004; Suan et al., 2012). The Westbury Formation documents a series of highly productive lowstands and less productive highstands. The first lowstand occurs within the first 2.5 m of the Westbury Formation, and the second 4–6 m above the base (Suan et al., 2012, fig. 5). At Doniford, the peaks of these events correspond roughly to the upper bone bed and a thick shelly limestone (Fig. 2). The increased primary production during these lowstands may have triggered a proliferation of bivalves and other shelled molluscs, which would explain the high number of durophagous taxa found in the upper Doniford bone bed, including *Lissodus*, *Sargodon*, and cephalopods (Duffin, 1999; Lombardo and Tintori, 2005; Cross et al., 2018). This is plausible as bivalves have been found in association with durophagous vertebrates at other marine sites in the Bristol area (Allard et al., 2015; Moreau et al., 2021). The greater abundance of *Severnichthys* can similarly be explained as *Sargodon* has been inferred as its main source of prey (Cross et al., 2018).

The faunal composition of the lower Doniford bone bed resembles the basal bone beds at Aust Cliff, the M4–M5 Motorway Junction (South Gloucestershire), Manor Farm, and Saltford (Fig. 9; Table 1): each of them is dominated by *Lissodus*, followed by high counts of *Rhomphaidon* and roughly equal numbers of *Severnichthys* and *Gyrolepis*. As these bone beds were probably deposited 2–4 km from the shore (Lovegrove et al.,

2021, fig. 11), like Doniford, as discussed above, this faunal assemblage may be characteristic of offshore shallow marine environments. This is further supported by the presence of different faunas in contemporary beds from coastal environments. For instance, the fauna of the basal bone bed at Hampstead Farm Quarry is dominated by *Severnichthys* rather than *Lissodus*, whilst that of Charton Bay is taxonomically more diverse than other sites (Fig. 9; Table 1; Lovegrove et al., 2021, fig. 11). The bone bed at Westbury Garden Cliff also suggests high diversity in coastal environments; however, this bone bed appears to be younger than the basal bone beds and cannot be compared directly with them (Williams et al., 2022). Williams et al. (2022) concluded that there were no similarities between the basal bone beds, but our re-tallying of specimens confirms a similarity. Unlike the lower Doniford bone bed, the upper one shares no apparent similarity with bone beds from similar levels in terms of faunal composition (Figs. 9, S2). Instead, its fauna shows a higher proportion of *Lissodus* and a smaller proportion of *Rhomphaidon*. These differences may be due to the deepening of water or collector bias.

## 6. Conclusion

The Rhaetian bone beds at Doniford provide insights into the depositional environment of the lower Westbury Formation within the Bristol basin. By studying microfossils from the lower and upper bone beds, in conjunction with analysis of the overall Rhaetian stratigraphy at Doniford, we find evidence to suggest that:

1. The south of the Bristol basin underwent a series of marine transgressions and regressions throughout the early Rhaetian, with the lower bone bed being deposited during the onset of this series and the upper Doniford bone bed being deposited during a period of peak flooding and primary production;
2. Sediments from both the lower and upper bone beds were deposited after long-distance transportation from a beach or river;
3. Material from the upper bone bed does not derive from the basal bone bed;
4. Rhaetian bone beds within the Bristol Basin are characterised by particular faunas depending on their depositional depth, with coastal deposits featuring a more diverse fauna than deep-water ones.

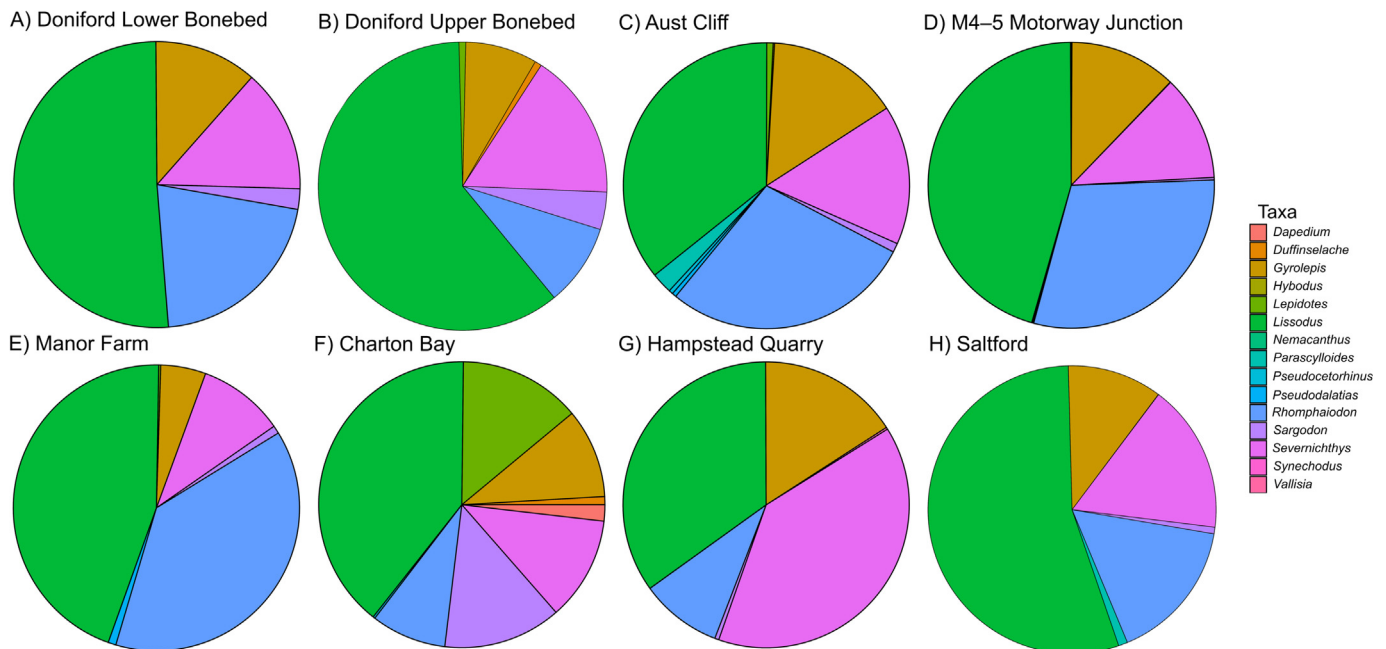


Fig. 9. Pie charts showing relative proportions of taxa found in the lower (A) and upper (B) Rhaetian bone beds at Doniford Bay as well as in the basal Rhaetian bone beds of Aust Cliff (C), M4–5 Motorway Junction (D), Manor Farm (E), Charton Bay (F), Hampstead Quarry (G), and Saltford (H).

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.pgeola.2023.01.004>.

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