



Late Triassic island dwarfs? Terrestrial tetrapods of the Ruthin fissure (South Wales, UK) including a new genus of procolophonid

Matthew Skinner^{a,*}, David I. Whiteside^{a,b}, Michael J. Benton^a

^a School of Earth Sciences, University of Bristol, Bristol, BS8 1RJ, UK

^b Palaeontology Section, Earth Science Department, The Natural History Museum, Cromwell Road, London, SW7 5BD, UK

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ABSTRACT

Ancient cave deposits across South Wales and southwest England have yielded Late Triassic to Early Jurassic tetrapod faunas that occupied a sub-tropical island archipelago. Here we present a hitherto little studied fissure at Ruthin Quarry in South Wales. A tooth of the primitive neoselachian shark *Rhomphaiodon minor* indicates the age of the fissure as early Rhaetian, some 205 Ma, possibly equivalent to the first bone-bed horizons in the Westbury Formation. We identify 11 taxa, including chondrichthyans, procolophonids including a new genus and species named here *Smilodoterpeton ruthinensis*, rhynchocephalians, the trilophosaurid *Tricuspisaurus thomasi* and archosaurs, including a small crocodylomorph like *Terrestrisuchus*. Ruthin is dominated by procolophonids and secondarily by archosaurs. Rhynchocephalians are rare at Ruthin, unlike at penecontemporaneous fissure localities. Many of these faunas are reminiscent of those found in Carnian-Norian deposits from North America, some of them 25 Myr older, suggesting the Ruthin faunas are relictual. In exploring the palaeogeography of Ruthin and other British Late Triassic fissure deposits, we find that factors in addition to island size may affect the recorded species richness of these islands. Further, most of the taxa appear to be 'primitive' (i.e. possess closest relatives that are much older stratigraphically), and their body sizes are small, so this could be the oldest record of insular dwarfism.

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1. Introduction

Fossiliferous fissure deposits are widely spread across South Wales and southwest England. The caves were formed in ancient karst land surfaces, and then filled with terrestrially derived sediment sometimes containing skeletons and isolated bones, as well as other fossils. The host rock comprises numerous formations of Early Carboniferous marine limestones that were uplifted in the Late Carboniferous and Permian and eroded to form a palaeotopography in the Permian and Triassic. Typical tetrapods from the fissures include procolophonids, rhynchocephalians, trilophosaurids, small dinosaurs, other archosaurs and, at some localities, early mammals (Whiteside and Marshall, 2008; Whiteside et al., 2016; Whiteside and Duffin, 2017). The fissures fall into two categories that reflect their age, the Late Triassic 'sauropsid' fissures and the later, Early Jurassic 'mammalian' fissures (Robinson, 1957a; Whiteside et al., 2016). A key problem in

studying all these fissures and their faunas is that there are only rarely clear indicators of their age.

Originally described as 'upland' faunas on the basis that the animals were small and found in limestone caves (Robinson, 1957a), the Late Triassic sauropsid fissure faunas were later recognised as insular when both terrestrial and marine palynomorphs (Marshall and Whiteside, 1980) in addition to glauconitic clay (Whiteside and Robinson, 1983) were discovered in a fissure at Tytherington, indicating nearshore marine conditions. This new understanding of the environmental setting indicates that, during the Late Triassic, the Bristol Channel fissure faunas lived on an island archipelago.

Today, animals living on islands can show a number of special characteristics. First, the 'species-area relationship' is especially clear: small islands have fewer species than large islands (Lomolino and Weiser, 2001). In a classic example, Darlington (1957) showed that numbers of lizard species on islands of the Greater and Lesser Antilles ranged from three on Redonda (2.6 km²) to 84 on Hispaniola (76,000 km²). Can we detect the species-area effect among the reptiles living on islands in the Bristol Channel Triassic-Jurassic archipelago?

* Corresponding author.

E-mail address: mattsk1271@gmail.com (M. Skinner).

Second, islands can show marked size shifts, whereby small animals may become larger (insular gigantism) and large animals may become smaller (insular dwarfism), sometimes termed the 'island rule' (Foster, 1964; Lomolino, 1985; Lokatis and Jeshke, 2018). Many examples of insular dwarfing have been cited from the fossil record, for example among species of proboscideans (Vartanyan et al., 1993; Agenbroad et al., 1999; Guthrie, 2004; Agenbroad, 2012), artiodactyls (Marra, 2005), *Homo* (Brown et al., 2004), ornithomimid dinosaurs (Benton et al., 2010), and sauropod dinosaurs (Sander et al., 2006; Marpmann et al., 2015). Island gigantism has also been reported (Cooper et al., 1993; Pavia, 1999, 2004; Baker et al., 2005; Bunce et al., 2005; Benton et al., 2010; Rick et al., 2012). There are many explanations for these size shifts, but insular dwarfing likely reflects the limited availability of land and food, as well as the smaller numbers of species and consequent body size displacement to fill empty niches. However, the generality of the island rule has been severely questioned (e.g. Meiri et al., 2005; Lokatis and Jeshke, 2018), and at best it can be said to apply to mammals (Foster, 1964; Lomolino, 1985; Lokatis and Jeshke, 2018), and not to be general (i.e. it happens as often as it does not happen). In other words, examples of size shifts can be identified among certain species on islands, but not all. We explore here whether we can identify insular dwarfism, as well as cognate effects noted before in dinosaurs, such as that species on islands seem more primitive than their coeval mainland relatives (Benton et al., 2010).

One of the sauropod fissure deposits, from Ruthin Quarry in South Wales, has been known since the 1940s, but was not described in detail, despite the abundance of its fossils (Fraser, 1994) and uniqueness of the fauna (Fraser, 1986; Edwards, 1998; Edwards and Evans, 2006), including the type materials of the enigmatic tetrapod *Tricuspisaurus thomasi* (Robinson, 1957b). Here, we describe the fossils of the Ruthin fissure and reconstruct the palaeoecosystem.

Repository abbreviations. BATGM, Bath Geological Museum, Bath; BRSMG, Bristol City Museum, Geology collection; BRUG, University of Bristol, Geology collection; CAMZM, University of Cambridge, Museum of Zoology; NHMUK, Natural History Museum, London; NMW, National Museum of Wales, Cardiff; NSMNH, Nova Scotia Museum of Natural History, Canada.

2. Geological setting

2.1. Geological setting of the Ruthin fissure

The area around Ruthin Quarry, east of Bridgend, South Wales, is dominated by numerous formations of Lower Carboniferous limestones, showing multiple faulting (Fig. 1A). To the west and east are Triassic clastic sediments of the Mercia Mudstone Formation, overlain by the Penarth Group. Pleistocene and Holocene soils, tills, and alluvium cover low-lying areas to the southeast of the quarries. The Ruthin quarries used to be worked for the grey oolite and shelly limestones of the Carboniferous Limestone Supergroup (Thomas, 1952). Occasionally the quarrymen would encounter fissures in the limestone filled with Triassic-aged sediments.

At Ruthin, there are four quarries (Fig. 1A, B): a small, abandoned northern quarry (National Grid Reference, SS 975795), a large southern quarry (SS 975793), a small abandoned north-eastern quarry (SS 977795), and the large Garwa Quarry further to the north east (SS 980798). Only the northern quarry is currently accessible.

We describe the geology of the Ruthin fissure site from our own field observations, from Thomas (1952), and from field notes by Kenneth A. Kermack from 1962 to 1970 held in the NHMUK. Keeble et al. (2018, fig. 3a) show examples of the notes kept by Kermack

during the many visits by researchers from University College London to the South Wales fissure sites. Thomas (1952) reported that the north face of the north-eastern quarry had a large outcrop of Triassic deposits that sat unconformably on the limestone, approximately 30 m long, 12 m wide and 9–11 m deep. The Triassic outcrop consisted of angular limestone blocks of varying length, up to 10 cm to the west and 2.5 m to the east, within an infill of red marl and moderately coarse red breccia. The nature of the infill suggested it came from the collapse of a cave formed by limestone dissolution. Stalagmitic calcite found coating major joints near the fissure supported this. Other fissure deposits may have been formed by faults or joints (Thomas, 1952); examples exist at Llanharry Quarry, but not at Ruthin.

A large joint was also recognised 30 m south-west of the outcrop (Thomas, 1952). The joint was only up to 1 m or so wide and infilled with red sandy marl which was replaced by calcite veins with haematite at depth. Fissures in the southern half of the quarry are unobservable now, having been fenced off by the quarrying company.

The final Triassic deposit which Thomas (1952) reported is significant for its high abundance of reptilian remains. Remnants of this reptile-rich fissure can still be seen today (Fig. 2A, B), immediately north of the demolished quarry offices, on the west side of the abandoned northern quarry (Fig. 1B). The original fissure is now obscured by soil and vegetation but observed dipping surfaces on top of the cliff suggest the presence of more fissure infill debris, though this is covered by vegetation. The fissure sits on a well-defined bedding plane (Fig. 2B), within the Cornelly Oolite Formation, and Thomas (1952) reported a metre or so of oolite overlying it. The fissure infill comprises a mixture of brown shale, red marly sandstone and yellow-grey limestone. Sandstone dominates the deposit and contains a high quantity of reptilian bones; the limestone and shale preserve no such fossils. This fissure deposit is described as a "pothole filling" and is divided into two, as shown by Thomas (1952, fig. 5). The fissures were probably more extensive across the northern face as indicated by heavy, red-coloured staining of the limestone, likely caused by haematite carried in solution from the fissure deposits or indirectly from overlying soil produced from the fissure material.

Kermack's field notes from 1962 report brown, Recent or Pleistocene-aged clay overlying the rocky deposits. No Mesozoic fissures were recognised in 1962, suggesting the original fissures were unobservable, lost or destroyed. A new fissure was found in 1963, running north to south along the west side of the south face of the quarry. The infill consisted of fine limestone and red material with variably coloured clay ("brown", "sandy", "red"). The fine material was described as being bedded. Originally thought to be artificial, because they followed the bedding planes, the cavities were later determined to be natural in origin. Bedding suggests infill was gradual, hence not due to a cave collapse.

Many rock samples from the quarry, likewise, contain an accumulation of rusty, red, yellow and brown-coloured marl, medium- to coarse-grained sandstone and breccia. The samples also include crystalline veins of calcite. Only a few samples preserve any bedding/lamination. All samples likely originated from the "pothole filling" deposit described by Thomas (1952). The rocks used to compile the faunal assemblages described below were collected by Walther G. Kühne (1911–1991) in 1949 and held in unopened lidded boxes in the NHMUK store so we can be certain that the prepared fossils come from the original bone bed from which *Tricuspisaurus* derived. Indeed, we have seen a note (and invoice) dated 9th October 1948 sent by Kühne to the NHMUK with a description of "three jaws of a new reptile (now *Tricuspisaurus*), possibly related to *Trilophosaurus* from a bone bed in Ruthin".

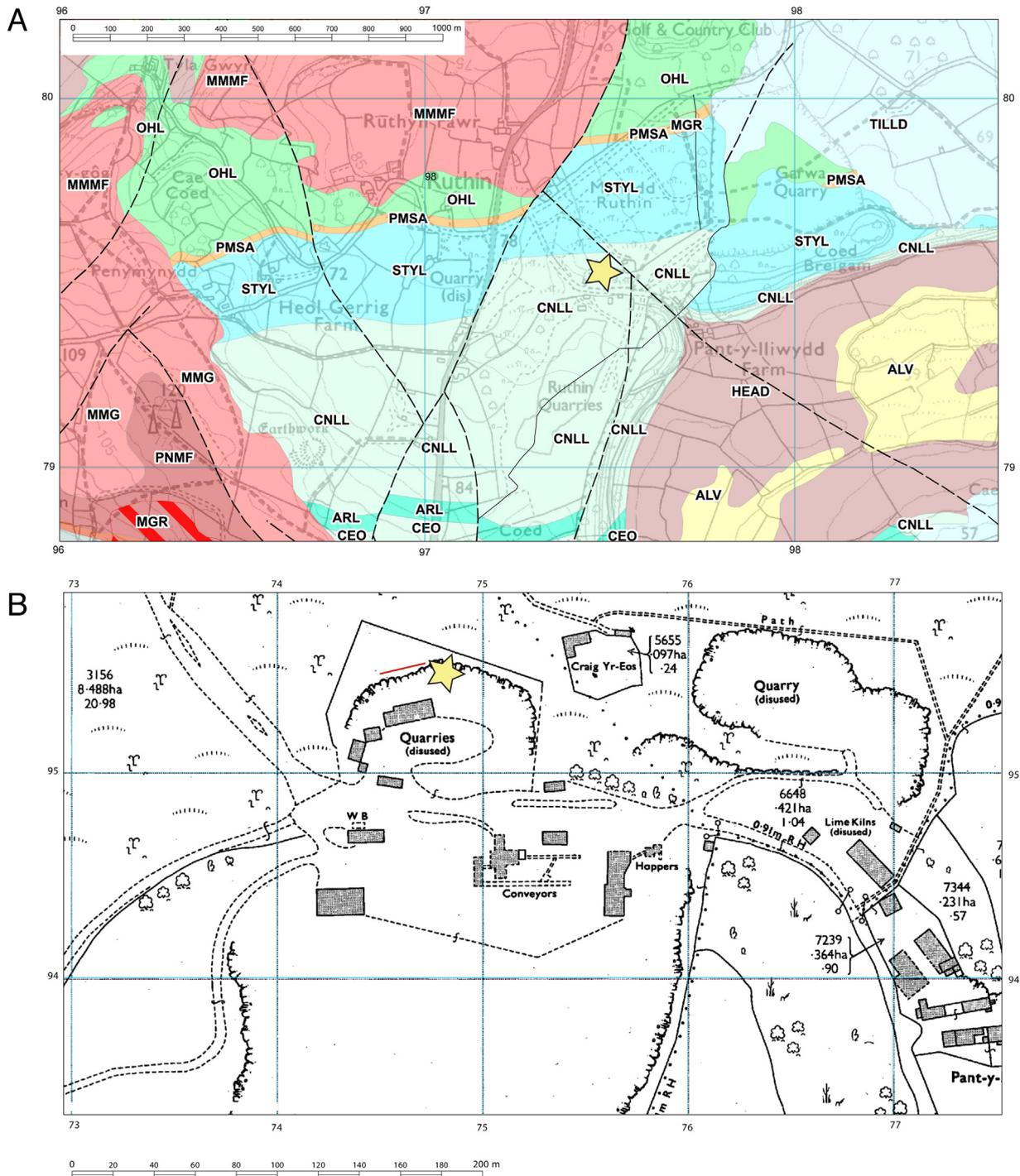


Fig. 1. Maps of Ruthin Quarry. (A) Geological map, showing quarry location (gold star) in the setting east of Bridgend. Stratigraphic unit abbreviations are from the Carboniferous (ARL, Argoed Limestone Member; CEO, Cefnyrhendy Oolite Member; CNLL, Cornelly Oolite Formation; OHL, Oxwich Head Limestone; PMSA, Pant Mawr Sandstone Member; STYL, Stormy Limestone Formation), Triassic (MMG, Mercia Mudstone Group; MMMF, Mercia Mudstone marginal facies; PNMF, Penarth Group marginal facies), and superficial (ALV, Alluvium; HEAD, Head – clay, silt, sand and gravel; MGR, made ground; TILLD, Till, Devensian). (B) The 1970 topographic map, showing detail of the quarries at Ruthin and the main buildings. Location of the fossiliferous fissure is marked with a red line (width of the fissure) and gold star (position of the square inset in Fig. 2A). Both maps © Crown Copyright and Database Right 2017. Ordnance Survey (Digimap Licence).

2.2. Thin section of the fissure sediment

A thin section of a rock sample (BRSUG 20549), collected from the Ruthin bone bed in the 1970s by R.J.G. Savage (1927–1998) shows a grain-supported sand comprising largely of light blue, pink and yellow calcite grains (Fig. 2C–G). Some show brightly coloured lamellar twinning (Fig. 2F), but most do not. Dolomite is also present. Many of the grains are overgrown or

outlined by haematite (Fig. 2G). Some 15–18% of the grains are composed of quartz, most of which have very sharp extinctions (Fig. 2C, D), suggesting an igneous origin, perhaps eroded from high-latitude Palaeozoic strata. In places, the calcite cement replaces the quartz, as indicated by wavy outlines of quartz grains, where the calcite appears to be etching its way into the quartz (Fig. 2C). Lithic grains are rare (5–6%) and consist primarily of siliceous rock fragments and mudrock. One notable

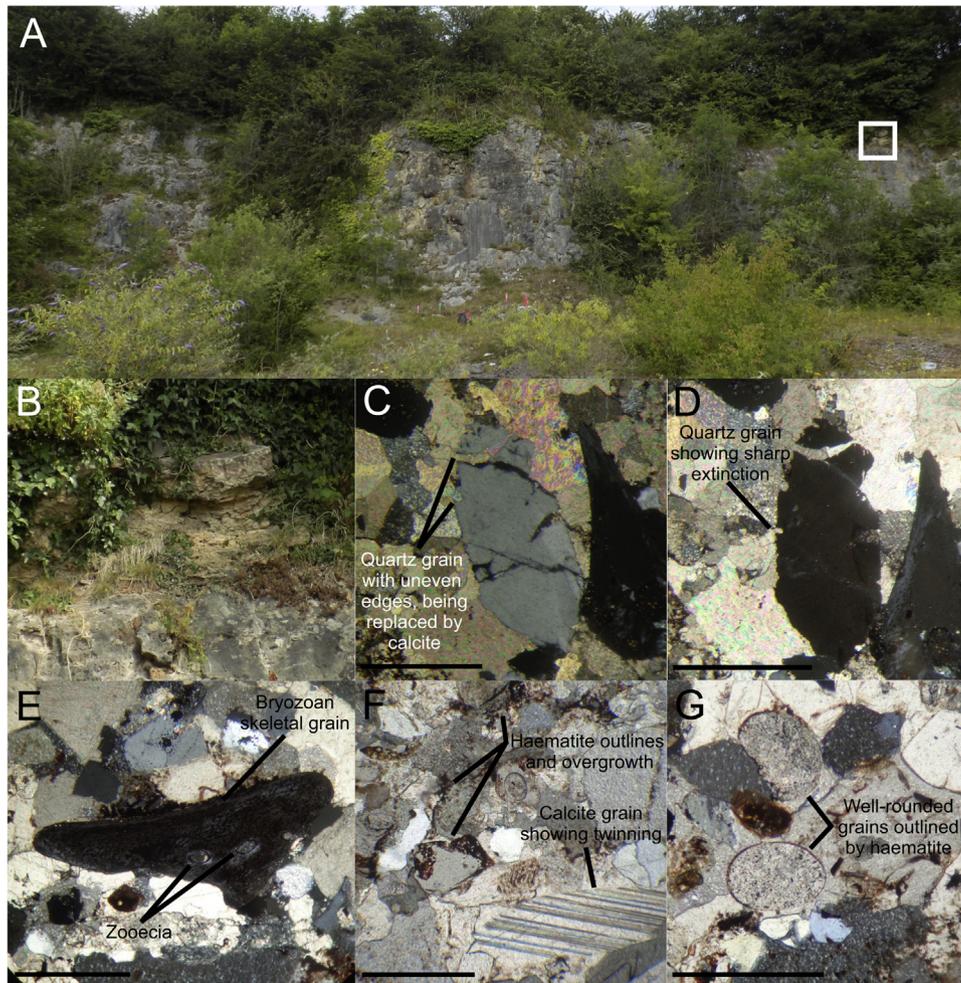


Fig. 2. Ruthin Quarry and its geology. (A, B) The north-west corner of the abandoned north face of the quarry, showing the area of the original 'reptile-rich fissure' (A) and a close-up of exposed remains of the fissure (B) outlined in A by a white square, both as in 2019. It is 8 m from the floor to the top of the old quarry face. (C–G) Images of a thin section from a block of bone-bearing fissure sediment, showing a quartz grain being replaced by calcite around the edges (C), the same quartz grain showing sharp extinction (D), a bryozoan skeletal grain, preserving holes interpreted as zoecia (E), brightly coloured twinning of calcite grain, and grains outlined or overgrown by haematite (F), and well-rounded calcite grains outlined by haematite (G). Scale bars are 0.5 mm for C–G.

lithic is chert, possibly eroded from a deep marine environment or the Carboniferous limestone before being deposited in the fissure. Mudrock lithics show fine, wavy laminations. Grains are outlined and sometimes overgrown by variably low to moderate amounts of haematite.

The sediment is poorly sorted, with grain sizes varying from fine to very coarse. Grains are variably angular to rounded, suggesting a mix of clasts derived from a variety of sources.

A single bryozoan fossil, about 1.25 mm wide, was recognised (Fig. 2E) by the flow-like structure of the grain and consistent line of holes along its surface. This fossil was likely eroded from the Carboniferous limestone.

The sample appears to have undergone diagenetic change, as evidenced by the precipitation of calcite cement and overgrowth over limestone clasts, likely precipitated from carbonate-rich water that flowed through the sediments. In addition, hand specimens show common calcite veins, suggesting tension jointing and infill from solution. The surrounding Carboniferous limestone was uplifted and folded during the Hercynian Orogeny in the Late Carboniferous and Early Permian, but the diagenetic effects observed in the fissure-filling sediments presumably date from after the Late Triassic, and are perhaps associated with Early Jurassic faulting, linked to the opening of the North Atlantic.

Haematite rims formed around the edges of the older, clastic grains, under arid conditions.

3. Materials and methods

Descriptions are based on collections from the NHMUK and NMW, including material from Kühne's rock collection in the NHMUK newly acid digested by us. Only fossils that preserve diagnostic features, primarily tooth-bearing bones, are assigned to genera or species. Fossils lacking recognisable features are not described. Descriptions, where possible, are based primarily on the best-preserved specimens of each species. Measurements were taken using a hand-held ruler or Leica Application Suite (LAS) V3.7 for microscopic materials. Measurements of the height, width and length refer to dorso-ventral, lateral to medial, and anterior-posterior measurements respectively, unless stated otherwise. Measurements with reference to the transverse plane are medio-lateral.

The microvertebrate fossils vary in size from <1 to 27 mm across, but most are between 1 and 2 mm. A light microscope (Nikon C-LEDS Hybrid LED Stand) was used to observe the fossils, which were photographed using a microscope camera setup (Leica DFC425/DFC425 C and LAS V3.7). Where more detailed images of

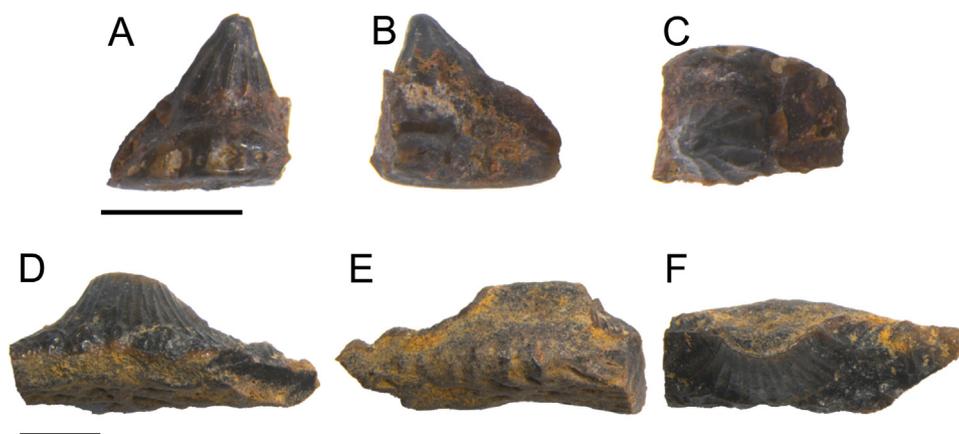


Fig. 3. Chondrichthyan fossils. (A–C) *Rhomphaiodon minor* tooth (NHMUK PV P 75820) in lingual (A), labial (B) and occlusal views (C). (D–F) *Polyacrodus cloacinus* tooth fragment (NHMUK PV P 75821) in lingual (D), labial (E) and occlusal (F) views. Scale bars are 1 mm.

the surface structure were required, a Hitachi S3500 N Variable Pressure Scanning Electron Microscope (SEM) was used with uncoated specimens. Internal structures were viewed and 3-dimensional (3D) models were produced using a Nikon XTH 225ST X-ray Computed-Tomography (CT) scanner. CT data were viewed and segmented using Avizo 8.0.

To analyse relative faunal abundance, a fresh dataset was required. Rock samples from the Walter Kühne collection in the NHMUK store were prepared using the standard acid digestion method (Foffa et al., 2014; Klein et al., 2015; Keeble et al., 2018). They were placed in acid baths containing 5% acetic acid (enough to cover the rocks), 0.5 g/l anhydrous sodium carbonate, and 0.167 g/l tribasic calcium phosphate. The latter two were bases to prevent acid digestion of the fossils. Rate of digestion varied depending on grain size, composition and lithification of samples. Every 24–48 hours, the samples were removed from the baths, acid solution was drained, and digested material fractionated using 2 mm, 0.5 mm and 0.18 mm sieves, while thoroughly rinsing the material to remove the acid. Very fine material was considered unusable. The fractionated material was left to dry on filter papers in funnels. To neutralise any remaining acid, the rock samples were placed in water with alkaline washing-up liquid for twice the time they had been left in acid. Any large fossils exposed on the rock surface during the process were coated with Paraloid to provide extra acid protection. The acid baths were then reset, and the process started again. This cycle was continued until either the rocks were fully dissolved, or time ran out.

The fractionated samples, once dried, were picked using a fine brush. Samples consisted mostly of fine rock grains and unidentified fossil fragments. Only about 5–10% of fossils were confidently identifiable and included in the abundance count. Because all the fossil material was disarticulated and fragmentary, unless a fossil/fragment could confidently be associated with another (fitting perfectly together), all fossil specimens were counted as separate individuals (following the procedure of Keeble et al., 2018).

To test for changes in body size, the faunas of Ruthin were compared to their phylogenetically closest recognisable mainland relatives. To test biodiversity changes, the number of terrestrial animal genera relative to the area in km² of Triassic–Jurassic islands in the Bristol Channel area was recorded. A standard palaeogeographic map of the Bristol Channel area (produced based on those from Foffa et al., 2014 and Whiteside et al., 2016) was gridded into 1 km² squares, and the number of squares over each island was counted (see later, Fig. 16). If an island occupied less than 50% of a square, that square was not counted. Genera were used instead of species, because all taxa were most confidently identified to the

genus level, and most genera are monospecific in the context of individual islands. Estimated island sizes in km² are as follows: Twyn-yr-Odyn (5), St Brides (15), Ruthin (34), Pant-y-ffynnon (16), Cromhall (14), Durdham Down (22), and Emborough (112). The numbers of tetrapod genera per island and per named locality were counted (Whiteside et al., 2016; Whiteside and Duffin, 2017; Keeble et al. 2018), and plotted against island area to test for correlation (see Supplement). Because there is a degree of uncertainty in taxon identifications, we plot both the minimum and maximum numbers of genera for each island.

4. Systematic palaeontology

The vertebrate fauna from the Ruthin fissure consists of two chondrichthyans, four procolophonids, three rhynchocephalians, one trilophosaurid and at least one archosaur.

4.1. Chondrichthyans

Class CHONDRICHTHYES Huxley, 1880
 Subclass ELASMOBRANCHII Bonaparte, 1883
 Infraclass EUSELACHII Hay, 1902
 Clade NEOSELACHII Compagno, 1977
 Genus *Rhomphaiodon* Duffin, 1993
Rhomphaiodon minor (Agassiz, 1837)
 Figs. 3A–C

Description. The single specimen consists of an upright, cone-shaped tooth crown bearing twelve well-defined, vertical ridges radiating from cusp apex to crown base (Fig. 3C). The tooth crown is positioned occluso-lingually on the flat plinth of the root, which bears three fine and two moderately sized pores on the lingual surface (Fig. 3A). Part of the root has been broken off, and one fine and one moderately sized pore are suspected to have been lost, as indicated by the pattern of the preserved pores and shape of the lingual surface of the root.

Remarks. The species was named on the basis of a fin spine (Agassiz, 1837), but later associated with isolated teeth (Storrs, 1994). It remains uncertain whether the teeth and original fin spine are from the same taxon (Slater et al., 2016). The teeth, noted for their similar morphology to those of *Rhomphaiodon nicolensis* by Duffin (1993b), were later reassigned from *Hybodius* to *Rhomphaiodon* by Cuny and Risnes (2005).

This is the first stratigraphically significant fossil from Ruthin that has not been reworked from the surrounding Carboniferous deposits, and our stratigraphic conclusions do not depend on any taxonomic uncertainties about which name ought to be applied.

This species is uncertainly recognised in Ladinian deposits in Germany but confidently in Norian strata in Germany and Rhaetian-aged deposits across Europe (Duffin and Delsate, 1993). The earliest occurrence of *R. minor* in British Triassic sequences was recorded by Landon et al. (2017) towards the top of the Blue Anchor Formation (Norian-Rhaetian) from a borehole at Stoke Gifford, Bristol, as well as within 2 m of the top of the Blue Anchor Formation at Goldcliffe. Duffin (pers. comm., 2020) states that 'R. minor is not found in any of the Carnian faunas from the UK or any other Norian sediments from the UK to the best of my knowledge; it appears to come in with the Rhaetian marine transgression in Britain.' The presence of crinoids in the Stoke Gifford deposits suggested stenohaline conditions to Landon et al. (2017), 'very similar' to the environment of the Westbury Formation. *R. minor* is found throughout the biostratigraphically well-documented Rhaetian Westbury Formation (Lakin et al., 2016) but is reportedly most common in the basal Westbury Formation bone beds (e.g. Mears et al., 2016; Slater et al., 2016). Considering the U.K. occurrences of *R. minor*, this fossil therefore indicates that the Ruthin deposits were formed as the Rhaetian transgression progressed and at the earliest at the Norian/Rhaetian boundary but most likely early Rhaetian (= Lower Penarth Group), approximately 206–205 Ma. At that time, sea level would have to have been high enough for some marine sediments to enter the fissures of the Ruthin area.

Order HYBODONTIFORMES Maisey, 1975
 Family POLYACRODONTIDAE Glükman, 1964
 Genus *Polyacrodus* Quenstedt, 1858
Polyacrodus cloacinus Quenstedt, 1858
 Figs. 3D–F

Description. The single specimen consists primarily of the lingual half of the base of a large cusp, which if complete would have been tall and elongate. The labial half of the tooth, presumably including the distinctive labial node (Mears et al., 2016), is not preserved. The preserved surface of the cusp (Fig. 3D) is covered in many apically oriented, well-defined vertical ridges which would have extended to the cusp apex. Fifteen such ridges are recognisable from the top of the preserved cusp (Fig. 3F), but some ridges bifurcate towards the base. In occlusal view, the cusp base extends slightly further from the main cusp body mesially than distally.

The base of the tooth appears elongate mesiodistally. More of the tooth (inferred) mesial of the cusp is preserved than the (inferred) distal region. The occlusal surface of the tooth, around the base of the large cusp, is rough and lumpy. Small remnants of two cusplets remain, occlusally on the inferred mesial side of the large cusp (Fig. 3E).

Remarks. Identification of this species is tentative as the specimen is poorly preserved. This species has previously been assigned to *Polyacrodus* or *Hybodus*; classification remains uncertain.

Looking at the teeth of modern sharks, recurved teeth point backwards, and we can apply this observation to *Polyacrodus*. The tooth is elongate mesiodistally with a single large cusp and multiple surrounding cusplets, with one on one side of the cusp and several on the other side. More complete *Polyacrodus* teeth (Mears et al., 2016, fig. 6i, j) preserve the curvature of the cusplets and from these we infer that the side with more cusplets is the more anterior/mesial side of the tooth (depending on the relative view of the jaw and position of the tooth).

This species has a wider reported stratigraphic range than *R. minor*, namely Late Triassic to Early Jurassic (Duffin and Delsate, 1993; Lakin et al., 2016; Mears et al., 2016; Slater et al., 2016), but is mostly present in Rhaetian-aged deposits and Jurassic records are uncertain (Duffin, 1993b; Duffin and Delsate, 1993). It has been

reported at the base of the Westbury Formation, but absent at the top (Slater et al., 2016), supporting an early Rhaetian age for Ruthin. The presence of this taxon and *Rhomphaiodon minor*, which are marine fish, further supports a high sea level at the time of fissure infilling and is best explained by the progress of the Rhaetian transgression with marine waters reaching just a few metres below the fissure.

4.2. Procolophonids

Class REPTILIA
 Subclass PARAREPTILIA Olson, 1947
 Order PROCOLOPHONOMORPHA Romer, 1964
 Superfamily PROCOLOPHONOIDEA Romer, 1956
 Family PROCOLOPHONIDAE Seeley 1888
 Genus *Haligonia* Sues and Baird, 1998
Haligonia cf. *bolodon* Sues and Baird, 1998
 Figs. 4A–E

Description. The primary specimen is an incomplete right maxilla (Fig. 4D, E), accompanied by a tooth from a separate individual (Fig. 4A–C). The maxilla is 5.2 mm long and the tooth approximately 1.5 mm wide.

Occlusally, the posterior 2/5 of the maxilla (Fig. 4D, E) is smooth and structureless, forming the posterior jugal ramus. Centrally, the fragmentary enamel outline of the base of the posteriormost tooth may be seen (Fig. 4D). The tooth was acrodont and would have been very broad and roughly dome-shaped. The isolated tooth (Fig. 4A–C) is very slightly smaller but was also likely the posteriormost tooth of the jaw. It is basally broad, with a sloping lateral surface (Fig. 4A) and a steep opposite lateral surface (Fig. 4C), resulting in a less bulbous, central apex consisting of a very narrow ridge (Fig. 4B). Anterior to the posteriormost tooth of the maxilla are four alveoli, lacking teeth (Fig. 4E). The alveoli are significantly smaller, being approximately 1/3 the length of the posteriormost tooth. Laterally (Fig. 4D), the bone surface is covered with extremely fine pits and striations. A small foramen is present at the base of the tooth alveolus anterior to the large posteriormost tooth and a larger one sits laterally between the second and third alveoli.

Remarks. The length, narrow shape, presence and positioning of the foramen and lack of curvature of the occlusal surface of the bone suggests this bone is a maxilla and not a dentary. The character of having the large tooth posterior to much smaller teeth suggests affinity with *Haligonia* (Sues and Baird, 1998, fig. 2B). Alveolar foramina in similar positions are present in *Haligonia bolodon*. The posterior ramus of our specimen is not as strongly curved as in the specimen described by Sues and Baird (1998, fig. 2) and so we have referred our specimen to *Haligonia* cf. *bolodon*.

Genus cf. *Scoloparia* Sues and Baird, 1998
 Cf. *Scoloparia* sp.
 Figs. 4F–N

Description. This taxon is recognised from multiple, isolated premaxillae, up to 3.5 mm long. Their surfaces are smooth, lacking noticeable pits and grooves. Posterolaterally, a large, flat ramus curving gently posterodorsally is present, forming an attachment surface with the maxilla and potentially the nasal as well. Anteriorly, the dorsal surface curves gently dorsally, outlining the anterior margin of the naris. Dorsally, the dorsally curving ramus appears very wide and flat surfaced (Fig. 4M, N). Medially, a bony ridge is present just above the tooth row which likely would have formed a palate. More extensive palates are unknown from Ruthin. All specimens lack well preserved crowns but do preserve the bases and alveoli of three acrodont teeth, the most anterior of which is considerably larger than the rest. The tooth row is strongly curved lingually, particularly the most anterior end. The sockets

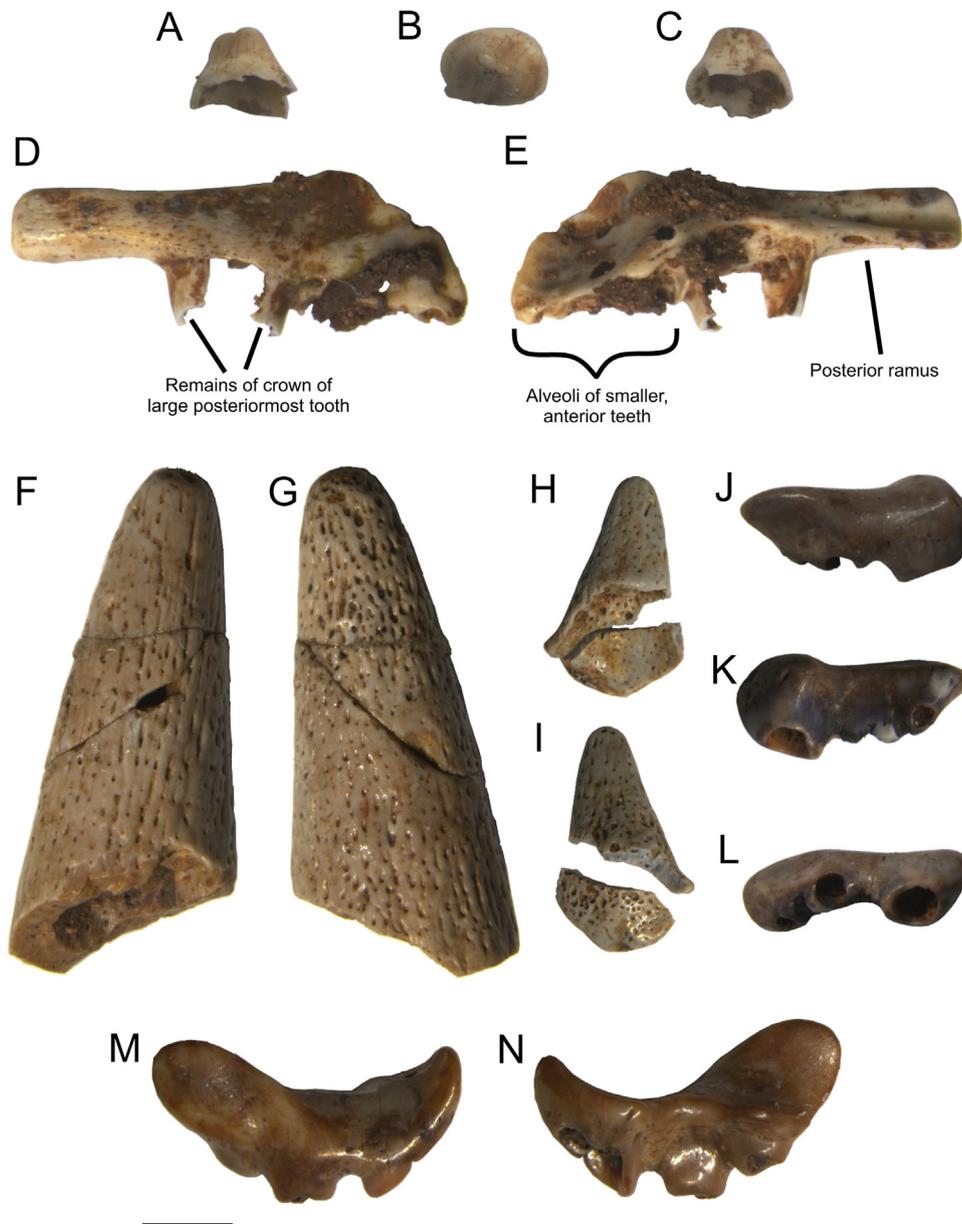


Fig. 4. Procolophonid fossils. (A–C) *Haligonia*, isolated, large tooth from NMW 88.12 G.52 in lateral (A), occlusal (B) and opposite lateral (C) views. (D, E) *Haligonia*, interpreted right maxilla from NMW 88.12 G.52 in lateral (D) and medial (E) views. (F, G) *Scoloparia*, large cephalic spine in opposite views (NHMUK PV R37480). (H, I) *Scoloparia*, small cephalic spine in opposite views (NHMUK PV R37481). (J–L) Cf. *Scoloparia*, abraded right premaxilla (NHMUK PV R37475) in lateral (J), medial (K) and occlusal (L) views. (M, N) Cf. *Scoloparia*, right premaxilla (NMW 88.12 G.89) in lateral (M) and medial (N) views. Scale bar is 1 mm for A–E and J–N, and 2 mm for F–I.

are circular (Fig. 4L) and the expected tooth shape is largely conical. The anteriormost tooth is noticeably larger than those behind.

Two cephalic spines from the quadratojugal are preserved. The spines are long and slender. The smaller spine (Fig. 4H, I) is 6 mm long, narrow, cone-shaped and covered in fine pits and grooves, which suggest it had a keratinous covering in life (Sues and Baird, 1998). It also preserves a widened base on which pits and grooves are considerably larger. The larger spine (Fig. 4F, G) is very similar, but is 12 mm long and the base is absent. Both spines are rounded at the apex but may have once been sharper before being worn away as most preserved procolophonid spines have a pointed apex.

Remarks. A similar but more complete specimen of a premaxilla was mis-identified as *Tricuspisaurus*, believed to be a procolophonid by Fraser (1986, fig. 5). We explain below why *Tricuspisaurus* is not a procolophonid.

Late Triassic procolophonids such as *Leptopleuron* (Säilä, 2010) and *Hypsognathus* (Sues et al., 2000) have two premaxillary teeth. *Scoloparia* can have two or three premaxillary teeth (Sues and Baird, 1998), which suggests that the Ruthin premaxillae are from this genus. This is confirmed from images of *Scoloparia* specimens provided by T. Fedak (NSMNH 996GF78.1, NSMNH 996GF70.1, NSMNH 996GF81.1). Three-toothed premaxillae are common in the Late Permian (Piñeiro et al., 2004) and Early Triassic (Borsuk-Bialynicka and Lubka, 2009). Of taxa already identified from Ruthin, our specimens could belong to *Haligonia* whose premaxilla is unknown, or to the new Ruthin taxon *Smilodonterpeton ruthinensis* but clear differences in morphology of known teeth suggest that this is unlikely. The medial bony ridge seen in our specimens is mirrored in *Scoloparia* (NSMNH 996GF70.1).

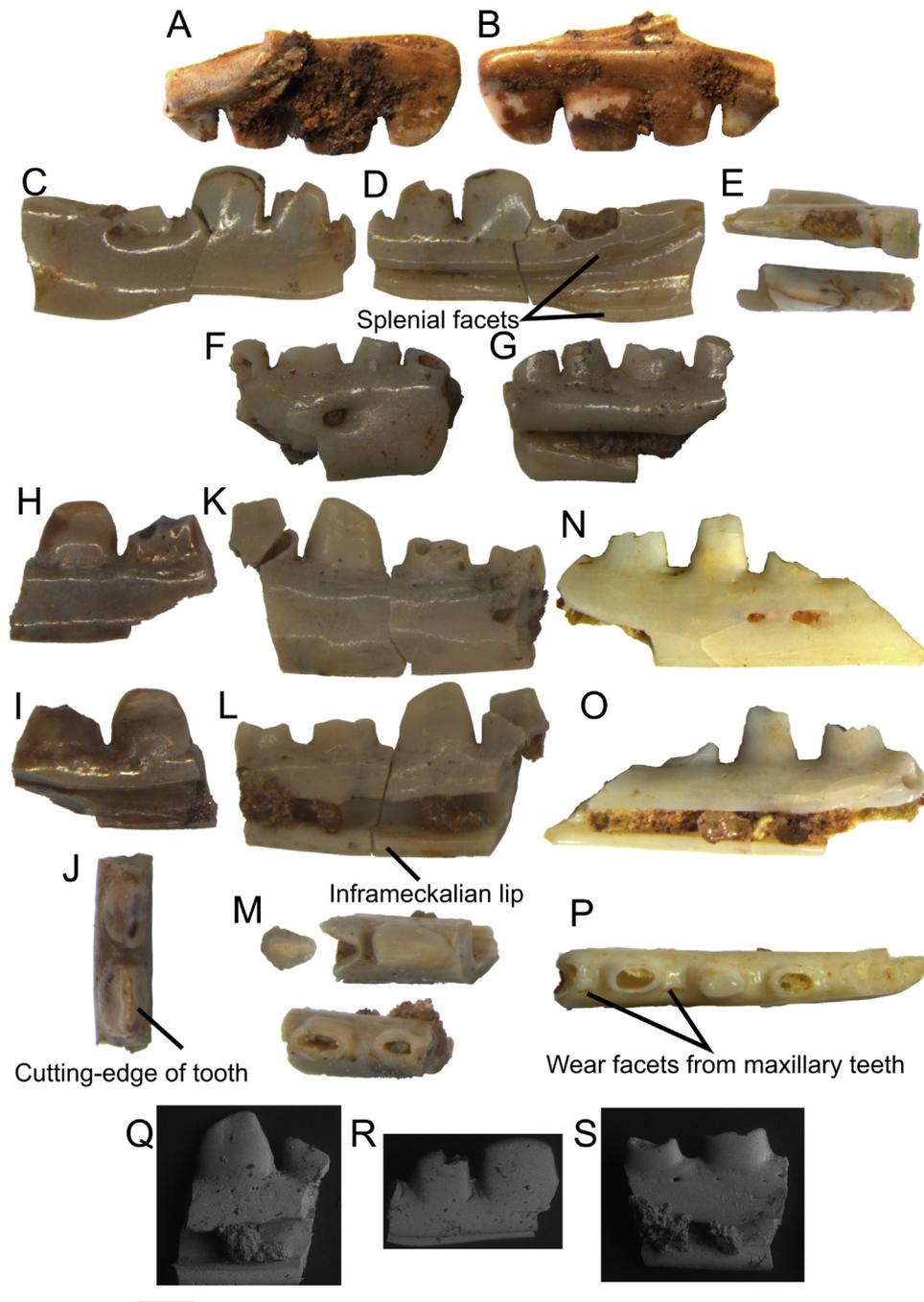


Fig. 5. *Smilodonteipeton ruthinensis* n. gen. n. sp. fossils and SEM images. (A, B) Right maxilla (NHMUK PV R37474) in lateral (A) and medial (B) views. (C–E) Holotype specimen: partial right dentary (NHMUK PV R37469) in lateral (C), medial (D) and occlusal (E) views. (F, G) Anterior right dentary portion (NHMUK PV R37472) in lateral (F) and medial (G) views. (H–J) Partial dentary (NHMUK PV R37470) in lateral (H), medial (I) and occlusal (J) views. (K–M) Partial right dentary (NHMUK PV R37471) in lateral (K), medial (L) and occlusal (M) views. (N–P) Right dentary (NHMUK PV R37473) in lateral (N), medial (O) and occlusal (P) views. (Q–S) SEM images of medial views of NHMUK PV R37471 (Q, S) and NHMUK PV R37469 (R), revealing chisel-shaped teeth, deep grooves anteriorly and posterior base of teeth and poorly-defined tooth-to-bone boundaries. Scale bar is 0.5 mm.

It is uncertain whether the Ruthin premaxillae relate to the cephalic spines that share their long, slender shape with *Scoloparia* (Sues and Baird, 1998), or what the shapes of their dentary tooth crowns were.

Genus *Smilodonteipeton* gen. nov.

Derivation of generic name. From *smili-*, Greek for 'chisel'; *dont-*, Greek for 'toothed'; and *erpeton*, Greek for 'reptile', referring to the distinctive shape of the teeth.

Type species. *Smilodonteipeton ruthinensis* sp. nov.

Smilodonteipeton ruthinensis sp. nov.

Fig. 5

Derivation of species name. Greek meaning 'from Ruthin', referring to the Ruthin Quarry where the fossils were discovered.

Holotype. Two fragments of a partial right dentary (NHMUK PV R37469, Fig. 5C–E).

Referred specimens. One partial right maxilla (from NHMUK PV R37474; Fig. 5A, B); one anterior fragment of dentary (NHMUK PV

R37472, Fig. 5F, G); one fragment of a right dentary (NHMUK PV R37470, Fig. 5H–J); three fragments of a right dentary (NHMUK PV R37471, Fig. 5K–M); one right dentary fragment with emplacements for five teeth (NHMUK PV R37473, Fig. 5N–P); one additional jaw fragment without teeth (from NHMUK PV R37474); four dentary fragments, one hypothesized left and two right and one uncertain, from NMW 88.12 G.94. The proposed species is known from eleven specimens comprised of 13 dentary fragments (Fig. 5C–S) and one maxilla fragment (Fig. 5A, B).

Type locality and horizon. Upper Triassic (Latest Norian to Early Rhaetian) fissure infill within Lower Carboniferous Limestone, Ruthin Quarry, St. Mary on the Hill, The Vale of Glamorgan, South Wales, UK (NGR SS 975 796).

Diagnosis. A procolophonid with the following autapomorphies: (1) at least three, near-square or sub-trapezoid (in labial or lingual views), posterior acrodont dentary teeth parallel or near-parallel to the long axis of the dentary; (2) a defined anterior and posterior groove that pinches the base of the teeth, absent laterally; (3) a shallow, rather than deep, dentary possessing a deep Meckelian groove outlined ventrally by a well-defined inframeckelian lip.

Description. Based on 14 fragmentary remains of tooth-bearing dentary bones. Some comprise two pieces that fit together (Fig. 5C, D, E, K, L, M), producing specimens approximately 2.8 mm long. The skull length is estimated to have been less than 20 mm, based on comparison of the fossils with whole skull reconstructions of other Late Triassic procolophonids.

One maxilla is known (NHMUK PV R37474), a specimen from the right side with four teeth that was acid-prepared from the Kühne rocks. The middle teeth have the characteristic sub-trapezoid shape of many dentary teeth, but the anterior and posterior teeth have a curved shape in lateral or medial views. The mesial side of the anterior cusp curves ventro-posteriorly whilst the distal edge of the smaller, posterior tooth, curves antero-ventrally.

The dentary is shallow compared to other procolophonids. The distance between the alveolar and ventral margins increases very gradually posteriorly, producing a gradient more akin to that of *Scoloparia* or *Acadiella* than the drastic changes seen in *Hypsognathus* or *Leptopleuron* (Sues and Baird, 1998). The lateral surface in better preserved specimens is well-rounded (Fig. 5K), though this surface is sometimes worn smooth and flat, so is in line with the labial surfaces of the teeth (Fig. 5C, M). Two moderately-sized foramina are recognised along the lateral surface (Fig. 5N), although only one is usually preserved (Fig. 5F, K). The medial surface (Fig. 5D, G, I, L, O) is very smooth, interrupted by a prominent, deep Meckelian groove just under half-way down the height of the dentary from the alveolar surface. The groove is dorsoventrally widest posteriorly, narrowing anteriorly very gently while remaining a significant gap. In other procolophonids, this groove is described as being shallow in *Scoloparia* and *Hypsognathus* or reduced to a sulcus in *Haligonia* (Sues and Baird, 1998; Sues et al., 2000). The inframeckelian lip, seemingly absent in *Acadiella* (Sues and Baird, 1998, fig. 1C), forms the medially projecting ventral border of the groove and is about half as dorso-ventrally thick as the rounded and well-defined bone dorsal of the groove (Fig. 5L, O). The lip in more abraded specimens is often missing or poorly defined (Fig. 5D, I). In some specimens, facets have been recognised at the back of the dentary (Fig. 5D), suggesting the presence of a splenial. The splenial bone is not recognised, but given facets are only recognised most posteriorly, it was likely absent anteriorly, as seen in other procolophonids such as *Leptopleuron* (Säilä, 2010) and *Scoloparia* (Sues and Baird, 1998).

Acrodont teeth are slightly dorsoventrally shorter than the dentary fragment they are ankylosed to, and similar in

proportions to those of *Acadiella* (Sues and Baird, 1998, fig. 1C, D), but the teeth are relatively taller than those of *Leptopleuron* (Säilä, 2010, fig. 8B–G) and *Scoloparia* (Sues and Baird, 1998, fig. 6 A, B). The teeth are generally preserved with their lingual surface in line with that of the dentary (Fig. 5D, E, I, J, L, M, O, P, Q–S). Wear on the teeth is likely to be from occlusion with the maxillary teeth which are similar in shape. The dentary teeth are separated by variably sized gaps, about 12–16% of the anteroposterior tooth length in the posterior teeth but which can range to over 30% in the more anterior dentition. Anteriorly, the teeth are circular in cross-section, but lack fully preserved crowns, interpreted to have been cylindrical or near-conical in shape (Fig. 5F, G, M). Posteriorly, complete tooth crowns are preserved. Such teeth are broadened anteroposteriorly, increasingly so posteriorly, and are near-square or sub-trapezoid in shape laterally. In occlusal view, posterior teeth are sub-rectangular to sub-oval in shape, the tooth base length being nearly twice the width, with an apical, labio-lingually narrowed crest positioned parallel to the length of the dentary (Fig. 5E, J, M, P). The anterior and posterior bases of the posterior teeth possess grooves where the bone appears to pinch the base of the teeth (Fig. 5R), not recognised in other procolophonids. These grooves are absent labially and lingually, where the boundary between the bone and enamel is poorly defined to unrecognizable (Fig. 5Q–S).

The right dentary NHMUK PV R37473 has two small ‘cusplets’ placed mesially and distally on the apex edge of the middle tooth (Fig. 5P). Most noteworthy, however, is that this specimen has clear wear facets caused by the occluding maxillary teeth. The wear facets are positioned on the lateral side, at, and just in front of, the base of the dentary teeth. They are most prominent on the bone of the two most posterior teeth emplacements but can also be discerned in similar position at the base of two anterior teeth (Fig. 5N, P). These wear facets appear to match well with the cutting edge of the maxillary teeth and suggest a shearing mechanism between the upper and lower dentition.

Remarks. We attribute the specimens to the Procolophonidae as they show the same type of acrodonty and a splenial was probably present. Initially, we considered that the animal might have been a rhynchocephalian, but the remnant dental shelf found at the base of acrodont teeth in that group is absent in *Smilodonterpeton*. Also, the skirting groove at the base of the teeth of *Smilodonterpeton* is absent in rhynchocephalians and the rhynchocephalians lack a splenial bone. The Meckelian groove lacks the anteriorly narrowing feature of the dentary in rhynchocephalians such as *Gephyrosaurus* (Evans, 1980, fig. 2C), *Diphydontosaurus* (Whiteside, 1986, fig. 28b), *Planocephalosaurus* and *Clevosaurus*. Rhynchocephalian teeth are usually more closely packed together and herbivorous forms have transversely broadened teeth. As it happens, abraded premaxillary teeth of *Clevosaurus* and *Sphenodon* (Fraser, 1982) have been described as being “chisel-like”. However, the teeth here are certainly not from the premaxillae and are fresh and unabraded.

Similar square teeth are seen in Late Cretaceous iguanas (Simões et al., 2015; Apesteguía et al., 2016), but these iguanian teeth are transversely broad in occlusal view (despite lateral appearances), packed close together and often offset. *Smilodonterpeton* teeth also resemble the anterior teeth of the Carnian *Xenodiphyodon petraios* (Sues and Olsen, 1993), whose dentition (as it also has tricuspid posterior teeth) is most similar to the trilophosaur, *Tricuspisaurus*. However, *Smilodonterpeton* is unlikely to be a trilophosaurid as the described dentaries are very shallow and lack tricuspid teeth.

The dentition pattern in *Smilodonterpeton*, of cylindrical or conical teeth anteriorly and broadened teeth posteriorly is often seen in leptopleuronine procolophonids such as *Hypsognathus*, *Leptopleuron* and *Scoloparia* (Colbert, 1946; Sues and Baird, 1998; Säilä, 2010). In such taxa, the posterior teeth differ as their long

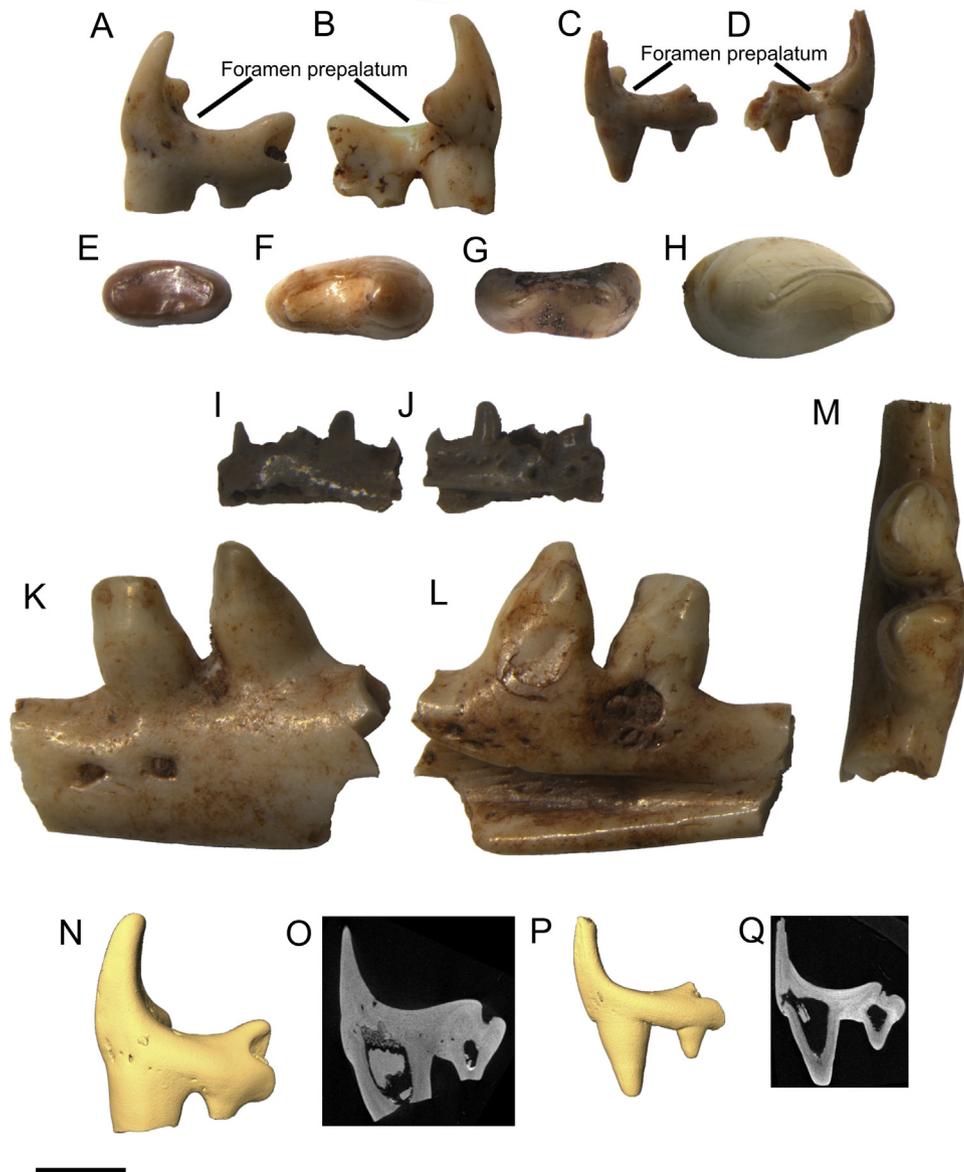


Fig. 6. Leptopleuroninae fossils and CT images. (A, B) Left premaxilla (NHMUK PV R37476) in lateral (A) and medial (B) views. (C, D) Left premaxilla (NHMUK PV R37477) in lateral (C) and medial (D) views. (E–H) Maxillary teeth from NMW 88.12 G.79 in occlusal views. (I, J) Anterior fragment of left dentary (NHMUK PV R37479) in lateral (I) and medial (J) views. (K–M) Left dentary fragment, from NMW 88.12 G.83 in lateral (K), medial (L) and occlusal (M) views. (N, O) Left premaxilla (NHMUK PV R37476) 3D model (N) and CT image (O), showing acrodont dentition. (P, Q) Left premaxilla (NHMUK PV R37477) 3D model (P) and CT image (Q), showing acrodont dentition. Scale bar is 1 mm for A–H and K–Q and 0.5 mm for I and J.

axes are perpendicular to the dentary length. *Acadiella* has a cutting ridge that runs more anteroposteriorly (Sues and Baird, 1998, fig. 1E) and *Kapes* and *Soturnia* have mesiodistally elongated teeth with respect to the upper dentition (Cisneros, 2008), but the apical crests of *Smilodonterpeton* are more in line with each other and the teeth are more transversely compressed and not as cylindrical in shape (Fig. 5J). The dentition is also unlike the procolophonid genera with bulbous teeth such as *Halignia* (Sues and Baird, 1998).

As it cannot be matched with any named procolophonid taxon, we name this as a new genus and species. Further assignment within the Procolophonidae is difficult as the teeth do not closely resemble those of any other known procolophonid. The broadness of the teeth indicates a leptopleuronin, but the orientation of the teeth and the shape and depth of the dentary is closer to other procolophonids.

These *Smilodonterpeton* teeth may have had a similar action to the posterior slicing acrodont teeth of *Diphydontosaurus* and it is therefore plausible that these similarly sized taxa were ecological competitors but the rhynchocephalian replaced the procolophonid in younger fissure deposits. The “chisel-like”, worn teeth of *Clevosaurus* (Fraser, 1982) may reflect particular prey such as coleopterans known to be present in the Late Triassic.

Subfamily LEPTOPLEURONINAE Ivakhnenko, 1979
Genus cf. *Hypsognathus* Gilmore, 1928 or cf. *Leptopleuron* Owen, 1851

Fig. 6

Description. Specimens include numerous isolated premaxillae, bicuspid teeth and dentary fragments. Specimens are all small with jaw fragments up to approximately 4 mm long, broadened teeth up to 2 mm wide and premaxillae up to 2 mm long.

The premaxilla (Fig. 6A–D) outlines the anterior and ventral sides of the nares. The nares are large and roughly circular in shape. Each premaxilla has three rami, one that bears the teeth and two that branch from the most anterior end of the bone, one dorsally and one medially. The dorsal ramus is termed the internarial bar, as it probably connected to the nasal bones between and behind the nares (Säilä, 2010). It is almost as long as the tooth-bearing ramus, but is smooth and slender, becoming increasingly thinner towards the apex. The medial ramus is comparatively short, about half the length of the dorsal ramus; it follows the medial plane and appears to outline the foramen prepalatum (Fig. 6A–D). The premaxilla outlines the anterior and lateral sides of the foramen, and the posterior and medial sides were probably outlined by more posterior cranial bones such as the vomer. The whole shape of the foramen is expected to be a thin oval. The posteriormost end of the tooth-bearing ramus is almost twice as thick dorsoventrally and has two very short branches with rounded ends, forming an ear lobe shape.

The premaxilla bears two teeth, conical in shape and separated by a small, variably sized gap. The anterior tooth is approximately twice as wide at the base and twice as long from the base to the tip than the posterior tooth.

The maxilla is unknown. Transversely widened teeth (Fig. 6E–H), likely from the maxilla, are bicuspid with one lingual cusp and one buccal cusp, and with a slightly curved, thin, blade-like ridge that connects them from tip to tip. Some maxillary teeth distinctly show one cusp, interpreted as the labial cusp, which is larger than the other (Fig. 6E–G), as seen in *Kapes bentoni* (Spencer and Storrs, 2002). The connecting ridge was likely convex anteriorly. In some specimens (Fig. 6E, F), the ridge has been worn away, leaving a wide, shallow, smooth groove between the cusps. The cusps are also partially worn down this way. This wear pattern is also seen in *Hypsognathus* and *Kapes* (Colbert, 1946, fig. 15; Spencer and Storrs, 2002, fig. 3).

The dentary (Fig. 6I–M) possesses at least two large vascular foramina, positioned centrally between the ventral and dorsal surfaces, on the lateral surface (Fig. 6K). There were likely more foramina, but the number can be variable in these procolophonid genera (Spencer and Storrs, 2002). The dentary becomes dorsoventrally shorter anteriorly. In medial view, a deep and dorsoventrally wide Meckelian groove is visible (Fig. 6L). The groove

becomes narrower anteriorly and rotates to the ventral side of the dentary at the anterior apex.

The dentary would have borne approximately six teeth. The two most anterior teeth are similar to those of the premaxilla, with a long-based tooth in front and a far smaller tooth, over twice as small, immediately behind. The original shape of the large tooth is unknown, but its base is long and narrow. The smaller tooth is worn at the apex but is otherwise a narrow column in shape. Posterior to these, the teeth are more like maxillary teeth, but are morphologically different, being less transversely wide and more columnar in shape. The same bicuspid dentition is present, but less well defined and sits on the highest point of the occlusal surface of the tooth. The ridge that connects the cusps has its convex side facing anteriorly in posterior teeth, and anterolaterally in anterior teeth.

All teeth are ankylosed to the bone, indicating an acrodont dentition (Fig. 6N–Q).

Remarks. These fragments are collected together because of their similar dental morphologies to *Hypsognathus fenneri* (Colbert, 1946, fig. 15) and *Leptopleuron lacertinum* (Säilä, 2010, fig. 7), with anterior cone-shaped teeth and transversely broadened, bicuspid posterior teeth. This procolophonid likely belongs to the same subfamily, and so is assigned here to the Leptopleuroninae.

Most procolophonids have previously been described as being protothecodont, having teeth with shallow or fairly deep roots ankylosed into the socket by bone, and with no space for soft tissue between the socket and the base of the tooth (Small, 1997). This differs from ankylothecondont forms whose teeth are deeply rooted such as rhynchosaur (Benton, 1984). However, more recent studies using polarised light microscopy (Cabreira and Cisneros, 2009) and CT scanning (Zaher et al., 2018) in addition to the CT scans demonstrated (Fig. 6O, Q) show that procolophonid teeth lack deep implantation structures such as sockets and roots, indicating that this previous classification of implantation is incorrect and that procolophonids actually bear acrodont dentition.

4.3. Rhynchocephalians

Subclass DIAPSIDA Osborn, 1903

Order RHYNCHOCEPHALIA Günther, 1867

Family SPHENODONTIDAE Cope, 1869

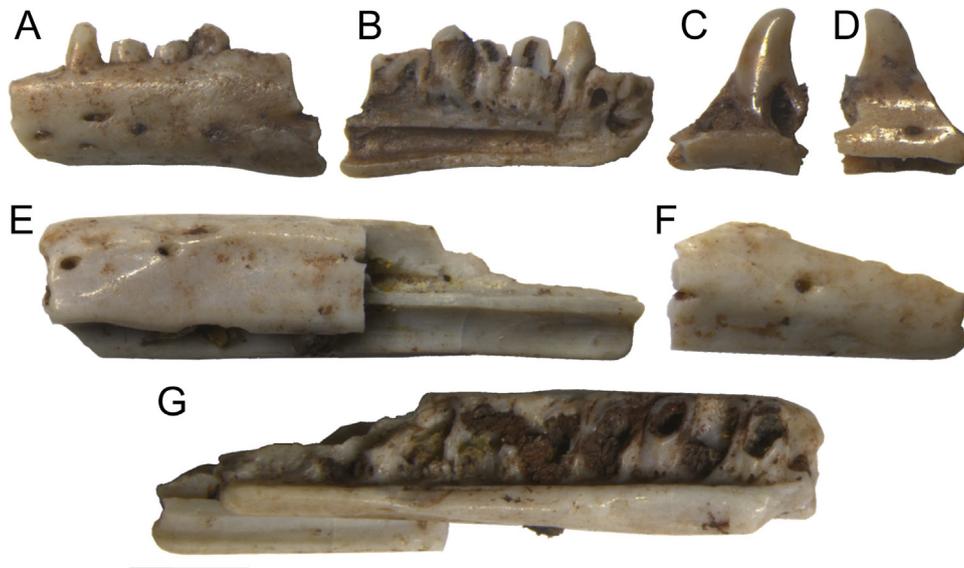


Fig. 7. Cf. *Diphydontosaurus* (Taxon 1) fossils. (A, B) Abraded left dentary fragment (NHMUK PV R37483) in lateral (A) and medial (B) views. (C, D) Isolated right-sided tooth (NHMUK PV R37484) in medial (C) and lateral (D) views. (E–G) Fragmented left dentary (NHMUK PV R37485) in ventral (E, F) and occlusal (G) views. Scale bar is 1 mm.

Genus cf. *Diphydontosaurus* (Whiteside, 1986) Taxon 1
Fig. 7

Description. We describe two dentary fragments and an isolated tooth bearing pleurodont dentition, with similar tooth implantation and replacement to *Diphydontosaurus avonis*. The taxon is about 30% larger and more robust than *D. avonis*, and with fewer teeth per mm. Small (Fig. 7A, B) and large (Fig. 7E–G) dentary fragments are approximately 2.5 mm and 5.5 mm long respectively.

The lateral surface of the small fragment (Fig. 7A) possesses multiple foramina, four anteriorly, which outline a very thin parallelogram, and one more posteriorly. The larger specimen (Fig. 7E–G) preserves a line of widely spaced foramina laterally. The medial surface in the smaller specimen (Fig. 7B) has been worn away, but preserves a deep, well-defined Meckelian groove, which would have been partially obscured by bone. The lateral bone of the larger specimen (Fig. 7E, F) is transversely moderately thick, forming a small, round, well-defined dorsal ridge next to the lateral surface of the tooth base. The dentaries preserve up to nine teeth, which are varyingly complete, with a count of about 2.5 per mm. The smaller jaw has alveoli for seven teeth, three of which are only visible on the medial side (Fig. 7B), otherwise obscured by the lateral ridge. Teeth are long, narrow and recurved, but otherwise conical, lacking serrations and likely had pointed apices before they were broken. Resorption pits are visible towards the base of the teeth in medial view (Fig. 7B).

An isolated tooth (Fig. 7C, D) is also long and recurved, but larger than those on the dentaries. A large hole present medially at the base of the tooth is probably a resorption pit and suggests frequent tooth replacement, as do the many resorption pits of NHMUK PV R37483 (Fig. 7B) and NHMUK PV R37485 (Fig. 7G). Laterally of the isolated tooth, there is a small foramen. The medially orientated bone, which supports the tooth, curves upwards medially to form a small, dorsal ridge which can partially obscure the base of the teeth, though not to so great an extent as the lateral bone. Bone ventral to the tooth row is missing.

Remarks. These specimens probably represent a large, previously undescribed species of *Diphydontosaurus*. Compared with the same region of the dentary, the Ruthin specimens have larger teeth than *D. avonis* but are of similar size (approximately 0.45 mm in mesiodistal width) to those of the 'basal' rhynchocephalian *Gephyrosaurus bridensis* (Evans, 1980, fig. 41). However, the teeth are more frequently replaced than in *Gephyrosaurus*, a feature characteristic of *Diphydontosaurus*, and lack the radial ribbing seen on teeth of *G. bridensis* (BRSUG 29384, Whiteside and Duffin, 2017, fig. 4J). None of these specimens has the posterior region of the dentary where the acrodont teeth occur in *Diphydontosaurus*, so we cannot use this character to confirm identity with that genus.

The specimens also have similarities to a left dentary (BATGM CD2) from Holwell described by Whiteside and Duffin (2017) as *Gephyrosaurus* sp., being either similar to or actually *G. bridensis*. One defining feature of *Gephyrosaurus* (thick, round, medial bone which largely obscures or closes the Meckelian groove) is largely absent on these Ruthin specimens, though is perhaps partially preserved in NHMUK PV R37485. The Ruthin specimens could therefore be early representatives of *Gephyrosaurus*, but the tooth morphology and implantation suggest that they are more likely to be *Diphydontosaurus*.

Genus *Diphydontosaurus* (Whiteside, 1986)
Diphydontosaurus sp. Taxon 2
Fig. 8

Description. Specimens consist of multiple small, isolated skull bones and fragments, primarily maxilla and dentary fragments, but also two jugals and a palatine fragment. The pleurodont tooth-bearing maxilla and dentary fragments are up to 3 mm

long, and thicker, more robust skull bone fragments are up to 3.5 mm long.

The maxilla is mostly very thin and bears a moderately sized foramen along its lateral surface above the tooth row (Fig. 8A). The complete maxilla likely bore more such foramina along the length of the jaw. The ventral surface consists of a medially orientated dental shelf on which sit up to 11 pleurodont teeth (Fig. 8B, D, F, S) with alveoli suggesting an additional one. The anterior maxillary pleurodont dentition forms a more regular sequence with clearly discrete recurved teeth compared to the variable orientation and some development of basal bone of attachment of the dentary teeth (contrast Fig. 8A, B, R, S with the anterior of N and O). The posterior region of the maxilla (Fig. 8A–D) has pleurodont tooth implantation which contrasts with the equivalent area in *D. avonis* where the teeth are acrodont in an alternating size sequence (Whiteside, 1986, fig. 7).

The jugals show an ear lobe shape posteriorly (Fig. 8G–J). They possess three rami, anterior, posterior and posterodorsal. The anterior ramus, presumably the longest in life and the widest dorsoventrally, bears a foramen on the lateral surface, at the posterior end (Fig. 8I). This foramen can also be seen medially, but is positioned more dorsally, at the base of the dorsal ramus. The posterodorsal ramus is the shortest as preserved but, being abraded, this probably was not the case originally. The posterior ramus is the thinnest dorsoventrally but appears to be slightly thicker mediolaterally and is angled at approximately 45° to the posterodorsal ramus.

The lateral edge of the palatine preserves four acrodont teeth; the posteriormost shows a possible nutrient foramen in medial view (Fig. 8L). The bone fragment possesses a foramen in lateral view (Fig. 8K) and the teeth sit, below a medial ridge, on a ventrally directed ridge of bone (Fig. 8L).

The dentary is long and thin, with the lateral surface bearing narrow foramina along its length (Fig. 8N). The medial surface reveals a dental shelf dorsally whilst the ventral region curves medially forming a well-defined Meckelian groove ventrally outlined by an inframeckalian lip (Fig. 8O, Q). The tooth-bearing shelf projects further medially than the lip. This specimen bears up to nine pleurodont teeth, but has alveoli for ten (Fig. 8N, O). Posteriorly, foramina are not preserved, and the dentary becomes thicker dorsoventrally as the dorsal surface of the bone curves upwards. The tooth-bearing region of the bone is about 1.25 mm thick, excluding the teeth, but is almost 2 mm thick most posteriorly. The lateral ridge which obscures the base of the teeth in lateral view is absent here. The inframeckalian lip of the bone becomes less well-defined posteriorly.

The pleurodont teeth are long, thin and recurved. They lack serrations, and small resorption pits are often visible on the medial surface of their bases (Fig. 8B, F, O) suggesting frequent tooth replacement. A ridge of bone on the lateral side of the maxilla obscures the basal third to half of the lateral surface of the teeth, depending on the tooth height. About five pleurodont teeth are present per mm, which is 20% greater than in *D. avonis*. Posteriorly, where the tooth obscuring ridge is absent (Fig. 8T–V), the teeth are acrodont and much broader at the base, becoming shaped like short, wide cones. The posterior acrodont dentary tooth base of the Ruthin specimen is about 0.8 mm mesiodistally wide in labial view which is very slightly larger than in *D. avonis*. The posteriormost three teeth of *D. avonis* were emplaced at an angle of about 10° from the jaw axis (Whiteside and Duffin, 2017), but here the tooth is worn posteriorly, and such measurements cannot be taken.

Remarks. We identify the partial palatine fossils as *Diphydontosaurus* rather than *Planocephalosaurus* based on their small size. Currently, *D. avonis* is the only named species, but the apparently greater frequency of pleurodont teeth per unit length in the

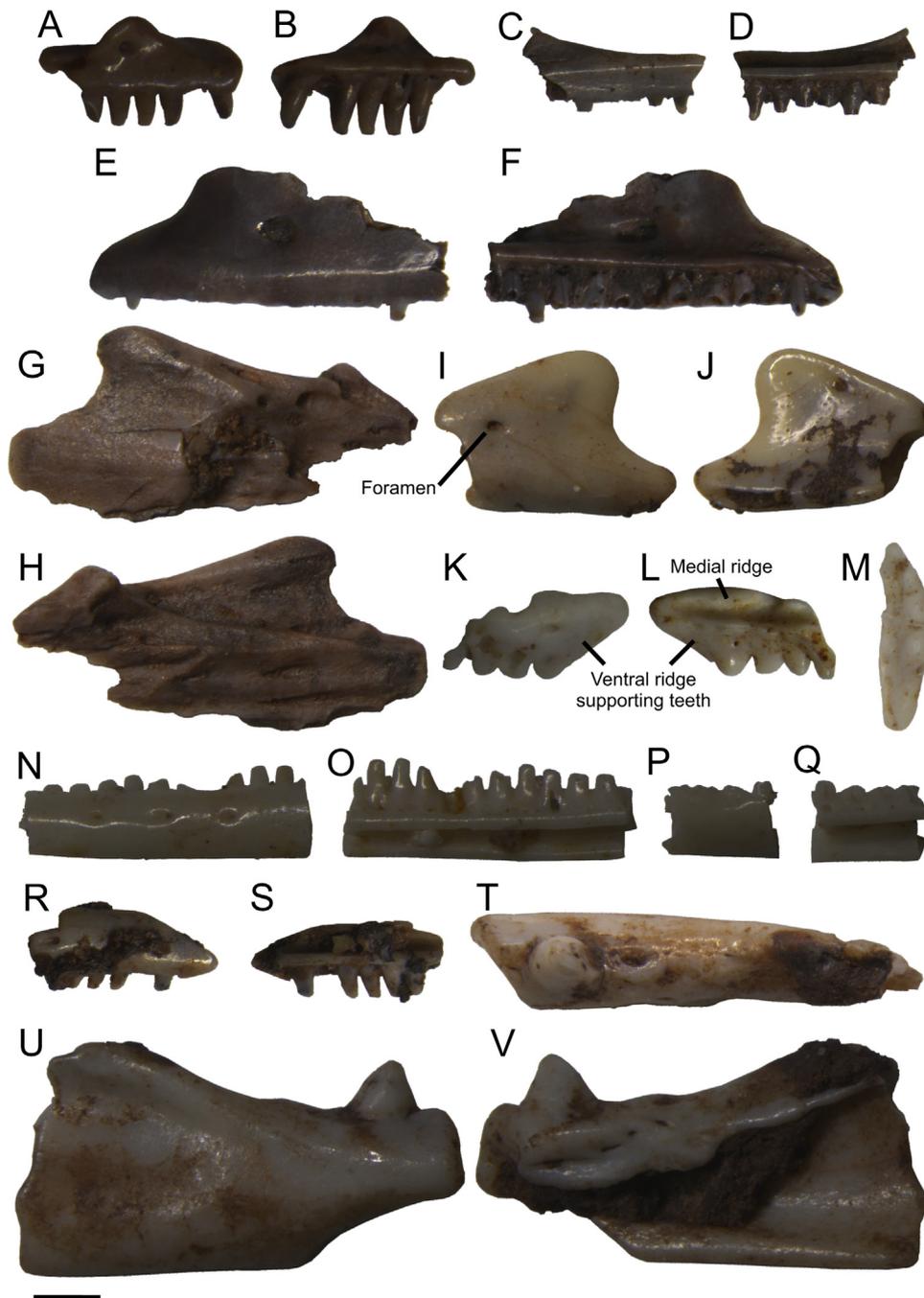


Fig. 8. *Diphodontosaurus* (Taxon 2) fossils. (A, B) Right maxilla fragment bearing pleurodont dentition, from NMW 88.12 G.68, in lateral (A) and medial (B) views. (C, D) Left maxilla fragment bearing pleurodont dentition (NHMUK PV R37486) in lateral (C) and medial (D) views. (E, F) Left maxilla fragment bearing pleurodont dentition (NHMUK PV R37487) in lateral (E) and medial (F) views. (G, H) Right jugal from NMW 88.12 G.81 in lateral (G) and medial (H) views. (I, J) Left jugal fragment from NMW 88.12 G.81 in lateral (I) and medial (J) views. (K–M) Right side palatine tooth row fragment (NHMUK PV R37488) in lateral (K), medial (L) and occlusal (M) views. (N, O) Right dentary fragment bearing pleurodont dentition, from NMW 88.12 G.64, in lateral (N) and medial (O) views. (P, Q) Right dentary fragment bearing pleurodont dentition, from NMW 88.12 G.64, in lateral (P) and medial (Q) views. (R, S) Right maxilla fragment bearing pleurodont dentition (NHMUK PV R37489) in lateral (R) and medial (S) views. (T–V) Posteriormost fragment of right dentary preserving one acrodont tooth and one alveolus, from NMW 88.12 G.65, in occlusal (T), lateral (U) and medial (V) views. Scale bar is 0.5 mm.

maxilla and dentary and the greater posterior extent of pleurodont dentition in the maxilla in the Ruthin specimens suggests they might represent a different species. However, as we have evidence of both pleurodont and acrodont marginal teeth on the jaws we feel that it is reasonable to refer the specimens to the genus rather than just cf. *Diphodontosaurus* as in taxon 1.

Genus *Planocephalosaurus* Fraser, 1982
Planocephalosaurus cf. *robinsonae* Fraser, 1982
 Fig. 9

Description. The collection consists of three premaxillae, a jugal and squamosal, three palatine tooth rows, four maxillary bone or tooth fragments, multiple dentary fragments and a claw. Skull fragments are up to 4.5 mm long, but most tooth-bearing bones are approximately 2–3 mm.

The premaxilla (Fig. 9A, B) forms the ventral and anterior margins of the nares, with a dorsal process and a posterior process bearing teeth. The narial margin is smooth. The lateral surface is smooth and unornamented. Medially, dorsal of the teeth and posterior to the dorsal ramus is a short palatal shelf. There are

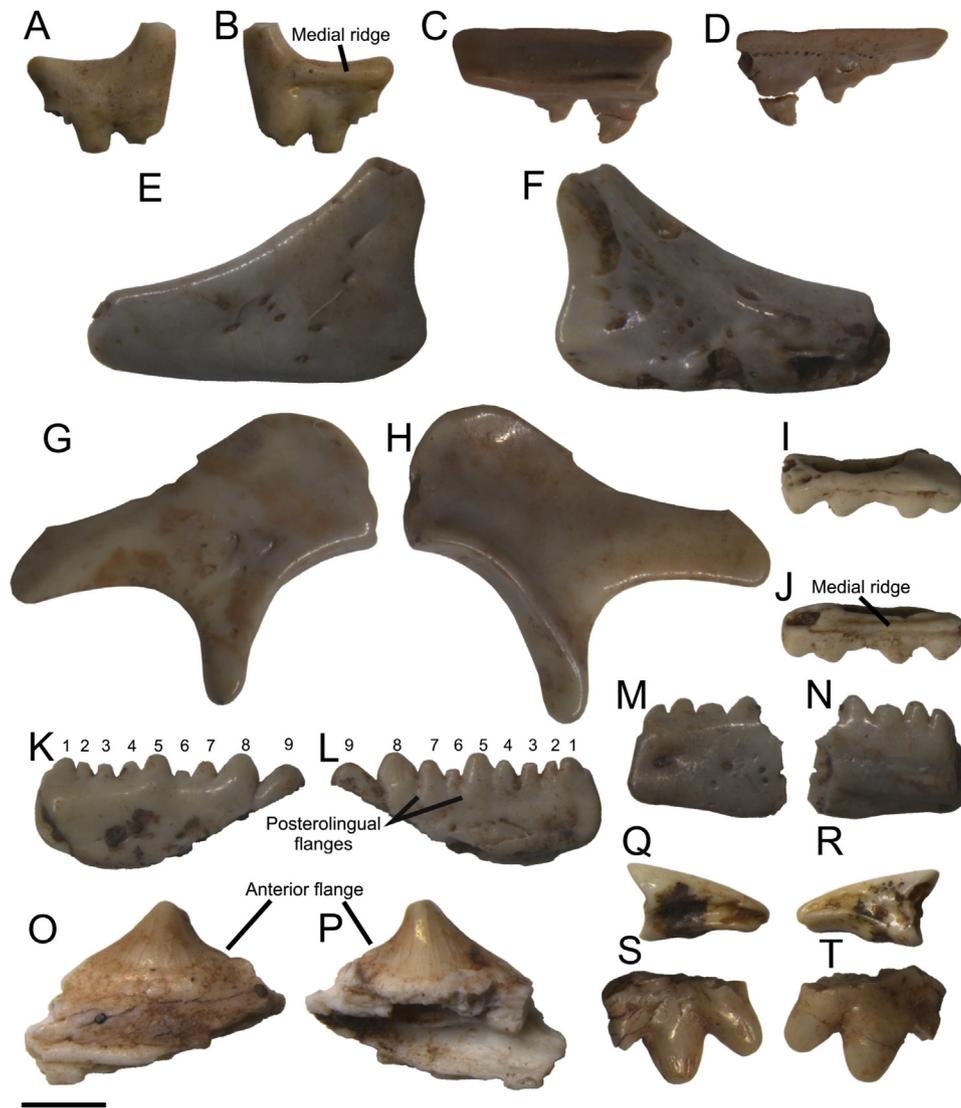


Fig. 9. *Planocephalosaurus* fossils. (A, B) Abraded right premaxilla (NHMUK PV R37490) in anterior (A) and medial (B) views. (C, D) Right maxilla fragment bearing acrodont dentition (NHMUK PV R37491) in lateral (C) and medial (D) views. (E, F) Left jugal (NMW 88.12 G.70) in lateral (E) and medial (F) views. (G, H) Left squamosal (NMW 88.12 G.72) in lateral (G) and medial (H) views. (I, J) Interpreted right side palatine tooth row (NHMUK PV R37492) in lateral (I) and medial (J) views. (K, L) Left dentary fragment bearing acrodont dentition, from NMW 88.12 G.67, in lateral (K) and medial (L) views. (M, N) Left dentary fragment bearing acrodont dentition, from NMW 88.12 G.67, in lateral (M) and medial (N) views. (O, P) Posteriormost tooth of right dentary (NHMUK PV R37493) in lateral (O) and medial (P) views. (Q, R) Claw (NMW 88.12 G.93) in opposite lateral views. (S, T) Right? premaxilla (NHMUK PV R37339) in medial/posterior (S) and anterior (T) views. Scale bar is 1 mm for A–D, I–T and 2 mm for E–H.

three, variably broken, conical teeth with the acrodont implantation (where the palatal shelf is visible) typical of *Planocephalosaurus*. The anteriormost tooth preserves less than half its height, the second approximately half its height and the posteriormost only its base. The second tooth shows radial ribbing medially. This medial ribbing is observed in the medial view of specimen NHMUK PV R37339 (Fig. 9S) which also has pronounced wear facets formed by occlusion with the anterior dentary teeth. Examining carefully under a good microscope reveals a thin rim of enamel forming the outside of each tooth. The anterior view of the specimen is shown in Fig. 9T.

The maxilla is described from a single fragment bearing two teeth (Fig. 9C, D). These teeth are interpreted as the flanged tooth series (Fraser, 1982), where each tooth bears a posterolingual flange, and they are recurved towards the apex.

The jugal fragment (Fig. 9E, F) is larger and more robust than that of *Diphydontosaurus* and lacks the large foramen found in the genus (see Whiteside 1986; fig. 15a). The fragment consists of the

main body with the thin posterior ramus almost completely missing and the thicker anterior and posterodorsal rami (of similar thickness) the length of which have largely been lost. The missing posterior ramus would have acted as the lower temporal bar of the lower temporal fenestra. The specimen lacks lateromedially thin bone that would indicate contact with another bone, indicating that such contacts occurred towards the distal ends of the jugal rami. Laterally, the jugal has nine small foramina, widely scattered across its surface. In medial view (Fig. 9F), a well-defined ridge of lateromedial bone is present from the anterior ramus to the posterodorsal one.

The squamosal fragment (Fig. 9G, H) consists of the ventral ramus, the anterior ramus, with most of the bone that was overlapped by the postorbital and jugal (Fraser, 1982) broken off; and the base of the dorsoventrally wide dorsal ramus. The size and shape of this specimen coincides with the description of Fraser (1982, e.g. fig. 1). Four foramina are present on the lateral surface (Fig. 9G); three outlining a triangle between the

ventral and anterior rami, about halfway up its dorsoventral height. The ventral ramus was originally described (Fraser, 1982) as having followed the lateral edge of the quadratojugal, with only one of the many described specimens possessing an anteriorly expanded ventral end to contact the jugal. This specimen does not have this ventral extension and instead seems to have been an attachment ramus to the quadratojugal and quadrate only. In lateral view, the anterior ramus is long, flat and rounded distally. The area of the anterior ramus that in life would have been obscured by the jugal and postorbital is wide and lateromedially thinner than the rest of the bone. This thinner bone extends 3/4 the length of the dorsal surface of the bone fragment. In medial view, a bony shelf is present around the concave-shaped, posterior edge that would have connected to the quadrate (Fraser, 1982).

The single preserved palatine tooth row (Fig. 9I, J) possesses up to four, wide-based, conical acrodont teeth which sit on a narrow ridge of bone. Laterally, the teeth are flattened and sometimes preserve wear facets. The tooth row would have run parallel to the maxillary dentition (Fraser, 1982). A small ridge of bone is faintly recognisable medially at the base of the teeth.

The dentary bears a medial, irregular line of fine foramina along its lateral surface (Fig. 9K, M). A moderately sized foramen is also preserved towards the anterior end. The Meckelian groove is positioned ventrally but becomes more ventrolateral posteriorly (Fig. 9N). The biggest fragment (Fig. 9K, L) preserves nine worn, smooth and often rounded, acrodont teeth. The anteriormost tooth is very slightly recurved but the others are more conical in appearance with the largest teeth posteriorly positioned. Teeth 2, 3 and 4 are very thin and flat in appearance, increasing slightly in size posteriorly. Teeth 5 and 7 are considerably larger than the teeth anterior to them and show moderately defined posterolingual flanges, although no such feature was noted by Fraser (1982). Tooth 6 deviates from the general pattern of increasing size posteriorly, being much smaller than its neighbours. Of the teeth present, the two most posterior are considerably larger than the rest, being over twice as high and wide. Wear facets lingually on the big posterior teeth indicate occlusion with palatine teeth. The original description (Fraser, 1982) states that the teeth are radially ribbed. This is best seen on the medial surface of the most posterior teeth. The teeth appear more laterally compressed in lingual view than in labial view. The large posteriormost tooth preserved on the right dentary (Fig. 9O, P; about 2.4 mm wide at the base) is a characteristic feature of *Planocephalosaurus* (Fraser, 1982). The base is greatly broadened, and the apex is angled at approximately 70° from the dorsal surface of the dentary, pointing anterodorsally. A slight flange is present at the anterior base of the tooth.

A single claw (Fig. 9Q, R), c. 2 mm long, is referable from its similar shape and size to *Planocephalosaurus*. In lateral and medial views of the claw, indistinguishable from each other (Fig. 9Q, R), the posterior end is crescent-shaped, where it would have attached to the phalange. The ventral surface is expanded, forming a ridge below the lateral depression, which fills the lateral and medial faces (Fig. 9Q, R). The apex of the claw is missing. The dorsal half of the claw, dorsal to the groove, is narrow and pointed anteriorly.

Remarks. The Ruthin specimens have three teeth per premaxilla whereas four teeth are characteristic of *Planocephalosaurus robinsonae* from Cromhall (Fraser 1982). However, *Planocephalosaurus* premaxillae from fissure 2 at Tytherington also have three teeth (Mussini et al., 2020) but other *Planocephalosaurus* elements found there are otherwise very similar to those of Cromhall. Therefore, the Ruthin *Planocephalosaurus* may possibly be a different species, but the overall features of our specimens suggest they are compatible with *P. robinsonae*. Previously suspected *Clevosaurus* remains (Fraser, 1994) may be posterior dentary teeth of *Planocephalosaurus*.

4.4. Archosauromorphs

Clade ARCHOSAUIROMORPHA Huene, 1946

Family TRILOPHOSAURIDAE Gregory, 1945

Genus *Tricuspisaurus* Robinson, 1957b

Tricuspisaurus thomasi Robinson, 1957b

Fig. 10

Description. The collection consists exclusively of teeth or tooth-bearing bones, more dentary than maxilla, and there is no premaxilla specimen. Only one near complete bone, a single dentary originally described by Robinson (1957b), is preserved (Fig. 10D, E). All other bone remains are fragmentary.

The maxilla specimen reported by Robinson (1957b, p. 290), termed P.L.R. 500, could not be located in the NHMUK collections, so we use the published description. The maxilla (Fig. 10A) is 16 mm long and 5 mm tall. It is badly damaged posterodorsally and in the anterior region. The dorsal surface, where preserved, appears level. The ventral surface of the bone, also level, is parallel with the dorsal surface, maintaining a constant, low maxillary thickness, until the maxilla turns ventrally by approximately 45°. The maxillary wall thickens posteriorly, suggesting a jugal ramus may have been present (Robinson, 1957b, p. 288).

The tooth row of the maxilla is 14 mm long and probably had twelve teeth, of which only six are relatively complete. Each tooth, at its base, possesses a 'neck' where it becomes notably narrower (Fig. 10A, B) and giving a pronounced bulbous appearance. This is best defined in larger, more posterior teeth. The first tooth is small and circular in cross-section. The following two teeth are also small, but transversely widened. Such widened teeth are positioned with their longest axes perpendicular to the edge of the jaw. The rest are probably tricuspid, but only the two teeth anterior of the posteriormost tooth have well preserved crowns. The posteriormost tooth is broken, but small. The largest maxillary tooth is no. 9 (Fig. 10A), at 2 mm wide. More posterior teeth deviate from the general alignment, with their lingual sides being positioned more anteriorly. The ventral angle of the occlusal surface of the dentary also means that such teeth are angled with their cusps pointing more anteroventrally.

The dentary (Fig. 10D, E) is 27 mm long, 10 mm tall and mostly very thin, the thickest part being the tooth-bearing region, approximately 3.5 mm wide. The anterior end is damaged anteriorly and laterally, but the occlusal surface is preserved. The symphysis is mostly preserved suggesting the anterior end is more or less complete. The ventral surface is a transversely thin edge. The lower posterior end is damaged but appears to retain this thin edge. The coronoid process is tall and well-rounded.

The dentary (Fig. 10D, E) bears in total nine teeth and alveoli; the anteriormost of these teeth has been misplaced in preparation so the cusp is directed anteriorly (rather than dorsally) and the base posteriorly. Anterior to the definite teeth sockets there is rough area on the crest which bears about five very small 'cusps' which may be highly worn very small teeth. Without removing the lacquer and getting a more detailed CT scan it is not possible to confirm or refute this idea but there also appear to be some tiny alveoli. The tooth row is 17.5 mm long. In occlusal view, the dentary at the anterior end is very narrow labiolingually and has a rough surface, likely a beak (also suggested by Robinson, 1957b). Posterior to the 'beak' region, about one fifth up its length, the dentary widens slightly and flattens. The dorsal surface carries circular alveoli for two small anterior teeth, but these teeth are not preserved. The following tooth is transversely widened, approximately twice as wide as long. Sculptural features are unclear. The next three teeth are tricuspid and possess fine, well-defined ridges anteriorly and posteriorly to the cusps, which disappear into the tips of the buccal and lingual cusps. These teeth are slightly larger towards the posterior end. A triangular gap separates them from

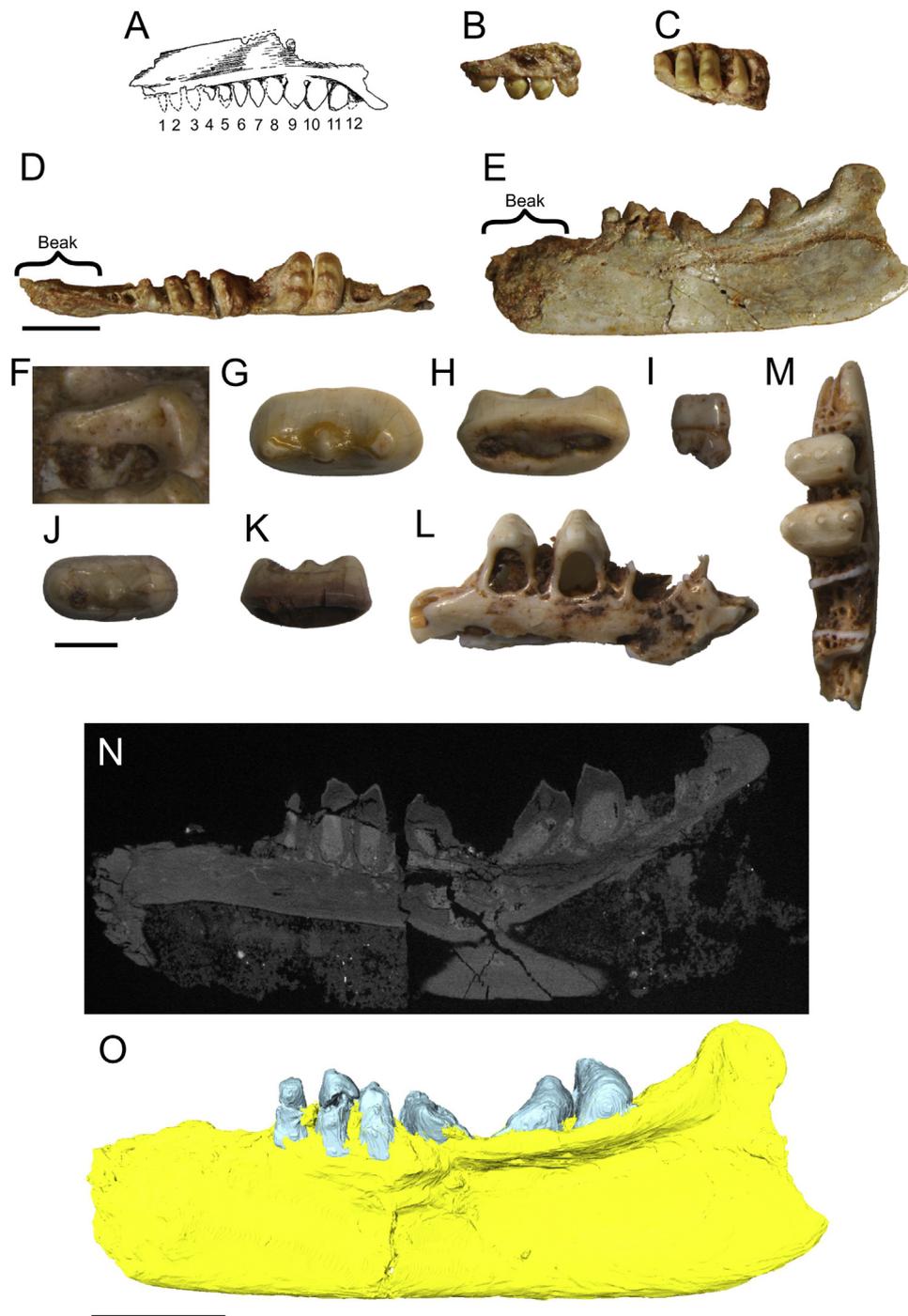


Fig. 10. *Tricuspisaurus* fossils, diagrams and CT images. (A) Diagram of the left maxilla (P.L.R. 500) in lateral view. Image from [Robinson \(1957b\)](#). (B, C) Maxilla fragment (NHMUK PV R6107) in lateral (B) and occlusal (C) views. (D, E) Holotype left dentary (NHMUK PV R6106) in occlusal (D) and lateral (E) views. (F) Damaged tooth from maxilla fragment (NHMUK PV R6107) in anterior view showing the abraded surface and exposed pulp cavity. (G, H) Isolated tricuspid tooth, from NMW 88.12 G.73, in occlusal (G) and ventrolateral (H) views. Cingula on this tooth are poorly defined. (I) Tricuspid tooth with a root, from NMW 88.12 G.73, in lateral view. (J, K) Tricuspid tooth, from NMW 88.12 G.73, in occlusal (J) and ventrolateral (K) views. Cingula on this tooth are well-defined. (L, M) Left dentary fragment with teeth, from NMW 88.12 G.36, in lateral (L) and occlusal (M) views. (N, O) Holotype dentary (NHMUK PV R6106) CT image (N) and model (O), showing protothecodont dentition. Scale bars are 5 mm for A–E and N–O and 1 mm for F–M.

the next tooth behind. Although [Robinson \(1957b\)](#) and [Spielmann et al. \(2008\)](#) suggest that the gap was edentulous it is plausible that a tooth was present in life. There are some splinters, possibly from a missing tooth present in the socket but it is also true that there is no discernible pulp cavity and the bone of attachment observed in the posterior missing tooth is absent here so the evidence is equivocal. However, no other specimen has such a gap (NHMUK PV R6108, NMW 88.12 G.36) and the abnormal teeth positioned

anteriorly and posteriorly to the gap are not recognised anywhere else.

One feature present on the lower lateral side of the teeth immediately anterior and posterior to the gap, are the prominent vertical ridges of bone of attachment ('fibrous bone' of [Robinson 1957b](#)). All teeth anterior to the gap are angled with the buccal side slightly more posterior than the lingual side. The two teeth posterior to the gap are the largest, equal in width at 4 mm, and

positioned where the occlusal surface of the jaw turns dorsally by about 12°. These two teeth have relatively larger, more well-defined cusps, have very slight ridges between the cusps, are angled with their longest axes more perpendicular to the edge of the jaw and have a large, anterior slope. The slope of the more anterior tooth has a large bulge anterobuccally and a small one anteromedially. The anterior cingulum is poorly defined. The anterior slope of the second tooth is proportionally smaller and both cingula are poorly defined. The unusual shape of these two teeth may have been caused by the triangular gap, perhaps by occlusion with an abnormal tooth on the maxilla (Robinson, 1957b, p. 290). The posteriormost tooth is missing, but likely followed the same pattern as the two in front. This tooth sits just anterior to the coronoid process.

All loose teeth (Fig. 10G–K) are tricuspid. Where teeth are missing (Fig. 10D), sockets are visible, with a well-defined smooth surface ridge outline. Cross sections of the sockets reveal the edges of the teeth to be ankylosed to the bone (Fig. 10L), indicating acrodont dentition, as suggested by Fraser (1986). However, a root was present on a small tricuspid tooth (Fig. 10I), indicating a partially thecodont dentition. Additionally, CT scans of the dentary (Fig. 10N) reveal that the teeth were deeply embedded into the bone with large pulp cavities. Taking these points together, *Tricuspisaurus* evidently showed protothecodont tooth implantation.

Remarks. The holotype dentary specimen NHMUK PV R6106 is by far the best preserved of all known *T. thomasi* remains. The maxilla described by Robinson (1957b) is lost. In the original description, NHMUK PV R6107 was not specified as a maxilla or dentary. Fig. 3 of that description shows a lateral view of the maxilla described, which displays teeth with a basal 'neck'. NHMUK PV R6107 also shows this condition, whereas the holotype dentary does not. We, therefore, describe it as a maxilla fragment.

The original description (Robinson, 1957b) includes reference to a transverse ridge on the crown of a tooth on specimen NHMUK PV R6107 (Fig. 10B, C, F). We consider two interpretations of this tooth. Firstly, Robinson's (1957b), description is 'the crown of this type of tooth bore a transverse ridge, sometimes curving anteriorly at its buccal end. She further added that 'One or two isolated teeth of this type are to be found in the Cardiff Museum collection'. Thus, one interpretation is that the blade-like morphology of the tooth, albeit with a very poorly developed or rudimentary tricuspid morphology, is as it appears. However, one of us (M.S.), suggests another view, that the shape relates to breakage or tooth wear, likely occurring in life. The pulp cavity is partly visible in the anterior view of the tooth (Fig. 10F). In this interpretation, the tooth would have been clearly tricuspid, with an anterior and posterior ridge, like the others.

The triangular gap on the holotype specimen has been noted as a feature of *Tricuspisaurus* (Spielmann et al., 2008). So far, no other specimen of *Tricuspisaurus* or a close relative has such a gap or any recognised form of occlusion where the teeth occlude with the bone/gum. Therefore, we argue that the gap could reflect damage or individual conditions and would be an equivocal autapomorphy for the species.

Tricuspisaurus has been the subject of debate since Fraser (1986) argued that it might be a procolophonid based on similarities in dentition. However, *Tricuspisaurus* shows protothecodont rather than acrodont tooth implantation and possesses more uniform dentition. The hypothesised beak is a feature seen in Trilophosauridae, including *Trilophosaurus* from North America, but not Procolophonidae. Other morphological similarities between *Tricuspisaurus* and *Trilophosaurus* include the possession of tooth rows with similar numbers of transversely broadened tricuspid teeth and tooth-bearing bones appearing triangular in shape occlusally with teeth sockets being larger more posteriorly. *Trilophosaurus* also has sharp edges between the cusps of its teeth

(Heckert et al., 2006, fig. 3; Spielmann et al., 2008, figs. 4, 8 and 9). *Tricuspisaurus* possesses these on some of its teeth, but they are reduced and, although sometimes hard to see, are confirmed here. In conclusion, we confirm that *Tricuspisaurus* is a trilophosaurid and not a procolophonid.

Tricuspisaurus has been reported from Cromhall and Tytherington, on the basis of tricuspid teeth. However, examination of the teeth found at Cromhall (BRSMG Cf609–611, 644, 645) suggests they are actually from an undescribed procolophonid. These teeth have the same morphology as those found at Tytherington (Whiteside and Marshall, 2008), suggesting that neither locality yields *Tricuspisaurus*.

Subdivision ARCHOSAURIA Cope, 1869
Superorder CROCODYLORMORPHA Hay, 1930
Suborder SPHENOSUCHIA Huene, 1942
Small crocodylomorph

Fig. 11

Description. Specimens of a small crocodylomorph similar to *Terrestrisuchus* include 12 jaw fragments, over 60 teeth and multiple osteoderms. Preserved teeth are up to 3 mm tall, osteoderms up to 4.5 mm long and jaw fragments up to 4 mm long.

The medial view of a left dentary fragment (NHMUK PV R 37531; Fig. 11A) demonstrates the thecodont implantation (with sockets) of the teeth of archosaurs. Medially, just below the tooth row (Fig. 11A) is the Meckelian canal. The tooth row preserves six complete tooth sockets with two more, incomplete, at each end; all lack teeth. Fraser (1985, fig. 20) featured a similar jaw from Cromhall Quarry that he identified as a pseudosuchian and another from Ruthin (Fraser, 1986, fig. 8b) that he identified as a 'thecodontian'.

The ventral surface of a fragment of the anterior end of a right dentary (Fig. 11B), is covered in variably sized, but mostly fine, circular, deep pits, interpreted as sensory pits found in skulls of modern crocodylians. Medially, just below the tooth row (Fig. 11C) on the dorsal surface, is a smooth area interpreted as the symphysis. In dorsal view (Fig. 11C), internal, largely porous bone is visible. Anteriorly, the dorsal surface of the ridge is also covered in fine pits, though it is unclear whether they are sensory or blood vascular foramina or both. Given their size, high abundance and relative position, they are likely to have been sensory. The tooth row preserves up to eight tooth sockets, small and lacking teeth. The six most anterior sockets (or alveoli) are more circular, while more posterior sockets are sub-rectangular, suggesting conical and serrated teeth were positioned here, respectively.

One specimen (CAMZM 12; Fig. 11D) is a large tooth that fulfils the criteria that Crush (1980) specified for *Terrestrisuchus* teeth. He described the recurved pointed teeth as having well-developed oval roots, medio-laterally flattened crowns, a carina and serrations on mesial and distal edges. However, archosaur teeth are very variable, and it is difficult to assign to any taxon (Nesbitt, 2011) such as pseudosuchian or dinosaur with any degree of confidence. Therefore, CAMZM 12 could be from a coelophysoid rather than a crocodylomorph, so we refer the specimen to *Terrestrisuchus* very tentatively.

Additional teeth that can possibly be assigned to a small crocodylomorph (Fig. 11E–O) have several morphologies. They are variable in height, but most are not taller than c. 2 mm. All are recurved and pointed at the apex. Some are narrow, producing an anterior and posterior edge serrated from apex to base with at least 10 serrations per mm, but almost all are preserved with serrated edges worn smooth. The recurved posterior edge is sharper than the anterior. Other teeth are almost perfectly circular in cross section and appear to lack serrations. One tooth preserves a swollen apex, likely an example of abnormal growth (Fig. 11K, L). Other teeth are of a morphology that is midway between these

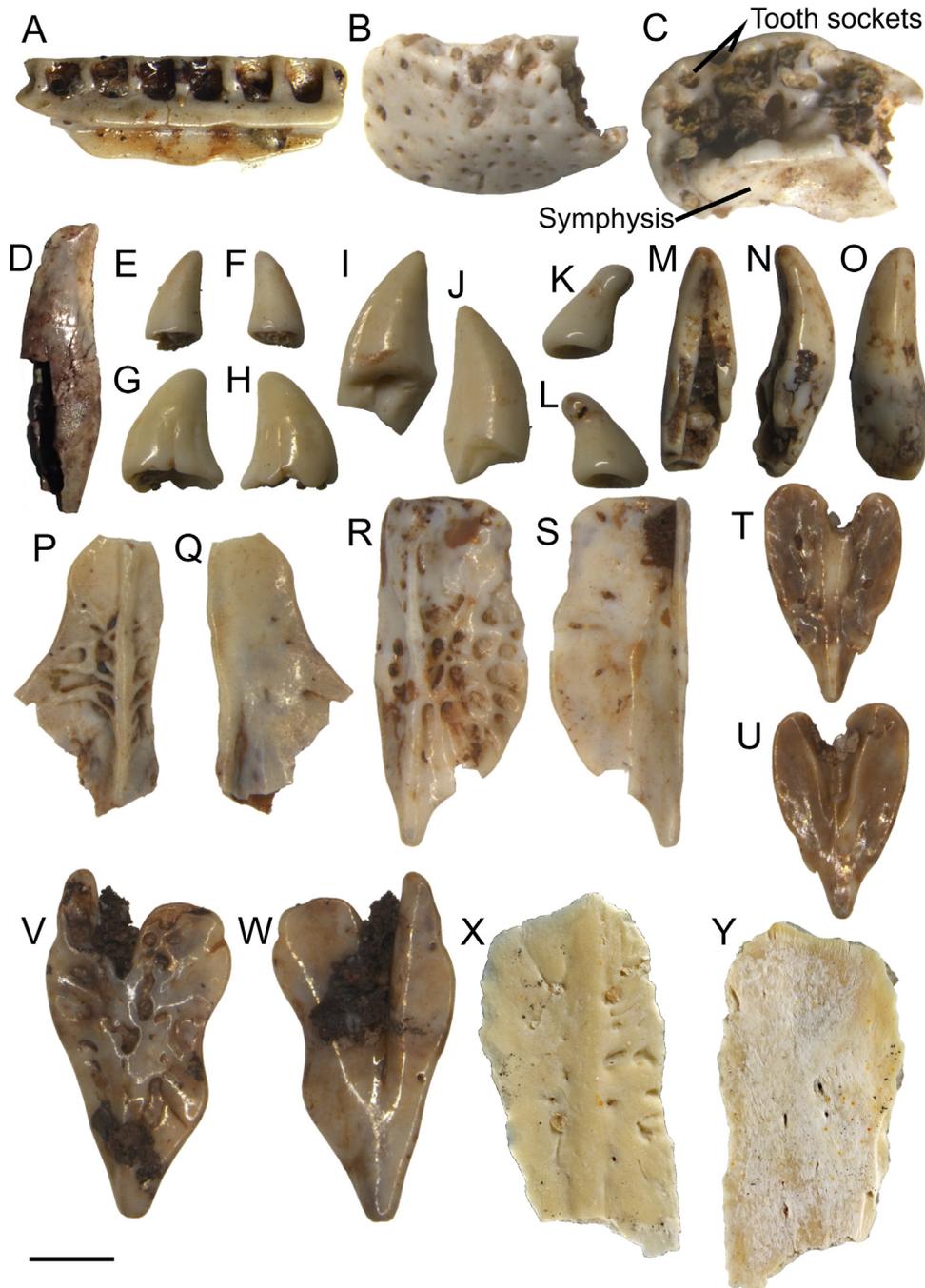


Fig. 11. Small crocodylomorph fossils. (A) Right dentary fragment with six complete sockets (NHMUK PV R37531) in medial view. (B, C) Jaw fragment (interpreted anterior of a right dentary) (NHMUK PV R37494) in ventral (B) and dorsomedial (C) views. (D) Possible *Terrestriusuchus* tooth (UCMCZ 12) in left lateral view. (E, F) Lateral/medial views of conical tooth NMW 88.12 G.77. (G, H) Lateral/medial views of sharp-edged tooth, from NMW 88.12 G.77. (I, J) Lateral/medial views of tooth, NMW 88.12 G.77 with carina present (I). (K, L) Lateral/medial views of conical tooth NMW 88.12 G.77, displaying an abnormal growth at the apex. (M–O) Conical tooth (NHMUK PV R37495) in posterior (M), right lateral (N) and anterior views (O). (P, Q) Keel-bearing osteoderm, from NMW 88.12 G.31.8, in dorsal (P) and ventral (Q) views. (R, S) Keel-bearing osteoderm, from NMW 88.12 G.31.8, in dorsal (R) and ventral (S) views. (T, U) Heart-shaped osteoderm, from NMW 88.12 G.31.8, in dorsal (T) and ventral (U) views. (V, W) Heart-shaped osteoderm from NMW 88.12 G.31.8, in dorsal (V) and ventral (W) views. (X, Y) Keel-bearing osteoderm from Pant-y-ffynnon (NHMUK R.10002) in dorsal (X) and ventral (Y) views. Scale bar is 1 mm for A–C and E–W and 2 mm for D, X and Y.

two. Some show a flat to concave surface where they split (Fig. 11M–O), anteriorly or posteriorly, often resulting in a medial line being visible in the dentine.

Two morphotypes of osteoderms are described here. The first scute morphotype resembles that of *Terrestriusuchus* (NHMUK P V R10002; Fig. 11X, Y) in morphology and size range. It is sub-rectangular in shape, and variably possesses pits and furrows (Fig. 11P–S). Pits are generally sparse, most prominent around the keel and they vary in shape and size, being generally small and

narrow. Pits sit perpendicularly to the well-defined keel running medially along the external surface, parallel to its longest axis. Osteoderms are moderately to strongly folded, at an angle of approximately 90° – 130° . The keel runs along the fold axis. Broader specimens often display more abundant pits, equally distributed across the external surface, and the keel is less well preserved. The dorsal surface is often worn smooth and/or bone is partially missing on the lateral side of the keel. One large specimen (NMW 88.12 G.62) lacks dorsal pits and the ventral surface is covered in

shallow, sub-circular/sub-rectangular pits. The smooth ventral surface was probably abraded, revealing the internal, pitted bony texture, as seen in other osteoderms.

The second osteoderm morphotype, with a similar size range to the first, is much rarer and shaped like a tall, narrow heart (Fig. 11T–W). A thin smooth ridge runs down the dorsal midline of the osteoderm with a well-defined furrow running in line with it on the ventral surface. The furrow disappears and the ridge becomes better defined towards the pointed, inferred anterior end. Given the furrows and ridges, it seems likely that osteoderms of this morphotype partially overlapped each other. A large fragmentary osteoderm (from NHMUK OD10) preserves the same groove and ridge seen in this morphotype.

Remarks. We assign these teeth and osteoderms to a small-crocodylomorph, based on the observation that they are all archosaurian, and that some of them are very similar to *Terrestrisuchus* remains. However, we cannot with any degree of confidence assign more than a few (e.g. Fig. 11D, P–S) to this genus. Tooth morphology in *Terrestrisuchus* varies along the jaw (Crush, 1984, fig. 2A). A maxilla fragment of the type specimen (NHMUK P34/1a) possesses tooth sockets that are rounded anteriorly but narrower posteriorly. Teeth are taller and anteroposteriorly narrower anteriorly, but shorter and broader posteriorly. This is seen more clearly in NHMUK PV R7557. Similar tooth morphologies from Cromhall, labelled “Thecodont”, but likely crocodylomorph, include a broad and recurved tooth (NHMUK R8611) and a narrower, taller tooth (NHMUK R8610). Both preserve very fine serrations on both the anterior and posterior edges. Fraser (1986, fig. 8c) also figures a serrated archosaur tooth from Ruthin. The number of teeth from Ruthin associated with this taxon is large, but crocodylomorphs were probably continuously replacing teeth throughout their lifetime.

As for osteoderms, Crush (1988, pp. 146–147, fig. 10C) describes the thoracic scutes as ‘basically leaf-shaped with an anterior peg that fitted into a triangular groove on the ventral surface of the adjacent plate. Each scute bears a prominent ridge along its midline and is sculptured medial to this ridge. A muscle scar is present postero-laterally.’ The scutes described here morphologically resemble those assigned to *Terrestrisuchus* (NHMUK R10002; Fig. 11X, Y). These scutes also resemble mid-dorsal osteoderms in other sphenosuchian crocodylomorphs (Sues et al., 2003, fig. 4). Caudal osteoderms are not recorded for *Terrestrisuchus*. By comparison, in rauisuchians (Cerda et al., 2013, fig. 1E), including taxa related to Crocodylomorpha, there is a single dorsal row of heart-shaped osteoderms over the tail, like those we assign to the *Terrestrisuchus*-like crocodylomorph here (Fig. 11T–W).

Subdivision ARCHOSAURIA Cope, 1869

Archosaur teeth

Numerous teeth from Ruthin (Fig. 12A–G) are identified as those of archosaurs, as they show evidence of thecodont implantation (no signs of basal damage expected if the tooth had been fused to the bone as with acrodont or pleurodont dentition). They are all teeth of carnivores and, because of the variation of tooth morphology along archosaurian jaws, it is possible that two or more morphotypes may derive from the same species. We distinguish a number of morphotypes, as in previous descriptions of such faunas (e.g. Van den Berg et al., 2012), but do not attempt to assign them to clades.

Tooth morphotype 1

These teeth (Fig. 12A, B) are basally broad and roughly circular in cross-section. They are recurved, conical and robust, with thick enamel. The recurved surface is worn smooth. No serrations or edges that could bear serrations are evident.

Tooth morphotype 2

These teeth (Fig. 12C–E) are the largest from Ruthin, with an estimated 8–9 mm tall crown. One specimen (Fig. 12C) is tall,

narrow, largely conical, weakly recurved, double-edged (anteriorly and posteriorly) and finely serrated with 5–6 serrations per mm, becoming finer towards the apex. The external surface bears vertical lines from the tip to the base of the crown. In cross section, lines radiate from the centre of the tooth to the edge. Laterally, the tooth crown surface appears more well-rounded than the medial surface. This tooth size suggests the total length of the animal was about 1 m, by comparison with more complete archosaur specimens.

One tooth fragment of this type (Fig. 12D, E) we first assigned to *Thecodontosaurus*, but the more complete tooth (Fig. 12C) suggests otherwise. Teeth were compared to the neotype of *Thecodontosaurus antiquus* (BRSMG C4529; Benton et al., 2000) and while serration shape and count are similar, NMW 88.12 G.53 (Fig. 12C) has a more rounded lateral surface, is taller, narrower and more cone-shaped. *Thecodontosaurus* has more leaf-shaped teeth with flatter lateral surfaces towards the serrations. The more complete tooth (Fig. 12C) came from a large archosaur, likely a saurischian dinosaur or phytosaur.

Tooth morphotype 3

This tooth type (Fig. 12F, G) is transversely thin, moderately recurved, dorsoventrally tall and likely to have possessed serrations that have been worn away. Given the size of the tooth, 6 mm tall and 3 mm wide at the base, it likely belonged to a carnivorous crocodylomorph, rauisuchian or theropod dinosaur.

4.5. Uncertain reptilian remains

Clade TETRAPODA

Class REPTILIA

Tetrapod claws

A number of isolated claws (Fig. 12H–O) could also belong to archosaurs, sphenodontians, or procolophonids. The specimens are identified as claws based on their curvature and lateral vascular grooves. They are often morphologically identical in closely related groups with the only difference being size, as seen for example in sphenodontians (Fraser and Walkden, 1984).

Claw morphotype 1

The single specimen (Fig. 12H, I) is long and narrow. The proximal end is deep, and the claw curves and narrows to the distal end. There is a groove on the right lateral surface at the proximal end (Fig. 12H). Markings are inconsistent on each side, and it is unclear what is a natural groove or a result of wear.

Claw morphotype 2

The most common morphotype at Ruthin (Fig. 12J–O). These claws vary greatly in size and completeness, but are often large, most being c. 2 mm long, but the largest up to 5 mm long and 3 mm tall, but only 1 mm wide. The claws are lightly recurved and bear a shallow, typically poorly defined lateral groove that starts ventrally at the posterior end and curves anteroventrally to meet the dorsal surface anteriorly. Given their abundance, some of these, at least, likely belong to procolophonids.

Osteoderms

During the Late Triassic, animals with osteoderms included crurotarsan archosaurs (crocodiles and relatives), lepidosaurs (possibly), placodonts and procolophonids, as well as chroniosuchian and temnospondyl amphibians. Osteoderms are common at Ruthin and various morphotypes are recognised (Fig. 13) in addition to those assigned to the *Terrestrisuchus*-like crocodylomorph (Fig. 11P–W). Osteoderms can be hard to assign to taxa because they can be highly variable in morphology within a single species, they may be similar between different taxa, and the full armament has not been described especially in small tetrapods.

Morphotypes 1–2 resemble those of the procolophonid *Scoloparia glyphanodon* (Sues and Baird, 1998; fig. 4) and the Permian pareiasaurs (Bulanov and Yashina, 2005, fig. 3). These

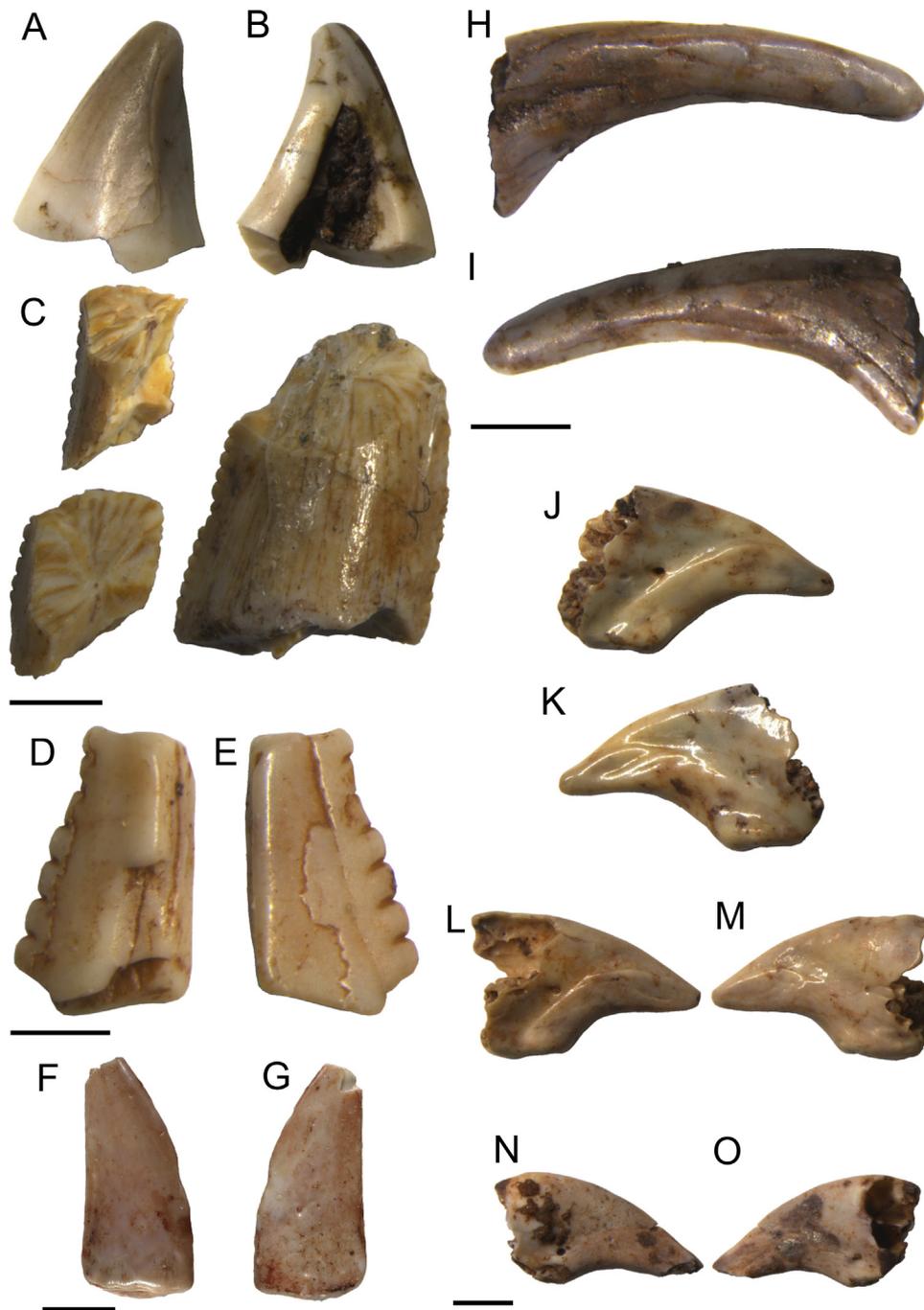


Fig. 12. Archosaur teeth (A–G) and claws (H–O). (A, B) Fragment of tooth of morphotype 1 (NMW 88.12 G.85), in external (A) and internal (B) views. (C) Teeth fragments of tooth of morphotype 2 (NMW 88.12 G.53). (D, E) Fragment of tooth of morphotype 2 (NMW 88.12 G.75), lateral/medial views. (F, G) Tooth of morphotype 3 (NHMUK PV R37495), in lateral/medial views, respectively. (H, I) Long, narrow claw of morphotype 1, from NMW 88.12 G.82, in lateral/medial views. (J, K) Large claw of morphotype 2, from NMW 88.12 G.31.14, in lateral/medial views. (L, M) Claw of morphotype 2, from NMW 88.12 G.31.14, in lateral/medial views. (N, O) Claw of morphotype 2, from NMW 88.12 G.31.14, in lateral/medial views. Scale bars are 1 mm for A–C and J–O, 0.5 mm for D–E and H–I and 2 mm for F–G.

osteoderms are not regarded as *Tricuspisaurus*, as previously suggested (Edwards, 1998), since we argue it is not a procolophonid. There is no evidence that trilophosaurs had osteoderms.

Osteoderm morphotype 1

The most common morphotype recognised (Fig. 13A–F), these osteoderms vary considerably in size and include some of the largest osteoderms from Ruthin, ranging from 2 to 9 mm wide when complete. They are sub-circular to sub-rectangular in shape with a moderate, well-defined, central boss which is greatly variable in height and thickness. Irregular abrasion of the boss can produce keel-like structures on their surfaces. Where bosses are

absent, circles of fine pits and/or large holes in the external surface are left in their place. The external surface is covered with circular pits, rather small on and immediately around the boss, but wider and deeper as they radiate away from it. Towards the edge of each osteoderm, the pits are increasingly long, fine, shallow and less well-defined, becoming absent at the osteoderm border which is smooth surfaced.

Osteoderm morphotype 2

In this morphotype (Fig. 13G–J), the external surface structure resembles morphotype 1, but two bosses are present instead of one. These bosses are generally close to each other with their

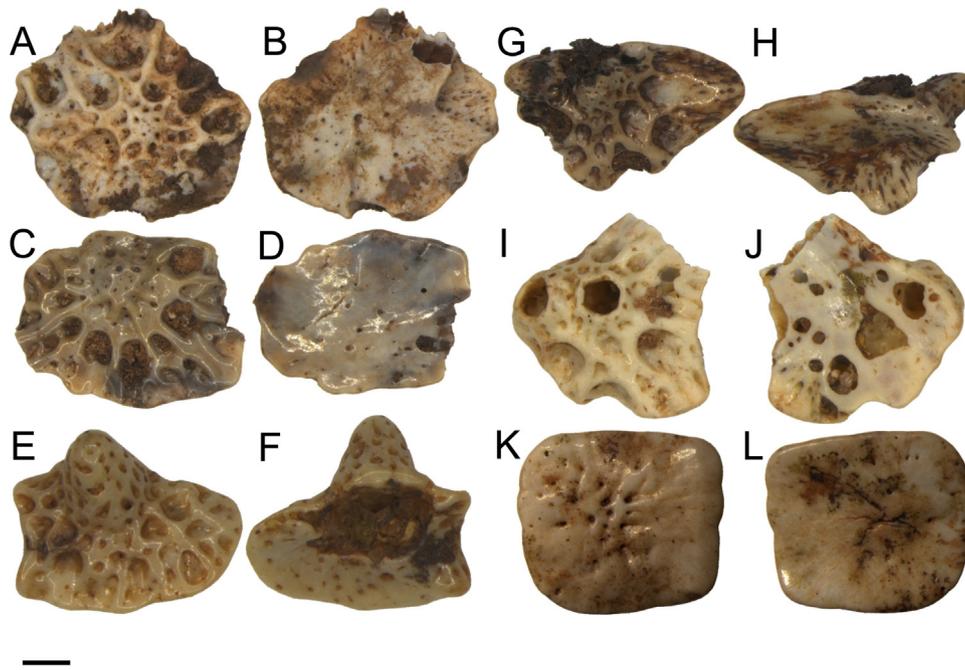


Fig. 13. Osteoderms. (A, B) Osteoderm of morphotype 1, from NMW 88.12 G.31.18, in dorsal (A) and ventral views (B), respectively. (C, D) Osteoderm of morphotype 1, from NMW 88.12 G.31.18, in dorsal (C) and ventral (D) views. (E, F) Osteoderm of morphotype 1, from NMW 88.12 G.31.18, in dorsal (E) and ventral (F) views. (G, H) Osteoderm of morphotype 2, from NMW 88.12 G.31.18, in dorsal (G) and ventral (H) views. (I, J) Osteoderm of morphotype 2, from NMW 88.12 G.31.18, in dorsal (I) and ventral (J) views. (K, L) Osteoderm of morphotype 3 (NHMUK PV R37482) in dorsal (K) and ventral (L) views. Scale bar is 1 mm for A–D and G–L and 0.5 mm for E–F.

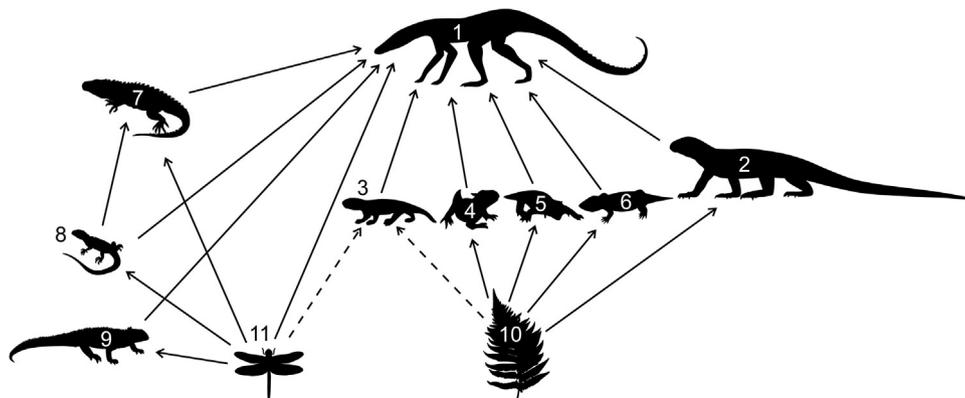


Fig. 14. Food web reconstruction of the faunas of Ruthin. Organisms represented are confidently identified; there may be at least one other small archosaur present, but we do not have enough fossil evidence to confirm. Key: 1. *Terrestrisuchus*-like crocodylomorph; 2. *Tricuspisaurus*; 3. *Smilodonterpeton*; 4. cf. *Scoloparia*; 5. cf. *Hypsognathus*/cf. *Leptopleuron*; 6. *Haligonia*; 7. *Planocephalosaurus*; 8. *Diphydontosaurus* (taxon 2); 9. cf. *Diphydontosaurus* (taxon 1) or possibly cf. *Gephyrosaurus*; 10. plants; 11. insects.

considerably thickened bony bases overlapping. The bosses stand approximately 10° apart.

Osteoderm morphotype 3

Some osteoderms (e.g. NHMUK PV R37482) are noticeably of morphotype 1, but most are very smooth, flat, sub-rectangular or sub-circular and bear few surface structures other than a small collection of fine pits and grooves in a centrally positioned sub-circular array (Fig. 13K, L). It is possible that these specimens are of morphotype 1 but are so badly worn that surface structures are lost. One specimen from the NHMUK has fine pits more widely distributed across the dorsal surface.

5. Ecosystem reconstruction

The reconstructed food web (Fig. 14) reflects dietary interpretations of each taxon, based on tooth morphology, size and comparison to modern analogues.

It is clear that the fauna, uniquely among the Late Triassic UK fissure deposits, has a high proportion of procolophonids comprising at least four taxa. It is also apparent that all the tetrapods are of small adult size (maximum length 1 m).

The top carnivore is a slender crocodylomorph, possibly *Terrestrisuchus* or *Terrestrisuchus*-like. Numerous teeth suggest there were other flesh-eating archosaurian taxa, but we could not confidently identify dinosaurs or rauisuchians for example. They presumably preyed opportunistically on all the other tetrapod taxa.

While no plant or arthropod fossils have been found, the dietary requirements of the tetrapods indicate their presence. The rhynchocephalians possess slightly recurved, conical teeth, and their small size and similarity to modern lizards indicates an insectivorous diet. Fraser (1982) suggested that *Planocephalosaurus* might also have preyed on small vertebrates because of its larger, more blade-like posterior teeth. We cannot be sure what *Smilodonterpeton* ate as its blade-like teeth perhaps indicate an

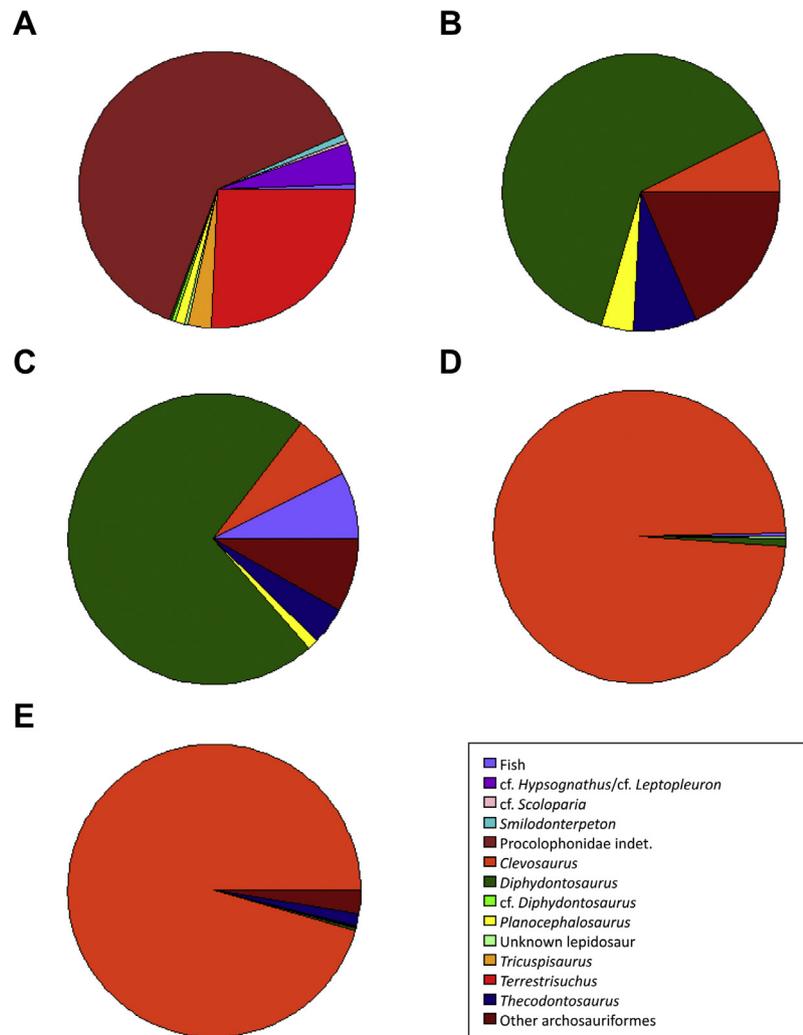


Fig. 15. Plot of relative abundance of faunas from Late Triassic fissure deposits at Ruthin (A), Durdham Down (B), Tytherington (C), Woodleaze (D) and Pant-y-ffynnon (E). For the purpose of this study, reworked fossils are not included in this analysis. Plots for localities other than Ruthin are produced from published data (Keeble et al., 2018).

arthropodous diet but it may have consumed particular plant material like the other procolophonids. *Tricuspisaurus* and the procolophonids (*Haligonia*, *Scoloparia* and a leptopleuronine), with their low bodies and broad incisor/molariform teeth were likely herbivores, feeding on low-lying plants. Spielmann et al. (2008) suggest that *Trilophosaurus* might have been arboreal but we have no evidence that *Tricuspisaurus* had a similar niche.

6. Palaeobiogeography and island effects

6.1. Relative abundance

The acid-digested fossil material shows a clear dominance of procolophonid remains (primarily osteoderms) and secondarily of archosaurs (Fig. 15 A). Rhynchocephalians are comparatively rare, making Ruthin unusual for a British Triassic fissure deposit. Most relative abundance data plots for fissures (Foffa et al., 2014; Klein et al., 2015; Keeble et al., 2018) show a 60–99% dominance of rhynchocephalians with procolophonids being absent (Fig. 15B, C). This difference in faunal composition could reflect geographic differences in the faunas, but this cannot explain all differences: the Pant-y-ffynnon locality (Fig. 15E) is on the neighbouring island in South Wales, separated from it by about 1 km of seaway (Fig. 16), and its fauna is different, but comparable in rhynchocephalian dominance to that of the Cromhall fissures (Fraser 1985), on an

island 50 km away. Perhaps most likely is that Ruthin represents a faunal assemblage that predates the other fissures, when rhynchocephalians had yet to dominate ecologically.

Some of the Ruthin taxa (e.g. *Haligonia*, *Scoloparia*, *Tricuspisaurus*) are most similar to North American relatives, perhaps reflecting a different source of the fauna, at a different time.

6.2. Species-area effect

We considered whether the Ruthin fauna showed any of the characteristics of island faunas, such as the species-area effect, insular dwarfism, insular gigantism, and primitiveness of the taxa. At a superficial level, in a survey of the faunas of the various Triassic-Jurassic islands in the Bristol Channel area, the larger palaeo-islands seem to support more genera of tetrapods than smaller islands (Fig. 16). However, when the data are plotted fissure by fissure (Fig. 17A), there is a broad scatter of points and the best fitting line is negative with a non-significant fit, suggesting unexpectedly that large islands support fewer taxa. Removing the large Emborough (= Mendip) palaeo-island results in a correlation (Fig. 17B) that provides some support for the species-area effect, although the R^2 value is not significant (Table 1).

This study is a first attempt and it is likely that our anomalous result reflects sampling problems, as the species-area effect is so widespread (Darlington, 1957; Lomolino and Weiser, 2001). First,

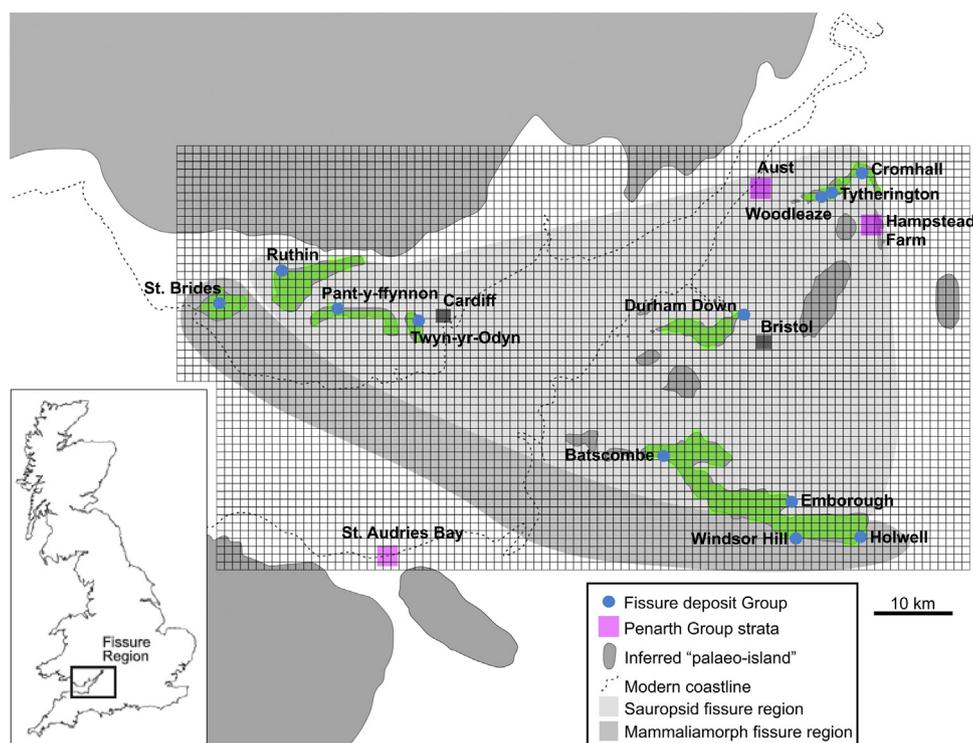


Fig. 16. Palaeogeographic map of the Bristol Channel area during the Late Triassic. Overlying grid demonstrates area in km². Squares in light green were counted as part of an island's area. Map modified from Whiteside et al. (2016) with a more accurate map of the Durham Down and Cromhall islands from Foffa et al. (2014). Islands are named after the locality of one of their respective fissure deposits. In other reconstructions, the island with Hampstead Farm is shown to be connected to Cromhall Island, which would add approximately 6 km² to the estimated island area.

the genus richnesses of individual fissures do not necessarily measure the biodiversity of a whole island, as there might be a variable range in geological ages of fissures on any one island, fissures might sample only one of many habitats, and the available or studied fissures might be unrepresentative (some are known to have been restricted to parts of the typical faunas; Klein et al., 2015; Keeble et al., 2018). Therefore, when a maximum and minimum genus count was estimated for each island, based on a combination of all fissures on that island, the result (Fig. 17C) displays the species-area effect, but R^2 values are statistically non-significant (Table 1). Removing the small island Twyn-yr-Odyn, which has fish but has not been investigated in any detail for terrestrial tetrapods does not improve the result (Fig. 17D).

A comparison of Emborough and Cromhall islands illustrates sampling effects. Emborough Island, represented by Holwell, Emborough and Batscombe fissures, is probably insufficiently documented overall, because although Holwell has been sampled by many researchers (e.g. Moore, 1867; Whiteside and Duffin 2017) the other two localities are relatively poorly known and warrant a thorough exploration. On the other hand, Cromhall Island, represented by fissure samples from Cromhall and Tytherington, has been very extensively studied, with thesis works by Fraser and Whiteside respectively and more recent study (Foffa et al., 2014; Klein et al., 2015; Whiteside et al., 2016; Mussini et al., 2020). Further, both Tytherington and Cromhall each host several fossiliferous fissures, and those at Cromhall span a broad age range (c. 3 Myr), from early to late Rhaetian (Whiteside et al., 2016), also contributing to the higher-than-expected genus counts.

The poor support for the species-area effect probably also reflects variations in the geological age and scope of environments sampled. Age ranges across the localities are great: Ruthin is early Rhaetian, Cromhall early to late Rhaetian (Morton et al., 2017) and the St. Brides palaeo-islands very late Rhaetian to Early Jurassic (Evans and Kermack, 1994), an overall span of 5–10 Myr.

Sedimentological and palynological evidence also supports the great variety of environments, with Ruthin being evidently arid (this study), Woodleaze being a saline, coastal environment (Klein et al., 2015), Tytherington possessing a wide diversity of terrestrial plants (Whiteside and Marshall, 2008), whereas St. Brides is dominated by conifers (Kermack et al., 1973; Whiteside et al., 2016). Our faunal richness counts reflect only what was washed into the fissures, which could sample a single flash flood event, or a time-averaged assemblage from a wide geographic area and representing multiple seasons of the year. Woodleaze and Pant-y-fynnon fissures show an assemblage that is 95% *Clevosaurus* (Klein et al., 2015; Keeble et al., 2018) and Cromhall and Tytherington fissures, which represent a small island (Foffa et al., 2014) of probably a few million years duration, show a greater diversity than fissures that represent larger islands, suggesting that sampling of the tetrapods on the islands is incomplete. Until we can control for these time-averaging and other variables, we might not find evidence for the species-area effect in the Bristol Channel palaeo-archipelago.

6.3. Insular dwarfism

The fauna of Ruthin documented here comprises nine named genera of terrestrial tetrapods, including procolophonids, rhychocephalians, archosaurs and a trilophosaur, all characterised by numerous individuals of small size. None of the fossils in the collections at the NHMUK, NMW or CAMZM represents an individual larger than 1 m long. Whiteside and Marshall (2008) emphasised that the absence of large animals is a feature of modern-day small islands. The Ruthin island would have been small at the time of the tetrapods, a maximum of 34 km² (based on the archipelago map of Whiteside et al., 2016). However, our discovery of two Rhaetian marine fish, *Rhomphaiodon minor* and? *Polyacrodus cloacinus*, indicates that marine waters were present in

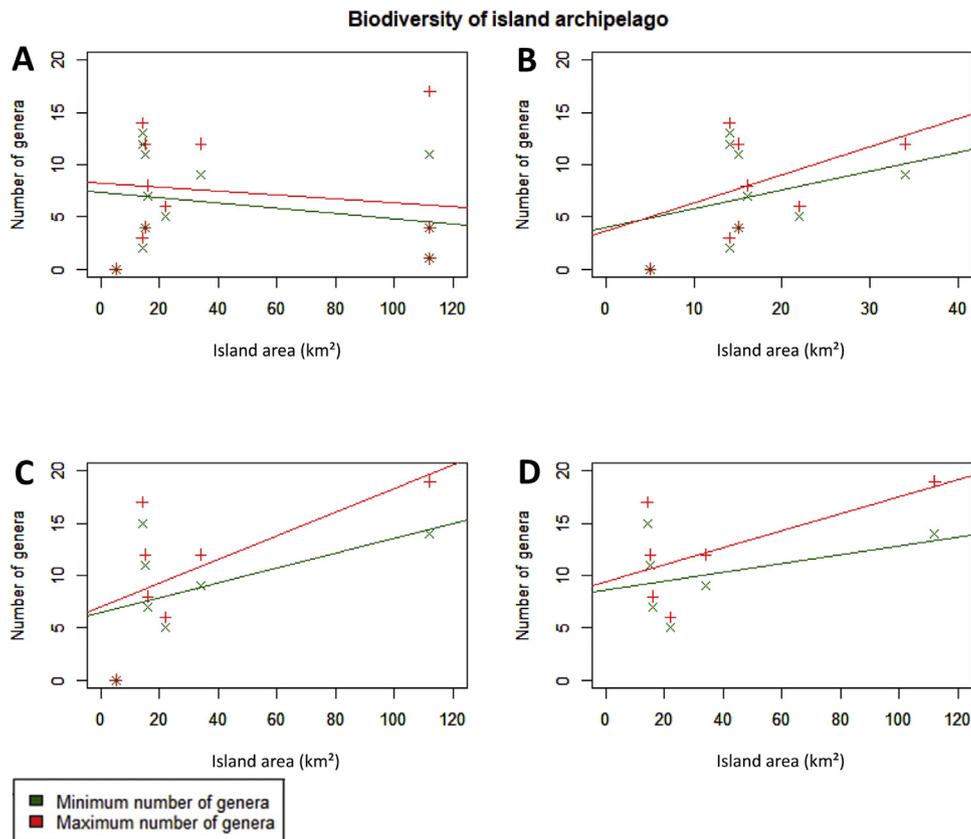


Fig. 17. Biodiversity charts presenting the current evidence for the species-area effect in Bristol archipelago island faunas, produced using island area data from Foffa et al. (2014) and Whiteside et al. (2016). Both the minimum and maximum numbers of genera are plotted for each island to account for uncertainty in taxon identifications. A, Biodiversity preserved in individual fissures. B, Biodiversity preserved in individual fissures without suspected anomalies. C, Cumulative biodiversity of fissures from the same islands. D, Cumulative biodiversity of fissures from the same islands without suspected anomalies.

Table 1

The species-area effect on the Rhaetian-aged palaeoislands of South Wales and the Bristol area, UK. Values shown here are calculated using the map from Foffa et al. 2014 for Cromhall Island and Durdham Down Island and Whiteside et al. 2016 for the rest. The values for 'Fissure biodiversity' show correlations between genera richness of individual fissures against island area. The values for 'Island biodiversity' show correlations between genera richness for each island (summed from all fissures on the island) against island area. 'Anomalies removed' means removal of Emborough Island for the fissure biodiversity measures, and Twyn-yr-Odyn for the island biodiversity. The 'min' and 'max' values relate to those for the 'minimum number of genera' and 'maximum number of genera' respectively.

Test	Fissure biodiversity		Island biodiversity	
	Whole dataset	Anomalies removed	Whole dataset	Anomalies removed
R ² (min)	-0.02321	-0.03583	0.09239	-0.04199
P value (min)	0.4118	0.4232	0.2603	0.422
R ² (max)	-0.06558	0.05136	0.2793	0.2208
P value (max)	0.6192	0.2702	0.1278	0.195

close proximity and the island is likely to have been much smaller than their estimate. Furthermore, the dating of the fauna as Norian/Rhaetian-early Rhaetian, based on the *Rhomphaiodon minor* tooth, corresponds to the time when the Rhaetian transgression was inundating the Palaeozoic rock landmasses, so the island area would have been contracting.

The other Late Triassic sauropsid faunas of SW Britain are also composed of taxa with small-sized individuals, generally dominated by rhynchocephalians but also including small archosaurs with a maximum length of about 2.5 m, such as *Thecodontosaurus* from the Durdham Down and Tytherington fissures (Whiteside and Marshall, 2008). In those localities, it is difficult to compare the taxa with continental species as the fissure animals except *Clevosaurus* are little known elsewhere. However, Whiteside and Marshall (2008) suggested that *Thecodontosaurus* might have been

a dwarfed plateosaurid sauropodomorph; relatives from Germany were 4–10 m long. Uniquely, for the sauropsid faunas, Ruthin does have a number of genera that are the same or closely related to continental taxa from the Late Triassic so it is possible to consider whether dwarfism or gigantism might have occurred.

Tricuspisaurus is closely related to *Trilophosaurus* which lived in the North American Late Triassic until the mid-Norian (Spielmann et al., 2008). While *Tricuspisaurus* lacks a complete skeleton, the jaw bones, when scaled against *Trilophosaurus* indicate a total length of c. 1 m, compared to 2–2.5 m for the latter. The leptopleuronine procolophonid remains are also generally very small, approximately 15 cm in body length, compared to the Carnian *Leptopleuron lacertinum* at 30 cm (Säilä, 2010) or the Norian–Rhaetian *Hypsognathus fenneri* at 33 cm (Sues et al., 2000; Sues and Olsen, 2015). Remains of *Haligonia* and *Scoloparia* from

Ruthin, if correctly identified, are half the size of those described by Sues and Baird (1998). It is clear, therefore, that many of the Ruthin species are much smaller than their continental closest relatives.

It is unlikely that there is a taphonomic sorting effect where larger animals were present but left no fossils because the fissures are essentially pit fall traps – why would larger animals, or bits of them, not have entered the fissures? In all fissures examined in SW Britain by a wide range of researchers over 160 years, no example of any large individual has been recorded; there are not even any teeth, small bones (e.g. phalanges) or fragments of larger bones of larger individuals >2.5 m in length. In other Triassic formations where small tetrapods are common, such as those of the Middle Triassic Otter Sandstone, isolated teeth, jaws, osteoderms and dermal bones of larger tetrapods such as temnospondyls, rhynchosaurs, and rauisuchians are commonly found (Coram et al., 2019). Large animals seem to have been absent from the fissures, but also from the islands as a whole.

In the Ruthin fauna there are no fossils indicating an animal longer than 1 m; the fossils of *Tricuspisaurus* indicate an animal of that size. Further, the individual bones do not suggest juvenility; for example, the jaw bones commonly bear multiple, well-worn teeth.

Our data suggests that the Ruthin procolophonids, the trilophosaur and probably some of the archosaurs, are unusually small and inhabited a reducing landmass with diminishing resources over a short period, possibly only a few thousand years. In that environment a dwarfed species is more likely to maintain a minimum viable population compared to its larger ancestors. Selection, in those circumstances will favour a population formed of small individuals. In support of the concept that ectotherms can be very small on islands, the two smallest living reptiles (and in fact the smallest amniotes) are found on tiny Caribbean islands; *Sphaerodactylus ariasae* from Beatu island (27 km²) and *S. parthenopio* from Virgin Gorda (21 km²) in the British Virgin islands (Hedges and Thomas 2001). The smallest chameleon *Brooksia micra* was recently discovered on Nosa Hara islet (2.7 km²), Madagascar by Glaw et al. (2012).

Therefore, we find that most of the Ruthin tetrapods were insular dwarfs. Exceptions are *Planocephalosaurus* and the large *Diphydontosaurus*, which are the same size as closely related sphenodontians elsewhere in the Late Triassic. We can identify no examples of insular gigantism. This example supersedes the oldest reported case of insular dwarfism previously reported, of the Late Jurassic sauropod *Europasaurus holgeri* from northern Germany (Sander et al., 2006).

6.4. Insular primitiveness

Most of the taxa, where close relatives can be determined, show affinities with much older mainland taxa. For example, the procolophonids *Haligonia* and *Scoloparia* occur otherwise in the Wolfville Formation of Nova Scotia, dated as late Carnian (Sues and Baird, 1998). The closest relative of *Tricuspisaurus* is *Trilophosaurus* from the Sonsela Member, Chinle Group, southwestern USA, dating as mid-Norian (Sues et al., 2003; Heckert, 2004), some 15–20 Myr before the early Rhaetian. The rhynchocephalians *Diphydontosaurus* and *Planocephalosaurus* are definitively known only from the fissures, and they sit low in the phylogenetic tree (Herrera-Flores et al., 2019), so are plesiomorphic ('primitive'), but associated phylogenetically with a variety of Late Triassic to Jurassic taxa.

This is not true for all Ruthin taxa. *Terrestrisuchus* in the phylogeny of Crocodylomorpha, sits midway between *Saltoposuchus* from the mid-Norian to Rhaetian of Germany and *Litargosuchus* from the earliest Jurassic of South Africa, so this taxon cannot be said to be primitive with regard to nearest relatives (Leardi et al., 2017).

7. Discussion

We confirm the independent findings of Edwards and Evans (2006). The Ruthin fauna is dominated by armoured procolophonids similar to *Scoloparia* (they found 46.6%, we found 63.5%), followed by a *Terrestrisuchus*-like crocodylomorph (they found 16%, we found 26.3%) and small pleurodont lepidosaurs similar to *Diphydontosaurus* or *Gephyrosaurus* (they found 16%, we found 0.7%). Among other taxa, they also reported cf. *Thecodontosaurus* (including an ilium; Edwards 1998), but we doubt that the ilium is from *Thecodontosaurus* and did not find any other specimens confidently attributable to the genus in our collections. They also recognised *Haligonia* as a component of the Ruthin fauna, but it was not figured.

Ruthin was possibly more arid than suggested for other fissure localities (Whiteside et al. 2016), as water-indicative fossils (non-marine fishes, plants, arthropods and pelynomorphs) are not recognised, though preservation might have been biased against such smaller, softer fossils. The prevalence of procolophonids and a trilophosaur, rather than high proportions of rhynchocephalians, might correlate with this aridity.

Fragmentary tooth plates of the Carboniferous holocephalian *Deltodus* are more common than Triassic fishes. These fossils are identified as derived from the Carboniferous limestone because of their preservation and because they are known elsewhere from that system, and bradyodonts such as *Deltodus* became extinct in the Permian (White, 1936; Stahl, 1999). The Ruthin procolophonids are different and much more diverse than at other fissure localities. Procolophonid specimens from Cromhall Quarry (BRSMG Cf609-611, 644, 645), with the same morphology as those described from Tytherington (Whiteside and Marshall, 2008), show maxillary tooth morphology similar to *Leptopleuron*, but a third cusp is recognised towards the buccal anterior edge of the tooth. The dentary teeth of the procolophonid from Cromhall (BRSMG Cf609-611) are also more blade-like than those of other procolophonids. These morphological differences suggest that the Ruthin procolophonids are different species to those from Cromhall and Tytherington.

Procolophonid osteoderms, while apparently absent in primitive forms, have been recognised in the two derived genera *Sclerosaurus* and *Scoloparia* (Cisneros, 2008). Ruthin is rich in procolophonid osteoderms, perhaps the richest locality in the world, but they are all disassociated so it is uncertain to which procolophonid they belong. Admittedly, our species abundance counts might exaggerate the relative abundance of the *Scoloparia*-like animal, because we treated each osteoderm as a new individual animal, even though one individual could shed dozens of osteoderms from its carcass.

Our case that *Tricuspisaurus* is a trilophosaurid could suggest that other animals that resemble it, but were formerly classed as procolophonids, might now be tested as possible trilophosaurids. These include *Xenodiphydon* (Sues and Olsen, 1993), known from tricuspid teeth like those of *Tricuspisaurus* and, though the anterior parts of its jaws remain undiscovered, possibly a beak as well.

This study provides some rudimentary support for the species-area effect on the Late Triassic/Early Jurassic palaeo-islands of the SW UK. This is likely influenced by incomplete understanding of the biodiversity of faunas on the islands, precise dating for each faunal assemblage, as well as uncertain estimates of the size of the islands, as there is no accurate map of the whole palaeo-archipelago for each sub-stage of the Rhaetian or Early Jurassic.

The Ruthin faunal assemblage is shown here to have been much more diverse than previously recorded. This may be because it is derived directly from continental areas, as indicated by the inclusion of faunas that show unexpected linkages to those of the

Wolfville Formation of Nova Scotia (*Haligonia* and *Scoloparia*; Sues and Baird, 1998). Further, *Trilophosaurus* (Chinle Group, south-western USA) and *Dromicosuchus* (Lithofacies Association II, North Carolina) are related to *Tricuspisaurus* and to *Terrestrisuchus* respectively (Sues et al., 2003; Heckert, 2004). The Wolfville Formation fauna is Carnian in age, and the other North American taxa are also either late Carnian or Norian. However, British Carnian taxa such as *Hyperodapedon* are absent or unrecognised in Ruthin and the fissure is most likely early Rhaetian, as supported by the presence of *Rhomphaiodon minor*. This indicates that the fauna of Ruthin is derived from North American taxa, but relict compared to other Rhaetian taxa. This also makes Ruthin the oldest fissure deposit known in the south-west of the UK.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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