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Microvertebrates from the Rhaetian basal bone bed of Saltford, near Bath, SW England



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ABSTRACT

The famous Rhaetian bone bed (Late Triassic, 205 Ma) is well known because it marks a major switch in depositional environment from terrestrial red beds to fully marine conditions throughout the UK and much of Europe. The bone bed is generally cemented and less than 10 cm thick. However, we report here an unusual case from Saltford, near Bath, S.W. England where the bone bed is unconsolidated and up to nearly 1 m thick. The exposure of the basal beds of the Westbury Formation, Penarth Group includes a bone bed containing a diverse Rhaetian marine microvertebrate fauna dominated by sharks, actinopterygian fishes and reptiles. Despite the unusual sedimentary character of the bone bed, we find similar proportions of taxa as in other basal Rhaetian bone beds (55–59 % *Lissodus* teeth, 13–16 % *Rhomphaiodon* teeth, 12–14 % *Severnichthys* teeth, 6–9% *Gyrolepis* teeth, 3–4% undetermined sharks' teeth, 1–3% undetermined bony fish teeth, and < 1% of each of *Hybodus*, *Parascylloides*, and *Sargodon*), the only differences being in the proportions of *Rhomphaiodon* teeth, which can represent 30–40 % of specimens elsewhere. This suggests that taphonomic bias of varying Rhaetian bone beds may be comparable despite different sedimentary settings, and that the proportions of taxa say something about their original proportions in the ecosystem.

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1. Introduction

The Rhaetian (205.5–201 Ma) is the final stage of the Triassic, and in Europe this corresponds to a continent-scale marine transgression. The base of the Westbury Formation of the Penarth Group in the U.K. is generally marked by a bone bed comprising in some cases large pebbles of locally derived Blue Anchor Formation, the underlying unit, as well as transported bone pebbles and coprolites, as well as microscopic teeth and bones. The bone bed is usually indurated, being cemented by calcite, as seen at the classic Aust Cliff site (Cross et al., 2018). The bone bed is usually interpreted as having been deposited by storm activity, as the advancing marine beds flooded the landscape, from western England to Poland, and churned and reworked the new, developing sea-bed (Macquaker, 1999).

In the area around Bristol, the Late Triassic landscape comprised a topography of eroded Carboniferous Limestone, forming hills and lowlands. The Rhaetian sea flooded over the lower-lying areas, some already filled with red beds of the Mercia Mudstone Group, as at Aust, and others comprising bare surfaces of Carboniferous limestone, as at Vallis Vale (Ronan et al., 2020). As sea levels rose, the Mesozoic sediments accumulated around the shorelines, leaving the Carboniferous hills as islands in a new archipelago, lying at the time in tropical latitudes.

The sharks, bony fishes and marine reptiles, primarily ichthyosaurs, of the day were key elements of new ecosystems in the shallow seas where there had previously been evaporitic sabkhas and dinosaurs trotting around. In the turbulent times of sea level rise, the vertebrates died, and their carcasses fell to the bottom. Meanwhile brachiopods, bivalves, gastropods, crinoids, and barnacles attached to rocks and developed new shoreline and lagoonal communities (Ronan et al., 2020). Shrimps burrowed in the hardgrounds formed by consolidated sediments of the underlying Triassic sediments (Korneisel et al., 2015).

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Occasional tropical storms (Macquaker, 1999) whipped up the waves, tearing invertebrates from the rocks and sediment, and churning the carcasses of sharks and ichthyosaurs. Masses of fossil-rich sediment were washed up and down the beach as tides rushed in and out, and storms sifted out the sand and mud, often leaving concentrated masses of bones, some larger specimens perhaps transported for a considerable distance and abraded into rounded pebbles. Trapped between these larger specimens are delicate teeth and bones that had not been transported so far (Cross et al., 2018). Coprolites became invested with calcium phosphate from the sheer concentration of bones, and then generally the whole bone bed was buried under later mudstones, sandstones, and limestones, and the weight of overlying sediment, and passage of mineral-rich waters often invested the bone bed with a cement largely of calcium carbonate. The classic, cemented basal bone bed of the Westbury Formation, as at Aust, occurs as a discontinuous bed, ranging from 0 to 20 cm in thickness.

The situation is different at Saltford, near Bath. Here the bone bed is an order of magnitude thicker, 0.89 m, and it is not indurated. The aim of this paper is to describe the sedimentology and palaeontology of the Saltford bone bed and to seek to understand how it fits the general model for deposition of the Rhaetian. Importantly, we use this unusual occurrence of the Rhaetian basal bone bed to test how far the proportions of fossils of different taxa might be a result of taphonomic versus ecological processes.

2. Geological setting

The Rhaetian bone bed at Saltford has not been reported before. Over the years, many geologists have described the Lias at Keynsham and Saltford (e.g. Buckland and Conybeare, 1824, pp. 300–302; Vaughan and Tutchter, 1903; Tutchter, 1923; Donovan, 1956), notably from the Saltford railway cutting (ST 685671–681676) and the Saltford Midland Region cutting (ST 686678), both described by various authors in Victorian times and summarised by Donovan (1956, pp. 184–188). In fact, the Saltford railway cutting is the type section for the Saltford Shale Member of the Blue Lias Formation, Hettangian in age (Donovan, 1956; Donovan and Kellaway, 1984; Ambrose, 2001), which overlies the Wilmcote Limestone Member, which in turn overlies the Penarth Group (Rhaetian) succession. The Saltford successions then begin above

the Rhaetian-Lias contact, and indeed Reynolds and Vaughan (1904, p. 211) noted that “no true Bone-bed has been recorded at the Rhaetic sections of . . . Saltford . . .”.

The Rhaetian was identified, however, on the Midland Railway section at Tennant's Wood, Saltford (ST 689671) by Bristow et al. (1873, section 10). These authors (Fig. 3A) record 6 ft. (1.8 m) of ‘Black Paper-shales, weathering rusty’, identified here as the Westbury Formation, overlying 4 ft. (1.2 m) of ‘Soft, green marls’, identified here as the Blue Anchor Formation, but they make no mention of any fossils, and yet this corresponds to the section we observed at Folly Wood (Fig. 3B). This location now lies on the Bristol and Bath Railway Path, about 1 km north-east of Folly Wood.

The Rhaetian bone bed exposure at Folly Wood, Saltford (NGR ST 681661; Fig. 1), was first discovered by one of the authors, Simon Carpenter (S.C.) in the late 1970s. It was found when he visited a local badger sett and chanced upon a lump of fossil-rich clay at the surface packed with small fish teeth and scales. This prompted a more thorough search of the site and much to his surprise and delight, he discovered a layer of clay in a tunnel entrance at the far end of the site. The in-situ clay could only just be reached at arm's length.

The badger sett is located on the lower slope of Folly Wood in an area of mixed deciduous woodland occupying a valley on the south-west edge of Saltford (Fig. 1). The head of the valley forms part of Saltford Golf Course and this in turn is part of the Duchy of Cornwall Estate.

Over the next decade or so, S.C. collected a number of bagged samples of the bone bed to sieve and process at home. In 1984, he contacted Christopher Duffin (C.D.), who identified over a dozen species of fishes and reptiles from the bone bed. This early collection of fossils from Folly Wood was then given to the late Mike T. Curtis, a Gloucester geologist with a passion for Rhaetian microvertebrates who then donated it to Bristol Museum in 1997. Then, in summer 2018, a controlled excavation was made at the original badger sett site (Fig. 2), when S.C. and C.D. directed a group of students from the University of Bristol, who bagged up 50 kg or more of the soft sediment in the bonebed layer, dividing the samples into five levels (Fig. 3B). This material forms the basis of the current paper.

At Folly Wood, a natural linear outcrop of limestone occurs along the upper part of the wooded valley (Fig. 1). Although the

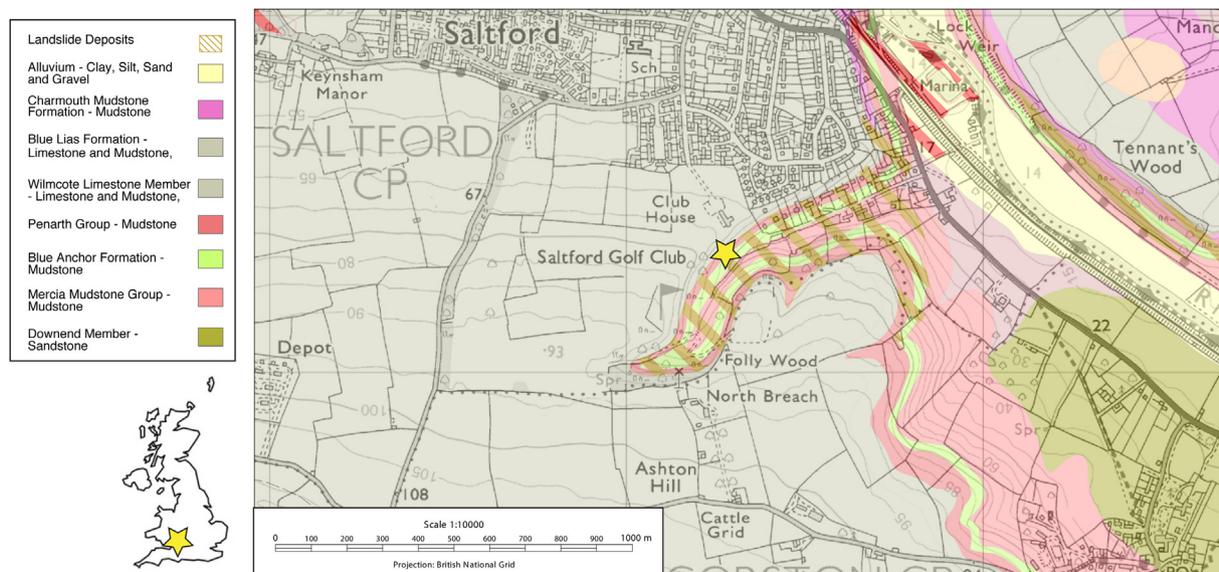


Fig. 1. Geological map of Saltford and the Folly Wood locality at Saltford Golf Course, and the Late Triassic stratigraphic succession in the deep gorge cut into the Lias. © Crown Copyright and Database Right 2017. Ordnance Survey (Digimap Licence).



Fig. 2. Excavating the Rhaetian section on the east slope of the Folly Wood gorge in summer 2018, showing M.J.B. in the excavated hole (A), the upper part of the Westbury Formation basal bone bed (B), and the lower part of the bone bed section (C). The scale bar is marked in 10 cm segments. Photographs by C.J.D.

outcrop is heavily vegetated, there are a few places where the sequence can be examined. At one locality, several metres above the 'bone bed' horizon, the 'Sun Bed' is seen, a conspicuous, pale, fine-grained limestone that has a characteristic flat erosion surface with abundant burrows (*Diplocraterion*, *Arenicolites*). The 'Sun Bed' marks the top of the Langport Member (formerly White Lias) in the area. The Langport Member is the upper division of the Lilstock Formation, which in turn is the upper division of the Penarth Group, overlying the Westbury Formation, at the base of which is the bonebed. The limestones and mudstones above the 'Sun Bed' are the pre-Planorbis beds and basal limestones of the Lias Group.

A few metres below the 'bone bed' horizon, and exposed in some of the tunnel entrances, is a pale, weathered, creamy sandstone. This has been identified as the sandstone bed at the top of the Blue Anchor Formation and part of the Mercia Mudstone Group. Between the sandstone bed at the top of the Blue Anchor Formation and the earliest Jurassic rocks, a late Triassic (Rhaetian) succession occurs (Fig. 3B). This includes the Westbury Formation and Cotham Member of the Lilstock Formation as well as the

Langport Member. Although we are uncertain of the thickness of these units at Folly Wood, their occurrence is at least confirmed by the digging activities of the badgers.

The bone bed (Fig. 3B) consists of a sandy clay containing abundant fish and reptile remains. The clays are weathered and oxidized and, although the majority of fossils are small, they can still be seen with the naked eye in hand specimens. The base of the bone bed contains coarser elements including coprolites, larger fragments of bone and small phosphatic concretions. Fragments of crinoid ossicles have been found in the bone bed and are likely to have been derived from the underlying Carboniferous limestone which would have been the source of some of the clastic material entering the lower Rhaetian depositional environment.

The faunal elements of the bone bed are generally well preserved. The small white borings on the surfaces of some of the teeth could be modern, or could indicate prolonged exposure and bioturbation on the sea floor before final incorporation into a bone bed. All the fossils show signs of abrasion (incomplete

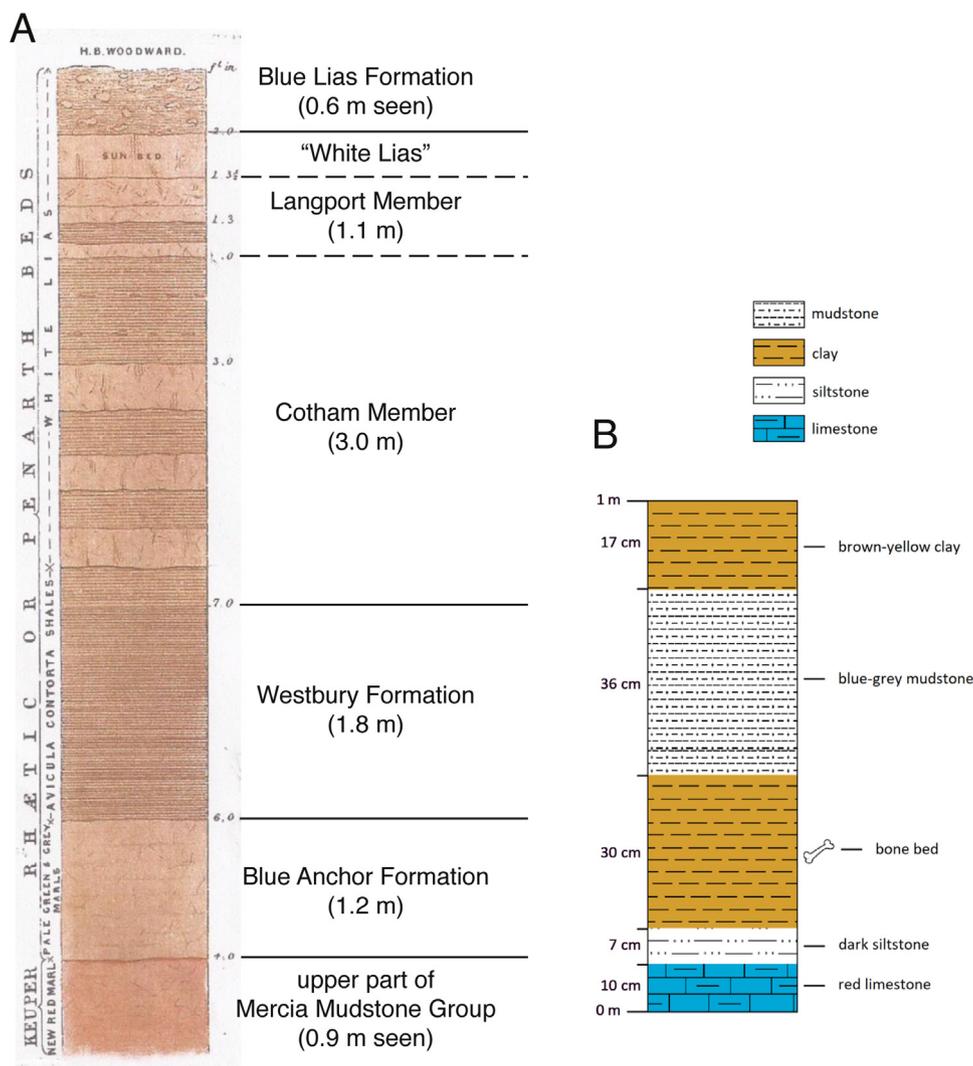


Fig. 3. Rhaetian sections at Saltford. (A) Section from Tennant’s Wood, from Bristow et al. (1873). (B) Section measured in the Folly Wood gorge in summer 2018, showing a calcareous sandstone of the Blue Anchor Formation at the base, overlain by the bone bed, and then mudstone units above. Numbers 1–5 mark the locations of five samples taken from different levels through the 89-cm thick bone bed.

specimens with rounded or eroded surfaces) and sorting by currents (the fossils fall into a very similar size range). Many teeth display wear facets.

3. Materials and methods

The unconsolidated arenaceous clay of the bone bed was processed in the laboratories of the Palaeobiology Research Group at the University of Bristol. Standard procedures were used, although acid was not required because the bone bed material was unconsolidated. The sediment was initially soaked in boiling water, and the heating of the clay was enough to dissociate it. Then for each of the five sampling levels the sediment was passed through a stack of sieves, at sizes 2 mm, 500 μm and 180 μm. A great deal of hot water was required to remove the clay from the microfossils. The washed sediment was drained through filter paper and dried, ready for picking.

Picking was done under a binocular microscope, separating all teeth and bones and fossil fragments into small plastic boxes using a slightly wetted, fine paint brush. The teeth were identified where possible or listed as undetermined. Other remains were separated into boxes identified as scales, spines, placoid scales, coprolites, bone fragments and other remains. The identifications were made

by reference to standard sources (e.g. Swift and Martill, 1999) and previous papers describing Rhaetian bone beds. Measurements in the descriptions of fossils were taken to tenths of a millimetre using the eyepiece graticule.

The most complete and typical teeth were photographed in order to show the diversity in terms of species, of morphotypes and of colours, using a Leica DFC425 C camera on an optical microscope with multiple image-stacking software. On average, between 15 and 17 pictures were taken per specimen, and they were fused automatically to produce a single digital image that reduces depth-of-field effects. These pictures were processed with GIMP to remove the backgrounds and with Paint 3D to restore the original colours of the specimens.

The next step was to estimate the relative abundance of each species by counting the numbers of specimens, and we followed the principles laid down in previous studies (e.g. Korneisel et al., 2015; Nordén et al., 2015; Cross et al., 2018). Each tooth, spine, placoid scale or bone fragment was counted as a single individual. Teeth were divided into three categories: complete teeth, incomplete teeth less than 50 %, and incomplete teeth more than 50 % preserved. Furthermore, we determined two levels of abrasion, a low level characterised by surface ornaments that are

noticeable and in relief, with a rough appearance and few digestion markings, and a higher level of abrasion with ornament removed, a smooth look and the presence in some cases of tiny holes or several digestion stains.

4. Systematic palaeontology

4.1. Chondrichthyans

Four distinct chondrichthyan tooth types have been assigned to named taxa, most of which are fairly common in the British Rhaetian, with the exception of *Parascylloides turnerae* (Thies et al., 2014).

4.1.1. *Lissodus minimus* (Agassiz, 1839)

We found 1871 teeth of *Lissodus minimus*, the most common species in the collection, and representing half of all teeth found.

These teeth (Fig. 4A–F) are boomerang-shaped in occlusal view, as is very typical of this species, and their maximum height at the central cusp ranges from 1.0 to 3.5 mm. The crown is elongated and low, with a short, symmetrical and upright central cusp. There are up to four pairs of additional lateral cusplets, smaller, very short and upright. The teeth have a labial peg, a little ball at the base of the central cusp which helped stabilise adjacent teeth in the same tooth file. A horizontal longitudinal ridge runs around the crown base on the crest of the crown shoulder. Roots are very rarely preserved. They are fine, represent 2/5 of the total tooth height and possess numerous small vascular foramina. We observed three variants in the collection: anterior teeth (Fig. 4A, B) which are fine, narrow, smooth, with ornamentation restricted to single, non-branching ridges descending the crown from the cusp apices, especially labially (Fig. 4B), and which are filiform in occlusal and basal views; lateral teeth (Fig. 4C, D) that are more elongated than anterior teeth, with a basally-directed labial peg and more

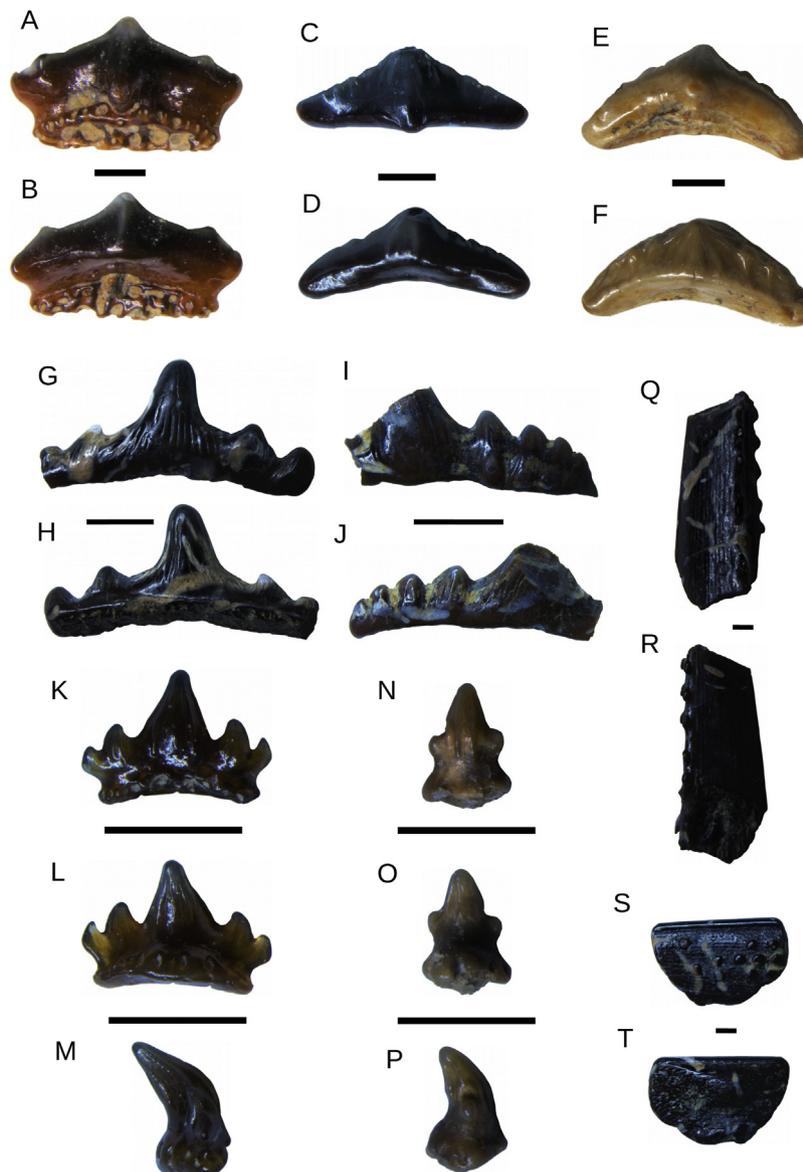


Fig. 4. Chondrichthyan species. A–F, *Lissodus minimus* anterior tooth (A, B: BRSUG 29951–10) and posterior teeth (C, D: BRSUG 29951–50; E, F: BRSUG 29951–11) in labial (A, C, F) and lingual (B, D, F) views. G, H, *Hybodus cloacinus* anterior tooth (BRSMG A27) in labial (G) and lingual (H) view. I, J, *Hybodus cloacinus* anterior tooth (BRSMG A50) in labial (I) and lingual (J) views. K–M, *Rhomphaiodon minor* anterior tooth (BRSUG 29951–32) in labial (K), lingual (L), and lateral (M) views. N–P, *Parascylloides turnerae* anterior tooth (BRSUG 29951–36) in labial (N), lingual (O), and lateral (P) views. Q, R, *Nemacanthus monilifer* dorsal spine (BRSMG B122) in lateral views. S, T, *Nemacanthus monilifer* fragmentary dorsal spine (BRSMG E56) in lateral views. All scale bars equal 1 mm.

numerous and more pronounced vertical ridges on the crown; posterior teeth (Fig. 4E, F) which are thicker, with distinct coronal ridges and which are diamond-shaped in occlusal and ventral views. We also observed intermediate morphotypes, identified as antero-lateral and postero-lateral teeth, matching those morphotypes described in previous studies (Slater et al., 2016; Cross et al., 2018). These tooth morphotypes seemingly represent the full range of monognathic heterodonty displayed by this species (Duffin, 1985). The teeth are generally not well preserved, having sustained a high level of abrasion so that the roots are nearly always missing.

Lissodus minimus was originally placed in the genus *Acrodus* by Agassiz but was reassigned to *Lissodus* (Duffin, 1985). This shark is a common and ubiquitous component of the Rhaetian microvertebrate fauna, having been recorded in all previous studies of the British Rhaetian bone beds. The fishes were durophagous, as indicated by the morphology of their teeth and they probably fed on benthic shelled invertebrates (Allard et al., 2015).

4.1.2. *Hybodus cloacinus* (Quenstedt, 1858)

We found 15 teeth of *Hybodus cloacinus* (Fig. 4G–J). This taxon is uncommon in our collection, but S.C. found more during his explorations. The isolated teeth are elongate (Fig. 4G, H) and have a high crown. The central cusp is lingually inclined and surrounded by up to four pairs of lateral cusplets that decrease in size the further they are from the central cusp, themselves lingually inclined too (Fig. 4I, J). The ornamentation comprises a series of vertical ridges, as in the other species like *Rhomphaiodon minor* and *Parascylloides turnerae*. They have quite large vascular foramina punctuating the root on the lingual side, and smaller foramina labially. The abrasion level of these teeth is generally high.

This taxon was referred to *Polyacrodus* by Quenstedt (1858), a genus which remains poorly defined, but the species was referred to *Hybodus* by Duffin (1999, p. 196). This species has been found in all previous studies of the British Rhaetian bone beds, but always in small quantities. It is present throughout the Rhaetian of western Europe (Duffin and Delsate, 1993) and ranges into the overlying Hettangian (Duffin, 1993). The number and shape of the central cusp and lateral cusplets indicate very probably a carnivorous diet.

4.1.3. *Rhomphaiodon minor* (Agassiz, 1837)

We found 543 teeth of *Rhomphaiodon minor*, another common Rhaetian species, representing 17 % of all teeth found (Fig. 4K–M). They show a great range of sizes, from tiny undamaged specimens to larger abraded specimens, ranging in maximum basal width from 0.8 to 6 mm and height of central cusp of 0.5–7 mm, and appear to be narrower than those from the Marston Road bone bed (Nordén et al., 2015). The crown bears two lateral cusplets (Fig. 4K, L) on either side of the high central cusp, mostly symmetrical and curved lingually (Fig. 4M). The ornamentation comprises a series of sparse vertical ridges extending from the apex of the central cusp to the base of the crown. Roots are generally quite well preserved, thick and represent around 30 % of the tooth height at the central cusp. They have between five and nine large vascular foramina for blood irrigation on the lingually extended part of the root and they are crescent-moon-shaped in ventral view. Teeth of this species show a wide range of abrasion, with the lateral cusplets often missing.

A remarkable feature of the Folly Wood collection is that there are so many tiny teeth of this species, in the size range of 0.5–1.0 mm high central cusps. These tiny examples are preserved in two ways, some as deep-orange, honey-coloured, semi-transparent specimens, similar in appearance to the various denticles and placoid scales, and others as yellowish-white specimens. In nearly all cases, many are complete and show little sign of abrasion. Larger

examples are nearly all abraded, with no sharp edges or points, and colours are white, black and mottled.

This species was named *Hybodus minor* by Agassiz (1837), but the genus was reviewed by Cuny et al. (2000) and they incorporated it into the genus *Rhomphaiodon*, and in doing so transferring it from the hybodonts to the neoselachians. These sharks have been found in all previous sites and studies on the British Rhaetian. The shape of the teeth, sharpened for piercing and catching prey and curved to avoid their escape, indicate their carnivorous diet (Cross et al., 2018).

4.1.4. *Parascylloides turnerae* Thies et al., 2014

We found 35 teeth of *Parascylloides turnerae*. This is the third occurrence of this species in the United Kingdom (Fig. 4N–P), and it is quite a rare component of the Rhaetian microvertebrate fauna. The teeth are high-crowned, but tiny, typically 0.8–2.5 mm in maximum height (Fig. 4N, O). The crown has a long central principal cusp, symmetrical and significantly recurved lingually (Fig. 4P), with one pair of additional cusplets whose bases are fused with that of the central cusp. The ornamentation of the central cusp comprises a few superficial vertical ridges running from the apex of the cusp to the crown/root junction. Roots are most of the time quite well preserved and represent around 25 % of the tooth height at the central cusp. They are very thick and have few vascular foramina. They form a protuberance lingually and are spherically shaped in basal view. The teeth of this species are in reasonably good preservation, showing minor abrasion.

This rather rare species was previously recorded from two localities in Germany (Thies et al., 2014; Sander et al., 2016). In the UK, it has previously been reported from two localities, from a former railway cutting through a section of Rhaetian and Lower Lias sediments, about 0.8 km east of the village of Barnstone, Nottinghamshire (Thies et al., 2014), and then about 30 specimens were noted in large collections from the Aust Cliff bone bed (Cross et al. 2018, p. 645). Before these discoveries, Agassiz (1837) identified these teeth as symphyseals or parasymphyseals of *Rhomphaiodon minor* (Thies et al., 2014, p. 1). Their morphology also shows some similarities to the upper teeth of *Pseudodalatias barnstonensis*, with which it might be confused (Sykes, 1974); the morphologies displayed by these teeth suggest that this species may also have been carnivorous.

4.1.5. *Nemacanthus monilifer* Agassiz, 1837

We found several chondrichthyan spines too but cannot assign them to a particular taxon. However, one spine type can be identified (Fig. 4Q–T). One specimen (Fig. 4Q, R) is elongate, with a narrow anterior margin, and denticulated posterolateral margins flanking the rather thicker posterior face of the spine. The spine has the shape of an isosceles triangle in cross section. Both lateral faces have longitudinal striations, and some fragments (Fig. 4S, T) also show geometrically arranged enamelled tubercles.

Spines of *Nemacanthus* were reported by Agassiz (1833–43), in the earliest descriptions of Rhaetian bone bed fish remains, and he identified two species, *N. monilifer* and *N. filifer*. Our specimens correspond to the middle-distal portion of the spine (Agassiz, 1833–43; see also Cross et al., 2018, Fig. 4f); in the complete spine, the proximal half lacks marginal denticulation, whereas the distal portion is exposed and denticulated on the posterior margin. *Nemacanthus* is a palaeospinacid shark, a group close to the base of Neoselachii, and they were large predators that probably fed on the hybodontoids and other fishes. In life, the spines sat in front of the two large dorsal fins, with the thin anterior margin acting as a cut-water, and the broader, posterior margin attached to the fins supported on multiple series of vertical ceratotrichia (Maisey, 1977).

4.1.6. Other chondrichthyans remains

4.1.6.1. Denticles. We found 145 denticles in roughly equal proportion at the different levels, but they are quite uncommon. Because various shark teeth are abundant components of the fauna, shark denticles should also be abundant (Cavicchini et al., 2018). However, the denticles are tiny and so could either be missed during sieving or fossil picking (although we made a special effort to retain and search the finest-grained residues from washing) or might be removed from the bone bed by winnowing under reasonably active currents.

Isolated denticles cannot be referred to a particular taxon because of their great variability in morphology depending on the age of the shark and their place on the body (Duffin, 1999). Therefore, they are described as three morphotypes according to shape, all of which were originally described by Reif (1978).

4.1.6.1.1. Placoid (neoselachian) scales. This first denticle type (Fig. 5A, B) consists of a crown placed on a pedicle attached to a basal structure (Johns, 1996), and measuring 1.0 mm along its

longest axis, but with smaller examples as little as 0.2 mm. The base is flat and rhomboidal or ellipsoidal with a small pedicle that is smooth or ridged. The crown is leaf-shaped, inclined backward, has a rounded margin and possesses a series of longitudinal, non-branching, fine ridges on the upper surface of the scale. These scales show considerable variability, with different degrees of development of the ridges and irregular edge of the crown. These denticles are typical of neoselachian sharks and pre-Rhaetian hybodonts (Landon et al., 2017).

4.1.6.1.2. Hybodontiform scales. Hybodontoid scales (Fig. 5C–E) consist of a shallow, flared base which has a larger diameter than the unicuspid crown which it supports, and they measure about 1 mm wide. The robust, upright crown sits more-or-less directly on the base with only a shallow pedicle between them. Stud-like in overall shape, the crown possesses a single, blunt cusp. Coarse, non-branching vertical ridges radiate from the cusp apex and descend the cusp sides, terminating just above the top of the pedicle. Despite the excellent quality of preservation, these scales cannot be assigned to a particular hybodont taxon, although

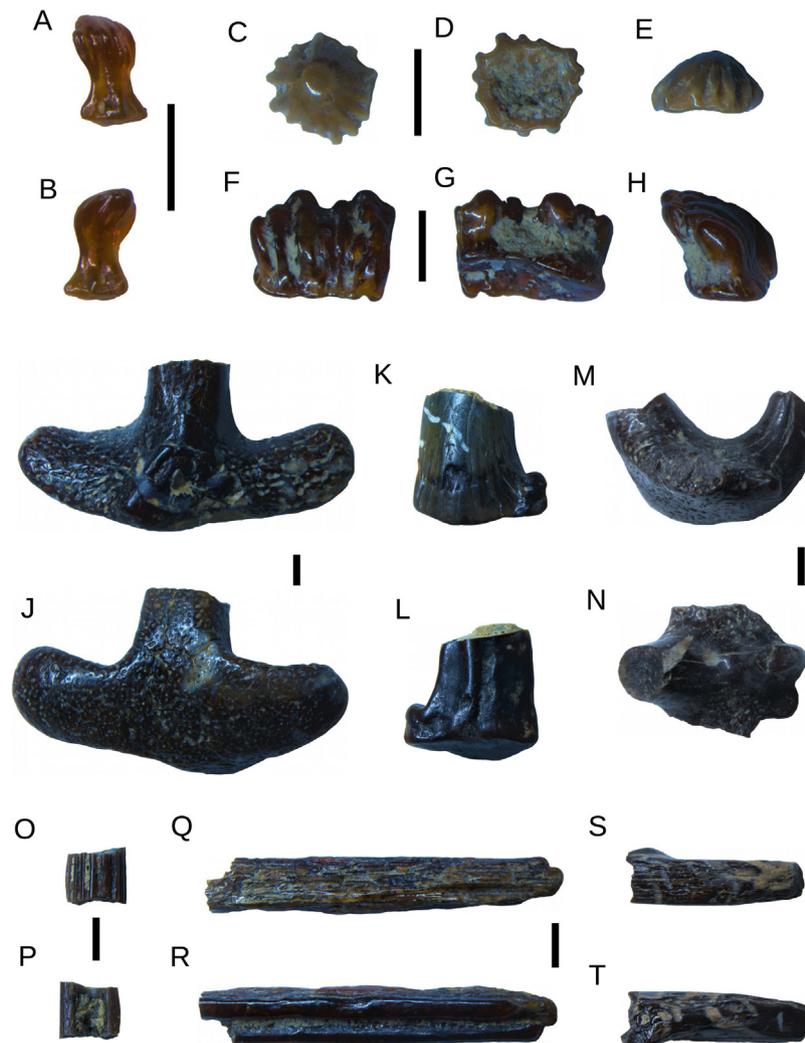


Fig. 5. Other chondrichthyan remains, denticles (A–H) and hybodont dorsal spines (I–P). (A, B) Placoid scale (BRSUG 29951-61-1) in lateral views. (C–E) Hybodontoid scale (BRSUG 29951-61-2) in dorsal (C), ventral (D), and lateral (E) views. (F–H) Ctenacanthid scale (BRSUG 29951-61-3) in posterior (F), anterior (G), and lateral (H) views. (I–L) Hybodont cephalic spine, basal part (I, J: BRSMG B119) in anterior (I) and posterior (J) views, and broken spine (K, L: BRSMG A15) in anterior (K) and posterior (L) views. (M–T) Hybodont dorsal spines, fragmented segment (M, N: BRSUG 29951-62-1) in exterior (M) and interior (N) views, broken spines (O, P: BRSUG 29951-62-2; Q, R: BRSUG 29951-62-3; S, T: BRSUG 29951-62-4) in lateral views. All scale bars equal 1 mm.

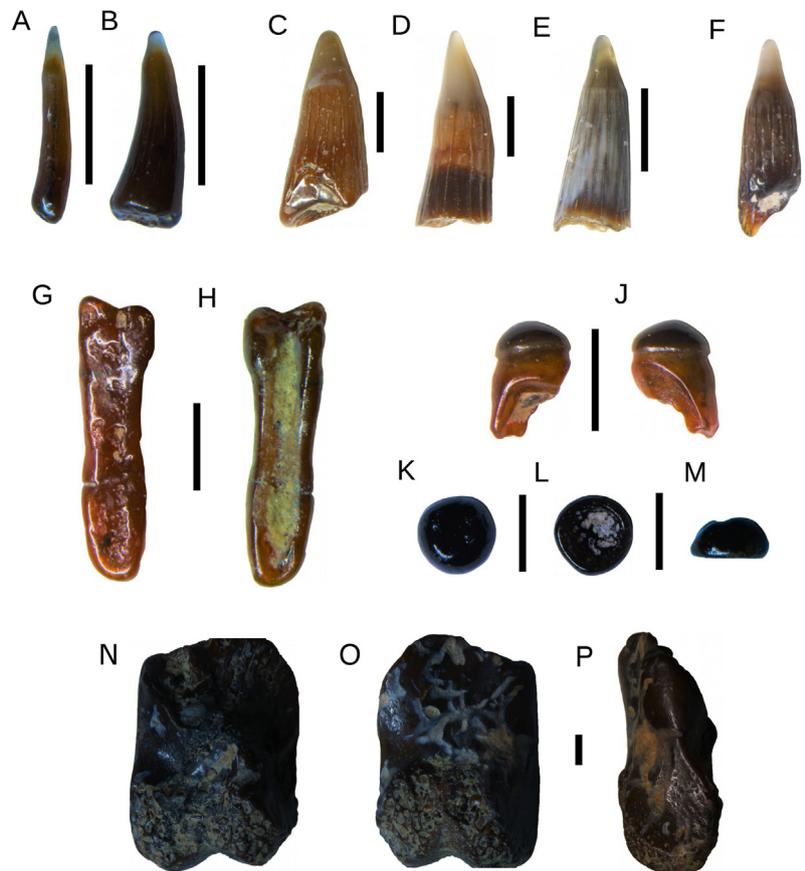


Fig. 6. Actinopterygian teeth and jaw fragments. (A, B) *Gyrolepis albertii* teeth (A: BRSUG 29951-54; B: BRSUG 29951-55) in lateral views. (C–E) *Severnichthys acuminatus* teeth, (C–E) *Birgeria acuminatus*-type (C: BRSUG 29951-16; D: BRSUG 29951-17; E: BRSUG 29951-18) in lateral view. (F) *Saurichthys longidens*-type (BRSUG 29951-19) in lateral view. (G–M) *Sargodon tomicus* teeth; (G, H) incisoriform tooth (BRSUG 29951-21) in labial (G) and lingual (H) views; (I, J) molariform tooth (BRSUG 29951-22) in lateral views; (K–M) molariform tooth (BRSUG 29951-58) in lateral (K), occlusal (L), and ventral (M) views. (N–P) Coelacanth quadrate fragment (BRSMG C1) in posterior (N), anterior (O) and lateral (P) views. All scale bars equal 1 mm.

Hybodus cloacinus and *Lissodus minimus* must be strong candidates.

4.1.6.1.3. Ctenacanthid scales. The bases of the third kind of denticle (Fig. 5F–H) are rectangular, concave, short and laterally elongated and the pedicle is very short; they measure 1–2 mm along their longest axis. The crown is multicuspoid, anteroposteriorly flattened, and inclined backward. It is strongly grooved and irregular in terms of shape and number of cusps. These cusps are erect, curved and laterally connected. They also have a pronounced ornamentation with vertical striations running from the base of the denticle to the apex. This identification is problematic because ctenacanth sharks are not found at the end of the Triassic (Cavicchini et al., 2018; Cross et al., 2018).

4.1.6.2. Cephalic spines. The hybodont cephalic spines are composed of two parts, a base and a spine (Fig. 5I–N). There is one reasonably complete specimen that shows an overall T-shaped, tri-radiate base comprising three equally-wide branches each 4–5 mm in diameter (Fig. 5I, J). These branches have rounded ends and bend slightly. The surface is rough and very porous (Fig. 5I). At the junction of these three branches there is a foramen (Fig. 5J). The spine is flattened laterally and curved backwards (Fig. 5M). It has one pair of lateral cusplets located at its base (Fig. 5K, L). The full shape is slightly asymmetrical and consists of a four-branched spine (Fig. 5N).

Hybodont cephalic spines are rare at Saltford and they have not commonly been noted in the UK Rhaetian bonebeds, with an older record from Aust Cliff (Duffin, 1982, p. 2).

4.1.6.3. Dorsal spines. Many fragments of dorsal spines have been found (Fig. 5O–T). They are very long and thin cylinders with a rounded end, but this could be a result of abrasion (Fig. 5Q, R). They have longitudinal and very pronounced ridges. Sometimes they have some cusplets along one margin (Fig. 5S, T). These spines probably belonged to hybodont sharks.

4.2. Osteichthyans

Four distinct actinopterygian tooth types are identified, all of which have been reported commonly from other Rhaetian bone beds. In addition, we report a coelacanth quadrate and abundant actinopterygian scales, fin ray elements, vertebral hemicentra, and fin spines.

4.2.1. *Gyrolepis albertii* Agassiz, 1835

Gyrolepis albertii is represented by 362 acutely pointed and slightly curved isolated teeth, ranging in length from 0.5 to 3.0 mm (Fig. 6A, B). They consist of a very fine tip, long, symmetrical and curved backwards towards the inside of the mouth of the fish. They vary greatly in thickness and are ornamented by superficial and fine vertical lines from the apex to the base. The tips of these teeth are very sharp and translucent, representing around 20 % of the

total tooth height. Teeth of *Gyrolepis* are found in good quantity, and most of the time sites where they are found also present a huge quantity of scales, but they cannot be assigned confidently to this taxon. The majority of these teeth are broken or incomplete and their striations are often not visible as a result of high abrasion.

Gyrolepis albertii is very common in the British and continental European Rhaetian and was found in every previous geological site, but of the six named species of *Gyrolepis*, only this one has been found in the Penarth Group (Davis, 1871). Moreover, the teeth of this species are often the most abundant in the samples. Their sharpness suggests they belonged to a carnivore that dealt with slippery prey, thus probably fishes that were smaller than them.

4.2.2. *Severnichthys acuminatus* (Agassiz, 1835)

This is the most common species of actinopterygian we found at our site (Fig. 6C–F), with a total of 570 teeth, representing around 17% of all the teeth found, and ranging in height from 0.4 to 10 mm. There are two morphotypes of *Severnichthys acuminatus*: the *Birgeria acuminata* type (Fig. 6C–E), with a distinct tip forming up to the half of the total tooth height, a massive appearance, quite thick and sometimes curved; and the *Saurichthys longidens* type (Fig. 6F), with a shorter sharp, translucent tip comprising up to 20% of the tooth. These teeth are quite elongate, more delicate than the *Birgeria*-type specimens and sigmoidally curved. This morphotype can be confused with *Gyrolepis albertii*, but there is a more obvious 'shoulder' between the clear, acrodin tooth tip and the main portion of the crown. The ornamentation is vertical, characterised by strong non-branching ridges running from the limit between the acrodin tip and the rest of the tooth to the base.

Originally, these two morphotypes were classified as two separate species, based on their different morphologies (Stensiö, 1925), but Storrs (1994) reported a jaw containing both types and he combined them into the new genus, *Severnichthys*. This is the second most common actinopterygian species in the British Rhaetian bone beds. These fishes were carnivorous predators, as indicated by their very sharp teeth, and probably ate a large variety of fishes.

4.2.3. *Sargodon tomicus* Plieninger, 1847

Sargodon tomicus is represented by 25 teeth from Saltford, ranging in maximum diameter from 0.7 to 4 mm (Fig. 6G–M). We

found two types of teeth, incisiforms and molariforms. The incisiform teeth (Fig. 6G, H) are long, flat, and excavated longitudinally on both labial and lingual sides by heavy post-mortem wear (Fig. 6H). Molariform teeth (Fig. 6I–M) are concave hemisphere-shaped (Fig. 6M), like a turned over bowl supported by brown basal portions (Fig. 6I, J). Their crowns are convex in occlusal view (Fig. 6K) and concave in ventral view (Fig. 6L), and they are all black, round, shiny, irregular and smooth punctuated by very small holes on the occlusal surface, representing the exposure of characteristic cavities in the dentine by wear. These teeth have no ornamentation. Most of these teeth from Saltford are incomplete and highly abraded.

Sargodon is known also from the Rhaetian of Germany and was named by Plieninger (1847). It has since been found throughout northwest Europe, but also in the Norian of Italy (Tintori, 1983). *Sargodon* has been reported in every previous British Rhaetian study, but usually occurs in very small numbers. The molariform teeth suggest a durophagous diet adapted to eating shells and other invertebrates by breaking and crushing (Tintori, 1983).

4.2.4. *Coelacanth* sp

One isolated bone fragment has been found that we identify as a partial quadrate of a coelacanth (Fig. 6N–P). The upper portion is nondescript, but at the lower edge is a double process with an arch between, and this matches the morphology of the heavily built articular surface of a quadrate bone into which the corresponding joint surface of the mandible would have fitted. This double condyle for articulation with the lower jaw is typical of coelacanths (Cavin and Grădinaru, 2014). Coelacanth remains are rare in the Penarth Group, previously known from Holwell (Duffin, 1999), Blue Anchor Point, Somerset (Hauser and Martill, 2013), and Manor Farm (Allard et al., 2015), so this is the fourth record.

4.2.5. Other actinopterygian remains

4.2.5.1. *Scales*. Collectively, more than 2000 actinopterygian scales have been found in our samples. They are generally rhomboid in shape, extended along the diagonal axis, and with angles that range from reasonably sharp to rounded (Fig. 7A–D). The long axis lengths are 1–5 mm. The internal and external

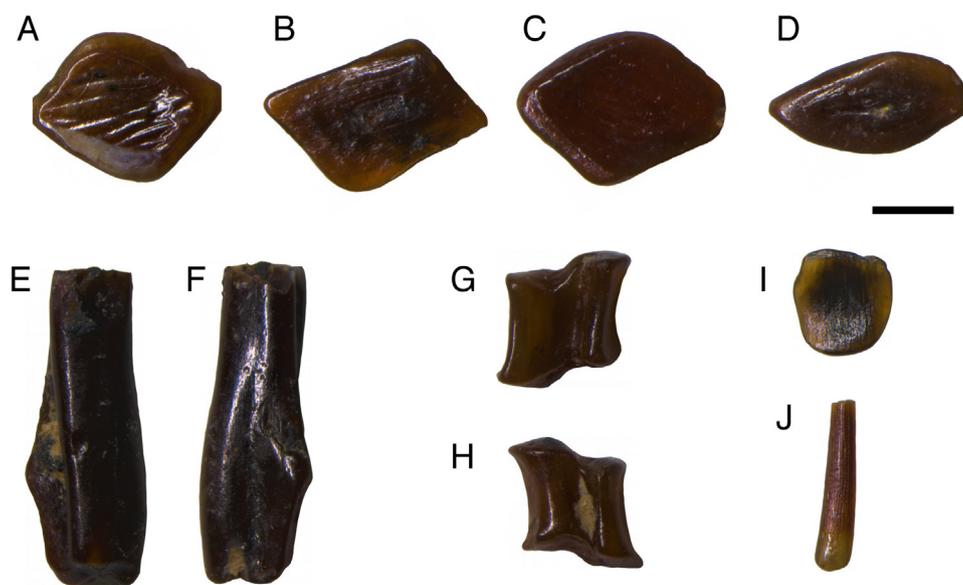


Fig. 7. Other actinopterygian remains. (A–D) Scales, morphotype 1 (A: BRSUG 29951-24-1), morphotype 2 (B: BRSUG 29951-24-2), morphotype 3 (C: BRSUG 29951-24-3), morphotype 4 (D: BRSUG 29951-24-4). (E–H) Fin ray elements, broken fin ray element (E, F: BRSUG 29951-63-1) in lateral views; fin ray element segment (G, H: BRSUG 29951-63-2) in lateral views. (I) Hemicentrum (BRSUG 29951-27-2) in exterior view. (J) Fin spine portion (BRSUG 29951-26) in lateral view. All scale bars equal 1 mm.

rhombic faces are slightly offset, accommodating the overlap along all four sides. In external view there always are some diagonal striations on the black ganoine layer, and in internal view the scales show numerous sequential growth lines, starting from a rectangular shape at the middle and becoming more rhomboid with growth (Fig. 7B). There are three morphotypes: morphotype 1 is seen in different forms, as a parallelogram-shaped scale with quite curved edges and longitudinal striations (Fig. 7A), or slightly more elongate and sharp-angled (Fig. 7B), or with rounded angles, probably as a result of abrasion (Fig. 7C); morphotype 2 (Fig. 7D) is a leaf-shape scale that is more elongated than morphotype 1 also possessing diagonal striations.

The scales from Saltford are too abraded to be able to distinguish those of *Gyrolepis* from other, similar morphotypes, as was done for the specimens from Hampstead Farm (Mears et al., 2016, Fig. 10); our morphotype 2 was not identified from that locality. Morphotype 2 is a fulcral scale, from the midline of the body, and reported also from Bristol Parkway station (Landon et al., 2016, Fig. 6M) and Stowey Quarry (Cavicchini et al., 2018, Fig. 8e, f).

4.2.5.2. *Fin ray elements.* Fin ray elements consist of more or less elongate segments with irregular shapes and smooth edges (Fig. 7E–H). These fin ray elements resemble morphotypes 4 and 2 respectively of Mears et al. (2016, fig. 11) from Hampstead Farm.

4.2.5.3. *Vertebral hemicentra.* Vertebral hemicentra (Fig. 7I), presumably from actinopterygians, are thin structures, oval and curved and with many fine ridges.

4.2.5.4. *Fin spines.* Fin spines (Fig. 7J) are very small rod-like structures ornamented by many numerous fine longitudinal striations all around their circumference. They range in diameter from 0.1–0.7 mm and many taper towards a narrow end, and some even show a pointed tip, and they may show a gentle curve. The example figured here is similar to one from Stowey Quarry (Cavicchini et al., 2018, Fig. 8k).

4.3. Other fossilized remains

4.3.1. Bone fragments

A large number of bone fragments has been discovered in our samples most of which are not identifiable (e.g. Fig. 8A, B).

4.3.2. Neoselachian vertebrae

These are circular, concave discs. The convex side (Fig. 8C) shows a series of concentric growth lines. The concave side (Fig. 8D) is smooth. These specimens represent cyclospindylous vertebrae which have been broken in half (e.g. Mears et al., 2016, p. 489).

4.3.3. Coprolites

Several coprolites have been found (Fig. 8E). These take the form of irregular cylinders with a generally smooth external surface not broken by the presence of inclusions and showing evidence of spiral structure. Such coprolites, mainly 3–10 mm long when complete, are usually ascribed to the most common vertebrates, the hybodont sharks (e.g. Mears et al., 2016, fig. 16).

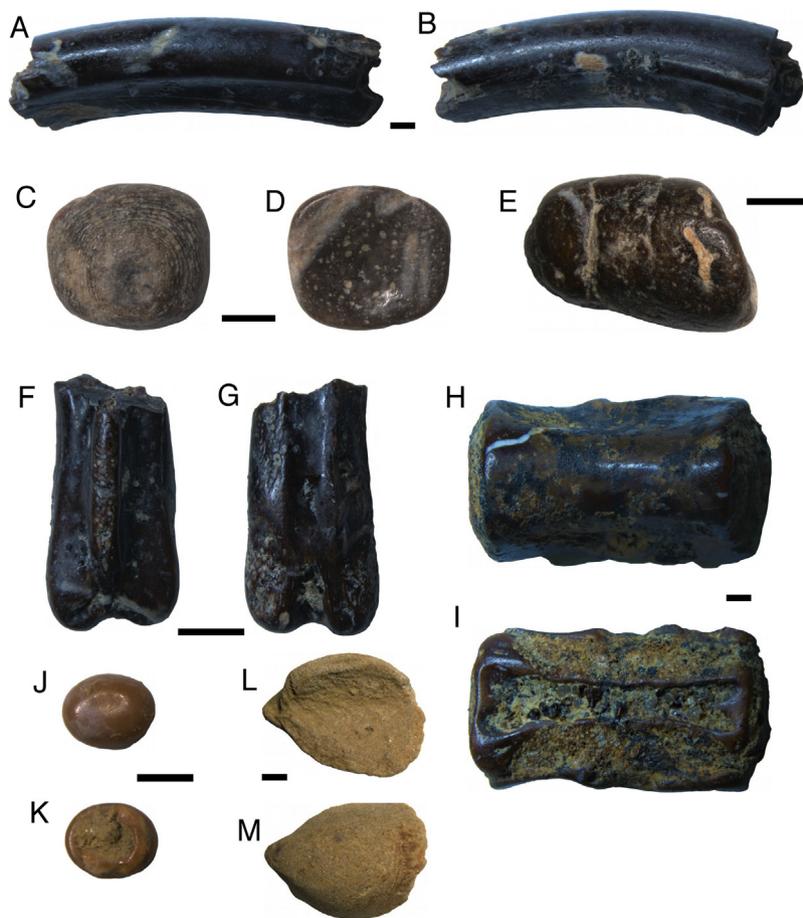


Fig. 8. Other fossilized remains. (A, B) Bone fragment, rib (BRSMG F41) in lateral views. (C–D) Vertebrae, posterior or anterior part (C, D: BRSUG 29951-27-1) in exterior (C) and interior (D) views. (E) Coprolite (BRSUG 29951-77) in lateral view. (F–I) *Pachystropheus* sp. bones, partial neural arch (F, G: BRSMG F112) in dorsal (F) and ventral (G) views, and vertebral centrum (H, I: BRSMG B117) in dorsal (H) and ventral (I) views. (J, K) *Psephoderma* sp. palatal tooth (BRSUG 29951-72) in occlusal (J) and ventral (K) views. (L, M) Bivalve valve steinkern (BRSUG 29951-89) in interior (L) and exterior (M) views. All scale bars equal 1 mm.

4.3.4. Reptiles

Some rare reptile bones and fragments have been found, which come from the small aquatic reptile *Pachystropheus*. Typical examples include a partial neural arch of a vertebra (Fig. 8F, G), showing the central neural spine and postzygapophyses at the lower margin as figured (Fig. 8F) as well as abraded margins of the neural canal in ventral view (Fig. 8G) and a vertebral centrum (Fig. 8H, I). The latter is elongate, showing a rounded ventral face (Fig. 8H) and a pair of ridges representing the bases of the neural arches flanking a groove in the midline, the floor of the neural canal, in dorsal view (Fig. 8I).

The locality has yielded a single isolated tooth (Fig. 8J, K) which probably belongs to a placodont rather than an actinopterygian. The specimen is a slightly elongate oval in outline (Fig. 8J) with a concave underside (Fig. 8K) and relatively thick walls with the tooth edges curving underneath to leave a pulp cavity about half the diameter of the whole tooth. The occlusal surface is quite flattened, and generally smooth, but possesses a slightly off-centre, somewhat crescentic depression (Fig. 8J). The tooth measures 2.0×1.6 mm and is unlike any fish tooth so far described from the British Rhaetian. By comparison with skull material from the Rhaetian of Italy and the Holwell fissure filling material, the Saltford specimen is probably an anterior palatine tooth belonging to *Psephoderma alpinum* (cf. Pinna, 1976, Fig. 1E), the sole placodont taxon recorded from the British Rhaetian (Nordén et al., 2015). The size of the specimen suggests that it is probably from a juvenile. Previous examples from the British Rhaetian have been larger, generally more than 5 mm on the long axis (e.g. Nordén et al., 2015, Fig. 10E, F; Whiteside et al., 2016, Fig. 2E). The shape of this type of tooth is typical of a durophagous diet.

The only other possible contender for the identity of this specimen would be an otherwise unknown pycnodont actinopterygian. The pycnodonts characteristically possess a medial row of teeth with elongate oval form, and the group makes its first appearance during the Late Triassic (Delsate and Kriwet, 2004). The pycnodont teeth described and figured in the

literature generally have tuberculated crowns, rather than possessing arcuate occlusal depressions as in the Saltford specimen.

4.3.5. Mollusc shells

Twenty-three complete and partial bivalve steinkerns (internal moulds in fine sandstone) have been found, but their poor state of preservation makes it difficult to assign them to a particular taxon. One specimen (Fig. 8L, M) is a reasonably complete cast of a single valve, 11 mm long.

4.3.6. Derived Carboniferous fossils recycled into the Rhaetian

4.3.6.1. Crinoid fragments. Crinoids are rare in Rhaetian samples, and yet we found 17 good examples all seemingly pertaining to the same species (Fig. 9A–L). Specimens include multiple ossicles that have been pyritised, isolated ossicles showing a central lumen and 30–40 radiating ridges and smooth outer edges (Fig. 9H–K). These isolated ossicles sometimes show a convex, unornamented face (Fig. 9G, H). The margin of the ossicle is sometimes marked by a centrally placed shallow groove around the outer circumference (Fig. 9C, F). Some specimens show blocks of 2–10 ossicles in close connection, forming part of the column. All examples shown here appear to be columnals, with no evidence of arm ossicles.

Most specimens are circular in ventral and dorsal views (Fig. 9A, B, G, H, J, K) but some present more irregular forms (Fig. 9D, E) possibly as a result of abrasion. Some specimens show pronounced radiating ridges in dorsal view (Fig. 9A). Moreover, there seem to be two types of connections between ossicles, one less packed and with larger inter-ossicle spaces and thicker ossicles in lateral view (Fig. 9I) and one more packed and with narrow inter-ossicle spaces and thinner ossicles in lateral view (Fig. 9L).

These crinoids cannot be assigned to either *Isocrinus* or *Pentacrinites*, the most common forms in the Late Triassic, because those Mesozoic forms are shaped like five-rayed stars. Our specimens look much more like classic Early Carboniferous taxa such as *Pentagonocyclicus* (Bouman & Donovan, 2015, Figs. 1H, I, 2O,

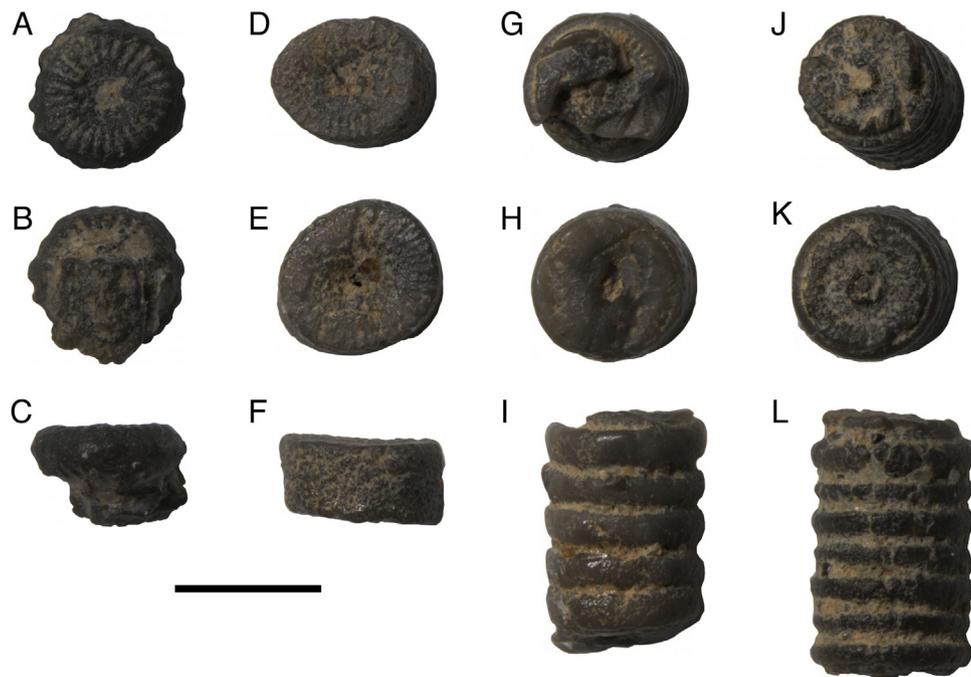


Fig. 9. Carboniferous crinoid ossicles. (A–C) BRSUG 29951-28-2, in dorsal (A), ventral (B), and lateral (C) views. (D–F) specimen 2 (BRSMG E99), in dorsal (D), ventral (E), and lateral (F) views. (G–I) specimen 3 (BRSMG E107), in dorsal (G), ventral (H), and lateral (I) views. (J–L) specimen 4 (BRSMG D118), in dorsal (J), ventral (K), and lateral (L) views. Scale bar equals 1 mm.

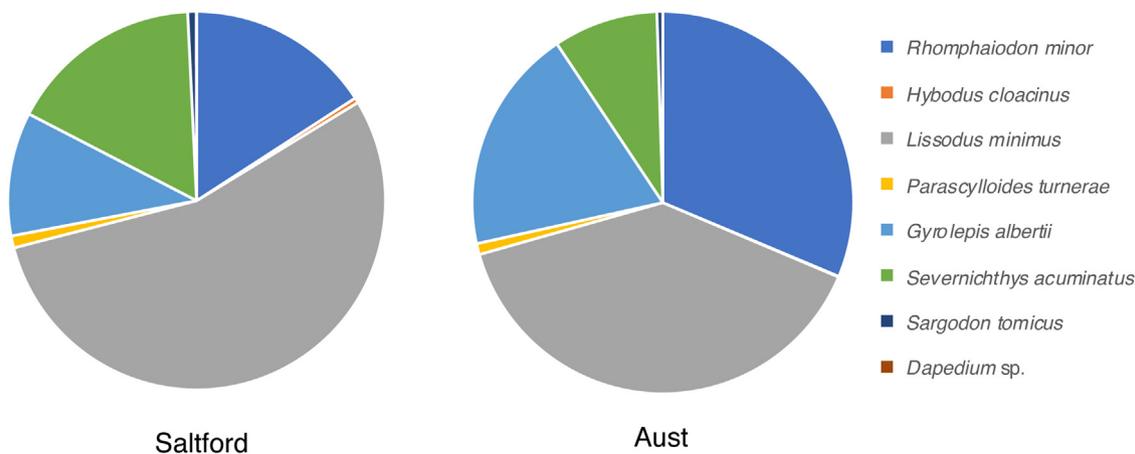


Fig. 10. Pie charts showing relative proportions of key fish taxa from all horizons at Saltford (left) and Aust (right). The data for Saltford are in the Supplement, and for Aust are from Cross et al. (2018, table 2).

P). We therefore class them as derived material from Carboniferous limestones. Here, the Rhaetian bone bed sits on Triassic sediments, but these rest unconformably on Carboniferous limestones. There are Carboniferous sediments around the Saltford-Keynsham area, but they are mostly Late Carboniferous clastic rocks associated with coal deposits.

5. Discussion

5.1. Faunal composition and comparison

We tested for evidence of sorting among the five levels we sampled from the basal bone bed at Saltford (Figs. 2,3). However, the faunal composition of each fossiliferous sample is remarkably uniform (Table 1). Samples from the lowest and highest levels (1, 5) show only rare fossils (bed 1) or none at all (bed 5). The three horizons in the middle of the bone bed, levels 2, 3, and 4 show near-identical proportions of the key taxa, with 55–59 % *Lissodus* teeth, 13–16 % *Rhomphaiodon* teeth, 12–14 % *Severnichthys* teeth, 6–9% *Gyrolepis* teeth, 3–4% undetermined sharks' teeth, 1–3% undetermined bony fish teeth, and < 1% of each of *Hybodus*, *Parascylloides*, and *Sargodon*. Further, the other fossil remains, including actinopterygian scales, spines, denticles, etc, also show similar proportions between horizons 2, 3 and 4 (Table 1), suggesting similar taphonomy throughout. Had we found proportional differences

Table 1
Proportions of microvertebrate remains in each of the five divisions of the basal bone bed at Saltford. The counts are taken from all size fractions. Abbreviations: Actin., actinopterygian; Chond., chondrichthyan.

Horizon	1	2	3	4	5	TOTAL
<i>Rhomphaiodon minor</i>	4	162	188	193	x	547
<i>Hybodus cloacinus</i>	0	7	5	3	x	15
<i>Lissodus minimus</i>	1	656	589	626	x	1872
<i>Parascylloides turnerae</i>	0	8	16	11	x	35
Chond. undetermined	0	58	50	46	x	154
<i>Gyrolepis albertii</i>	1	93	131	138	x	363
<i>Severnichthys acuminatus</i>	0	201	194	175	x	570
<i>Sargodon tomicus</i>	0	8	8	9	x	25
Actin. undetermined	5	12	27	16	x	60
TOTAL	10	1206	1208	1217	x	3641
scales	6	566	632	809	x	2013
spines	0	34	52	72	x	158
denticles	0	37	55	53	x	145
crinoid	0	6	3	1	x	10
other remains	14	661	759	787	x	2221
TOTAL	20	1304	1524	1722	x	4550

through the Saltford bone bed, this might have suggested deposition under different sedimentary conditions or over a long span of time. However, the similarities suggest little change, and presumably relatively rapid deposition of the whole 1-m-thick unit.

The same approach can be taken for comparison of the Rhaetian basal bonebeds more widely. In earlier work, when we compared several basal bone beds (Cross et al., 2018, fig. 14), we found evidence of a possible geographic split in the relative proportions of the two shark tooth types *Lissodus* and *Rhomphaiodon*. In all cases, *Lissodus* is the most abundant identifiable fossil, but *Rhomphaiodon* represents 10–15 % of all specimens at Manor Farm, Charton Bay and Stowey (Allard et al., 2016; Korneisel et al., 2015; Cavicchini et al., 2018). Elsewhere, *Rhomphaiodon* makes up 30–40 % of all teeth, as for example at Aust Cliff (Cross et al., 2018, table 2), Hampstead Farm (Mears et al., 2016, fig. 20), and the M4 junction (Slater et al., 2016), and here at Saltford (Fig. 10). This could be partially a geographic division, in that Aust Cliff, Hampstead Farm, and the M4 junction locations are physically close to each other. However, Manor Farm shows a different pattern, and yet is close geographically to Aust Cliff, whereas Saltford is some distance away.

The shared occurrence of more-or-less the same taxa in all the basal bone beds suggests that they are all sampling the same fauna of fishes, even though the conditions of deposition vary subtly from location to location. The presence and absence of small numbers of teeth from some rare taxa such as *Pseudocetorhinus pickfordi*, *Pseudodalatias barnstonensis*, and *Parascylloides turnerae* is likely a sampling artefact – they were presumably rare elements in the faunas, and so may or may not be found in any bone bed sample simply by chance. The discrimination into two assemblage types based on the relative proportions of *Rhomphaiodon minor* is interesting, as samples of this taxon are large, and so the range from 10 to 15% of all specimens at some sites and 30–40% at others is likely a real difference. Whether it reflects different faunal compositions by chance or season of the year cannot be said. Because the teeth are similar in size and shape to many others, it would be harder to explain this by some kind of physical taphonomic sorting process.

The fact that the Saltford basal bone bed differs so substantially from all others in both lithology (uncemented, un lithified) and thickness (nearly 1 m thick, compared to the more usual 10 cm) suggested we ought to expect some differences in faunal composition. We did not find these. Therefore, the taphonomic regime was probably similar between both bone bed types, and the Saltford bone bed appears to be sampling the early Rhaetian

marine fauna in a similar way to the thinner, consolidated bone beds at Aust and Hampstead Farm, for example. At one level, this gives some confidence that the sedimentological variations we see between different Rhaetian basal bone beds around Bristol are distorting the sample proportions in similar ways, or at least allowing us to make more direct comparisons that might identify other factors that generate differences, such as the apparent differences through time seen in comparing the basal and higher bone beds (e.g. Mears et al., 2016) and the differences just noted in proportions of *Rhomphaiodon* between sets of locations.

5.2. Palaeoecology and palaeoenvironment of Saltford

All chondrichthyans and actinopterygians from Saltford are marine nektonic carnivorous species that presumably formed a food web somewhat like that at Aust (Cross et al., 2018, fig. 15), with *Severnichthys* preying on all the smaller bony fishes and sharks. We do not have examples of ichthyosaurs or plesiosaurs from Saltford, but the limited remains of *Pachystropheus* show that the ecosystem included this predatory form, which also doubtless preyed on a variety of the fishes. *Gyrolepis* and the small hybodont sharks such as *Lissodus* and *Rhomphaiodon* presumably preyed on smaller fishes and soft-bodied invertebrates. The durophagous *Sargodon* and *Psephoderma* presumably fed on molluscs and other shelled prey.

Collections note

Specimens are housed in Bristol City Museum Geology collections (BRSMG, Carpenter collector numbers) and University of Bristol Geology Collections, School of Earth Sciences (BRSUG).

Declaration of Competing Interest

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

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.pgeola.2020.11.003>.

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