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The Rhaetian vertebrates of Chipping Sodbury, South Gloucestershire, UK, a comparative study

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ABSTRACT

Microvertebrates are common in the basal bone bed of the Westbury Formation of England, documenting a fauna dominated by fishes that existed at the time of the Rhaetian Transgression, some 206 Myr ago. Two sites near Chipping Sodbury, south Gloucestershire, Barnhill Quarry and Chipping Sodbury railway cutting, show differing faunas. Top predators are the large bony fish *Severnichthys* and the shark *Hybodus cloacinus*, which preyed on smaller sharks such as *Lissodus* and *Rhomphaiodon*. These fishes in turn may have fed on a mixed diet of other fishes and invertebrates, and *Lissodus* was a shell crusher. Comparisons of these faunas with others described recently from the Bristol region, and from Devon, indicate remarkable faunal similarities in the Rhaetian basal Westbury Formation bone bed over a wide area, based on a variety of ecological statistics that document species diversities and relative abundances. Only the fauna from the Chipping Sodbury railway cutting differs significantly.

1. Introduction

The Rhaetian was a significant stage of the Triassic, during which there were profound changes in the Earth's climate and topography, and biosphere. During this short span of time (205.7–201.3 Myr ago; Maron et al., 2015), Pangaea began to break up (de Lamotte et al., 2015), and this presumably greatly influenced the global climate system by driving cyclical extremes of climate (Trotter et al., 2015). The Rhaetian was terminated by the end-Triassic mass extinction, which saw the rapid, global extinction of ~50% of marine and terrestrial genera (Deenen et al., 2010), including the conodonts and many marine reptiles and invertebrates, as well as many archosaurs, some therapsids, and most temnospondyl amphibians.

Rhaetian outcrops in the UK, assigned to the Penarth Group, extend from Teesside in the north-east of England to Dorset on the south coast, and on both sides of the Severn Estuary, in South Wales and around Bristol (Swift and Martill, 1999). The stratigraphy of the Rhaetian follows a common pattern throughout the UK, but differs in continental European locations. However, one constant throughout all occurrences is that there is generally a basal bone bed that yields abundant bones and microfossils of bony fishes, sharks, and reptiles. A number of British Rhaetian bone bed sites have been described (Swift and Martill, 1999; Allard et al., 2015; Korneisel et al., 2015; Nordén et al., 2015) and many of them share the key elements of their faunas in common; however, there has never been a numerical comparison of the faunal lists, key taxa and relative abundances between different sites. Are they constant, representing unbiased preservation of a common fauna, or are there differences in diversity and relative abundance, perhaps reflecting palaeoenvironmental or taphonomic differences?

The aim of this paper is to explore variations in the composition of the vertebrate faunas from the Rhaetian bone beds of southern England. Here, we examine two sites, Barnhill and Chipping Sodbury railway cutting, chosen because they are located geographically adjacent to each other. Further, we analyse census data from these sites, and others, to assess the variation in faunal assemblages and relative abundances of taxa among a number of Rhaetian bone bed sites

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2. History and geological setting

2.1. Historical setting

The two sites, Barnhill Quarry (National Grid Reference [NGR] ST 72604 82620) and Chipping Sodbury railway cutting (NGR ST 71484 80904 to ST 75242 81473) are approximately 1.1 km apart, both being located towards the eastern end of Chipping Sodbury (Fig. 1). Barnhill Quarry, sometimes called Arnold's Quarry (Murray and Wright, 1971), was first mentioned on a tithe map printed in 1839, when the quarry was much smaller and shallower than it is today, and quarrying operations were small-scale. From 1844, however, the quarry was presumably a much larger undertaking, and was recruiting workers from the Sodbury Union Workhouse. In 1859, records show a specialist limestone quarry, as well as a limekiln on the site (Ridge Wood, 2015). At this time, the quarry covered 11 acres, 2 rods and 7 perches (approx. 46,719 m^2). From the 1860s, there is evidence of a railway siding leading into the quarry (Ridge Wood, 2015), built and run by the Midland Railway Company. It is likely that packhorses and mules were used to carry cut stone from the quarry to the railway line. After the First World War, quarrying became the principal source of employment in the area, as the demand for limestone increased with the growing network of roads being laid at the time.

In 1928, several small-scale West Country quarries were grouped together to form the British Quarrying Company (Hopkins, 1979), which later became the Amalgamated Roadstone Corporation (ARC); Barnhill Quarry was used as the headquarters for what was at the time the largest stone company in the world. Eventually, however, the limestone yield of the quarry began to decline, and by 1955, the quarry had been abandoned. The site was declared an SSSI for its twofold stratigraphic significance; in representing the Lower Cromhall Sandstone of the Carboniferous, which is noted for the demonstration of sedimentary structures, and in demonstrating an excellent Rhaetian section sitting directly on Carboniferous Limestone (Benton et al., 2002; Cossey et al., 2004). However, there is much ongoing debate about the future of the site. Houses and a supermarket were built (2014–2016) in the southern part of the quarry, and the remainder could become a household waste landfill site. Today, the site covers just 7.7 acres (31,160.8 m^2), but the geological sections forming the east, north and west faces of the quarry are still intact.

Chipping Sodbury railway cutting was excavated by the former Great Western Railway Company, which had been the primary railway company in the west since its establishment in 1835 (Roden, 2010). Following successful completion of the Severn Railway Tunnel in 1887 (Walker, 1888), the construction of a new railway line between Swindon and the tunnel began in November, 1897 (Robertson and Abbott, 1989). This would allow South Wales coal traffic bound for London to bypass Bristol. In order to lay a track bed across such an uneven landscape, great volumes of rock and earth were excavated to build tunnels and cuttings, and a large number of embankments and viaducts also had to be erected (Husband, 1902).

Chipping Sodbury railway cutting leads into Chipping Sodbury tunnel, which is the second longest railway tunnel in the Great Western region (4433 m), exceeded in length only by the Severn tunnel (7008 m). Construction of the former was made possible by 'shaft excavation', and at one point the tunnel had up to 40 gangs of navvies tunnelling ventilation shafts directly down into the hill, then tunnelling horizontally at the correct depth to link up with other shafts (Husband, 1902). Work on the line was completed in 1903, and by this time, excavation of the cuttings had required the work of 4000 navvies, 44 steam locomotives, 17 steam shovels, 11 steam cranes and 1800 wagons (Robertson and Abbott, 1989).

2.2. Geology of Chipping Sodbury railway cutting

Chipping Sodbury is located on low-lying Upper Triassic and Lower Jurassic sediments (Fig. 1), and the succession youngs eastwards, passing up through Lower and Middle Jurassic sediments, with outcrops all trending roughly north to south at this point. About 1 km east of the eastern limit of Chipping Sodbury, the landscape rises as a ridge formed from the Dyrham

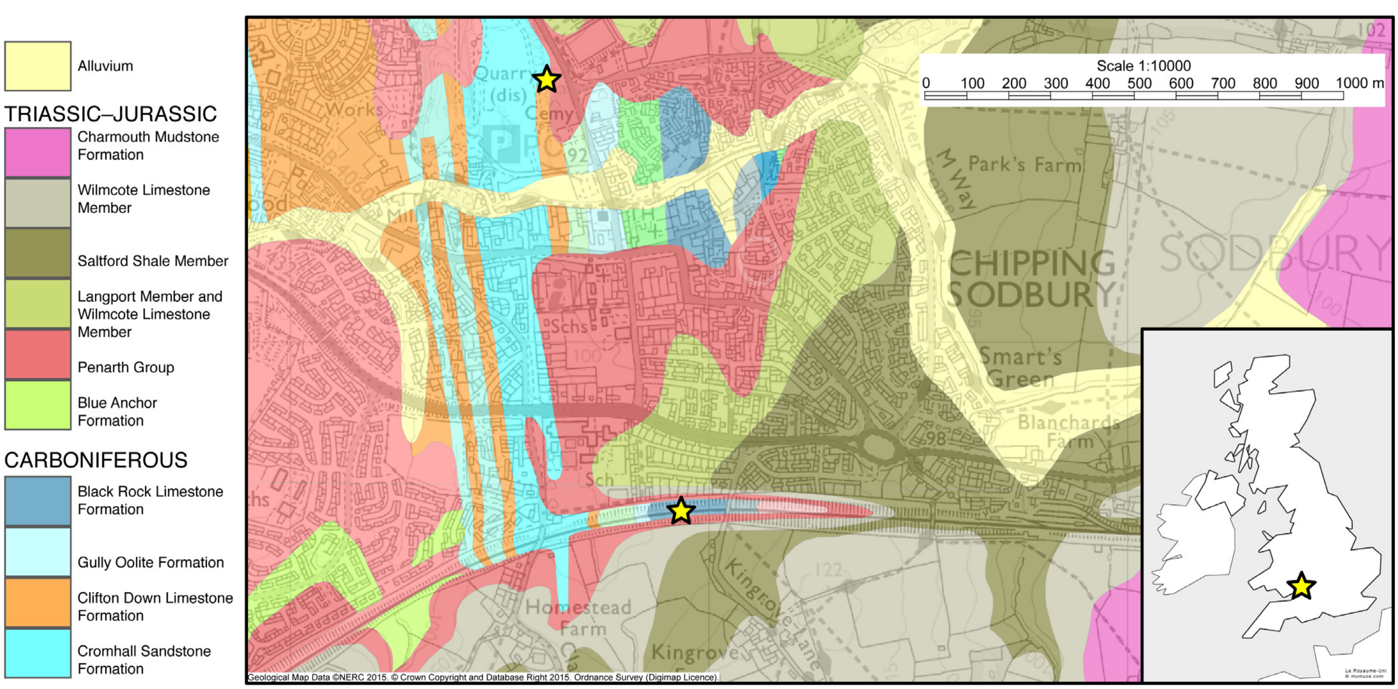

Fig. 1. Geological map of the Chipping Sodbury area, with Barnhill Quarry and the Chipping Sodbury railway cutting marked (yellow stars). Key geological formations are indicated, separated into four key Carboniferous units (bottom of column) and the key Triassic–Jurassic units above. © Crown Copyright and Database Right 2015. Ordnance Survey (Digimap Licence).

Formation and Bridport Sand Formation (both Lower Jurassic; Pliensbachian and Toarcian respectively), and the Inferior Oolite Group (Aalenian to Bathonian) and overlying Middle Jurassic units. This Lower–Middle Jurassic ridge is penetrated by the Chipping Sodbury tunnel. East of the tunnel is a 3.5-km-long cutting through a succession of formations, from west to east, descending through the Charmouth Mudstone Formation (Sinemurian–Pliensbachian) and the Rugby Limestone Member (Hettangian–Sinemurian) east of the former Chipping Sodbury station, the Saltford Shale Member (Rhaetian–Hettangian) from Chipping Sodbury station to Lilliput Bridge, the Wilmcote Limestone Member (Rhaetian–Hettangian) west of Kingrove Bridge, and then the Cotham Member and Westbury Formation (Rhaetian), Blue Anchor Formation (Norian–Rhaetian), and older red beds of the Mercia Mudstone Group (Early Triassic – Rhaetian) further west. The Chipping Sodbury quarries, including Barnhill Quarry, cut down through the Triassic and Jurassic sediments to reach various limestone formations of the Lower Carboniferous. The railway cutting also exposes these Carboniferous units in small patches at track level, from west to east (Avon Group mudstone, Black Rock Group limestone, Friars Point Limestone Formation, Gully Oolite Formation, Cromhall Sandstone Formation, Oxwich Head Limestone Formation; Courceyan to Brigantian). Reynolds and Vaughan (1904) described the geology of the railway cutting, based on their field work as it was being excavated. Their descriptions provide a remarkable longitudinal sketch of rocks exposed along the section when it was clean (it is now entirely overgrown), as well as summary sedimentary logs taken at several points along the track (Fig. 2).

Reynolds and Vaughan (1904) note that the outcrop of Rhaetian bone bed they uncovered was very clear, and extended from a point 'east of the Lilliput Bridge' as far as 'the Old-Red-Sandstone outcrop lying west of Chipping Sodbury railway-station' (Fig. 2). The railway station no longer exists, but it was located at ST 742816, and the BGS map shows a small exposure of Old Red Sandstone, the Tintern Sandstone Formation, dated as Late Devonian to Early Mississippian, located in the track bed of the railway cutting at ST 732817, and underlying the Black Rock Limestone Subgroup, dated from the Tournaisian (Courceyan–Chadian substages), immediately to the west in the railway cutting. Along the cutting, Reynolds and Vaughan (1904, p. 197) note that the Rhaetian 'varies a great deal in thickness, being thickest where the Palaeozoic rocks have been much denuded. At two points where large rounded hummocks of the Palaeozoic project into the Rhaetic, the Black Shale is deposited on them in an arched manner, forming an anticline of bedding.' Thus, the picture is of Rhaetian sediments overstepping underlying Palaeozoic rocks unconformably from the west, with the basal parts of the Triassic sequence draped over discontinuities in the eroded surface.

The basal bone bed occurred sporadically (Fig. 2): as Reynolds and Vaughan (1904, pp. 197–198) note, '[i]t is first met with as one

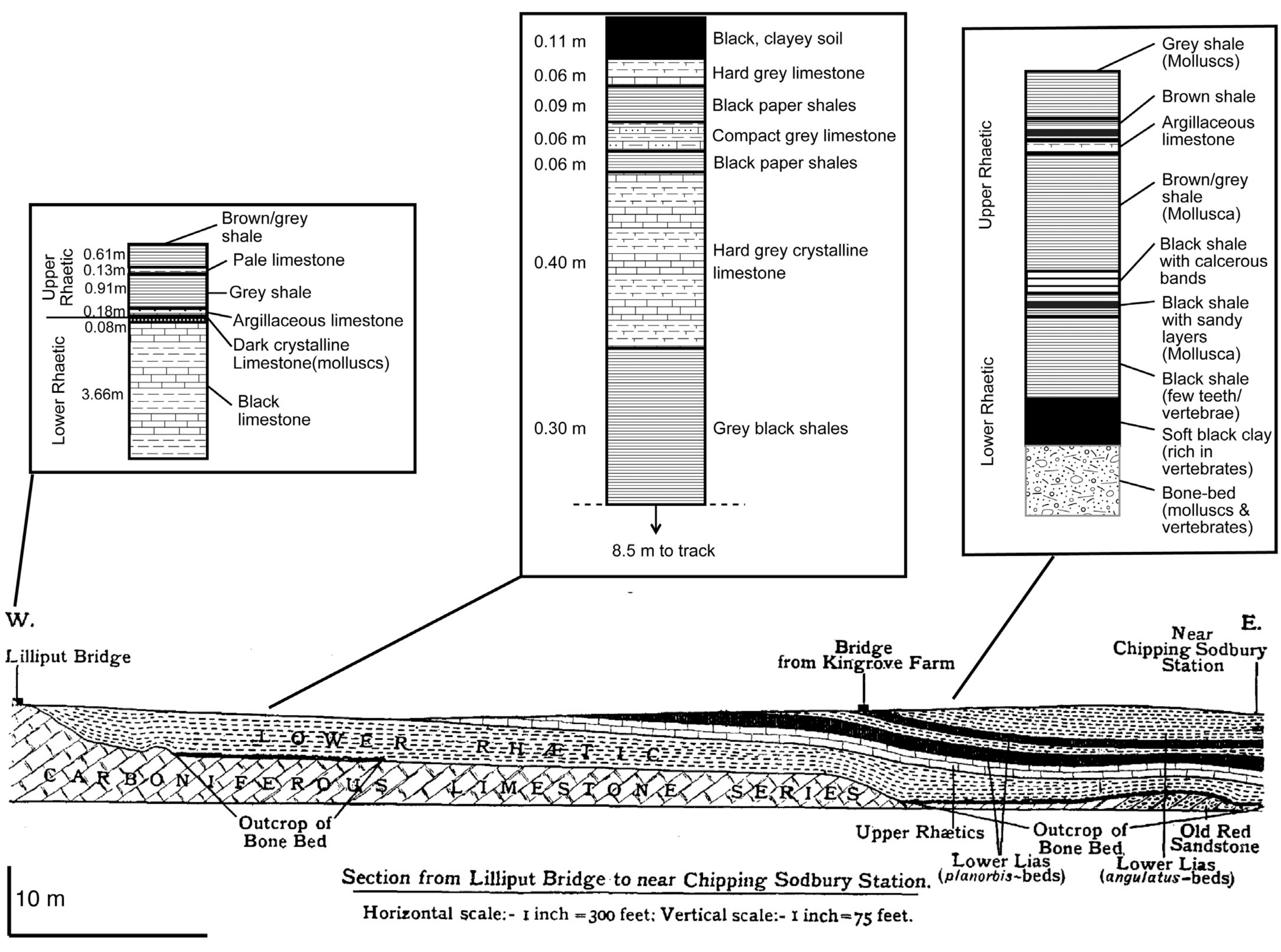

Fig. 2. Cross-section of the section of railway line where the bone bed is exposed (NGR ST 728816), with three stratigraphic columns through the Rhaetian succession, as documented by Reynolds and Vaughan (1904). The longitudinal section is from Reynolds and Vaughan (1904). Metric scales are added.

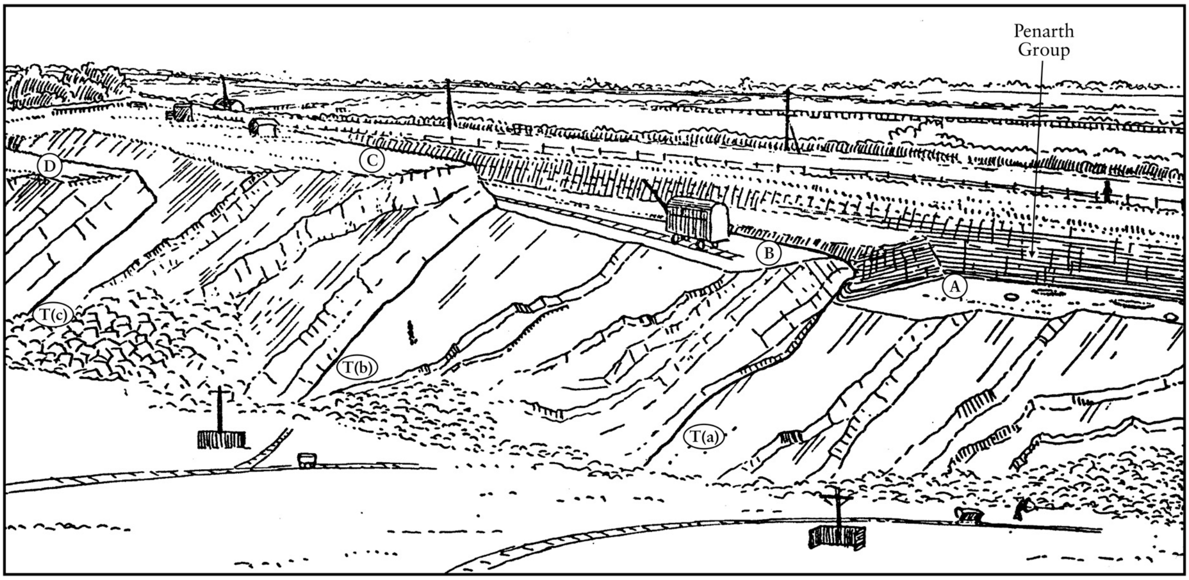

Fig. 3. Illustration of Barnhill Quarry taken from Reynolds (1938) to show the position of the Penarth Group within the quarry, with buildings and figures for scale. The four quarried platforms, marking the top of the Carboniferous Limestone are labelled 'A'–'D', and the overlying Penarth Group is labelled at top right. T(a), T9B), and T(c) are three overthrusts, structural features noted by Reynolds (1938).

passes east from Lilliput Bridge at a point about 150 yards from the bridge: it extends for a distance of about 130 yards, and then again disappears, reappearing after some 200 yards, and extending continuously to the end of the Palaeozoic outcrop'. They describe it as a 'Hard Bone-Bed, containing quartz-pebbles and crowded with vertebrates; *Plicatula cloacina* is not infrequent', being 3 inches [7.5 cm] thick, and immediately overlaid by a thin unit of 'Soft black clay, crowded with vertebrates'. They do not note any other bone-bearing horizons in the section, despite their being aware of such multiple bone beds at other sites.

2.3. Geology of Barnhill Quarry

Barnhill Quarry excavates the Clifton Down Limestone and the Lower Cromhall Sandstone formations (Visean: Arundian to Brigantian). The Clifton Down Limestone sequence, which include coral beds and stromatolite horizons, has received detailed study and environmental interpretation (e.g. Murray and Wright, 1971). It shows a cycle of sedimentation passing from intertidal algal mats, through lagoons, barrier and open shelf deposits and back through the same sequence to intertidal algal mats.

The Penarth Group is exposed around the edges of Barnhill Quarry, especially in the south-east corner, where a 6-m section shows Westbury Formation, Cotham Member, and some overlying Lias Group (Figs. 3 and 4). The Westbury Formation, and the basal bone bed, sit directly on the eroded and karstified Carboniferous Limestone ('A', Figs. 3A and 4B). The exposed upper surface of the Carboniferous Limestone forms four platforms ('A'–'D', Fig. 3), two of which display well-developed clints and grykes, karstic solution channels produced by subaerial weathering (Reynolds, 1938). The other top surfaces of the Carboniferous Limestone are smooth, perhaps eroded by the Rhaetian transgression.

The Rhaetian sediments are typical of the area, starting with 3.8 m of Westbury Formation, largely dark grey and black fissile shales and thin interbedded limestones and sandstones, and

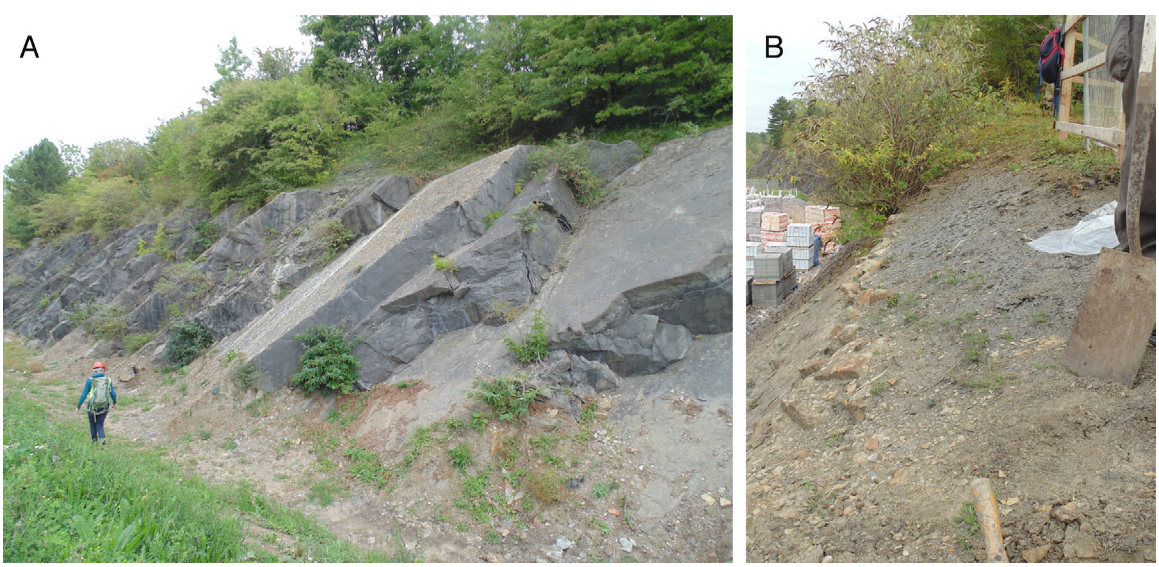

Fig. 4. The Carboniferous-Triassic unconformity at Barnhill Quarry. (A) Dipping Carboniferous Limestone beds overlain with Rhaetian at the level of the vegetation. (B) Close-up of the contact between Carboniferous and Rhaetian sections, with the bone bed just above the blocky, orange-stained limestone.

overlain by 1.7 m of the Cotham Member of the Lilstock Formation, comprising typical pale buff-coloured shales and thinly bedded limestones (Fig. 3B). Reynolds (1938) characterised two lithologies of the basal bone bed, the first being a dark-coloured crystalline limestone containing phosphatic nodules, coprolites, and bone fragments, and the second characterised by large (up to 1.2 m long) rounded blocks, some of them partially coated with pyrite. In many cases, these blocks are isolated, but when they occur in groups, bone-bearing and quartz pebble-rich sediment often infills the spaces, producing a very coarse-grained conglomerate. This coarse conglomerate occurs only sporadically.

In attempting to understand the Rhaetian of Barnhill Quarry, a field drawing by Reynolds (1938), showing the quarry when it was still working, in the late 1930s, is very helpful (Fig. 3). The small building at the top left appears on Ordnance Survey maps until the 1960s, at which point it was presumably pulled down. It, as well as the road marked by fence posts, and the orientation of the illustration, confirm that this drawing was made from the west side of Barnhill Quarry, facing east, with the telegraph poles (and a person) marching along the side of the Wickwar Road (B4060). The boundary between the large, steeply dipping beds of the Carboniferous Limestone and the overlying thinly bedded, dark-coloured Westbury Formation is clear, as it is today, although much overgrown (Fig. 4). An annotated, detailed 25-inch-to-the mile (1:2500) Ordnance Survey map of Barnhill Quarry in the Curtis archive at BRSUG shows exactly where he collected his fossiliferous samples, and that is from the base of the Westbury Formation at the extreme right of the diagram, below the arrow pointing to the 'Penarth Group' (Fig. 3), namely at NGR ST 72606 82675.

Bench 'A' in Fig. 3 is the location of the fossil collections made by Mike Curtis in 1976 from the basal Westbury Formation bone bed. On revisiting the site in August 2015, bench 'A' was located, close to a fence beside a footpath that runs behind some new houses and close to the boundary fence of the quarry site. The Carboniferous-Triassic contact is clear (Fig. 4B), and samples of the basal Westbury Formation bone bed were collected.

3. Materials and methods

The microvertebrate fossils described here were collected from 1975–1977 by Mike Curtis (1951–2009), an amateur geologist from Gloucestershire. Throughout his life, Curtis collected vast quantities of fossil material from Bristol and the surrounding area, and is hailed as a highly reliable source of information owing to his methodical collecting, identification and labelling (Nordén et al., 2015). Curtis kept meticulous records of his collecting, and wrote detailed summaries of his observations. When these collections were made, Curtis was Quarry Manager of the Chipping Sodbury Quarries.

Curtis' field notebooks and annotated maps of the region, although helpful in describing the geology of the localities, unusually yield no information about the horizons at Barnhill Quarry or in Chipping Sodbury railway cutting from which the material was gathered or the original volume of unprocessed material gathered, and no lab books have been found which describe the preparation of this material. However, we assume that he followed his usual meticulous procedures, as outlined by Korneisel et al. (2015).

Initial identifications of the microvertebrates were by Curtis, and these have all been thoroughly checked and revised here. As much as half of the unidentified material in his collection has now been identified, based on published works (Swift and Martill, 1999; Allard et al., 2015; Nordén et al., 2015), as well as comparisons with collections from other sites. The materials described here represent a tiny proportion (<5%) of the tens of thousands of identified Rhaetian-age microvertebrates that Curtis collected during his lifetime, and which are now lodged in the collections of Bristol City Museum (BRSMG) and the University of Bristol (BRSUG).

4. Systematic palaeontology

Specimen numbers from both sites are small (Table 1). The fossils from both localities are generally of good quality, some with signs of abrasion. No morphotypes have been allocated, since the majority of the unidentified material is heavily eroded, fragmented and difficult to group. We describe materials from both sites together, but clarify the sources throughout.

4.1. Chondrichthyans

In total, the remains of three taxa of sharks, as well as some partially identifiable shark and holocephalan remains, were recovered from the two locations, all of which are previously known from the Rhaetian. Most of the chondrichthyan remains come from members of the Hybodontiformes.

4.1.1. Lissodus minimus *(Agassiz, 1839)*

By far the most common species from the railway cutting, the teeth of *L. minimus* are distinctive (Allard et al., 2015), being broadly triangular and carrying strong ridges. The teeth exhibit clear monognathic heterodonty, and several different morphs may be found (Fig. 5); some possess tricuspid crowns (Fig. 5A), whereas others show a more pronounced single, central cusp (Fig. 5B–E). In occlusal view (Fig. 5D), the teeth possess narrow, flattened crowns that taper mesially and distally from the centre, with rounded tips. In labial view (Fig. 5E), the characteristic labial peg is located low on the crown, at the base of the very low central cusp, which is flanked by even lower pairs of lateral cusplets. In some specimens, the occlusal crest, a ridge running from end to end of the occlusal surface of the crown and passing through all of the cusp apices, appears almost crenulated. Vertical ridges descend both labial and lingual faces of the crown from the occlusal crest, usually terminating at the crown shoulder, which is commonly marked by a horizontal ridge. Specimens vary from 1.5–3 mm in maximum dimension, and 0.5–1 mm in height. The flattened shape of these teeth suggests durophagous feeding. Many specimens are incomplete.

4.1.2. Hybodus cloacinus *(Quenstedt, 1858)*

This large species is reasonably common at Barnhill, representing up to 10% of specimens, but represented by only a single tooth at the railway cutting. The specimens found at Barnhill are remarkably well preserved, and several virtually complete pentacuspid crowns have been found (Fig. 6A and B). The principal

Table 1
Abundance table of taxa from Barnhill Quarry and Chipping Sodbury Railway Cutting, showing raw numbers of specimens.

Taxon	Barnhill Quarry	Chipping Sodbury Railway Cutting
Lissodus minimus	102	774
Hybodus cloacinus	17	3
Rhomphaiodon minor	33	33
Holocephali	1	0
Nemacanthus	0	1
Misc. Hybodontiforms	2	12
Gyrolepis albertii	53	173
Severnichthys acuminatus	105	104
Sargodon tomicus	1	0
Ceratodus sp.	2	0
Total	316	1100

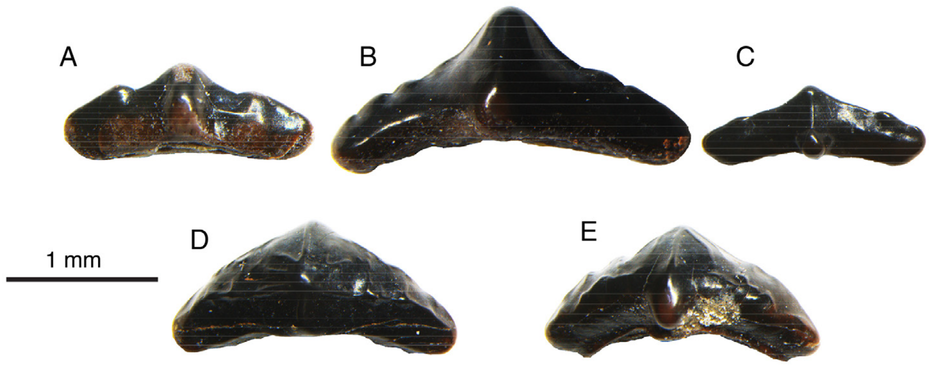

Fig. 5. Teeth of the shark *Lissodus minimus* from Barnhill Quarry and the Chipping Sodbury railway cutting. (A) BRSMG Cf14012; (B) BRSMG Cf14013; (C) BRSMG Cf14014; (D and E) BRSMG Cf14015, in occlusal (D) and lateral (E) views.

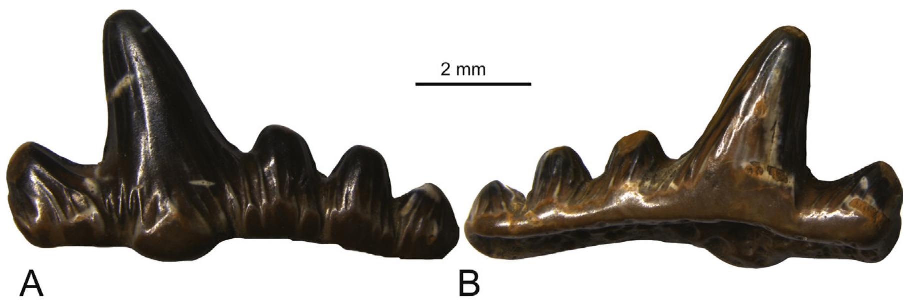

Fig. 6. Anterolateral teeth of the shark *Hybodus cloacinus* from Barnhill Quarry. (A) BRSMG Cf14204 in labial view; (B) BRSMG Cf14205 in occlusal view.

cusp, over twice the height of the adjacent lateral cusplets, is situated slightly off-centre, and possesses a distinctive and characteristic labial node at its base. Relatively coarse vertical ridges descend the crown, especially labially, often bifurcating basally and occasionally swollen towards their base to form nodes. Up to three pairs of lateral cusplets are present. The principal cusp is inclined distally in anterolateral teeth, which are also asymmetrical in labial view. The complete teeth represent the largest specimens recovered from either site, with the largest measuring 7.9 mm × 4.5 mm. Accompanying these specimens are many examples of worn and broken teeth.

The material from Barnhill and Chipping Sodbury railway cutting agrees well with the morphological variation shown by this species from other Rhaetian localities (see Section 6), and an articulated dentition from the Lower Lias (Lower Jurassic) of Lyme Regis (Duffin, 1993b, 2010, pl. 59, Fig. 2).

4.1.3. Rhomphaiodon minor *(Agassiz, 1837)*

This species is abundant at Barnhill quarry, but scarcer at the railway cutting. Several tooth morphs are present at Barnhill, as well as fin spines recovered from the railway cutting. A complete specimen of one morph is shown in Fig. 7A and B. The central cusp

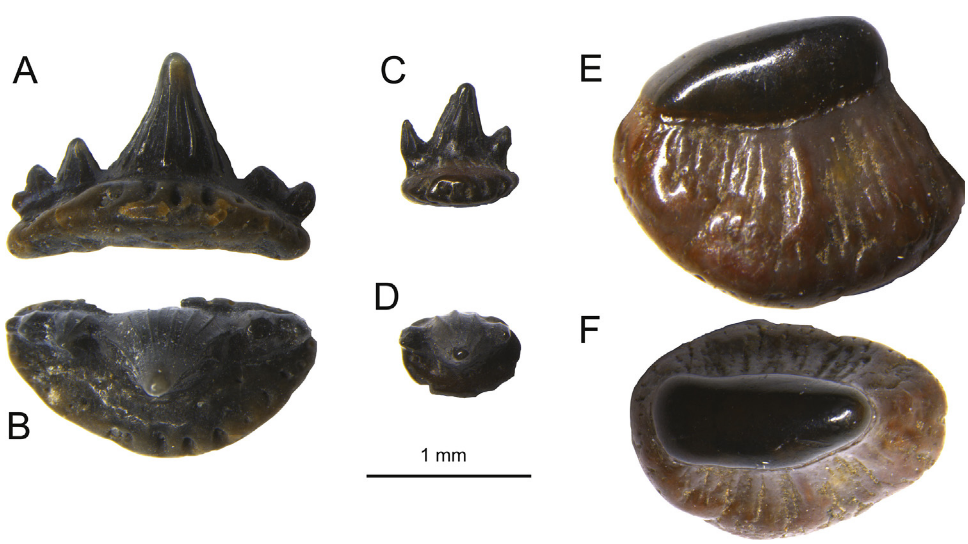

Fig. 7. Teeth of the shark *Rhomphaiodon minor* from Barnhill Quarry and the Chipping Sodbury railway cutting. (A and B) Complete pentacuspid tooth (BRSMG Cc6321) in occlusal (A) and labial (B) views. (C and D) Complete tricuspid tooth (BRSMG Cc6322) in occlusal (C) and labial (D) views. (E and F) Unidentified holocephalan dermal denticle (BRSMG Cc6323) in lateral (E) and dorsal (F) views.

in teeth of *R. minor* is symmetrical, unlike those of *H. cloacinus*. The teeth commonly possess five cusps; the central cusp is flanked by two pairs of low lateral cusplets. The central cusp is over twice the height of the smaller lateral cusplets. All cusps are triangular in shape, have an elliptical cross-section and are inclined lingually (Fig. 7B). There are broad, shallow, non-branching vertical ridges running down both labial and lingual faces of the cusps, but these are less well defined in the smaller cusplets. The root is very broad, with the distance between the most proximal and most distal parts of the root being over 70% of the height of the entire tooth. The entire tooth is small, measuring 1.25 mm $H \times 1.94$ mm $W \times 0.95$ mm D.

Another tooth type (Fig. 7C and D) is tricuspid and laterally flattened. The root is bulbous, and pitted with vascular foramina, and the crown is broadly ridged and triangular. It could be argued that this tooth morphotype should be allocated to the morphologically slightly similar synechodontiform shark *Parascylloides turnerae* recently described from the Rhaetian of Barnstone, Nottinghamshire and several localities in Germany (Thies et al., 2014). The teeth described by Thies et al. (2014) are more laterally compressed than the specimens described and figured here, their lateral cusplets are much lower in comparison to the height of the central cusp, and the ornamentation of the crown is also different, especially on the lingual face of the central cusp. The tooth type in Fig. 7C and D clearly belongs to *R. minor*.

4.1.4. Holocephali

A single dermal denticle of an unidentified holocephalan chondrichthyan was recovered (Fig. 7E and F) at Barnhill Quarry. It comprises a small crown sitting on top of a more massive root that expands to twice the diameter of the crown. The enamel on the rounded crown is black and smooth. The larger root of the denticle tapers from the base upwards, and bears irregular longitudinal ridges. This identification is based on close similarity to specimens identified as Group C morphotype by Sykes (1974, p. 59) from Barnstone in Nottinghamshire, suggested to come from a chimaeriform by him, and a very similar example is given by Korneisel et al. (2015, Fig. 6A and B).

4.1.5. Nemacanthus *sp.*

A single portion of a fin-spine (Fig. 8A and B) from an unidentified species of *Nemacanthus* was recovered from Chipping Sodbury railway cutting. The fragment consists of an irregularly dimpled golden brown shaft with a furrow running longitudinally along the posterior edge, to accommodate the anterior margin of the dorsal fin. On the anterior edge of the spine is a black enamel ridge, presumably to give the fin stability and to act as a prow to streamline the fin and aid in 'cutting' through the water. Complete specimens of *Nemacanthus* fin spines from localities such as Aust Cliff show that the enamelled anterior ridge extended the full length of the exserted portion of the fin spine (Storrs, 1994, p. 225; Duffin, 1999, p. 204).

4.1.6. Hybodontiform dorsal fin spines

Some dorsal fin spine fragments are incomplete, and lack both a tip and base. They are, however, recognisable by the deep, regular longitudinal ridges (costae) and furrows on the lateral walls of the exserted portion of the spine (Fig. 8C), and by the series of small downturned denticles along the posterior margin of the spine. These two aspects of the spine ornament are diagnostic of hybodontiforms, and differ from fin spines of neoselachians, which have smooth enamelled lateral walls, and those of ctenacanthiforms, which usually possess a tuberculated ornament on the lateral walls. The spines supported the leading edge of the dorsal fins during life, acting both defensively and as a cutwater. It is impossible to assign the dorsal fin spine fragments to a particular species of hybodontiform shark.

4.1.7. Hybodontiform dermal denticles (scales)

A small number of hybodontiform dermal denticles were recovered from the railway cutting, but not from Barnhill Quarry. These denticles could not be characterised to species level, although many are of extremely good quality. One example (Fig. 9A and B) is of a type described by Sykes (1974) as simply a 'Rhaetian hybodont denticle', and measures approximately 700 μm in length. Although the base is flared and subquadrate in shape, there is a distinct 'waist' forming a narrow pedicel below the expanded crown, which is flattened along the lateral axis. Nine vertical ridges ascend the pedicel and the outer (=anterior) face of the crown, which is produced into a series of denticles along the posterior margin. The anterior and posterior facets are irregularly ridged and furrowed.

4.2. Osteichthyans

Four osteichthyan taxa were recovered from both sites, all of which are known to occur in the Rhaetian (Duffin, 1982). Three of these are actinopterygians, and one a sarcopterygian.

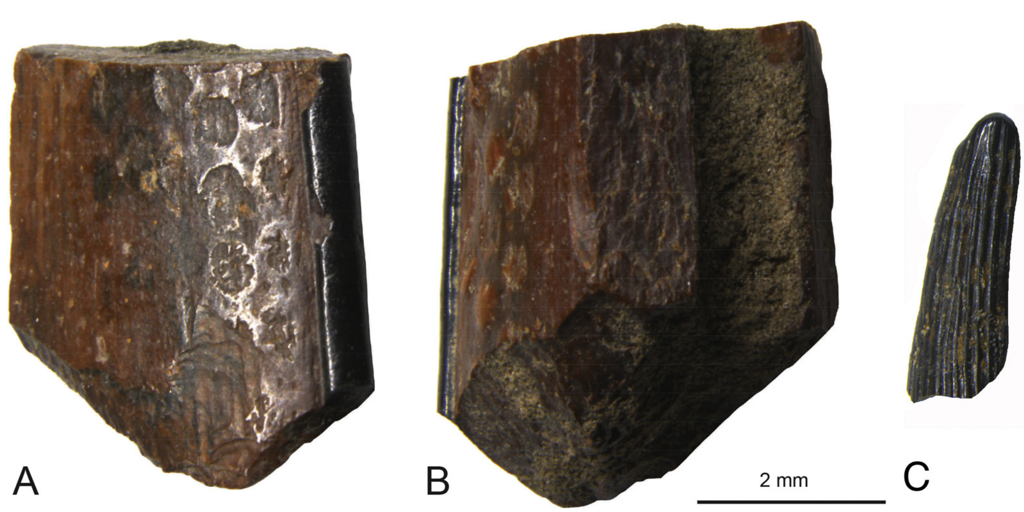

Fig. 8. Shark fin spines from Chipping Sodbury railway cutting. (A and B) *Nemacanthus* sp. fin spine (BRSMG Cc6324), in two views (A, B). (C) Unidentified hybodontiform fine spine fragment (BRSMG Cf14082.52).

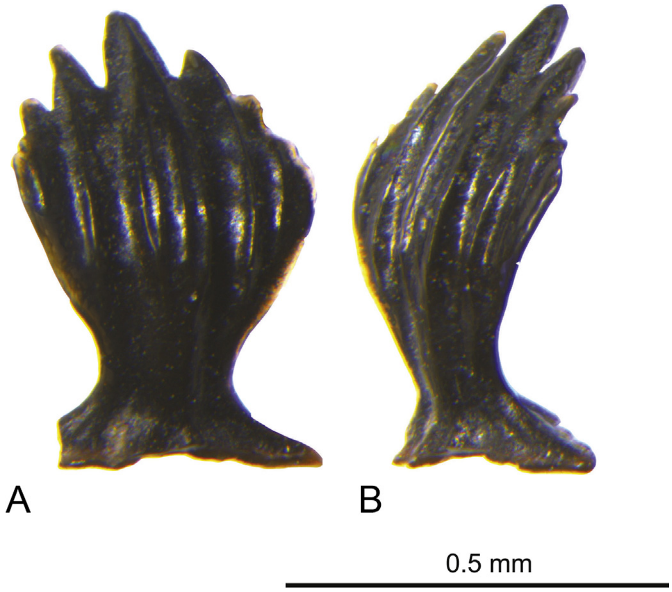

Fig. 9. Hybodont dermal denticle (BRSMG Cc6325), from Chipping Sodbury railway cutting, in anterior (A) and lateral (B) views.

4.2.1. Gyrolepis albertii *(Agassiz, 1835)*

This species makes up a large proportion of fossil material recovered from the railway cutting, where teeth and scales are abundant. This species was identified from Swift and Martill (1999), and of the six known species of *Gyrolepis*, only *G. albertii* is found in the Penarth Group (Davis, 1871). The scales (Fig. 10A and B), as in many Rhaetian beds, are ubiquitous (Allard et al., 2015), and are laterally flattened, with a thick base, which varies in colour from honey gold to chestnut, topped with a thinner, jet-black patterned enamel covering with a diagonal rippled pattern of enamel ridges running in the cranial-caudal direction. The teeth are slender, long and tapered, with a distinctive, gentle hook-like curve (Fig. 10C and D), finely ridged at the base and smooth at the offset, clear-coloured tip.

4.2.2. Severnichthys acuminatus *(Agassiz, 1844)*

The teeth of *S. acuminatus* are very common in these deposits, and were described from the Chipping Sodbury railway cutting by Reynolds and Vaughan (1904), although they did not differentiate between the different tooth types of this species. Here, we report two heterodont morphs from both deposits, the '*Birgeria acuminata*' tooth type and the '*Saurichthys longidens*' tooth type. These were previously considered to be separate species, but were synonymised by Storrs (1994) when a single jaw containing both tooth types was identified.

At Barnhill Quarry, the '*B. acuminata*'-type teeth dominate. These are particularly well preserved, but otherwise unexceptional. In some specimens, the complete, enamel-tipped tooth has been preserved with the root, and even the pulp cavity is readily distinguishable (Fig. 11A and B). The teeth are deeply but sparsely ridged in the lower 50%, and the root is both ridged and pitted. The tooth cap is smooth as a result of post mortem abrasion.

In the '*Sa. longidens*' tooth type (Fig. 11C and D), there is no mark to distinguish the root from the crown, other than the distal cessation of shallow grooves that run longitudinally along the surface. This tooth type is represented in our samples by incomplete teeth, all of which are missing the root. Some specimens retain the translucent, pearl-coloured enamelled tip, and all are ridged along the length of the crown.

Superficially, the '*B. acuminata*'-type teeth of this species are difficult to distinguish from the teeth of *G. albertii*, but they differ in shape, with those of *G. albertii* being more steeply curved and hook-shaped, with the cap forming a much smaller percentage of the total tooth height. Both types of *S. acuminatus* teeth are slender and needle-shaped, with deep grooves on the sides of the root, and the transition from root to crown takes place three-quarters of the way along the tooth from the base. The crown of the tooth finishes in an enamelled tip that is smooth. In the '*B. acuminata*' tooth type, there is a shallow but pronounced groove that distinguishes the ridged root from the smooth crown.

4.2.3. Sargodon tomicus *(Plieninger, 1847)*

A single good-quality tooth of this species was found at Barnhill Quarry (Fig. 11E and F). The specimen is approximately 57 mm in length, and has a smooth, dark coffee-coloured tip, separated from the rest of the tooth by a small circular ridge and groove. The crown has a smooth, marbled pattern, and the inferior face is concave (Fig. 11E). The root is missing.

4.2.4. Ceratodus *sp.*

Two very worn sarcopterygian teeth belonging to an unknown species of *Ceratodus* were identified from the Barnhill collection. The occlusal surfaces of these teeth (Fig. 12A–D) are composed of pleromic hard tissue (tubular dentine) containing pillars of hypermineralised dentine. Although heavily worn, shown by their high polish, and fragmentary nature, there is some evidence of the transverse ridges, characteristic of more complete specimens of *Ceratodus* tooth plates from localities such as Aust Cliff, which gave a sectorial component to the process of occlusion.

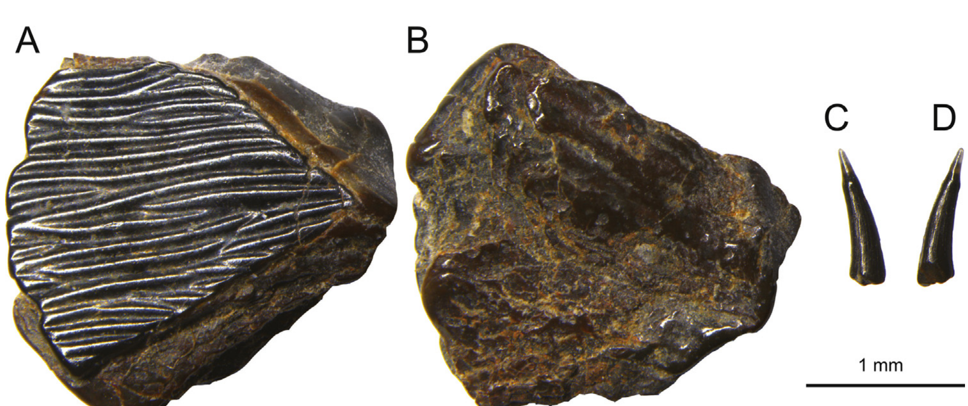

Fig. 10. Remains of the osteichthyan *Gyrolepis albertii* from Barnhill Quarry and the Chipping Sodbury railway cutting. (A and B) Dermal scale (BRSMG Cc6326) in external (A) and internal (B) views. (C and D) Tooth (BRSMG Cf14266) in lateral distal (C) and proximal (D) views.

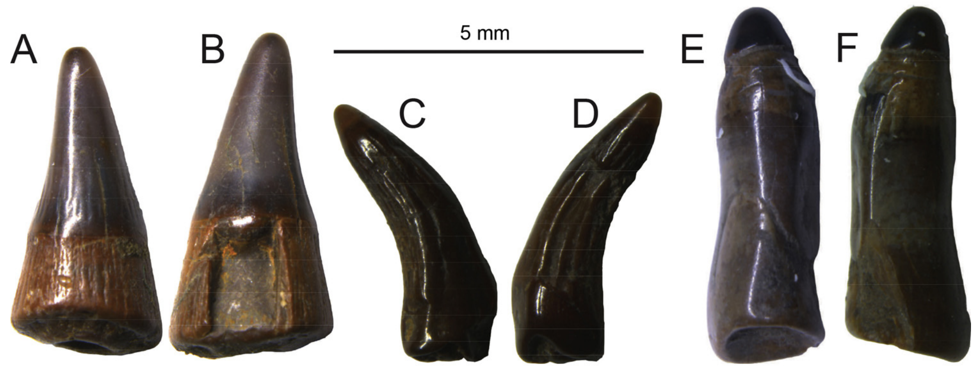

Fig. 11. Teeth of bony fishes from Barnhill Quarry and the Chipping Sodbury railway cutting. (A and B) *Birgeria acuminata*-type tooth (BRSMG Cf14308) of *Severnichthys acuminatus*, (C and D) *Saurichthys longidens*-type tooth (BRSMG Cf14322) of *Severnichthys acuminatus*. (E and F) A tooth of *Sargodon tomicus* (BRSMG Cf14379).

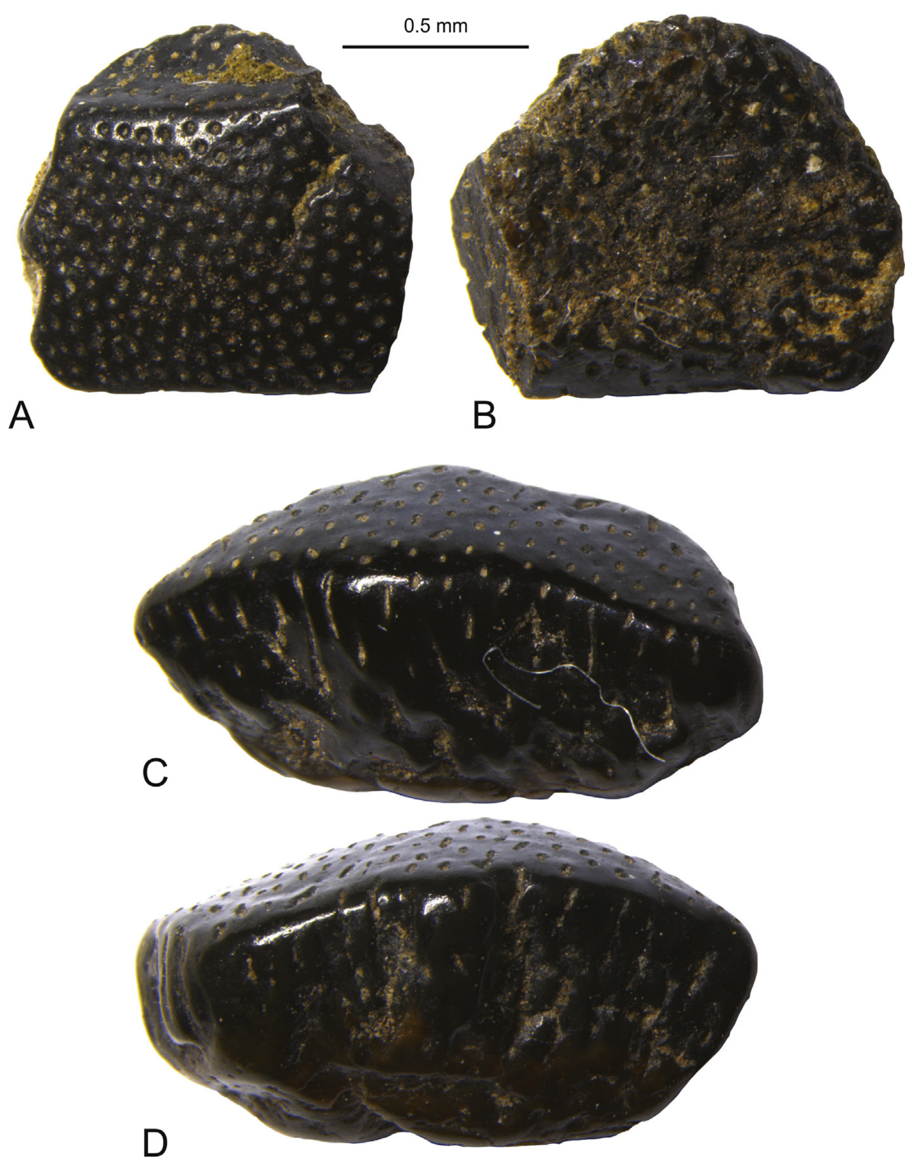

Fig. 12. Teeth of *Ceratodus* sp. from Barnhill Quarry. (A and B) Partial tooth BRSMG Cf14250, in occlusal (A) and ventral (B) views. (C and D) Partial tooth BRSMG Cf14251, in occlusal (C) and lingual (D) views.

4.3. Miscellaneous vertebrate material

From both sites, there was an abundance of unidentifiable vertebrate material, none of which could be further characterised, and so is not presented here.

5. Diversity and relative abundance

Comparison of the two sites shows that Barnhill Quarry has a more species-rich fauna (nine identifiable taxa) than the railway cutting (seven identifiable taxa), with six species shared, and ten taxa identified in total. Sample sizes were different, with 1100 identifiable specimens from the railway cutting and 316 from Barnhill Quarry. The relative proportions of taxa differ quite substantially (Table 1), with *L. minimus* and *S. acuminata* equally abundant at Barnhill (Fig. 13A), but *L. minimus* overwhelmingly abundant in the railway cutting, and *S. acuminata* much less frequent in the railway cutting (Fig. 13B). Oddly, *G. albertii* is equally abundant at both sites, and other taxa are quite rare in the railway cutting due to the overwhelming abundance of *L. minimus* there (Fig. 13A and B).

The higher species diversity at Barnhill is exaggerated when the relative proportions of specimens per species are considered. The Shannon–Wiener Index of Biodiversity (H') is higher at Barnhill (1.524) than at Chipping Sodbury (0.938), as is the Species Evenness (J') (0.69 and 0.48, respectively). This shows that the Barnhill Quarry fauna is considered to be more diverse because the relative proportions of specimens among species are more unequal (Tuomisto, 2010). This is confirmed by Simpson's Index of Diversity (D), which is 0.529 for the railway cutting and 0.254 for Barnhill. This index reflects the probability that two species sampled from each site will be of the same species (Simpson, 1949), and therefore the lower figure for Barnhill suggests higher overall diversity.

When the two species samples are compared, they turn out to be similar, based on a reasonably high Sørenson–Dice Coefficient (0.75).

There is a wider question of how typical such values might be, and how the faunas of geologically comparable Rhaetian bone beds might differ or resemble each other. The current data set was compared with other recently studied samples, from Manor Farm Quarry (NGR ST 574896), near Aust Cliff, South Gloucestershire (Allard et al., 2015), Charton Bay (NGR SY 281893), on the south Devonshire coast (Korneisel et al., 2015), and Marston Road Quarry (NGR ST 73114485), near the village of Nunney in Somerset (Nordén et al., 2015).

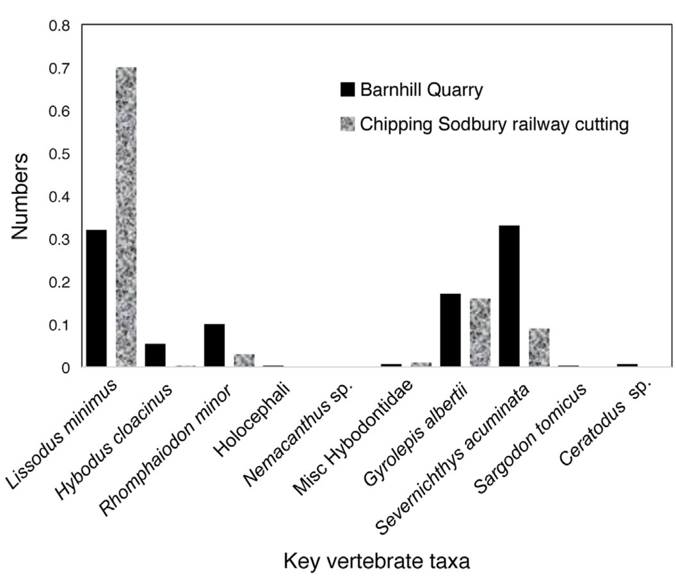

Fig. 13. Pie charts illustrating relative species frequencies, among identifiable material from Barnhill Quarry (A) and the Chipping Sodbury railway cutting (B). Species are named in the key; Misc., Miscellaneous.

Table 2
Comparison of five Rhaetian bone beds, according to some standard ecological statistical measures, the Shannon–Wiener Biodiversity Index (H'), Species Evenness (J'), and Simpson's Index of Biodiversity (D).

Locality	H'	J'	D
Barnhill Quarry	1.524	0.69	0.254
Chipping Sodbury Railway Cutting	0.938	0.48	0.529
Manor Farm Quarry	1.539	0.62	0.274
Charton Bay	1.729	0.79	0.223
Marston Road Quarry	1.735	0.72	0.237
Interquartile range	0.205	0.10	0.037

The comparisons (Table 2) show that most localities have statistically indistinguishable index values, except for the values of H' and D from Chipping Sodbury railway cutting. These outliers were determined using the Interquartile Range, and these confirm that the overall ecological diversity at the railway cutting, based on species richness and on individual species frequencies, is smaller than that found at any other sampled locality. This difference emerges despite the fact that there is no statistically significant difference between the species evenness (J') of any of the localities.

These comparisons confirm the general similarity in Rhaetian bone bed samples among localities that are geographically widespread, from Gloucestershire to the south Devon coast, a distance of about 150 km. The stratigraphic evidence is that the Rhaetian basal bone beds at all these locations are likely of exactly the same age, representing an event that took place geologically instantaneously, namely the termination of the Triassic red beds of the Mercia Mudstone Group by the Rhaetian transgression, and the exactly coeval basal Westbury Formation bone bed that has been proved to have been deposited at the same time as marine shrimps were excavating burrows on the top of the eroded Blue Anchor Formation (Korneisel et al., 2015).

Therefore, in trying to understand the difference between the majority of the sites and the Chipping Sodbury railway cutting microfauna, four hypotheses should be considered, namely that the differences could result from differences in stratigraphic age, geographic differences, facies and environmental differences, or sampling. The first three can probably be rejected based on the evidence of generally close matching between samples – the bone beds are all the same age, there is no evidence for geographic variation, and the facies are seemingly similar from site to site – indeed the Rhaetian succession is highly predictable (Swift and Martill, 1999). One slight caveat is that we do not have primary evidence of the exact horizon from which Mike Curtis excavated his Chipping Sodbury railway cutting Rhaetian bone bed samples, and it could have been from a bone bed higher in the Westbury Formation for example. However, the Westbury Formation basal bone bed was clearly present in the railway cutting (Reynolds and Vaughan, 1904), and these authors mention no other occurrences of bones from their first-hand observations of the freshly cut sections, so it is most likely that Curtis sampled from the basal bone bed. The railway cutting sample yielded 1100 identifiable specimens, compared to 316 from the Barnhill Quarry sample, so the difference cannot simply be explained by sampling, but in the end, sampling bias of some kind would seem to be the most likely explanation of the fact that the Chipping Sodbury railway cutting sample shows such different proportions of taxa from the other Rhaetian basal bone beds.

Table 3
Comparison of five Rhaetian bone beds using the standard statistical measure of the Sørenson–Dice Coefficient.

Bhl	Rly	MF	Ch	MR	
Bhl	X	X	X	X	X
Rly	0.75	X	X	X	X
MF	0.67	0.63	X	X	X
Ch	0.67	0.63	0.76	X	X
MR	0.70	0.67	0.87	0.80	X

Key: Bhl – Barnhill Quarry. Rly – Chipping Sodbury Railway Cutting. MF – Manor Farm Quarry. Ch – Charton Bay. MR – Marston Road Quarry.

The Sørenson–Dice Coefficient (CC) for all five sites together was calculated to be 0.63. This statistic is a measure of similarity between communities (Dice, 1945; Sørenson, 1948), and ranges from 0 to 1, 0 indicating entirely independent and separate communities, and 1 indicating identical communities. The relatively low value suggests that the similarity between the five localities is reasonable, perhaps indicating they are essentially from the same age and environment. Table 3 outlines the individual CC values for each pair of sites.

6. Discussion

6.1. The Chipping Sodbury railway cutting fauna

L. minimus dominates this ecosystem, making up 70% of identifiable material from this site, as noted earlier (Reynolds and Vaughan, 1904), and as is the case at other Rhaetian sites (Duffin, 1999; Korneisel et al., 2015). The teeth of this species suggest that it was a shell crusher (Korneisel et al., 2015), feeding opportunistically on molluscs and arthropods, which are known to be numerous in the Westbury Formation and Cotham Member (Reynolds and Vaughan, 1904; Mander and Twitchett, 2008; Marquez-Aliaga et al., 2010).

The second most common species, comprising 15% of the sample, is the palaeoniscid chondrostean *G. albertii*, which had previously been reported from the railway cutting (Reynolds and Vaughan, 1904). *G. albertii* was a large, predatory fish; a specimen from Pfersdorf, in the Schweinfurt district of Germany measured 31 cm in length (Steinkern, 2012), and the long, needle-like hooked teeth suggest that it was a piscivore (Tintori, 1998; Korneisel et al., 2015). It is possible that *G. albertii* preyed on the abundant, and smaller *L. minimus*.

Of the remaining ~15% of identifiable fossil material, the most common species is *S. acuminatus*, which was described by Reynolds and Vaughan (1904) as dominating this locality along with *L. minimus*, but in this collection it occurs at a frequency of just 9%. In other regions of the Westbury Formation, *Severnichthys* represents the top predator (Storrs, 1994), and is similar to *G. albertii*, in as much as it is a large predatory species, and probably fed on small chondrichthyans and osteichthyans.

Some 3% of the total material is made up of the remains of *R. minor*. This small shark is found throughout the Westbury Formation, and only a single specimen has previously been noted from Chipping Sodbury cutting. Reynolds and Vaughan (1904) describe finding 'one small tooth...probably to be referred to this species [*Rhomphaiodon minor*]'. Elsewhere in the Westbury Formation, the heterodont teeth and fin spines of this species are common (Duffin, 1999). *R. minor* likely represents a small, opportunistic predator, or possibly even a scavenger (Tintori, 1998), but would also likely have been prey to *Gyrolepis* and *Severnichthys*.

The small number of specimens assigned to *H. cloacinus* was slightly unexpected, especially as Reynolds and Vaughan (1904) also recorded *H. cloacinus* from this site.

6.2. The Barnhill Quarry fauna

The ecology of the Rhaetian fishes from Barnhill Quarry is more diverse, with relatively even proportions of species frequencies compared to the railway cutting. Here, the '*B. acuminata*' type teeth of *S. acuminatus* dominate the ecosystem, at a species frequency of 33%. Also common here is *G. albertii*, found here at a species frequency of 17%, opposite proportions to those of the railway cutting.

As well as these two large actinopterygians, other predators are found at Barnhill. The largest specimens are the teeth of the hybodontiform shark *H. cloacinus*, which occur at a frequency of 9.4% at Barnhill, and are classified as clutching type teeth (Cuny and Benton, 1999), adapted to grasping and tearing flesh from large prey, as opposed to a habit of pursuing smaller species. *L. minimus* also occurs here, but at a relatively low frequency compared to the railway cutting (32%).

Some of the best-preserved teeth in the Curtis collection are those of *R. minor*, a small synechodontiform shark that occurs at a frequency of 10% in the Barnhill collection. This species is known from Triassic deposits in many European countries including Belgium (Duffin and Delsate, 1993; Duffin et al., 1983), France (Cuny et al., 2000) and Luxembourg (Godefroit et al., 1998) as well as the UK (Nordén et al., 2015). Due to the curved, knife-shaped structure of the teeth, it is reasonable to suggest that *R. minor* may have fed on smaller osteichthyans and invertebrates known to have been found in the Rhaetian (Smith et al., 2014).

A single tooth of *Sargodon tomicus* was also found in the Barnhill collection. This species is relatively rare in the Westbury Formation, and is entirely absent from the Cotham Member (Allard et al., 2015).

6.3. Wider comparison

The fish species found at the two sites are typical of the Westbury Formation (Duffin, 1999), and the majority are also the most common in shallow-sea biomes (Storrs, 1994). Associated fossils, such as bivalves and other marine invertebrates have been noted in association with similar vertebrate faunas from other localities nearby (Reynolds and Vaughan, 1904; Nordén et al., 2015; Allard et al., 2015) and from other parts of the region (Richardson, 1906; Korneisel et al., 2015). However, because the fossiliferous sediment was treated with acetic acid, invertebrate remains were likely to have been damaged or destroyed, and so were not reported here.

In our comparison of faunas, we established two points, namely (1) that most of the basal bone bed samples showed essentially identical faunal compositions, and (2) the railway cutting assemblage showed most differences from the others. We have over 1000 identified specimens from this latter assemblage, so it is not likely to be simply a question of sample size. However, we cannot rule out that other sampling biases might have come into play, such as some selectivity in preservation of remains, or in the collection and processing procedures used by Mike Curtis. Perhaps, however, the human aspect was minimal because Curtis, so far as we know, applied the same methods in all his field and laboratory work, and so would not have used some different means of excavation or different methods of chemical treatment or sample sieving, but we cannot prove that. So, perhaps there was some taphonomic sorting of fossil remains before deposition, and the sporadic wedging in and out of the basal bone bed along the railway cutting, reported by Reynolds and Vaughan (1904) might be slight evidence in support of such a tentative conclusion.

How typical are these British faunas when compared with those from elsewhere in Europe? We compare the composition of the

Table 4
Wider comparison of Rhaetian fish faunas based upon personal observations and Allard et al. (2015), Duffin (1980a,b), Duffin and Delsate (1993), Duffin et al. (1983), Godefroit et al. (1998), Korneisel et al. (2015), Nordén et al. (2015), Sykes et al. (1970). GB = Great Britain, B = Belgium, L = Luxembourg.

Group	Taxon	Barnhill Quarry (GB)	Chipping Sodbury Railway Cutting (GB)	Manor Farm Quarry (GB)	Marston Road (GB)	Holwell Quarry (GB)	Chilcompton (GB)	Charton Bay (GB)	Barnstone (GB)	Habay-la-Vieille (B)	Attert (B)	Syren (L)
Hybodontiformes	*Lissodus minimus*	X	X	X	X	X	X	X	X	X	X	X
	Lissodus lepagei											X
	Hybodus cloacinus	X	X	X	X	X			X	X	X	X
	Palaeobates reticulatus					X						
Neoselachii	*Rhomphaiodon minor*	X	X	X	X	X	X	X	X	X	X	X
	Duffinselache holwellensis			X	X	X	X	X		X		
	Synechodus rhaeticus				X	X				X		X
	Nemacanthus fin spines		X			X	X		X	X		X
	Vallisia coppi			X		X				X		
	Pseudodalatias barnstonensis			X	X				X	X	X	
	Pseudocetorhinus pickfordi			X	X	X		X		X	X	X
	Parascylloides turnerae								X			
Holocephali	*Agkistracanthus mitgelensis*					X						
	Holocephalan scales	X	X	X	X	X		X	X			
Osteichthyes	*Gyrolepis albertii*	X	X	X	X	X	X	X	X	X	X	X
	Severnichthys acuminatus	X	X	X	X	X	X	X	X	X	X	X
	Sargodon tomicus	X		X	X	X	X	X	X		X	X
	Lepidotes sp.			X	X			X				
	Dapedium sp.							X				?
	cf. *Colobodus*				X	X				X	X	
	Indet. coelacanth (quadrates)			X		X						
	Ceratodus latissimus	?							?			

Barnhill Quarry and Chipping Sodbury railway cutting ichthyofaunas with those sampled from other Rhaetian sequences in the West Country, the East Midlands and further afield in continental Europe (Table 4). Only those faunas which have been directly examined by us, or which have been the subject of good quality illustration have been included so as to avoid any significant variation in taxon identification. It is clear that some species are extremely rare in the Rhaetian as a whole, being recorded at very few localities and in small numbers (e.g. the sharks *Palaeobates reticulatus*, *P. turnerae*, *Vallisia coppi*, the holocephalans *Agkistracanthus mitgelensis* and *Myriacanthus paradoxus*, and coelacanths and dipnoans). Some species are based on occasional records outside their standard time range; *Lissodus lepagei* was originally described from the Norian of Medernach in Luxembourg (Duffin, 1993a) but has since been recorded at Syren, Lorraine-Luxembourg by Godefroit et al. (1998).

H. cloacinus, which ranges into the Lower Jurassic (Hettangian to Sinemurian of Lyme Regis; Duffin, 1993b), is widely distributed but, having rather large teeth that are subject to taphonomic filtering, is usually a minor component of Rhaetian vertebrate faunas. The teeth of *L. minimus* and *R. minor* may vary in frequency but are ubiquitous components of the Rhaetian fish fauna. The teeth of *Pseudodalatias barnstonensis*, *Duffinselache holwellensis*, *Pseudocetorhinus pickfordi* and *Synechodus rhaeticus*, although not so widespread or common as the former two species, are nevertheless sufficiently well represented across a range of localities to be counted amongst the shark species which are useful indicators of deposits of Rhaetian age.

7. Conclusion

The geographic proximity of the sites from which these collections were gathered, located about 1 km apart, was an important driver of this study and, unexpectedly, the relative proportions of taxa differ substantially. Not only do these faunas differ statistically from each other according to several standard ecological indices, but the Chipping Sodbury railway cutting fauna was found to be substantially different from a number of other Rhaetian basal bone bed faunas reported from Devon to Gloucestershire, a distance of 150 km, whereas these faunas all show considerable resemblances to each other. This anomaly cannot immediately be investigated as the site is now densely overgrown and, being within a deep cutting of an active railway line, is not readily accessible. If equal samples of Rhaetian sediment could be obtained from each of the five sites investigated here, and possibly from other well-known sites, then this hypothesis of sampling bias could be tested.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at http://dx.doi.org/10.1016/j.pgeola.2016.02.010.

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