



# Microvertebrates from multiple bone beds in the Rhaetian of the M4–M5 motorway junction, South Gloucestershire, U.K.

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## ABSTRACT

The Rhaetian (latest Triassic) is best known for its basal bone bed, but there are numerous other bone-rich horizons in the succession. Boreholes taken around the M4–M5 motorway junction in SW England provide measured sections with multiple Rhaetian bone beds. The microvertebrate samples in the various bone beds differ through time in their composition and in average specimen size. The onset of the Rhaetian transgression accumulated organic debris to form a fossiliferous layer high in biodiversity at the base of the Westbury Formation. The bone bed at the top of the Westbury Formation represents a community with lower biodiversity. The bone beds differ in their faunas: chondrichthyan teeth are dominant in the basal bone bed, but actinopterygians dominate the higher bone bed. These differences could be taphonomic, but are more likely evidence for ecological-evolutionary changes. Further, a change from larger to smaller specimen sizes up-sequence allows rejection of an earlier idea that the successive bone beds represented multiple reworkings of older bone beds.

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## 1. Introduction

The Rhaetian is a short span of time at the end of the Triassic, 205.7–201.3 Myr ago (Maron et al., 2015), that is important in Earth history as the prelude to, and including, the end-Triassic mass extinction. It also marks major environmental changes across Europe, and perhaps more widely, some of them influenced by the Central Atlantic Magmatic Province eruption (Suan et al., 2012). The Rhaetian Sea flooded much of central Europe, from Poland to France and the UK. This is documented widely in geological sections, which show how Rhaetian marine bone beds suddenly terminate the thick red-bed, largely terrestrial deposits of the Carnian and Norian.

The Rhaetian is especially known for the famous basal bone bed that marks the base of the Westbury Formation of the Penarth Group in the UK (MacQuaker, 1999) and its equivalents throughout

Europe. This dense fossiliferous layer is coarsely conglomeratic and has a sharp, erosive base that is situated atop the Blue Anchor Formation in many locations in the UK (Hamilton, 1961; Duffin, 1980; MacQuaker, 1999). Although bone beds are commonly found in the lowest 2–3 m of the Westbury Formation, bone beds located higher (and lower = 'infra-Bone-bed deposits') in the formation have been mentioned in several reports (Richardson, 1911; Storrs, 1994). Multiple Rhaetian bone beds have been reported from many localities (see Section 2.3). Allard et al. (2015) reported five bone beds through the Westbury Formation and overlying Cotham Member of the Lilstock Formation, at Manor Farm, near Aust, Bristol. These thinner, higher bone beds may be independent, or they may be the result of shoreward reworking of previous bone beds, or an upwards grading of the basal bone bed (Swift and Martill, 1999). Here we will assess these two models, and especially whether the stratigraphically higher bone beds are reworked variants of the basal Westbury Formation bone bed.

The Rhaetian and its classic basal bone bed is perhaps best known from the area north of Bristol, in south Gloucestershire. The most famous site is Aust Cliff (UK National Grid Reference,

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NGR, ST 565 894), where the Penarth Group is well exposed and has yielded abundant Rhaetian marine shark and fish fossils, and rare terrestrial reptile fossils (Storrs, 1994). Aust Cliff has been exceptionally well studied, with early descriptions from the 1820s onwards, and thorough documentation by Reynolds (1946) and Hamilton (1977). Near to Aust Cliff, and with a similar geological exposure, Manor Farm Quarry has been described by Allard et al. (2015).

Two motorways were constructed from the 1960s onwards through this area: the M4 runs from London to Swansea, and the M5 runs from Exeter to Birmingham. Unfortunately, opportunities were missed at the various times of construction to document the stratigraphic sequence, and to sample for fossils. However when gantries and cantilevered Enhanced Message Signs were erected along the M4 and M5 near Almondsbury, south Gloucestershire in 2001 and 2002, many boreholes were cored on the motorway hard shoulders and central reservations. Geotechnical Engineering Ltd. of Gloucester thoroughly documented these boreholes with engineering logs. Local geologist Mike Curtis sampled the cores, and his notes give a detailed account of their stratigraphy, sedimentology, and fossil content. This allows for study of the Rhaetian fauna where exposure is absent and allows for investigation of lateral continuity. Furthermore, it is unusual to have the opportunity to work from samples taken from measured levels in borehole cores.

Here, we describe the M4 and M5 motorway boreholes from the Almondsbury region of south Gloucestershire. We use these to investigate the number of bone-bearing horizons and their variations in faunal composition, and hence to consider models for their deposition.

## 2. Geological setting

### 2.1. Geological overview

The Triassic succession in the southwest of England (Fig. 1) comprises the largely terrestrial, thick red-brown mudstones of the Mercia Mudstone Group, of which the Blue Anchor Formation is the uppermost unit, representing more marine, coastal conditions. This succession is capped by the marine Penarth Group, which comprises the black mudstones of the Westbury Formation overlain by mixed grey mudstones and limestones of the Lilstock Formation. The Westbury Formation also contains rare calcareous sandstones that are either ripple laminated or bioturbated, as

evidenced by trace fossils such as *Thalassinoides* (MacQuaker, 1999; Suan et al., 2012; Korneisel et al., 2015). Deposition appears to have been cyclical, with three or four fining-upwards successions. Shell beds and intraformational conglomerates at the base or higher in the succession provide evidence for numerous flooding events (MacQuaker, 1999). The unlaminated mudstones form most of the succession and indicate oxidizing conditions at the time of accumulation (MacQuaker, 1999). When taken together, the Westbury Formation illustrates a rapidly changing marine environment with fluctuating levels of oxygen, salinity, and water depth.

The overlying Cotham Member of the Lilstock Formation comprises interbedded limestones deposited during times of regression, and occasionally containing algal deposits that form the signature 'landscape Cotham Marble' (Hamilton, 1961). Fewer fossils are found in the Cotham Member than in the Westbury Formation because there were fewer marine incursions. The overlying White Lias, part of the Langport Member of the Lilstock Formation, comprises pale grey limestone and calcareous shales, formed by another marine transgression. During times of regression, surfaces were well exposed, leaving desiccation cracks (Swift and Martill, 1999).

The Penarth Group is well exposed on coasts in south Wales and the southwest of England, and runs northeast through England, with additional exposures in Northern Ireland. Dramatic climate changes were occurring during the Rhaetian: the CAMP eruptions at the end of the Rhaetian increased the amount of phosphorus entering the oceans, interrupting carbon and oxygen cycles in warmed, deep and shallow waters (Suan et al., 2012). Temperatures were more equable from the equator to the poles than today, encouraging lower oceanic circulation and consequently supporting the preservation of vertebrate remains in a low-energy setting (Trueman and Benton, 1997).

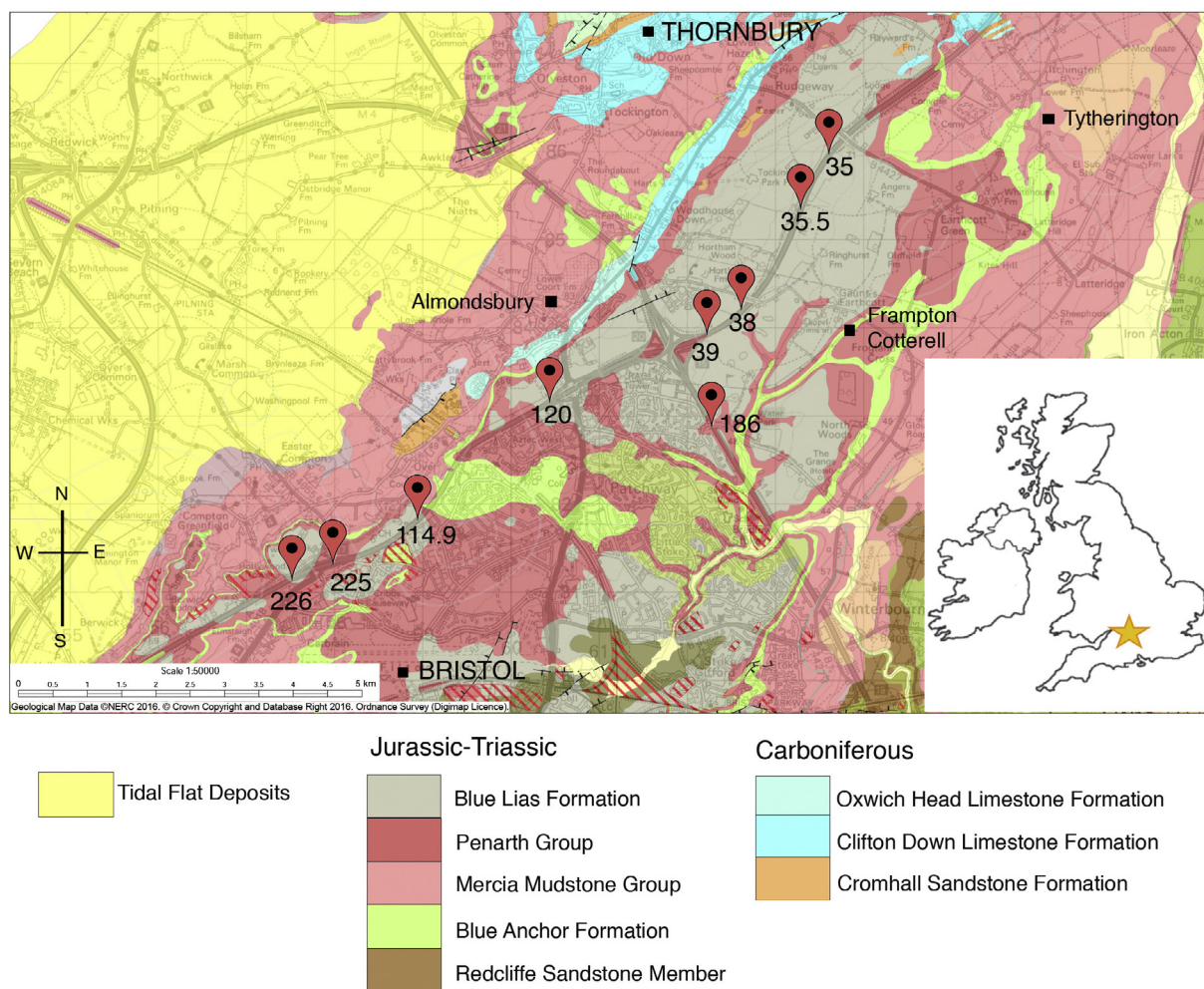
Deposition of the Westbury Formation likely lasted for about 2 Myr (MacQuaker, 1994; Mears et al., 2016), beginning with flooding and high-energy storms that transported highly phosphatized organic material to form the basal bone bed, often interpreted as a 'tempestite' (Short, 1904; Reif, 1982; MacQuaker, 1994; Storrs, 1994; Suan et al., 2012). Generally, the Rhaetian follows conformably above the Blue Anchor Formation, but in the Mendips and South Wales, the Penarth Group lies atop contemporaneously karstified Carboniferous limestone that once formed palaeoislands, providing a few examples of Rhaetian bone beds containing reworked Carboniferous fossils (Swift, 1999; Behan et al., 2012). Fissures in these limestone palaeoislands in South Wales and the area around Bristol had formerly been dated throughout the Late Triassic, but most or all may in fact be of Rhaetian age, matching palynological evidence from Tytherington (Marshall and Whiteside, 1980; Whiteside et al., 2016).

### 2.2. Geology surrounding the M4–M5 motorway junction

The boreholes used in this study are spaced over some 8.28 km along the M5, and around the M4–M5 junction (Fig. 2), and topography ranges from 54.8 m OD to 88.7 m OD (Fig. 3A). The boreholes then vary in their starting point at the current land surface, and they also vary in depth (Fig. 3B), but because of their geographic propinquity, the distinctive lithologies can be correlated readily. The sequence begins with up to 4 m of the Blue Anchor Formation, characterized by laminated green-greyish mudstones with thin beds of fine-grained limestone. Two borehole logs (186, 35) intersect fractures parallel with the bedding that are filled with stiff green-grey siltstone and gravel. In addition, boreholes 226, 225, 120, 114.9, and 39 show closely spaced subhorizontal and subvertical planar fractures, also filled with siltstone, indicating the lateral persistence of fractures. Boreholes

Lithostratigraphic Units			Chronostratigraphic Units	
Blue Lias Group	planorbis zone		Jurassic	Hettangian
	pre-planorbis zone			
Penarth Group	Lilstock Formation	Langport Member	Triassic	Rhaetian
		Cotham Member		
	Westbury Formation			
Mercia Mudstone Group	Blue Anchor Formation			Norian
	Keuper Marl Formation			

Fig. 1. Summary of Late Triassic and Early Jurassic stratigraphy in England (after Swift, 1999; Trueman and Benton, 1997).



**Fig. 2.** Geological map of the M4–M5 motorway junction area, each flag showing the site of drilled boreholes. The classic Aust Cliff section lies to the left, just south of the M4 bridge running to Wales. ©Crown Copyright and Database Right 2015. Ordnance Survey (Digimap Licence).

35, 38, and 114.9 all show bioturbation on the uppermost bedding plane. That from borehole 38 is compacted with dark grey mudstone and tubular fossil fragments. Bioturbation at the top of the Blue Anchor Formation has also been reported in Devon, UK, where *Thalassinoides* burrow systems preserve a marine assemblage of teeth from the overlying basal Westbury Formation bone bed (Korneisel et al., 2015).

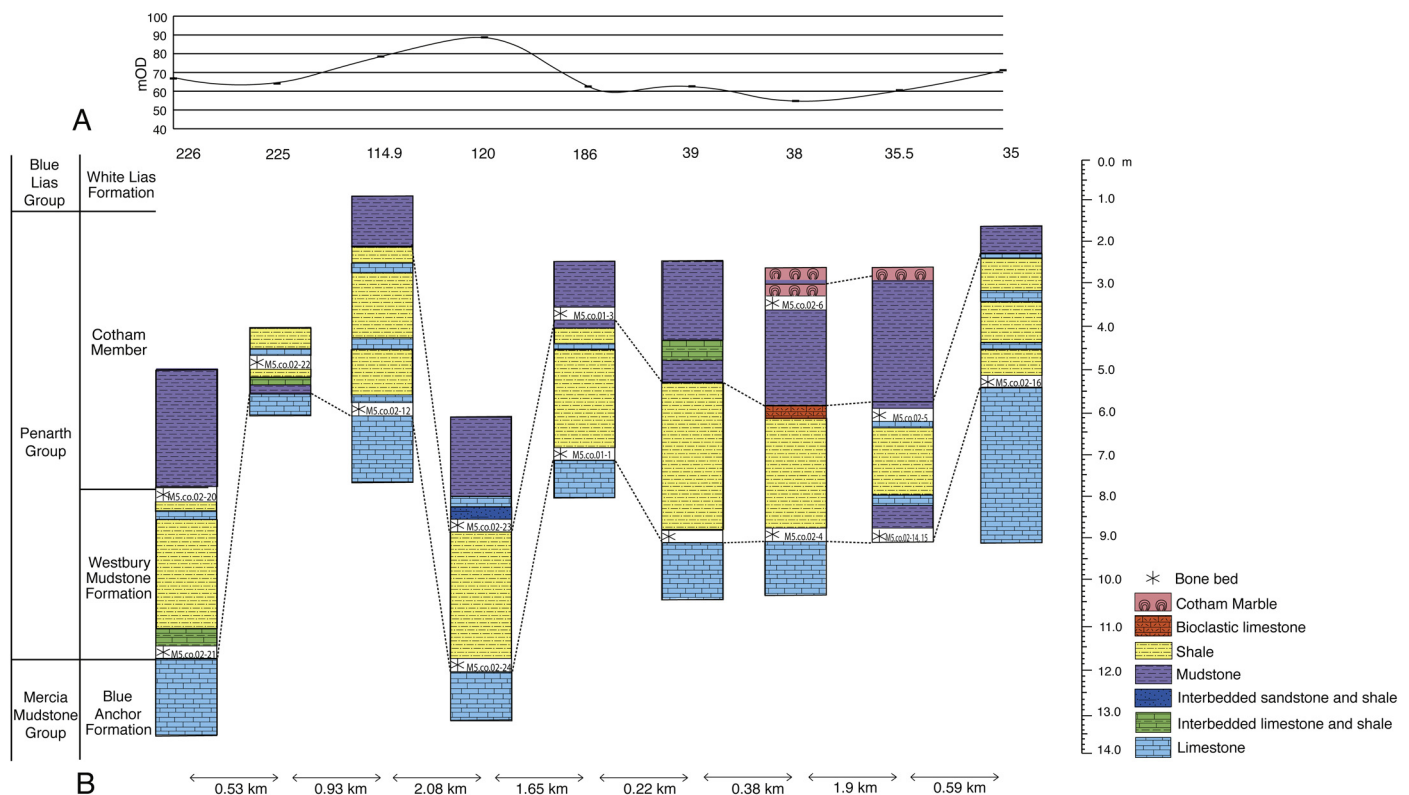
The Blue Anchor Formation is followed by 3–5.5 m of the Westbury Formation, composed of finely laminated black shales with bands of pyritic sandstone, and silt-rich ossiferous and calcareous mudstones. It also contains large amounts of organic matter and pyrite, with conglomerates at the base or higher in the formation (Richardson, 1911; Storrs, 1994; MacQuaker, 1999; Gallois, 2009). Multiple boreholes (226, 225, 114.9, 35.5, 35) have thin beds (10–60 mm) of dark grey, fine-grained, and strongly laminated limestone. These beds are occasionally bioturbated and contain clasts of dark grey mudstone. Borehole 38 shows a larger bed of bioclastic limestone, measuring 70 mm thick. The bone bed at the base of the Westbury Formation measures 2–10 cm thick, and comprises a matrix of dark grey shale and limestone with occasional rounded quartz and calcareous sandy aggregates. The basal bone bed of borehole 35.5 (Fig. 3B, 02–14,15) is preserved in a layer of lenticular mudstone. Sample 02–14 is then situated slightly above this basal bone bed in a layer of grey ossiferous mudstone with shale fragments. Bone beds restricted to the top 7–10 cm of the formation are found in a lighter grey matrix of

alternating laminated silty clay and fine sandstone. The bone bed at the top of the Westbury Formation in borehole 186 (Fig. 3B, 01–3) is approximately 10 cm thick, and consists of grey-green mudstone.

The overlying Cotham Member (2–8.8 m, this study) is marked by its greenish-grey colour, and it often contains layers of finely laminated mudstone, deposited cyclically in turbulent shallow waters (Storrs, 1994; Swift, 1999). The boreholes occasionally exhibit bands of non-bioturbated sandy limestone throughout the Cotham Member sequence (Fig. 3B, 39, 120). Borehole 186 shows alternating grey-green and yellow-brown fine-grained mudstone. The uppermost bone bed is found in borehole 38 at the top of the Cotham Member and contains few vertebrate fossils, but many invertebrates (Fig. 3B, 02–6) preserved in grey-green sandy mudstone and very angular grey limestone with quartz grains. A double layer of Cotham Marble with pyrite is situated above bone bed 02–6, separated by approximately 30 cm of green sandy calcareous mudstone. In addition, borehole 38 shows two layers of Cotham Marble and both have shell fragments on their fracture surfaces.

The Cotham Member terminates the Penarth Group succession in the area of the M4–M5 motorway junction, and indeed the Blue Lias is absent from all boreholes (Fig. 3B). In other locations, the White Lias Formation comprises pale grey limestone and calcareous shales, and the overlying Watchet Mudstone Formation, the uppermost unit of the Langport Member, is also absent here.





**Fig. 3.** Sections through the Rhaetian in boreholes along the M4–M5 motorway junction. (A) Graph showing topography and metres above ordnance datum (mOD) for each borehole. (B) Fence diagram showing sedimentary logs for each borehole core. Boreholes and bone bed horizons are labelled with Curtis' respective accession numbers. Bone beds at the top of the Westbury Formation are horizons labelled: M5.co.02-20; M5.co.02-23; M5.co.01-3; M5.co.02-5. Bone beds at the base of the Westbury Formation are horizons labelled: M5.co.02-21; M5.co.02-22; M5.co.02-12; M5.co.02-24; M5.co.01-1; M5.co.02-4; M5.co.02-14, 15. Horizon M5.co.02-6 lies at the top of the Cotham Member. Scale for borehole depth. Horizontal distances in kilometres between each borehole are specified. Lithologies and the key stratigraphic divisions of the Mercia Mudstone Formation and Penarth Group are indicated.

### 2.3. Multiple bone beds in the Westbury Formation

It is well known that multiple bone-bearing horizons are present in the Penarth Group (Storrs, 1994; Martill, 1999), as documented at several localities, including nearby Aust Cliff (Short, 1904) and at Westbury Garden Cliff (Storrs, 1994). Gallois (2009) and Suan et al. (2012) reported at least three bone beds in the middle and upper parts of the Westbury Formation at Penarth Bay in south Wales. Five bone beds were reported at Barnstone, Nottinghamshire (Sykes, 1977). The Westbury Formation at Barrow-on-Soar, Leicestershire shows the striking number of eight fossiliferous layers, and these were interpreted as having been produced by shoreward reworking in the form of scatter and trace bone beds above several primary bone beds (Sykes, 1977). Although Sykes (1977) reported on the number of bone beds at various localities in the UK, he did not compare their faunas.

Several bone-bearing layers were also reported by Allard et al. (2015) at Manor Farm Quarry, with the basal bone bed at the bottom of the Westbury Formation, one located at the top of the Westbury Formation, and three in the Cotham Member. Of most importance is the compositional difference in the diversity and abundance of taxa in the five beds, with more chondrichthyans present in the basal bone bed, and nearly absent in the overlying bone-bearing horizons (Allard et al., 2015). This substantial difference calls for further research on localities that contain multiple bone-bearing horizons.

The phosphatic conglomerate at the base of the Westbury Formation typically contains (i) numerous coprolites, (ii) rounded quartz-pebbles, identified as possible gastroliths of *Ichthyosaurus*

and *Plesiosaurus*, (iii) angular or subangular pebbles of the underlying sediment, whether Blue Anchor Formation or Carboniferous Limestone, and (iv) bones and teeth ranging from tiny, unabraded teeth and scales to large, rounded bone pebbles derived from vertebrae and ribs of marine reptiles. The basal bone bed measures up to 20 cm thick at Aust Cliff and rests only millimetres above the base of the Westbury Formation, as it does in many other exposures in the UK, such as Westbury Garden Cliff and Lilstock Bay (Roberts, 1862). However, study of exposures at Lavernock Point and Watchet reveals some variations, with the basal bone bed lying slightly higher in the succession (MacQuaker, 1999). In some locations such as the Chipping Sodbury quarries the basal bone bed is sporadic or absent, where the ancient sea lapped against areas of higher topography (Curtis, 1981; Lakin et al., 2016; Mears et al., 2016).

The basal Westbury Formation bone bed is assumed to be contemporaneous across the region, with numerous coprolites and the common fish taxa *Rhomphaiodon* ('*Hybodus*'), *Lissodus*, *Nemacanthus*, *Gyrolepis*, and *Severnichthys*. Louis Agassiz was first to identify the fishes from the basal bone bed from Aust Cliff, where he described as many as 18 species (Roberts, 1862). In each of the M4–M5 boreholes, we found the Rhaetian bone bed at the base of the Westbury Formation (Fig. 3B). Layer 02-21 from borehole 226 in this study does contain less numerous remains than the others, but the basal bone bed is known to be discontinuous in the Aust area (Hamilton, 1977).

Five of the boreholes used in this study show additional bone-bearing layers. In boreholes 226, 120, 186, and 35.5, a bone bed lies at the top of the Westbury Formation (Fig. 3B). In addition,

borehole 35.5 also exhibits an additional, third bone bed (Fig. 3B, 02-14) that rests on a thin layer of mudstone slightly above the basal bone bed (Fig. 3B, 02-15). Fossils extracted from this layer are highly fractured and abraded. Borehole 35 also possesses a similar bone bed (2 cm) that rests on a bed of limestone above the basal bone bed (5 cm). However, these were both processed by Curtis as one sample, so a comparative study between these two fossiliferous horizons could not be performed. Horizon 02-20 from borehole 226 and 01-3 from borehole 186 are dense in vertebrate contents and coprolites, showing minimal transport abrasion. Fossils in horizon 02-23 from borehole 120 show more signs of transport abrasion, but the contents are very similar to 02-20. From borehole 35.5, horizon 02-5 is much less dense in vertebrate remains. At the top of the Cotham Member, horizon 02-6 from borehole 38 marks the highest bone-bearing horizon found in this study, and contains a large quantity of invertebrates.

### 3. Methods

Geotechnical Engineering Ltd., Gloucester provided thorough documentation for each of the nine boreholes along the M4 and M5, spaced at roughly equal intervals along the M5 (Fig. 2). These cores were examined by Mike Curtis (1950–2008), a well-known amateur palaeontologist and fossil collector, who at the time worked in the laboratories of the company. He acquired some complete borehole core samples and focused on sampling from the Westbury Formation. These borehole specimens comprise a small portion of the Mike Curtis collection, which is held in part at the Bristol Museum and Art Gallery (BRSMG), donated in 1997, and at the University of Bristol School of Earth Sciences (BRSUG), donated after his death in 2009. In addition to his contribution towards significant fossil finds such as *Thecodontosaurus* (Benton et al., 2012), his large collection consists of Rhaetian vertebrate microfossils that he avidly excavated across the Bristol-Gloucester area. The Curtis collection has been used in previous studies to examine the faunal composition of various Rhaetian-age fossil localities around Bristol and the southwest of England, including Charton Bay, Devon (Korneisel et al., 2015), Marston Road Quarry, Holwell (Nordén et al., 2015), Manor Farm Quarry, Aust (Allard et al., 2015), Barnhill Quarry, Chipping Sodbury (Lakin et al., 2016), and Hampstead Farm Quarry (Mears et al., 2016).

Atkins/Highway Agency maps that detail the location of each borehole are held in the Mike Curtis collection (BRSUG) alongside borehole logs produced by Geotechnical Engineering Ltd. Borehole engineering logs were transcribed by Curtis to detail the geological sequence. These stratigraphic diagrams also note the horizon from which he took samples. Here we examine all fossiliferous horizons sampled by Curtis from boreholes 226, 120, 186, 38, and 35.5. Boreholes 225, 114.9, and 35 contained only one fossiliferous horizon that has been identified as the basal Rhaetian bone bed, and were not used in this study. However, Curtis's notes on the geological sequence for all borehole logs were used to inform the summary fence diagram (Fig. 3).

The BRSUG collections contain microvertebrate material processed by Curtis, using his usual thorough methods, as detailed by Korneisel et al. (2015). Sediment samples were repeatedly placed in 10% acetic acid until no longer reactive, and residual material was processed through four sieves with gauges measuring 2.4 mm, 1.2 mm, 600 µm, and 300 µm. Specimens obtained were then sorted by their respective sieve size, identified, and catalogued. Additional rock material from boreholes in the collection was processed for fossils by T.S.S. and T.G.D. in summer 2015 (M5.co.02-21; M5.co.02-23; M5.co.02-24; M5.co.02-4). This material was placed in a 5% acetic acid solution, with the addition of tri-calcium as a buffer, until no longer reactive. Material was then placed in water to allow it to neutralize for 2–3 days.

Processing was done using four sieves, with gauges measuring 2 mm, 800 µm, 600 µm, and 150 µm. Cataloguing was then carried out according to Curtis's protocol, for integration into the BRSUG collection.

Registered specimens in the Curtis collection (BRSUG 29371-1) were analyzed and counted with reference to his methods and notes. Species are more or less subject to fragmentation and abrasion depending on tooth morphology. For this reason, rules were followed when counting specimens to ensure a reasonable assessment for the relative abundances of species. These rules are adapted and revised from Curtis's methods and Korneisel et al. (2015).

Chondrichthyan teeth are among the most heavily fragmented and abraded, as many exhibit lateral cusps in addition to the central cusp. *Rhomphaiodon minor* was counted as complete when the central cusp and lateral cusps were complete. *Lissodus minimus* was counted as complete when the central cusp and labial peg were present and intact. *R. minor* and *L. minimus* were both counted as 'halves' when either the central cusp or lateral cusps/labial peg were present and clearly identifiable. *Duffinselache holwellensis*, *Hybodus cloacinus*, and *Pseudodolatias barnstonensis* were counted when a portion of the central cusp was present.

Actinopterygian teeth were often less abraded. *Severnichthys acuminatus* and *Gyrolepis albertii* were counted as complete when roughly 70% or more of the crown and shaft were intact; any identifiable specimens comprising 30% or less of the crown and shaft were counted as 'halves'. *Sargodon tomicus* teeth were counted as complete when the entire circular occlusal surface was present, and '*Lepidotes*' sp. teeth were counted as complete when the crown was present and intact.

Specimens identifiable only to broad taxa, such as denticles, scales, and fin ray elements, were only included in the broad taxonomic analysis, and not assigned to species in the absence of diagnostic characters. 'Miscellaneous' and 'unidentifiable' bone fragments were omitted from the census, including isolated fragments of teeth and roots.

### 4. Systematic palaeontology

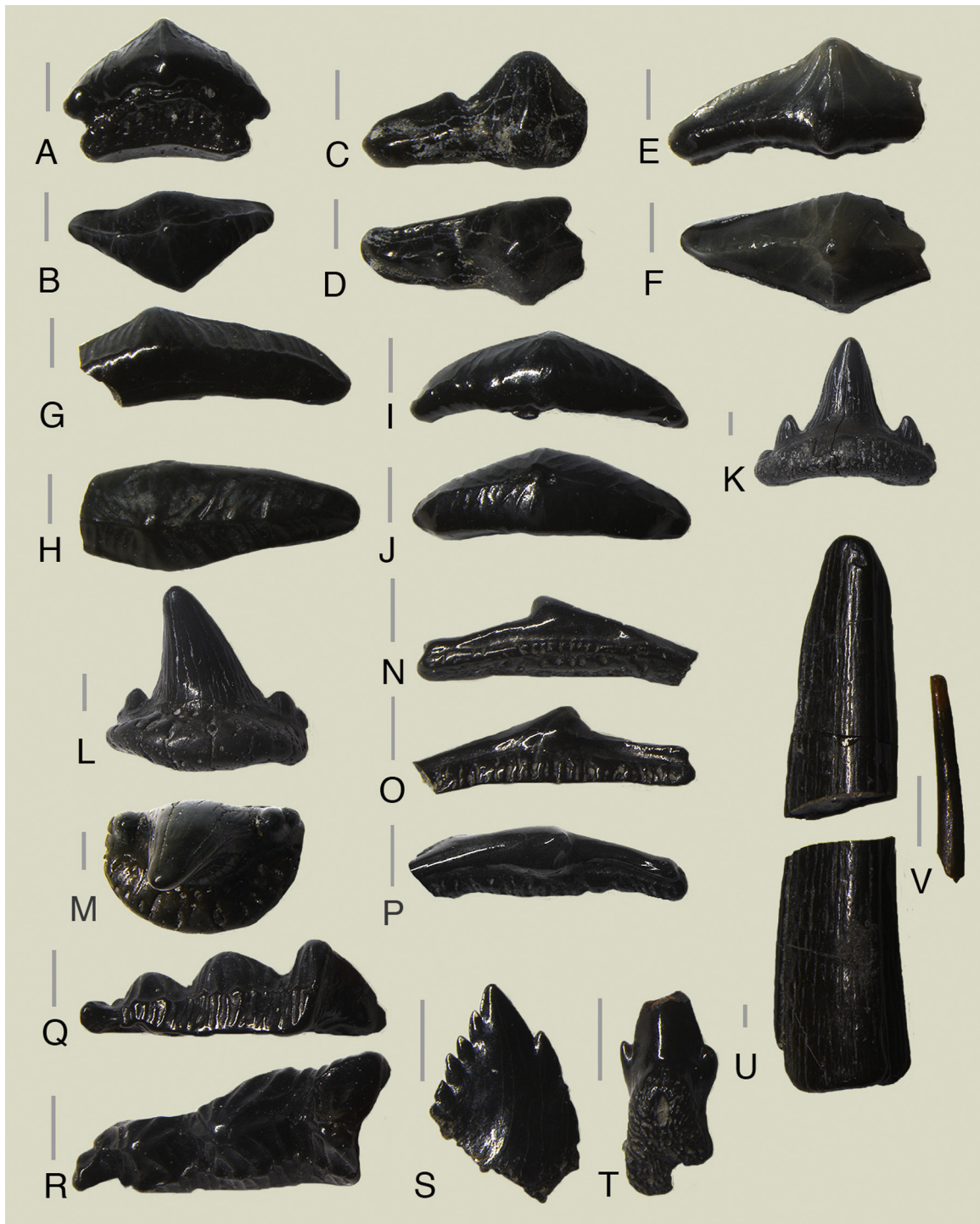
#### 4.1. Chondrichthyans

Seven species of sharks have been identified in material collected from the M4–M5 motorway, all having been recorded previously in the British Rhaetian (Duffin, 1999).

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

Teeth from the hybodont shark *L. minimus* represent the majority of fossils in the collection, as they do in several other quantitative studies of the Rhaetian (Lakin et al., 2016). This shark shows monognathic heterodonty characterized by five distinct tooth morphotypes: anterior, anterolateral, lateral, posterolateral, and posterior (Duffin, 1999), all of which are presented in this study (Fig. 4A–J).

Anterior teeth of *L. minimus* are diamond-shaped in occlusal view due to the bulbous labial peg. In lateral view the mesio-distal parts are steeply angled to form a central cusp with a minuscule lateral cusplet on either side (Storrs, 1994). This makes the base of the tooth deeply concave where the porous root is sometimes attached, running parallel to the cusps with a flat base (BRSUG 29371-1-1803; Fig. 4A). The occlusal crest divides the crown into lingual and labial faces and is elevated throughout the length of anterior teeth (BRSUG 29371-1-1803; Fig. 4B). Bifurcating vertical ridges run from each cusp down the labial and lingual faces of the crown and terminate at a horizontal ridge that runs the length of the tooth on top of the crown shoulder. The largest anterior tooth



**Fig. 4.** Chondrichthyan teeth from the M4–M5 motorway junction. (A and B) *Lissodus minimus* anterior tooth (BRSUG 29371-1-1803) in labial (A) and occlusal (B) views. (C and D) *Hybodus cloacinus* anterolateral tooth (BRSUG 29371-1-1785) in labial (C) and occlusal (D) views. (E and F) *Lissodus minimus* posterolateral tooth (BRSUG 29371-1-1785) in side (E) and occlusal (F) views. (G and H) *Lissodus minimus* lateral tooth (BRSUG 29371-1-1785) in labial (G) and occlusal (H) views. (I and J) *Lissodus minimus* posterior tooth (BRSUG 29371-1-1788) in side (I) and occlusal (J) views. (K) *Rhomphaiodon minor* anterior tooth (BRSUG 29371-1-2013-20) in lingual view. (L and M) *Rhomphaiodon minor* anterior tooth (BRSUG 29371-1-301) in lingual (L) and occlusal (M) views. (N, O and P) *Duffinselache holwellensis* tooth (BRSUG 29371-1-1701) in labial (N) lingual (O) and occlusal (P) views. (Q and R) *Hybodus cloacinus* anterior tooth (BRSUG 29371-1-1746) in lingual (Q) and occlusal (R) views. (S) *Pseudodalatias barnstonensis* lower median tooth (BRSUG 29371-1-1875-2) in labial view. (T) *Pseudodalatias barnstonensis* central upper tooth (BRSUG 29371-1-1876) in lingual view. (U) *Nemacanthus monilifer* fragmented fin spine (BRSUG 29371-1-291) in side view. (V) *Pseudocetorhinus pickfordi* gill raker (BRSUG 29371-1-1278-10) in side view. All scale bars are 0.5 mm.

in the collection is 750  $\mu\text{m}$  in height from the tip of the central cusp to the base of the crown, and 2 mm mesiodistally.

An anterolateral tooth from the collection is 2.4 mm long mesiodistally and carries three cusps that decrease distally in circumference; 0.8 mm in height at the mesial cusp, 0.72 mm at

the central cusp, and 0.5 mm at the distal cusp (BRSUG 29371-1-1785; Fig. 4C–D). In occlusal view, these cusps are closer along the lingual edge. The labial side in occlusal view is asymmetrically curved, as the mesial end is 1.1 mm wide at the largest cusp and narrows to 0.5 mm wide at the distal cusp. Each cusp has a rounded



tip with strong bifurcating ridges that run to the crown shoulder, and then descend laterally and non-branching to the base. The crown shoulder for each cusp forms a prominent horizontal ridge.

Lateral teeth are longer than anterior teeth and show less angulation of mesio-distal parts in lateral view. Lateral teeth measure 1.2 mm in height from the tip of the central cusp to the base of the tooth (BRSUG 29371-1-1785; Fig. 4E). Although this tooth exhibits a break at its mesial end, it measures 2.6 mm in length mesio-distally (BRSUG 29371-1-1785; Fig. 4F). Lateral teeth possess an occlusal crest with an associated central cusp that is more prominent than in other morphotypes. The central cusp also has bifurcating vertical ridges that run down to the horizontal ridge. A prominent labial peg is situated adjacent to the horizontal ridge. Elongate morphotypes such as this one are most often broken at the distal end of the central cusp, but both fragments are easily identified from the bifurcating vertical ridges and concave nature of the tooth base.

Posterolateral teeth have a similar width-to-length ratio as lateral teeth, but are less angulated in lateral view, giving rise to a less concave base. A typical example (BRSUG 29371-1-1785; Fig. 4G and H) measures 950 µm in height from the tip of the central crown to the base of the tooth and 2.8 mm in length mesio-distally, although one end is broken. The central cusp is laterally flattened when compared to lateral teeth and bears bifurcating ridges that run to the horizontal ridge, which is situated more closely adjacent to the cusp. The labial peg is much less prominent in posterolateral teeth, with a gentle convex shape to the labial and lingual faces.

Posterior teeth exhibit a very subtle curve in lateral view that reaches one central flattened cusp. One specimen (BRSUG 29371-1-1788; Fig. 4I and J) measures 0.74 mm in height from the tip of the central crown to the base of the tooth and 2.9 mm in length mesio-distally. The occlusal crest, bifurcating vertical ridges and horizontal ridge are less pronounced than in other morphotypes, and the labial peg is very weak.

**Remarks.** Remains of *Lissodus*-like sharks have been reported from the Upper Devonian to Upper Cretaceous (Duffin, 1985, 2001). In the original description, Agassiz (1839) named these teeth *Acrodus minimus*, but they were later assigned to the genus *Lissodus*, which had accumulated several species previously identified as *Acrodus* and *Polyacrodus* (Fischer, 2008). The genus *Lonchidion* was previously seen as synonymous with *Lissodus* (Duffin, 1985), but it is now considered a separate genus (Duffin, 1985; Rees and Underwood, 2002, 2008).

The five *Lissodus* tooth morphotypes and their intermediates are much longer than they are wide, and bear a low crown suitable for benthic-durophagous feeding in marine and non-marine environments (Fischer et al., 2009). They are convex at the base of the tooth when no roots are present, and the root varies in depth. At the base of the central crown, a perpendicular labial peg can be seen clearly in occlusal view on the anterior, anterolateral and lateral teeth, but is more discreet in posterolateral and posterior teeth. Tooth replacement in this durophagous fish would require multiple rows of teeth growing in succession to those being used. The labial peg may have acted as a stabilizer to teeth growing in succession, preventing their movement and thus any usage before necessary (Rees and Underwood, 2002).

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

The second most abundant species is the neoselachian shark *R. minor*. Teeth from this species have an upright, triangular central cusp that is characterized by strong vertical ridges running from the tip of the cusp to the base of the crown (BRSUG 29371-1-2013-20, BRSUG 29371-1-301; Fig. 4K–M). There may be one or two

lateral cusplets on either side of the central cusp that are much smaller in size than the central cusp itself. All cusps are located close to the labial side and curve lingually, presumably to reduce the chance for prey to escape. If present, a porous root forms a bulbous lingual torus and remains flat on the labial side of the tooth (Storrs, 1994). The largest *R. minor* teeth in the M4–M5 collection measure 2.5 mm in height at the central cusp and 2.5 mm mesio-distally at the base of the lateral cusplets.

**Remarks.** This species is well known in the Rhaetian and the early Jurassic, and there have been further records (requiring verification) from the Ladinian and Norian (Duffin, 1993a; Duffin and Delsate, 1993, p. 38). ‘*Hybodus*’ *minor* was originally described from fin spines by Agassiz (1837) and the name was later applied to isolated teeth belonging to several tooth morphotypes (Storrs, 1994). It is still not certain whether fin spines assigned to this genus can be associated with any teeth. It was first suggested by Maisiey (1977) that ‘*Hybodus*’ *minor* teeth might be from a neoselachian shark rather than a hybodont. Noted as similar to teeth of *Rhomphaiodon nicolensis* by Duffin (1993b), they were reassigned to *Rhomphaiodon* (Synchodontiformes) by Cuny (2005) based on both tooth morphology and enameloid microstructure.

#### 4.1.3. *D. holwellensis* (Duffin, 1998b)

*D. holwellensis* teeth are long and slender and more gracile than most shark teeth in this collection. There are four complete teeth and an additional fragment representing *D. holwellensis* in the M4–M5 collection, the largest measuring 2 mm mesiodistally and 0.4 mm in height from the central cusp to the base of the crown (BRSUG 29371-1-1701; Fig. 4N–P). There is a slight mesiodistal lingual curvature. The central cusp sits slightly distally from the centre of the tooth and is inclined distally. There are no accessory cusplets or lateral cusplets. Non-branching vertical ridges begin at the crown shoulder and run to the base on both labial and lingual sides of the crown. The root is equal in height (0.4 mm) to the crown and is directed lingually with a flat base. On the labial side the root is divided into two, the lower portion being more concave and having more vascular foramina (Duffin, 1998b).

**Remarks.** *D. holwellensis* is known only from the Rhaetian. Teeth from this species were previously classified under the hybodont genus ‘*Polyacrodus*’ by Duffin (1998b), and were reassigned to *Duffinselache* within the Neoselachii by Andreev and Cuny (2012), based on the presence of triple-layered enameloid microstructure.

#### 4.1.4. *H. cloacinus* (Quenstedt, 1858)

*H. cloacinus* is represented by a single morphotype in the M4–M5 collection. A partial crown of this taxon measures 2.3 mm in length mesiodistally and 1.2 mm in height from the largest cusp to the base of the crown (BRSUG 29371-1-1746; Fig. 4Q and R). Three cusps are present on the fragment, but the tooth is broken and heavily abraded. Strong vertical ridges descend from the cusp apices to the crown shoulder on both the labial and lingual sides. An occlusal crest runs along the middle of the tooth through the tips of the cusps. A horizontal ridge meets the crown shoulder on both the labial and lingual sides. Along the horizontal ridge there is a labial node.

**Remarks.** Originally named *Polyacrodus cloacinus* (Quenstedt, 1858), this generic identification is uncertain, and the taxon was referred to *H. cloacinus* by Duffin (1999). The species has been recorded from the Rhaetian of Germany, France, Britain and

Belgium through to the Sinemurian of Lyme Regis (Duffin and Delsate, 1993). This species is postulated also to have fin spines, but these cannot presently be distinguished from those of *Lissodus* or *R. minor* (Storrs, 1994).

#### 4.1.5. *P. barnstonensis* (Sykes, 1971)

Two morphotypes of the dignathic heterodont *P. barnstonensis* are represented in the M4–M5 collection. The lower parasymphyseal tooth (BRSUG 29371-1-1875-2; Fig. 4S) is very narrow labio-lingually and measures 1.25 mm in height at the central cusp and 0.9 mm mesiodistally. Non-branching lateral striations accent the labial and lingual sides, and these appear 'crack-like' (Sykes, 1971). This tooth is heavily abraded on the mesial side and therefore only one worn serration is evident. On the distal end there are four serrations, each with a translucent tip. The central cusp has a slight distal curvature that becomes more pronounced in posterior teeth of the lower jaw. Teeth of the lower jaw strongly resemble this morphotype and show more serrated edges on the distal end (Tintori, 1980).

The central upper tooth (BRSUG 29371-1-1876; Fig. 4T) is heavily abraded at the tip of the central cusp but measures 1.2 mm in height and 0.6 mm mesiodistally. The central cusp is straight and conical in shape, with one small lateral cusplet protruding from each mesial and distal end. A porous root is present with a large lateral median canal through which blood vessels pass to the next series of teeth (Sykes, 1971). Furthermore, teeth of the upper dentition show an increase in distal curvature of the central cusp.

**Remarks.** Teeth of this species were originally described as '*Dalatiidae*' by Sykes (1971, 1974) and are known from the Ladinian, Norian, and Rhaetian (Tintori, 1980; Storrs, 1994). *P. barnstonensis* teeth are peculiar as they resemble both extant Dalatiidae and extinct Hybodontiformes in their serrations (Andreev, 2010). Teeth of this species were classified under Selachii as *Pseudodalatias* according to their single-crystalline enameloid (Reif, 1978). The systematic position of this genus is still unknown and is the subject of considerable discussion (Cappetta, 1987, 2012; Botella et al., 2009). The dignathic morphology of these teeth suggests a 'cutting-clutching' feeding behaviour (Botella et al., 2009).

#### 4.1.6. *Nemacanthus monilifer* (Agassiz, 1837)

A single partial fin spine, in addition to a separate fragment, represents *N. monilifer* in the M4–M5 collection (BRSUG 29371-1-291; Fig. 4U). It is presumed to have broken during handling as the striations and ornamentation align perfectly. The fragment measures 12.4 mm in length and 2.9 mm in width at the proximal end. The spine is triangular in cross-section, with the posterior end being wider (Storrs, 1994). An enamelled keel runs the preserved length of the two fragments along the anterior margin of the spine. The posterior portion of the spine has a central groove running the entire length of the fin spine. Intermittent non-branching striations representing unroofed mantle canals run from the proximal to the distal end. There are no denticles along the postero-lateral margins of the spine.

**Remarks.** *N. monilifer* was named by Agassiz (1837) for fin spines found at Aust Cliff, and is synonymous with *N. filifer* and *N. minor* (Storrs, 1994). These fin spines slightly resemble those of *Hybodus* in the striations, but are considered more structurally similar to those of *Palaeospinax* since they are without node ornamentation (Maisey, 1975, 1977; Duffin, 1982). No teeth have been assigned to this species, as *Nemacanthus*, *Palaeospinax*, and *Hybodus* are all found in association with one another, and so isolated teeth and spines cannot be associated. Consequently the systematic position of *Nemacanthus* is very uncertain.

#### 4.1.7. *Pseudocetorhinus pickfordi* (Duffin, 1998a)

The M4–M5 collection contains a single gill raker from *P. pickfordi*, which measures 0.4 mm long (BRSUG 29371-1-1278-10; Fig. 4V). It is long and slender, laterally flattened, and has a brown tip.

**Remarks.** *P. pickfordi* represents the earliest basking shark and is known from several Rhaetian sites (Allard et al., 2015; Korneisel et al., 2015; Nordén et al., 2015). It possesses oral teeth resembling other extinct basking sharks (Neoselachii: Galeomorphii: Cetorhinidae) (Duffin, 1998a). Its position as the earliest planktivorous basking shark has been disputed based on the lack of resemblance of oral teeth to extant forms, such as *Cetorhinus maximus* (Shimada, 2015). However this species is also associated with gill rakers that would aid in passive planktonic filter feeding.

#### 4.1.8. Other selachian remains

Numerous small (<0.6 mm) chondrichthyan denticles were found in the collection in addition to a smaller number of unidentifiable prismatic cartilage and neoselachian vertebrae. Previous studies have assigned denticles to morphotypes, but further research is required to assign denticles to a genus or species (Duffin, 1999). Denticles found in the M4–M5 collection were not counted or assigned a morphotype and are consequently not described further.

### 4.2. Osteichthyans

Four actinopterygian taxa were identified from the M4–M5 collection, all typical of the British Rhaetian (Duffin, 1999).

#### 4.2.1. *G. albertii* (Agassiz, 1835)

The most common actinopterygian in the M4–M5 collection is *G. albertii*, represented by teeth and scales. These teeth have a very large range in size, with some measuring less than 0.35 mm and some as large as 5.8 mm in height. Smaller teeth are very gracile in their conical shape and have a smooth translucent tip that is roughly 1/6 of the height of the tooth (BRSUG 29371-1-199; Fig. 5A). They have very weak ornamentation of vertical non-branching striations. A jaw fragment with one complete tooth and the base of another tooth was also found in the collection (BRSUG 29371-1-90; Fig. 5B). The attached root is heavily vascularized and measures 1.7 mm from the base of the tooth to the base of the root.

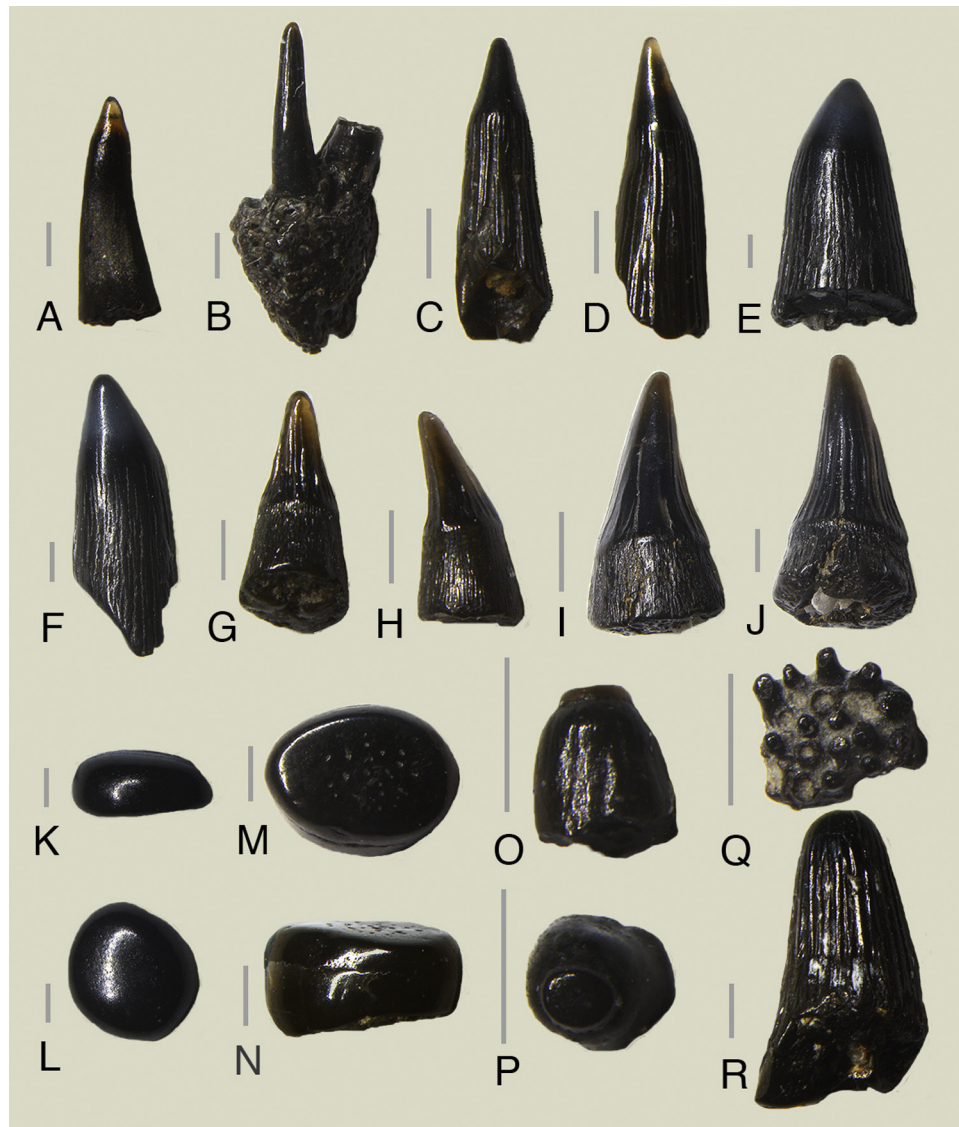
**Remarks.** This taxon was erected by Agassiz (1835) for remains from the Muschelkalk of Germany and the Rhaetian bone bed of Wickwar, near Bristol. Scales and teeth of *G. albertii* are ubiquitous in Rhaetian strata, and the scales show a considerable amount of morphological variation (Duffin and Gazdzicki, 1977; Mears et al., 2016).

#### 4.2.2. *S. acuminatus* (Agassiz, 1835)

Bony fish of the genus *Severnichthys* were large predators that roamed the seas in the Late Triassic. They possess two distinct tooth morphotypes, with several intermediates. Both of these morphotypes were originally assigned to separate taxa, '*Birgeria acuminata*' and '*Saurichthys longidens*', respectively. Dentary bones from the Westbury Formation of Aust Cliff, UK later confirmed an association between the morphotypes, and '*B. acuminatus*' and '*S. longidens*' are now treated as synonyms of *S. acuminatus* (Storrs, 1994).

Teeth of the '*Saurichthys longidens*' morphotype (Fig. 5C–F) are upright, conical, and sit perpendicular to the jaw (Duffin, 1999). They have a large range in size, but smaller teeth (BRSUG 29371-1-142, Fig. 5C and D, ~2.3 mm) are more slender and have a smooth





**Fig. 5.** Actinopterygian and marine reptile teeth from the M4–M5 motorway junction. (A) *Gyrolepis albertii* tooth (BRSUG 29371-1-199). (B) *Gyrolepis albertii* jaw fragment (BRSUG 29371-1-90) in side view. (C and D) '*Saurichthys longidens*' type of *Severnichthys acuminatus* tooth (BRSUG 29371-1-142) in side view. (E and F) '*Saurichthys longidens*' type of *Severnichthys acuminatus* tooth (BRSUG 29371-1-2013-19) in side view. (G) '*Birgeria acuminata*' type of *Severnichthys acuminatus* (BRSUG 29371-1-222) in side view. (H) '*Birgeria acuminata*' type of *Severnichthys acuminatus* (BRSUG 29371-1-223) in side view. (I and J) '*Birgeria acuminata*' type of *Severnichthys acuminatus* (BRSUG 29371-1-2013-17) in side view. (K and L) *Sargodon tomicus* tooth (BRSUG 29371-1-2013-16) in side (K) and occlusal (L) views. (M and N) *Sargodon tomicus* tooth (BRSUG 29371-1-1563) in occlusal (M) and side (N) views. (O and P) '*Lepidotes*' sp. tooth (BRSUG 29371-1-1551) in side (O) and occlusal (P) views. (Q) Actinopterygian jaw fragment (BRSUG 29371-1-89) in occlusal view. (R) *Ichthyosaurus* sp. (BRSUG 29371-1-2013-15) in side view. All scale bars are 0.5 mm.

translucent acrodin cap that accounts for roughly a third of the tooth height. Larger '*S. longidens*' teeth (BRSUG 29371-1-2013-19; Fig. 5E and F, ~3.8 mm) have a more robust base and become gradually thinner towards the tooth cap. The caps of larger teeth are less translucent, and instead exhibit a white colouring. '*S. longidens*' teeth have fine, non-branching, vertical striations that terminate at the tooth cap ridge.

The '*Birgeria acuminata*' (BRSUG 29371-1-222, BRSUG 29371-1-223, BRSUG 29371-1-2013-17; Fig. 5G–J) teeth are also conical and sit perpendicularly on the jaw, but many possess a distal curvature in the tooth cap. The tooth cap accounts for roughly half of the tooth height, and has a strong circumferential ridge at the base of the cap. Numerous fine striations run vertically below the circumferential ridge, while thicker and more prominent vertical striations begin at the circumferential ridge and run to the apex of the tooth. Similar to the '*Saurichthys longidens*' type, '*Birgeria*' teeth also have a translucent tip.

#### 4.2.3. *S. tomicus* (Plieninger, 1847)

*S. tomicus* shows three types of tooth morphology: incisiform, hemispherical, and pointed. Eight of the hemispherical teeth were found in the M4–M5 collection and are either circular or ovate in shape (Fig. 5K–N). One hemispherical tooth is 2 mm across in occlusal view (BRSUG 29371-1-2013-16; Fig. 5K and L). Its crown is dome-shaped and smooth, similar to those of an adult specimen. The second hemispherical tooth measures 1.8 mm across in occlusal view and is more ovate in shape (BRSUG 29371-1-1563; Fig. 5M and N). In lateral view this crown is very flat and the surface is pitted where antemortem wear has breached the surface tissue exposing clusters of dentine canals beneath.

**Remarks.** *S. tomicus* is a semionotid that was named by Plieninger (1847) and is known from entire specimens and isolated teeth from the Norian and Rhaetian across Europe (Tintori, 1983). The hemispherical shape of the teeth indicates *Sargodon* was a durophage.

There is evidence that tooth morphology differs in each ontogenetic stage, unlike the usual situation in other fish such as predatory sharks (Tintori, 1998).

#### 4.2.4. *Lepidotes* sp. (Agassiz, 1832)

There is one *Lepidotes* tooth in the M4–M5 collection that measures 0.5 mm in height from the apex of the crown to the base and 0.32 mm across in occlusal view (BRSUG 29371-1-1551; Fig. 5O and P). It has very smooth non-branching lateral striations.

**Remarks.** *Lepidotes* is another semionotid known from complete specimens and isolated teeth and is found nearly worldwide from the Rhaetian to the Late Cretaceous (Jain, 1983, 1984; Thies, 1989). Further research is required to confidently identify teeth from the Rhaetian as belonging to Semionotiformes, and in particular those assigned to *Lepidotes*. This genus is well documented in the Jurassic from a plethora of scales, but no scales have been found in Rhaetian sections (Duffin, 1999). *Lepidotes* teeth are characterized by a small apical tubercle that sits asymmetrically on the occlusal face (Storrs, 1994). Its morphology has perhaps led to the over assignment of generally bulbous teeth to this genus and the genus *Sphaerodus*, which is a junior synonym of *Lepidotes* (Storrs, 1994). In addition it is often difficult to identify *Lepidotes* to species level, as there are 19 taxa. *Lepidotes* has been reported in the Rhaetian section of Marston Road by Moore (1867), in various Rhaetian sections studied by Richardson (1911), and in the Rhaetian of Nottinghamshire by Sykes (1979). The specimen identified here as *Lepidotes* is based on criteria used by Allard et al. (2015), Korneisel et al. (2015), and Nördén et al. (2015) in their Rhaetian bone bed studies.

#### 4.2.5. Other osteichthyan remains

Another osteichthyan jaw fragment was found in the collection, but could not be identified. It measures 0.5 mm mesiodistally (BRSUG 29371-1-89; Fig. 5Q). Six teeth are broken on the mesial edge, and there is evidence of at least 11 heavily worn teeth distal to the mesial row of teeth. The collection also includes numerous well-preserved fin rays, scales, and central vertebral rings that could not be identified to a specific osteichthyan taxon. Consequently these remains were not counted and are not further described here.

#### 4.3. Marine reptiles

Isolated marine reptile teeth identified as *Ichthyosaurus* sp. were found in material collected along the M4–M5 motorway and are typical of the Rhaetian basal bone bed. Other reptile remains such as ichthyosaur vertebrae, plesiosaur vertebrae or teeth, or bones of *Pachystropeus* were not identified.

##### 4.3.1. Undetermined *Ichthyosaurus* sp.

Two conical teeth and an additional tooth fragment were identified as belonging to *Ichthyosaurus*. The largest tooth measures 2.9 mm in height from the base to the apex and 1.6 mm in width at the base (BRSUG 29371-1-2013-15; Fig. 5R). It is heavily worn, has very strong vertical ridges that run the entire length, and a relatively narrow pulp cavity exposed in the broken base.

**Remarks.** Disarticulated *Ichthyosaurus* remains, such as isolated vertebrae, ribs, paddle bones, and teeth, are occasionally found in the Rhaetian, but are not easily identified to species level (Storrs, 1994). The Late Triassic was a significant time for these large marine predators. Dominating the seas from the Early Triassic, at the end of the Triassic their numbers were reduced to just three or four lineages (Thorne et al., 2011; Fischer et al., 2014), before the neoichthyosaurs recovered in the Early Jurassic.

#### 4.4. Other fossilized remains

##### 4.4.1. Coprolites

Although previously described by others as plant materials, Buckland recognized these enigmatic structures as fossil faeces in 1829 (Duffin, 2009). The basal bone beds surrounding the M4–M5 junction are rich in coprolites (most >2 mm), which is to be expected in a Rhaetian basal bone bed. As proposed by Duffin (1979), coprolites of the Rhaetian can be separated by morphotype and assigned to their creators. Although coprolites were not assigned to morphotype in this study, most were of spiral form and were likely produced by selachians (BRSUG 29371-1-2013-23(-29); Fig. 6A–N). The spiral pattern extends within the coprolite, and specimens often break across flat planes corresponding to the spiral faces (e.g. Fig. 6A, B, F, M, N). Broken surfaces (e.g. Fig. 6C) show irregular internal structures, but these cannot be identified as particular scales, teeth, or bones.

From the basal bone bed 02-24, 202 coprolites were measured across their width. The measured faecal structures can be divided into three size categories of 5 mm, 7 mm, and 10 mm maximum diameter (Fig. 7). These size categories perhaps originate from the varied size and diet of their originators, but assignments to particular genera are not made here.

The M4–M5 coprolites differ from those reported from the basal Rhaetian bone bed at Hampstead Farm Quarry (Mears et al., 2016, Fig. 16) in several ways. Our specimens are black, theirs generally white, reflecting greater phosphatisation of the Motorway Junction specimens. In addition, the M4–M5 specimens are straight-sided cylinders with rather blunt, rounded terminations, whereas many of the Hampstead Farm coprolites have more pointed terminations. The M4–M5 specimens compare well morphologically with those assigned to Type 2 of Duffin (1979).

##### 4.4.2. Invertebrates

The bone bed lying at the top of the Westbury Formation in borehole 38 was not introduced to acetic acid prior to sieving and contains an abundance of invertebrate fossils such as ophiuroids, and echinoid plates and spines. These invertebrate remains are most certainly identifiable to their respective taxa, but were not the focus of this study.

##### 4.4.3. Unidentified bones

The majority of the fossilized vertebrate remains are fragmented bones displaying no anatomical characters and have consequently not been included in this study.

## 5. Discussion

### 5.1. Faunal composition and comparison

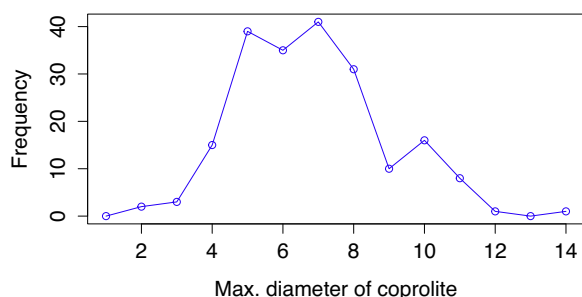
The M4–M5 motorway collection includes 2693 identifiable fossils in total, with 2425.5 from the basal bone bed and 267.5 from the bone bed at the top of the Westbury Formation (Table 1). Fractions represent partial examples of large teeth. It is unknown how much sediment was collected from each borehole and therefore the density of fossils in the sediment could not be calculated (cf. Allard et al., 2015). However, the higher number of fossils found in the basal bone bed is not regarded as a result of sampling bias.

#### 5.1.1. Comparison of fossil sizes

Cumulative values from bone beds at the top and base of the Westbury Formation (omission of 02-6 at top of Cotham Member) were analyzed using a Pearson's Chi-squared test (Table 2). There is a highly significant association ( $\chi^2$ -squared = 451.54,  $df$  = 3,  $p$  < 0.001) between the distributions of microvertebrate fossil



**Fig. 6.** Coprolites from the M4–M5 motorway junction. (A and B) Coprolite (BRSUG 29371-1-2013-23) showing transverse section (A) and side view (B). (C and D) Coprolite (BRSUG 29371-1-2013-24) showing transverse section (C) and side view (D). (E and F) Coprolite (BRSUG 29371-1-2013-25) in side views. (G and H) Coprolite (BRSUG 29371-1-2013-26) in side views. (I and J) Coprolite (BRSUG 29371-1-2013-27) in side views. (K and L) Coprolite (BRSUG 29371-1-2013-28) in side views. (M and N) Coprolite (BRSUG 29371-1-2013-29) in side views. All scale bars are 1 cm. Photographs credited to Hollie Morgan.



**Fig. 7.** Frequency polygon showing maximum diameter of coprolites from the M4–M5 motorway junction. Sample size of 202 coprolites from the base of the Westbury Formation of borehole 120, horizon 02-24.

**Table 1**

Table of fossils identified to a species level from bone beds at the base and the top of the Westbury Formation.

	WF-basal	WF-top
<b>ACTINOPTERYGII</b>		
<i>'Birgeria acuminata'</i>	143	27
<i>Gyrolepis albertii</i>	292	212
<i>Sargodon tomicus</i>	7	1
<i>'Saurichthys longidens'</i>	144.5	15.5
<i>Lepidotes</i> sp.	1	0
Total	587.5	255.5
<b>CHONDRICHTHYES</b>		
<i>Lissodus minimus</i>	1098.5	8
<i>Rhomphaidon minor</i>	720.5	0.5
<i>Duffinselache holwellensis</i>	1	3.5
<i>Hybodus cloacinus</i>	3	0
<i>Pseudodolatias barnstonensis</i>	3	0
<i>Nemacanthus monilifer</i>	1.5	0
<i>Pseudocetorhinus pickfordi</i>	1	0
<i>Ichthyosaurus</i> sp.	2.5	0
Total	1831	12
Overall total	2425.5	267.5

**Table 2**

Contingency table of fossil sizes identified to a species level from respective bone beds at the base and the top of the Westbury Formation.

	–650 $\mu$ m + 180 $\mu$ m	–850 $\mu$ m + 600 $\mu$ m	–2 mm + 850 $\mu$ m	+2 mm
<i>WF-top</i>				
M5.co.02-5	96.5	4	0	0
M5.co.02-6	6.5	0	0	0
M5.co.02-20	66.5	15	0	3
M5.co.01-3	19.5	5.5	0	0
M5.co.02-23	33.5	15	2.5	0
Total	222.5	39.5	2.5	3
<i>WF-basal</i>				
M5.co.02-21	0	2	1	0
M5.co.02-24	1	0	0	59
M5.co.01-1	435	823.5	182.5	0
M5.co.02-4	12.5	47.5	53.5	0.5
M5.co.02-14	0	91	25.5	0.5
M5.co.02-15	0	311.5	106	8.5
Total	448.5	1275.5	368.5	68.5
Overall total	671	1315	371	71.5

size and bone bed horizon. Fossils from the base of the Westbury Formation are predominantly  $>600 \mu$ m in size, while fossils from the top of the formation are primarily  $<600 \mu$ m in size (Table 1). This difference could reflect biology or geology.

Among biological reasons for the marked difference in mean sizes between the bone beds could be evolution or ecology. Perhaps the assemblage of organisms sampled in the higher bone bed evolved to be smaller than earlier in the Rhaetian, or there might be some ecological reason that smaller organisms prevailed. However, these size measurements do not assess actual body size, but are merely relative sizes of preserved teeth. The size differential much more likely represents a taphonomic sorting effect, whereby the basal bone bed was deposited by higher energy currents than the later bone beds. The storms associated with the initial Rhaetian transgression in this case might have been more energetic, and so capable of transporting materials larger than 0.6 mm, and often  $>2.4$  mm. Fossils deposited at the base of the formation therefore best represent larger predators that were



transported from a benthic marine environment. This would also explain the large number of invertebrates that were found in the 02-6 assemblage, and the lack of abrasion seen in many bone beds higher in the stratigraphic sequence. Further analysis of rare earth element signatures might inform the length of transport and method of deposition (cf. Trueman and Benton, 1997).

### 5.1.2. Analysis of species composition

Of the 13 species present in the basal bone bed, seven are shared with the bone bed at the top of the Westbury Formation. Species absent in the higher fossiliferous layer are *H. cloacinus*, *P. barnstonensis*, *P. pickfordi*, *Lepidotes* sp., *Ichthyosaurus* sp., and *N. monilifer*. Much reduced is *R. minor*, and significantly more rare are *L. minimus*, *D. holwellensis*, and *S. tomicus*. Despite these differences, the two bone bed samples are highly similar in terms of their large number of shared species as indicated by a high percentage of similarity (Sørensen-Dice coefficient, 0.7).

The higher species diversity of the basal bone bed is confirmed by calculation of Simpson's Index of Diversity (DI), with a value of 0.684, compared to 0.359 for the upper Westbury Formation bone bed. The Shannon-Wiener Diversity Index (SWDI), which measures species richness and evenness (H), produces an H value of 1.365 for the basal bone bed and 0.775 for the upper Westbury Formation bone bed. This indicates that the basal bone bed is more species rich, and relative abundances are more evenly distributed amongst the species. For species evenness (I), the basal bone bed has a value of 0.052, and the upper bone bed 0.202, confirming the lower species evenness of the former. This reflects the large number of specimens identified as *L. minimus* and *Hybodus minor* (Table 1).

As the SWDI calculation for evenness (I) indicated, there is a transition from mostly chondrichthyans (75.6%) in the basal bone bed, to mostly actinopterygians (95.5%) in the upper Westbury Formation bone bed (Fig. 8). This trend was further analyzed taxonomically by comparing the observed numbers of Actinopterygii, Chondrichthyes, and marine reptiles by using SWDI. This produced an H value of 0.562 for the basal bone bed, and 0.183 for the upper bone bed, meaning there is 56% certainty that a fossil chosen at random from the basal bone bed will be a chondrichthyan, and that there is 18% certainty that a fossil chosen at random from the upper bone bed will be an actinopterygian. The lower level of certainty for the higher bone bed probably reflects the substantial decrease in relative abundance of fossils, and consequently a smaller sample size than the basal bone bed.

A limiting factor in this study is the inability to compare faunal compositions of the higher bone beds of different boreholes because of their small sample sizes. Further limiting factors are the ontogenetic stages of the organisms represented, the variation in numbers of teeth between species, and their respective modes of tooth replacement. There is potential for overestimation of

predatory fish and shark numbers because they replace their teeth more frequently than some herbivores and durophages (Tintori, 1998). However, we propose the above quantitative findings as general evidence of ecological change through geological time.

### 5.2. Multiple Rhaetian bone beds

Our study leads to consideration of the competing explanatory models for multiple Rhaetian bone beds. Sykes (1977) argued that only the basal bone bed was primary, and even that one contained 'pre-fossilised' elements that had been fossilized, eroded, and finally transported before their final deposition in the basal Westbury Formation bone bed. This view was also promoted by Duffin (1980) and Martill (1999), but queried by Antia (1978), who stated each bone bed is different simply because they are of different ages and sedimentary regimes.

Sykes (1977) reflected his views in his classification of the Rhaetian-age bone beds, as either primary, secondary, scatter, or trace bone beds depending upon the depositional characters and amount of abrasion and fragmentation of fossils. This classification has been questioned, as the evidence for transport and abrasion differ between well-studied sites such as Aust and Westbury Garden Cliff (Trueman and Benton, 1997). A transgressive lag depositional model was proposed by MacQuaker (1994) and Martill (1999), suggesting that transgressions accumulated organic debris that was previously deposited, forming the basal bone bed and those higher in the stratigraphic sequence. There is, however, no evidence that all or most of the microvertebrates are reworked from older beds, nor that the amount of abrasion increases up through successive Rhaetian bone beds. In addition, bone beds higher in the formation are probably not part of the same stratigraphic event, as the Westbury Formation accounts for roughly 2 Myr of the Rhaetian. Reports on bone beds higher in the sequence have also varied in number, and there has yet to be any evidence of continuity in nearby locations (Roberts, 1862; Sykes, 1977; Allard et al., 2015). The inability to correlate these bone beds suggests that they were not deposited by regional transgressions, contrary to the suggestion of Martill (1999).

Our study confirms the rejection of the Sykes' (1977) proposal. An upwards reworking of the basal bone bed would presumably replicate fossiliferous layers close above the basal bone bed. In fact, the topmost Westbury Formation bone bed presumably followed some 0.3–1 Myr after the basal bone bed and appears to be a laterally continuous event (Fig. 3) (MacQuaker, 1999). Sustaining a sedimentary basinal system that strictly recycled older bone beds over such a time span seems unlikely. There are two further, and more decisive reasons to reject the Sykes (1977) model. First, bones and teeth in higher bone beds show no sign of additional abrasion or breakage of the specimens when compared to those in the basal bone bed. In fact, some delicate teeth and bones are in better condition than their counterparts from the older bed. Second, if these 'secondary' beds were a result of shoreward reworking, taxa would be represented in a non-biased fashion. As we note here (Fig. 8), the species composition and sizes differ substantially between the two bone bed horizons. Both of these findings would be hard to explain by reworking, especially the introduction of novel taxa not seen at all in the basal bone bed. Both findings are therefore seen to support the hypothesis that bone beds originated from separate stratigraphic events to represent different ecological communities.

It is likely that the bone beds found at the top of the Westbury Formation in this study are equivalent to the Upper *Pecten*-Beds described at several localities by Short (1904). However, the Upper *Pecten*-Bed at the nearby Aust Cliff exhibits a high number of invertebrate remains, coprolites, *Ichthyosaurus*, *Plesiosaurus*, and

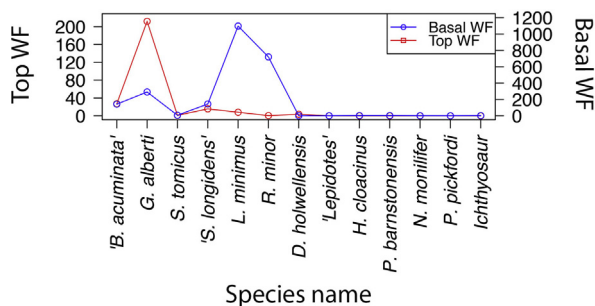


Fig. 8. Faunal composition of fossiliferous beds found at the base and top of the Westbury Formation surrounding M4–M5 motorway junction. Species identified in the (A) upper and (B) basal bone bed of the Westbury Formation based on identifiable material (teeth/jaw fragments) to a genus or species level. Sample sizes are 267.5 for the upper bone bed and 2425.5 for the basal bone bed.

*Rhomphaiodon*. Although Short's (1904) description was not quantitative, none of the aforementioned taxa are present in the upper bone beds surrounding the M4–M5 junction. Furthermore, the contents of higher bone beds at Garden Cliff include additional taxa than those described in this study, such as the reptile *Pachystropheus rhaeticus* (Storrs, 1994). Therefore, although there may have been some lateral persistence of this upper bone bed, it appears that it varies taphonomically across the local region.

In conclusion, each Rhaetian bone bed is likely unique and genetically unconnected with others in the succession. Like the basal Rhaetian bone bed, the upper Westbury Formation bone bed is a 'tempestite', with the clasts condensed by a shoreward storm (Short, 1904; Reif, 1982; Storrs, 1994), but the preserved fossils were derived locally at the time, and there is no evidence they were reworked from pre-existing bone beds.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.pgeola.2016.07.001>.

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