



## Microvertebrates from the classic Rhaetian bone beds of Manor Farm Quarry, near Aust (Bristol, UK)



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### ABSTRACT

Manor Farm Quarry shows a detailed record of the entire Rhaetian section typical of southwest England. It has yielded a standard Rhaetian marine fauna, including eight species of sharks, four species of actinopterygian fishes, and the reptiles *Pachystropeus* and *Ichthyosaurus*, all of which are widely known from coeval sites. An unusual feature is the occurrence of an unidentified coelacanth, represented by nine isolated quadrates showing a broad range of sizes. The site has also provided information on the occurrence of vertebrates through five distinctive bone-bearing horizons, including the famous basal Westbury Formation bone bed, as well as a second horizon with bones at the top of the Westbury Formation, and three within the overlying Cotham Member of the Lilstock Formation. These show substantial differences, especially between the basal bone bed and the four overlying bone-rich units. The basal Westbury Formation bone bed is dominated by shark remains (73%, compared to 23–30% in the four overlying units), most notably, teeth of *Rhomphaiodon minor* and *Lissodus minimus*, which are absent or rare in higher beds. Further, teeth of the bony fishes *Gyrolepis albertii* and *Severnichthys acuminatus* are rare in the basal bone bed, but abundant at the top of the Westbury Formation and through the Cotham Member, and the sharks *Duffinselache holwellensis* and *Pseudocetorhinus pickfordi*, absent in the basal bone bed, are relatively abundant in the four overlying bone-bearing units. These differences in faunal lists and in relative proportions probably do not reflect sampling, but some major differences in ecology and evolution.

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## 1. Introduction

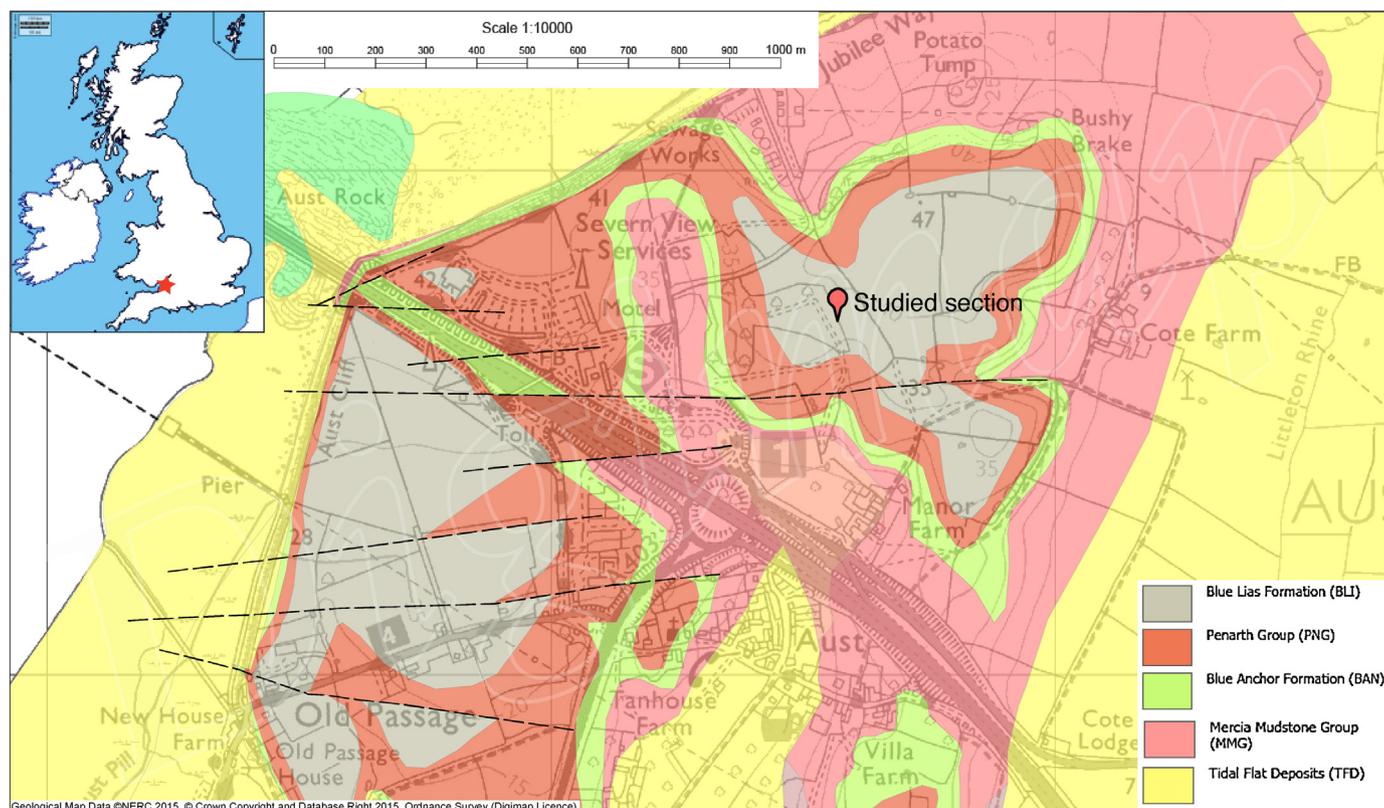
The Triassic–Jurassic boundary exposed at Aust Cliff, near Bristol, SW England (Fig. 1), is one of the most evocative and famous geological sites of the United Kingdom. Here, in 1824, William Buckland and William Conybeare, the leading palaeontologists of their day, were the first to describe the Carboniferous, Triassic, and Jurassic successions around Bristol; they figured Aust Cliff, and noted the abundant vertebrate fossils in the bone bed near the top of the cliff. Later accounts of this famous site include those by Strickland (1841), Etheridge (1868), Short (1904), Reynolds (1946), Hamilton (1977), Storrs (1994), and Benton

and Spencer (1995). Buckland and Conybeare (1824) noted a succession, from the bottom, through red sandstone, gypsum, and red marl with pale stripes (=Mercia Mudstone Formation), light greenish-grey marl (=Blue Anchor Formation), bone bed (basal Rhaetian bone bed), dark marl with compact shelly beds (=Westbury Formation), grey marl (=Lilstock Formation), and grey lias (=Pre-*planorbis* Beds, *planorbis* Beds, Blue Lias). Since then, the Rhaetian bone bed at Aust has yielded important collections of ichthyosaurs, plesiosaurs, the marine reptile *Pachystropeus*, and dinosaurs, as well as fishes. Because of the significance of the site for stratigraphy and for palaeontology, the whole of the Aust Cliff section (National Grid Reference, NGR ST 565895–ST 572901) has been designated as a Site of Special Scientific Interest (Benton and Spencer, 1995, pp. 75–80).

The bones and teeth from the Aust bone bed are generally isolated, and heavily abraded. We use the term 'bone bed' to refer

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**Fig. 1.** Geological map of the Aust-Manor Farm area, showing the site of the studied Manor Farm section, and its relation to the Late Triassic and Early Jurassic stratigraphic succession. The classic Aust Cliff section lies to the left, on either side of the M48 road bridge, running from the 'Pier' to the 'Sewage Works'. ©Crown Copyright and Database Right 2015. Ordnance Survey (Digimap Licence).

to horizons, often with an erosive base, in which bones and teeth are concentrated, and may be associated with phosphatised coprolites and inorganic phosphate nodules (Martill, 1999). Bones and teeth in bone beds may be relatively undamaged, or abraded, as at Aust. This is true in particular for the rare dinosaur remains; it is likely that they are allochthonous components that had been transported for some distance. This condition contrasts with less abraded, more delicate fossils found in the basal Rhaetian bone bed at other nearby sites such as Westbury Garden Cliff, south Gloucestershire (NGR SO 718128), where transport distances were presumably lower. This difference between the bone beds was confirmed by study of the rare earth elements (REE), which showed matching of REE signatures between sediment and bones in the less transported materials, but not at Aust, where bones and sediment have different REE signatures, indicating different sources (Trueman and Benton, 1997). The presence of mixed terrestrial and marine fauna, and clasts from the Blue Anchor Formation, in the Rhaetian bone bed, have suggested an origin of this unit from shoreward storm surges accumulating the material in a shelf setting, in a rapidly deposited 'tempestite' (Storrs, 1994; Suan et al., 2012).

Late Triassic fossiliferous sediments, whether the marine Rhaetian bone beds, or terrestrial bedded and fissure deposits, document important elements of contemporary vertebrate faunas.

The latest Triassic was a time of great importance in the history of life, with major extinctions and originations of new groups. Extinctions occurred at different points through the Late Triassic, including during the end-Triassic mass extinction itself, and there were major extinctions and turnovers among sharks (Cappetta, 1987; Friedman and Sallan, 2012) and marine reptiles (Thorne et al., 2011). Bony fishes, on the other hand, were apparently little

affected by the end-Triassic event, with all families crossing the boundary into the Jurassic (Friedman and Sallan, 2012; Romano et al., 2014). On land, dinosaurs were rising in importance, and the precursors of many modern tetrapod groups had emerged in the Late Triassic, among them the first lissamphibians (frogs and salamanders), turtles, lepidosaurs (basal sphenodontians), crocodylomorphs, and mammals (Sues and Fraser, 2010; Benton et al., 2014).

The Rhaetian Transgression was a Europe-wide event, when a major transgression flooded across central Europe, France, and southwest and central England, perhaps triggered by the initiation of the breakup of Pangaea (Fischer et al., 2012; Suan et al., 2012). Throughout most of this area, the marine Rhaetian beds overlie eroded terrestrial Triassic red beds, but in places, such as around the Mendip Hills of Somerset, the basal Rhaetian beds can also rest directly, and unconformably, on uplifted Carboniferous Limestone. In most cases, the unconformable base of the Rhaetian succession is formed from a pebbly lag deposit rich in vertebrate remains, the basal Rhaetian bone bed (Storrs, 1994; Swift and Martill, 1999; Suan et al., 2012). In places, there is evidence that the bottom currents swept bone-bearing sediments into coeval *Thalassinoides* burrows constructed by callianassid shrimps that then reworked the bone-bearing sediment, producing meniscate packing structures (Korneisel et al., 2015).

Here, we describe an occurrence of the basal Rhaetian bone bed from Manor Farm, south Gloucestershire, close to the classic Aust Cliff section (Fig. 1), and showing the Rhaetian and earliest Jurassic horizons much more clearly than at the top of the cliff. The Manor Farm pit was excavated in the 1990s, and a section was conserved as an accessible site for visitors and collectors. The geology of the site has been described (Radley and Carpenter, 1998), but the fossils are presented here for the first time.

## 2. Geological setting

In the Aust area, south Gloucestershire, the Upper Triassic sequence consists of the Mercia Mudstone Group, which represents arid or semi-arid coastal sabkha environments (Norian to early Rhaetian), overlain by fossiliferous sediments of the mid to late Rhaetian Penarth Group, which records the environmental change to shallow marine and lagoonal facies (Macquaker, 1999; Swift, 1999). The uppermost Rhaetian sediments are the Pre-*planorbis* Beds, with an abundance of benthic marine fauna but no ammonites. The first occurrence of ammonites (*Psiloceras*) marks the base of the Hettangian stage of the Jurassic System. These stratigraphic terms were standardised by Warrington et al. (1980) and Donovan and Kellaway (1984).

Between 1995 and 1996, extensive exposures were created at Manor Farm, Aust (NGR, ST 574 896), for the excavation of construction materials required for the second Severn road crossing. These exposures provide sections from the upper Mercia Mudstone Group (red-brown mudstones and the Blue Anchor Formation), the Penarth Group (Westbury Formation and Cotham Member of the Lilstock Formation), up to the Pre-*planorbis* Beds of the Blue Lias. Importantly, this replicates the higher portion of the nearby Aust Cliff. As much of the upper part of Aust Cliff has long been inaccessible, study of the fossils from this section often relies on fallen blocks from the Penarth Group and Pre-*planorbis* Beds.

The section at Manor Farm (Fig. 2) begins with about 1 m of unfossiliferous, blocky, brick-red, silty mudstone of the Mercia Mudstone Group at the base, and is followed by about 3 m of the green-grey silty mudstones of the Blue Anchor Formation, which form sloping banks above. The Norian-Rhaetian boundary is generally taken to lie within the Blue Anchor Formation (Kellaway and Welch, 1993), which exhibits a conspicuous 20-cm-thick muddy sandstone marker bed, also seen at Aust Cliff (Reynolds, 1946; Hamilton, 1977).

The next unit is the Westbury Formation, some 3.5 m thick, comprising grey-black cyclic shales, thin fossiliferous sandstones, and tabular, muddy bioclastic limestones. At its base, the basal Rhaetian bone bed (formerly sometimes called the '*Ceratodus* bone bed') occurs as discontinuous lenses, up to 20 cm thick, occupying shallow depressions on the eroded top of the Blue Anchor Formation. At some levels, the shales are packed with convex-up, crushed bivalves, including *Rhaetavicula contorta*, and the thin sandstones contain euhedral pyrite crystals, and horizons packed with mouldic, disarticulated, convex-up bivalves, including current-aligned *Pleurophorus elongatus* and scattered vertebrate remains, including fish teeth and isolated remains of *Pachystropheus*. Other thin sandstones contain trace fossils, including the U-shaped burrow *Arenicolites*, and the bases of bivalve resting traces, *Pelecypodichnus*, possibly formed by infaunal bivalve shells found on neighbouring horizons, including *Eotrapezium*. Near the top of the Westbury Formation there is a laterally persistent unit of muddy, dark-grey, rust-weathering bioclastic limestone, approximately 8 cm thick, which is probably equivalent to the Upper Pecten Bed of Aust Cliff (Reynolds, 1946). The upper surface of this unit displays abundant, disarticulated *Chlamys valoniensis*, sometimes accompanied by *Rhaetavicula contorta*. Within the unit, the sediment is a mixture of mud-grade sediment and compacted shell debris, with localised concentrations of small, articulated, spar-filled bivalves, suggesting, as for the basal bone bed, rather rapid deposition.

Among larger fossils from the basal Rhaetian bone bed, Radley and Carpenter (1998) noted a large ichthyosaur vertebral centrum (with a diameter of 150 mm), a fragmentary propodial of a plesiosaur, a possible theropod dinosaurian vertebra, shark fin spines, a jaw fragment of the large carnivorous actinopterygian *Severnichthys*, and coprolites. In addition, the basal bone bed

yielded some recrystallized, disarticulated bivalves, including *Mytilus cloacinus*. In other cases, articulated, calcite spar-filled bivalves from the basal Rhaetian bone bed have been interpreted (Storrs, 1994) as evidence of storm conditions that would exhume such bivalves from offshore beds, and mix them with the long-transported phosphatic material (bones, teeth, coprolites, inorganic pebbles). The upper portion of the Westbury Formation had relatively fewer fossils, but did yield to S.C.C. a large mandible element from an ichthyosaur measuring almost a metre in length.

Above the predominantly grey-coloured Westbury Formation, there is a step in the section, marked by the cream-coloured marls and fine-grained limestones of the 3-m-thick Cotham Member. The lower portion comprises 0.8 m of grey shelly clay with some cemented bands, becoming increasingly marly towards the top. At the base of this unit, abundant and disassociated fish teeth and scales occurred as well as a fragmentary propodial of a plesiosaur. The bivalve *Chlamys valoniensis* is abundant in the lower part. This is equivalent to 'band 8' of Reynolds (1946), and he assigned it to the top of the Westbury Formation. However, here, following Radley and Carpenter (1998, p. 64), we regard it as the lower part of the Cotham Member (Fig. 2). In the Manor Farm section, lenses of grey 'pecten limestone' with *C. valoniensis* occur in the lower part of the unit, and are lithologically similar to the lower, laterally persistent bed. The undersides of some of these lenses, as seen in loose slabs, display irregular pod-shaped to sinuous casts, representing remains of a burrow system. Other loose pieces yield common fish vertebrae. Higher parts of the Cotham Member comprise pale-coloured marls with some beds of chalky, micritic, tabular to nodular limestone, approximately 1.4 m above the base, equivalent to Reynolds' (1946) 'insect bed', his 'band 10'. Loose blocks of this contain scattered casts of *Tutcheria cloacina* and *C. valoniensis*, as well as occasional ichthyosaur and plesiosaur vertebrae, a coprolite, and a probable theropod phalanx (Radley and Carpenter, 1998, p. 64).

Examples of the stromatolitic 'landscape marble' were exposed in trial pits at the top of the Cotham Member. At this location the layer was up to 15 cm thick and rested on soft, unfossiliferous khaki-coloured mudstone. Loose blocks of 'crazy' Cotham Marble (intraformational micrite-flake breccia) were found nearby, and probably represent channel fills between the stromatolites (Reynolds, 1946; Hamilton, 1961). In some specimens, the mud-flake breccia is overlain by stromatolitic growths, while in others it is intercalated with splintery, cream-weathering micrite, packed with small, disarticulated *Modiolus cf. hillanus*.

The Langport Member ('White Lias') of the Lilstock Formation is absent here, as at Aust Cliff, and the highest strata preserved in the quarry brow and subsoil comprise the distinctive flaggy, brown-grey bioclastic limestones and mudstones of the Pre-*planorbis* Beds. These limestones are full of disarticulated bivalves, including *Liostrea hisingeri* and *Pteromya tatei*, with rarer *Oxytoma longicostata* and *Modiolus minimus* (Radley and Carpenter, 1998, p. 65). Minute echinoid spines stud the surfaces of some slabs, and an ichthyosaur vertebra was found at this level by S.C.C. Associated mudstones are also rich in *L. hisingeri*.

The Manor Farm quarry site remained open for some time after active excavation in 1995 and 1996, and many collections were made by local geologists and palaeontologists. Restoration of the site occurred in 2002 but not before S.C.C. was able to successfully negotiate with the landowner and the restoration contractor, RMC Aggregates South West, to keep part of the exposure open for geologists and other visitors (Fig. 3A–C). A large number of basal bone bed blocks were rescued from across the site and left to weather naturally, close to the saved section (Fig. 3D). Funding was provided in 2004 by the Curry

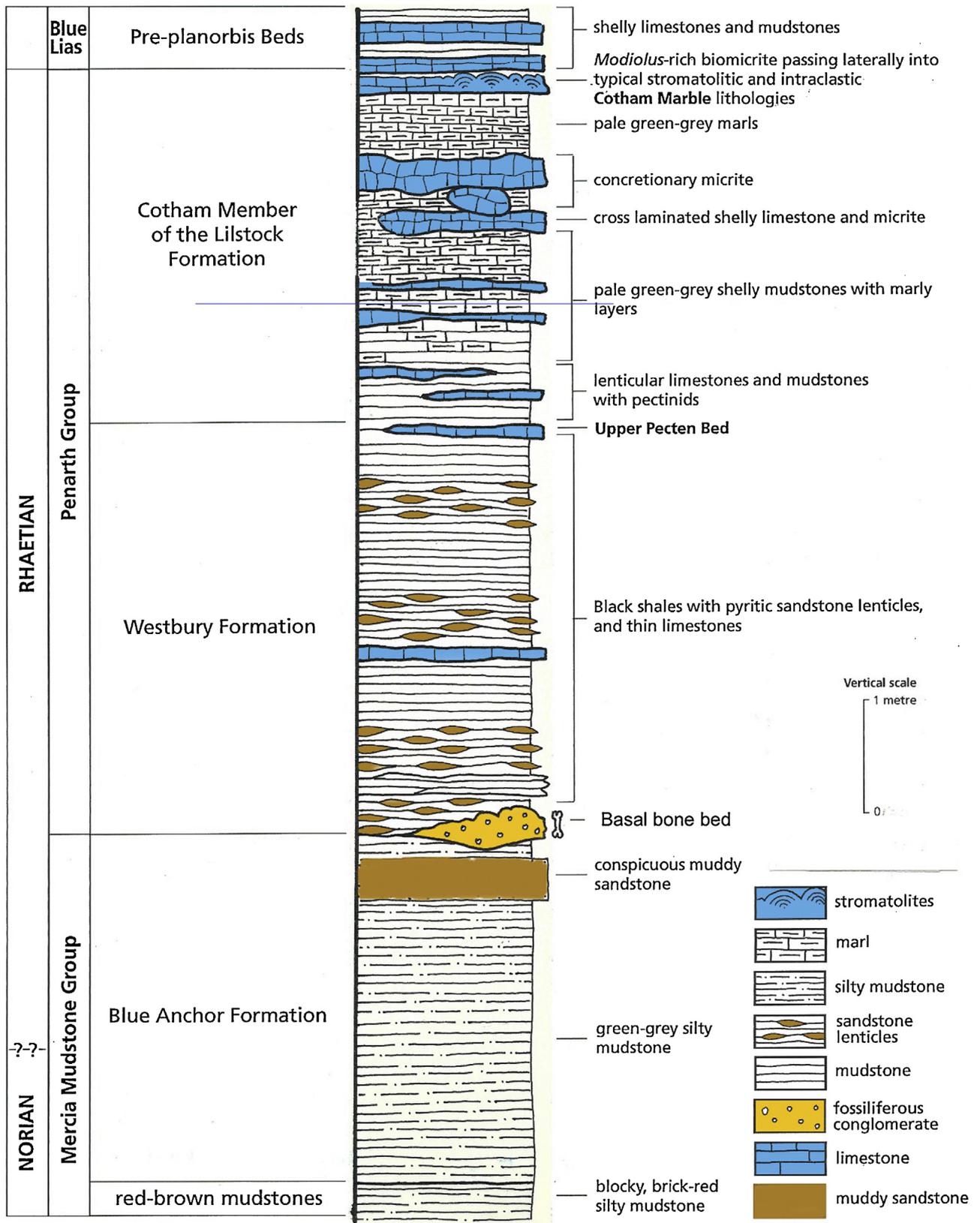


Fig. 2. Sedimentary log through the latest Triassic and earliest Jurassic at the Manor Farm site, Aust, South Gloucestershire (ST 574896). Lithologies and the key stratigraphic divisions of the Mercia Mudstone and Penarth groups are indicated.

Fund of the Geologists' Association, the Bristol Naturalists' Society, and Bath Geological Society to fund an interpretation board on site, depicting a late Triassic palaeo-environment. At the time of writing, there are plans to clean up the site by

removing unwanted talus currently obscuring many of the interesting features and providing improved interpretation. The logged section (Fig. 2) is from the conserved section seen in Fig. 3A–D.



**Fig. 3.** The Manor Farm pit, as excavated in 1995, and conservation of a reference section. (A) The restoration contractors, RMC Aggregates, reshaping the edge of the Manor Farm site to keep a geological section for visiting geologists. (B) A view of the rock face preserved intact during the restoration phase to provide a permanent section for visiting geologists; this exposure shows the very top of the Mercia Mudstone Group (quarry floor), the Penarth Group and the lower part of the Blue Lias (below quarry edge). (C) The edge of the larger pit showing the dark Westbury Formation with overlying lighter rocks of the Cotham Member. (D) Richard Wilkins, an amateur geologist from Abingdon near Oxford, excavating the basal bone bed during the final restoration phase. All photographs by S.C.C.

### 3. Materials and methods

As in previous studies (e.g. [Korneisel et al., 2015](#); [Nordén et al., 2015](#)), the microvertebrate collection described here was made by Mike Curtis (1950–2008), a renowned fossil collector from Gloucester whose special enthusiasm was the Rhaetian vertebrate fossils; he had been instrumental in other major fossil finds around Bristol ([Benton et al., 2012](#)). The collection was accumulated over several years, based on 13 samples made by Curtis in 1999, 2000, 2006, and 2007. He records in his notes that these came from five horizons (sediment sample sizes listed): the basal bone bed of the Westbury Formation (0.33 kg), the uppermost bed of the Westbury Formation (43.205 kg), the lowermost bed of the Cotham Member (29.005 kg), a horizon about 50 cm above the base of the Cotham Member (50.585 kg), and a horizon 1.9 m above the base of the Cotham Member (1.27 kg). The total of all processed samples was 124.395 kg.

The bone bed material was processed by Curtis according to his usual protocols (summarised by [Korneisel et al., 2015](#)). He first washed adhering mud from the sediment, which 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  $\mu\text{m}$ , and 300  $\mu\text{m}$  gauge. The material greater than 2.4 mm contained no recoverable vertebrate remains. The remainder of the material was sorted first according to size by sieve, and then into groups of similar fossils. Some 1991 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.

We estimated the number of specimens in the collection by first distinguishing identifiable and unidentifiable materials. Shark teeth were counted when at least the central cusp was present, and actinopterygian teeth were counted when approximately 70%, or more, of the intact crown was present. These counts excluded isolated fragments of tooth, such as portions of root, isolated cusplets, and small crown fragments. The small numbers of reptilian teeth were all near-complete, and all were counted. With other material, which included denticles, scales, reptilian bone fragments and coelacanth quadrates, we included everything possible.

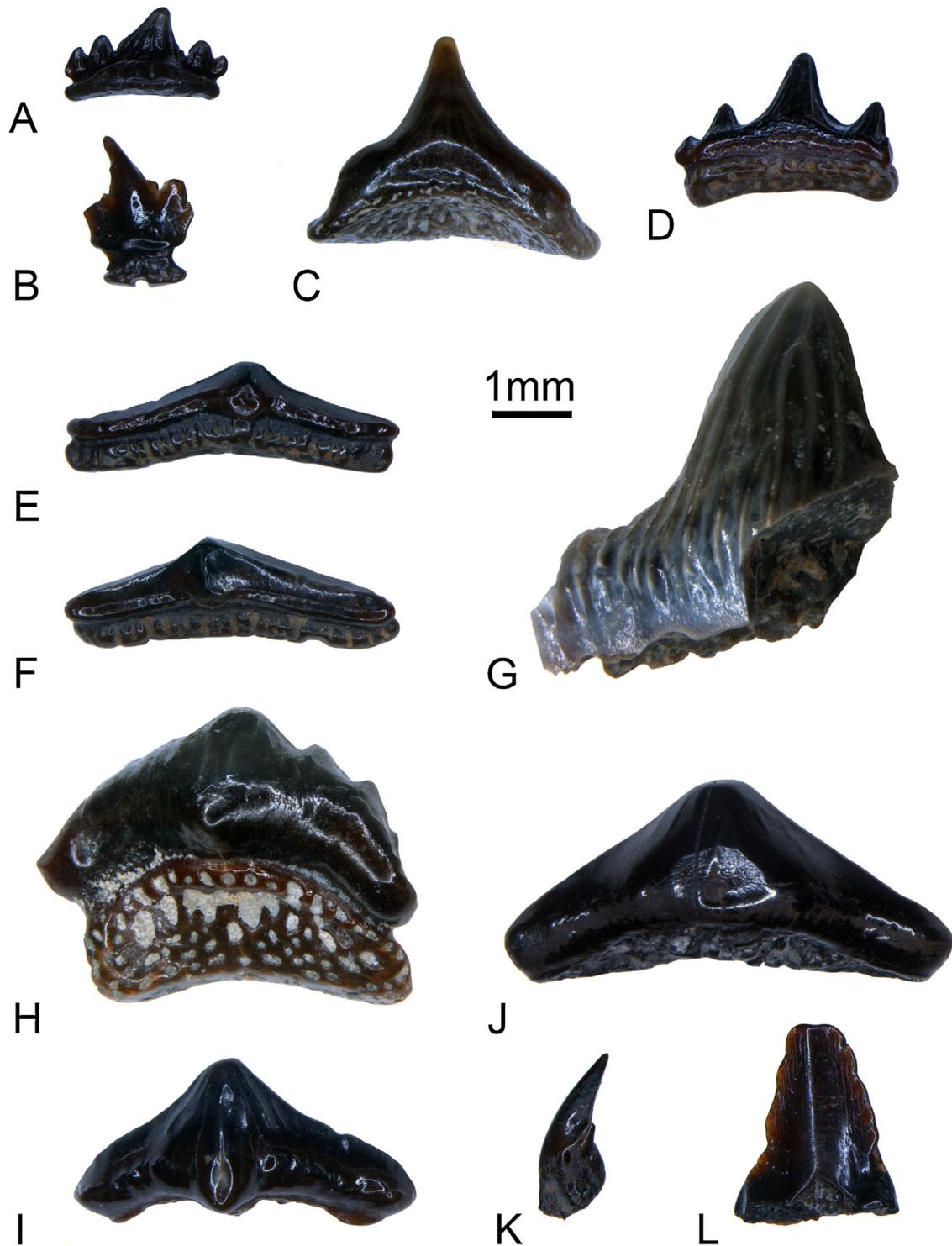
### 4. Systematic palaeontology

#### 4.1. Chondrichthyans

Eight species of sharks have been identified from teeth present in the Manor Farm collection, all of which have been previously recorded in the British Rhaetian ([Duffin, 1999](#)).

##### 4.1.1. *Rhomphaiodon minor* ([Agassiz, 1837](#))

The specimens range from fragments of central cusps to complete teeth with intact roots. The teeth are small but vary in size, with a central cusp up to 3 mm in height. The crown ([Fig. 4A](#)) is strongly vertically ridged, with a longer, slightly flattened labio-lingually, primary central cusp and a pair or two pairs of small lateral cusplets. The first two lateral cusplets on either side of the central cusp are usually around 50% of the total height of the central cusp. When a second pair of lateral cusplets is present they



**Fig. 4.** Chondrichthyan teeth from the Manor Farm Rhaetian section. (A) *Rhomphaiodon minor* tooth in lingual view (BRSUG 29371-1-1547-1). (B) *Vallisia coppi* tooth in lingual view (BRSUG 29371-1-1574). (C) *Pseudocetorhinus pickfordi* tooth in labial view (BRSUG 29371-1-1593). (D) *Synechodus rhaeticus* tooth in labial view (BRSUG 29371-1-1617). (E and F) *Duffinselache holwellensis* tooth in labial (E) and lingual (F) view (BRSUG 29371-1-1733). (G) *Hybodus cloacinus* tooth in oblique labial view (BRSUG 29371-1-1749). (H) *Lissodus minimus* tooth in labial view (BRSUG 29371-1-1771 1). (I) *Lissodus minimus* tooth in labial view (BRSUG 29371-1-1769). (J) *Lissodus minimus* tooth in lingual view (BRSUG 29371-1-330). (K) *Pseudodalatias barnstonensis* tooth in lateral view (BRSUG 29371-1-1886). (L) *Pseudodalatias barnstonensis* tooth in lingual view (BRSUG 29371-1-1873-2).

are usually around 50% of the height of the first pair of cusplets. The central cusps and lateral cusplets are curved lingually.

Originally described by Agassiz (1837) as '*Hybodus minor*', the type specimen was a small dorsal fin spine retrieved from the Westbury Formation bone bed of Purton Passage, located further

up the Severn Estuary. Agassiz subsequently assigned teeth to this taxon, although the validity of this association is uncertain. Further complicating this identification is the lack of diagnostic features on the originally described fin spines, which are indistinguishable from the fin spines of other Penarth Group hybodont shark taxa.

Duffin (1999, p. 195) noted similarities between '*Hybodus*' *minor* and *Rhomphaiodon nicolensis* (Duffin, 1993a). This similarity was further studied by Cuny and Risnes (2005), who discovered that '*H.*' *minor* also possessed a haphazard crystalline enameloid previously thought to be present in *R. nicolensis* only. Based on this discovery, Cuny and Risnes (2005) reassigned British '*Hybodus*' *minor* teeth to the genus *Rhomphaiodon* and identified this genus as a member of the Order Synchodontiformes.

#### 4.1.2. *Vallisia coppi* Duffin, 1982b

*Vallisia coppi* is represented in the Manor Farm assemblage by a single tooth. This specimen (Fig. 4B) is small, with a central cusp just over 1 mm high, and consists of a partially damaged crown with an intact root. The crown is multicuspid, inclined lingually with flattened labial and lingual faces, with a higher, distally inclined central cusp. Although the apices of the lateral cusplets are broken off on one side, the other (mesial) side is intact. On the intact side there are two lateral cusplets. The cusplets are only partially separated from each other and the central cusp. The base of the crown extends outwards as a lip, overhanging the incised junction between root and tooth. The root comprises around 30% of the tooth's total height, and its basal surface is bisected with an open canal. The base of the root is slightly flared.

*Vallisia coppi* is known from two sites in Somerset: the Vallis Vale type locality and the Holwell fissure fillings, as well as from the Belgian Rhaetian (Duffin et al., 1983). It is difficult to determine the taxonomic affinities of *V. coppi* – some teeth have been shown to contain median canals (Duffin, 1982b), a feature unknown in neoselachians, and Cuny and Benton (1999) confirmed that the ultrastructure of the enameloid in teeth of *Vallisia* is not neoselachian. While the enameloid of *Vallisia* is similar to that of a hybodont, the incised root/crown margin present on *Vallisia* teeth is not. The most recent taxonomic assessment of *V. coppi* places it in the Neoselachii *incertae sedis* (Cappetta, 2012, p. 327). Note that the genus has also been tentatively recorded from the Upper Famennian of Belgium (Ginter et al., 2010, p. 107), but such an age range for a single species seems unlikely.

#### 4.1.3. *Pseudocetorhinus pickfordi* Duffin, 1998a

*Pseudocetorhinus pickfordi* is represented by a number of complete teeth (Fig. 4C). These have a low, lingually inclined cusp. The cusp is thorn-shaped, and some specimens exhibit a distal inclination. There are no lateral cusplets. Some teeth have fine vertical striations on the surface of the crown. The root, which is often flared, curves lingually from the base of the crown, resulting in a shallow labial face to the root.

*Pseudocetorhinus* is classified as a member of the Cetorhinidae, a clade of neoselachian galeomorphs that includes the extant basking shark (*Cetorhinus maximus*). Assignment to the Cetorhinidae may need revision (Cappetta, 2012, p. 330), and the conclusion that *Pseudocetorhinus pickfordi* is the earliest known filter-feeding shark (Duffin, 1999, p. 204) has recently been challenged (Shimada et al., 2015) since its teeth have a wider base, mesiodistally, than those of demonstrably planktivorous species from Upper Cretaceous and younger deposits of Russia and the USA.

#### 4.1.4. *Synechodus rhaeticus* (Duffin, 1982a)

Teeth of *Synechodus rhaeticus* are wide and multicuspid, each crown featuring a central cusp and at least one pair of lateral cusplets on either side (Fig. 4D). They also show pronounced longitudinal ridges on both labial and lingual crown shoulders. The lateral cusplets decrease in size with increasing mesial and distal distance from the central cusp. The cusp is upright, though there is some variation in lingual inclination, which is related to the monognathic heterodonty shown through the dentition.

The species was originally described on the basis of a complete dorsal fin spine from the basal bone bed of the Westbury Formation at Aust Cliff, as well as fragments found in the Holwell fissure fillings, assigned then to *Palaeospinax rhaeticus* (Duffin, 1982a). Numerous fragments and complete teeth subsequently found in bone beds at a large number of sites were later assigned to *Synechodus rhaeticus*.

#### 4.1.5. *Duffinselache holwellensis* (Duffin, 1998b)

The crown of typical *Duffinselache* teeth (Fig. 4E and F) is very low, with vertical ridges ascending from the outer edges of the crown to the apex, on both labial and lingual faces. There are no lateral cusplets. The root and crown are equal in height, with a small degree of incision at the crown/root boundary. The root is marked with vascular foramina, forming strong longitudinal patterns of ornamentation.

Described from specimens discovered at Holwell Quarry, Somerset and the base of the Cotham Member at Chilcompton, Somerset (Duffin, 1998b), this species was assigned to the poorly defined genus *Polyacrodus* as *P. holwellensis*. The genus *Polyacrodus* was established by Jaekel (1889), based on histological differences between his specimens and the teeth of *Hybodus*. Andreev and Cuny (2012) later reassigned "*Polyacrodus*" *holwellensis* to their new genus *Duffinselache* on the basis of enameloid ultrastructure, the identification we use here.

#### 4.1.6. *Hybodus cloacinus* Quenstedt, 1858

Specimens representing *Hybodus cloacinus* in the Curtis collection are all fragmented, missing parts of the crown and root (e.g. Fig. 4G). The central cusp in these specimens is conical with pronounced vertical ridges, and the lateral cusplets show similarly pronounced ridges. The ridges on the crown may bifurcate basally.

Originally described from the German Rhaetian around Tübingen, southern Germany, *Hybodus cloacinus* is now found at most European Rhaetian sites, although it is a fairly rare faunal component. There is one record from the lower Jurassic, which expands the species' known range to Rhaetian to Sinemurian (Duffin, 1993b).

#### 4.1.7. *Lissodus minimus* (Agassiz, 1839)

*Lissodus minimus* is common in the Manor Farm collection, represented by isolated crowns and complete teeth that exhibit moderate monognathic heterodonty (Fig. 4H–J). The multicuspid crown possesses a low profile, with a central cusp and up to five pairs of extremely low lateral cusplets. Crowns may be smooth or vertically ridged on both labial and lingual sides. The occlusal crest runs the mesiodistal length of the crown, passing through the apices of the central cusp and lateral cusplets, forming their poorly defined cutting edges. Positioned low on the labial side of the tooth is a labial peg, a feature of varying prominence throughout the collection, which may have locked each tooth in place with the succeeding member of the same tooth file. The root/crown margin is incised, with the root projecting lingually from the base of the crown. The labial surface of the root is very shallow, and its base is concave.

Originally described as "*Acrodus*" *minimus*, this species was later allocated to the genus *Lissodus* (Duffin, 1985). This species is widespread and well known throughout the Penarth Group and the European Rhaetian (Fischer, 2008). The structure of these teeth is indicative of the shark's durophagy, and it presumably fed on shelled, benthic invertebrates.

#### 4.1.8. *Pseudodalatias barnstonensis* (Sykes, 1971)

Although teeth belonging to this taxon are uncommon in the Curtis collection, the dignathic heterodonty described by Duffin (1999, p. 201) is evident. Upper teeth (Fig. 4K) are curved lingually

with a low incline and near-circular cross section; their central cusps are pronounced and flanked laterally by a pair of short lateral cusplets. The collection also contains fragmented crowns of lower teeth (Fig. 4L), which are bladelike and labiolingually compressed, with strongly serrated lateral cutting edges.

The dentition of this species is similar to that of extant species of the Order Squaliformes, such as the Cookiecutter shark, *Isistius brasiliensis*. Like these sharks, *Pseudodalatias barnstonensis* would have shed its lower teeth in one complete strip, maintained by the complex articulations connecting adjacent teeth. These articulated strips of lower teeth have been found in Norian deposits in Italy (Tintori, 1980).

#### 4.1.9. Other selachian remains

As well as these teeth, the Manor Farm collection also contains other selachian fossils such as denticles, vertebrae and prismatic cartilage. Of the approximately 800 denticles, termed also placoid scales, we identify both Sykes' (1974, p. 59) 'Group B' and 'Group C' morphotypes. 'Group B' denticles are varied in appearance, as described by Sykes (1974, p. 59) and are associated with hybodont sharks. The 'Group C' denticles are squat, with a low, enameloid crown. The base of the denticle is slightly flared and ornamented with vertical grooves, and the underside is concaved. Sykes described these denticles as chimaeriform in origin.

There are over 100 neoselachian vertebrae in the Manor Farm collection, each up to 5 mm in length. Each has an abraded surface, though both concave faces of the vertebral centrum may be seen.

Finally, there are over 200 possible specimens of selachian prismatic cartilage in the collection. Prismatic cartilage is the mosaic-like layer of small apatite tiles bound together by a lattice of collagen fibres near the surface of the cartilaginous skeleton, unique to chondrichthyans (Maisey, 2013).

#### 4.2. Osteichthyans

Four actinopterygian taxa and one lungfish were identified among the Manor Farm collection, all previously known from the British Rhaetian (Duffin, 1999). Most notable are some quadrates belonging to an undetermined coelacanth, only the third report of coelacanths in the British Rhaetian.

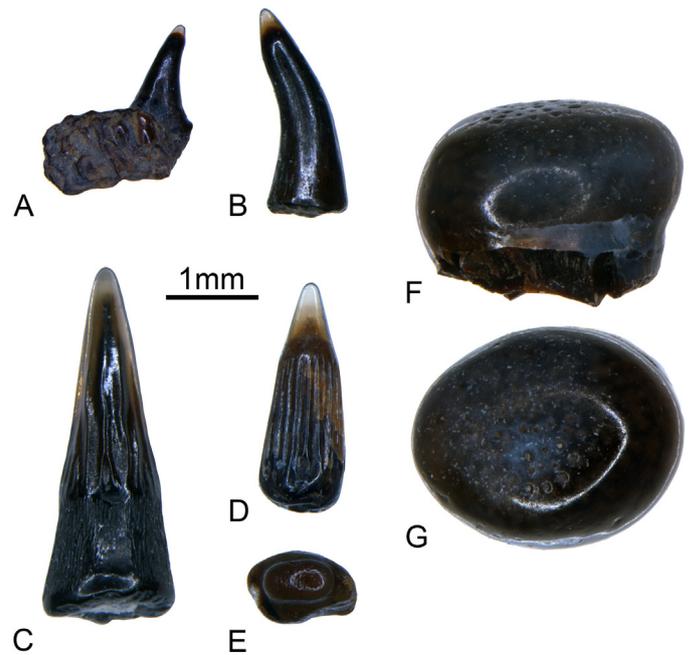
##### 4.2.1. *Gyrolepis albertii* Agassiz, 1835

*Gyrolepis albertii* teeth (Fig. 5A and B) are conical, with a slight curve and a sharp, translucent, enamelled apical cap. This cap is no more than 35% of the tooth's length, and is separated from the rest of the tooth by a ridge and a change in direction of the tooth's curvature, commonly resulting in a slightly sigmoidal shape. Below the cap, the tooth is marked with fine, vertical striations. While most samples are disarticulated crowns without a root, our specimens also included teeth attached to small jaw fragments (Fig. 5A).

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

*Severnichthys acuminatus* was a large, predatory osteichthyan with two types of teeth in the jaw – each previously ascribed to distinct taxa. Curtis attributed *Severnichthys acuminatus* teeth to these separate species and identified them accordingly. The 'Birgeria acuminata' type teeth (Fig. 5C) are conical and upright, with a semi-translucent cap accounting for up to 50% of the tooth's total height. The cap is often vertically ridged, with fine ridges continuing below the cap. The cap is separated from the rest of the tooth by a prominent ridge or collar.

'*Saurichthys longidens*' teeth are passingly similar in appearance, but may have a slightly sigmoidal lateral outline (Fig. 5D). These teeth have a smaller cap, often under 10% of the tooth's total length. Below the cap, these teeth are also vertically ridged, but



**Fig. 5.** Actinopterygian teeth from the Manor Farm Rhaetian section. (A) *Gyrolepis albertii* tooth attached to jaw fragment (BRSUG 29371-1-1691). (B) *Gyrolepis albertii* tooth in side view (BRSUG 29371-1-1663-1). (C) 'Birgeria acuminata' type *Severnichthys acuminatus* tooth (BRSUG 29371-1-1644-1). (D) '*Saurichthys longidens*' type *Severnichthys acuminatus* tooth (BRSUG 29371-1-129-1). (E) *Lepidotes* sp. tooth in occlusal view (BRSUG 29371-1-1550). (F and G) *Sargodon tomicus* tooth in side (F) and occlusal (G) views (BRSUG 29371-1-414).

these ridges are noticeably more pronounced than those on the lower part of the 'Birgeria acuminata' type teeth.

*Severnichthys acuminatus* was, in all likelihood, similar in appearance to the well-studied *Birgeria*, a genus to which these Penarth Group fossils had formerly been assigned (as *Birgeria acuminata*). However, fossils from the Aust Cliff and Westbury Garden Cliff sites include examples where both *Birgeria acuminata* and *Saurichthys longidens* type teeth, and intermediates between these two extremes, exist on the same jaw (Storrs, 1994, pp. 229–236).

##### 4.2.3. *Sargodon tomicus* Plieninger, 1847

The Curtis collection includes molariform teeth of *Sargodon tomicus* (Fig. 5F and G). These isolated crowns are domed, and elliptical in occlusal view. The occlusal surface of the crown is often partially concave due to wear. This wear reveals the histology of the dentine beneath the crown's surface, consisting of a network of cavities terminating in finely branching canaliculi that result in a pattern of small pores on the surface of the worn area (Duffin, 1999, p. 217).

Originally described from isolated teeth from the German Rhaetian (Plieninger, 1847), near-complete specimens from the Norian of Northern Italy reveal that the species is a deep-bodied actinopterygian fish up to 1 m in length, with three to six incisoriform teeth on the dentary and a further three teeth on the premaxilla (Tintori, 1983).

##### 4.2.4. *Lepidotes* sp.

*Lepidotes* teeth exist in the Manor Farm collection as isolated tooth caps and as teeth in jaw fragments (Fig. 5E). These teeth are domed, commonly featuring a protuberance of acrodin on the occlusal surface. Otherwise, there is a large amount of variation in these teeth and few diagnostic characteristics, meaning that *Lepidotes* is a wastebasket genus for the bulbous teeth of unknown fish species.

#### 4.2.5. Undetermined coelacanth

The Manor Farm collection also includes its most unusual component, nine isolated quadrates of an undetermined coelacanth (Fig. 6). These bones are rod-like, flaring at the base into a double articulation, with a distinctive grooved articular surface; this double glenoid for articulation with the lower jaw is typical of coelacanths (Cavin and Grādinaru, 2014). The rod-like, central shaft portion in some specimens forms a broader flange. Coelacanth remains are rare in the Penarth Group, previously known from Holwell (Duffin, 1999), where the single specimen was initially identified as a reptilian phalange (Duffin, 1978). More recently, an isolated right gular plate of a coelacanth was reported from the Rhaetian bone bed at Blue Anchor Point, Somerset (Hauser and Martill, 2013). Our record here, from Manor Farm, is therefore the third report of coelacanth remains from the British Rhaetian.

The fossilised quadrates of the Curtis collection are quite abraded and do not feature distinct characteristics, and so they cannot be identified to generic or specific level.

#### 4.2.6. Other osteichthyan remains

The Manor Farm collection includes a large number of unidentified actinopterygian remains, including scales, fin ray elements, ring centra, indeterminate bones, jaw fragments and teeth, lacking the diagnostic features required for confident identification.

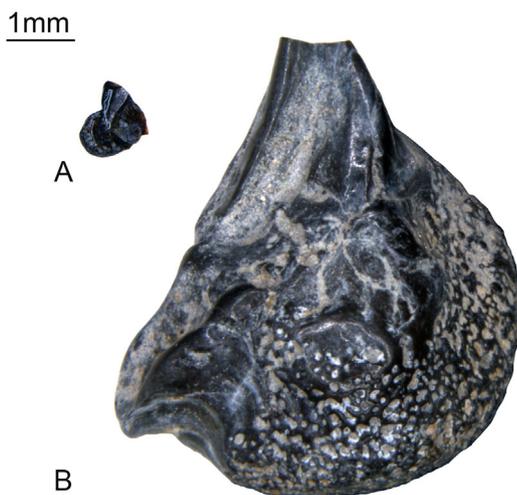
There are over 7300 rhombohedral actinopterygian scales, varying in size and worn to varying degrees. The less worn specimens reveal a glossy surface of fine ridges attached to the unadorned rhombohedral base. Fin ray elements are numerous and fragmented, with over 950 specimens, varying greatly in fragment size and shape. While some fragments are generally rod-like, others are flattened and broad. Most of these specimens are domed on one side, with a longitudinal groove on the other.

#### 4.3. Reptiles

Reptile remains from Manor Farm include isolated specimens of the typical Rhaetian forms *Pachystropeus* and *Ichthyosaurus*.

##### 4.3.1. *Pachystropeus rhaeticus* E. von Huene, 1935

*Pachystropeus rhaeticus* is represented in the collection by a number of bone fragments, including neural spine fragments, and one nearly complete element. This element (Fig. 7A and B) is



**Fig. 6.** Coelacanth quadrates from the Manor Farm Rhaetian section, showing the full size range. (A) Smallest undetermined coelacanth species quadrate (BRSUG 29371-1-61). (B) Largest undetermined coelacanth species quadrate (BRSUG 29371-1-410).

64 mm long, flat and slightly curved. It tapers from an 8-mm-wide broken end to a 155-mm-wide, more complete articular end. The surface of the bone is longitudinally lightly striated, and it is brown in colour. The size, shape, and mode of preservation suggest this is a limb bone from the small reptile *Pachystropeus*, but it does not quite match the figured humeri and femurs (Storrs and Gower, 1993; Storrs et al., 1996). It most resembles the shaft and distal end of a juvenile humerus (Storrs et al., 1996, fig. 8B), but could equally be a lower limb bone, such as an ulna or tibia, not previously figured. Storrs et al. (1996) report humeri measuring up to 90 mm in total length, and the femur of the holotype is 63 mm long. A smaller limb bone specimen (Fig. 7C and D) is preserved black, but is otherwise consonant in shape and size with *Pachystropeus* limb bones.

Other remains of *Pachystropeus* (Fig. 8D–P) are identified on the basis of shape, preservation, internal bone porosity (pachyostotic) patterns (Fig. 8D, L–P), and size. Neural spine fragments include one from a dorsal vertebra (Fig. 8D and E), two further specimens showing the prezygapophyses (Fig. 8F) and the prezygapophyses and neural spine (Fig. 8G and H), and a possible partial neural arch from a short sacral vertebra (Fig. 8I). These are identified by comparison with more complete vertebrae in the holotype and related materials (e.g. Storrs et al., 1996, text-figs. 5, 6, pls. 1, 2). These specimens are all tiny, much smaller than the typical specimens described by Storrs et al. (1996), but they may come from juveniles, having separated from the centra possibly because of an absence of co-ossification. Other *Pachystropeus* fossils include two larger, striated neural spines from dorsal vertebrae (Fig. 8J, M and N), a possible centrum (Fig. 8L), a possible distal humerus (Fig. 8K), and possible vertebral fragments (Fig. 8O and P).

*Pachystropeus* was initially described on the basis of fragmented material from the Westbury Formation of Somerset and Gloucestershire and its equivalents in Germany at Gaisbrunnen and Olgahain, as well as Rhaetian fissure fillings in Holwell, Somerset (E. von Huene, 1933, 1935; F. von Huene, 1902, 1956). Another Rhaetian species, *Rysosteus oweni*, described by Owen (1842), is synonymous (Duffin, 1978), but the lack of useful descriptions or illustrations and the loss of the holotype fossils have left *Rysosteus* as an undiagnosable taxon and *nomen dubium*.

The affinities of *Pachystropeus* have been debated. It was assigned to the choristoderes by Storrs and Gower (1993), which extended the known fossil record of the group back by around 45 Myr. *Pachystropeus* was the only known choristodere not found in freshwater deposits. However, this identification has been queried: Matsumoto and Evans (2010) noted that the diagnostic characters of choristoderes are in the skull, and yet only one cranial bone of *P. rhaeticus* has been found. Renesto (2005) suggested that *Pachystropeus* might be related to *Endennasaurus* from the Late Triassic of Italy, a possible thalattosaur, based on the common occurrence of 22 characters regarded by Storrs and Gower (1993) as unique to choristoderes; thalattosaurs are marine.

Whatever its correct phylogenetic placement, the similarities between *P. rhaeticus* and the slender, long-bodied choristoderes and thalattosaurs, indicate a similar, semi-aquatic, coastal lifestyle. It was a small animal, with an estimated adult length of 1 m or less, though some, rarer fossils indicate lengths of 2–2.5 m. It was superficially crocodylian in appearance, and presumably hunted fish in the shallow Rhaetian seas.

##### 4.3.2. Undetermined *Ichthyosaurus* sp.

Four ichthyosaur teeth were identified among the Manor Farm fossils. These teeth (Fig. 8A–C) are conical, with a wide, heavily ridged root formed of plicidentine. The crown is also vertically ridged, though this is less pronounced than the ornamentation of the root. One of these teeth has a pronounced incision marking the



**Fig. 7.** *Pachystropheus rhaeticus* elements from the Manor Farm Rhaetian section. (A and B) *Pachystropheus* bone (BRSUG 29371-2-192). (C and D) *Pachystropheus* bone fragment (BRSUG 29371-2-202).

root/crown junction. All specimens are damaged to a varying degree, with all missing the crown apex.

The Late Triassic saw an extensive turnover of ichthyosaur species, with the demise of the large shastasaurid ichthyosaurs and the rapid radiation of neoichthyosaurians into the Jurassic (Thorne et al., 2011; Fischer et al., 2014). Most Rhaetian ichthyosaur fossils are isolated fragments, and so the majority are classified as *Ichthyosaurus* sp., although this may not be accurate (Storrs, 1994).

#### 4.4. Other fossilised remains

##### 4.4.1. Invertebrates

There are a significant number of invertebrate specimens in the Manor Farm collection, including crustaceans, ophiuroids, echinoids, bivalves, gastropods and the fragmentary remains of further, indeterminate invertebrates. There are also 1859 specimens of indeterminate invertebrate remains, consisting of fragments and undifferentiated partial invertebrate microfossils.

The crustacean specimens include a single fragmented specimen of an unidentified barnacle genus, possibly *Eolepas*, and three unidentified, articulated ostracods. *Eolepas rhaetica* was first recorded by Moore (1861) from Vallis.

Ophiuroids are represented by 589 fragments, including ambulacral plates and vertebrae from the arms. There are also 101 echinoid specimens, comprising partial plates and spines.

There are 96 indeterminate bivalve specimens, including disarticulated valves, fragmentary remains and argillaceous casts, some with an ochreous coating. Gastropods are numerous, represented by 717 specimens. These include fragmentary and complete arenaceous internal casts ('steinkerns'), including limonitised and compressed examples.

##### 4.4.2. Unidentified bones

Around 1932 bone fragments could not be confidently assigned to taxa. These specimens lack diagnostic features, varying in levels of abrasion and the degree of fragmentation.

##### 4.4.3. Coprolites

Coprolites are common in the Manor Farm collection, as in other Rhaetian deposits, with approximately 1091 in this collection. These vary in size, shape and colour, and are very difficult to assign to any particular taxon.

## 5. Discussion

### 5.1. Faunal composition and comparison

The fauna of the Manor Farm collection presents a similar ecosystem to that represented at other Rhaetian formations,

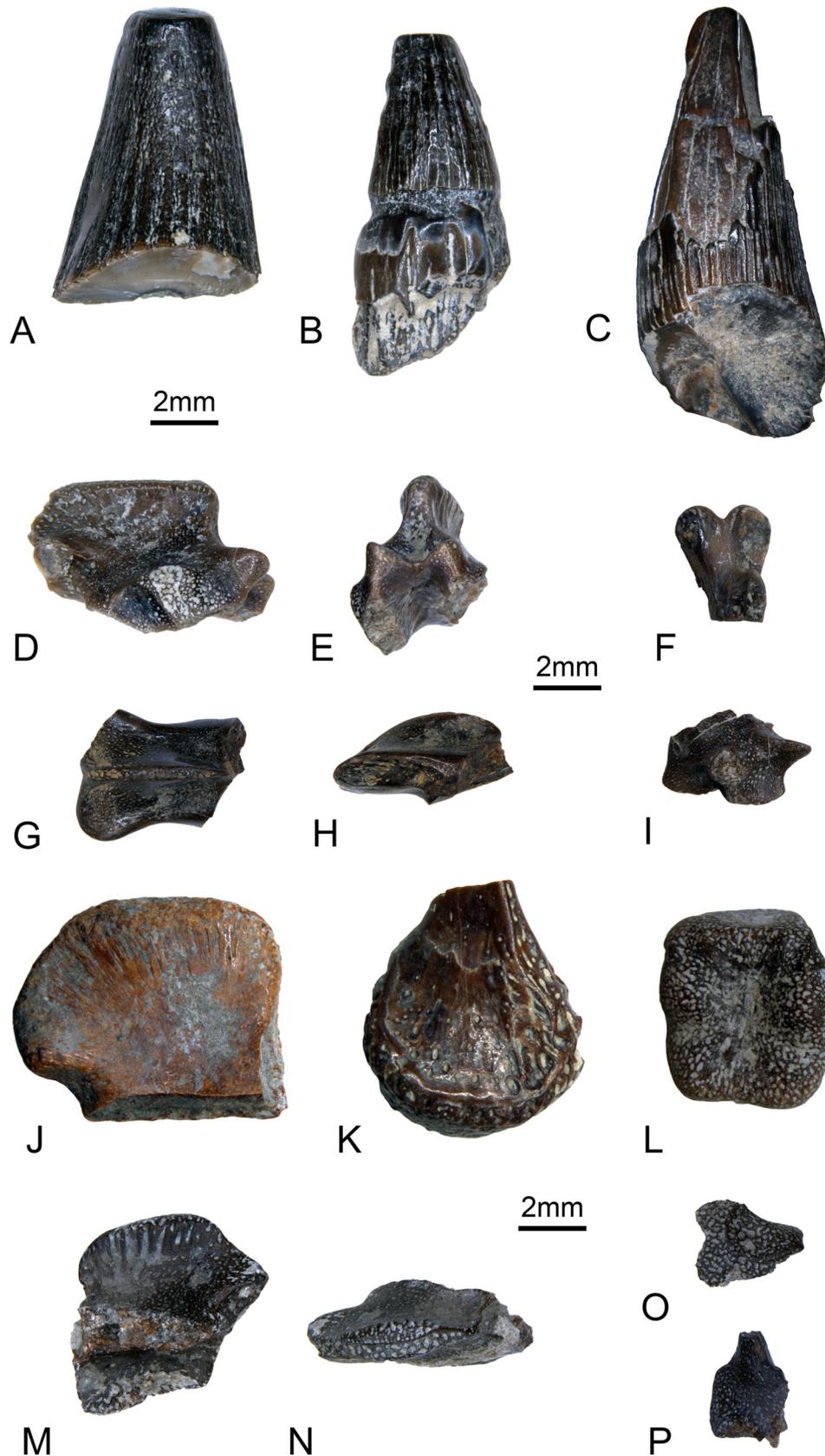
including nearby Aust Cliff. In particular, the species of chondrichthyan and actinopterygian fishes in this collection correspond with those commonly found in the British Rhaetian, although the presence of coelacanth quadrates is unexpected. The Manor Farm collections amassed by Mike Curtis comprise 19,521 specimens. Of this total, osteichthyan scales account for 37%, chondrichthyan denticles for 5%, and unidentified bones for 10% (Fig. 9A). Non-scale or denticle chondrichthyan and osteichthyan fossils account for 6% and 20%, respectively. When these poorly identifiable fossils are excluded, 1965 identifiable fossils remains, of which chondrichthyan teeth make up 32% and osteichthyan teeth 62% (Fig. 9B). The final 6% comprises all other fossils identified to the genus level. The three most commonly identified species are *Lissodus minimus*, *Severnichthys acuminatus* and *Gyrolepis albertii*, with these three species' teeth together comprising 80% of the identified fossils. Although quantitative studies of Rhaetian fossil material are uncommon, the recent studies of Rhaetian material from Charton Bay in Devon by Korneisel et al. (2015) and Marston Road Quarry, Somerset (Nordén et al., 2015) found similar distributions of species among their identified material.

As well as the various identified fish species, our collection contains four ichthyosaur teeth and 12 specimens belonging to the semi-aquatic reptile *Pachystropheus rhaeticus*, together comprising only 0.6% of the vertebrate collection. The majority of these *P. rhaeticus* specimens are fragments under 10 mm in length, but there are two bones over 30 mm, BRSUG 29371-2-192 and BRSUG 29371-2-202.

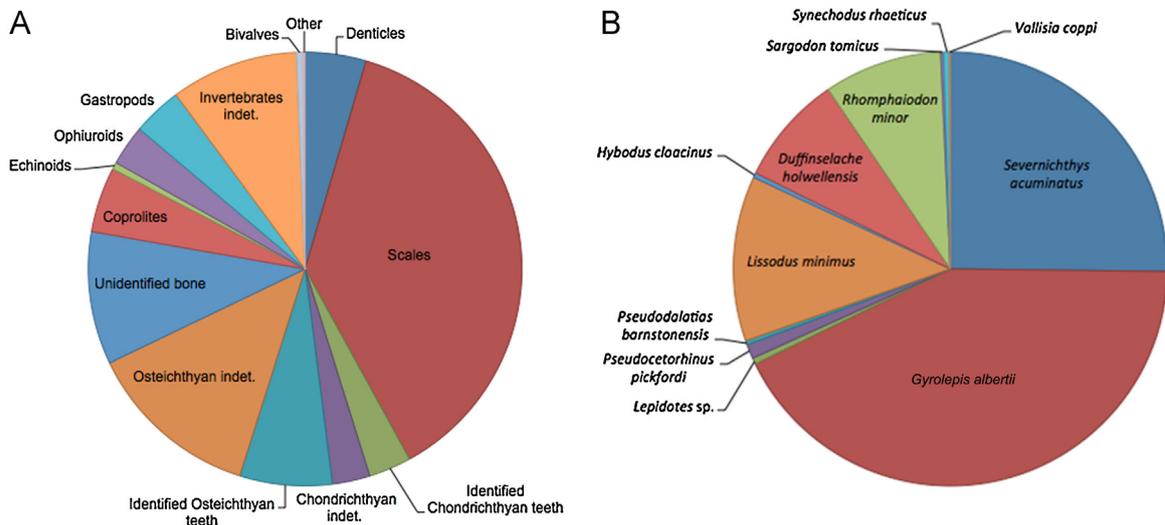
Invertebrates account for 17% of the total Manor Farm collection when all specimens are included. Only one genus is confidently identified among this material, the barnacle *Eolepas rhaetica* (Moore, 1861). Undetermined echinoids, ophiuroids, gastropods and bivalves are also included. The known invertebrate fauna of the British Rhaetian is described by Storrs (1994), and we do not explore these materials further. Note that here, as in other comparable studies of microvertebrates, the invertebrates are likely under-counted because the acid digestion process presumably preferentially dissolves calcium carbonate exoskeletons when compared to the calcium phosphate in bones, teeth, and scales.

### 5.2. Multiple Rhaetian bone beds

The main focus in studies of the British Rhaetian has been on the basal Rhaetian bone bed. However, collectors have long known that there are further bone beds, higher in the sequence, which may be less rich, but nonetheless produce diverse faunas. Mike Curtis, in various unpublished studies, spent time seeking to determine how many bone-bearing horizons there were, and how their faunas differed. Here, thanks to his careful collecting, we are



**Fig. 8.** Other reptilian material from the Manor Farm Rhaetian section. (A) Ichthyosaur tooth (BRSUG 29371-2-249). (B) Ichthyosaur tooth (BRSUG 29371-2-250). (C) Ichthyosaur tooth (BRSUG 29371-2-251). (D and E) *Pachystropeus rhaeticus* dorsal neural arch fragment in lateral (D) and anterior (E) views (BRSUG 29371-2-203-1). (F) *Pachystropeus rhaeticus* anterior neural arch fragment (BRSUG 29371-2-203-2). (G and H) *Pachystropeus rhaeticus* neural spine fragment in dorsal (G) and lateral (H) views (BRSUG 29371-1-988-1). (I) *Pachystropeus rhaeticus* sacral neural spine fragment (BRSUG 29371-1-988-2). (J) *Pachystropeus rhaeticus* dorsal neural arch from adult (BRSUG 29371-2-205-1). (K) *Pachystropeus rhaeticus* possible distal humerus, or other limb element (BRSUG 29371-2-205-2). (L) *Pachystropeus rhaeticus* centrum, in dorsal view (BRSUG 29371-2-205-3). (M and N) *Pachystropeus rhaeticus* dorsal neural arch and spine in lateral (M) and ventral (N) views (BRSUG 29371-1-990-1). (O) *Pachystropeus rhaeticus* bone fragment (BRSUG 29371-1-990-2). (P) *Pachystropeus rhaeticus* bone fragment (BRSUG 29371-1-990-3).



**Fig. 9.** Census of specimens from Manor Farm. (A) Relative proportions of all fossils in the Manor Farm collection. Total number of specimens: 19,521. The “other” category includes coelacanth quadrates, *Eolepas* sp., ichthyosaur teeth, ostracods and *Pachystropeus rhaeticus* fossils. (B) Relative proportions of fish teeth identified to the genus level. Total number of specimens: 1965.

able to report the faunal compositions of five bone-bearing horizons (Table 1; Fig. 10).

The most striking observation is the substantially differing yields of specimens per kg of sediment sample. Mike Curtis sampled each of five layers – the basal Westbury Formation bone bed, a further horizon at the top of the Westbury Formation, and three levels in the Cotham Member, at the base, 50 cm above the base, and just below the top of the unit, and the yields range from over 900 identifiable specimens per kg from the basal Westbury Formation bone bed to 30 specimens per kg at the top of the Westbury Formation, and only 1–12 identifiable specimens per kg in the three Cotham Member microvertebrate-bearing units

**Table 1**

Summary of specimen counts from each of five bone-bearing horizons, showing changing occurrences, relative abundances, and overall yield of specimens per kg of sample.

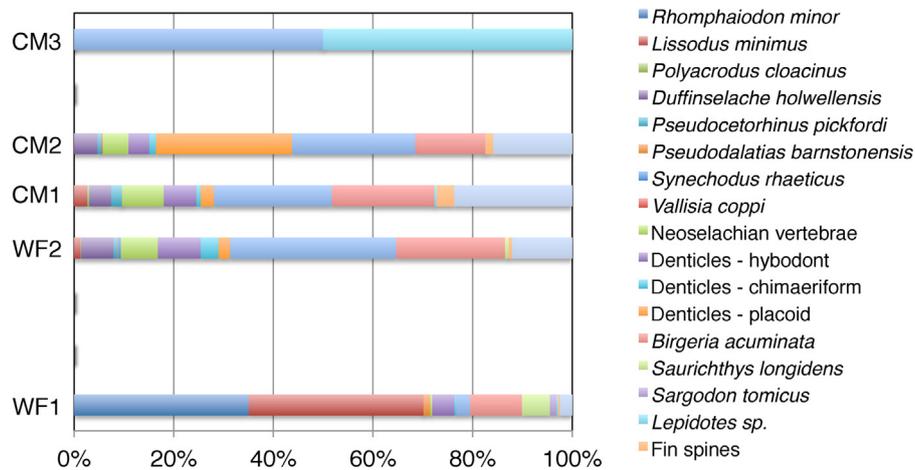
	WF-basal	WF-top	CM-base	CM-mid	CM-top
<b>Chondrichthyes</b>					
<i>Rhomphaiodon minor</i>	101	0	0	0	0
<i>Lissodus minimus</i>	101	13	6	0	0
<i>Hybodius cloacinus</i>	0	1	1	0	0
<i>Duffinselache holwellensis</i>	0	66	10	18	0
<i>Pseudocetorhinus pickfordi</i>	0	8	5	3	0
<i>Pseudodalatias barnstonensis</i>	4	1	0	0	0
<i>Synechodus rhaeticus</i>	0	6	0	0	0
<i>Vallisia coppi</i>	0	0	0	1	0
Neoselachian vertebrae	1	75	19	20	0
Denticles – hybodont	13	87	15	16	0
Denticles – chimaeriform	1	36	2	5	0
Denticles – placoid	0	23	6	105	0
<b>Total</b>	<b>221</b>	<b>321</b>	<b>65</b>	<b>173</b>	<b>0</b>
<b>Osteichthyes</b>					
<i>Gyrolepis albertii</i>	8	337	54	95	1
<i>Birgeria acuminata</i>	30	221	47	54	0
<i>Saurichthys longidens</i>	16	7	0	0	0
<i>Sargodon tomicus</i>	4	0	0	0	0
<i>Lepidotes</i> sp.	1	0	1	0	1
Fin spines	1	7	8	6	0
Fin ray elements	7	122	54	61	0
<b>Total</b>	<b>67</b>	<b>694</b>	<b>164</b>	<b>216</b>	<b>2</b>
Coprolites	14	274	37	185	0
<b>Overall total</b>	<b>302</b>	<b>1289</b>	<b>266</b>	<b>574</b>	<b>2</b>
Sample weight (kg)	0.33	43.21	29.01	50.59	1.27
Sharks/Bony fishes	0.73	0.25	0.24	0.30	0.00
Fossils/kg	915.15	29.83	9.17	11.35	1.57

(Table 1; Fig. 10). Whereas the basal Rhaetian bone bed appears to be ubiquitous, these four higher bone-bearing horizons may be locally occurring phenomena, or may be more widespread – further exploration is required.

In terms of taxa, there are major changes through the sequence. The basal Westbury Formation bone bed is dominated by teeth of the sharks *Rhomphaiodon minor* and *Lissodus minimus*, making up 66% of all finds. Next most abundant is *Severnichthys acuminatus* (*Saurichthys longidens* type). Overall, the first two taxa ensure that the basal bone bed is dominated by sharks (73% of the fauna; Table 1), whereas the other four bone-bearing horizons show much lower proportions (24–30% sharks).

The bone-bearing horizon at the top of the Westbury Formation is dominated by teeth of *Gyrolepis albertii* and *Severnichthys acuminatus* (*Birgeria acuminata* type), then fin ray elements, hybodont denticles, neoselachian vertebrae, and the most abundant shark teeth, *Duffinselache holwellensis*. This last form is absent in the basal bone bed, and continues relatively abundant through the Cotham Member. The same is true of the teeth of the bony fishes *Gyrolepis albertii* and *Severnichthys acuminatus* (*Birgeria acuminata* type), which are relatively rare in the basal bone bed. On the other hand, the shark teeth *Duffinselache holwellensis* and *Pseudocetorhinus pickfordi* are absent in the basal bone bed, relatively abundant at the top of the Westbury Formation, and diminish somewhat in abundance in the Cotham Member (Table 1; Fig. 10). Among other unusual occurrences, chimaeriform denticles appear to be relatively abundant at the top of the Westbury Formation, but not above or below. Further, *Severnichthys acuminatus* (*Saurichthys longidens* type) and *Sargodon tomicus*, while present in the Westbury Formation, are absent in the Cotham Member.

The variations in apparent dominance, as well as appearances and disappearances of different taxa, with especially marked differences between the base and top of the Westbury Formation, do not seem to reflect sampling, as the specimens span the range of sizes sampled through sieves of different sizes – each of the five fossiliferous horizons yields macroscopic remains, as well as a full range of microvertebrate specimens in the size ranges from 300 µm to 2 mm. Comparison with carefully sampled materials from other sites may confirm some of these patterns, and suggest there are real appearances and disappearances of certain taxa, perhaps reflecting facies and ecology or evolution.



**Fig. 10.** Relative proportions of key taxa in five bone-rich horizons, two in the Westbury Formation (WF1, WF2), where WF1 is the basal Westbury Formation bone bed, and three in the overlying Cotham Member (CM1, CM2, CM3). Based on data in Table 1, taxa and main categories are identified in the key, and these read from left to right, as proportions of 100%, on the x-axis.

The differences in relative abundance of the two tooth types of *Severnichthys acuminatus* are surprising; these are widely interpreted as morphs of a single species, and so might be expected to occur in equivalent proportions throughout the succession. The occurrence of one type in the basal Westbury Formation bone bed, and the other in higher bone-bearing horizons could then suggest that the allocation of both types to a single species is at fault, or more likely that there is some taphonomic sorting – the teeth do differ slightly in size (cf. Fig. 5C and D).

### 5.3. Rhaetian coelacanth

The nine coelacanth quadrates from Manor Farm collection were unexpected finds. This is only the third report of coelacanth from the British Rhaetian, following previous finds by Duffin (1978, 1999) of small putative coelacanth quadrates from Holwell, Somerset and Hauser and Martill (2013), who reported a single coelacanth gular plate from Blue Anchor, Somerset.

The earliest known coelacanth is *Euporosteus yunnanensis*, from the early Devonian (Pragian) of Zhaotong, Yunnan, China (Zhu et al., 2012), and the clade had a history of substantially varying diversity through time until the famous gap in their fossil record from the latest Cretaceous to the present, and the living *Latimeria* (Cloutier and Forey, 1991; Forey, 1998; Friedman and Coates, 2006; Wen et al., 2013). The Triassic was an unusual time in coelacanth evolution, beginning with a sharp peak in diversity (14–21 species) in the Early Triassic, having risen from 2 to 3 species in the Late Permian, and then declining to 3–4 species in the Anisian, and 1–2 species in the Rhaetian and Early Jurassic (Forey, 1998; Wen et al., 2013).

The Early Triassic peak was the highest ever in coelacanth evolution, and it could represent an artefact of unusually high sampling, although the species come from many localities and many formations, so it is as likely to be a true reflection of relative coelacanth diversity. In the latter case, Wen et al. (2013) suggested that this is evidence that coelacanth were in some way acting as disaster taxa, recovering well from the Permo-Triassic mass extinction, and in fact flourishing in the perturbed environmental conditions, with bursts of global warming and ocean-floor anoxia at times. The modern coelacanth, *Latimeria*, is able to survive in low-biomass, oxygen-deficient waters because of a low metabolic rate, specialised breathing and gill physiology and unique electroreceptor organ in the rostrum (Fricke and Hissmann, 2000). Anoxic conditions at the Permo-Triassic boundary and

Early Triassic oceans were widespread (Wignall and Twitchett, 1996). If the Early Triassic coelacanth shared aspects of the physiology of *Latimeria*, they might have diversified in the Early Triassic at a time when other marine clades were struggling, but there is no evidence for the physiology of these early forms.

In any case, by Rhaetian times, only isolated remains are reported, including *Chinlea sorenseni* and an unidentified coelacanthid from the upper Rock Point Member of the Chinle Formation in western Colorado (Milner et al., 2006), as well *Undina picena* and some undescribed species in the Norian to Rhaetian of North Italy (Lombardo and Tintori, 2005; Dalla Vecchia, 2006), and some coelacanth remains in the late Norian–early Rhaetian Ørsted Dal Member in east Greenland (Milàn et al., 2004), and from Morocco and Germany (Forey, 1998). Most of these coelacanth records, except those from North Italy, are from freshwater deposits. Coelacanth were overall rare by the Late Triassic and Early Jurassic, but their diversity peaked again, with 5–10 species worldwide in the Tithonian and Aptian–Albian (Forey, 1998; Wen et al., 2013). Much more work is required to determine the true diversity of Rhaetian coelacanth worldwide, as well as the role of the end-Triassic mass extinction on their longer-term evolution.

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### Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.pgeola.2015.09.002>.

### References

- Agassiz, L.J.R., 1833–1844. *Recherches sur les Poissons Fossiles. Tome 3 Concernant l'Histoire de l'Ordre des Placoïdes*. Imprimerie Petitpierre, Paris 390 + 34 pp.
- Andreev, P.S., Cuny, G., 2012. New Triassic stem selachimorphs (Chondrichthyes, Elasmobranchii) and their bearing on the evolution of dental enameloid in Neoselachii. *Journal of Vertebrate Paleontology* 32, 255–266.

- Benton, M.J., Spencer, P.S., 1995. Fossil Reptiles of Great Britain. Chapman & Hall, London 386 pp.
- Benton, M.J., Schouten, R., Drewitt, E.J.A., Viegas, P., 2012. The Bristol Dinosaur project. Proceedings of the Geologists' Association 123, 210–222.
- Benton, M.J., Forth, J., Langer, M.C., 2014. Models for the rise of the dinosaurs. Current Biology 24, R87–R95, <http://dx.doi.org/10.1016/j.cub.2013.11.063>.
- Buckland, W., Conybeare, W.D., 1824. Observations on the south-western coal district of England. Transactions of the Geological Society of London, Series 2 1, 210–316.
- Cappetta, H., 1987. Mesozoic and Cenozoic Elasmobranchii Chondrichthyes II. In: Schultze, H.-P. (Ed.), Handbook of Paleichthyology 3B. Gustav Fischer Verlag, Stuttgart, pp. 1–193.
- Cappetta, H., 2012. Chondrichthyes. Mesozoic and Cenozoic Elasmobranchii: Teeth. In: Schultze, H.-P. (Ed.), Handbook of Paleichthyology 3E. Verlag Dr Friedrich Pfeil, München, pp. 1–512.
- Cavin, L., Grădinaru, E., 2014. Dobrogeria aegyssensis, a new early Spathian (Early Triassic) coelacanth from North Dobrogea (Romania). Acta Geologica Polonica 64, 161–187.
- Cloutier, R., Forey, P.L., 1991. Diversity of extinct and living actinistian fishes (Sarcopterygii). Environmental Biology of Fishes 32, 59–74.
- Cuny, G., Benton, M.J., 1999. Early radiation of the neoselachian sharks in Western Europe. Geobios 32, 193–204.
- Cuny, G., Risnes, S., 2005. The enameloid microstructure of the teeth of synchondontiform sharks (Chondrichthyes: Neoselachii). PalArch's Journal of Vertebrate Palaeontology 3 (2), 1–19.
- Dalla Vecchia, F.M., 2006. The tetrapod fossil record from the Norian–Rhaetian of Friuli (northeastern Italy). New Mexico Museum of Natural History Science Bulletin 37, 432–444.
- Donovan, D.T., Kellaway, G.A., 1984. Geology of the Bristol district: Lower Jurassic rocks. Memoir of the British Geological Survey Bristol Special Sheet (England and Wales).
- Duffin, C.J., 1978. The Bath geological collections. The importance of certain vertebrate fossils collected by Charles Moore: an attempt at scientific perspective. Newsletter of the Geological Curators Group 2, 59–67.
- Duffin, C.J., 1982a. A palaeospinacid shark from the Upper Triassic of south-west England. Zoological Journal of the Linnean Society 74, 1–7.
- Duffin, C.J., 1982b. Teeth of a new selachian from the Upper Triassic of England. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1982 (3), 156–166.
- Duffin, C.J., 1985. Revision of the hybodont selachian genus *Lissodus* Brough (1935). Palaeontographica, Abteilung A 188, 105–152.
- Duffin, C.J., 1993a. Late Triassic sharks teeth (Chondrichthyes, Elasmobranchii) from Saint-Nicolas de Port (north-east France). Professional Paper of the Belgian Geological Survey 264, 7–32.
- Duffin, C.J., 1993b. Teeth of *Hybodus* (Selachii) from the Early Jurassic of Lyme Regis, Dorset (Southern England): preliminary note. Professional Paper of the Belgian Geological Survey 264, 45–52.
- Duffin, C.J., 1998a. New shark remains from the British Rhaetian (latest Triassic). 1. The earliest Basking shark. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1998 (3), 157–181.
- Duffin, C.J., 1998b. New shark remains from the British Rhaetian (latest Triassic). 2. Hybodonts and palaeospinacids. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 240–256.
- Duffin, C.J., 1999. Fish. In: Swift, A., Martill, D.M. (Eds.), Fossils of the Rhaetian Penarth Group. Field Guide to Fossils 9. Palaeontological Association, London, pp. 129–148.
- Duffin, C.J., Coupatez, P., Lepage, J.C., Wouters, G., 1983. Rhaetian (Upper Triassic) marine faunas from le golfe du Luxembourg in Belgium (preliminary note). Bulletin de la Société belge de Géologie 92, 311–315.
- Etheridge, R., 1868. Physical structure of west Somerset and north Devon and the palaeontological value of Devonian fossils. Quarterly Journal of the Geological Society of London 23 (251–252), 568–598.
- Fischer, J., 2008. Brief synopsis of the hybodont form taxon *Lissodus* Brough, 1935, with remarks on the environment and associated fauna. Freiburger Forschungshefte C 528, 1–23.
- Fischer, J., Voigt, S., Franz, M., Schneider, J.W., Joachimski, M.M., Tichomirowa, M., Götze, J., Furrer, H., 2012. Palaeoenvironments of the late Triassic Rhaetian Sea: implications from oxygen and strontium isotopes of hybodont shark teeth. Palaeogeography, Palaeoclimatology, Palaeoecology 353–355, 60–72.
- Fischer, V., Cappetta, H., Vincent, P., Garcia, G., Goolaerts, S., Martin, J.E., Roggero, D., Valentin, X., 2014. Ichthyosaurs from the French Rhaetian indicate a severe turnover across the Triassic–Jurassic boundary. Naturwissenschaften 101, 1027–1040.
- Forey, P.L., 1998. History of the Coelacanth Fishes. Chapman & Hall, London.
- Fricke, H., Hissmann, K., 2000. Feeding ecology and evolutionary survival of the living coelacanth *Latimeria chalumnae*. Marine Biology 136, 379–386.
- Friedman, M., Coates, M.I., 2006. A newly recognized fossil coelacanth highlights the early morphological diversification of the clade. Proceedings of the Royal Society B 273, 245–250.
- Friedman, M., Sallan, L.C., 2012. Five hundred million years of extinction and recovery: a Phanerozoic survey of large-scale diversity patterns in fishes. Palaeontology 55, 707–742.
- Ginter, M., Hampe, O., Duffin, C.J., 2010. Chondrichthyes. Paleozoic Elasmobranchii: Teeth. In: Schultze, H.-P. (Ed.), Handbook of Paleichthyology 3D. Dr Friedrich Pfeil, München, pp. 1–168.
- Hamilton, D., 1961. Algal growth in the Rhaetic Cotham Marble of southern England. Palaeontology 4, 324–333.
- Hamilton, D., 1977. Aust Cliff. In: Savage, R.J.G. (Ed.), Geological Excursions in the Bristol District. University of Bristol, pp. 110–118.
- Hauser, L.M., Martill, D.M., 2013. Evidence for coelacanths in the Late Triassic (Rhaetian) of England. Proceedings of the Geologists' Association 124, 982–998.
- Huene, F. von, 1902. Uebersicht über die Reptilien der Trias. Geologische und paläontologische Abhandlungen 6, 1–84.
- Huene, E. von, 1933. Zur Kenntnis der Württembergischen Rhabdomebeds mit Zahnfunden neuer Säuger und säugerähnlicher Reptilien. Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg 1933, 65–128.
- Huene, E. von, 1935. Ein Rhynchocephale aus dem Rhät (*Pachystropeus* n.g.). Neues Jahrbuch für Mineralogie, Geologie und Paläontologie 74, 441–447.
- Huene, F. von, 1956. Paläontologie und Phylogenie der niederen Tetrapoden. Gustav Fischer, Jena.
- Jaekel, O., 1889. Die Selachier aus dem Oberen Muschelkalk Lothringens. Abhandlungen zur Geologischen Spezialkarte von Elsass-Lothringen 3, 275–332.
- Kellaway, G.A., Welch, F.B.A., 1993. Geology of the Bristol district. Memoirs of the Geological Survey, U.K. .
- Korneisel, D., Gallois, R.W., Duffin, C.J., Benton, M.J., 2015. Latest Triassic marine sharks and bony fishes from a bone bed preserved in a burrow system, from Devon, UK. Proceedings of the Geologists' Association 126, 130–142.
- Lombardo, C., Tintori, A., 2005. Feeding specializations in Norian fishes. Annali dell'Università degli Studi di Ferrara Museologia Scientifica e Naturalistica, Volume Speciale 2005, 25–32.
- Macquaker, J.H.S., 1999. Aspects of the sedimentology of the Westbury Formation. In: Swift, A., Martill, D.M. (Eds.), Fossils of the Rhaetian Penarth Group. The Palaeontological Association, pp. 39–48.
- Maisey, J.G., 2013. The diversity of tessellated calcification in modern and extinct chondrichthyans. Revue de Paléobiologie 32, 355–371.
- Martill, D.M., 1999. Bone beds of the Westbury Formation. In: Swift, A., Martill, D.M. (Eds.), Fossils of the Rhaetian Penarth Group. Field Guide to Fossils 9. Palaeontological Association, London, pp. 49–64.
- Matsumoto, R., Evans, S.E., 2010. Choristoderes and the freshwater assemblages of Laurasia. Journal of Iberian Geology 36, 253–274.
- Milán, J., Clemmensen, L.B., Bonde, N., 2004. Vertical sections through dinosaur tracks (Late Triassic lake deposits, East Greenland) – undertracks and other subsurface deformation structures revealed. Lethaia 37, 285–296.
- Milner, A.R.C., Kirkland, J.I., Birthisel, T.A., 2006. The geographic distribution and biostatigraphy of Late Triassic–Early Jurassic freshwater fish faunas of the southwestern United States. New Mexico Museum of Natural History Science Bulletin 37, 522–529.
- Moore, C., 1861. On the zones of the Lower Lias and the *Avicula contorta* Zone. Quarterly Journal of the Geological Society 17, 483–517.
- Nordén, K.K., Duffin, C.J., Benton, M.J., 2015. A marine vertebrate fauna from the Late Triassic of Somerset, and a review of British placodonts. Proceedings of the Geologists' Association, <http://dx.doi.org/10.1016/j.pgeola.2015.07.001>.
- Owen, R., 1842. Report on British fossil reptiles. Report of the British Association for the Advancement of Science 1841, 60–204.
- Plieninger, T.H., 1847. Abbildungen von Zähnen aus der oberen Grenzbreccie der Keupers bei Degerloch und Steinenbronn. Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg 3, 164–167.
- Quenstedt, F.A. von, 1858. Der Jura. H. Laupp, Tübingen.
- Radley, J.D., Carpenter, S.C., 1998. The Late Triassic strata of Manor Farm, Aust, south Gloucestershire. Proceedings of the Bristol Naturalists' Society 58, 57–66.
- Renesto, S., 2005. A possible find of *Endennasaurus* (Reptilia, Thalattosauria) with a comparison between *Endennasaurus* and *Pachystropeus*. Neues Jahrbuch für Geologie und Paläontologie Monatshefte 2005, 118–128.
- Reynolds, S.H., 1946. The Aust section. Proceedings of the Cotteswold Naturalists' Field Club 29, 29–33.
- Romano, C., Koot, M.B., Kogan, I., Brayard, A., Minikh, A.V., Brinkmann, W., Bucher, H., Kriwet, J., 2014. Permian–Triassic Osteichthyes (bony fishes): diversity dynamics and body size evolution. Biological Reviews, <http://dx.doi.org/10.1111/brv.12161> (Epub ahead of print).
- Shimada, K., Popov, E.V., Siverson, M., Welton, B.J., Long, D.J., 2015. A new clade of putative plankton-feeding sharks from the Upper Cretaceous of Russia and the United States. Journal of Vertebrate Paleontology, <http://dx.doi.org/10.1080/02724634.2015.981335> (Epub ahead of print).
- Short, A.R., 1904. A description of some Rhaetic sections in the Bristol district, with considerations on the mode of deposition of the Rhaetic Series. Quarterly Journal of the Geological Society of London 60, 170–193.
- Storrs, G.W., 1994. Fossil vertebrate faunas of the British Rhaetian (latest Triassic). Zoological Journal of the Linnean Society 112, 217–259.
- Storrs, G.W., Gower, D.J., 1993. The earliest possible choristodere (Diapsida) and gaps in the fossil record of semi-aquatic reptiles. Journal of the Geological Society of London 150, 1103–1107.
- Storrs, G.W., Gower, D.J., Large, N.F., 1996. The diapsid reptile, *Pachystropeus rhaeticus*, a probable choristodere from the Rhaetian of Europe. Palaeontology 39, 323–349.
- Strickland, H.E., 1841. On the occurrence of the Bristol bone-bed on the Lower Lias near Tewkesbury. Proceedings of the Geological Society of London 3, 585–588.
- Suan, G., Föllmi, K.B., Adatte, T., Bormou, B., Spangenberg, J.E., Van De Schootbrugge, B., 2012. Major environmental change and bone bed genesis prior to the Triassic–Jurassic mass extinction. Journal of the Geological Society, London 169, 191–200.

- Sues, H.-D., Fraser, N.C., 2010. *Triassic Life on Land*. Columbia University Press, New York.
- Swift, A., 1999. Stratigraphy (including biostratigraphy). In: Swift, A., Martill, D.M. (Eds.), *Fossils of the Rhaetian Penarth Group*. The Palaeontological Association, pp. 15–30.
- Swift, A., Martill, D.M., 1999. *Fossils of the Rhaetian Penarth Group*. Field Guides to Fossils 9. Palaeontological Association, London 312 pp.
- Sykes, J.H., 1971. A new dalatiid fish from the Rhaetic Bone Bed at Barnstone, Nottinghamshire. *Mercian Geologist* 4, 13–22.
- Sykes, J.H., 1974. On elasmobranch dermal denticles from the Rhaetic Bone Bed at Barnstone, Nottinghamshire. *Mercian Geologist* 5, 49–64.
- Thorne, P.M., Ruta, M., Benton, M.J., 2011. Resetting the evolution of marine reptiles at the Triassic–Jurassic boundary. *Proceedings of the National Academy of Sciences, United States of America* 108, 8339–8344.
- Tintori, A., 1980. Teeth of the selachian genus *Pseudodalatias* (Sykes, 1971) from the Norian (Upper Triassic) of Lombardy. *Rivista Italiana di Paleontologia e Stratigrafia* 86, 19–30.
- Tintori, A., 1983. *Hypsisomatic Semionotidae (Pisces Actinopterygii) from the Upper Triassic of Lombardy (N. Italy)*. *Rivista Italiana di Paleontologia e Stratigrafia* 88, 417–442.
- Trueman, C.N., Benton, M.J., 1997. A geochemical method to trace the taphonomic history of reworked bones in sedimentary settings. *Geology* 25, 263–266.
- Warrington, G., Audley-Charles, M.G., Elliott, R.E., Evans, W.B., Ivimey-Cook, H.C., Kent, P.E., Robinson, P.L., Shotton, F.W., Taylor, F.M., 1980. A correlation of Triassic rocks in the British Isles. *Geological Society of London Special Report* 13, 78 pp.
- Wen, W., Zhang, Q.-Y., Hu, S.-X., Benton, M.J., Zhou, C.-Y., Tao, X., Huang, J.-Y., Chen, Z.-Q., 2013. Coelacanths from the Middle Triassic Luoping Biota, Yunnan, South China, with the earliest evidence of ovoviviparity. *Acta Palaeontologica Polonica* 58, 175–193.
- Wignall, P.B., Twitchett, R.J., 1996. Oceanic anoxia and the end-Permian mass extinction. *Science* 272, 1155–1158.
- Zhu, M., Yu, X., Lu, J., Qiao, T., Zhao, W., Jia, L., 2012. Earliest known coelacanth skull extends the range of anatomically modern coelacanths to the Early Devonian. *Nature Communications* 3, 772.