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The first tetrapod track recorded from the Rhaetian in the British Isles

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ABSTRACT

Terrestrial vertebrate trace fossils are relatively abundant in mid-to-late Triassic and early Jurassic deposits in the British Isles but to date none at all have been recorded from the Rhaetian, the final stage of the Triassic. This represents a persistent gap in the terrestrial ichnological record. We present the first Rhaetian track to be recognised in the British Isles, found at Aust Cliff on the south bank of the Severn Estuary near Bristol in SW England. This locality is well known for disarticulated remains of Rhaetian fossil reptiles including some terrestrial species but in 2006 a track (TECMAG0161) was found for the fist time. Although the specimen was found ex-situ the palynological data from the surrounding matrix confirms a Rhaetian age. The track was examined with CT scanning and photogrammetry. We tentatively assign the track to the ichnogenus *Procolophonichnium* based on size and digit proportions. The isolated nature of the specimen offers little concrete information about the track maker but such tracks have previously been attributed to parareptiles or therapsid trackmakers. The specimen adds a datapoint to an otherwise ichnologically empty period of time in the British Isles. The track also provides solid evidence for a [locally] terrestrial environment in a sequence that is otherwise considered predominantly marine or estuarine. This discovery suggests that there may be more such tetrapod tracks of Rhaetian age preserved, at least at Aust, and further searching will hopefully lead to the current minimal dataset being expanded.

1. Introduction

Fossilised tracks are a valuable palaeontological resource providing direct insight into the lives of extinct organisms otherwise unavailable from bones alone. In the absence of body fossils, tracks can provide unique evidence of the producer's presence in the fauna at that time and setting, as well as information about limb motion, soft-tissue anatomy and palaeoenvironment (Padian and Olsen, 1984; Minter et al., 2007; Falkingham, 2014). To date, no terrestrial vertebrate trace fossils have been recorded from the Penarth Group of the Upper Triassic, including the Aust section (Swift and Duffin, 1999), nor indeed from any deposits in the UK dating to the Rhaetian (Sarjeant, 1975; Delair and Sarjeant, 1985), being the final division of the Triassic lasting from 205.7–201.3 Ma (Maron et al., 2015).

In 2006 a small slab was found at the base of the cliff exposure at Aust (Fig. 1) on the south bank of Severn Estuary near Bristol in SW England by Mr and Mrs Chinn. Recognising that the impressions on one surface of the block looked like a possible track, they took the specimen to Bristol City Museum and Art Gallery for identification. It was donated, then accessioned as TECMAG0161 / Cg2406.

Aust Cliff exposes a sequence across the Triassic-Jurassic boundary. It is one of the best-known geological sites in the country and is the most prolific site for Rhaetian reptiles in the British Isles (Benton and Spencer, 1995). The locality was first described by Buckland and Conybeare (1824) and the exposure reveals a section through Upper Triassic (Norian to Rhaetian) and the lowermost rocks of the Lower Jurassic (Hettangian). Because of the significance of the site for both stratigraphy and palaeontology, the whole of the Aust Cliff section was designated as a Site of

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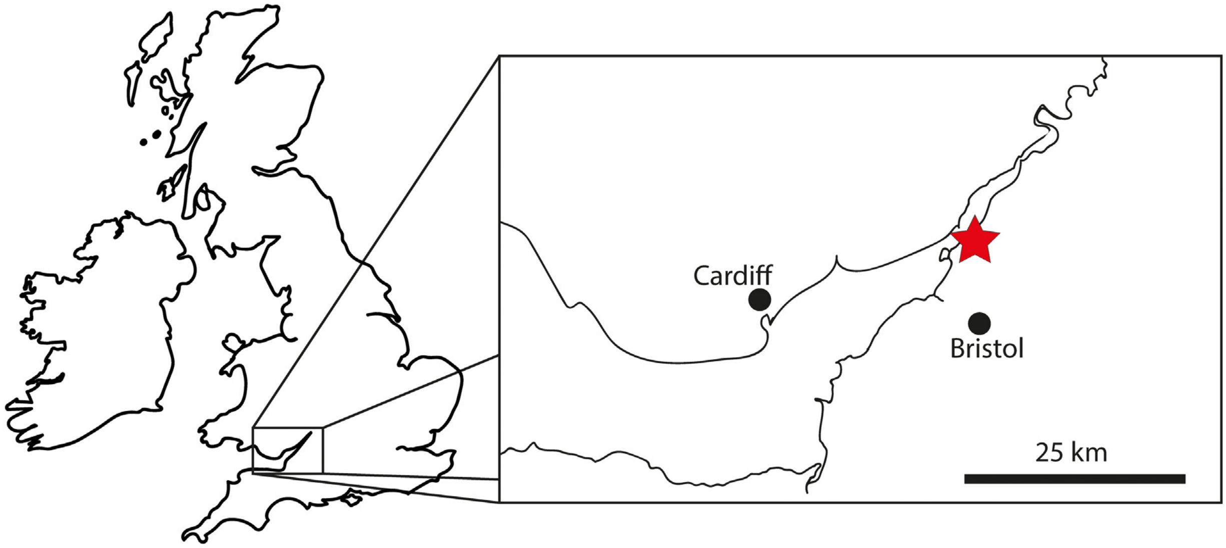

Fig. 1. Map of the British Isles, showing the location of the site at Aust, South Gloucestershire, on the eastern side of the River Severn.

Special Scientific Interest (SSSI) by the then Nature Conservancy Council (Benton and Spencer, 1995).

The base of the cliff exposes the Mercia Mudstone Group (Warrington et al., 1980), deposited in an arid coastal environment. Two formations are presented here. The lowermost Branscombe Mudstone Formation (Gallois, 2001) was formerly known as the 'Upper Keuper Marls' and comprises a sequence of calcareous mudstones and siltstones which are reddish in colour and represent coastal sabkha deposits, with gypsum veins and nodules suggestive of playa lakes. The succeeding grey-green siltstones and mudstones of the Blue Anchor Formation (Kellaway and Welch, 1993), formerly called the 'Tea Green Marls', indicates deposition in less arid conditions. This formation is overlain by the Penarth Group which comprises the black shale sequence of the Westbury Formation, recording the initial phases of the Rhaetian marine transgression. Temporary shallowing took place during the deposition of the Lilstock Formation, the basal unit of which is the Cotham Member. The succeeding carbonates of the Langport Member of the Lilstock Formation marks the onset of renewed marine transgression (Swift, 1999), giving way to limestones and shales at the top of the cliff forming the lowest part of the Lias (Benton and Spencer, 1995).

The well-known 'Rhaetic Bone Bed' that yields fish and reptile fossils as well as copious quantities of coprolites is found at the base of the Westbury Formation (Cross et al., 2018). The black shale sequence of this formation is interrupted by two arenaceous layers – the 'Lower Pecten Bed' and 'The Upper Pecten Bed'. These are less well known than the basal bone bed, but preserve an invertebrate fauna with occasional isolated vertebrate remains. The name refers to the common occurrence of the pectinid bivalve *Chlamys valoniensis*. Both of these beds are located towards the upper section of the high cliff. As such, these fossiliferous layers cannot be collected *in situ* at Aust, but specimens that have fallen from the cliff are frequently found at the base of the exposure and on the intertidal beach. The complete Rhaetian succession can be examined *in situ* just a short distance inland at Manor Farm (Allard et al., 2015; Radley and Carpenter, 1998). The Manor Farm pit was excavated in the 1990s, and a section was conserved as an accessible site for visitors and collectors.

Although specimen TECMAG0161 / Cg2406 was found at the base of the cliff at Aust, the distinctive colour and composition of the matrix indicates that it originates from the Upper Pecten Bed of the Westbury Formation (Simon Carpenter, pers. comm.). This is a hard grey limestone (Reynolds, 1947) of the Upper part of the Westbury Formation of the Penarth Group positioned just below the Cotham Member of the Lilstock Formation (Fig. 2), placing it near the top of the lower Rhaetian (Reynolds, 1947; Cross et al., 2018, p. 642).

Herein we describe the track and the microfaunal and palynological analyses undertaken on the matrix, and compare the specimen to known body fossils and ichnofossils from the Rhaetian period in the British Isles.

2. Material and methods

Specimen TECMAG0161 / Cg2406 was discovered in 2006 at the base of the cliff at Aust on the Severn Estuary (National Grid Reference, NGR ST 565,895-ST 572,901). It had had been on the beach for an unknown period of time prior to discovery. The block is 215 × 176 × 45 mm and weighs 1.389 kg. The underside is convex, whilst the upper surface is flatter, even slightly concave, and possesses two distinct impressions. These are here referred to as 'impression 1′ and 'impression 2′ as labelled in Figure 3. The surface around these impressions is uneven and has been eroded somewhat to a smooth, rounded appearance.

The rock is a yellow-grey limestone containing numerous bivalve remains, and is attributed to the Rhaetian Upper Pecten Bed (Allard et al., 2015). The bivalves are generally exposed as broken cross sections through single valves.

2.1. CT scanning and 3D imaging

To aid visual analysis, digital 3D models of the specimen were produced through photogrammetric methods, as well as CT scanning. Following the protocol described by Falkingham et al. (2018), all data including CT slices, photographs, and 3D models are made openly available (DOI: 10.6084/m9.figshare.7998173).

2.1.1. 3D digital model made using photogrammetry

A photogrammetric model (Matthews et al., 2016) was produced from 615 images taken using a Sony Nex-6 (16mp) and 16–50 mm lens. The images were processed using the open-source AliceVision Meshroom (https://alicevision.github.io/). The large number of photos resulted in a high-resolution textured mesh consisting of 3,645,173 triangles and 10,935,519 vertices.

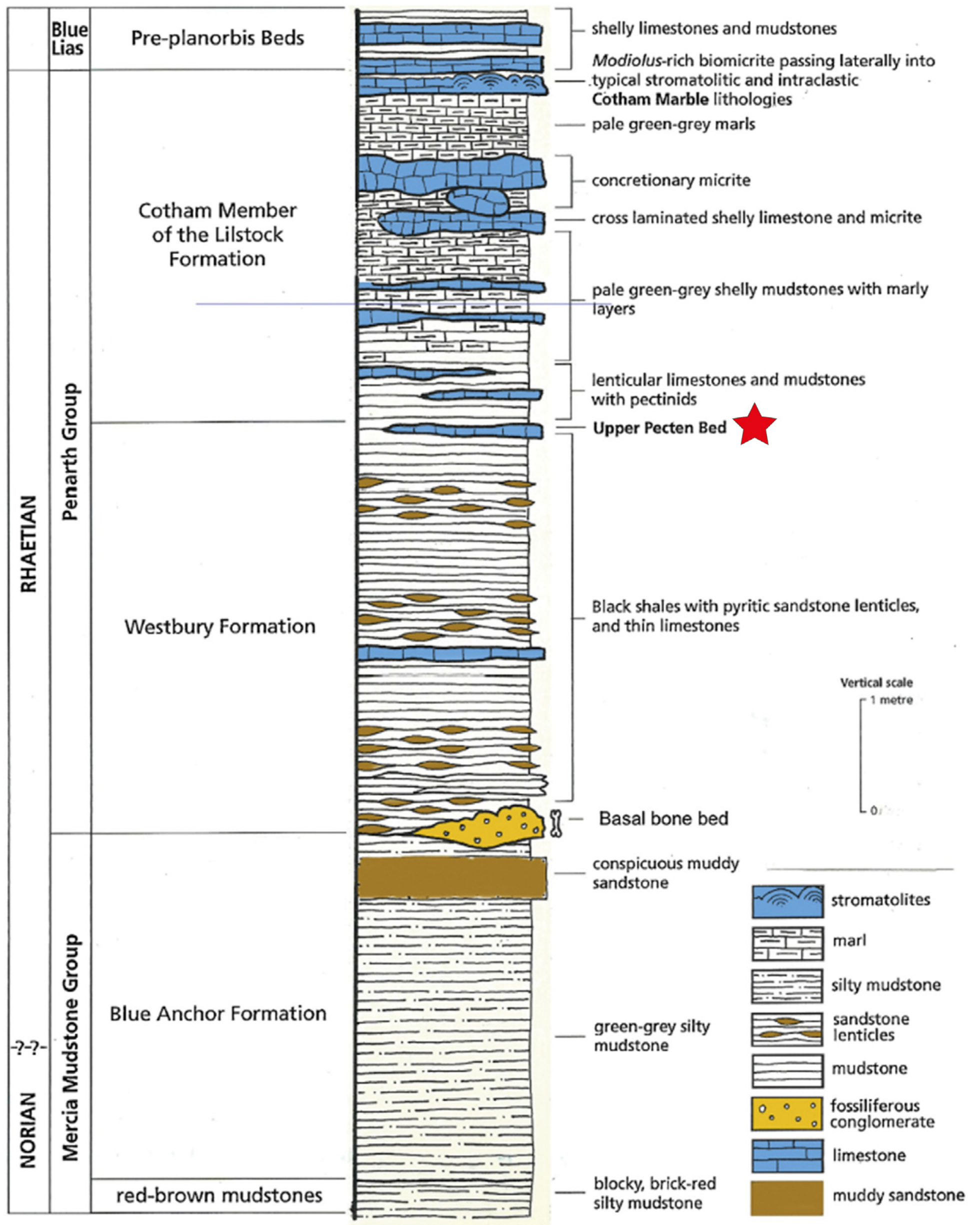

Fig. 2. Sedimentary log through the latest Triassic and earliest Jurassic at Manor Farm Aust, South Gloucestershire (ST 574,896). Lithologies and the key stratigraphic divisions of the Mercia Mudstone and Penarth groups are indicated. Red star indicates stratigraphic position of the specimen. Modified from Allard et al., 2015.

2.1.2. 3D digital model made using CT scanning

The specimen was scanned at the Royal Veterinary College (University of London, Hatfield, UK) using a LightSpeed Pro 16 CT scanner at 100 kV. Pixel size per slice was 0.48 mm (480 μm), and slices were spaced 0.625 mm (625 μm) apart. Unfortunately, no internal geometry (*e.g.,* deflected laminations *via* penetration or transmission) was discernible in the CT slice data (Fig. 4) so only a surface model could be produced from the data. This 3D digital model was produced using 3D Slicer (www.slicer.org). Scanning artefacts produced some lines in the surface model running across the width of the specimen, but these were relatively minor and indistinct.

2.2. Microfossil analyses

A small (~20 g) sample of matrix from the underside of the specimen was taken for microfauna analysis. This sample was disaggregated in ~1% solution of H_2O_2 (hydrogen peroxide) for 30 min, then rinsed, dried and sorted under a binocular microscope.

A small (<5 g) sample of matrix from the underside of the specimen was taken for palynological analysis. The sample was treated with concentrated hydrochloric acid (37%) to remove carbonate material and then with hydrofluoric acid (40%) to remove silicates to leave an organic residue. The resulting residue was sieved using a 10 μm mesh and mounted onto a coverslip and glass slide using Glue4Glass.The slide was examined using a Leica DMRE microscope and imaged on a Leica DMRX microscope.

3. Description

Impression 1 (Fig. 5) is the larger of the two, being 40 mm in length and 43 mm in width, and is interpreted as a vertebrate track. There are 4 straight, conical, digit impressions, each 14–17 mm long. The total interdigital angle between the outermost digits is 98°, and ~25–38° between each other digit. The rear of the impression is the deepest part, ~6 mm deeper than the surrounding surface. The digit impressions are deepest at the posterior and shallower at their distal

Fig. 3. Digital model of the specimen. A) Orthographic views of all sides of the specimen, B) True-colour, C) red-white-blue height map (red-blue = 23 mm), and D) interpretive outline drawing to highlight impressions 1 and 2.

tips. Sediment has been raised up between digits and around the track to form a displacement rim. There are three deeper pits within the rear half of the track, approximately aligned with the digit impressions. Given the regular nature of the digit impressions, and general morphology, we confidently interpret this impression as a vertebrate track.

Upon first inspection, impression 2 (Fig. 6) looks superficially similar to impression 1, albeit smaller at ~28 mm in length, and with only 2–3 distinct 'digit impressions'. However, close analysis of the apparent digit impressions reveals bivalve shell portions in cross section (Fig. 6, bottom) in two of them, while the third is not connected to the rest of the impression. We interpret this impression as a preservational or erosional artefact, rather than as a track, as discussed below.

4. Results

4.1. Comparisons of the digital 3D models

That no internal structure could be identified in the CT data is unsurprising given the size of the specimen and apparent homogeneity of the rock itself. However, a surface model was produced from the CT data. We had hoped that a CT scan of the specimen would provide additional information about sub-surface morphology, and possibly evidence as to whether the smaller impression really was a track based on possible undertracks. Although the data contained a few artefacts from the scanning process, the CT scanning and photogrammetric scanning produced very similar surface models (supplemental figure/supplemental data).

4.2. Microfossil analyses

No microfauna were observed. Whilst pollen specimens extracted from the sample are poorly preserved and extremely pale in appearance, this is to be expected from a sediment that has been exposed to surface erosion processes and therefore likely subjected to considerable oxidation (Traverse, 2007). Due to the oxidised nature of the sediment, it is unlikely that a full primary assemblage is present (Traverse, 2007). This is why a quantitative analysis is not performed. However, the present taxa (Table 1) are enough to give an indication of age.

5. Discussion

5.1. Dating

There has been some discussion about the exact age of the Penarth Group but palynological and conodont studies have shown

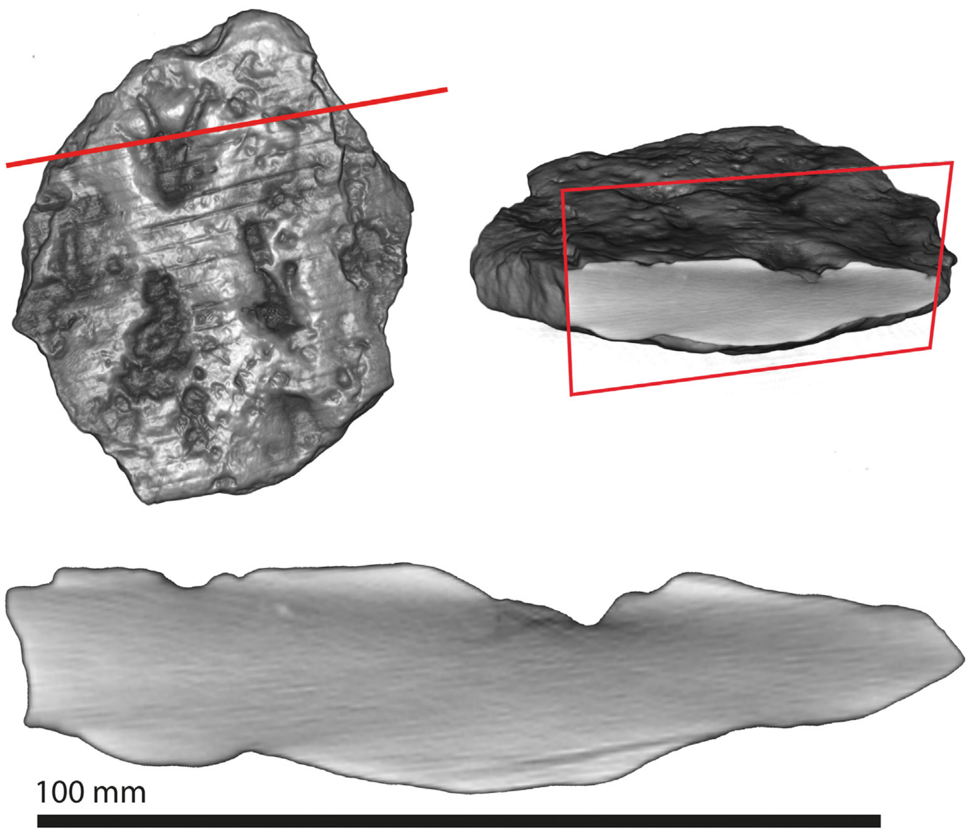

Fig. 4. CT data presented as volume render and single slice, illustrating the lack of detail and structure visible beneath impression 1. Scale bar for lower slice = 100 mm.

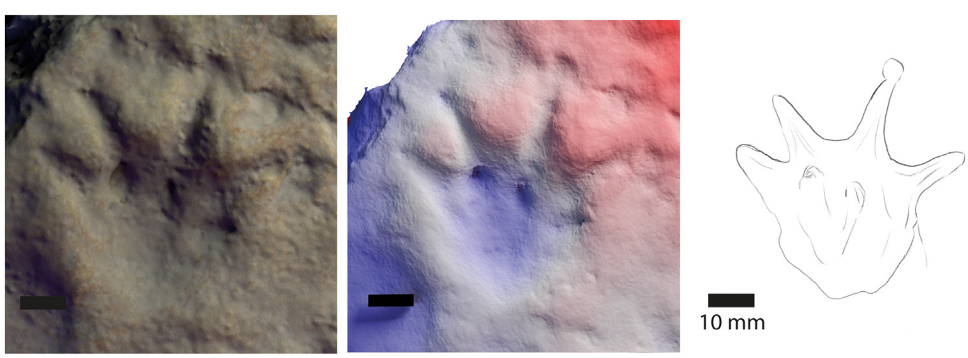

Fig. 5. Zoomed view of Impression 1 as photo-textured model, height mapped model, and interpretive outline. Scale bar = 10 mm, red-blue = 23 mm.

it to lie wholly within the Rhaetian stage of the latest Triassic (Swift and Martill, 1999). As the specimen TECMAG0161 / Cg2406 has been determined to be from the Upper Pecten Bed located at the top of the Westbury Formation of the Penarth Group, we infer it to be of Rhaetian age. This conclusion is reinforced by the qualitative relative-age assignment from the palynological analysis of the matrix, based on a comparison with the St. Audries Bay site (Bonis et al., 2010). The apparent lack of *Krauselisporites reissingeri* - a robust and distinctive spore that would be easily observed if present, even in a weathered sample – but the presence of *Dapcodinium priscum, Polypodiisporites polymicroforatus* and possible *Rhaetipollis Germanicus* is consistent with assemblages prior to the Blue Lias Formation.

It is also within the Lilstock Formation at St. Audries Bay that sporomorphs such as *Vitreisporites* spp., *Perinopollenites elatoides*, *Quadraeculina anellaeformis* and *Polypodiisporites polymicroforatus* occur consistently together, as observed here. Therefore the assemblage of palynomorphs identified (Table 1) is consistent with a Late Rhaetian age, possibly Lilstock Formation of St. Audries Bay equivalent (c.f. Bonis et al., 2010).

5.2. The environment

The whole of the Westbury Formation – including the Upper Pecten Bed at Aust - is considered to be exclusively marine, although the consistent presence of a low number of terrestrial specimens indicates a nearshore environment. Significantly, very deep desiccation cracks have been recorded in the upper part of the Rhaetian sequence, particularly in Somerset sections (*e.g.*, Duffin, 1980). This means that fleeting terrestrial conditions would not be so surprising. Although body fossil remains may be the result of post-mortem transportation, tracks must necessarily be preserved *in situ* providing certainty over environmental reconstruction (Conti et al., 2005; Falkingham, 2014). Specimen TECMAG0161 /

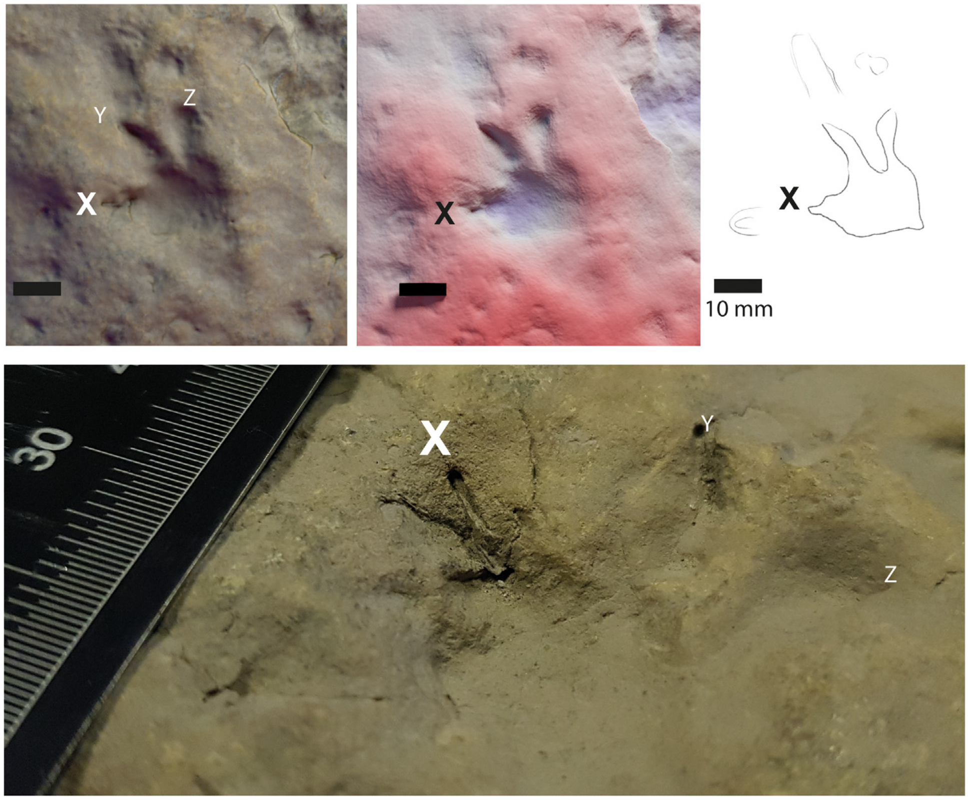

Fig. 6. Top: Close view of Impression 2 as photo-textured model, height mapped model, and interpretive outline. Bottom: Photo highlighting the broken bivalve shell around which an apparent 'digit impression' has formed at 'X', indicating this impression is unlikely to be a track, and may in fact be an erosional artefact. Y and Z indicate tips of other features to aid in visual orientation. Scale bar = 10 mm in top row, and markings indicate mm in bottom image. Red-blue colour scale = 23 mm.

Table 1
Pollen taxa present in sample from TECMAG0161 / Cg2406.

Dinoflagellate cysts
Dapcodinium priscum
Acritarchs
Micrhystridium spp.
Prasinophyte algae
Cymatiosphaera polypartita
Spores and pollen
Quadraeculina anellaeformis
Pityosporites spp.
Vitreisporites spp.
Perinopollenites elatoides
?Tsugaepollenites spp.
?Rhaetipollis germanicus
Polypodiisporites polymicrofuratus

Cg2406 is the first fossil known to show the presence of a (presumably marginal) terrestrial environment in the entire Westbury Formation - indicating perhaps a supra-tidal bedding plane.

5.3. Track interpretations and possible track makers

On first inspection specimen TECMAG0161 / Cg2406 appears to represent two vertebrate track impressions of different size and digit number, not unlike a manus-pes pair. However, upon closer examination we believe impression 2 is an artefact, created by weathering and erosion of the rock around at least one embedded bivalve shell. That the exposed bivalve shell appears to be broken lends support to the idea that this is not a combination of preservational artefact and real track, but we cannot rule out that an animal placed a foot in this position, and that the location of the bivalve shell is coincidental. The most conservative interpretation, and the one we adopt here, is that TECMAG0161 / Cg2406 contains only a single track, rather than partial trackway as initially thought. Although this makes the track more difficult to interpret, the specimen does serve to illustrate that care and close inspection are necessary in identifying tracks.

Impression 1 possesses regularly spaced digit imprints and is generally better defined, and as such we are confident that this is a track. The morphology and overall size of the impression, particularly digit proportions (relatively short), shape (tapered), and orientation (interdigital angle roughly equal between digits), in conjunction with the geological age, lead us to tentatively assign the impression to *cf. Procolophonichnium* (Nopcsa, 1923). The approximately equal length of the digits precludes assignment to similar ichnotaxa *Rhynchosauroides* or *Dromopus. Proclophonichnium* is a? Late Permian/Early to Late Triassic ichnogenus reported from Africa, Europe, and North and South America. Ichnospecies within this ichnogenus display pes impressions between ~15–35 mm in length and ~15–40 mm in width, usually slightly wider than long. Although *Procolophnichnium* is diagnosed as a pentadactyl trace, many examples of the ichnogenus lack impression of digit I, making many visible tracks only tetradactyl (Klein et al., 2015). However, the rear portion of the track described here is much larger and rounder than the many *Procolophonichnium* specimens figured in the comprehensive review by Klein et al. (2015), and so we emphasise the tentative nature of our assignation.

Prior to the Rhaetian, Mid Triassic tetrapod tracks in the UK include *Chirotherium*or *Rhynchosauroides* (King and Thompson, 2000) attributed to rauisuchian trackmakers, and one indeterminate specimen, possibly also of chirotheroid affinities (King and

Benton, 1996). Upper Triassic tetrapod tracks include the oldest dinosaur prints in the UK, and other archosaur footprints (King and Benton, 1996) in the Mercia Mudstone Group in South Wales dated to the Norian Stage which preceded the Rhaetian. Hitherto, no tetrapod tracks have been known from the Westbury Formation, and the next oldest trackways known in the UK after the Rhaetian are the Middle Jurassic (Aalenian) dinosaur tracks found in Yorkshire (Whyte and Romano, 1994, 2001; Whyte et al., 2007; and Whyte et al., 2010).Therefore, a gap exists in the tetrapod footprint record throughout the Rhaetian in the British Isles.

The vertebrate fauna of the Westbury Formation consists of isolated disarticulated skeletal elements and as such the material is of limited taxonomic value. The fauna is dominated by the marine component. The fishes include six species of shark, four actinopterygian taxa, a myriacanthid holocephalan and a lungfish and they are represented by scales, teeth, fin elements, isolated bones and occasional pieces of cartilage (Cross et al., 2018). Marine reptiles present include ichthyosaurs and plesiosaurs and these mostly comprise isolated vertebrae and long bones, together with other bone fragments from the post-cranial skeleton and isolated teeth (Storrs, 1999).

Terrestrial tetrapod remains are less numerous in the fauna, are similarly disarticulated and are therefore even less well understood. They include dinosaurs (*Camelotia borealis, Megalosaurus? cambrensis* and *Thecodontosaurus antiquus* (Storrs, 1999) but see Lomax et al., 2018) and some small and putative cynodont and mammal material (Boyd Dawkins, 1864). Significantly, these sediments also contain possible phytosaurs (Storrs, 1999) and potentially the earliest representative of the semi-aquatic choristoderes (*Pachystropheus rhaeticus)* that may have inhabited coastal or estuarine environments (Storrs and Gower, 1993). Most examples of *Pachystropheus* suggest an animal about 1 m long or less but some adult specimens seem to have reached lengths of 2–2.5 m (Storrs, 1999, p. 231).

Beyond the immediate vicinity of the Aust section, the coeval deposits of the Late Triassic fissure faunas of South Wales and the West of England also preserve fossil vertebrates. These represent contemporary infills of karstic features developed in the underlying Carboniferous Limestone on a series of palaeo-islands. Recent reviews of these fissure deposits have concluded that, rather than ranging from Carnian to Rhaetian in age, all are likely to be Rhaetian, with the exception of some examples in the St Brides area of South Wales. These are probably Hettangian to Sinemurian in age (Whiteside et al., 2016; Whiteside and Duffin, 2017). The fissures have been divided into two faunal groups (see Whiteside et al., 2016, Fig. 4). The 'sauropsid' fissures (Robinson, 1957) include Cromhall, Tytherington, Durdham Down, Woodleaze, Emborough, Batscombe, Pant-y-ffynnon, and Ruthin. The 'mammaliamorph' fissures (Whiteside et al., 2016) include Holwell, Windsor Hill, and the St Brides quarries (Pant, Pontalun, Ewenny, and Duchy). The fissure faunas preserve a wide range of small (generally less than 0.5 m long) reptiles (see Whiteside et al., 2016 Table1 for a summary), including a fairly diverse set of sphenodontian rhynchocephalians (*Diphydontosaurus*, *Gephyrosaurus*, *Penegephyrosaurus, Clevosaurus, Planocephalosaurus, Pelecymala, Sigmala*) as well as the gliding 'lizards' *Kuehneosuchus* and *Kuehneosaurus*. Larger (2−3 m long) reptiles are represented by the possible basal sauropodomorphs *Thecodontosaurus* and *Pantydraco*, trilophosaurs (*Tricuspisaurus* and *Variodens*) and putative phytosaur, aetosaur, drepanosaur and pterosaur remains. The sphenosuchian crocodylomorph, *Terrestrisuchus*, was approximately 0.5 m long, with a manus around 20 mm in length (Crush, 1984). Procolophonid remains have been recorded from Cromhall, Ruthin and Holwell quarries (Whiteside et al., 2016; Whiteside and Duffin, 2017, p. 695).

Confidently associating tracks with trackmakers is notoriously difficult even in the best cases. When a track is isolated, weathered, and not associated with a comprehensive body fossil record, as in this case, that difficulty verges on impossibility. *Procolophonichnium* was originally attributed to procolophonids, then later to turtles and most recently a therapsid trackmaker (Klein et al., 2015). The lack of anatomical detail (*e.g.* phalangeal pads) and trackway context associated with the track described here means that we cannot even ascertain if it is a pes or manus impression. The size of the impression, and digit proportions lead us to reject any of the small reptile or sauropodomorphs listed above as trackmakers.

6. Conclusions

Specimen TECMAG0161 / Cg2406 is the first tetrapod track from Rhaetian deposits to be recorded in the British Isles. Despite first appearances, we consider it a single track rather than a trackway. This, coupled with the isolated nature of the specimen, offers little concrete information about the trackmaker. The track resembles the ichnogenus *Procolophonichnium*, which has most recently been attributed to a therapsid trackmaker. Known mammaliamorph body fossils are too small to represent the trackmaker. Our specimen lacks enough anatomical fidelity to confidently assign a trackmaker even at a high taxonomic level.

However, the specimen does add an important data point to an otherwise ichnologically empty hiatus. The track also provides solid evidence for a locally terrestrial environment in a sequence otherwise considered to represent predominantly marine and estuarine environments. There are likely to be more such tetrapod tracks of Rhaetian age preserved, at least at Aust, and any further discoveries of this nature will add to our understanding of this crucial period in terrestrial tetrapod evolution.

Declaration of competing interest

None

Declaration of Competing Interest

The authors report no declarations of interest.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.pgeola.2020.07.012.

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