



Latest Triassic marine sharks and bony fishes from a bone bed preserved in a burrow system, from Devon, UK



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ABSTRACT

The Rhaetic Transgression, 210 Myr ago, which marked the end of continental conditions in the European Triassic, and the arrival of marine deposition, may have been heralded by the arrival of burrowing shrimps. Here we document an unusual taphonomic situation, in which classic basal Rhaetic bone bed is preserved inside a *Thalassinoides* burrow system at the base of the Westbury Mudstone Formation, in the highest part of the Blue Anchor Formation, at Charton Bay, Devon, UK. The fauna comprises four species of sharks and five species of bony fishes. The sharks, *Rhomphaiodon* ('*Hybodus*'), *Duffinselache*, *Lissodus*, and *Pseudocetorhinus* are small, and include predatory and crushing/opportunistic feeders. The top predator was the large *Severnichthys*, typical of Rhaetian ichthyofaunas, and *Gyrolepis* was a smaller predator. Late Triassic bony fishes generally included many shell-crushers, and the Charton Bay assemblage is no exception, with teeth of *Sargodon*, '*Lepidotes*', and *Dapedium*, the last being a rare record for the British Rhaetic. This kind of burrowed and filled contact occurs elsewhere at the base of the Westbury Mudstone Formation, and so may be a typical marker of the early phases of the Rhaetic Transgression.

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1. Introduction

The latest Triassic was a time of great environmental upheaval, with major changes in depositional systems across Europe, and waves of extinction, culminating in the end-Triassic mass extinction itself. In the oceans, there were major extinctions and turnovers among sharks (Cappetta, 1987) and marine reptiles (Thorne et al., 2011). In general, bony fishes were apparently unaffected by the end-Triassic event, with all families crossing the boundary into the Jurassic (Friedman and Sallan, 2012). On land, dinosaurs were rising in importance, and the precursors of many modern tetrapod groups had emerged, among them the first lissamphibians (frogs and salamanders), turtles, lepidosaurs (basal sphenodontians), crocodylomorphs, and mammals (Sues and Fraser, 2010; Benton et al., 2014). The scale of the end-Triassic mass extinction, the relative timings of events on land and in the

sea, and indeed the duration of the event, and whether there might have been earlier bouts of extinction in the preceding Norian and Rhaetian stages, are all much debated (e.g. Tanner et al., 2004; Mander et al., 2008; Deenen et al., 2010).

In the early part of the Rhaetian Stage, the last stage of the Triassic, continental red-bed environments that had covered much of central Europe and the UK throughout the Permo-Triassic were transformed by the Europe-wide Rhaetic Transgression into marine environments that were to last in places until the end of the Cretaceous. In SW Britain the unconformity at the base of the Rhaetic succession is almost everywhere marked by pebbly lag deposits rich in vertebrate remains, hence the name Rhaetic bone bed (Storrs, 1994; Swift and Martill, 1999; Suan et al., 2012).

In the topographically higher areas adjacent to the Rhaetic Sea, a fissured karstic landscape was developed on the Carboniferous Limestones of the Bristol area, the Mendip Hills and in South Wales (Fig. 1). Some of the fissures were infilled with tropical soils, many of which contain the bones of small terrestrial vertebrates. Some of the 'Bristol fissures' are of known Rhaetian age, others of indeterminate, possibly 'Late Triassic age'. The faunas have been

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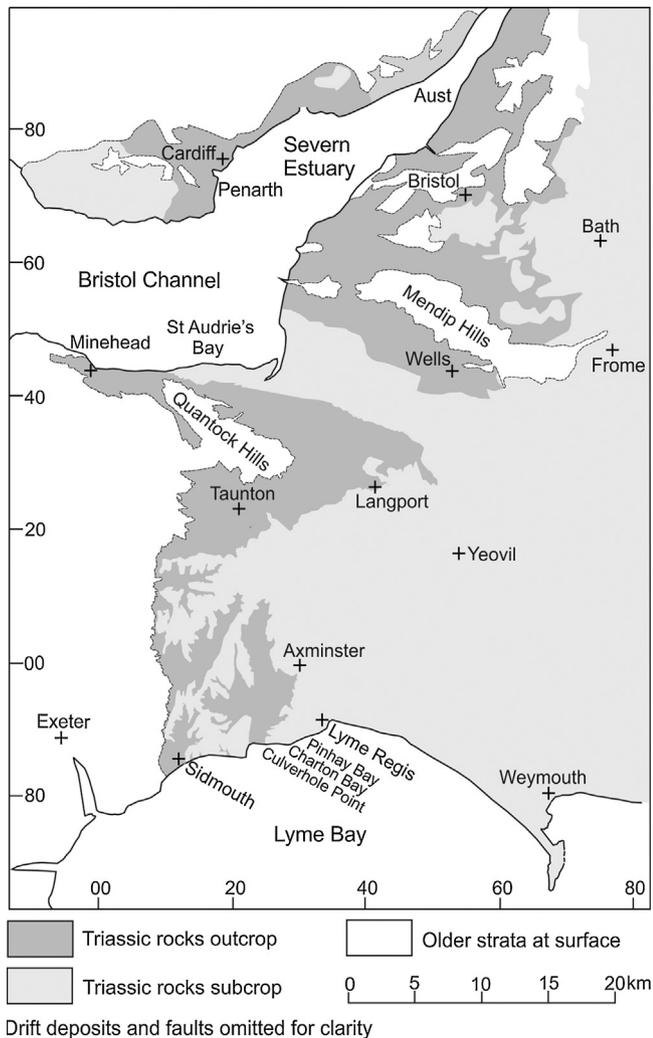


Fig. 1. Distribution of Triassic rocks in south-west Britain, showing the positions of Penarth Group outcrops referred to in the text.

studied since the 1830s, and they yield microvertebrates and marine elements, including the teeth of sharks and actinopterygian fishes (e.g. Whiteside and Marshall, 2008; Van den Berg et al., 2012; Foffa et al., 2014).

Here, we describe an occurrence of the basal Rhaetic bone bed from Charton Bay, east Devon in which the bone bed occurs in a well preserved burrow system, an unusual taphonomic situation that may be more widespread at this stratigraphic level than previously recorded. The pulsed onset of the Rhaetic Transgression may have been marked by the arrival of marine shrimps that became established in burrow systems on a firmground of Blue Anchor Formation mudstones, and associated with transported bone and phosphatic debris that fell to the bottom under gravity, was winnowed by bottom currents, and filled the burrows, and occasionally underwent reworking by the burrowers.

2. Geological setting

2.1. The Rhaetic of Devon

In the UK, the Rhaetic Stage is represented by rocks of the Penarth Group and the lowest part of the Lias Group (pre-*Planorbis* Beds). These groups can be traced at outcrop from the Devon coast, through Somerset and the Severn Estuary area (Fig. 1), and across the Midlands to the Yorkshire coast. The Penarth Group is well

exposed on the Glamorgan, Somerset and Devon coasts where the Westbury Mudstone Formation at the base of the group rests unconformably on the Blue Anchor Formation at the top of the Mercia Mudstone Group. The highest formations in the Penarth Group, the Watchet Mudstone Formation, and its lateral correlative the White Lias Formation, are overlain with lithological contrast but only minor sedimentary break by the Lias Group.

The beds that we now know to be of Rhaetic age were noted by some of the earliest geologists. The oldest image of a Rhaetic fossil seems to be a polished section of Cotham Marble figured as 'Dendropotamites' by Nehemiah Grew (1641–1712) in his 1681 catalogue of the collections of the Royal Society (Grew, 1681: Part III, p. 268, pl. 20), with a further reference dating to 1754 (Swift and Martill, 1999). Rhaetic bone bed fossils from the Devon coast were noted first in the 1820s by collectors, including Mary Anning (1799–1847), and by the local geologist William Buckland (1784–1856) (Swift and Martill, 1999). This early work coincided with similar discoveries in Germany, and the name Rhaetic was Anglicized from the German term 'Rhät' (from the Rhätische Alpen, now spelled Rätische, a mountainous area of the central Alps), which had been applied to fossiliferous rock units of comparable age. The Somerset geologist, Charles Moore (1815–1881) was the first to formally identify rocks of this age in Britain (Moore, 1861).

The Rhaetic deposits were widely noted, and recognized as marking a sudden change from the thick underlying terrestrial successions to marine environments as indicated by sharks' teeth, the bones of marine reptiles, and marine/brackish-water bivalves. Most of the early attention was focused on the bone bed at the base of the Westbury Formation. This is especially fossiliferous and well exposed at Aust Cliff (National Grid Reference, NGR, ST 565 894), on the Severn Estuary where it includes clasts torn up from the underlying Blue Anchor Formation, phosphate pebbles, and a mélange of often abraded bones, and teeth of all sizes. A second, and sometimes as many as three, thinner bone beds may occur in the lower 2–3 m of the Westbury Mudstone Formation.

The chemistry of the basal Rhaetic bone bed has been interpreted (Suan et al., 2012) as evidence for widespread perturbation in phosphorus and carbon cycling in the oceans, associated with dramatic climate change. These changes may have been triggered by volcanic eruptions in the Central Atlantic Magmatic Province (CAMP), which elevated the rifting margins of the early North Atlantic, causing an increase in runoff and phosphorus input into coastal waters. This led to oxygen depletion, which in turn favoured redox-driven phosphorus regeneration and massive phosphatization of vertebrate hard parts in shallow waters. Phosphatized bones, teeth, coprolites, and other clasts were then transported into deeper waters episodically by storm events. This model (Suan et al., 2012) accounts for the widespread occurrence of bone beds at apparently the same time across Europe, and also for the substantial differences between coeval bone bed categories, interpreted as of proximal and distal (transported) type (Trueman and Benton, 1997). The 'proximal' bone beds show minimal physical evidence of transport, comprising delicate, unabraded, small teeth and bones, with rare earth element (REE) signatures similar to those of the hosting rock. The 'distal' transported bone beds comprise much larger bones, coprolites, and inorganic phosphatized fragments, mostly heavily abraded, and with REE signatures unlike the hosting sediment (Trueman and Benton, 1997). The model further explains why the majority of fossils in the Rhaetic bone beds are from marine animals, but with associated rare insects, plants, and dinosaur remains, presumably derived from terrestrial runoff into the ocean (Swift and Martill, 1999). Further, this model, which links bone bed formation to climatic change and initial CAMP eruptions, points to the likelihood of continued disturbances to the biosphere, as well

as perhaps some extinction events before the end-Triassic mass extinction (Tanner et al., 2004; Deenen et al., 2010), or at least the need to disentangle regional extinction signals from global evidence.

The Rhaetic bone bed has been recorded at three localities on the east Devon coast, at Culverhole (SY 272 893), Charton Bay (SY 281 893), and Pinhay Bay (SY 319 908). All three are in the intertidal zone and are overlain by beach deposits for most of the time. Woodward and Ussher (1911) noted that the full thickness of the Westbury Mudstone had been exposed at Culverhole in 1888 and thereafter, and that the bone bed comprised a black calcareous grit with small quartz pebbles, an occasional reptilian bone, and numerous fish remains including *Acrodus minimus*, *Gyrolepis albertii*, *Hybodus cloacinus*, *Lepidotus*, *Saurichthys acuminatus*, *Sargodon tomicus*, some of which infilled cracks in the underlying Blue Anchor Formation mudstones. Mary Anning collected fishes and marine reptiles from the bone bed at this locality (Egerton, 1841). Richardson (1906) published a similar description of this section, which contains many of the same details.

At Charton Bay, c. 18 m of Penarth Group sediments are exposed in a low cliff (SY 3015 2003) that is affected by landslides. The succession comprises c. 7 m of Westbury Mudstone overlain by 2 m of the Cotham Formation and 9 m of the White Lias overlain by the basal beds of the Blue Lias Formation (Fig. 2). A cliff 400 m west exposes the youngest 20 m of the Blue Anchor Formation overlain by landside debris that conceals the junction with the Westbury Mudstone.

The cliff section is separated from outcrops in the intertidal area by a fault that brings the highest part of the Blue Anchor Formation down to beach level (Fig. 3). There, the dark grey pyritic mudstones of the Westbury Mudstone rest unconformably and with marked lithological contrast on pale grey-green massive mudstones in the upper part of the Blue Anchor Formation. The outcrop of the junction emerges from beneath beach deposits to crop out in the lower part of the intertidal area adjacent to a N–S trending fault that cuts out most of the Westbury Mudstone. The Rhaetic Bone Bed infills shallow (20–30 mm deep) depressions in the Blue Anchor Formation mudstone and infills a complex burrow system that penetrates the top 20–50 mm of the mudstone (Fig. 4A).

2.2. The burrow systems

The burrows comprise complex networks of gently undulating horizontal to subhorizontal partially crushed cylinders infilled with bone-bearing, dark grey silty and sandy mud that stands out in marked lithological and colour contrast to the green mudstone host rock (Fig. 4A). The burrows appear to radiate out for 0.5–0.6 m from shallow depressions (20–30 mm deep and 0.2–0.3 m across) that are infilled with the same dark grey lag deposit (Fig. 4A and B). They are connected to the depressed areas by 10–20 mm long vertical shafts and low-angle curved burrows, with the net result that the complete burrow system probably does not occupy more than the top 50 mm of the Blue Anchor Formation mudstone. When traced away from the depressions, the individual burrows appear to be discontinuous (Fig. 4C) due to the irregular nature of the present-day erosion surface. Many have rounded ends presumably because their cross section is a flattened circle and they are moving in and out of the plane of view. The burrow walls are unlined and unornamented. Many of the burrows fall in two size ranges, measuring 4–5 mm and 10–12 mm in diameter. The smaller diameter burrows commonly join the larger diameter burrows at a high angle. In many cases the contents and textures of the infilling materials of both burrows are the same, indicating that the burrows form part of a single network not two intersecting networks. In the areas closer to the depressions many of the

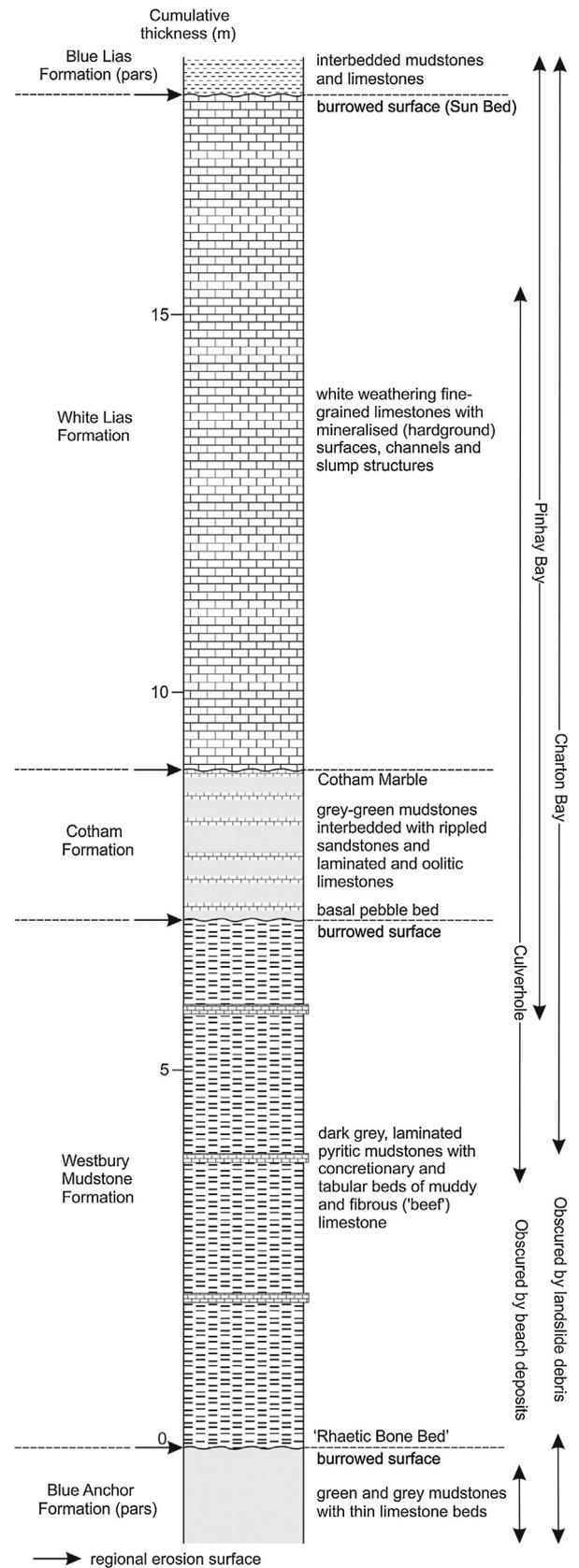


Fig. 2. Generalized vertical section for the Penarth Group succession exposed on the east Devon coast.



Fig. 3. Charton Bay, Devon and the Rhaetic bone bed. The junction of the Blue Anchor and Westbury Mudstone Formations is concealed by landslide deposits in the cliffs. An E–W trending fault brings the burrowed unconformity surface down to beach level (foreground). View NE.

burrows are up to 20 mm wide and are locally widened to form nodes or widened ends. Some of the larger burrows are amalgamated to form irregular shapes that may have been joined to vertical access shafts. The smaller diameter burrows appear to be single-use tunnels, and the larger diameter burrows multi-use access tunnels with turning areas where widened.

The burrows are filled with compacted, mostly grain-supported silt- and sand-grade debris in a dark grey silt matrix. The clasts comprise vertebrate remains (5–10%), angular silt-grade and well

rounded sand-grade frosted clear quartz grains that appear to have been derived from a desert environment (20–25%), perhaps reworked from the Triassic rebeds below, and numerous small (mostly 1–5 mm across) angular green clasts of the host-rock mudstone (up to 20%). These last indicate that the Blue Anchor Formation mudstones were already lithified at the time of the burrowing. The absence of organic nutrients in the mudstones indicates that the burrows were made for shelter. The compacted nature of the infilling material throughout the whole burrow

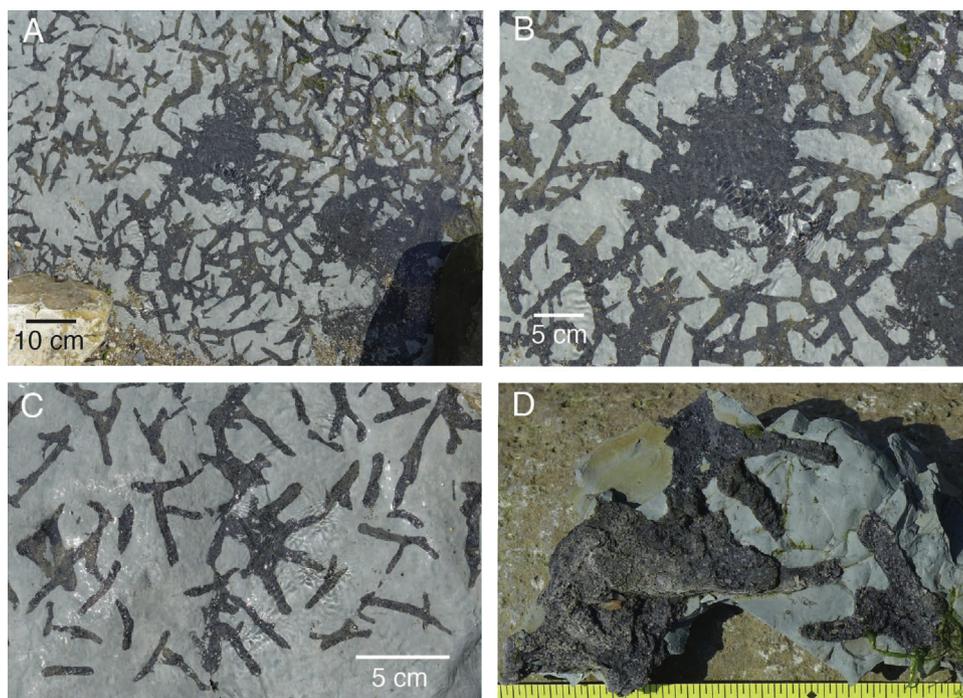


Fig. 4. The burrow system *Thalassinoides*, containing bone bed infill. (A) Top surface of the Blue Anchor Formation, showing branching burrow systems, clustering around a depression, infilled with dark-coloured bone bed material. (B) Close-up of the depression. (C) Burrows nearby, eroded and appearing disconnected. (D) Upper surface of part of the burrow system partially weathered out in low relief. Scale bars on each image; millimetres indicated on ruler in D.

system, including in the smaller diameter burrows most distant from the access shafts, together with a few examples of meniscus-fill structures, suggests that the lag deposit represents feeding waste, or at least that the burrowing animals reworked, and packed the bonebed material as they moved through the burrow system. Similarly, the concentration of the lag deposit in the depressed areas around the access shafts may be a concentration of similar waste.

The overall architecture of the burrow system and the shapes of the individual burrows are closely similar to that of *Thalassinoides* Ehrenberg, 1844, an ichnogenus comprising linked, branching systems, with Y- and T-junctions between burrows, and with occasional swellings at nodes (Bromley and Frey, 1974). Such burrows are mostly attributed to decapod crustaceans, especially callianassid and thalassinidean shrimps, building systems for feeding and protection that may extend 1 m below the sea floor. *Thalassinoides* burrows have been reported from strata ranging from Cambrian to Recent and from deep-water (in turbidites) to intertidal environments. The ichnogenus has been commonly reported from the Rhaetian and Jurassic where sedimentary horizons dominated by *Thalassinoides* are interpreted as those of shallow, oxygenated marine settings above fair-weather wave base (upper shoreface) associated with high-energy depositional processes (Sharafi et al., 2012).

3. Methods

3.1. Collection

Fossiliferous burrow-infilling sediment collected from the Charton Bay outcrop in 2005 was processed by Mike Curtis (1950–2008), a renowned fossil collector from Gloucester who had previously worked with Rhaetian vertebrate fossils and had been instrumental in major fossil finds around Bristol (Benton et al., 2012). Mr. Curtis recorded in his notes (Curtis MS Report on DE.RG.02-1, October 2006) that he prepared 65 g of sediment infill from Charton Bay from which he washed the adhering mud. The material was then treated with 10% acetic acid until the reaction had stopped, and the residue was washed with water through four sieves, of 2.4 mm, 1.2 mm, 600 μm , and 300 μm gauge.

The material greater than 2.4 mm contained no recoverable vertebrate remains. The remainder of the material, about 1870 vertebrate fossil remains, was sorted first according to size by sieve (2.4–1.2 mm, 1.2 mm to 600 μm , 600–300 μm), and then into groups of similar fossils. About 600 specimens were identified as teeth of individual species, and many more were marked as miscellaneous remains and undifferentiated teeth, denticles, scales, and fragments. This material, forming part of the Mike Curtis collection, was donated to Bristol Museum and Art Gallery (BRSMG) in 1997, and the University of Bristol School of Earth Sciences (BRSUG), after his death, in 2009.

Mr Curtis noted that 'the fish assemblage is similar to, but more diverse than, that of the Rhaetic Bone Bed at Westbury on Severn and other localities in Avon and contains two genera of bony fish, *Dapedium* and '*Lepidotes*', not previously recorded from the Rhaetic Bone Bed (Mike Curtis, pers. comm., 2006, in Gallois, 2007, p. 292). In fact, '*Lepidotes*' had been listed from Rhaetic vertebrate faunas by Moore (1861) and Richardson (1911), as well as being described on the basis of isolated teeth from Barnstone in Nottinghamshire (Sykes, 1979), and paired vomers recovered from the Rhaetic sequence at Watchet by Jain (1983).

3.2. Species relative abundances

Previous to donation, Mr. Curtis counted the specimens and graphed the relative abundance of species, as part of his report to

R.W.G. This formed a preliminary part of a proposed study of the fish contents of the basal Rhaetic Bone Bed and bone beds from the same and other levels in the Rhaetic elsewhere in SW Britain. Unfortunately, these comparisons were not completed. For our study, we checked all the registered specimens in the Curtis collection (BRSUG 29371-1), and compared our counts of relative abundances with his. After setting aside the 'miscellaneous' and 'undifferentiated' remains, we counted the identifiable specimens, according to rules, followed also by Curtis, that were designed to ensure as fair an assessment as possible, and especially to avoid the risk of over-estimating the relative abundances of certain taxa whose teeth were commonly broken into fragments.

Among the sharks' teeth, *Rhomphaiodon minor* specimens were counted when the central cusp and a portion of the root were present. *Lissodus minimus* specimens were counted when the central cusp was present and complete, along with the labial peg, except for posterolateral teeth, in which there is not a prominent labial peg. The single *Pseudocetorhinus pickfordi* specimen was counted based on an apparently whole cusp of the tooth and associated root. For *Duffiniselache holwellensis*, the tooth was counted when a portion of root and of the cusp was present.

Among the teeth of actinopterygians, both *Severnichthys acuminatus* and *Gyrolepis albertii* specimens were counted when the tooth cap and a portion of the shaft were both present. For *Dapedium* sp., a specimen was counted when the whole circular occlusal surface was present, along with the definitive molariform features, as the potential length of the tooth is not known, nor the root morphology. *Sargodon tomicus* specimens were considered to be whole for counting when the definitive occlusal surface was visible and unbroken. '*Lepidotes*' sp. remains were counted as whole when an unbroken cusp was present.

A second count was also completed for *Lissodus minimus* specimens, with the addition of a system to account for teeth represented by large fragments (isolated tooth arms), which were excluded from the original count. This second count divided teeth into two classifications, 'wholes' and 'halves'.

Whole teeth fell under the same description as for the first. The category of 'halves' was added, and defined as full arms of the tooth not necessarily including part of the cusp. Segments that were split in half longitudinally, therefore missing half the cusp and sometimes the labial peg, and other pieces with a partial cusp, were counted as halves for this estimate.

4. Systematic palaeontology

4.1. Sharks

Duffin (1999) described ten taxa of sharks based on teeth from the British Rhaetic, and we have identified four of these among the Charton Bay bone bed material.

4.1.1. *Rhomphaiodon minor* (Agassiz, 1837)

Our specimens range from isolated central cusps to whole teeth with some of the root intact. The teeth are moderately to strongly ridged, and have a long, conical primary cusp and one set of smaller cusplets. There can be a second pair of cusplets or, more frequently, a stray single cusplet protruding from one end of the tooth (Fig. 5A). The central cusp is commonly curved lingually, and ranges in size widely, up to nearly 3 mm long. Cusplets are half the height of the central cusp or less. Any extra cusplets seem to decrease in size at about the same ratio.

This is the second most common chondrichthyan species in the collection. The previous generic assignment of this tooth, *Hybodus*, was problematic for two reasons. First, numerous species of shark teeth were assigned to the genus, and it was evidently a

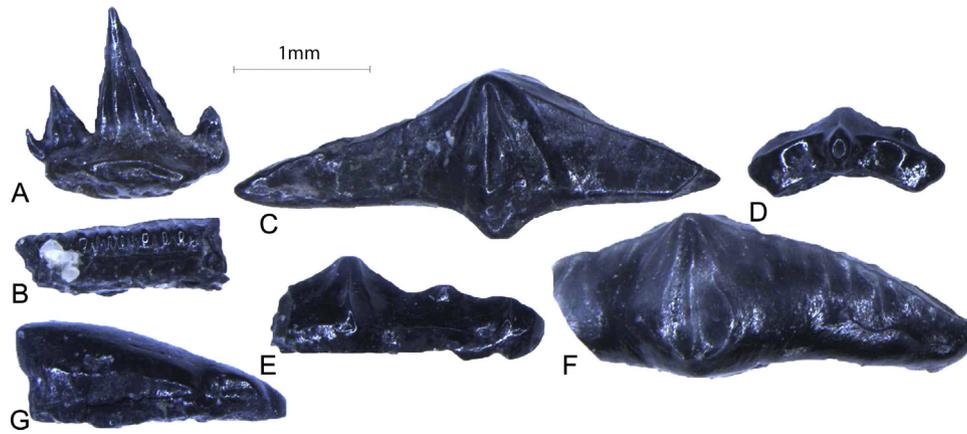


Fig. 5. Sharks' teeth from the Charton Bay Rhaetic bone bed. (A) *Rhomphaiodon minor* tooth (BRSUG 29371-1-532 B1) in lingual view. (B) *Duffinselache holwellensis* tooth (BRSUG 29371-1-56 1) in side view. (C–F) Teeth of *Lissodus minimus* in labial view, (C) lateral tooth (BRSUG 29371-1-550 B1), (D) anterior tooth (BRSUG 29371-1-529 A13), (E) anterolateral tooth (BRSUG 29371-1-569 B4), (F) posterolateral tooth (BRSUG 29371-1-550 A1). (G) *Pseudocetorhinus pickfordi* tooth (BRSUG 29371-1-537) in side view. Scale bar 1 mm.

wastebasket taxon. Further, because the type specimen of *Hybodus minor* Agassiz, 1837 was a dorsal fin spine, it had always been controversial to assign teeth to this taxon. Duffin (1999, p. 195) noted similarities between the British '*Hybodus*' *minor* teeth and those he had assigned (Duffin, 1993) to his new genus *Rhomphaiodon*, from the Norian of France and Germany. Cuny and Risnes (2005) confirmed this insight, and assigned British '*Hybodus*' *minor* teeth to *Rhomphaiodon*, identifying this genus as a member of the Order Synchodontiformes based on enameloid ultrastructure, and we follow that designation here.

4.1.2. *Duffinselache holwellensis* (Duffin, 1998b)

We identify four tooth fragments of this taxon in the Curtis collection, but these lack the central cusp. These teeth (Fig. 5B) are narrow and long, but lack cusplets. They have very low crowns. These teeth have a large and very flared root about the same height as the crown. The tooth crowns are strongly ridged, even abnormally so.

This species was originally described as *Polyacrodus holwellensis* by Duffin (1998b), based on specimens from fissure fills at Holwell Quarry, Somerset and the base of the Cotham Formation at Chilcompton, Somerset, but he noted (Duffin, 1999, p. 197) that '*Polyacrodus* is a poorly defined taxon'. In light of this, and the discovery that the species possesses some features typical of neoselachians, Andreev and Cuny (2012) erected the new genus *Duffinselache* for this taxon.

4.1.3. *Lissodus minimus* (Agassiz, 1839)

The most abundant shark at Charton Bay is the heterodont *Lissodus*, represented by isolated cusps and small crown fragments, identified based on their wide arched shape and/or distinctive ridges (most common in anterior and posterolateral teeth), to full cusps with varying amounts of wear. We identify the four tooth morphotypes from different parts of the jaw (Fig. 5C–F), noted by Duffin (1999, pp. 199–201), namely anterior, anterolateral, lateral, and posterolateral (see also Duffin, 1985, 2001). These occur both as distinct examples and as a variety of intermediate forms. *Lissodus* teeth are generally long and low-crowned, probably used for crushing hard shelled benthic prey, commonly with a pronounced labial protuberance, generally known as the labial peg (Cappetta, 1987). This peg protrudes from the base of the central cusp, which can be quite prominent and pronounced in some of the tooth morphotypes, but is short or low in others; it was probably used as a locking device to stabilize successional teeth in the same row.

The cusp is commonly divided by a sharp longitudinal ridge (often called the occlusal crest) running along the length of the tooth (Storrs, 1994, pp. 222–224). Some teeth curve lingually at the ends, creating a convex curve to the labial side. This is most common in anterior teeth. Most of the teeth have no cusplets, though one pair is common in lateral teeth, but some teeth from this species are recorded as having up to five pairs of cusplets (Duffin, 1999, p. 201), which usually varies between morphotypes. If the root were present on any of the teeth from our sample, we would expect it to be flat and approximately perpendicular to the tooth cap. The crown may be smooth or have bifurcating grooves in its surface (Cappetta, 1987, p. 36). In the Curtis collection, the large majority of *Lissodus* teeth are ridged to varying degrees. None of these teeth has a significant root fragment, and with the root missing, the underside of the crown is concave.

Lateral teeth (Fig. 5C) are quite robust, with a prominent cusp made somewhat pyramidal-shaped by the longitudinal crest and the labial peg. The tooth is strongly ridged and has a low bulging labial peg, giving the protuberance a 'U' shape in labial view.

Anterior teeth (Fig. 5D) are the most gracile type and, in side view, the cusp is more raised from the ends of the tooth than in the other types, giving it a curved appearance. The labial peg is very protuberant, looking circular in labial view. A pair of smaller cusplets is common in these teeth, and they are less ridged than the other types. The cusp is generally narrow but sharply peaked.

Anterolateral teeth (Fig. 5E) have a very prominent sharply peaked cusp, but the tooth itself is otherwise very thin. These teeth are variable in the prominence of ridging, and can have many small cusplets, similar to those on anterior teeth. Anterolateral teeth are quite long compared to their height.

Posterolateral teeth (Fig. 5F) are the most robust tooth type in *L. minimus*. The cusp rarely protrudes from the regular dome-like curve of the tooth. These teeth have widely spaced short ridges perpendicular to the tooth length, except at the centre, where they tend towards a point.

Lissodus minimus is similar to, and has historically been classified in the same grouping as, the genus *Lonchidion* (Cappetta, 1987); in his original description, Louis Agassiz assigned the teeth to *Acrodus* (Agassiz 1839). This species is the most abundant selachian present in our collection by tooth remains, making up nearly half of the material. All four morphotypes (Duffin, 1999, p. 200) are present. Many of the teeth, though, have a combination of traits that put them between the four types, instead of clearly matching one or another, as would be expected in teeth coming from different tooth files. *Lissodus* is identified as a member of the

Family Lonchidiidae, a long-lived hybodont clade ranging from the Late Devonian to Late Cretaceous. Many species assigned to the genus were removed to other genera by Rees and Underwood (2002), but *L. minimus* is retained in *Lissodus*.

4.1.4. *Pseudocetorhinus pickfordi* Duffin, 1998a

There is only a single tooth belonging to this taxon in the Curtis collection. This tooth (Fig. 5G) has a low inclined cusp with a slight dent in the centre. It appears quite worn, and the indentation in the peak of the cusp may be an ante-mortem wear facet. The root is flared, more on one side than the other.

This specimen is consistent with previous descriptions (Duffin, 1998a, 1999, p. 204), although previously reported materials show considerable variation. The rarity of the species in the collection matches its wider occurrence, in that it is always rare in the Rhaetic. *Pseudocetorhinus* is assigned to the Family Cetorhinidae, a neoselachian, galeomorph clade comprising the Basking Sharks, although the assignment is uncertain (Duffin, 1999, p. 204).

4.1.5. Other selachian remains

In addition to identifiable teeth, we report two other kinds of selachian remains: dermal denticles and prismatic cartilage. The Charton Bay dermal denticles show a great range of shapes. Some are columnar, while others are ridged or plate-like; placoid and hybodontoid scales are both represented in the collection (see Duffin, 1999, p. 205 ff.).

Dermal denticles vary substantially over different parts of the body in selachians, and there may be very little difference between species (see Duffin and Ward, 1993, p. 78 for further discussion). This means that it is usually not possible to assign isolated denticles to any particular taxon, or even clade.

Two of the Charton Bay denticles are relatively large (up to 3 mm long and 2 mm high) and robust. A squat, featureless enamelled crown sits on a slightly flared base with a flat to convex undersurface (Fig. 6). These denticles conform to those of the Group C morphotype as described by Sykes (1974, p. 59) from Bamstone in Nottinghamshire, and suggested by him as being chimaeriform in origin. The presence of myriacanthoid holocephalans in the British Rhaetic was established by Duffin (1994, 1999), who described a series of tooth plates, and *Squaloraja* has been recorded from both Somerset and the

Bristol area (Moore, 1861; Short, 1904). Holocephalans have a much-reduced squamation in comparison to that of selachians; *Squaloraja*, for example, has denticles scattered over the surface of the body (Duffin, 1992, p. 295), and a closely spaced amature of scales on the ventral surface of the frontal clasper and the opposing dorsal surface of the head in male specimens. The denticles from Charton Bay, which may indeed belong to a holocephalan, differ from those of *Squaloraja* in their more robust base and rather squat crown, which is not extended into a cusp (see Delsate et al., 2002, fig. 21).

Four possible pieces of prismatic cartilage from an unidentified chondrichthyan are present in the collection. Prismatic cartilage comprises a mosaic of minute tiles or tesserae of apatite, linked together by collagen fibres, and forming just below the cartilage surface in extant and fossil chondrichthyan (Maisey, 2013). The Rhaetic tesserae are each hexagonal pieces (originally with six unbroken sides), though some are missing edges or corners following breakage. Fossilized cartilage is quite rare, since cartilage is neither as calcified nor as durable as bone and, possessing a higher proportion of organic material, decays more quickly.

4.2. Bony fishes

We identify five actinopterygian species based upon teeth among the Charton Bay microvertebrates, as well as other unidentifiable materials. This compares with the nine species noted by Duffin (1999) for the entire British Rhaetic.

4.2.1. *Gyrolepis albertii* Agassiz, 1835

G. albertii teeth are shaped like elongate cones, somewhat curved, and ranging in length from 0.7 to 2.5 mm, with the longer teeth generally more curved and narrow relative to their length (Fig. 7A). *G. albertii* teeth are the fourth most common osteichthyan in the Charton Bay assemblage, making up just over ten percent of the teeth present. They have a sharp, translucent enamel cap that is separated from the rest of the tooth by a ridge and, commonly, a pronounced change in slope of the cone. This cap is usually no more than 35% of the length of the tooth (Duffin, 1999, p. 213). Some teeth show fine striations below the cap, along the length of the tooth.

Our specimens are small, compared to sizes up to 3 mm long elsewhere (Duffin, 1999, p. 213). *Gyrolepis* is assigned to the

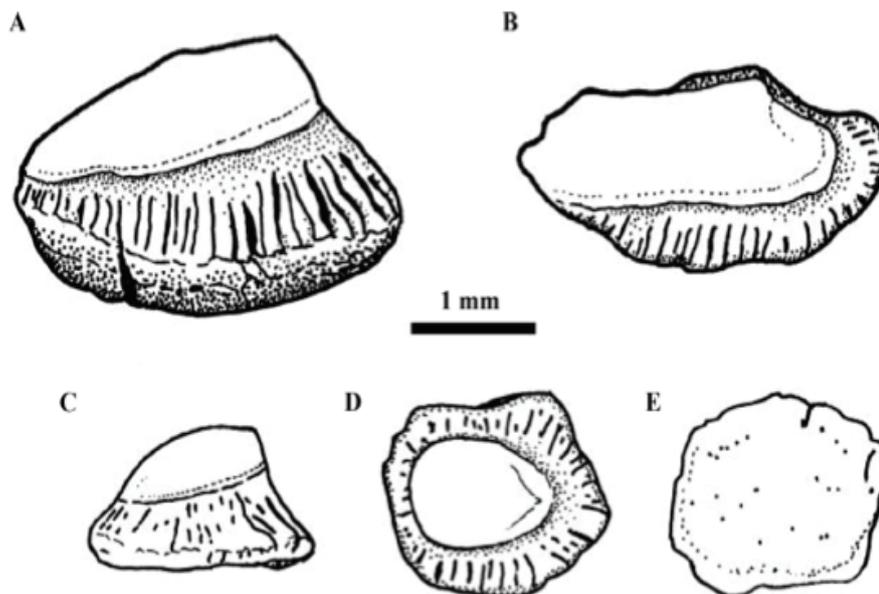


Fig. 6. Dermal denticles, possibly belonging to an unidentified holocephalan, from the Charton Bay Rhaetic Bone Bed. BRSUG29371-1-552A in (A) side view, (B) surface view. BRSUG29371-1-552B in (C) side view, (D) surface view, (E) basal view.

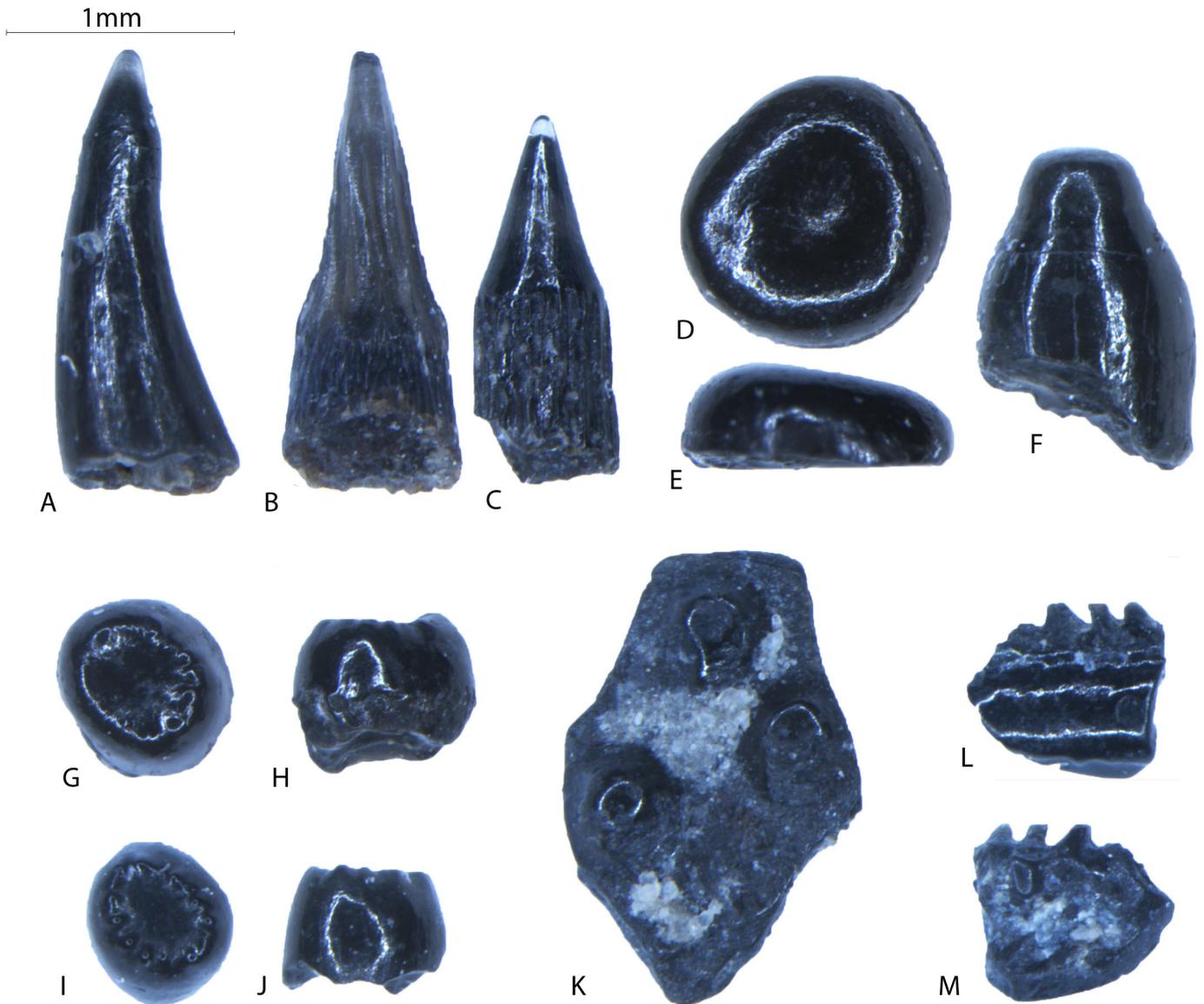


Fig. 7. Actinopterygian teeth from the Charton Bay Rhaetic bone bed. (A) *Gyrolepis albertii* tooth (BRSUG 29371-1-539 A4) in side view. (B) '*Birgeria acuminata*' type *Severnichthys longidens* (BRSUG 29371-1-542 B4). (C) '*Saurichthys longidens*' type *Severnichthys longidens* (BRSUG 29371-1-538 3). (D and E) *Sargodon tomicus* tooth (BRSUG 29371-1-544 B1) in occlusal (D) and side (E) views. (F) '*Lepidotus*' sp. tooth (BRSUG 29371-1-545 1) in side view. (G and H) *Dapedium* sp. tooth (BRSUG 29371-1-546 3) in occlusal (G) and side (H) views. (I and J) *Dapedium* sp. tooth (BRSUG 29371-1-546 1) in occlusal (I) and side (J) views. (K) Actinopterygian palatal fragment (BRSUG 29371-1-524 A) in occlusal view. (L and M) Actinopterygian jaw fragment in buccal (L) and lingual (M) views.

Palaeoniscidae, a group typical of the Carboniferous and Permian, but also a wastebasket 'family' and likely to be paraphyletic.

4.2.2. *Severnichthys acuminatus* (Agassiz, 1835)

S. acuminatus was a large predatory fish with at least two types of teeth, both originally classified in distinct taxa (Storrs, 1994, pp. 229–236), and both present in this sample. The first type, '*Birgeria acuminata*' (Fig. 7B), is conical with a translucent cap of up to 50% of the tooth height (Duffin, 1999, p. 215). This cap is separated from the tooth shaft by a prominent ridge. There may be ridges on the cap, but they are more prominent below the cap. The '*Saurichthys longidens*' (Fig. 7C) type is sigmoidal and the enamel cap is less than 10% of the tooth height. These teeth are strongly ridged below the cap, with a somewhat flared base, which may get a somewhat folded appearance from the strong ridges of the tooth (Duffin, 1999, p. 215).

The classification of *Birgeria acuminata* and *Saurichthys longidens* as two types of teeth in the species *Severnichthys acuminatus* by Storrs (1994, pp. 229–236) has been debated, but is widely

accepted as reasonable (e.g. Duffin, 1999, pp. 215–216; Błażejowski, 2004; Whiteside and Marshall, 2008).

4.2.3. *Sargodon tomicus* Plieninger, 1847

The second most abundant teeth from Charton Bay, and the most abundant osteichthyan teeth, belong to *Sargodon tomicus*. There were two tooth morphs (Duffin, 1999, p. 217). The first type, incisiform, is represented in the collection by only a single broken crown fragment, recognizable from its distinctive crown histology (vascular acrodin). When complete, these were long teeth with deep roots and a chisel-like crown. Molariform teeth, the second type, are usually found heavily worn and isolated from their roots (Fig. 7D–E). These are domed cusps, useful for heavy grinding, and circular to elliptical in shape, and can be up to 7 mm in diameter at other localities (Duffin, 1999, p. 217). However, the largest teeth in our sample were about 3 mm in diameter, and they show very little variation. Some of them, though, show a small rise or boss in the centre of the dome, probably produced by wear or abrasion.

Sargodon tomicus is present throughout the Penarth Group and is widely known from isolated tooth caps as well as rare articulated remains in other units (Duffin, 1999, p. 217). The teeth come from a large fish, known from complete and articulated specimens from the Norian of Italy (Tintori, 1983), measuring up to 1 m in total length, a member of the Semionotiformes, which were otherwise rather smaller, and abundant throughout Late Triassic and Early Jurassic marginal seas and lakes. The teeth have been described as prehensile, and they were probably used for crushing shells and other hard prey (Andreev, 2012).

4.2.4. *Lepidotes* sp.

Sixty teeth in our collection have been assigned to the genus '*Lepidotes*', but the species cannot be determined because of the great variability in tooth shape. Teeth assigned to this genus are highly variable, with few distinguishing characteristics. The most distinctive teeth (Fig. 7F) are bulbous, with a short peg on the occlusal surface. Other teeth are shorter and dome-like, with a small cusp on the occlusal surface, otherwise very similar to *S. tomicus*.

'*Lepidotes*' has long been a wastebasket genus for undifferentiated, generally bulbous tooth remains of actinopterygians, especially from the Jurassic. Rhaetic materials, such as these, could be assigned to the Triassic genus *Paralepidotus*, but the specimens are inadequate for detailed assignment (López-Arbarello, 2008); therefore we retain them here under the traditional, informal name '*Lepidotes*' sp. Mr. Curtis described *Lepidotes* 'gill rakers' from Charton Bay, showing the same shape as those from Late Jurassic *Lepidotes glorioae* (Thies, 1989). However, we cannot confirm that these are '*Lepidotes*' gill rakers with certainty.

4.2.5. *Dapedium* sp.

We identify eight teeth tentatively as *Dapedium* sp. (Fig. 7G–J). *Dapedium* teeth are round multi-cusped teeth, and have not been found with their roots, so their full length is unknown. Godefroit et al. (1998) report *Dapedium* teeth from the Late Triassic of Luxembourg, but they describe them as 'mammiliform' or 'molariform', with five to twelve tubercles. Our specimens show seven to ten tubercles. The occlusal surface is generally round. Godefroit et al. (1998) note another type, a two-tubercle bifurcated tooth, but none of these are present in our sample.

This may be only the second record of teeth of this genus from the British Rhaetic, as Godefroit et al. (1998, p. 324) noted a possible find from Aust. *Dapedium* was a deep-bodied fish, with durophagous dentition, known from complete specimens from the Norian of Italy (Tintori, 1983) and more widely from the Early Jurassic (Thies and Hauff, 2011).

4.2.6. Other actinopterygian remains

Other actinopterygian remains include two skull portions, some vertebral centra, some fin rays, and some scales. These probably pertain to one or other of the five actinopterygian taxa identified on the basis of their teeth, but there is no evidence to help us match teeth and non-tooth fossils.

A small piece of actinopterygian jaw, measuring 2 mm × 0.25 mm, bears three protuberances and the remains of some heavily worn teeth, and is apparently broken on all sides (Fig. 7K). The specimen is similar to an actinopterygian palatal fragment in Foster and Heckert (2011, fig. 2E). Of the taxa otherwise represented in this sample, *Dapedium* sp. is known to have had palatal teeth (Godefroit et al., 2008).

A second actinopterygian skeletal element is a jaw containing a few very abraded teeth (Fig. 7L–M). One side has a deep groove perpendicular to the teeth, along the length of the jaw fragment. The fragment is just under 1 mm in length and slightly shorter in height, with tooth studs less than 0.25 mm in length.

The collection also includes 18 curved actinopterygian hemicentra, measuring up to 1.5 mm at their greatest dimension.

There are also 25 fin rays, long cylindrical pieces of bone, sometimes showing a gradual tapering of diameter in one direction. The longest fragments are about 2.5 mm in length, but they are broken at the tips, and so would have been longer originally. Some fine, delicate elements in this group of specimens may be partial fragments of gill rakers, as suggested for *Pseudocetorhinus* (Duffin, 1998a, 1999).

Some fin ray elements are stouter, thicker and somewhat flattened, and these may be jointed elements from the tail of *Sargodon*. They are generally domed on one side, and have a longitudinal groove along the other, creating the appearance of two rods stuck together. Our sample contains thirteen of these fragments.

Finally, many rhombohedral scales are present in our collection. Though worn to various degrees, some show a glossy surface with branching ridges, attached to a larger unadorned rhombohedral base. These scales cannot be identified with any confidence, although such scales have been identified with species such as *G. albertii*, with teeth present in this collection, and with other taxa without remains in this sample such as *Colobodus* (Duffin, 1999).

4.3. Other fossilized remains

The collection also includes 13 coprolites, ranging in length from 300 µm to 1.2 mm, and of varying shades of brown, even though the vast majority of other material is dark grey. Rounded, sub-spherical, slightly flattened or semi-cylindrical, they are sometimes mottled in colour, though no discernible specific contents are apparent. They conform to Type 3 coprolites as described by Duffin (1979, 1999). Coprolites are notoriously difficult to assign to a specific producer.

5. Discussion

5.1. Formation of the bone bed

The Charton Bay bone bed is, unusually, largely preserved inside a *Thalassinoides* burrow system (see Section 2). We reconstruct the sequence of events in its formation (Fig. 8) as proceeding in five stages. The youngest part of the Blue Anchor Formation of the Severn Estuary and Devon areas was exposed and became partially lithified and eroded (Fig. 8A). This produced an extensive, low-relief coastal plain that was rapidly inundated by the Rhaetic transgression to form shallow-water, current-swept marine environments. Extensive *Thalassinoides* burrow systems were produced in the near-surface layer of the lithified seabed ('firm-ground') at this time, probably by a small crustacean for shelter and feeding purposes (Fig. 8B). The waters above supported a diverse fish population at a time when the seawater chemistry was especially conducive to the preservation of phosphatic remains (see Section 2.1). Carcasses of the varied fishes fell to the bottom, and their skeletons were broken up, and washed around by bottom currents, and broken up and abraded. These bones and phosphatic fragments became part of the lag deposit known as the Rhaetic bone bed, the result of winnowing by currents that removed much of any input of siliciclastic sediment from nearby land areas, and it was deposited over the surface eroded by its transporting currents, filling irregularities in the underlying seabed, including occupied *Thalassinoides* burrow systems (Fig. 8C). The shrimps, or other crustaceans, that formed and occupied the burrows moved through the incoming fine-scale bone-bed material, packing it in some burrows with meniscate packing structures.

In the fourth stage (Fig. 8D), deposition of the Westbury Mudstone continued, compacting the bone bed and lower

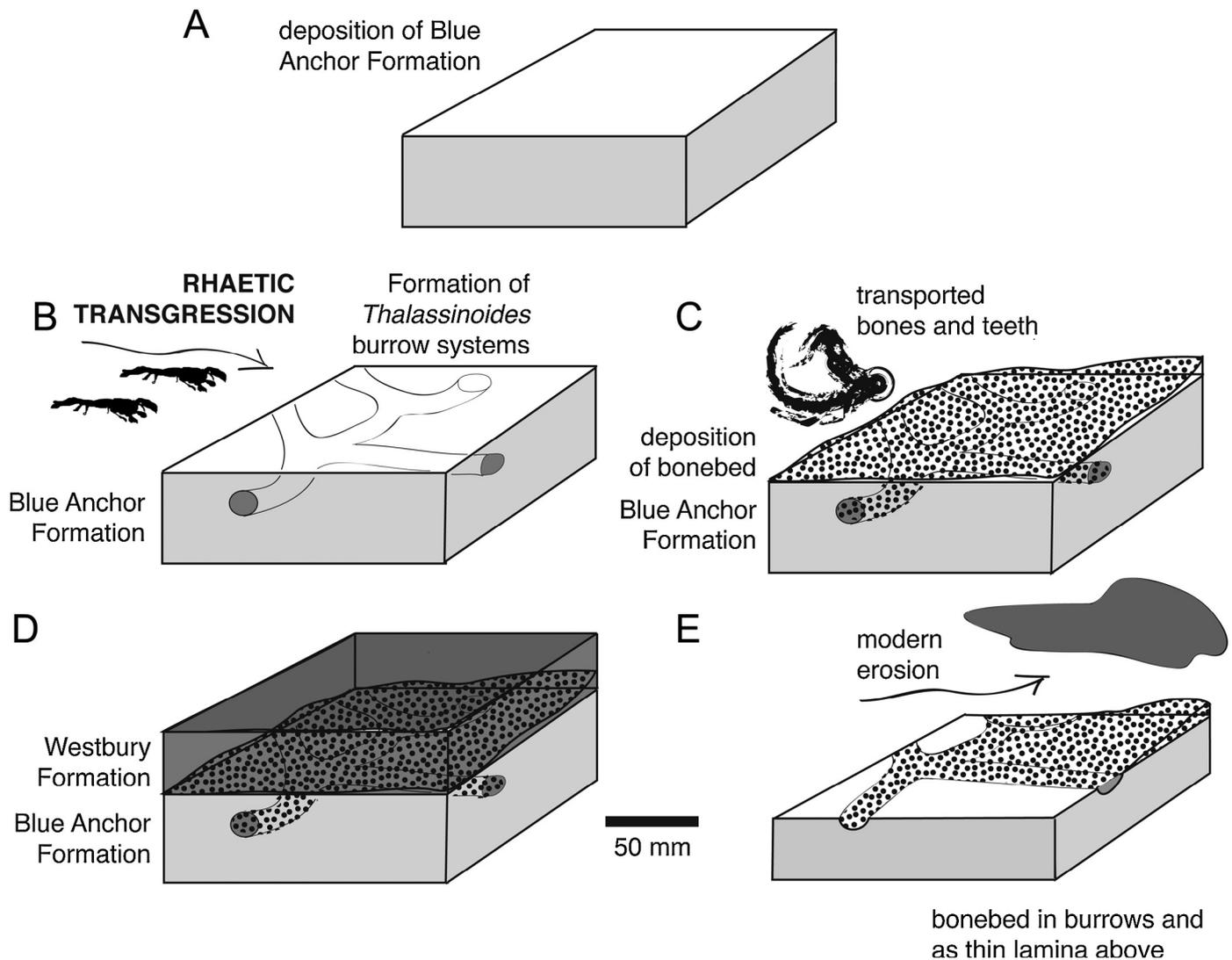


Fig. 8. Model for deposition of the Rhaetic bone bed at Charton Bay, Devon, as a burrow infill. (A) Deposition of the Blue Anchor Formation. (B) Beginning of the Rhaetic transgression, with arrival of burrowing shrimps that excavated the *Thalassinoides* burrows near the top of the Blue Anchor Formation. (C) Coeval deposition of basal Rhaetic bone bed sediments over the top of the Blue Anchor Formation, and reworked by shrimps into the *Thalassinoides* burrows. (D) Continuing deposition of the Westbury Formation sediments over the basal bone bed. (E) Modern erosion on the foreshore at Charton Bay exposes the top of the Blue Anchor Formation, with the bone bed-filled burrows and thin sheets of bone bed between.

sediments. In the fifth and final stage (Fig. 8E), recent marine erosion has exposed the unconformable junction of the Westbury Mudstone and the Blue Anchor Formation in the intertidal area at the western end of Charton Bay. The Rhaetic Bone Bed lag deposit rests on a slightly irregular surface of Blue Anchor Formation mudstones and extends down up to 50 mm into the mudstones as reworked infills in a complex *Thalassinoides* burrow system.

5.2. Wider occurrence of Rhaetic bone beds in burrow systems

This is the first detailed description of the Rhaetic bone bed reworked in a burrow system, although such occurrences have been noted briefly before. The junction of the Blue Anchor Formation and the Westbury Mudstone is marked by an erosion surface and a lithological contrast throughout SW Britain (Richardson, 1911). In addition to the burrowed junction at Charton Bay described here, burrowed surfaces have been recorded, but not described in detail, at Penarth (ST 188 695) and Lavernock Point (ST 188 682), Glamorgan (Richardson, 1905) and St Audrie's Bay (ST 104 431), Doniford Bay (ST 082 435), Lilstock (ST 177 454), and Blue Anchor (ST 039 438) on the

Somerset coast (Duffin, 1980), in the St Fagan's Borehole (ST 1169 7813), Cardiff (Waters and Lawrence, 1987) and in the Burton Row Borehole (ST 3356 5208) in Somerset (Whittaker and Green, 1983). Re-examination of the Glamorgan and Somerset coast sections by the present authors has confirmed the presence at St Audrie's Bay of the Rhaetic Bone Bed preserved in a thalassinoid burrow system in green mudstones that is morphologically closely similar to that at Charton Bay. Elsewhere on the Somerset coast, the bone bed rests on an irregular surface of bioturbated limestone in which *Chondrites* and *Thalassinoides* burrows are common, but these pre-date the unconformity and the formation of the bone bed.

At Penarth (ST 188695) and Lavernock Point (ST188682), the burrow/bone bed association occurs at two levels. At the Blue Anchor Formation/Westbury Formation Boundary, a thin conglomeratic basal bone bed, comprising rounded quartz pebbles, phosphatic clasts, teeth, and bones, with largest clasts up to 20 mm across, forms an irregular layer 0–20 mm thick, and infiltrates small, subvertical burrows. The second occurrence is in a 50–100 mm thick sandy limestone located 1.3–1.8 m above the base of the Westbury Mudstone formation. Here, *Thalassinoides* and other burrows, some up to 80 mm in diameter, contain sporadic bones

and teeth together with other arenaceous clasts and clay pellets. None of the burrow systems in Somerset or Glamorgan is currently as well exposed or well preserved as that at Charton Bay, and none contains such a high concentration of fish debris.

5.3. Faunal composition

The collection from the Charton Bay Rhaetic basal bone bed comprises 1868 specimens. Of these 1425 are identifiable (not bone fragments), consisting of 894 teeth, and 531 other elements (Fig. 9). Of these, 466 specimens can be identified as chondrichthyan, and 941 as osteichthyan. Of the chondrichthyan remains, 172 are teeth that belong to *L. minimus*, 37 to *R. minor*, 4 to *D. holwellensis*, and 1 to *P. pickfordi*. The remainder are dermal denticles or uncountable tooth fragments. A more liberal count of *L. minimus* teeth resulted in an estimate of 191 teeth, when accounting for halves. Of the osteichthyan remains, 60 are teeth belonging to the genus '*Lepidotes*', 58 belong to the species *S. tomicus*, 51 to *S. acuminatus*, 44 to *G. albertii*, and 8 to the genus *Dapedium*. The remainder comprises scales, unidentifiable teeth, and jaw fragments, gill rakers, etc.

In any such numerical study, there are many potential sources of error. For example, in the first count of *L. minimus*, we failed to include the many large fragments of tooth which either had a broken off cusp, or were broken in half, having been split transversely through the cusp and peg. The category 'halves' was added in the second count to account for these pieces, with each piece in the final total counting as half a tooth. Omitting the tooth halves clearly underestimated the numbers of *Lissodus*, whereas including the halves might overestimate this taxon in comparison to others for which tooth fragments were not counted.

Another potential source of error could be the loss of specimens smaller than 300 µm in any dimension as this was the smallest sieve mesh size used during processing of the material (Curtis notes, unpublished). We found many examples of teeth larger in one dimension than a sieve that they had passed through. The lateral *L. minimus* tooth in Fig. 5, for example, is nearly 4 mm long, but came from the material between 1.2 and 2.4 mm. Teeth of the *B. acuminatus* type of *S. acuminatus* as well as specimens of *G. albertii* were also longer from root to tip than the 1.2 mm sieve through which they had passed. In addition, we could not confirm that there were no vertebrate remains in the material greater than 2.4 mm (the largest sieve used), as this material was discarded.

Even with a perfect count of the fossil remains in such a microvertebrate assemblage, it is unlikely that these teeth represent relative faunal abundances other than in a very general way (Fig. 9). For example, animals with piercing teeth would

probably have lost more teeth than those with crushing teeth, but a counter-bias would have been that such crushing teeth are more likely to be preserved, surviving transport and abrasion, better than the pointed teeth of grasping hunters. Nonetheless, we find that many species in our sample were durophages, at least pointing to the importance of shell crushing in the Rhaetic marine fish assemblage. Other general biases in the tooth assemblage include the fact that different fishes had different numbers of teeth in their jaws, and differing lifespans, so their potential productivity of teeth would have varied. Added to this is the fact that sharks shed their teeth regularly, both during feeding and as a consequence of the continuous, conveyor-belt like renewal of the dentition; an individual shark could potentially produce thousands of teeth during its lifetime. Further, the assemblage is presumably spatially and time-averaged to some extent, so we cannot know the mix of original foraging areas, nor of seasons of the year, that are represented in the single deposit.

5.4. Late Triassic marine fish feeding ecology

The Late Triassic was an important time in fish evolution, documenting the transition from faunas dominated by hybodontiforms and other basal sharks, and chondrosteans, to those dominated by nesoselachians and neopterygians (Friedman and Sallan, 2012). The Charton Bay assemblage includes a mix of taxa belonging to the older and newer clades.

The top predator may have been *Severnichthys*, estimated at 1 m long, and with powerful predatory teeth and jaws. Elsewhere in the Somerset Rhaetic, rare coelacanths vied for top predator role (Hauser and Martill, 2013). This may have been a generally slow-moving lunge or ambush predator that lurked among water weeds, like the modern pike, and rushed out to snatch smaller prey. *Gyrolepis*, with its long, needle-like teeth, was also evidently a predator, feeding perhaps on smaller fishes and invertebrates. The other Charton Bay osteichthyans, *Sargodon*, '*Lepidotes*', and *Dapedium*, were all durophages, feeding on the abundant bivalves and other shelled invertebrates known from associated Rhaetic units (Gallois, 2007). This relative importance of durophages has been noted in the Late Triassic before: Lombardo and Tintori (2005) explain the phenomenon by the new skull arrangements in the neopterygians, in which the maxilla was free posteriorly and so enabled the development of a more powerful muscular system which could bring strong pressure to bear on any broad teeth in the jaw margins or palate. Late Triassic neopterygians were thus able to exploit new diets that were not available to less derived actinopterygians with their simpler jaw mechanisms, and these new diets included echinoids, crustaceans, and bivalves. It should

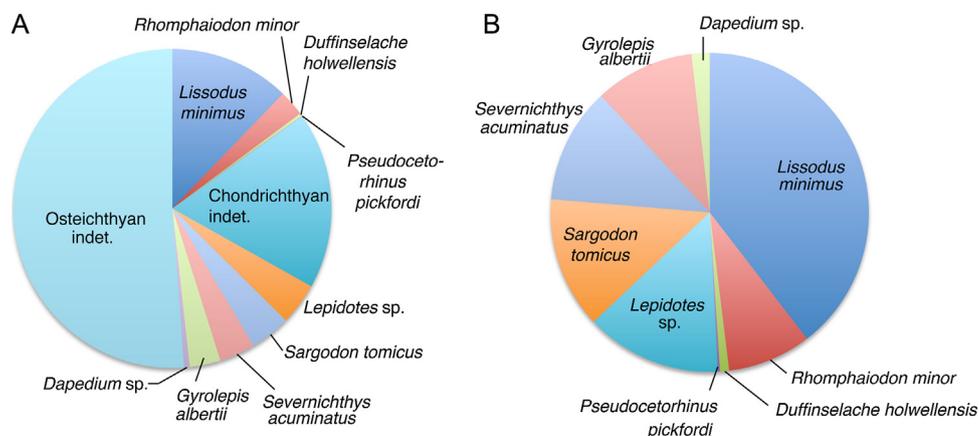


Fig. 9. Relative proportions of fish remains in the Charton Bay Rhaetic bone bed, based on all identifiable material (A) and on material identifiable to genus or species level (B). The fauna comprises one-third sharks, when all material is considered (A), and half sharks, for identifiable material (B).

also be noted that these three clades represent part of the Mesozoic to modern marine invertebrate fauna that had flourished after the Permo-Triassic mass extinction, replacing less meaty Palaeozoic precursor taxa such as brachiopods, crinoids, and trilobites.

The Charton Bay sharks, *Rhomphaiodon*, *Duffinselache*, *Lissodus*, and *Pseudocetorhinus*, are a typical selection of British Rhaetic forms (Storrs, 1994; Duffin, 1999). The teeth at least are generally small, suggesting these sharks were also small, perhaps subsidiary predators to some of the osteichthyans in the fauna. Tooth shape varies substantially, from the triangular, pointed teeth of *Pseudocetorhinus* to the low, blade-like teeth of *Lissodus*, presumably indicating differing diets and feeding modes. The *Lissodus* dentition has been interpreted (Cuny and Benton, 1999, p. 200) as of 'crushing type, indicating more opportunistic feeding behaviour', and *Pseudocetorhinus* may have been a filter feeder. The other sharks may have been adapted for clutching and piercing prey animals, including even some of the new, fast-moving neopterygian fishes.

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