Contents lists available at ScienceDirect

Proceedings of the Geologists' Association

A Rhaetian microvertebrate fauna from Stowey Quarry, Somerset, U.K.

Iacopo Cavicchini[a], H. Cecilia Heyworth[a], Christopher J. Duffin[a,b,c], Claudia Hildebrandt[a], Michael J. Benton[a,*]

[a] School of Earth Sciences, University of Bristol, Wills Memorial Building, Queens Road, Bristol BS8 1RJ, UK
[b] 146 Church Hill Road, Sutton, Surrey SM3 8NF, UK
[c] Earth Sciences Department, The Natural History Museum, Cromwell Road, London SW7 5BD, UK

A B S T R A C T

Rhaetian bone beds have been described from many locations in south-west England, around Bristol. One site that has never been reported is Stowey Quarry, some 13 km south of Bristol. This quarry yielded Lias, and revealed thin Rhaetian units in the quarry floor, including two bone beds, the basal Rhaetian bone bed, and a second, higher bone bed, also within the Westbury Formation. The fossil fauna of both includes elements typical of Rhaetian bone beds elsewhere, but showing differences in faunal composition between the two. The basal bone bed yielded more specimens and more species, with three taxa (*Sargodon tomicus*, *Rhomphaiodon minor* and *Hybodus cloacinus*) exclusive to this bed and eleven identified in total. *Severnichthys acuminatus* accounts for more than 50% of the countable teeth from the basal bone bed, followed by *Gyrolepis albertii* with 20%, *Lissodus minimus* with 14% and *Rhomphaiodon minor* with 9%. The basal bone bed, as ever, is dominated by chondrichthyans, whereas the upper bone bed is dominated by osteichthyans, which form 90% of the non-dental remains. The only unique taxon is *Dapedium*, and *Gyrolepis albertii* is the most abundant species with 45% of countable teeth, followed by *Severnichthys acuminatus* with 38% and *Duffinselache holwellensis* with 11%. These faunal differences, and the equally good condition of specimens between both samples confirms that the upper bone bed is independent of the basal bone bed, and is not a reworked subsample.

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1. Introduction

During the Rhaetian, the final division of the Triassic, lasting from 205.7 to 201.3 Ma (Maron et al., 2015), a series of marine transgressions flooded much of what is now northern and central Europe, bringing about dramatic changes in the European flora and fauna (Swift and Martill, 1999; Suan et al., 2012). Some of the most notable traces of this marine transgression are the thin, dark, fossil-rich layers identified since the 1800s as the Rhaetian bone beds, most notably the bone bed that marks the base of the Rhaetian in the U.K. Such levels are widespread across Europe in Rhaetian sediments, although their genesis is still debated and not fully understood: theories about their formation propose reworking of existing material during flooding episodes (Macquaker, 1999), or drastic changes in the water's geochemical conditions (Suan et al., 2012) induced by volcanism.

In the south-western U.K., across South Wales and around Bristol, the Rhaetian transgression formed a shallow sea with

structural palaeo-highs emerging from it as an archipelago of karstic islands (Fig. 1; Whiteside et al., 2016). Rocks belonging to the Penarth Group record this phase of dynamic fluctuations of relative sea level and the definitive disappearance of the continental arid conditions that had persisted for over 100 myr through the Permian and Triassic.

The Penarth Group comprises the Westbury Formation and the Lilstock Formation, which is further divided into the Cotham Member and the Langport Member. The Penarth Group outcrops from southwest to northeast England, and exposures are also present in Ireland and Scotland, although outcrops are typically limited in area (Swift and Martill, 1999). The Penarth Group is succeeded by the Lias Group, which includes the Triassic-Jurassic boundary above its basal unit, the Pre-*planorbis* Beds.

The best-known bone bed in south-western U.K. generally lies at the base of the Penarth Group, although it can occur above the base of the Westbury Formation or within the underlying Blue Anchor Formation. Nonetheless, the bone-rich horizon termed informally the "basal bone bed" is dense with chondrichthyan and osteichthyan fish remains, as well as fossils of marine reptiles such as ichthyosaurs and plesiosaurs, and the enigmatic *Pachystropheus*. Most palaeontological studies of Rhaetian microvertebrates have

* Corresponding author.
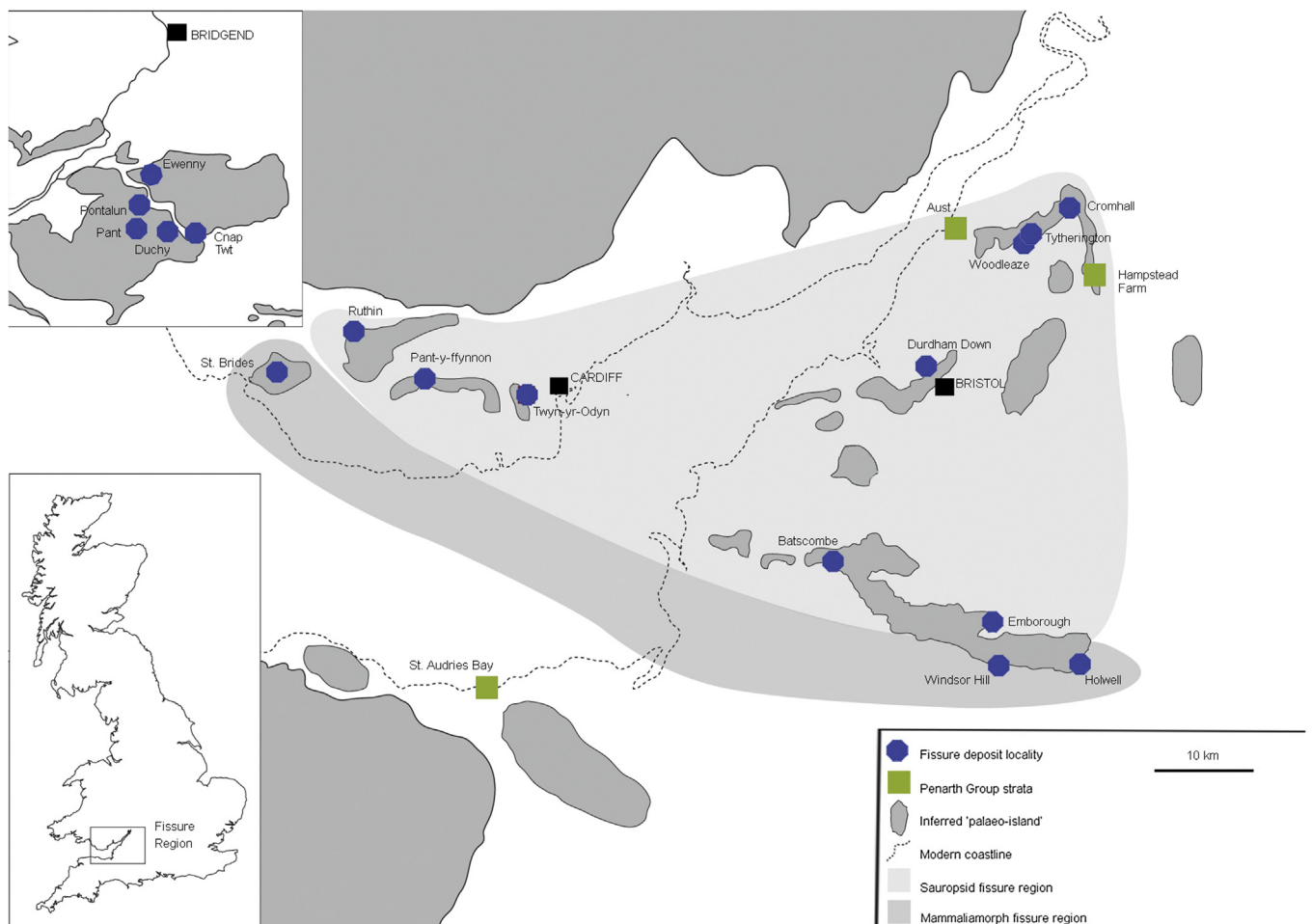*E-mail address:* mike.benton@bristol.ac.uk (M.J. Benton).

Fig. 1. A simplified Rhaeto-Liassic geography of the palaeo-archipelago of islands around Bristol and South Wales. Light grey is the region of Rhaetian-age fissures and dark grey that of the principal Early Jurassic localities. Upper left inset is a close-up of the quarries in the St. Brides area. Key Rhaetian bone bed localities are marked. Modified from Whiteside et al. (2016).

focused on the basal bone bed, but there are as many as four or five further bone-rich units higher in the Westbury Formation and low in the Cotham Beds (Duffin, 1980; Macquaker, 1999; Storrs, 1994; Allard et al., 2015; Mears et al., 2016; Slater et al., 2016). Most of these locations are in south Gloucestershire, close to the shores of the present-day Severn Estuary.

Here we present the first report of Rhaetian vertebrates from more than one bone bed in a location south of Bristol, in Stowey Quarry, Somerset. This site was a well-known exposure of the Rhaetian and Lower Jurassic, but has now been largely lost to science, and so it is important to record the field collecting and borehole data from the site.

2. Geological setting

Stowey Quarry (ST597586), also previously called Sutton Hill Quarry (Donovan, 1956), is located roughly 1 km south-east of the village of Bishop Sutton, on top of Sutton Hill. In the 1880s, Stowey Quarry was a long, narrow strip, running north–south, but since then it expanded eastwards, with planning permission for extraction of the Lias for building and road foundations in 1954 and 1998, forming a roughly square excavation of more than 20 acres (Figs. 2, 3c ; Carpenter, 2001). The quarry owners received planning permission for tipping of demolition and construction waste and other inert materials, in 1980, with a further permission in 2007 to develop a materials recycling facility. After 2010, the quarry has been filled with rubble and waste, and was the site of

extensive protest in 2012–2016 when it was proposed to become an asbestos dump. The earth-covered quarry fill has now obscured the floor of the quarry and most of the exposed quarry walls.

The fields around Bishop Sutton and nearby Stowey village were dotted with several limestone quarries since the 1800s, but by the mid-20th century most were abandoned. One small quarry lay east of Stowey village, on the east side of the small stream, at ST599600, and a larger, drive-in quarry at the White Cross cross-roads of the road running south of Bishop Sutton, at ST591587. Pits and small crags may still be seen beside the road just south of Stowey village, past the steep zig-zag that rises up the Triassic to Lower Jurassic section, at ST603593–604594 and ST600593–the 1880s Ordnance Survey map shows these as two long pits, each with a track branching from the road. Indeed, the much-filled former pit at ST603593 was named as Stowey Quarry by Donovan (1956, pp. 192–193), who was able to report that "This large old shallow quarry is almost completely overgrown. but two or three beds of limestone are still exposed at the eastern end, and the higher part of the section . . . was exposed by excavation." Donovan (1956, p. 193) recorded a section of 11 beds, spanning the *angulata*, *conybeari*, and *rotiforme* subzones, and comprising a section of about 2 m in total.

These quarries all lie on Sutton Hill, which is a small plateau, 150–165 m above sea level and stretching in a SSW-NNE direction for around 3 km; the plateau's top coincides with a vast outcrop of Upper Triassic to Lower Jurassic rocks, particularly the Langport Member of the Lilstock Formation, and the top of the Blue Lias
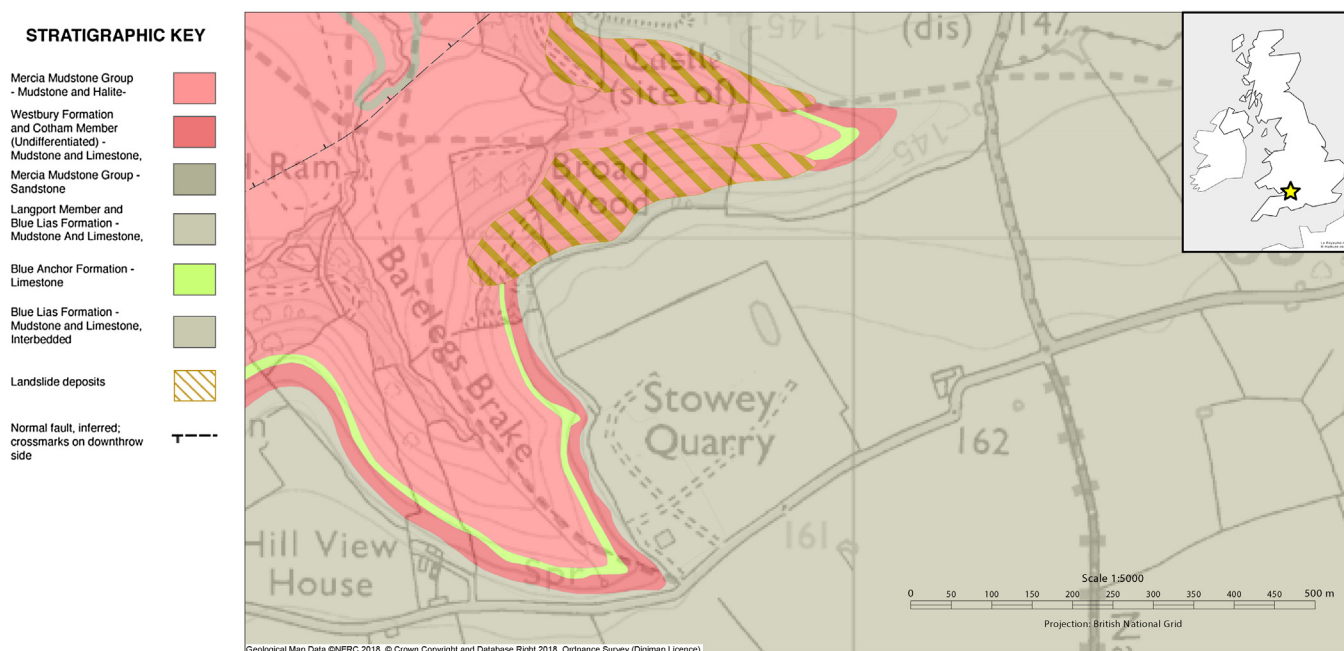
Fig. 2. Geology around Stowey Quarry (ST 597586). The morphological top of Sutton Hill is dominated by Early Jurassic outcrops, but the Penarth Group strata are buried just a few metres below the ground in Stowey Quarry and crop out on the plateau's slopes. Stowey Quarry was opened to work the Early Jurassic rocks, and the floor rested on the Rhaetian-Lias contact. © Crown Copyright and Database Right 2015. Ordnance Survey (Digimap License).

Formation (Fig. 2). These formations are more competent than the Cotham Member and the Westbury Formation below, being made up mostly of limestone and, therefore, they act like a protective cap against erosion; water action, however, has cut gullies into the plateau's slopes. The succession around the quarry is sub-horizontal or dips gently towards the NW. Owing to the morphology and stratigraphy of Sutton Hill, the Penarth Group, with the Rhaetian bone beds it contains, can be reached with relatively shallow pits or boreholes through the overlying Lias on top of the plateau.

The succession at Sutton Hill records a story of repeated marine transgressions, beginning at the bottom of the Westbury Formation with the basal bone bed and the erosive surface it rests upon (Swift and Martill, 1999). Sedimentation in the newly formed basin became predominantly clastic and relative sea level periodically rose and fell. Resulting fining-upward cycles with current-related sedimentary structures and erosive tops can be recognized throughout the whole Penarth Group, along with disturbances such as slumps (Duffin, 1980). Water exchange between the basin and the main ocean was discontinuous, favouring low oxygen levels; as a result of all the above, Rhaetian faunas (apart from the bone beds) are often not diversified and occur in patches, while pyrite and glauconite are very common (Swift and Martill, 1999).

While the Westbury Formation mainly comprises dark, organic-rich shales with subordinate calcareous sandstones, throughout the Penarth Group the calcareous fraction progressively increases, probably owing to reduced run-off from the continental areas nearby; emersion episodes marked by desiccation cracks are common, including the so-called "Sun bed" at the top of Lilstock Formation (Swift, 1995).

The Pre-*planorbis* beds, just above the Sun bed, mark the bottom of the Blue Lias Group and the definitive stabilization of the marine environment, testified by the presence of pelagic fossils such as ammonites (Donovan, 1956). Donovan (1956, pp. 191–192) noted that "several feet of the White Lias are exposed, succeeded by about 13 ft. of Blue Lias of the *planorbis* and *johnstoni* subzones. This exposure shows the thickest development in the district of the

beds between the Sun Bed and the *Psiloceras* Bed, and of the shales and limestones which form the lower part of the *johnstoni* subzone." He illustrated a short section, with 20 numbered beds, and reported specimens of *Planorbis* throughout, providing the zonal evidence. Donovan (1958, p. 138) reported a visit a few years later when the quarry was not "worked so deep" as it had been, and the White Lias was obscured.

The uncertainty over the naming of the Stowey quarries was highlighted by Loupekine (1956, p. 160) in his review of quarrying operations around the Bristol district, who referred to "Stowey Quarry", operated by the "Stowey Quarry and Lime Co. Ltd.", extracting Lias limestone, using the name we do, but differing from Donovan (1956, p. 191), Donovan (1958, p. 138) who called it 'Sutton Hill Quarry'. We stick to 'Stowey Quarry', however, the name used by local people and marked on current Ordnance Survey maps.

In 1999, Simon Carpenter and Richard Wilkins, two amateur palaeontologists, excavated a fossiliferous level occurring in the "Pre-Planorbis beds" (Fig. 2a and b), recovering a fossil assemblage rich in marine vertebrates, including marine reptiles, as well as fronds of the cycadeoid plant *Otozamites* and fish remains (Carpenter, 2001). At the same time, Hesselbo et al. (2004) were measuring stratigraphic thicknesses, sedimentary facies indica-tors, and stable isotopes through Triassic-Jurassic boundary sections across SW England, and they included Stowey Quarry as a key location, recording a composite section from Stowey and nearby Chilcompton (Hesselbo et al., 2004, Fig. 1) and noting a major negative carbon isotope excursion there corresponding to the level of the Cotham Marble. They noted also swaley and hummocky cross-stratification in the White Lias (Langport Member) of Stowey Quarry, indicative of storm deposition.

3. Materials and methods

In presenting the rock succession through the Rhaetian in Stowey Quarry, we use information from two sources, notes and specimens from Mike Curtis, and unpublished quarry reports. Mike Curtis, then working as a geologist for Geotechnical Engineering
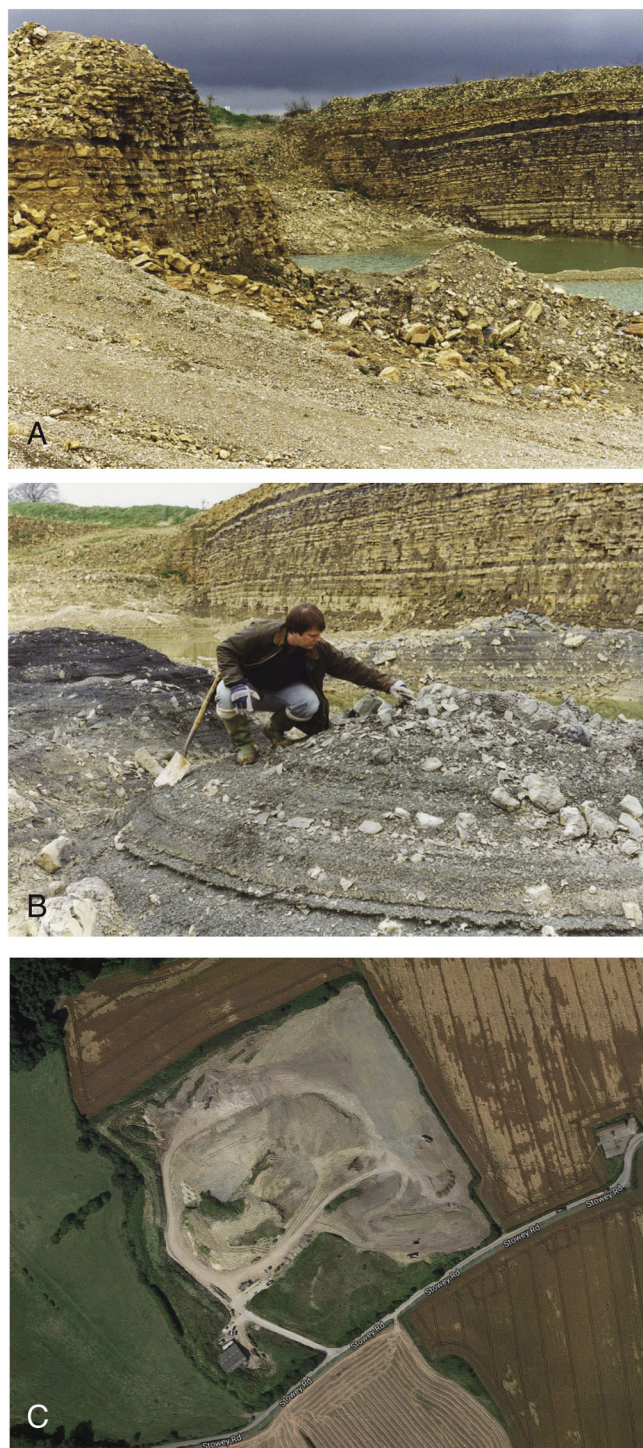
Fig. 3. Stowey Quarry, Bishop Sutton, Somerset, two views in April 1999, and an aerial photograph. A, General view of the quarry, showing the main section through late Triassic and early Jurassic strata – the lighter band some 2 m above water level is the top of the Langport Member with the 'Sun bed' at the very top. B, Close-up of Richard Wilkins crouching on a pile of unweathered clay/mudstone. This material came from several trial pits excavated in the floor of the quarry, each 2 to 3 m deep. The pits exposed the Cotham Marble at the top, so the mudstone below was presumably part of the Cotham Member. Simon Carpenter found a few small fish teeth and vertebrae, as well as part of a plesiosaur vertebra from this unweathered spoil, and the sediment and fossils were very similar to the fossils found in the lower zone of the Cotham Member at the Manor Farm site (Allard et al., 2015). The excavation stopped before it reached the Westbury beds. C, Aerial view, taken from Google maps. Photographs, and accompanying notes, by Simon Carpenter.

Ltd in Cheltenham, gained access to five borehole cores taken in the floor of the quarry in 1997. He processed the Rhaetian bone bed materials, identifying the basal bone bed, and one other bone bed, higher in the Westbury Formation, and retained the fossils, some borehole materials, and engineering geology reports, which were all donated on his death to Bristol University Geology collections in the School of Earth Sciences (BRSUG).

This collection also includes the previously unpublished Report 85555 by Geotechnical Engineering Ltd. We have extracted data on thicknesses, lithologies, and bone bed occurrences from these data sources, and we took data from another lithological log made during an excavation carried out by M.J. Carter Associates in September, 1998. This report was chosen amongst others for its reasonable quality and precision, and because it covers an area of the quarry unexplored by Curtis in 1997. We do not reproduce the original technical drawings or Mike Curtis' hand-written notes and logs, but present standardised, measured logs taken from their data. The unpublished site reports include detailed plans of the quarry floor, with the locations of the boreholes and sections marked, so we could present a redrafted version of this plan, together with the logs (Fig. 4).

The fossil collections described in this paper come from the cores drilled in 1997 (Fig. 4); the samples from the bone beds encountered during the drilling were collected and processed, partly by Mike Curtis at the time, and partly by us in summer 2016 and 2017. The samples are divided into four groups (following Curtis' own notation): the SQ.co.001 group comes from a bone bed located around 3 m below the quarry floor in borehole number 2; SQ.co.002 comes from the same borehole, around 6 m deep; SQ.co.003 comes from borehole number 4, at around 8.40 m below the quarry floor; and SQ.co.004 comes from the same borehole, at 3.20 m deep. In his notes, Curtis carefully recorded the microstratigraphy around the levels he sampled, never thicker than 3 cm, also noting that groups 001 and 004 come from the Westbury Formation-Cotham Member boundary, while groups 002 and 003 come from the Blue Anchor Formation-Westbury Formation boundary.

Processing of the samples was carried out by breaking down the sediment using a buffered 10% acetic acid solution (1.9 l of water in which 3 g of tri-calcium and 5 g of sodium carbonate anhydrous had been dissolved, and at least 100 ml of acetic acid was added). The resultant material was then sieved through five different filters: 2.4 mm, 1.2 mm, 600 μm, 425 μm, and 300 μm. Samples of SQ.co.003 and 004 were processed and sieved by Curtis, who then proceeded to identify the fossil material; on the other hand, the SQ.co.001 sample was processed but not sorted or identified, and SQ.co.002 was left unprocessed in the form of a block of sediment. Therefore, we processed it, using similar methods to Curtis; it was broken down using 10% acetic acid, sieved through various filters, and fossil material in the remaining sediment was separated. Curtis reported weights for each sample in his notebooks: 210 g for SQ.co.001, 189.5 g for SQ.co.002, 173.5 g for SQ.co.003, and 93.1 g for SQ.co.004.

Fossils were identified using an optical microscope and comparison with relevant field guides (Swift and Martill, 1999), and more recent papers, and we confirmed that most of the identifications by Mike Curtis were correct. Unidentified or unusual material was also categorised and identified as far as possible, although many fossils were too abraded or just broken into unrecognizable fragments. All the material was then assigned its own BRSUG identification number, keeping material of the same species and similar fossils together in trays or in small boxes, and setting apart unidentified bones and peculiar specimens.

Individual specimens that best represented a species or morphotype were selected, set apart from the rest and photographed using a microscope with Leica DFC425C built-in camera,
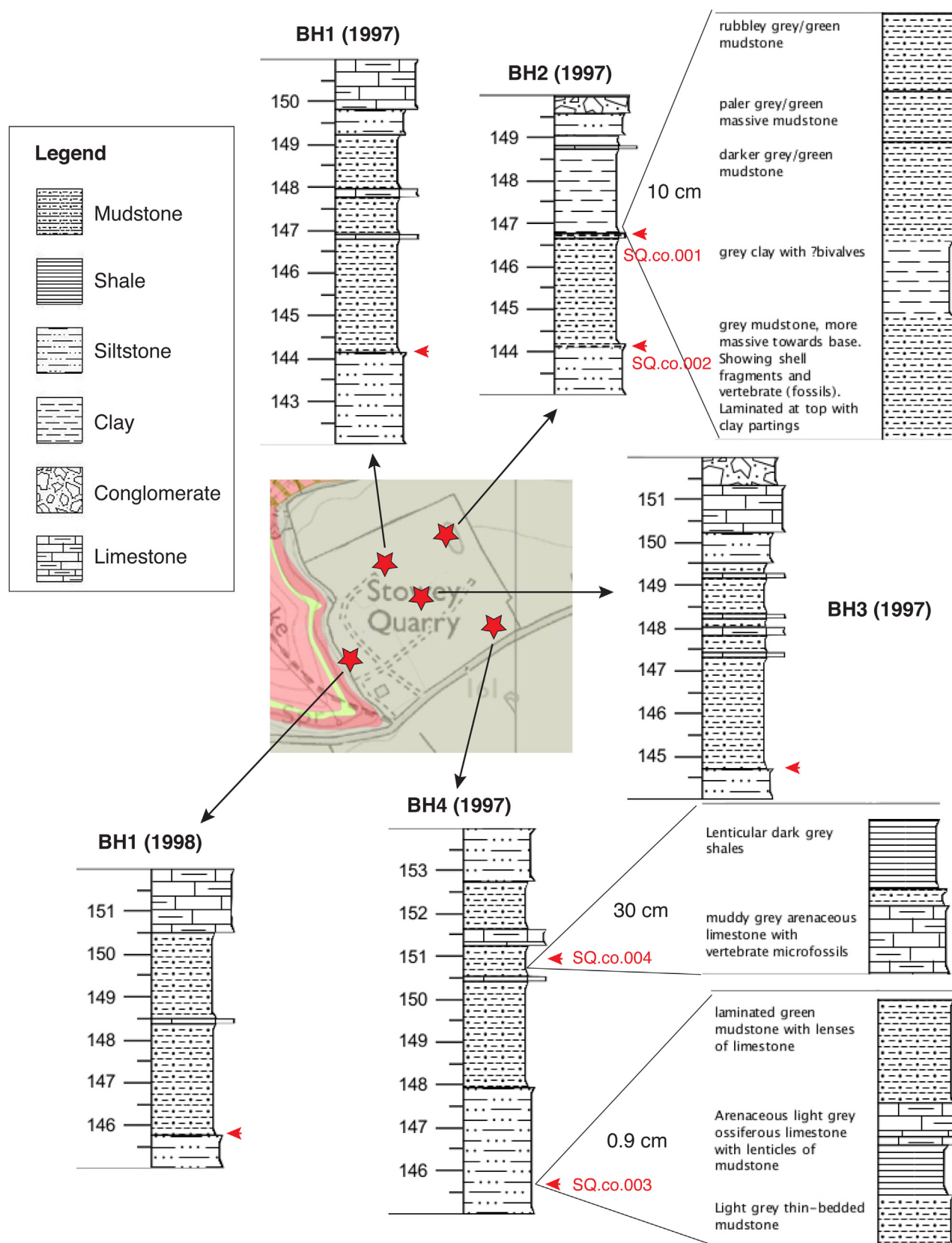
Fig. 4. Sedimentary logs from boreholes in Stowey Quarry. Key boreholes made at different points around the quarry floor in 1997 and 1998 are summarised, together with extra detail in two cases from logs made by Mike Curtis around the bone beds. Scale of the logs is in metres above sea level. Red arrows indicate positions of bone beds, the basal Rhaetian bone bed, at the contact of the Blue Anchor Formation and Westbury Formation above, and the higher Westbury Formation bone bed, in the cases of boreholes 2 and 4. The four numbered samples by Curtis (SQ.co.001, 002, 003, 004) are also indicated. Photo is an extract from the geological map; © Crown Copyright and Database Right 2015. Ordnance Survey (Digimap Licence). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and photo-stacking software, to reduce out-of-focus effects. Photographs were then processed using photo-editing software to crop out the background and adjust colour and contrast, to produce the specimen illustrations.

Since the fossil collection comes from multiple bone beds, care was taken in recording details and in the numerical and statistical analyses. Simply counting bones and teeth probably would not give an accurate summary of faunal content; for example, we have no information about how many teeth each animal possessed in life nor, for chondrichthyans, how many teeth each individual might have shed during its lifetime. Further, of course, the assemblages of fossils in each bone bed could well have derived from multiple sources. Nonetheless, we provide numerical count data, following principles used in previous papers in the series (e.g. Allard et al., 2015; Korneisel et al., 2015; Mears et al., 2016). In these counts, chondrichthyan teeth were included in the count only if they possessed an intact primary cusp, and osteichthyan teeth were included if 70% or more of the main cusp was intact. For scales, vertebrae, coprolites, denticles, and other assorted bone material, both fragments and whole specimens were included when counting, with no difference between them.

Subsequently, faunal assemblages and presence/absence of the various species or morphotypes were determined for each of the four fossil assemblages; this allowed assessment of how many bone beds were actually sampled and the faunal differences between them. Some species encountered were known to be heterodont: any different morphotypes belonging to a single species were put together in both classifications and statistical counting. The only exceptions are *Birgeria acuminata* and *Saurichthys longidens*, which are not separate species but two morphotypes of the osteichthyan *Severnichthys acuminatus* (Agassiz, 1835), as noted by Storrs (1994).

4. Systematic palaeontology

4.1. Chondrichthyans

Chondrichthyan remains make up around 30% of the specimens, fewer than Osteichthyes. Members of the Elasmobranchii were dominant among these chondrichthyans, but a minor holocephalan presence is testified by the presence of chimaeriform denticles. Tooth morphologies show that the chondrichthyans were either durophagous or predatory; heterodont forms were common, perhaps indicating opportunistic feeding habits. Teeth and denticles make up most of the shark remains identified, but more delicate specimens, like bits of prismatic cartilage, vertebrae and hemicentra, are also present, at times in a good state of preservation. The chondrichthyan fauna is typical of that from Rhaetian bone beds throughout Europe (Cuny and Benton, 1999; Duffin, 1999).

4.1.1. Duffinselache holwellensis (Duffin, 1998b)

This neoselachian shark is heterodont: anterior teeth are large (up to 4.9 mm in length), nearly symmetrical and with a sturdy, polygonal main cusp that is distally inclined (Fig. 5a and b). The base is flared and presents ridges (visible in the best preserved specimens) that never climb the crown, instead descending to the deep neck that separates the crown from the root. Heels of the crown can be straight or slightly curved labially. Posterolateral teeth are smaller overall, around half the length of anterior teeth, and show a smaller main cusp, asymmetrical and distally inclined (Fig. 5c and d); the heels are straight and present fainter ridges. In both morphologies, there are no visible lateral cusplets and the root's size is comparable to the crown; foramina punctuating the root are particularly evident since they are spaced by columns of tissue.

4.1.2. Lissodus minimus (Agassiz, 1839)

Teeth of this species vary in length from around 3 to 5.5 mm, and their finest features can be almost completely erased by mechanical wear. The presence of a low, conical central cusp and a labial peg on the labial side (made of a strong vertical ridge with a globular projection near the crown's base), however, make it possible to distinguish even the most worn out or broken specimens (Fig. 5g and h). The crown can be slightly curved or almost semicircular in occlusal view, and presents up to five pairs of lateral cusplets along a strong occlusal crest; bifurcating ridges descend radially from the cusps and from the occlusal crest (Fig. 5e and f). The root is not preserved in specimens from this collection; when present, it is at least the same depth as the crown and is punctuated by various foramina (Mears et al., 2016). Teeth of this species are the most common chondrichthyan teeth in the collection; their tendency to break at two thirds of their length, leaving the main cusp and one of the heels together, or almost in half, may introduce a high bias in the counting criteria (see below, Section 5).

4.1.3. Hybodus cloacinus Quenstedt, 1858

Some isolated fragments in the collection have been identified as lateral cusplets of *H. cloacinus*, although there are no complete specimens (Fig. 5i). The cusplets are robust, strongly ridged for their whole height (more on the labial side) and are slightly inclined lingually; the base of the crown is flared, but there are no remaining root tissues. Complete specimens of this species are not uncommon in Rhaetian beds: they reach 7 mm in length and are strongly asymmetrical (Lakin et al., 2016), probably belonging to a slow-moving durophagous predator (Tintori, 1998).

4.1.4. Pseudocetorhinus pickfordi Duffin, 1998a

This species is a rare sight in this collection and no complete specimens are preserved, although it has been reported widely in Rhaetian bone bed assemblages (Cuny and Benton, 1999). Teeth show one unornamented, asymmetrical and pointed cusp and no cusplets; the crown too is generally asymmetrical and distally inclined. The tooth shows a strong neck between the crown and the root, and this bears some nodes at the base of the crown (Fig. 5j) and vascular foramina lie around the slightly bulging elements of root tissue. A fraction of the root is preserved in one specimen, and it shows a rugose and punctuated surface (Fig. 5k). In more complete specimens the root extends beyond the limits of the crown but is roughly of the same height; our specimen would seem to be most likely part of a tooth from an anterior or anterolateral position (Mears et al., 2016, Fig. 5g, h).

4.1.5. Synechodus rhaeticus (Duffin, 1982)

Synechodus rhaeticus had some of the biggest teeth in the sample, with a crown up to 2.5 mm in height in the most complete specimen. The main cusp is mostly upright or slightly inclined distally and lingually, and can be positioned slightly off the crown's centre; an average of three cusplets on each side is present, although they can be unevenly distributed and up to four on each side (Cuny and Benton, 1999; Nordén et al., 2015). They are considerably smaller than the main cusp and decrease in size further away from it. Despite the cusplets' possibly irregular distribution, the tooth as a whole looks roughly symmetrical (Fig. 5l). All cusps and cusplets are conical and have ridges that descend the neck bifurcating and intersecting, on both sides of the tooth. The neck itself is deeply incised and gives way to a root randomly punctuated by foramina, approximately as wide as the crown, but smaller in size. The morphology described here belongs to an anterior tooth; although the dentition is known to show linear gradient heterodonty (Nordén et al., 2015), no other morphologies were recognized in this collection.

Fig. 5. Chondrichthyan teeth from Stowey Quarry. (a-d) *Duffinselache holwellensis*. (a and b) BRSUG 29371-1-1696, anterior tooth in dorso-lingual (a) and ventro-labial (b) views; (c and d) BRSUG 29371-1-1696, posterior tooth in lingual (c) and labial (d) views. (e-h) *Lissodus minimus*. (e and f) BRSUG 29371-1-2035-1, exceptionally well-preserved specimen in dorsal (e) and labial (f) views; (g and h) BRSUG 29371-1-2035-1, most common appearance of *L. minimus* in the collection, dorsal (g) and labial (h) views. (i) *Hybodus cloacinus* fragment, possibly a lateral cusplet (BRSUG 29371-1-939-8), in labial view. (j and k) *Pseudocetorhinus pickfordi* tooth (BRSUG 29371-1-1596) in oblique labial (j) and dorsal (k) views. (l) BRSUG 29371-1-1608, *Synechodus rhaeticus* tooth in lingual view. The specimen is broken but substantially complete and in good preservation. (m and n) *Rhomphaiodon minor* tooth (BRSUG 29371-1-1510-1) in labial (m) and lingual (n) views. Scale bar is 2 mm for (a), (b), (e), (f) and (l); 1 mm for the other specimens.

4.1.6. Rhomphaiodon minor (Agassiz, 1837)

Specimens of these teeth are the second most abundant in the collection, although not ubiquitous in every analysed bone bed. They are often found as complete, pentacuspid teeth, even in the smallest specimens, and are always lingually inclined with a sinuous outline (Fig. 5m and n); when found as fragments, the main cusp is usually intact. All cusps present a few, relatively coarse vertical ridges usually more pronounced lingually than labially, although the surface can easily be abraded until they disappear; ridges can branch at the level of the neck. The root is usually smaller than the crown and has a broad, foramina-punctuated lingual projection, called the lingual torus, which is a very useful distinctive character when it is preserved.

4.1.7. Other selachian remains

4.1.7.1. Denticles.
Denticles are fairly common in this collection, although not homogeneously distributed in each of the analysed levels. They are the remains from the skin of chondrichthyans, and thus are a kind of fossil expected in levels generally rich in shark remains. Being structurally homologous to teeth, sometimes they bear a close resemblance to them and are usually difficult to assign to taxa (Swift and Martill, 1999); in this collection, they were divided by morphology into several broad categories.

Placoid denticles (Fig. 6a, b): This morphology is the most common in the collection, and they show a variety of morphologies. We follow descriptive terminology from Johns (1996), who described such denticles as consisting of a crown on a pedicle, or basal structure. One type of placoid denticle (Fig. 6a) shows a moderately flared pedicle and a larger crown mounted on a narrow neck. The crown has longitudinal ridges that descend to the neck and is always posteriorly elongated; the overall morphology can be flat-topped or slightly concave and the posterior termination is pointed, with up to three cusps. The second type (Fig. 6b) is dominated by the elongate, pointed principal cusp, forming part of an arched crown, bearing longitudinal ridges, and separated by a short neck from the pedicle, which is only slightly larger than the neck. Dimensions rarely exceed 1 mm for these denticles.

Ctenacanthid denticles: The collection contains only one dubious, fragmented specimen of this morphology. The crown is multicuspid; each cuspid is almost upright and has strong vertical

Fig. 6. Other chondrichthyan remains from Stowey Quarry. (a–d) denticles. (a) Placoid denticle (BRSUG 29371-1-2048-6), in oblique anterior view. (b) Placoid denticle (BRSUG 29371-1-2048-7), in posterior view. (c) Chimaeriform denticle (BRSUG 29371-1-2048-6), in dorsal view. (d) Hybodont denticle (BRSUG 29371-1-1481-1), in oblique anterior view. (e) Selachimorpha prismatic cartilage (BRSUG 29371-1-43-1). (f and g) Chondrichthyan vertebra (BRSUG 29371-1-619), in lateral (f) and anterior (g) views. Scale bar is 1 mm for (c), 0.5 mm for all other specimens.

keels. The base is short and the neck is moderately incised, although the specimen is too damaged to be further characterized. Whether it is a ctenacanthid or not is hard to determine – this term has been used in previous papers (e.g. Duffin et al., 1983; Korneisel et al., 2015; Nordén et al., 2015), but ctenacanthids are otherwise generally Palaeozoic taxa.

Chimaeriform denticles (Fig. 6c): Chimaeriform scales are the second rarest morphology in the collection, but includes the biggest specimen of all. As the name suggests, this kind of denticle belongs to members of the Holocephali, although it is not possible to assign the scales to any particular genus, either from denticles or other remains. Our specimens resemble those figured as holocephalan denticles by Duffin et al. (1983) and Korneisel et al. (2015, Fig. 6). These chondrichthyans had only sparse scales on their bodies and as a result, denticles tend to be larger and rarer even in fossiliferous levels; the morphology is easily recognizable, here and elsewhere, presenting a large basal plate and a small (but robust), single, unornamented crown capped with enamel.

Hybodont denticles (Fig. 6d): The hybodont morphology consists of a large base, usually larger than the crown, although it is robust in appearance; it has a unicuspid or multicuspid termination, possibly due to odontode fusion (Swift and Martill, 1999). Each cusp has coarse ridges running down for the full height of the cuspid that tend to become thicker near the neck.

4.1.7.2. Prismatic cartilage. A few elements of the chondrichthyan cartilagineous endoskeleton were found (Fig. 6e). Some have retained their original regular outline (pentagonal and hexagonal), while others are worn and have lost their polygonal shape. Many such prisms, also called *tesserae*, fit together in chondrichthyan endoskeletal elements like a mosaic, along with unmineralised sections (Dean and Summers, 2006). Such prismatic cartilage may

be a chondrichthyan synapomorphy (Maisey, 1986), found in all extant and fossil forms.

4.1.7.3. Neoselachian vertebrae. Vertebrae from chondrichthyans are not very common in the collection, with just two specimens, but they ought to occur because of the high number of chondrichthyan remains of other kinds. Both specimens are roughly cylindrical in shape, with concave bases, and they are very abraded (Fig. 6f and g). This corresponds best to Morphotype V1 of the three neoselachian vertebrae distinguished by Mears et al. (2016, Fig. 8a, b) from Hampstead Farm Quarry, in that it has a subcircular articular face and lacks lateral constriction.

4.2. Osteichthyans

All identified osteichthyan remains are assigned to the Actinopterygii, and mostly the Neopterygii, with a total of five identified species. All specimens are from species that are already well known from the British Rhaetian. There are nearly twice as many identifiable bony fish remains as there are chondrichthyan remains.

4.2.1. Gyrolepis albertii Agassiz, 1835

Gyrolepis teeth are very common in the collection, and ubiquitous at all the levels sampled. The tooth shaft is conical due to a slight flaring towards the root, and has a characteristic, curved outline. The tip is pointed and made of acrodin; it can account for up to one quarter of the tooth's length, but can also be easily lost. The tip is unornamented, while the shaft bears fine vertical striations along its length (Fig. 7a). Dimensions of these teeth can be highly variable, with the biggest specimens measuring over 2 mm in height, but the morphology remains remarkably consistent in teeth of any height. Scales from this fish are also among

Fig. 7. Osteichthyan teeth from Stowey Quarry. (a) *Gyrolepis albertii* tooth (BRSUG 29371-1-2045-1), in side view. (b-f) *Severnichthys acuminatus*. (b-d) *Birgeria*-type *S. acuminatus* teeth (BRSUG 29371-1-209-1 (b) and 29371-1-2041-8 (c and d)), in side view and showing various morphologies. (e and f) *Saurichthys*-type *S. acuminatus* teeth (BRSUG 29371-1-2041-8) in side view, showing various morphologies. (g and h) *Sargodon tomicus* tooth (BRSUG 29371-1-2032-1), in dorsal (g) and ventral (h) views. (i and j) *Lepidotes* sp. teeth (BRSUG 29371-1-2041-17 and BRSUG 29371-1-2022-1 respectively). (k and l) *Dapedium* sp. tooth (BRSUG 29371-1-1272-1), in lateral (k) and oblique dorsal (l) views. Scale bar is 1 mm for (b), 0,5 mm for all other specimens.

the most common ones found in the collection and in Rhaetian strata across England (Storrs, 1994); they are described below.

4.2.2. Severnichthys acuminatus (*Agassiz, 1835*)

Two tooth morphologies are known for this fish: *Birgeria acuminata* and *Saurichthys longidens*, formerly thought to be two distinct species until both were found on the same jaw bone (Savage and Large, 1966; Storrs, 1994); the collection contains also a complete array of intermediate forms, combining characteristics of the two morphotypes to form a continuum.

B. acuminata: morphology is substantially conical, topped with an acrodin tip that can occupy more than half of the crown's length and is transparent in the better-preserved specimens. Tip and shaft are separated by a strong neck; both are moderately to strongly ridged and sometimes rugose in appearance, although they can be worn to the point of being completely featureless (Fig. 7b, c and d). They can be over 2.5 mm in height.

S. longidens: differentiated from *B. acuminata* principally by its sinusoidal shape and the unornamented tip occupying less space on the crown. There can be a neck separating tip and shaft, but it is not so pronounced as in *B. acuminata*. The shaft can have ridges descending to the root, straight down or describing helixes, but never reaching the rugose appearance of *B. acuminata* (Fig. 7e and f); the shaft's base can be flared. This morphology is the smaller one, both in diameter and in height.

4.2.3. Sargodon tomicus *Plieninger, 1847*

This fish is a known heterodont species, with a molar-like morphotype and an incisor-like morphotype (Duffin, 1980), but in this collection only fragments, or small molar-like teeth, were found. Teeth have a circular outline when seen in dorso-ventral view, and have a convex acrodine cap, which can be very worn (Fig. 7g and h); the inferior surface is usually just concave and irregular. Specimens in a good state of preservation still show dentine tubules in the

acrodine cap, but usually teeth are just dark and pebble-like. The diameter of complete teeth does not exceed 1 mm.

4.2.4. "Lepidotes" sp

Five specimens have been assigned tentatively to this genus; they are small teeth, never more than 1 mm in height, and with an upright, cylindrical crown, sub-circular in cross section. There is a small, pointed enamel cap (when preserved), which can be dome-shaped or even hook-shaped (Fig. 7i and j). One specimen shows what may be part of the root attached to the tooth, but in general these specimens do not show many distinctive features apart from the general appearance and the enamel tip. The hook-shaped specimen (Fig. 7i) may be a pharyngeal tooth. The name "*Lepidotes*" is applied to teeth of this kind from many levels in the Mesozoic, and we use it simply because it has been conventionally applied to such Rhaetian teeth before (e.g. Duffin, 1980, 1999; Allard et al., 2015; Nordén et al., 2015).

4.2.5. Dapedium sp.

Dapedium teeth are rare in Rhaetian strata; this collection is no exception, since only one, but nearly-complete, 1.5 mm high tooth was identified as belonging to this genus (Fig. 7k and l), based on comparison with previous studies (e.g. Godefroit et al., 1998, Fig. 7 (7); Korneisel et al., 2015, Fig. 7G–J). The tooth is roughly circular in section and has a cylindrical, barrel-like general appearance. The diameter of the crown top is roughly 0.7 mm and has six (possibly more) tubercles arranged around the tooth edge, while the lower half is marked by a row of very thin and short incisions and a slight indentation, which could mark the tooth-root division. The supposed root is broken, exposing the ellipsoidal pulp cavity. This may be only the third record of teeth of this genus from the British Rhaetic, as Godefroit et al. (1998, p. 324) noted a possible find from Aust, and Korneisel et al. (2015) some specimens from Devon. *Dapedium* was a deep-bodied fish, with durophagous dentition, known from complete specimens from the Norian of Italy and more widely from the Early Jurassic (Thies and Hauff, 2011).

4.2.6. Other osteichthyan remains

4.2.6.1. Scales.
As the dermal elements of Osteichthyes, scales are fairly common in the collection, and ubiquitous in all Rhaetian-age bone beds. The most common producer of such scales seems to be *Gyrolepis albertii* (Storrs, 1994; Whiteside and Marshall, 2008; Mears et al., 2016), with different morphotypes assignable to this taxon: they always comprise a roughly polygonal-shaped single piece (most regular ones are rhomboid or square, but elongated anterodorsally to posteroventrally). The external side can be recognized by a ganoine layer, ornamented antero-posteriorly by striations that can branch; when the layer is absent, concentric lines following the scale's outline can be seen on the underlying surface (Fig. 8a–d). The anteriormost portion of the scale is never covered by ganoine, presenting instead a chamfered edge to accomodate the preceeding scale's overlap. The scale's internal side often has an oblique, linear, wide ridge. Assigning scales to taxa can be tricky, since different morphologies could reflect either different taxa or different positions on a single individual's body and, although this is clear for *G. albertii*, it is not so evident for other taxa. As an example, this collection includes one complete, concave, apparently featureless fulcral scale (Fig. 8e and f), impossible to assign to a taxon. Past works highlight another particular morphotype, with a thick external ganoine layer presenting concentric polygonal ridges and belonging to *Pholidophorus* (Whiteside and Marshall, 2008; Mears et al., 2016, Fig. 10g, h) but the morphotype is rare and seems to be missing from the Stowey Quarry collection.

4.2.6.2. Fin ray elements and spines.
Osteichthyan fins comprise several skeletal elements; although they cannot be assigned to taxa, their function can sometimes be recognized, distinguishing a number of fin ray elements and fin spines. The first ones, also called lepidotrichia, are small bones with a rectangular, smooth-angled patch of striated ganoine, bilaterally paired and segmented, that make the fin's structure more robust (Fig. 8g–j). Different morphotypes are present in the collection and, despite the lack of a good number of complete specimens, there seems to be a distinction between bigger and smaller elements, judging by the length of the ganoine patch; a similar distinction, although based on more complete specimens, was made by Mears et al. (2016) for material from Hampstead Farm Quarry's multiple beds. In comparison, the Stowey Quarry collections seem to lack the elongated morphotype F4 (Mears et al., 2016, Fig. 11i, j). Fin spines, on the other hand, are elongated, moderately curved and sub-circular or elliptical in section (Fig. 8k). The surface presents very superficial longitudinal incisions.

4.2.6.3. Gill raker teeth.
Gill raker teeth are bony elements that project from the gill arch, and that were used for suspension feeding; they can be found in both chondrichthyans and osteichthyans that adopt this feeding mode. They superficially resemble regular teeth, albeit much smaller both in height and in section, and they are upright, unornamented and have a pointed, curved tip (Fig. 8l). Probably due to the diminutive size and section, these remains are very rare in the collection and no complete specimen was found. It has been suggested that *Pseudocetorhinus pickfordi* might have been the suspension feeder that possessed these teeth (Duffin, 1998a,b, 1999), but this cannot be proved. To reflect this, gill raker teeth have been categorized as unidentified specimens in all the statistical analyses.

4.2.6.4. Vertebral centra.
Osteichthyan vertebrae have a central centrum, which is a doughnut-shaped skeletal element, surrounding and protecting the notochord, and which also supports the ribs and neural spines (Fig. 8m). No vertebra was found articulated, however, and the centra were often in pieces.

4.2.6.5. Hemicentra.
In fishes, hemicentra form part of the condyles in the axial endoskeleton. They are platy in appearance, being concavo-convex and very thin when seen in anterior-posterior view. Because of this plate-like morphology, recognisable specimens are rare to come by both in this collection (just two recognisable specimens), and in British Rhaetian strata. Hemicentra fragments are probably much more common than is recorded, being part of fish skeletons, but among works on the British Triassic, only Nordén et al. (2015, p. 574) report a small number of actinopterygian hemicentra from Marston Road Quarry.

4.3. Other fossilised remains

4.3.1. Invertebrates
One of the beds investigated yielded around a hundred steinkerns of gastropods, produced by sediment filling the void left inside shell, which was then lost; most belong to the genera *Promathildia* (tall steinkerns with a turreted spiral), *Cylindrobullina* and *Solarioconus* (both having a bigger, oval last whorl and being shorter), based on comparison with earlier work (Barker and Munt, 1999; Mears et al., 2016, Fig. 17). Closer identification was impeded by the lack of details, especially of the outer features of the shells. Some of the gastropod steinkerns have vertebrate bone fragments or denticles attached, a necessarily post-mortem and probably also post-diagenetic event (Fig. 8n). The grain size categories with steinkerns did not yield any other recognizable fossil invertebrates.

Fig. 8. Osteichthyan remains and other non-vertebrate fossils from Stowey Quarry. (a-d) Osteichthyan scales (BRSUG 29371-1-777-1), in external (a and c) and internal (b and d) views; (a) shows the ganoine layer and the concentric pattern underneath. (e and f) Osteichthyan fulcral scale (BRSUG 29371-1-684-2), in external (e) and internal (f) views. (g-j) Fin ray elements (BRSUG 29371-1-739) (g and h) and BRSUG 29371-1-777-1 (i and j); with g and i showing an ornamented layer of ganoine. (k) Fin spine (BRSUG 29371-1-2041-1). (l) Gill raker tooth (BRSUG 29371-1-2041-11). (m) Ring centrum (BRSUG 29371-1-1315). (n) Steinkern of Gastropoda (probably *Promathildia* sp.), showing a bone fragment attached to the internal cast (BRSUG 29371-1-1380-3). (o and p) Coprolites (BRSUG 29371-1-1036-1 and BRSUG 29371-1-1035 respectively); (o) classifiable as a h- or i-type, produced by a fish. Scale bar is 2 mm for (p), 0.5 mm for (l) and (m), and 1 mm for all other specimens.

4.3.2. Unidentified bones

Most fossilized bones are fragments, making it impossible to identify them at any level. Together, unidentified bone fragments number more than 600 specimens.

4.3.3. Coprolites

Fossilized faeces are not ubiquitous in this collection, and count fewer than 60 specimens. Most of them are round or ellipsoidal and featureless, making it impossible to classify them (Fig. 8p); one

Table 1

Summary of counts of key taxa, group-level identifiable material and unidentified material from the four levels sampled at Stowey Quarry. Numbers for teeth include only countable specimens. Groups 001 and 004 are referred to the upper bone bed (Westbury Formation–Cotham Member boundary) while groups 002 and 003 are from the basal bone bed (Blue Anchor Formation–Westbury Formation boundary). Allocation of samples to basal bone bed (BBB) and a bone bed located at the top of the Westbury Formation (UBB) are indicated.

	Group 002 BBB	Group 003 BBB	Group 001 UBB	Group 004 UBB
Lissodus	128	54		2
Rhomphaiodon	63	49		
Duffinselache				11
Severnichthys	670	29	1	37
Gyrolepis	250	1	4	42
Sargodon	22	6		
Osteichthyan scales	68	71	6	361
Osteichthyan fin elements	93	1	3	108
Chondrichthyan denticles	357	12	4	30
Chondrichthyan cartilage				18
Gill raker teeth	14		1	
Coprolites		10		47
Gastropods				94
Unidentified bones	6	531	15	90

specimen (Fig. 8o) could be classified as an h- or i-type coprolite, produced by a fish (Hunt and Lucas, 2012).

5. Discussion

5.1. Faunal composition

Specimens collected by Mike Curtis in Stowey Quarry come from two bone beds, so our statistical analyses had the objectives to assess faunal variations between the sampled beds and to compare the faunas from Stowey Quarry with other Rhaetian outcrops. The specimens show variable degrees of post-mortem wear, from almost perfectly preserved specimens to fossils impossible to identify or to tell apart from rocky pebbles.

The collection comprises 4106 specimens, further divided among the four stratigraphic levels sampled: 39 in the 001 group (from borehole 2, 3.20 m deep); 2260 in the 002 group (from borehole 2, 6 m deep); 885 in the 003 group (from borehole 4, 8.40 m deep); and 910 in the 004 group (from borehole 4, 3.20 m deep). Curtis's notes assign the 001 and 004 groups to a bone bed located at the Westbury Formation–Cotham Member boundary, while groups 002 and 003 are assigned to the basal bone bed, at the Blue Anchor Formation–Westbury Formation boundary (see Table 1). Curtis's meticulous notes even report the exact weight in grams of material extracted from each bone bed in the cores and then processed. This has allowed us to extrapolate the number of fossils per unit of bulk weight, ranging from 5 to 12 fossils per gram; this figure could not be obtained for the 001 group, because that material was only partially processed by Curtis.

Without applying any counting criteria, Osteichthyes account for 50.93% of the specimens in the collection; Chondrichthyes are 29.08%, while 16.32% of the specimens remain unidentified. Gastropods and coprolites comprise only 3.86% of the collection. Looking at the vertebrate fossils, 45% are teeth, 28% are other kinds of remains and 16% remain unidentified. To further characterize and compare the two bone beds sampled, groups 002 and 003 are combined as the basal bone bed, and groups 001 and 004 as the upper bone bed (see Fig. 9).

As expected, the basal bone bed has yielded more specimens (76% of the total) and is more species-rich, with three taxa
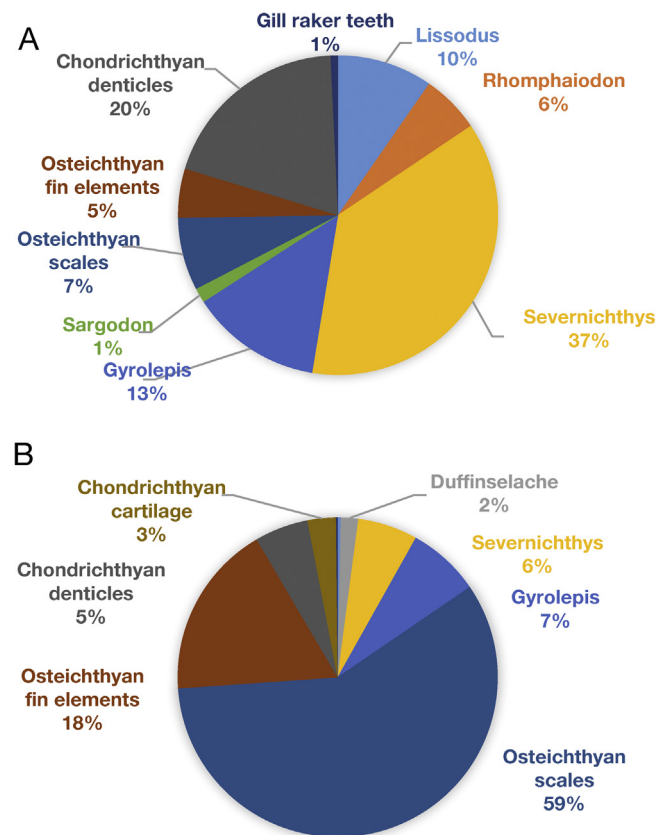
Fig. 9. Comparison of the principal faunal elements of the two bone beds sampled at Stowey Quarry, the basal bone bed (A) and the upper bone bed (B). The statistics include only countable teeth.

(*Sargodon tomicus*, *Rhomphaiodon minor* and *Hybodus cloacinus*) exclusive to this bed and 11 identified in total. Teeth are most common in the basal bone bed, making 55% of the total, while 20% comprise other microvertebrate fossils and 17% could not be identified. *Severnichthys acuminatus* alone accounts for 54.8% of the countable teeth from the basal bone bed, followed by *Gyrolepis albertii* with 19.7%, *Lissodus minimus* with 14.3% and *Rhomphaiodon minor* with 8.8%, and with minor presences of other taxa. The bed yields abundant chondrichthyan remains, with 385 specimens comprising denticles, spines and vertebrae; osteichthyan fossils, comprising scales, fin elements and spines, are less abundant, but still total 235.

Some discrepancies in figures between the two samples of the basal bed, though, are worth noticing: first, around 60% of the 003 group specimens are unidentified bone fragments; apart from that, the 003 group only accounts for 10% of countable teeth and for 14% of other kinds of remains for the basal bone bed. This leaves the majority of osteichthyan and chondrichthyan remains of the basal bone bed concentrated in the 002 sample, highlighting strong lateral variability. The discrepancy could indicate that we are sampling two different bone beds, although this seems unlikely, and lateral variability in bone bed content is more likely.

The upper bone bed contains roughly 24% of the collection; the only *Dapedium* sp. tooth of the collection was found in this bed, and it yielded nine species in all. We cannot conclude, however, that the reduced number of fossils is real, in light of the incomplete processing of the 001 sample. The bed is dominated by vertebrate remains, with 56% of specimens; teeth only reach 13%, with 11% of unidentified fossils and 16% between coprolites and gastropods (invertebrates were exclusive to the 004 sample). This time, *Gyrolepis albertii* is the most abundant species with 45.5% of

countable teeth, followed by *Severnichthys acuminatus* with 37.6% and *Duffinselache holwellensis* with 10.9%. Osteichthyes are also dominant when considering other kinds of identified fossils, with 90% of the upper bone bed non-dental remains comprising scales, fin elements and spines. The presence of coprolites and internal casts of gastropods is unique at this level, hinting at a less-energetic depositional environment compared to the basal bone bed.

Data from all the levels sampled reveals some concentrations of taphonomically similar fossils and of fossils of the same species. For example, sample 002 includes around 350 denticles (more than 85% of all denticles in the collection), an extraordinary 671 teeth of *Severnichthys acuminatus*, representing 90% of specimens of this species in the whole collection, and over 80% of all *Gyrolepis albertii* teeth. Further, sample 004 contains 70% of the collection's scales, and sample 003 has around 530 bits of unidentified bones, 82% of the total. There is no reason to believe that these are artificial counts, because the same sampling methods were used in all cases, and they likely reflect natural lateral variations in the bone beds dependent on sedimentology and taphonomy.

As a final remark, it was found that the counting criteria applied generated a group-focused and sometimes very high bias. Chondrichthyan teeth were to be included in the counting only if they possessed an intact primary cusp, while for osteichthyan teeth 70% of the main cusp had to be intact. Teeth excluded from the counting were 6.6% of the total for bony fish, while for sharks the figure is 57.1%, with a 65.4% peak for *Lissodus minimus* alone. It is clear how a thoughtless application of the criteria could lead to an underestimation of the presence of some taxa; it is equally clear, though, that including every fragment in the counting would lead to an overestimation of the same taxa. A more specific criterion should be adopted, taking into account the risk of damage to the more breakable teeth: as an example, *L. minimus* teeth in this collection were most often seen breaking in half dorso-ventrally or roughly at a third of their length, generating fragments without an intact main cusp in either case. Adding half or one third of the fragments into the counting would be more time-consuming, but would result in a more adequate estimation of the occurrence of this taxon.

5.2. Environment and modes of life

The Rhaetian bone bed environment was dominated by Osteichthyes, at least in numbers; for fishes like *Severnichthys acuminatus* and *Gyrolepis albertii*, it is easy to hypothesize a predatory lifestyle, judging from their pointed teeth; of these two, previous studies assign larger dimensions to *S. acuminatus* (Storrs, 1994). Other bony fishes show evidence of a durophagous diet, based on the development, during the Late Triassic, of augmented muscular power for the maxillary area (Lombardo and Tintori, 2005). Teeth of *Sargodon tomicus*, *Lepidotes* and *Dapedium* all have morphologies designed to crush shells of any kind; even though there is not a massive invertebrate presence in this collection, it is not uncommon to find all kinds of body and trace fossils produced by invertebrates in Rhaetian strata (Storrs, 1994; Allington-Jones et al., 2010; Mears et al., 2016; Korneisel et al., 2015). This absence could be mainly taphonomic, reflecting loss of specimens with originally aragonitic shells, or damage and winnowing in the strong bottom currents.

Durophagous, or generally opportunistic feeding habits, seem to be included among chondrichthyans too, with *Lissodus minimus* and *Duffinselache holwellensis* showing a heterodont dentition, with morphologies not quite as specialized as the osteichthyans previously mentioned, and possibly adapted to exploit different food sources. Other sharks were clearly predatory, like *Rhomphaiodon minor*, *Synechodus rhaeticus* and *Hybodus cloacinus*, with

their sharp, multi-cuspid teeth. Their dimensions are unknown, but could have been comparable to those of the predatory osteichthyans, complicating any possible hypothesis about the trophic chain of the palaeo-environment. Finally, the gill raker teeth in the collection show that at least one filter-feeding species was present in the British Rhaetian and it has been hypothesized that the shark *Pseudocetorhinus pickfordi* might have adopted this feeding habit (Duffin, 1998a,b, 1999).

The absence of terrestrial tetrapod remains, often found in coeval sediments filling karstic fissures in palaeo-highs in south-western England (Van der Berg et al., 2012; Klein et al., 2015; Nordén et al., 2015; Whiteside et al., 2016; Whiteside and Duffin, 2017) probably highlights that Stowey Quarry was located in an offshore area. Marine reptiles are absent from this collection, but have commonly been found (Storrs, 1994; Nordén et al., 2015; Mears et al., 2016) among sharks and bony fishes in the British Rhaetian, even in Stowey Quarry itself, although from sediments located at the top of the Penarth Group (Carpenter, 2001). It cannot be excluded that the absence of such tetrapod remains was a sampling or taphonomic artefact, reflecting the fact that our samples came from boreholes and we focused on processing sub-mm specimens. Larger bones and teeth might be absent, or simply might not have been sampled.

5.3. Bone bed origin and wider comparison

The occurrence of multiple bone beds in Rhaetian strata is not unusual and has been documented before: Sykes (1977), for example, listed some 40 Rhaetian outcrops and the bone beds they contain, and he proposed criteria for the characterization of supposed "primary" and "secondary" bone beds, based on elements that indicate reworking of fossils. Such multiple bone beds in the British Rhaetian have been confirmed many times since, by Martill (1999), Allard et al. (2015), Mears et al. (2016), and Slater et al. (2016), among others. However, Sykes' (1977) model, in which he argued that all Rhaetian bone beds have been reworked from elsewhere, and that the higher bone beds in particular show evidence that they were reworked from the basal bone bed, has been rejected on the basis of several lines of evidence, by Mears et al. (2016), Slater et al. (2016), and others: (1) the higher Rhaetian bone beds do not show any difference in abrasion levels from the basal bone bed; (2) basal Westbury Formation bone beds range from largely allochthonous (e.g. Westbury on Severn) to mixed or largely allochthonous (e.g. Aust), as demonstrated by their highly variable abrasion levels and by analysis of rare earth elements by Trueman and Benton (1997); (3) there is a considerable span of time, perhaps some million years between the basal and higher Rhaetian bone beds; and (4) there are definite faunal differences between the basal and higher bone beds, as noted also here, suggesting strongly that each bone bed is sampling a different fauna.

Both Stowey bone beds show characteristics that would classify them as mixed between a primary bone bed with next to no transport, and a secondary bone bed, in which theoretically all the material is allochthonous (following Sykes' definition). Granulometric sorting is absent, and delicate fossils beautifully preserved have been found alongside heavily abraded and unidentifiable remains. The upper bone bed seems to have a stronger primary component, with more fragile specimens in good state of preservation, while the basal bed has a higher percentage of teeth excluded from the counting because they did not meet the criteria. Such a mix of primary and secondary characteristics is commonplace for all bone beds of the Penarth Group, including the basal bed.

Considering now the vertebrate taphonomic assemblages of Stowey Quarry, they represent classic examples of the Penarth Group marine fauna from south-western England and south Wales

Table 2
Summary of counts of key taxa, group-level identifiable material and unidentified material from the basal bone bed (BBB) and a bone bed located at the top of the Westbury Formation (UBB) in three different localities. Data from Mears et al. (2016) for Hampstead Farm, and from Allard et al. (2015) for Manor Farm. Missing entries represent data not available. Abbreviations: Chondr., chondrichthyan; Osteich., osteichthyan.

	Stowey Quarry-BBB	Manor Farm-BBB	Hampstead Farm-BBB	Stowey Quarry-UBB	Manor Farm-UBB	Hampstead Farm-UBB
Lissodus	182	101	300	2	13	0
Rhomphaiodon	112	101	40	0	0	0
Duffinselache	0	0	0	11	66	0
Severnichthys	699	46	222	38	228	72
Gyrolepis	251	8	69	46	337	40
Sargodon	28	4	2	0	0	0
Osteich. scales	139		86	367		29
Osteich. fin elements	94	8	20	111	129	2
Chondr. denticles	369	14	52	34	146	84
Chondr. cartilage and vertebra	1	1		19	75	
Gill raker teeth	14		0	1		160
Coprolites	10	14		47	274	
Gastropods	0			94		
Unidentified bones	537		17	105		15

(Storrs, 1994; Swift and Martill, 1999; Allard et al., 2015; Nordén et al., 2015; Lakin et al., 2016; Mears et al., 2016) and even from other coeval European locations (Godefroit et al., 1998; Sander et al., 2015), although for these last ones an exact stratigraphic correlation would be difficult to achieve.

While most works have focused on the more fossiliferous and ubiquitous basal bone bed, although it varies in composition and stratigraphic level, the sections described at Manor Farm Quarry (Allard et al., 2015) and Hampstead Farm Quarry (Mears et al., 2016) include the basal bed and a bed at the top of the Westbury Formation perfectly correlatable with the upper bone bed at Stowey (see Table 2). This makes these studies particularly suitable to compare not only abundance of taxa, but also possible trends in relative abundance and taxa appearance/disappearance.

Some shared trends clearly emerge from a simple comparison: the absence of *R. minor* and *S. tomicus* at the top of the Westbury Formation, as also at Manor Farm (Allard et al., 2015) and Hampstead Farm (Mears et al., 2016), a dramatic drop in *L. minimus* and a rise of *D. holwellensis* (some teeth attributed to this shark have been found in Stowey Quarry's basal bone bed, but are omitted in Table 2 because they did not meet the counting criteria). The extent of these trends cannot be determined from these three occurrences alone, but, if further evidence should accumulate, these could become valuable biostratigraphic indicators for the Penarth Group. For other taxa, distribution is highly variable, with peaks of abundance unevenly distributed between the two bone beds in different locations. This trend can be seen in Stowey Quarry both vertically and laterally at a small scale, but it is probably expandable to the whole ancient basin, excluding recovery bias as a possible explanation. The upper bone bed is confirmed to have a higher percentage of primary components (*sensu* Sykes, 1977) in all the localities examined.

Acknowledgements

Appendix A Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.pgeola.2018.02.001.

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