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The Late Triassic microvertebrate fauna of Tytherington, UK

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ABSTRACT

The Late Triassic fissure fills from the region of Bristol, SW England and S Wales, preserve unique assemblages of small vertebrates derived from an archipelago of palaeo-islands that document aspects of a critical transition in the history of terrestrial ecosystems. Tytherington Quarry, in south Gloucestershire, is the site of several fossiliferous fissures, all dated as Rhaetian (terminal Triassic), and source of abundant remains of the 'Bristol dinosaur', Thecodontosaurus antiquus. In addition, the fissure sediments have yielded previously unreported microvertebrate assemblages, including over 400 jaw remains from three genera of sphenodontians and 100 archosaur teeth assigned to 15 morphotypes. The land fauna is dominated by sphenodontians, with Diphydontosaurus by far the most common form, followed by Clevosaurus, then the sauropodomorph dinosaur Thecodontosaurus, and then the sphenodontian Planocephalosaurus. There are, in addition, rare remains of contemporaneous bony fishes, as well as fossils apparently reworked from the Carboniferous limestones, namely conodonts, holocephalian (chimaeroid) teeth, and a shark tooth. Many typical latest Triassic animals, such as temnospondyls, phytosaurs, aetosaurs, rauisuchians, plateosaurids and dicynodonts are not represented at Tytherington, perhaps because these generally larger animals did not live on the palaeo-island, or because their carcasses could not fit into the fissures. The absence of tritylodonts and early mammals is, however, less easy to explain on the basis of size, although it is known that these forms were abundant here by the Early Jurassic.

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1. Introduction

The Late Triassic was a key time in the evolution of terrestrial ecosystems. In the wake of the devastating end-Permian mass extinction, faunas on land were slowly rebuilding themselves (Sahney and Benton, 2008; Irmis and Whiteside, 2011; Chen and Benton, 2012). The Palaeozoic world of therapsids was replaced by faunas consisting first of dicynodonts, rhynchosaurs, cynodonts, and basal archosaurs, and these gave way in the Norian to dinosaurs and the precursors of many modern terrestrial vertebrate groups, including the first lissamphibians (frogs and salamanders), the first turtles, the first lepidosaurs (basal sphenodontians), the first crocodylomorphs, and the first mammals (Benton, 1983; Sues and Fraser, 2010).

At the same time, Pangaea was beginning to break up, with massive rifting between the east coast of North America and the north-west coast of Africa and Western Europe. Climates were seasonal, being generally hot and dry, and pluvial conditions in the Carnian gave way to more arid climates in the Norian and Rhaetian (Tucker and Benton, 1982; Simms and Ruffell, 1990).

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At this time, the UK lay within 30 degrees north of the Equator, and the area around Bristol and the Severn Estuary consisted of an archipelago of small islands (Robinson, 1957; Whiteside and Marshall, 2008). The islands were composed of uplifted Palaeozoic rocks including Early Carboniferous marine limestones that developed karstic features in exposed areas, including deep fissures. Occasional, episodic rain washed red, lateritic soils into these fissures, and the sediments were occasionally accompanied by carcasses of the indigenous island fauna, including the dinosaur Thecodontosaurus, sphenodontians, as well as other archosaurs. When the islands were flooded, skeletal remains were transported by the water until they settled. Fissure deposits like this have been found in guarries around Bristol, on the southern side of the Severn Estuary (Tytherington, Cromhall, Durdham Down, Emborough, Batscombe, Highcroft, Barnhill, Holwell, Windsor Hill), and in South Wales, on the northern side of the Bristol Channel/Severn Estuary (Ruthin, Duchy, Pant-y-ffynon, Pant, Pont Alun) (Robinson, 1957; Fraser and Walkden, 1983; Benton and Spencer, 1995; Savage, 1993; Whiteside and Marshall, 2008). The fissures range in age from Late Triassic to Early Jurassic, with some fissures, including Tytherington, dated definitely as Rhaetian (Whiteside and Marshall, 2008).

The Triassic fissures of the Bristol and South Wales areas have yielded diverse fossils, including fishes, lepidosaurs (Swinton, 1939; Robinson, 1962, 1973; Evans, 1980; Fraser, 1982, 1988a;

0016-7878/\$ - see front matter © 2012 The Geologists' Association. Published by Elsevier Ltd. All rights reserved. http://dx.doi.org/10.1016/j.pgeola.2012.05.003 Whiteside, 1986), crocodylomorphs (Crush, 1984), the basal sauropodomorph *Thecodontosaurus* (Benton et al., 2000), pterosaurs (Fraser, 1988b; Fraser and Unwin, 1990), other archosaurs (Fraser and Walkden, 1983), cynodonts (Savage and Waldman, 1966; Savage, 1971), early mammals (Fraser et al., 1985), the crustacean *Euestheria* (Whiteside and Marshall, 2008), and millipedes (Fraser, 1988b), but no insects, lissamphibians or turtles. Most of the material is disarticulated, although some more complete remains have been found. The fauna of each fissure consists of different species lists and different relative proportions of taxa.

The aim of this paper is to present the first report of an intensive sampling exercise at Tytherington, documenting all identifiable fossils found in the original site of collection of rocks bearing *Thecodontosaurus* bones from fissure 2, especially the microvertebrates. The aim is to complete the picture of the latest Triassic tropical-belt terrestrial ecosystems of which *Thecodontosaurus* was a part.

Institutional acronym: BRSUG, Bristol University, School of Earth Sciences collection.

2. Geological setting

Tytherington Quarry (Ordnance Survey grid reference, ST 660890; Fig. 1) exposes primarily Early Carboniferous Limestone, which is guarried for road building. Over the years, Triassic-aged fissures have been identified, and these are generally discarded by the quarrymen. The fissure fill rocks consist of sandy limestone. conglomerate, and breccia (Whiteside, 1983) containing bones in a variety of layers, representing detrital palaeosols intercalated with clasts derived from erosion of the karstic Carboniferous limestone surface, from the cave walls, or from previously deposited surface sediment (sandstone). The larger and smaller clasts show some weathering, indicating that they have been moved by water. The presence of glauconite-smectite in one of the fissures indicates a marine influence on sedimentation (Whiteside and Robinson, 1983). Evidently, the terrestrial fossils and clasts were moved initially by fresh waters re-charged by rainfall on the limestone surface and through the caves where they mixed with marine waters at some point (Whiteside, 1983). Whiteside and Marshall



Fig. 1. Geology of the Bristol fissures. (A) Palaeogeographic map of the Bristol Channel area some 200 Ma, showing land (stippled) and sea (blank), and an archipelago of some 20 small islands, most of them bearing fissures with fossil remains (named by quarries). (B) Cross-section of the Tytherington fissures, showing cave formation and water courses that captured and transported the bones. From Whiteside (1983) and Whiteside and Marshall (2008).

(2008, Figs. 8 and 9) show the field relations of the dinosaurbearing rocks.

The sandy limestone layers in the Triassic fissures yield mainly small sphenodontian jaws and isolated teeth, while the conglomerates and breccias contain larger bone remains of *Thecodontosaurus* and the smaller reptiles. Other fossils in the sandy limestone layers include fish teeth and invertebrate remains, including crinoids and trace fossils. Many of these are reworked from the highly fossiliferous marine Carboniferous limestone, although some were exposed in the Carboniferous limestone clasts through acid digestion. Some of the fish teeth, however, appear to be Triassic, and so it is not clear whether these fishes lived in fresh or brackish waters in the caves, or were washed in from other sources. Whiteside and Marshall (2008) argued that such fishes were contemporaneous with the reptiles but very unlikely to have been cave dwellers.

Dating the Bristol fissure fills is a problem. It is widely accepted that they include a range of ages, from Late Triassic to Early Jurassic (Robinson, 1957; Whiteside, 1986; Savage, 1993; Fraser, 1994; Benton and Spencer, 1995; Whiteside and Marshall, 2008), and that most, but not all, localities exhibit fissures of a single age. There is no primary evidence of age from some of the Late Triassic fissures with red or green sediment infills. Tytherington, uniquely, has yielded a palynoflora that gives clear evidence of Rhaetian age (Marshall and Whiteside, 1980; Whiteside and Marshall, 2008). The Lower Jurassic fissures, such as Holwell, Duchy, Pont Alun, and Pant are dated as earliest Jurassic, Hettangian to Sinemurian, on the basis of *Hirmeriella* pollen that came from the conifer *Cheirolepis* (Harris, 1957).

3. Materials and methods

3.1. The rocks and fossils

The study is based on 26 large rocks collected in 1975 from fissure 2 (Whiteside and Marshall, 2008), part of a collection of some 5 tonnes of rock from Tytherington that have been under reduction and study since 1976, when DIW began his PhD work (Whiteside, 1983), and which have yielded abundant fossils of *Thecodontosaurus* (Benton et al., 2000; Whiteside and Marshall, 2008). This material, and the 'Bristol dinosaur' *Thecodontosaurus* in particular, has formed the basis of an active educational and outreach project over many years, funded variously by the Leverhulme Trust, the University of Bristol, and the Heritage Lottery Fund (Benton et al., 2012). As part of this endeavour, successive generations of students of the MSc in Palaeobiology at the University of Bristol have been trained and engaged to extract *Thecodontosaurus* bones, and since 2010 also to extract microvertebrate fossils. These form the basis of the present report.

The fossils in the Tytherington fissure fills are nearly all disarticulated, but the bones, whether large or small, are generally in good condition, suggesting modest physical transport. The bones range in colour from pure white and yellow to brown and sometimes, though rarely, bright red. Teeth are mostly white-yellow to orange in colour.

3.2. Rock and fossil processing

The process of preparation follows methods established by Whiteside (1983). Each rock was checked for visible fossils, which were glued with MowitalTM in ethanol, which dries to form a plastic layer that consolidates and protects the bone from acid digestion. The rocks were then processed in 5% acetic acid solution, with tri-calcium added as a buffer to protect the uncovered bone surface. Mowital was used in preference to ParaloidTM as it provides a strong bond and is more easily reset (Davidson and

Alderson, 2009). After 45–60 h, the rock was thoroughly cleaned with water, and the water and residue were run through a sieve with mesh size 250 μ m. The rock and residue were then returned to the water, with a drop of soap (sodium hydroxide) to neutralise any remaining acid, and left for a further 45–60 h, but fungus sometimes grew, and the process was stopped. After cleaning, the rock and residue were run through the acid and neutralising cycle repeatedly until there was no acid left.

The residue was then run through four sieves, with mesh sizes of 1180 μ m, 600 μ m, 425 μ m and 250 μ m. The residue was dried on filter paper in a funnel over a small bucket, and, when dry, was brushed into storage boxes labelled according to the source rock and the processing regime. The contents of each box were then tipped onto standard microfossil grids, and hand picked under a binocular microscope. Identifiable specimens were sorted into broad morphotypes.

Key specimens were photographed with a Leica MZ12.5 stereomicroscope equipped with a digital camera. Images were processed using QCapturePro 6.0. For every new specimen and after any modification to the microscope, light and white balance were adjusted. A black background was chosen to increase contrast. Because many of the specimens were teeth, one magnification was used for as many as possible (magn. 1.6×10). Adjustments were only made for conodont elements (magn. 4.0×10), fish teeth (magn. 4.0×10) and specimens that were very large, like sphenodontian jaws (magn. 1.0×10).

Measurements were made under the microscope using the built-in measuring device as well as a scale photographed beside the fossil. Measuring teeth was difficult; most are incomplete and therefore figures are minimal estimates. Tooth height is measured by placing the tooth with the base as horizontal as possible, before measuring the vertical line from the highest portion (tip if present) to the base. Tooth width is the width of the crown at its broadest part.

3.3. Identifying specimens and determining faunal composition

Over 1800 boxes were catalogued, containing more than 10,000 teeth, bones and bone shards from small animals to archosaurs and basal dinosaurs. Most of these bone shards were beyond recognition. More than 1100 specimens however were identifiable to some level. The sphenodontian remains were identified by comparisons with identified materials and using existing literature (see below). All teeth with a crystal tip, or teeth with the same shape but with the tip missing were catalogued as those of bony fish. Toothplates with tubules are holocephalian (chimaeroid) teeth. Teeth that were larger, and clearly not from bony fishes, chimaeroids, or sphenodontians, or that showed serrations were classified as archosaur teeth.

Microvertebrate collections readily provide information on the relative proportions of the taxa. However, this was more difficult than expected. First, the reworked, older materials had to be discarded. Then, decisions had to be made about how to quantify numbers when some taxa (e.g. archosaurs) are represented by isolated teeth, whereas others (e.g. sphenodontians) are represented mainly by partial jaws to which the teeth are firmly fused. Further, it is known that many Triassic archosaurs had a variety of tooth morphs at different positions along their jaws, and teeth may vary through ontogeny (Heckert, 2004). This makes it impossible to determine whether our 15 archosaurian tooth morphs represent 15 different taxa, or more likely some smaller number. Eventually it was decided to count every tooth fragment from archosaurs (including Thecodontosaurus), bony fish, shark, chimaeroid, and conodont, and to present results both with and without the older reworked materials. Some of the Palaeozoic fossils were reworked in the Late Triassic though others, more pristinely preserved such as some of the conodonts, derived from intercalated native Carboniferous limestone clasts dissolved out during acid preparation. The count for sphenodontians was based on an assessment of every bone and loose tooth that was attributable to a particular genus. This approach still probably overestimates the tooth taxa and underestimates the sphenodontians, but no other solution seemed possible.

4. Systematic palaeontology

4.1. Sphenodontians

More than 400 sphenodontian jaw fragments (loose teeth not included) have been found, belonging to three genera. Cranial material could usually be identified to genus level based on previous work (Fraser, 1982, 1986, 1988a; Fraser and Walkden, 1984; Whiteside, 1983, 1986). Postcranial material was harder to identify from the literature (Robinson, 1973; Whiteside, 1983; Fraser and Walkden, 1984; Fraser, 1988a, 1994) because of its fragmentary state. Materials are illustrated in Fig. 2.

4.1.1. Diphydontosaurus avonis Whiteside, 1986

The dentary (Fig. 2A and B) is long and thin, and contains more than 20 teeth, which vary from front to back: the anterior teeth are small and conical, middle teeth are slightly recurved, and the last three or four teeth are conical and robust (Whiteside, 1986). Some *Diphydontosaurus* teeth are ridged on top, but the ridges do not extend as far ventrally as in *Planocephalosaurus*.

4.1.2. Clevosaurus sp.

The *Clevosaurus* dentary (Fig. 2C and D) is thicker than that of *D. avonis*. The anterior teeth are sharp, conical, but slightly laterally compressed, and they alternate in size (Robinson, 1973). The last three posterior teeth are robust and round, with one primary sharp cusp and a large pit. The teeth from the maxilla and dentary fit together. The large posterior teeth have a thin layer of brown enamel. The teeth are often heavily worn, sometimes to the bone.

4.1.3. Planocephalosaurus sp.

Few *Planocephalosaurus* teeth have been found, and most of these are from the posterior part of the maxilla (Fig. 2E and F). The teeth are robust, like those of *Clevosaurus*, but the examples from Tytherington are mostly smaller. They are recurved, with ridges down from the surface of the crown and not just on the top as in *D. avonis*. The ridges are not always visible, often being partially worn away. The teeth from the premaxilla are more pointed and circular, but larger than those of *D. avonis*. It is likely that the material belongs to *Planocephalosaurus robinsonae* (Fraser, 1982; Fraser and Walkden, 1984), but the specimens are too fragmented and weathered to be certain.

4.2. Archosaur teeth

In total, 97 archosaur teeth were found. Many are broken and fragmented, which makes them difficult to compare. We distinguish 15 morphotypes, but it is difficult to assign these to taxa, except for *Thecodontosaurus*. As for the others, our morphotypes 8 and 9 are similar to archosaur morphotypes A and C from the Lower Kalgary locality in the Chinle Formation, USA (Heckert, 2004, Fig. 38). Morphotype B has a similar shape, but a much larger serration density. According to Heckert (2004), these teeth are not recurved enough to be associated with theropods. Both morphotypes also share similarities with *Euparkeria* (Senter, 2003, also suggested for morphotype B by Heckert (2004)), but that taxon is much too old (Anisian) to be considered here. Other teeth in this publication also appear similar in some ways, but overall, the shapes differ from the teeth shown here.

As for other possible identities, Whiteside and Marshall (2008) mention a theropod similar to *Megapnosaurus*, and this could account for some of our recurved teeth. In addition, some of the teeth could belong to a basal crocodylomorph, possibly *Terrestrisuchus* (Crush, 1984), which has been reported from Tytherington previously (Whiteside, 1983). Further, some of the Tytherington teeth resemble those of the pseudosuchian *Revueltosaurus* (Spielmann et al., 2007, Figs. 2 and 3), both from the Chinle Formation.

However, other Late Triassic archosaur groups cannot be recognised. For example, none of our teeth is like the *?Terrestrisuchus* sp. and *Agnosphitys cromhallensis* teeth from Cromhall illustrated by Fraser et al. (2002, Fig. 2), nor like the archosaur teeth from Durdham Down shown by Galton (2007, Fig. 32). Late Triassic pterosaurs have multicusped teeth, and our morphotype 2 might be similar to some anterior pterosaur teeth, for example *Eudimorphodon* cf. *ranzii* from Austria (Wellnhofer, 2003, Fig. 6), but as the tip of BRSUG 29372-525 is broken, nothing can be concluded.

4.2.1. Archosaur morphotype 1: Thecodontosaurus antiquus

These are some of the largest archosaur teeth (Fig. 3A and B), and 27 examples have been found. The tooth has a spatulate shape with the anterior side more strongly recurved. It is laterally compressed, asymmetrical and has denticles on both the anterior and the posterior sides, with a density of approximately 4 per mm. The denticles point to the tip of the tooth. Based on shape, this morphotype belongs to *Thecodontosaurus antiquus* (Riley and Stutchbury, 1840; Benton et al., 2000).

4.2.2. Archosaur morphotype 2

BRSUG 29372-525 is a recurved tooth, approximately 5 mm tall, with the tip missing (Fig. 3C and D). The tooth is practically circular (only slightly laterally compressed) and straight. No



Fig. 2. Sphenodontian jaws and teeth from Tytherington. (A, B) Right mandibles of *Diphydontosaurus avonis*, A – labial view and B – lingual view. (C, D) Right mandible of *Clevosaurus* sp., C – labial view, D – lingual view. (E, F) Maxilla fragment of *Planocephalosaurus* sp. Scale bars are 1 mm.



Fig. 3. Archosaur tooth morphotypes 1–15. (A, B) BRSUG 29372-42, morphotype 1 with A, lingual view and B, labial view. (C, D) BRSUG 29372-525, morphotype 2 with C – ?lingual and D – ?labial view. (E, F) BRSUG 29372-68, morphotype 3 in two views. (G, H) BRSUG 29372-12, morphotype 4 with G, labial and H, lingual view. (I, J) BRSUG 29372-40, morphotype 5 with I, labial and J, lingual view. (K, L) BRSUG 29372-41, morphotype 6 with K – ?labial and L – ?lingual view. (M, N) BRSUG 29372-535, morphotype 7 with M – labial and N – lingual view. (O, P) BRSUG 29372-11, morphotype 8 with O – labial and P – lingual view. (Q, R) BRSUG 29372-45, morphotype 9 with Q – labial and R – lingual view. (S, T) BRSUG 29372-13, morphotype 10 with S – ?labial and T – ?lingual view. (Q, R) BRSUG 29372-45, morphotype 9 with Q – labial and R – lingual view. (S, T) BRSUG 29372-13, morphotype 10 with S – ?labial and T – ?lingual view. (Q, R) BRSUG 29372-14, morphotype 10 with S – ?labial and R – lingual view. (S, T) BRSUG 29372-13, morphotype 10 with S – ?labial and T – ?lingual view. (V, V) BRSUG 29372-167, morphotype 11 with U – labial and V – lingual view. (W, X) BRSUG 29372-168, morphotype 12 with W – labial and X – lingual view. (Y, Z) BRSUG 29372-76, morphotype 13 with Y – lingual and Z – labial view. (AB–AC) BRSUG 29372-50, morphotype 14 in two views. (AD–AE) BRSUG 29372-50, morphotype 15 with AD – ?labial and AE – ?anterior-lingual view. Scale bars are 1 mm.

serrations are present. The crown is approximately one third of the tooth length, but without the tip it is hard to be precise. The base of the tooth shows the root with a resorption pit for the incoming replacement tooth.

4.2.3. Archosaur morphotype 3

BRSUG 29372-68 is a long, thin, recurved tooth slightly over 2 mm tall (Fig. 3E and F). It is split, with the posterior half missing. The anterior half does not show any serrations. The shape of the fragment suggests it was slightly compressed. Other teeth, like BRSUG 29372-1084, 1096, 1317 and 1868, are split in the same way and fit the overall description. Size and degree of recurvature seem to differ. Another tooth, BRSUG 29372-40, is split in the same way, but lacks the anterior side.

4.2.4. Archosaur morphotype 4

BRSUG 29372-12 is a nearly complete and very robust tooth (Fig. 3G and H). Only the tip is missing. It is recurved and laterally compressed but still with a thick circular cross section. It is approximately 1.8 mm wide, and at least 2.3 mm high. It is serrated on both sides, but serrations on the anterior side only start a quarter of the length above the base. Serrations on the posterior side have a density of 12 per mm close to the base, but this decreases slightly further from the base.

4.2.5. Archosaur morphotype 5

BRSUG 29372-40 is split, but only the posterior side is present (Fig. 3I and J). It is likely laterally compressed and its posterior end is serrated, with approximately 14 serrations per mm.

4.2.6. Archosaur morphotype 6

BRSUG 29372-41 is a large and robust tooth (Fig. 3K and L). It is approximately 4 mm in height (with the tip missing), at least 1.6 mm wide, quite recurved, and laterally compressed. Serrations are present on the posterior side, with approximately 13 per mm. This tooth is unique in size and robustness.

4.2.7. Archosaur morphotype 7

BRSUG 29372-535 is a recurved tooth over 2 mm in height and 1 mm in length (Fig. 3M and N). Its posterior side is partially serrated for about three-quarters of its height (though its tip is missing). There are approximately 13 serrations per mm. The tooth is laterally compressed.

BRSUG 29372-1772 is much like this tooth: it is approximately the same size, but a larger fragment of the top is missing. Still, it seems the serrations on its posterior size stop before they reach the tip, as in BRSUG 29372-535. The fragment BRSUG 29372-402 might also belong to this morphotype: it does not have serrations on the anterior side, and those on the posterior side are not present along the entire length.

4.2.8. Archosaur morphotype 8

BRSUG 29372-11 is a very slightly curved triangular tooth approximately 2 mm tall and 1.4 mm wide (Fig. 30 and P). It is laterally compressed and has serrations anterior and posterior sides. The serrations on the anterior side disappear closer to the base, but this may result from wear, in that the entire tooth shows abrasion. Serrations on the posterior side have a density of 11 per mm, but those on the anterior side cannot be measured as a result of the wear. BRSUG 29372-562, 603 and 48 seem to fit this morphotype. BRSUG 29372-562 and 603 also lack serrations on the lower half of their anterior side. BRSUG 29372-48 lacks both the base and the lower half of its anterior side, but seems to fit in this group by overall shape.

4.2.9. Archosaur morphotype 9

BRSUG 29372-45 is a slightly recurved triangular tooth (Fig. 3Q and R) that is very like the previous morphotype, which might be a worn version of morphotype 9. Serrations with a density of 11 per mm are present on both the anterior and posterior sides, and those on the former extend for almost the entire length. This tooth appears to be more gracile and less laterally compressed than morphotype 8. The fragments BRSUG 29372-196 and 565 may belong here.

4.2.10. Archosaur morphotype 10

BRSUG 29372-13 is a fragment of a large, recurved, and laterally compressed tooth (Fig. 3S and T). The surface is not smooth. It is at least 1.5 mm wide. The posterior side is serrated with a density of 12–14 per mm (density decreasing further from the base). The tooth fragment BRSUG 29372-1064 is much like BRSUG 29372-13, but appears to be less laterally compressed, so this might be an older or larger version, or a different part of the same tooth.

4.2.11. Archosaur morphotype 11

BRSUG 29372-1617 is a recurved slender tooth approximately 1.5 mm wide and slightly laterally compressed (Fig. 3U and V). It has serrations on its posterior side. At the base, the serrations are finer and denser (14 per mm), but this decreases (11 per mm) and then finally increases again closer to the top of the tooth.

4.2.12. Archosaur morphotype 12

BRSUG 29372-168 is a fragment of a slender recurved tooth over 1.7 mm wide and slightly laterally compressed (Fig. 3W and X). The posterior side is serrated. It is much like Morphotype 11, but slightly larger and with a lower density of serrations (\approx 10 per mm). It seems

as if the density in this tooth is also higher at the base, and then decreases upwards. This tooth may be a larger version of morphotype 11, with less dense serrations.

4.2.13. Archosaur morphotype 13

BRSUG 29372-76 is a slender, recurved tooth (Fig. 3Y and Z) much like morphotypes 11 and 12. It is, however, smaller, a little over 1.2 mm wide and even less laterally compressed. The serrations on its posterior side are also much denser, with at least 14 per mm, but perhaps more, although a length of only 1 mm could be measured because of damage. It could be the result of damage, but not all serrations seem to be equal in length.

4.2.14. Archosaur morphotype 14

BRSUG 29372-1038 is a small tooth, 0.7 mm in height and probably located in the posterior part of the jaw (Fig. 3AB and AC). It is recurved and laterally compressed with a smooth surface. It looks very simple and non-specialised.

4.2.15. Archosaur morphotype 15

BRSUG 29372-50 is another simple tooth, but larger (1.6 mm) and seemingly slightly more complicated than BRSUG 29372-1038 (Fig. 3AD and AE). It is recurved, laterally compressed and smooth. No serrations are present.

4.3. Actinopterygian teeth

We identify 62 complete or near-complete teeth as pertaining to actinopterygian (bony) fishes. Among these, three morphotypes can be identified, and the remaining teeth are described as 'miscellaneous' and probably represent numerous genera. Some of these fish teeth are well preserved, as evidenced by the crystal tips found during preparation, which are very fragile and break off easily. Teeth that no longer have a crystal tip could be Triassic teeth that have been transported or they could be reworked.

4.3.1. Fish morphotype 1

This tooth type is conical and bent, with the base usually thicker than the tip (Fig. 4A). The tip is not directly above the centre of the base, but more to one side. This group comprises 60 teeth. Though they are mostly conical, with a broader base and significantly smaller towards the tip, thickness, length and degree of curvature differ. It is hard to further subdivide these general tooth morphs. Some of the larger teeth may represent *Gyrolepis*, which was also found at Tytherington by Whiteside (1983). This group also contains teeth that no longer have a crystal tip and may therefore have been heavily worn during lengthy transport or perhaps reworked.



Fig. 4. Fish tooth morphotypes 1–3. (A) BRSUG 29372-7, example of morphotype 1. This particular tooth is a large version of this type. (B) BRSUG 29372-947, morphotype 2. (C) BRSUG 29372-1435, morphotype 3. Notice the 'dent'. Scale bars are 1 mm.

4.3.2. Fish morphotype 2

BRSUG 29372-947 is a circular, conical tooth with a crystal tip (Fig. 4B). It is slightly recurved and has part of the root still attached. The enamel and the crystal tip make up approximately 0.5 mm of the tooth.

4.3.3. Fish morphotype 3

BRSUG 29372-1435 is a small and slender fish tooth (Fig. 4C). It is circular in cross section, and quite recurved. This specimen is 0.5 mm in height and bright orange. The crystal tip is still present. Approximately 0.15 mm from the base is a hollow area that encircles the entire tooth; its function is not clear.

4.4. Chondrichthyan teeth

4.4.1. Thrinacodus ferox Turner, 1982

BRSUG 29372-14 is a shark tooth (Fig. 5A). Its base is long and narrow and the three cusps are asymmetrical, identifying this tooth as *Thrinacodus* and separating it from *Phoebodus* (Turner, 1982; Ginter et al., 2010). The middle and mesial cusp are reduced compared to the more distal larger cusp. No intermediate cusplets are present, another feature of *Thrinacodus* (Turner, 1982; Ginter et al., 2010). All three cusps are extremely curved. The largest cusp appears to have striations on its inner side, emanating from the base. The shape of this tooth, and the extreme asymmetry of its cusps suggest it belongs to the species *T. ferox* from the Late Devonian and Early Carboniferous (Ginter et al., 2010), and so this is clearly reworked.

4.4.2. Chimaeroid teeth

There are more than 200 fragments of chimaeroid teeth, but none complete. Sizes range from <1 mm to more than 5 mm (Fig. 5B and C). The tooth plates are curved and bear many straight tubules that cross the width. They occur in a wide range of colours, from stony grey to almost bright purple. Whiteside (1983) assigned teeth of this kind to the holocephalians *Psephodus* and *Helodus*, which are well known from the surrounding Carboniferous limestone. In this study it was not possible to identify the taxon more closely, and so it is not clear whether these are Rhaetian, or reworked from the Carboniferous.

4.5. Conodont elements

In total, 32 conodont elements have been identified, of which 22 may be assigned to four morphotypes. The remaining specimens were too fragmented to identify more closely. Of the 22 distinctive elements, 19 belong to morphotype 3, and the other three are

different. The specimens are all brown in colour, differing in shade, with the exception of the morphotype 5 specimen, which is transparent grey.

Rhaetian conodonts are rare (Mosher, 1968; Swift, 1989), and they are the very last of the clade (Clark, 1983). Supposed Early Jurassic examples have been noted, but these are likely reworked, and their presence or absence is not a reliable indicator of the Triassic–Jurassic boundary (Lucas et al., 2005). None of the Tytherington conodont elements fits the descriptions of Rhaetian taxa (Swift, 1989; Orchard, 2010, Fig. 15), so they are all regarded as reworked, a suggestion made already by Whiteside and Marshall (2008) for specimens from Tytherington, though not from fissure 2.

4.5.1. Conodont morphotype 1

BRSUG 29372-1283 (Fig. 5D) is a distinctive cone-shaped element and one of the smallest here. The base has two cusps, of which the distal is short and the mesial is very long, approximately twice as long as the length of the base. The surface of the large cusp is mostly smooth, but a rough surface may indicate a few very small denticles along the line of the large cusp.

4.5.2. Conodont morphotype 2

BRSUG 29372-1752 (Fig. 5E) is a platform element, with a broad leaf-shaped base and a short blade extending from the centre line. The blade appears to have three denticles, though a fourth may have been abraded; the mesial two denticles are approximately the same size, but the third is smaller and hardly visible. The basal plate has three rows of denticles, two along the margins, and one in the centre line. One of the lateral rows shows six denticles. The first five of which, from the blade, increase in length, and the sixth decreases. The other lateral row has a few 'bumps', but no obvious denticles. The centre row starts with three small denticles at the tip of the blade, which then disappear into the broad, midline groove.

4.5.3. Conodont morphotype 3

BRSUG 29372-613 (Fig. 5F) is a blade-type element, with a gently curved lower rim and basal cavity, and a partly smooth, partly denticulate upper margin. Three small denticles occur at one end of the upper margin, with a broken-off denticle base between them, and a long smooth margin behind, where denticles have probably been abraded. There are 19 specimens of this morphotype, and they all differ slightly in length and width.

4.5.4. Conodont morphotype 4

BRSUG 29372-866 (Fig. 5G) is poorly preserved, and might be an abraded version of morphotype 3. It lacks denticles. The base is pyramidal in side view. Three rows of irregular bumps extend



Fig. 5. Other material from Tytherington. (A) BRSUG 29372-14, tooth from *Thrinacodus ferox*. (B, C) Both BRSUG 29372-619, chimaeroid tooth fragments. (D–G) Conodont elements. (D) BRSUG 29372-1283, morphotype 1. (E) BRSUG 29372-1752, morphotype 2. (F) BRSUG 29372-613, example of morphotype 3. (G) BRSUG 29372-866, morphotype 4. (H) crinoid ossicle. (I, J) Trace fossils. (I) BRSUG 29372-1366, morphotype 2 and (J) BRSUG 29372-1117, morphotype 1. Scale bars are 1 mm.



Fig. 6. The faunal composition of microvertebrates from Tytherington fissure 2, showing proportions of identifiable remains based on all material (A), all material with reworked elements removed (B), and material from a single unit of red sandstone (C).

along the length of the specimen, one at each side and one in the centre line.

4.6. Other fossils

Many crinoid ossicles are visible in the surrounding Carboniferous limestone (Fig. 5H), and some have become mixed with the Late Triassic fissure fills. These isolated specimens are all treated as reworked.

Isolated trace fossils of two kinds are also identified. The first (Fig. 5I) is a tiny, straight structure with a roughened surface, little over 1 mm in total length and 270 μ m wide, and perhaps hollow. It is unclear whether this is a chance fragment of a burrow or boring and it may have broken from the Carboniferous limestone. A second trace fossil type (Fig. 5J) is curved and smooth-surfaced, some 1.5 mm long, and approximately 700 μ m wide. There are six examples.

5. Faunal composition, associations and discussion

The sphenodontian *Diphydontosaurus avonis* is the commonest faunal component, generally representing more than 50% of all identified specimens, whether with all material (Fig. 6A) or with reworked material excluded (Fig. 6B). *Clevosaurus* sp. is the second

most abundant sphenodontian (5–7%), followed by *Planocephalo-saurus* sp. (c. 1%). Among the sphenodontians, approximately 90% of specimens were identified as *D. avonis*, confirming earlier statements (Whiteside, 1983; Whiteside and Marshall, 2008). Of the archosaur teeth, 30% are certainly attributable to *Thecodontosaurus*, and some other archosaur morphotypes may be anterior mandibular or premaxillary teeth of this taxon, so it comprises minimally 2–3% of all material. Archosaurs as a whole comprise 6–8% of all identified specimens. Next in proportions come the teeth of bony fishes (5–7%), and then the sharks. Among the reworked material, holocephalians (probably chimaeroids) and conodonts dominate.

These proportions are similar to those noted by Whiteside and Marshall (2008, Fig. 17) as an average for fissure 2, although they found a higher percentage of *Clevosaurus* than in the current study of the horizon that yielded bones of *Thecodontosaurus*. Note that in our study and earlier studies, smaller remains may be undersampled; in the first half of the current study, the smallest sieve size was 425 μ m, and was only reduced to 250 μ m in processing the second half of the sediment sample. Therefore, conodonts and fishes are probably undersampled, but the other materials (sphenodontians, archosaurs, chimaeroids) should not have been affected.

A special count was made of the fossil content of an isolated block containing, unusually, clasts of Old Red Sandstone. This block

Table 1

The co-occurrence of contemporaneous vertebrate taxa with *Thecodontosaurus* and *Diphydontosaurus* from the rocks collected at the site of the discovery of *Thecodontosaurus* in fissure 2 at Tytherington. The probability of association by chance is shown as p, based on a Fisher exact two-tailed test using presence or absence between two taxa in a 2×2 contingency table. Total rocks sampled are 26.

	Diphydontosaurus present (rows 1 and 2) or Thecodontosaurus present (rows 3 and 4)	Archosaurs present	Clevosaurus present	Planocephalosaurus present	Contemporaneous fish present
Number of rocks where species present when <i>Thecodontosaurus</i> present	13	11	10	5	11
	<i>p</i> = 0.580	p=0.218	p=0.008	p=0.391	p=0.016
Percentage of species present when <i>Thecodontosaurus</i> present	92.9	78.6	71.4	35.7	78.6
Number of rocks where species present when <i>Diphydontosaurus</i> present	13	16	12	7	14
	<i>p</i> =0.580	p=0.268	p=0.225	<i>p</i> = 0.540	<i>p</i> = 0.085
Percentage of species present when Diphydontosaurus present	56.5	69.6	52.2	30.4	60.9

yielded 117 recognisable microvertebrate specimens, about onetenth of all the Tytherington material in this study. This rock contains specimens of every group of microvertebrates found at Tytherington, except sharks (although only 1 specimen in total is recorded from all samples) and *Planocephalosaurus* (only 10 specimens recorded from all samples). The faunal composition of this single sample (Fig. 6C) is similar to the overall samples, but with a decrease in proportions of fish teeth (from 6% to 3%) and the absence of *Planocephalosaurus*.

As most of the Tytherington material investigated here pertains to the sphenodontian *Diphydontosaurus avonis*, an attempt was made to document size variation in the population using width measurements of the frontal bone. Of the 17 *Diphydontosaurus* frontals in the collection, 12 could be measured. These showed a range in minimum interobital width from 1.2 to 1.6 mm, with a continuous distribution (not illustrated) and no apparent jumps in size. This measure therefore provides no evidence for age classes or sexual dimorphism.

Our sampling allows us to explore associations between the Late Triassic taxa (Table 1). *Diphydontosaurus* is recorded from 23/26 or 88.5% of all rock samples. Also *Diphydontosaurus* co-occurs nearly 93% of the time when *Thecodontosaurus* is present and in 100% of the samples when *Clevosaurus* or *Planocephalosaurus* are found (Table 2). Although these co-occurrences are strikingly high and above expected, they are not statistically significant, as sample sizes are too small and perhaps also because *Diphydontosaurus* predominates in the vast majority of rocks. It is noteworthy that *Thecodontosaurus* is present at Tytherington, and that both genera co-occur at Durdham Down (Whiteside, 1983), yet no other sphenodontians occur at that locality (*contra* Whiteside, 1983; Whiteside and Marshall, 2008).

The co-occurrences between the contemporaneous fish and the large *Thecodontosaurus*, and the small *Clevosaurus* are highly significant positive associations using the Fisher exact test (Tables 1 and 2). This suggests that there may have been an association in life between *Thecodontosaurus* and *Clevosaurus*, even though sampling of the living community has been modified by water transport. The statistically significant grouping of medium-sized and small reptile fossils suggests that smaller elements of larger reptiles, if present, should have been found in our sampling. There are also statistically significant positive associations between *Clevosaurus* and other archosaurs, *Planocephalosaurus* and *Clevosaurus*, and other archosaurs and contemporaneous fish (Table 2). The reptile/fish associations suggest that surface water was available on the limestone when the animals were present, and that these waters transported their bones into the fissures during floods.

There is a relatively low co-occurrence of Planocephalosaurus with either Thecodontosaurus or Diphydontosaurus (Table 1), and none of these associations is significant using the Fisher exact test. These comparisons are of interest as Diphydontosaurus and Planocephalosaurus are the smallest reptiles found, suggesting that the low co-occurrence cannot simply be attributed to sorting through water transport. Planocephalosaurus is common at Cromhall, where Diphydontosaurus is rarer, and the genus has not been recorded with Thecodontosaurus or Diphydontosaurus at Durdham Down. Also, considering Tytherington fissures 4 and 14 from Whiteside and Marshall (2008, Fig. 17), it is clear that where Planocephalosaurus is abundant Diphydontosaurus is rare. If these fissures are coeval, it seems that Diphydontosaurus and Planocephalosaurus were either ecological competitors tending to exclude each other, or had preferences for different habitats on the palaeoisland (Whiteside and Marshall, 2008), and so were less frequently transported together to deposition.

There is also a significant positive association between *Diphydontosaurus* and the reworked chimaeroid fossils

he co-occurrence and probab ccurs with the first (upper ro re 26.	vility of association betv w) and the probability c	ween various reptile taxa a of association by chance (l	nd contemporaneous fi ower row). This is basec	sh from hssure 2 at Tytherin I on a Fisher exact two-tailed	gton. The two figures b I test using presence or	eneath each species name absence between two tay	e represent the percentage c ta in a 2 × 2 contingency tal	if the second taxon that ile. Total rocks sampled
Taxa	Clevosaurus/	Planocephalosaurus	Other archosaurs/	Clevosaurus	<i>Clevosaurus</i>	Planocephalosaurus/	Planocephalosaurus/	Planocephalosaurus/
	Diphydontosaurus	Diphydontosaurus	Diphydontosaurus	/Contemporaneous fish	/Other archosaurs	Clevosaurus	Contemporaneous fish	Other archosaurs
Percentage co-occurrence	100	100	94.1	91.7	91.7	85.7	85.7	85.7
Probability of association	0.225	0.540	0.268	0.0005	0.015	0.009	0.081	0.357
Taxa	Clevosaurus/	Other archosaurs/	Planocephalosau	rus/ Other archosaurs/	Other archosaurs,	Clevosaurus/	Other archosaurs/	Chimaeroids/
	Thecodontosaurus	Contemporaneous fisl	1 Thecodontosauru	is Thecodontosaurus	Clevosaurus	Planocephalosaurus	Planocephalosaurus	Diphydontosaurus
Percentage co-occurrence	83.3	82.4	71.4	64.7	64.7	58.3	35.3	95.7
Probability of association	0.008	0.038	0.391	0.218	0.015	0.009	0.357	0.027

Table

(p = 0.027; Table 2), though associations between the terrestrial fauna and other reworked fossils are not significant. It is likely that the chimaeroid fossils were weathered out of the limestone in the locality where the *Diphydontosaurus* lived and all remains were transported together.

The Bristol fissures, including Tytherington, sample only a certain number of the major Late Triassic tetrapods. There are no temnospondyls, rhynchosaurs, dicynodonts, or plateosaurid sauropodomorphs (e.g. Plateosaurus), and phytosaurs and aetosaurs are rare, being represented only by Rileyasuchus from Durdham Down (Benton et al., 2000) and a probable aetosaur scute from Cromhall (Fraser, 1988c), which was later identified as Aetosaurus by Lucas et al. (1999). These are all larger animals, and perhaps more associated with damp low-lying areas. Robinson (1971) characterised the fissure faunas as coming from 'upland' areas, as opposed to the more usual finds of 'lowland' animals in the sediments of Late Triassic lakes and rivers. This distinction between habitats is unclear, however: the fissures formed in karst on islands, and so these were not uplands, but simply distinct from marginal, vegetated areas. The larger vertebrates just noted are probably absent for one of four reasons, or a combination: (1) the animals were present only on mainlands; (2) the animals lived in open, damp areas; (3) the animals were too large for any part of their carcasses to fit into the vertical portions of the fissures (although Thecodontosaurus is as large as many of them, and carcasses were likely broken down before entering the fissures); and (4) several of these groups were much diminished in diversity by Rhaetian times, and this includes the already extinct rhynchosaurs, and the dicynodonts, despite an isolated find from Poland (Dzik et al., 2008). Our evidence, based on the faunal associations discussion above, suggests that (2) and (3) are much less likely reasons.

The absence of cynodonts and mammals from Tytherington and nearly all other Triassic fissures (see Fraser et al. (1985) for the discovery of mammals at Emborough) is more surprising perhaps because these clades included small animals, in the size range of the immensely common sphenodontians. Further, mammals such as *Kuehneotherium* and *Morganucodon* as well as tritylodonts such as *Oligokyphus* are relatively common in the Lower Jurassic fissures (Kühne, 1956; Savage and Waldman, 1966; Savage, 1971; Kermack et al., 1973, 1981). In light of the intensive search for such remains, presumably these animals, although well known from Late Triassic, including Rhaetian, deposits elsewhere, were absent from the north Bristol archipelago until after the end-Triassic mass extinction.

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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.2012.05.003.

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