



Vertebrates from the Late Triassic *Thecodontosaurus*-bearing rocks of Durdham Down, Clifton (Bristol, UK)



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ABSTRACT

Since the discovery of the basal sauropodomorph dinosaur *Thecodontosaurus* in the 1830s, the associated fauna from the Triassic fissures at Durdham Down (Bristol, UK) has not been investigated, largely because the quarries are built over. Other fissure sites around the Bristol Channel show that dinosaurs represented a minor part of the fauna of the Late Triassic archipelago. Here we present data on microvertebrates from the original Durdham Down fissure rocks, which considerably expand the taxonomic diversity of the island fauna, revealing that it was dominated by the sphenodontian *Diphydontosaurus*, and that archosauromorphs, including sphenosuchian crocodylomorphs, coelophysoid theropods, and the basal sauropodomorph *Thecodontosaurus*, were diverse. Importantly, a few fish teeth provide new information about the debated age of the fissure deposit, which is identified as lower Rhaetian. *Thecodontosaurus* had been assigned an age range over 20–25 Myr of the Late Triassic, so this narrower age determination (209.5–204 Myr) is important for studies of early dinosaurian evolution.

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1. Introduction

The Late Triassic palaeogeography of the region around Bristol and South Wales (UK) consisted of an archipelago of small limestone islands lying in or near the tropics (Fig. 1A; Robinson, 1957; Whiteside and Marshall, 2008). Well-documented terrestrial vertebrate faunas from these fissure fills have been found in many limestone quarries of the area, some such as Cromhall (Fraser, 1994) and Tytherington (Whiteside, 1983; Whiteside and Marshall, 2008; Van den Berg et al., 2012) near Bristol (Fig. 1A), and Pant-y-ffynon (Galton et al., 2007) in South Wales. The first vertebrate fossils to be documented from these fissure fills were 'saurians' from Durdham Down in Bristol, named *Thecodontosaurus* by Riley and Stutchbury (1836), and with the species name *T. antiquus* added later (Morris, 1843).

Some additional taxa were reported from the Durdham Down fissure deposits. Riley and Stutchbury (1836, 1840) identified two species of their new genus *Palaeosaurus*, namely *P. cylindrodon* (= *Palaeosauriscus* Kuhn, 1959) and *P. platyodon* (= *Rileyasuchus* Kuhn, 1961), both of which are now considered *nomina nuda* (Benton et al., 2000; Galton, 2007). The first was based on a single

tooth that was destroyed in 1940 during the Second World War and it is now considered *Archosauria incertae sedis*, thus *nomen dubium* (Benton et al., 2000, 2012; Galton, 2007; Benton, 2012); the latter was originally represented by a heterodont phytosaur posterior tooth to which other undiagnostic material was added, and it is also considered invalid (Benton et al., 2000, 2012; Galton, 2007; Benton, 2012). Halstead and Nicoll (1971) incorrectly identified an articulated limb of the sphenodontian *Clevosaurus* from Durdham Down; the specimen is actually *Diphydontosaurus* (Whiteside, 1983; Whiteside and Marshall, 2008). The occurrence of *Clevosaurus* at Durdham Down has, in fact, never been confirmed; reports of its presence by Whiteside (1983) and Whiteside and Marshall (2008) were contradicted by Van den Berg et al. (2012), as the evidence was poor.

Historical materials from Durdham Down are in the collections of Bristol City Museum, the Natural History Museum, London, Yale Peabody Museum, and the National Academy of Sciences in Philadelphia (Benton, 2012). We have had the unique opportunity to acid prepare a representative sample of these original *Thecodontosaurus*-bearing rocks, collected in the 1830s from the quarries at Durdham Down, and can therefore for the first time make a detailed analysis of its poorly known microvertebrate fauna; moreover, we mechanically prepared and re-described controversial material from the historical collection. In this paper, we present the first extensive study on the microvertebrate fauna

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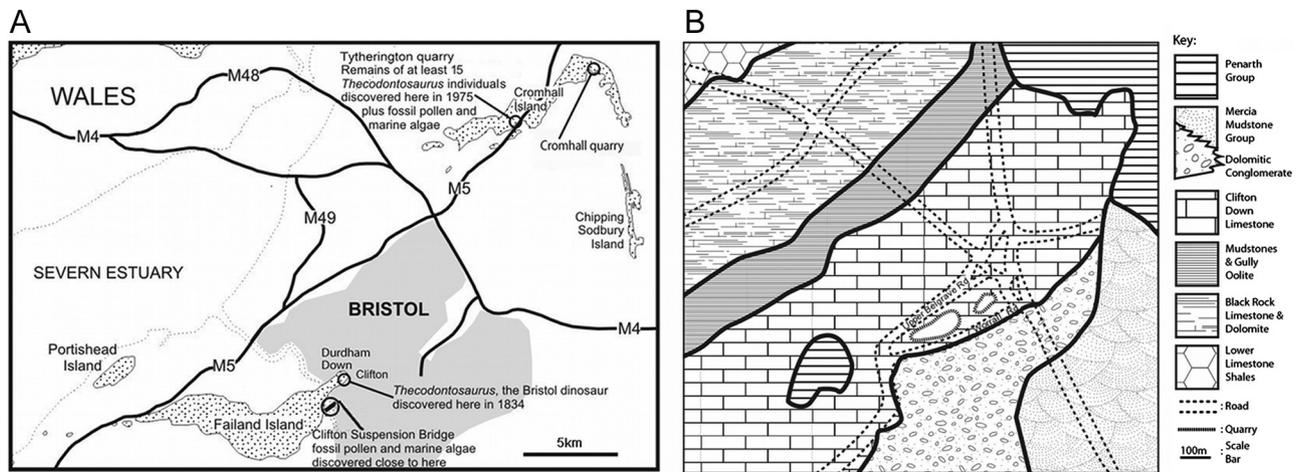


Fig. 1. Geology of Durdham Down fissure. (A) Palaeogeographical map of the Bristol area in the Late Triassic (205 Ma) showing inferred palaeo-highs with superimposed modern geography. (B) Simplified geological map of Durdham Down, with 19th century quarry locations. Geology mapping and column derived from BGS map 264. The Dolomitic conglomerate, Mercia Mudstone Group and Penarth Group are Late Triassic. The other strata are Early Carboniferous.

of the Durdham Down fissures to provide an overview of all identifiable fossils, to reconstruct the contemporary ecosystem in which the early dinosaur *Thecodontosaurus* lived, and to date the fauna. *Institutional abbreviations:* BRSMG, Bristol City Museum & Art Gallery collection; BRSUG, Bristol University, School of Earth Sciences collection.

2. Geological and palaeoenvironmental setting

The Durdham Down quarries in Clifton were exploited for the extraction of Carboniferous Limestone, which was used as a building material. When quarrying ended about 1840, the quarries were filled and/or became building sites; for this reason, the exact location of the fissure deposits of the 1830s cannot be certain. The *Thecodontosaurus* bones collected in the 1830s, and now in BRSMG, could have come from anywhere in the string of quarries between Worrall Road to the south, and Upper Belgrave Road to the north (Fig. 1B). No contemporary documents survive, but the sum of eyewitness accounts, and reported eyewitness accounts, was summarised in Benton et al. (2000), Galton (2007), and Benton (2012). The best surviving quarry wall, with a Triassic-age fissure cutting down into the Carboniferous Limestone is at the east end of the series of quarries, beside Quarry Steps, and this was designated as a Site of Special Scientific Interest (Benton and Spencer, 1995). Further evidence that this is the most likely location was established by a team from the Bristol Dinosaur Project, who found *Thecodontosaurus* and *Diphyodontosaurus* fossils in a collection of rocks from walls around the old quarry.

As in many similar sites in the SW of Great Britain, karstic features such as fissures and cave systems developed in the uplifted and steeply dipping Carboniferous limestones. The infills of the cavernous voids frequently contain fossils, following cavern collapse and meteoritic waters washing lateritic soil and limestone debris, including blocks of unaltered Carboniferous limestone, into these cavities. The fossil-bearing rock contains layers of conglomerate with grey Carboniferous limestone clasts and sandy limestone ranging in colour from red to pale ochreous yellow. Despite analysing all available historical documents, we cannot be sure of the relationships and succession of the layers from which the rocks derive. However, we can analyse the relative quantities of fossils from a range of rocks to discover the faunal composition and associations of these deposits. The age of the Durdham Down deposits has been a matter of debate. The fissure deposits around Bristol and in South Wales are generally dated to the Late Triassic–Early Jurassic (Robinson, 1957; Whiteside, 1986; Savage, 1993;

Fraser, 1994; Benton and Spencer, 1995; Whiteside and Marshall, 2008), but exact dating has been possible only for Tytherington. That age assignment is based principally on the association of Rhaetian palynomorphs and marine phytoplankton with *Thecodontosaurus* and/or other reptiles in six fissures including fissure 2 at Tytherington quarry, described by Marshall and Whiteside (1980) and Whiteside and Marshall (2008), who also reported an association of the terrestrial reptiles with fish fossils found in the Penarth Group, particularly the Westbury Formation (lower Rhaetian). Whiteside and Marshall (2008) also argued that there was no evidence that these Late Triassic fissure faunas are older than the Rhaetian transgression, through a comparison of the terrestrial faunas, Penarth Group fishes and geological field relations. Currently, the consensus is that the Durdham Down *Thecodontosaurus*-bearing deposits can be dated as Rhaetian (Whiteside, 1983; Galton, 2007; Benton, 2012) based on the conspecific *Thecodontosaurus* remains from fissure 2 at Tytherington.

This has not always been the view, and it is often assumed that *Thecodontosaurus* is Carnian in age, some 20–25 Myr older than the early Rhaetian. This discrepancy in age is significant because *Thecodontosaurus* is phylogenetically a basal sauropodomorph dinosaur, and the earlier date provides a different pattern of timing for this part of the dinosaur phylogenetic tree. The Carnian age was assumed early: for example, Moore (1881) did report ‘Rhaetic’ bone bed fossils from the quarry at Durdham Down, but decided that the *Thecodontosaurus* bones were more likely considerably older, equivalent to Carnian. Robinson (1957) viewed faunas from these types of fissure as Norian, and this view was followed by Benton (1991), who presented the time range of Thecodontosauridae as late Carnian to Rhaetian. Benton and Spencer (1995) noted the similarity of *Thecodontosaurus* from Durdham Down with materials from Tytherington, and its early Rhaetian age, but further noted also the phylogenetically basal position of the genus among sauropodomorphs, and so hinted at a late Carnian age. Benton et al. (2000) also tentatively suggested a late Carnian or early Norian age. Tanner et al. (2004) stated that the Thecodontosauridae (including *Thecodontosaurus*) had become extinct before the Rhaetian, and Lucas (2010) suggested that some of the fissure fills, including Durdham Down, could be as old as Carnian.

Counter-evidence came from the similarity of *Thecodontosaurus* materials from Durdham Down and Tytherington, already dated as early Rhaetian, and from palynomorphs and fish remains reported by Whiteside and Marshall (2008) from a fissure near the Clifton Suspension Bridge, 1.5 km from Quarry

Steps. These are representative of the Westbury Formation, Penarth Group, dated as lower Rhaetian. However, as no Rhaetian-age related fossils have been reported within the Durdham Down deposits, the dating is so far unconfirmed. The fish and marine phytoplankton associations from Tytherington suggested to Whiteside and Marshall (2008) that *Thecodontosaurus* lived on a small island with the sea nearby. Van den Berg et al. (2012) reported that there is a statistically highly significant association between *Thecodontosaurus* and Rhaetian fish, providing strong evidence that there was surface water at the time that the dinosaurs lived on the Tytherington palaeo-island. Whiteside and Marshall (2008) also regarded the Durdham Down *Thecodontosaurus* and associated terrestrial fauna as living on a separate, but nearby, Rhaetian island (termed the 'Failand' palaeo-island by J.E.A Marshall; see Fig. 1A). In the current analysis we have looked for evidence that could corroborate or negate this hypothesis.

3. Materials and methods

3.1. Rocks

This study is based on five samples of fissure rocks from Durdham Down, donated by the BRSMG, including the original 1834 collection (Riley and Stutchbury, 1836). Small blocks were removed from the rocks containing the original *Thecodontosaurus* materials, taking care not to damage the dinosaur bones. The samples weighed 7503 g altogether, and 1872 g of residue was treated. We also report materials from an additional rock associated with *Diphydontosaurus* from the Durdham Down collection studied by DIW during his Ph.D. thesis work.

The fossil-bearing rocks consist of breccias and conglomerates that include unchanged Carboniferous Limestone clasts (see Fig. 7B) and other clasts formed of hardened dolomitised limestone. The rock is frequently stained ochreous yellow or brown with limonite (e.g. Fig. 6A–D). This metasomatically changed matrix is observed attached to the fossils (Fig. 3A–C, G, H, M–O) and has also resulted in colouring of the fossils themselves (Fig. 3D and E). The Durdham Down rocks and their fossil preservation is strikingly similar to those at Tytherington reported by Whiteside and Marshall (2008) and this extends to specific sedimentological features such as aggregated ooids (Fig. 5D). This similarity in lithologies suggests that the Tytherington and Durdham Down fissures had similar or the same palaeoenvironment at infilling.

3.2. Processing

The processing consisted of ten cycles of acid digestion, neutralisation in water and sieving. Before starting acid preparation, each rock was weighed and checked for visible fossils that, if found, were stabilised with a 15–20%, Paraloid™ B-72 solution; this procedure has the double aim to protect the fossil both from chemical digestion and from physical damage during the later phases of the process. Once dry, the rocks were digested for 48–60 h in a 5% acetic acid solution buffered with tri-calcium orthophosphate to prevent further digestion of uncovered fossil material. The next step consisted of carefully cleaning the samples by rinsing in warm and cold water. The residue was also cleaned and collected by running water through a 75 µm sieve. Both sediment and rocks were then left in water for twice as long as the acid digestion (normally four days). A drop of soap was added in order to neutralise any residue of acid. Afterwards, the residue was sieved and the rock checked and then submitted to a new cycle of acid preparation. Five sieve meshes were adopted to collect the residue: 1400 µm, 710 µm, 425 µm, and 250 µm, to which a

75 µm sieve was added during the fourth cycle specifically for finding fish teeth, which could be useful for dating, as well as amber; the different mesh sizes provided a first-dimension classification. The residue was collected and left to dry in filter paper on funnels and once dried collected into plastic boxes, where rock of origin, mesh size and sieving date were recorded. At the end of the ten acid cycles, a few specimens were still embedded in the rock and were mechanically prepared with the fossil preparation facilities in the Palaeobiology Laboratory at the University of Bristol.

3.3. Identification and photography

Every fossil was hand picked under a stereoscopic microscope in a standard picking tray and placed into small plastic boxes. They were broadly classified into morphotypes and stored in receptacles between two layers of Plastazote® LD15 padding (Viegas and Clapham, 2012). Each specimen was individually identified at some taxonomic and/or anatomical level through comparisons with the literature, and labelled with all the information necessary for sound conservation (rock of origin, sieving date, picking date, identification, picker initials).

Multifocus photographs of the most representative specimens were taken using the photography tool on a Leica M205C microscope; processing and merging of the stack of pictures was automatically done using the software Leica Application Suite – LAS v3.7. We used one magnification, 4.58 × 10, for most of the specimens; only a few archosauromorph and larger sphenodontian specimens required a lower magnification. In order to obtain the best quality, each photograph was adjusted in terms of brightness, gamma and saturation, before and after the final picture was produced. Optimal contrast was achieved by arranging the pictures on a black uniform background.

The micrographs in Fig. 5 were obtained by fixing the specimens to double-sided sticky tape and placing them in the scanning electron microscope without any coating.

3.4. Fossils

The fossils of the Durdham Down fissures are typically disarticulated, and very fragmented and the colouration spans from dark brown, red-pink to yellow, without any discernible pattern for the type of animal, or anatomical part. Of 225 residue boxes, 107 specimens were identified at some taxonomic or anatomical level. Unsurprisingly, most of the acid-digested residue is bone shards; among the identifiable finds, most are teeth. Sphenodontian and *Thecodontosaurus* teeth show characteristic shapes, and different taxa could be identified. Only occasionally could postcranial material be anatomically identified and very seldom taxonomically.

4. Systematic palaeontology

4.1. Sphenodontians

4.1.1. *Diphydontosaurus*

Eighteen teeth and jaw fragments were assigned to *Diphydontosaurus*. They span the uniquely peculiar dentition of the taxon, which is pleurodont anteriorly and acrodon posteriorly on both the maxilla and the dentary. The first condition is unique among sphenodontians, while the latter is a shared feature of all Sphenodontidae (Whiteside, 1986). The *Diphydontosaurus* premaxilla bears five to seven small pleurodont teeth, round in cross section (Fig. 2A–E); anterior maxillary teeth are also pleurodont (not figured). Caudad to these are the acrodon teeth that show characteristic size alternation (4–9 depending on the specimen)

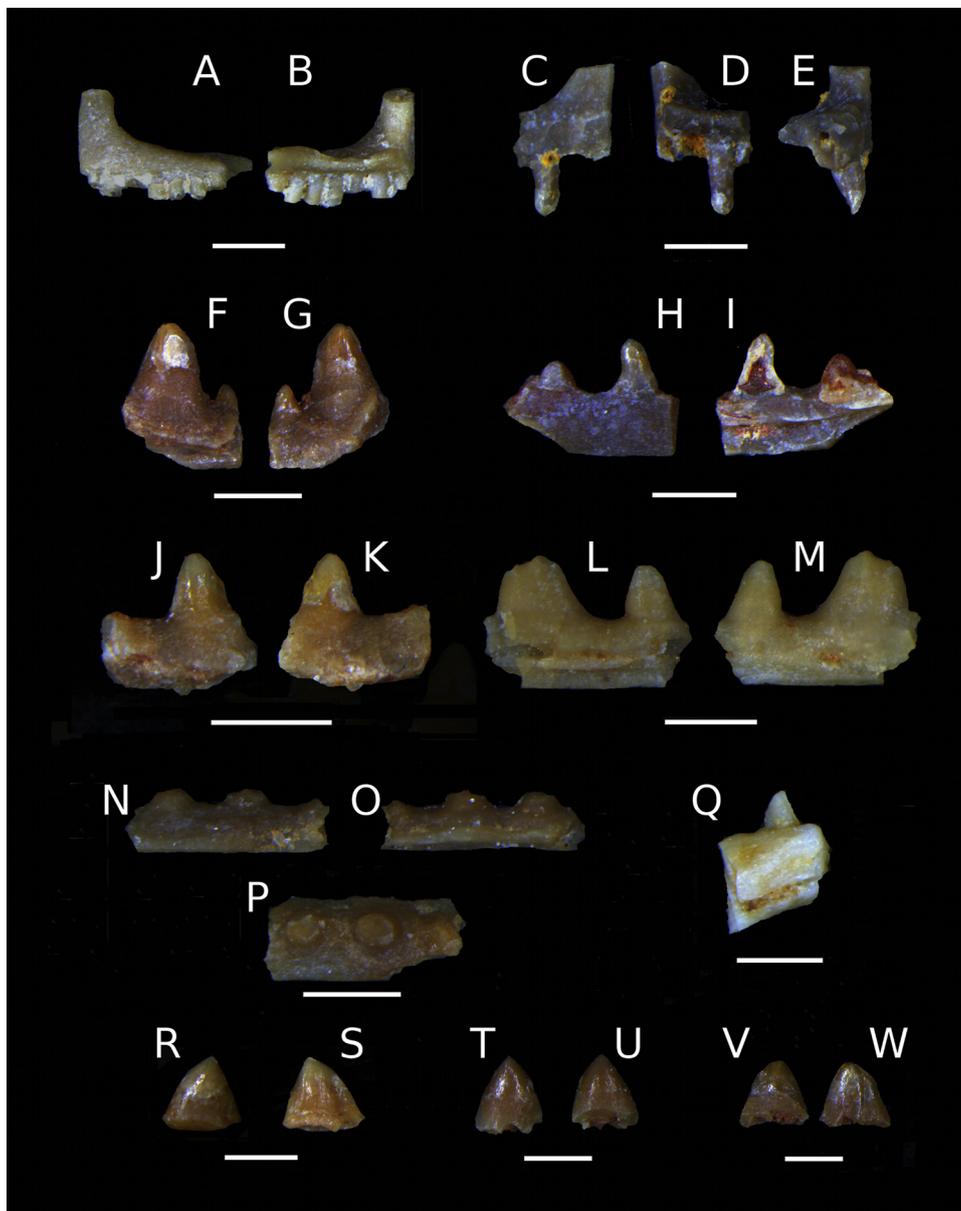


Fig. 2. *Diphydontosaurus* jaws and teeth from Durdham Down. (A and B) BRSMG Cb4277.2, left premaxillary fragment, in anterior (A) and posterior (B) views; (C–E) BRSMG Cb4213.1, right pre-maxillary fragment in anterior (C), posterior (D) and lateral (E) views; (F and G) BRSMG Cb4277.7 right maxillary fragment with small tooth on the lingual side, in labial (F) and lingual (G) views; (H and I) BRSMG Cb4277.1, dentary fragment; (J and K) BRSMG Cb4277.8, dentary fragment; (L and M) BRSMG Cb4277.4, dentary fragment; (N–P) BRSMG Cb4277.14, toothed palatal bone fragment; (Q) BRSMG Cb4196.1, isolated dentary fragment; (R and S) BRSMG Cb4277.3, isolated dentary acrodon tooth; (T and U) BRSMG Cb4277.5, isolated dentary acrodon tooth; (V and W) BRSMG Cb4277.9, isolated dentary acrodon tooth. Scale bars equal 500 μm .

with the smaller ones growing on the lingual side (Fig. 2F and G). A few further fragments (Fig. 2H–Q) of tooth-bearing bones were found, but their fragmentary nature makes it difficult to clearly identify their anatomical position; it was only possible to recognise a dentary fragment bearing two teeth (Fig. 2L and M) and a palatal fragment still carrying three rounded and worn teeth (Fig. 2N–P). Some single teeth were also found (Fig. 2R–W), showing a variety of shapes ranging from sharp triangular and laterally compressed to stout and conical; these teeth have wear facets caused by occlusion which are the same as in *Diphydontosaurus* dentaries found in the BRSUG Tytherington collection.

4.1.2. *Clevosaurus*

Incontrovertible evidence of *Clevosaurus* at Durdham Down is given by the incomplete right ramus of a lower jaw (Fig. 3A–C). One tooth, the most posterior on the dentary, was recovered before

damage occurred during mechanical preparation; a significant enamel layer is visible and still covers the surface of the tooth (Fig. 3B). In order to prevent further damage to the rest of the mandibular ramus, it was decided to leave it in the matrix. A second, heavily worn posterior tooth was picked from the residue and it is here assigned to *Clevosaurus* based on the peculiar lateral outline (Fig. 3D–F). *Clevosaurus* posterior dentary teeth show a unique round and stout morphology with a characteristic lateral profile with large posterior cusp (Fraser, 1988; Säilä, 2005; Van den Berg et al., 2012).

4.1.3. ?*Planocephalosaurus*

The last sphenodontian tooth (Fig. 3G and H) shows affinity with *Planocephalosaurus*. The tooth is acrodon and falls both into the size range of *Diphydontosaurus* teeth but also in the lowest range of *Planocephalosaurus*; however it differs from *Diphydontosaurus* teeth as it has more developed striations on both sides of the

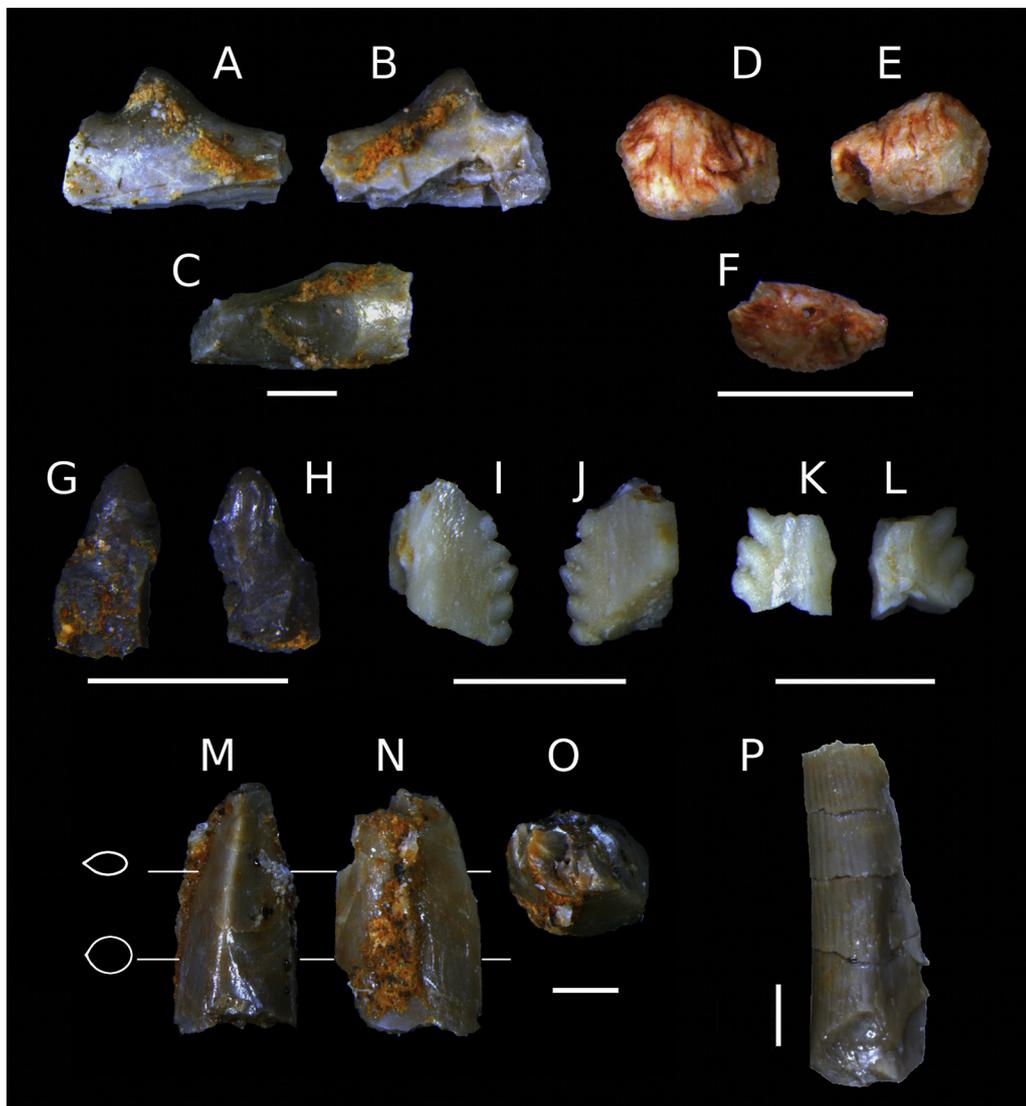


Fig. 3. Sphenodontian and archosauromorph isolated teeth from Durdham Down. (A–C) BRSMG Cb4196.2, *Clevosaurus* posterior dentary tooth; (D–F) BRSMG Cb4196.3, *Clevosaurus* worn tooth; (G and H) BRSMG Cb4213.2, *Planocephalosaurus?* acrodont tooth; (I and J) BRSMG Cb4195.2, *Thecodontosaurus* tooth fragment; (K and L) BRSMG Cb4196.4, *Thecodontosaurus* tooth fragment; (M–O) BRSMG Cb4261.1, '*Palaeosaurus*' tooth; (P) BRSMG Cb4196.5, '*Palaeosaurus*' tooth. Scale bars equal 1 mm.

crown. It does not match the range of morphology in *Clevosaurus*. The tooth is conical with an occlusion mark only on the lingual side, resembling the tooth from the middle section of the maxilla of *Planocephalosaurus* (cf. Fraser, 1982, pl. 69, fig. 4).

4.2. Archosauromorphs and others

Archosauromorph teeth are much rarer in the Bristol fissures than those of sphenodontian lepidosauromorphs, but they can be distinguished by their thecodont implantation, whereas the sphenodontians are acrodont or distinctively pleurodont. Sphenodontian acrodont teeth also have distinctive wear facets that often extend to the bone, because the maxillary and dentary teeth shear against each other; such wear facets are not found on archosauromorph teeth. Archosauromorph crowns are conical or mediolaterally compressed; the tooth crowns frequently display anterior and posterior, or only posterior, keels, distinctly serrated or with small denticles. However, it should be noted that these features, which are not infrequently lost and modified among archosaurs, have also been reported in non-archosaurian taxa (Godefroit and Cuny, 1997; Heckert, 2004). Other features that distinguish archosauromorphs from Triassic sphenodontians

include the universally amphicoelous vertebrae of the latter, in contrast to the platycoelous (e.g. *Terrestriusuchus*, Crush, 1984) or amphiplatyan centra of archosaurs.

4.2.1. *Thecodontosaurus*

The *Thecodontosaurus* dentition is highly characteristic and well documented from the Bristol and Tytherington fissures (e.g. Benton et al., 2000, fig. 3; Whiteside and Marshall, 2008, fig. 5i; Van den Berg et al., 2012, fig. 3A and B) and the teeth described here were found in blocks that had produced *Thecodontosaurus* bones. The teeth are leaf-shaped, laterally compressed, and with a serration pointing from the root to the tip of the tooth (Riley and Stutchbury, 1840; Benton et al., 2000; Galton, 2007; Van den Berg et al., 2012). Two shards, preserving the diagnostic lateral serration, were found (Fig. 3I–L).

4.2.2. Archosauromorph A

BRSMG Cb4277.15 is a fragment of a small and single finely serrated tooth; the serration is damaged and it is preserved only on one side of the shard. Considering the preservation, assigning it to any of the morphotypes in Van den Berg et al. (2012) is difficult.

4.2.3. *Phytosauridae* indet

Two large teeth (Fig. 3M–P) do not belong to any of the previously mentioned taxa. They both well exceed a diameter and height of 1 mm; unfortunately damage makes identification difficult. The first one, BRSMG Cb4261.1 (Fig. 3M–O), is a large tooth that is missing the tip; it has a stout, nearly round cross-section at the base, which gradually becomes more laterally compressed towards the tip; the crown shows a very faint base-apical striated ornamentation, bears a single well developed flange and lacks visible denticles. These characters are unfortunately insufficient for any kind of certain identification, although its stoutness, dimension, ornamentation and cross section strongly recall the anterior maxillary dentition of a heterodont phytosaur in the figures and descriptions of Godefroit and Cuny (1997), Heckert (2004) and Hungerbühler (2000). The second tooth, BRSMG Cb4196.5 (Fig. 3P), is less stout but also large. It is missing the tip and was found in four pieces; approximately one third of its cross-section is preserved. It is a long, conical-oval and slightly curved tooth with a vertical striated ornamentation running along its entire preserved length; a faint serration can be discerned on one side. Given this peculiar combination of features, it does not

match any morphotypes described by Van den Berg et al. (2012). The ornamentation and dimension of the tooth suggests it belongs to an archosauromorph. The lateral ornamentation resembles that depicted in an unclear hand drawing of '*Palaeosaurus*' *cylindrodon* (Riley and Stutchbury, 1836, 1840); the specimen was destroyed in World War II. However, we can identify this tooth as deriving from the anterior-middle premaxilla of a heterodont phytosaur by its size, serrations, lack of strong curvature, sub-circular cross section and widely spaced longitudinal striations.

Heterodont phytosaurs can show significant variation along the tooth row which includes striated, unstriated, flanged, unflanged, recurved and relatively straight teeth in genera such as the Norian *Nicrosaurus* (Hungerbühler, 2000). As shown by Hungerbühler, *Nicrosaurus* teeth can also have unserrated or serrated carinae with a varying degree of denticle density on the mesial and/or distal surfaces. A similar variety of teeth have been recorded at the Norian/Rhaetian deposits of St Nicolas-de-Port in France and assigned to an indeterminate heterodont phytosaur by Godefroit and Cuny (1997). However, phytosaur fossils from this locality were also assigned to the Rhaetian *Angistorhinopsis ruetimeyeri* by Sigogneau-Russell and Hahn (1994). Kimmig and Arp (2010) refer

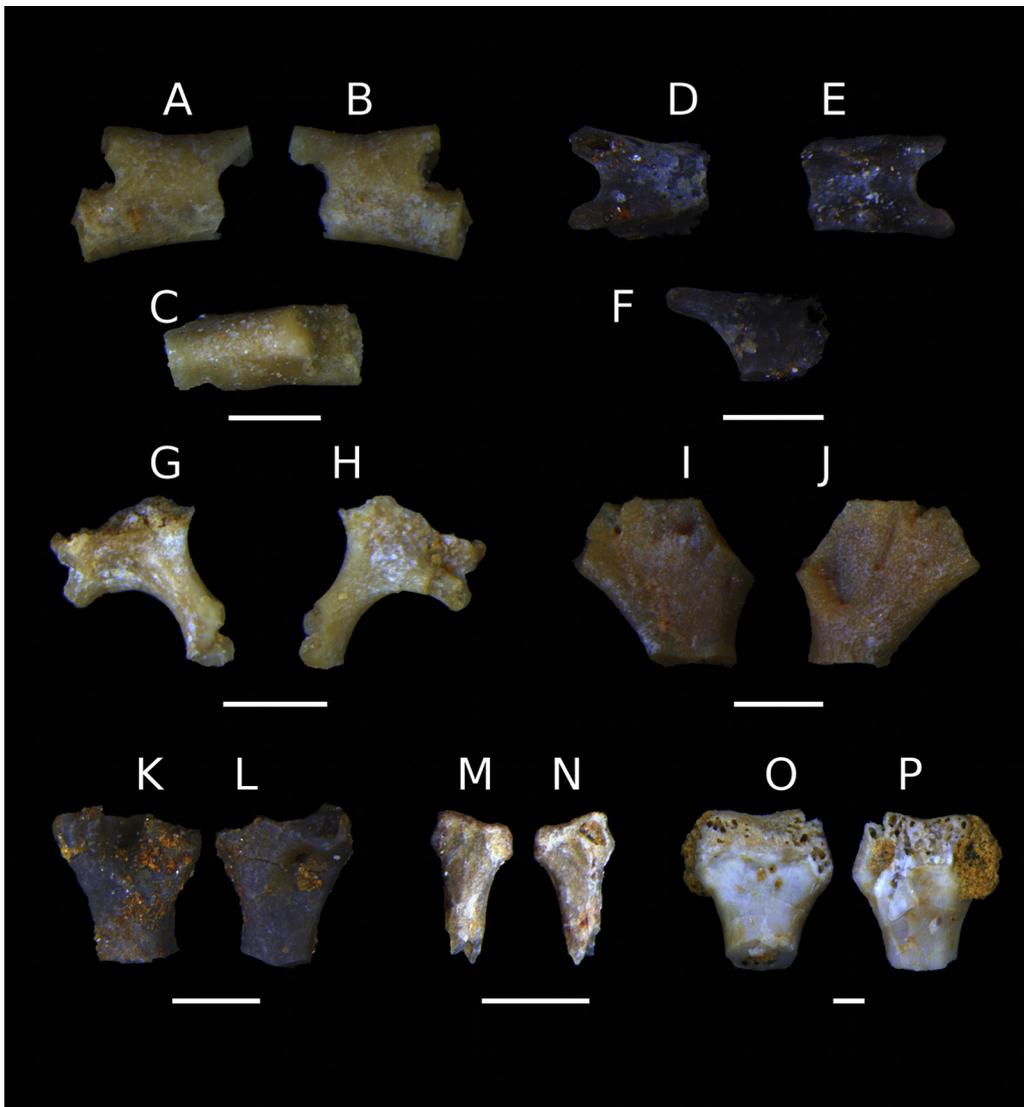


Fig. 4. Sphenodontian postcranial remains from Durdham Down. (A–C) BRSMG Cb4277.16, sphenodontian caudal vertebra; (D–F) BRSMG Cb4277.3, caudal vertebral arch; (G and H) BRSMG Cb4261.2, fragment of pterygoid? from a small sphenodontian; (I and J) BRSMG Cb4277.18 palatal bone, probably palatine; (K and L) BRSMG Cb4277.21, basipterygoid process of the parabasisphenoid; (M and N) BRSMG Cb4277.20 proximal end of metapodial of small sphenodontian; (O and P) BRSMG Cb4196.8 distal end of phalanx of larger sphenodontian e.g. *Clevosaurus*? Scale bars equal 500 μm .

to 'Nicrosaurus-like' or *Angistorhinopsis ruetimeyeri* fossils from the late Norian-Early Rhaetian of Germany and Switzerland. The first tooth from Durdham Down resembles the indeterminate phytosaur genus or *Angistorhinopsis* from St Nicholas-de-Port and also type 1 of Hunt (1994) (in Heckert, 2004) which is a *Nicrosaurus*-like maxillary tooth in comparison with Hungerbühler (2000). The second tooth, particularly with the putative serrated carina, fits an anterior-mid premaxilla position in the same or similar genus.

A posterior tooth originally named *Palaeosaurus platyodon* (Riley and Stutchbury, 1836), and later identified as that of a phytosaur (Huene, 1908a), was later considered a nomen dubium, as noted earlier. Our findings however, provide further evidence that a heterodont phytosaur was present at Durdham Down. Whiteside and Marshall (2008) also reported a Rhaetian '*Palaeosaurus*' tooth from Tytherington, very similar to '*P. platyodon*' and which has a distinct serrated carina, but otherwise resembles BRSMG Cb4261.1, and may also belong to a heterodont phytosaur. Overall, our analysis of the specimens from Durdham Down indicates similarities to a *Nicrosaurus*-like heterodont phytosaur but assignment to that genus is uncertain. We therefore refer these teeth to Phytosauridae indet.

4.3. Other microfossils

Among other fossils, the most common finds are 11 incomplete vertebrae (Fig. 4A–F), cranial elements (Fig. 4G–J), ten bone epiphyses, mostly metapodials and phalanges (Fig. 4N–Q) and twelve diaphyses. The latter specimens come in various dimensions and shapes, but the lack of epiphyses prevents more precise identification. There does not seem to be any preferential preservation of one kind of bone compared to the others. The variety of fragmented bones and long bone shafts of different shapes and dimensions emphasises the range of taxa in the samples.

4.3.1. Vertebrae

Probably the best preserved of these specimens is a caudal vertebra, with a neural arch and amphicoelous centrum (Fig. 4A–C), which is of the same morphology and size as the posterior tail bones of a small sphenodontian such as *Diphydontosaurus*. Referencing the descriptions, figures and plates in Whiteside (1983) we attribute these specimens to that genus. The second vertebral element is a partial neural arch (Fig. 4D–F). The bone lacks any transverse processes, but has two articular processes on the long axis. Given the fragmentary state of the fossil and the lack of any diagnostic features, a precise taxonomic identification cannot be provided.

4.3.2. Cranial elements

Among cranial elements (Fig. 4G–L), three were sufficiently preserved to be identified.

BRSMG Cb4261.2 (Fig. 4G and H) is probably a fragment of a lepidosaur pterygoid, but the absence of teeth means this cannot be confirmed. However, it displays a prominent process bearing a small facet that matches with the facet of the medial process of the ectopterygoid (see Whiteside, 1986, fig. 24). BRSMG Cb4277.18 (Fig. 4I and J) is a thin fragment of palatal bone. A number of features indicate that it represents the anterior part of the palatine; in particular a series of aligned foramina (for cranial nerves and arteries) as well as the distinct rim of a tooth base on one side of the bone (see Whiteside, 1986, fig. 22).

BRSMG Cb4277.21 (Fig. 4K and L) resembles a small section of the basipterygoid process of the parabasisphenoid, identified by a large foramen that would represent the internal carotid artery (see Whiteside, 1986, fig. 22). Therefore, all three elements lack any diagnostic features, which prevents a more certain taxonomic

identification but they fit in the size range and morphology of *Diphydontosaurus*.

4.3.3. Epiphyses

Both BRSMG Cb4277.20 and BRSMG Cb4196.8 (Fig. 4M–P) represent articular portions of long bones. The first (Fig. 4M and N) is the proximal end of a metapodial comparable in size and morphology with *Diphydontosaurus* described by Whiteside (1983).

A distal epiphysis of a phalanx (Fig. 4O and P) is comparable in size and morphology with *Clevosaurus*, and is found in the same rock specimen (BRSMG Cb4196) that yielded the teeth of that genus.

4.3.4. Rhaetian fish teeth

Two partial teeth of sharks (Fig. 5A and B) were found associated with articulated *Diphydontosaurus* limb bones. These teeth prepared in 1983 by one of us (DIW) from a separate rock (BRSMG Cb 4715). There is always a risk that fish teeth in the Bristol fissures, especially those of sharks, might derive from the Lower Carboniferous wall rock. However, we are convinced that these are Triassic fish teeth for two reasons: (1) they do not belong to any of the Lower Carboniferous fish genera found in the Durdham Down limestones, such as *Thrinacodus*, *Helodus* or *Psephodus*; and (2) they do not show the unique preservation colours of Carboniferous fish teeth in the Mesozoic fissures, such as the grey, blue or other lighter colours seen in chimaeroid teeth from Tytherington (Van den Berg et al., 2012; fig. 5C). The present teeth are preserved black, the same as produced by the anaerobic conditions of burial in the sediments of the local marine Westbury Formation (lower Rhaetian) described by Macquaker (1999). The best preserved of the fish teeth (Fig. 5A) has the low crown, central stubby cusp, and descending vertical ridges from the cusp apex on both the lateral and lingual surfaces described by Duffin (1999) for *Lissodus minimus* Agassiz, 1839. The broken subsidiary cusp

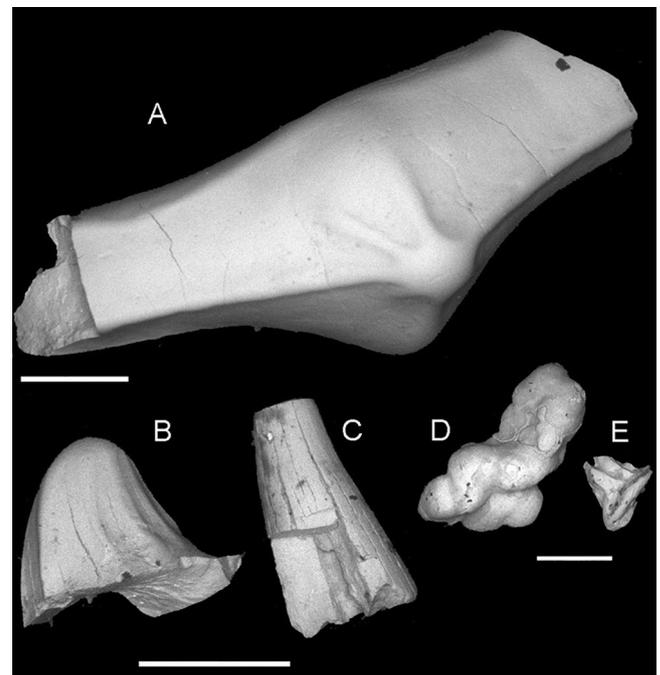


Fig. 5. Fish teeth and other remains from Durdham Down. The teeth and denticle are preserved black or brown but given a false white effect under the SEM. (A) Tooth of *Lissodus minimus*; (B) subsidiary cusp of tooth, most likely from *Rhomphaiodon minor*; (C) actinopterygian fish tooth; (D) aggregated ooid, cf. Whiteside and Marshall (2008, fig. 5m) at Tytherington; (E) denticle of hybodont shark? Scale bars equal 200 μm (A) and 500 μm (B–E).

(Fig. 5B) has the coarse vertical ridges that descend from the apex, as described by Duffin (1999) for *Rhomphaiodon* sp. The importance of these fossils is that they are from sharks that are typically found in this region in the bedded sequences of the local Westbury Formation (lower Rhaetian). Both genera are also known from early Rhaetian fissure fills at Holwell, and *Lissodus minimus* is found in the 'basal Penarth group' slot fissures (Westbury Formation, lower Rhaetian) of Cromhall (Fraser, 1994). In both these upper Triassic fissure localities, the assemblages include *Diphydontosaurus* and *Clevosaurus* (Fraser, 1994). We also note a dermal denticle from a shark (Fig. 5E) and part of a tooth from an actinopterygian (Fig. 5C) from rock specimen BRSMG Cb 4715, which indicates surface waters on or near the limestone at the time of fissure infilling.

4.4. Macrofossils

4.4.1. ?*Kuehneosauridae* indet

A long thin bone (Fig. 6A), which was exposed in rock sample BRSMG Cb4196 at the end of the acid cycles, was mechanically prepared. The bone, with a length of about 30 mm, is incomplete and shows a nearly round cross section of constant diameter (about 1 mm) that becomes oval at one end. It is almost straight, with very slight curvature. The fossil lacks both the epiphyses, which makes it difficult to identify; however its size and morphological features suggest it is too large to be a skeletal part of any of the sphenodontian lepidosaurs. Although an assignment to a gliding reptile such as *Mecistotrachelos* (Fraser et al., 2007) cannot be discounted, the dimensions and the unusual length of the specimen are compatible with the proximal half of the shaft of one of the elongate ribs in kuehneosaurids such as *Kuehneosaurus* and *Icarosaurus*; these diapsid gliding forms are both found in the Late Triassic to Early Jurassic of various localities in SW Britain and New Jersey (Robinson, 1962; Colbert, 1966). If confirmed, this report would be the first kuehneosaur from Durdham Down, whilst kuehneosaurs have previously been reported from Emborough, Pant-y-ffynon and Cromhall (Benton and Spencer, 1995; Whiteside and Marshall, 2008). Considering the archosauromorphs identified from the Durdham Down deposit, an alternative identification is as an ulna of *Terrestrisuchus* (Crush, 1984), which is of similar size and cross section, but the absence of epiphyses means that the decision between kuehneosaur rib or crocodylomorph ulna must be left open.

4.4.2. *Sphenosuchia* indet

A second long bone, exposed in anterior-lateral view in block BRSMG Cb4195 (Fig. 6B), is 74 mm long and slightly curved. After initial identification as "*Thecodontosaurus costa*" by Huene (1908b), the fossil received little attention until today; however, in the first stages of this project it was noticed that its dimensions and proportions differ from any *Thecodontosaurus* bone, and it is far too large and not sufficiently S-shaped to pertain to any of the fissure sphenodontians. Its size, slender structure, and particularly features of the proximal diaphysis (Fig. 6B–D), strongly match the femur of the sphenosuchian crocodylian *Terrestrisuchus gracilis* (Crush, 1984), from a Late Triassic fissure in Pant-y-ffynon quarry. In particular there is only a slight sigmoid flexure of the shaft, the epiphyses match, the distal one being expanded and the proximal weakly developed; the latter is also flattened and twisted with respect to the shaft. All these features, although shared with *Terrestrisuchus* (Crush, 1984), do not represent diagnostic characters at generic level. The presence of a poorly developed fourth trochanter would constitute a diagnostic feature, but sediment still covers the area where this could be observed. Thus, in the absence of any more specific character, we assign the fossil to 'Sphenosuchia indet.', based on the strong similarity to *Terrestrisuchus* (Crush, 1984).



Fig. 6. Sphenosuchian crocodylomorph femur and possible kuehneosaur rib from Durdham Down. (A) BRSMG Cb4196, kuehneosaur? rib; (B–D) BRSMG Cb4195, sphenosuchian crocodylomorph right femur in anterior (B), antero-lateral (C) and antero-medial (D) views. Ruler in cm is the scale for A; scale bar equals 5 cm in B–D.

4.4.3. Theropod dinosaur tibia

One of the original Durdham Down specimens (BRSMG Cb4277; Fig. 7) is a long bone (185 mm) whose medial side was roughly prepared, perhaps by quarry workers, before they sold the specimen. Probably as a consequence of this 'preparation', most of the medial side is missing or severely damaged, severely compromising the identification; the lateral side of the bone was still embedded in the rock. Originally the fossil was identified as a rib and assigned to *Thecodontosaurus antiquus* by Huene (as noted on the original label in the collection). Evidence that this specimen is not a rib includes the absence of curvature for two-thirds of its length, the proximal end shape with no sign of any rib articular processes, and the enlarged distal end with an articular facet.

Further preparation has allowed investigation of the previously hidden features of the bone (Fig. 7), which show that this is a tibia.

Key evidence comes from the newly prepared and well-preserved proximal epiphysis (Fig. 7C and D). Here, there are two depressions, separated by a low ridge and proximo-distally orientated, the fibular crest (fc, Fig. 7D). This is a theropod

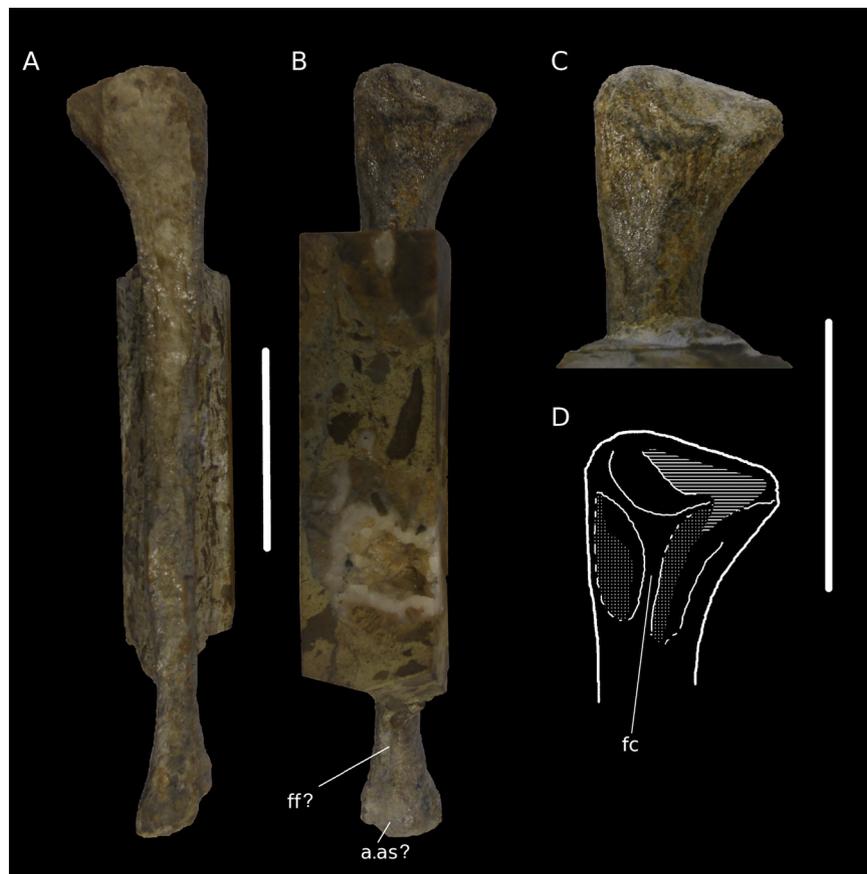


Fig. 7. Theropod tibia (BRSMG Cb4277) from Durdham Down, in medial (A) and lateral (B) views. Close up of the lateral face of the proximal epiphyses (C) and interpretative drawing (D). Notice the conglomeratic matrix in A, B. Abbreviations: a.as?, possible articulation with astragalus; fc, fibular crest; ff?, possible facet for fibula. Scale bars equal 5 cm.

synapomorphy (Gauthier, 1986; Rauhut, 2003; Nesbitt, 2011) that occurs in two morphologies. In BRSMG Cb4277, and other basal theropods including ‘*Syntarsus*’, it is proximally sited and gently connected with the proximal epiphysis; in most other theropods it is more distally placed and not connected to the proximal epiphysis of the tibia. In proximal view, the lateral posterior condyle of the fibula is gently confluent with the cnemial crest, giving the lateral surface of the proximal end a smooth concave profile, as opposed to the deep offset and strongly developed incisura tibialis seen in more derived theropods (Rauhut, 2003, p. 115, fig. 43). This, despite not being a synapomorphy, is a characteristic feature found in basal theropods such as *Coelophysis* and ‘*Syntarsus*’ (Rauhut, 2003).

The distal end of the specimen, despite initial appearances, does not provide dinosaurian synapomorphies. For example, the notch for reception of the ascending process of the astragalus (a.as, Fig. 7B) was until recently considered a diagnostic feature of dinosaurs, but has now been recognised also in non-dinosaurian dinosauromorphs (Benton, 1990; Brusatte et al., 2010; Nesbitt, 2011). The remaining outline suggests a rectangular profile in distal view, with a possible lateral process posterior to the astragalus facet, also seen in *Coelophysis*, ‘*Syntarsus*’ (*Megapnosaurus*) and other ‘traditional coelophysoids’ (Rauhut, 2003), but in BRSMG Cb4277 it might be an artefact of crushing and bad preservation. There is a possible facet for reception of the distal end of the fibula (ff?, Fig. 7B).

Overall, dimensions, morphology, and dating are all consistent with attribution of this tibia to a small basal theropod dinosaur, probably a member of ‘traditional Coelophysoidea’, following the

nomenclature of Ezcurra and Brusatte (2011); however the lack of diagnostic features prevents a more precise assignment to specific or generic level. The initial doubts that BRSMG Cb4277 might instead be a fibula vanish when the proximal end morphology is considered; in particular, the two fossae separated by a ridge are inconsistent with fibular morphology where a single fossa (for articulation with the tibia) would be expected; in this regard, we can also confidently exclude the possibility that the middle ridge is an artefact of crushing/preservation.

5. Faunal composition, comparisons and discussion

On the Late Triassic island archipelago in the Bristol area, the microvertebrate fauna of Tytherington quarry fissure 2 (Van den Berg et al., 2012) comprises the sphenodontians *Diphydontosaurus*, *Clevosaurus*, and *Planocephalosaurus*, and Rhaetian fishes, together with various archosauromorphs including the dinosaur *Thecodontosaurus*. Statistical comparison of the faunas from Tytherington and Durdham Down shows a strikingly similar terrestrial reptile composition (Fig. 8). Careful processing of the rocks, as also observed at Tytherington by Van den Berg et al. (2012), reveals that sphenodontians represent the vast majority of the fissure fauna at Durdham Down, contra Galton (2007), who nevertheless recognised that the perceived dominance of archosaurs in the same quarry was the result of a size bias.

Diphydontosaurus is by far the most common taxon at both localities, followed by archosauromorphs (excluding *Thecodontosaurus*), *Clevosaurus* and then *Thecodontosaurus*. *Planocephalosaurus* is the rarest terrestrial reptile identified at both localities,

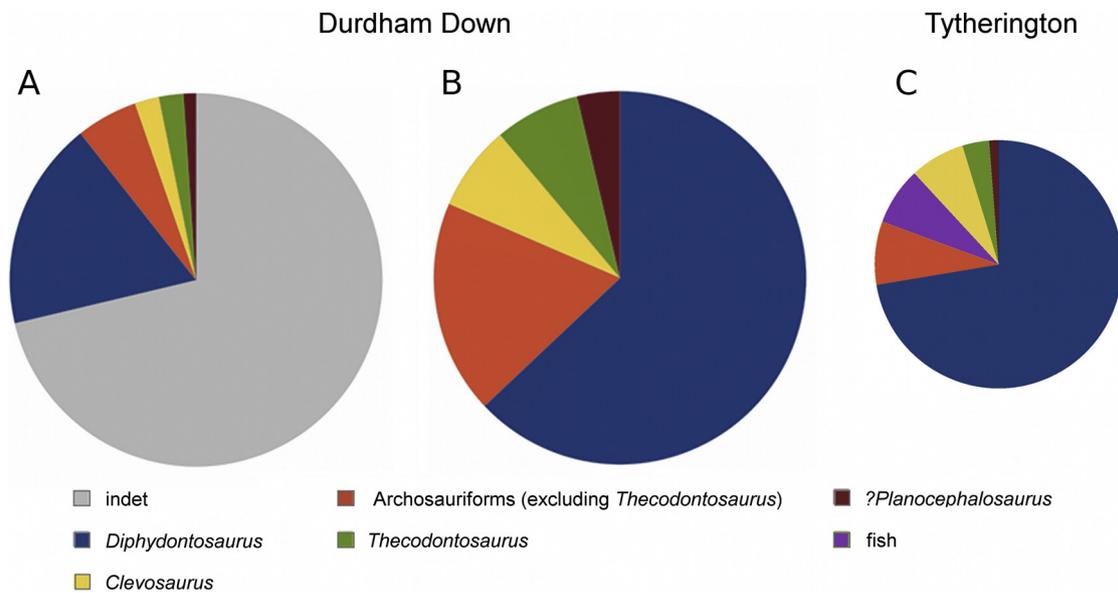


Fig. 8. Faunal composition of Durdham Down and Tytherington fissures, based on (A) all specimens and (B) taxonomically identifiable specimens (teeth/jaw fragments) from Durdham Down, and (C) material from Tytherington fissure 2 (reworked material removed). In order to produce a sound comparison, only specimens that were catalogued after acid digestion were considered.

Modified from Van den Berg et al. (2012).

although our identification at Durdham Down is tentative. *Diphodontosaurus* is found in 80% of the samples with *Thecodontosaurus*, which is similar to the high proportion at Tytherington fissure 2, where it is nearly 93% (Van den Berg et al., 2012). The Durdham Down samples differ from Tytherington in yielding no reworked Carboniferous conodont and chimaeroid fossils. This absence of reworked Carboniferous fossils may reflect the differing host rocks: the Durdham Down fissure is in the Clifton Down Limestone (see Fig. 1B), whereas fissure 2 at Tytherington is in the more fossiliferous Black Rock Limestone (Whiteside and Marshall, 2008, fig. 4). Nevertheless, in comparison with other fissure localities, it is clear that the Durdham Down microvertebrate fauna is most similar to that of Tytherington fissure 2. The samples from Durdham Down have some reptiles such as *Clevosaurus* in common with Cromhall, but *Thecodontosaurus* is not confirmed at that locality, and *Planocephalosaurus* is far more abundant there, comprising well over 50% of the specimens in the majority of sites; *Diphodontosaurus* is much rarer at Cromhall and always below 40% (Fraser, 1985, fig. 5). *Clevosaurus* found by us in the Durdham Down microvertebrate fauna, is also reported at Holwell (Fraser, 1994), Ruthin, and Pant-y-ffynon (Whiteside and Marshall, 2008). *Thecodontosaurus* is recorded from Holwell (Whiteside and Marshall, 2008) and the similar genus *Pantydraco* from Pant-y-ffynon (Galton et al., 2007). Quantitative analyses have not been reported for Holwell, Ruthin or Pant-y-ffynon, but observations of collections by the authors show that these have different faunal compositions from Durdham Down and Tytherington fissure 2. Moreover, whilst the confirmation of phytosaurs is not new, the discovery of probable *Terrestriuchus* and possible kuehneosaurid fossils in the Clifton fissure is significant and underlines some previously unknown similarities among the faunas of Failand and other (northern, southern and western) islands of the Triassic archipelago, noted also by Whiteside and Marshall (2008).

Supporting this point of view is the presence of remains of basal theropods. These are not a surprising finding, since theropod fossils were already described from Clifton (an ilium and a metacarpal; Galton, 2007), from Tytherington (a metatarsal II; Whiteside,

1983) and Pant-y-ffynon (various postcranial elements; Warrener, 1983; Rauhut and Hungerbühler, 2000). The last finds were originally reported as '*Syntarsus*' (*Megapnosaurus*) sp., a coelophysoid dinosaur closely related to *Coelophysus* (Rauhut, 2003), and also considered very similar to *Procompsognathus* from Germany (Rauhut and Hungerbühler, 2000). Unlike the common presence of contemporaneous bony fishes at Tytherington, we have recorded only one poor specimen of an actinopterygian tooth and none in our recent sampling, which may be explained by the small sample size. Importantly, associated with articulated *Diphodontosaurus* limb bones, we have found sharks' teeth with the same preservation as those typically found in the local strata of the marine Westbury Formation. Even if some hybodont sharks were able to live in fresh waters, as described by Murry (1981), the maintenance of surface waters on karstic limestone requires nearby marine waters to provide the freshwater lens (Whiteside and Marshall, 2008). Such an environment would most likely occur at a time of high sea level in a transgression, rather than in the more terrestrial conditions of deposition shown by the preceding Mercia Mudstones Group. These shark teeth therefore provide evidence of a nearby marine shoreline at the time of deposition. Our findings support the view of Whiteside (1983) and Whiteside and Marshall (2008) that the Durdham Down deposit is Rhaetian in age, most probably lower Rhaetian, with the dinosaurs and other terrestrial reptiles inhabiting a discrete palaeo-island (termed Failand island; Fig. 1A). It also provides evidence against a pre-Rhaetian age, as had been suggested by Robinson (1957) and Lucas (2010), and supports Moore's (1881) first idea of a 'Rhaetic age' for the Durdham Down deposit based on his finding of 'Rhaetic bone bed' material 'almost alongside the Clifton reptilia'.

The additional evidence for an early Rhaetian date for the sampled Durdham Down fissures matches the age of *Thecodontosaurus* at Tytherington (Whiteside and Marshall, 1983), and the closely related *Pantydraco* from South Wales (Rhaetian or Early Jurassic; Galton et al., 2007), and so moves the recorded origin of Thecodontosauridae 20–25 Myr forward in time to the early Rhaetian (209.5–204 Myr ago). However, this opens a potentially long ghost lineage for the clade, as Thecodontosauridae in most

cladograms falls near the base of Sauropodomorpha, whose minimal date of origin is late Carnian, based on other taxa such as *Saturnalia* from the Upper Santa Maria Formation of Brazil (Langer et al., 2010; Brusatte et al., 2010).

Despite processing a huge amount of rocks, mammaliomorphs or other cynodonts have not been recorded from Durdham Down, Tytherington or Cromhall, although they are present with similar reptiles at Holwell, well to the south. Cynodonts and mammals may have been exceedingly rare in the area, either occurring in habitats not sampled in the fissures, or excluded from Failand and Cromhall islands by some geographical barrier, and yet with an abundance of sphenodontians instead.

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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.2014.02.002>.

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