Abstract

Evidence of Late Triassic large tetrapods from the UK is rare. Here, we describe a track-bearing surface located on the shoreline near Penarth, south Wales, United Kingdom. The total exposed surface is c. 50 m long and c. 2 m wide, and is split into northern and southern sections by a small fault. We interpret these impressions as tracks, rather than abiogenic sedimentary structures, because of the possession of marked displacement rims and their relationship to each other with regularly spaced impressions forming putative trackways. The impressions are large (up to c. 50 cm in length), but poorly preserved, and retain little information about track-maker anatomy. We discuss alternative, plausible, abiotic mechanisms that might have been responsible for the formation of these features, but reject them in favour of these impressions being tetrapod tracks. We propose that the site is an additional occurrence of the ichnotaxon *Eosauropus*, representing a sauropodomorph trackmaker, thereby adding a useful new datum to their sparse Late Triassic record in the UK. We also used historical photogrammetry to digitally map the extent of site erosion during 2009–2020. More than 1 m of the surface exposure has been lost over this 11-year period, and the few tracks present in both models show significant smoothing, breakage and loss of detail. These tracks are an important datapoint for Late Triassic palaeontology in the UK, even if they cannot be confidently assigned to a specific track-maker. The documented loss of the bedding surface highlights the transient and vulnerable nature of our fossil resources, particularly in coastal settings, and the need to gather data as quickly and effectively as possible.

1. Introduction

The body fossil record of Late Triassic non-marine tetrapods from the UK is limited and most of our knowledge of these taxa comes from one of three sources: the diverse microvertebrate faunas recovered from fissure fill deposits in the Bristol Channel region of England and Wales (Fraser & Sues, 1994; Benton & Spencer, 1995; Whiteside et al. 2016); a series of taxa preserved largely as natural moulds in the Lossiemouth Formation of Elgin, Scotland (Newton, 1893; Benton & Walker, 1985); and as rare, usually isolated, elements from a few localities in SW England and Wales (Storrs, 1994; Galton, 1998, 2005; Redelstorff, 2012; Martill et al. 2016). Known tetrapod diversity includes temnospondyls, mammaliforms, procolophonids, rhynchosaurids, trilophosaurids, drepanosauroids, a variety of lepidosauromorphs (rhychocephalians and several stem-taxes), choristoderes, several pseudosuchian archosaurs (phytosaurs, euctosaurs, crocodylomorphs) and various avemetatarsals (including saurupodomorph and theropod dinosaurs; Rauhut & Hungerbühler, 2000; Galton, 2005; Galton & Kermack, 2010) although many of these, particularly the larger-bodied taxa, are known only from limited material. Taken together, these localities span the Carnian–Rhaetian stages and a range of palaeoenvironments, but the majority are currently thought to span a Rhaetian age (Whiteside et al. 2016; Lovegrove et al. 2021).

Several Late Triassic UK sites preserve ichnofossil assemblages that complement the skeletal record, demonstrating the presence of various trackmakers in either areas or stratigraphic levels where there is little or no bone preservation. The tetrapod ichnofossil record from this time in the UK is mostly attributed to small- to medium-sized trackmakers. These include rare Carnian records from the Lossiemouth Formation and the Arden Sandstone Formation of Warwickshire, usually attributed to either synapsids or crocodylomorphs (Tresise & Sarjeant, 1997), and isolated tracks from Aust, Gloucestershire that may have been made by therapsids (Larkin et al. 2020).

The most important track assemblage, however, comes from the Norian–Rhaetian-aged Mercia Mudstone Group of south Wales (Sollas, 1879; Thomas, 1879; Tucker & Burchette,
The marginal facies in which these assemblages occur cannot be attributed to a particular formation within the group (Howard et al., 2008), but tracks are known from three areas along the northern coast of the Severn Estuary, including Newton Nottage near Porthcawl and the Bendricks and Sully areas south of Cardiff. The most comprehensive account to date on these occurrences was published by Lockley et al. (1996), who reported a minimum of 88 trackways from about 10 stratigraphic levels that mostly pertain to tridactyl theropod dinosaurs. In addition, these authors discussed 16 bipedal trackways of tetradactyl morphology assigned to *Pseudotetrasauropus* (now *Eurosaurus*; see Nicosia & Loi, 2003) as well as four quadrupedal trackways assigned to *Tetrasauropus* (now *Eurasaurus*; see Lockley et al., 2006). Both types were possibly made by sauripodomorph dinosaurs, although a chirotheroid affinity was also discussed.

Here, we add to this record by describing a series of features that we interpret as Late Triassic tetrapod tracks from the Blue Anchor Formation (Mercia Mudstone Group) situated on the foreshore near Penarth, South Glamorgan, Wales.

### 2. Brief history of study

The tracks have been exposed intermittently over the past decade (and certainly long before this; Thomas, 1879), and the presence of these features was noted by several members of the public over this time, some of whom contacted the National Museum of Wales (Cardiff) and Cardiff University. However, to the best of our knowledge, JEM and GS were the first to attempt formal documentation of the site in 2009, with other teams led by LC and colleagues, CH and colleagues, and Chris Berry (Cardiff University) and colleagues, also mapping and examining the site subsequently. These teams developed different models for the formation of these features, with JEM/GS regarding the structures as tracks and LC, CH and others regarding the structures as ambiguous, and potentially of abiotic origin (see Section 6 for Discussion). However, although this work formed the basis for various student projects, it remained unpublished and was not discussed or disseminated more widely. Following a query from a member of the public to the Natural History Museum, PLF, SCRM and PMB visited the site in August 2020, unaware that other researchers had previously made independent assessments. However, consultation with CH and LC during and after this visit provided more background information on the history of study and led to the current collaboration. Given the exposed and publicly accessible nature of the site, it is highly likely that others have also examined it, although we are unaware of any other formal documentation attempts or any record of this site in the literature.

### 3. Material and methods

#### 3.a. Geological setting

The tracks occur on a single surface at the top of a 15-cm-thick grey, dolomitic siltstone. Small gypsum nodules occur near the top of the bed. The tracks are deeply impressed into the top surface and are partially infilled with a green siltstone with orange stringers. In the summer of 2020, the beds immediately above and below the track layer were unexposed and covered in pebbles and boulders, but the beds that were exposed on the beach appear to show a cyclical pattern of dolomitic mudstones, siltstones and limestones with gypsum nodules, similar to the track layer. These beds are attributable to the Blue Anchor Formation of the Mercia Mudstone Group, and those exposed on the beach are c. 5 m below the top of the Blue Anchor Formation. The Blue Anchor Formation has generally been considered to be late Norian–early Rhaetian in age (Howard et al., 2008). At St Audrie’s Bay (Somerset), the Blue Anchor Formation records a reversed polarity event and was tentatively assigned to the Norian stage using comparisons with the composite magnetostratigraphic polarity pattern of Tethyan marine sites (Hounslow et al., 2004). However, subsequent magnetostratigraphic studies of marine sites recording the Norian–Rhaetian transition in Austria have suggested that beds of the Blue Anchor Formation with reversed polarity are more likely to be entirely Rhaetian in age (Hounslow & Muttoni, 2010; Hüsing et al., 2011). Accordingly, the Blue Anchor Formation, and hence the tracks reported here, are most likely to be Rhaetian in age, especially given their stratigraphic location at the top of the Blue Anchor Formation.

The greenish-grey silty dolomitic mudstone beds of the Blue Anchor Formation have been interpreted as mostly subaqueous evaporitic lacustrine deposits with occasional marine influence, representing the early stages of the Rhaetian marine transgression (Tucker & Burchette, 1977; Tucker, 1978; Mayall, 1981; Howard et al., 2008; Suan et al., 2012). In the Penarth Bay area, there is a gradual transition between the Branscombe Mudstone Formation, a succession predominantly composed of red-brown silty dolomitic mudstone with gypsum nodules and veins deposited in a lacustrine setting, and the greenish-grey silty mudstone of the Blue Anchor Formation. This lithological transition is considered to record a shift from arid to less arid climatic conditions (Howard et al., 2008; Suan et al., 2012). The tracks were thus formed under predominantly semi-arid conditions on a low-lying mudflat alongside a marine-influenced lake that was prone to periodic shoreline retreat and sub-aerial exposure.

#### 3.b. Locality description

The track surface is exposed on the beach approximately 1 km south of Penarth pier (Fig. 1; 51.4253° N, −3.1710° W). This beach is usually covered in loose material (ranging in size from sand to small boulders) but, on rare occasions, exceptionally high tides strip away this overlying sediment to expose the surface.

The exposure documented in August 2020 consisted of two exposures of the same bedding surface; the northern being c. 30 m in length and c. 2 m wide, and the southern being c. 20 × 2 m. The two exposed surfaces are offset c. 10 m by a non-contemporaneous fault trending 052° across the beach, downthrown to the south (Fig. 2). Areas were brushed down prior to photography and measurement. Cleaning efforts during 2020 were focused on the northern section, but local tides constrained the time available for exposing and mapping the site, hence only a narrow strip was exposed. The bedding surface continues to the west beneath surficial sediment and overlying strata.

### 4. Photogrammetry and historical site assessment

During the summer of 2020, both exposed surfaces were recorded via photogrammetry with a total of 1386 photos taken using a Sony Nex–6 (16 mp) and 16–50 mm lens. Photogrammetric models were produced using AliceVision Meshroom v. 2019.2, then analysed and visualized using Blender v. 2.91.

During mapping in 2009, in addition to clearing and documenting the site via traditional means, JEM and GS took
285 photographs of what we label here the southern exposure, with a Pentax K10D (10 mp). These photographs were used here to generate a photogrammetric model (via AliceVision Meshroom v. 2019.2) using ‘historical’ or ‘post-hoc’ photogrammetry, that is, where photographs taken in the past, without the intention of creating 3D models, are used for photogrammetric reconstruction (Falkingham et al. 2014, 2018; Lallensack et al. 2015). The availability of two digital models (Fig. 3) produced from photographs taken over a decade apart provided a valuable opportunity to examine the extent of loss of the surface due to erosion, and to provide supplementary detail on the morphology of these features prior to this period of additional weathering and erosion. All data, photographs and models are available from Figshare (https://doi.org/10.6084/m9.figshare.14604567).

5. Description
The impressions are highly variable in shape and size (Fig. 4). They are all highly weathered, exhibiting both broken and smoothed surfaces, breakage being facilitated by numerous diaclases in the

![Stratigraphic log](https://doi.org/10.1017/S0016756821001308) Published online by Cambridge University Press
bedding plane. They are roughly circular to elliptical in outline, and almost entirely lack clear impressions of either individual digits, claws or footpads (but see below). They range over 20–60 cm in maximum diameter. Depth is likewise variable, but ranges mainly over 5–10 cm. Almost all of the depressions are surrounded by significant asymmetrical displacement rims that are often similar in height to the depth of the track, and that extend laterally from the tracks to make the maximum zone of deformation approximately 1.5–2 times the size of the area of negative displacement (Manning, 2004; Falkingham, 2016). The displacement rims are variable in height and width along the outline of the footprints, which is consistent with similarly pronounced displacement rims that have been recorded from other dinosaur tracksites (e.g. Farlow et al. 2012, fig. 15A).

The footprint outlines are highly irregular, but some impressions do reveal possible anatomical information. Indentations into the inner sides of the displacement rims can generally be attributed to the removal of chunks of rock by erosion and subsequent smoothing by weathering. However, in other cases, such indentations are distinctly caused by undulations of the displacement rims, although these are not necessarily related to foot anatomy (e.g. Marty et al. 2009, fig. 6). Nevertheless, at least some of the structures (Figs 3c, d, 4c, d) exposed in 2009 possessed regularly spaced indentations that are consistent in size and shape and which we interpret as digit impressions. Unfortunately, these tracks lost almost all of this detail in the intervening years due to erosion (Fig. 3c, d).

Tracks are distributed unevenly and for the most part without association. Several large and complex impressions are subdivided by shallow rims and might have been formed by partly overlapping impressions. The northernmost exposure has two sequences of tracks that appear to be arranged in lines with semi-regular spacing. Measuring from the centre of each depression, the northernmost sequence (Fig. 5) consists of 5–6 impressions 1.1–1.3 m apart (from north to south: 1.08, 1.13, 1.19 and 1.28 m). The second sequence of tracks on this exposure consists of 6–8 impressions, spaced 1.2–1.5 m apart (1.24, 1.27, 1.13, 1.33 and 1.53 m, from north to south or top to bottom in Fig. 3). The sequences are not contiguous on the exposed surface, but could conceivably extend and connect beneath the overburden. It is possible that these impressions form trackways, although the irregularity in spacing and the size variation of tracks makes this interpretation tentative.

All of the tracks exposed in 2020 were heavily distorted by weathering and erosion, and were often missing large parts from their displacement rims and interiors (Fig. 4). Tracks visible only in the 2009 dataset were of a similar level of preservation (sensu stricto; see Falkingham & Gatesy, 2020) to those visible in 2020. The few tracks visible in both 2009 and 2020 showed reduction in their displacement rims and shallowing in line with the simulated weathering experiments conducted by Henderson (2006), and also displayed some breakage of the rim, creating a jagged rather than smooth surface (Fig. 3).

Both exposures exhibited a high density of impressions. The heavy erosion, combined with the lack of anatomical detail, makes it difficult to unambiguously identify all of the impressions present as tracks (see Section 6 for Discussion). There are also many instances of overprinting, which makes an accurate count of individual tracks difficult. Nevertheless, track density is clearly high, with > 40 impressions on the southern surface and > 60 impressions on the northern surface (Fig. 2), equating to approximately four tracks per square metre of exposed surface.
6. Discussion

6.a. Are they tracks? Alternative explanations?

Because the surface lacks unequivocal evidence of detailed foot anatomy or trackways, alternative formational mechanisms for these impressions should be considered. The dense distribution, asymmetric raised rims and sunken floors of the roughly circular impressions raise questions of expansion and collapse of sediment. The role of gypsum in their formation might provide an explanation. Directly beneath this bed, and in others through the sequence, there are layers of gypsum nodules and dissolution cavities. Rimmed impressions are also present in other beds on the foreshore, although these are not as pronounced as on the main bed described here. Volume changes caused by the hydration and drying of evaporitic minerals (63%; Azam, 2007) in the semi-arid desert and lake edge environments envisaged for these beds might result in the bulging and collapse of overlying sediment. Notably, nodules fill, and sometimes line, impressions that are similar in size and spacing to the possible tracks, some of which are rimmed (see supplementary material at https://doi.org/10.6084/m9.figshare.14604567). Another possible process could involve the shallow liquefaction of uncompact mud sediment to form mud volcanoes, perhaps seismically induced in these Late Triassic environments (Mayall, 1983; Simms, 2003, 2007; Laborde-Casadaban et al. 2021). Both alternatives might result in a random distribution of rimmed pits or lead to some

Fig. 3. (Colour online) Comparison of the south track-bearing surface between 2020 and 2009. (a) Digital models and outline drawings of the surface from 2020 and 2009, aligned and overlain. (b) Close-up of three tracks X, Y and Z, identified in both models. (c) Photo-textured and (d) height-mapped close-up images of track W illustrating the detail and possible digit impressions present in 2009, compared with the heavily weathered appearance in 2020. Scale bar in (c) 1 m, height map in (d) blue to red: 10 cm (but height map could not be zeroed accurately between 2020 and 2009 models).
alignment of structures relating to the deformational setting. While not ruling out dinosaur trackways, these processes also merit consideration, not least to see whether there are discernible differences between the impressions regarded here as tracks and others.

As an alternative hypothesis, could the impressions be moulds of gypsum nodules that have since eroded away? We found no evidence of gypsum remaining within any of the exposed impressions interpreted here as tracks, either in 2009 or 2020. It is conceivable, although unlikely, that gypsum did previously reside within these impressions and has been completely removed through erosion, unlike those on the exposed part of the underlying bed. However, even if gypsum were originally present in the tracks, it may be possible that the impression came first, and the nodules formed within them, nucleating around the disturbance, rather than nodule formation creating the sediment deformation. Finally, in cases where two impressions are overlapped/beside each other, the displacement rims on one impression overwrite the other, implying a sequential forming of impressions while the first impression is empty. This strongly suggests that the impression formation is not related to gypsum formation.

Another possible origin for the impressions is that they are fish-feeding traces. Such traces have been repeatedly confused with tetrapod tracks in the past, particularly those of sauropods (Martinelli et al. 2001; Lucas, 2015). Fish-feeding traces can be aligned in rows that can resemble trackways (Lucas, 2015), and may show digit-like impressions at one end as well as smaller displacement rims (e.g. Pearson et al. 2007, fig 2). Belvedere et al. (2011) described a site of fish-feeding traces that was initially interpreted as a tetrapod tracksite. These authors noted that the regular spacing and lack of displacement rims were indicators that the impressions were not tetrapod tracks. At Penarth, the strongly pronounced displacement rims as well as the excessive overprinting and irregular distribution are good indicators that the impressions are not fish-feeding traces.

Fig. 4. (Colour online) Detail images of individual tracks. (a) Individual D-shaped impression recorded in 2020, presented as photo-textured and height-mapped digital models. (b) Two to three overlapping impressions recorded in 2020, with a displacement rim spanning the centre of the deepest areas, presented as photo-textured and height-mapped digital models. (c, d) Individual tracks recorded during 2009, but showing clearer morphology in the displacement rims that we interpret as digit impressions (marked with *) (c) located on the reconstructed model (Fig. 3a), shown here as a height map, but note that water and debris present in the track affect the accuracy and fidelity of the photogrammetric model; and (d) not recorded with enough photographs for a 3D reconstruction. White scale bar: 10 cm, red to blue height map spans 10 cm.
We consider the uneven outlines of the impressions, their large asymmetric displacement rims, and their arrangement and distribution to be, on balance, evidence supporting their interpretation as tetrapod tracks.

6.b. Possible trackmakers

The highly weathered condition of the vast majority of the tracks makes it difficult, or even impossible, to determine if they were all made by the same taxon, or by several species. The size range of the impressions indicates strongly that the surface was traversed by more than one trackmaker. Small and large tracks could represent manus and pes impressions, but small and large impressions do not appear to be associated consistently. Assuming the semi-regularly spaced impressions described above (Fig. 5) do constitute trackways, they were likely made by bipeds because they are incredibly narrow-gauged. The shorter, northernmost trackway exhibits a consistent pace angulation of 140° (138–143°), which is not

Fig. 5. (Colour online) Possible trackways observed on the northern surface, photo-textured models and interpretive outlines; dashed lines indicate extent of displacement rims. Tracks with approximately equal distancing are highlighted in black and connected with dashed lines. Other tracks are in red.
6.c. Formational mechanisms and comparison with modern tracks

Trample grounds are not uncommon in the dinosaur ichnological record, or for other trackmakers, extinct and extant (Marty et al. 2003; Da Silva et al. 2007; Mezga et al. 2007; Marty, 2008; Richter & Bohme, 2016; Lallensack et al. 2018). Sites such as the Penarth tracksite, where numerous tracks occur in high densities and are close to or even overprinting each other, would be given a moderate to heavy ‘dinoturbation index’ following Lockley & Conrad (1989). Such highly ‘dinoturbated’ sites can occur along herd movement paths (e.g. following the edge of a body of water, or along a migration trail), in which case the majority of tracks will be oriented in the same direction. Trample sites are also likely to occur beside bodies of water, either flowing or still, where animals congregate to drink. In these cases, the density of trackmakers is significantly increased over time, drawing animals from a much larger area than would otherwise be recorded in a tracksite. Animals will move to, from and around the body of water, leaving tracks in all directions. Additionally, the sediment conditions required for track formation are ideal. Particularly in an arid or semi-arid environment, as is interpreted to be the case when the Penarth tracks were made, sediment around a body of water will span the gamut from completely dry to completely saturated. Between these end points lies a ‘Goldilocks’ zone, where the sediment is soft enough to deform underfoot, but firm enough to retain its shape after foot withdrawal (Falkingham et al. 2011, 2014). Given the narrow exposure and lack of anatomical details, it is difficult to draw conclusions about the number of trackmakers, or the extent of the trampled area.

Modern tracksites beside bodies of water have previously been figured in the literature and used as analogues for fossil sites (Laporte & Behrensmeyer, 1980). We add to this existing literature by presenting in Figure 6 a trample ground made by cattle in mud, beside a small flowing stream. Photographs were also collected for photogrammetric reconstruction, but the presence of water made 3D reconstruction difficult, and so only a photo is presented here (photographs and 3D model are available; see supplementary data at https://doi.org/10.6084/m9.figshare.14604567).

The size of the cow tracks varies significantly across the site, ranging over 10–20 cm, although cattle of approximately consistent size were the only possible trackmakers. Tracks are generally larger when located beneath the water’s surface. The tracks were not observed at the time of formation, so it is unknown whether the larger impressions were formed underwater, or if they were inundated post-formation. The larger size of tracks is likely due to reduced friction and cohesion within the saturated sediment, which is able to collapse into bowl-shaped depressions, while retaining a significant displacement rim. Further away from the water, in the firmer substrate, displacement rims are taller and overall track size is smaller.

The general form of the cow tracks in Figure 6, particularly those near or under the water, is very similar to those recorded from Penarth in that tracks lack distinct features or sharp edges, but retain displacement rims including in overprinted impressions. Definitive trackways cannot be identified, because track density is so high and because trackmakers were likely not moving with consistent speed, and therefore consistent stride length, in this area. We consider this an approximate taphonomic analogue for the Penarth tracks. While the feet and tracks of cows are very different from those of dinosaurs, the mechanics of sediment flow and deformation are the same, and so we present this comparative...
example to illustrate a possible mechanism that might produce tracks like those at Penarth.

6.d. Extent of weathering and erosion since 2009

It was fortunate that a large number of photographs were taken during the fieldwork carried out in 2009, enabling the construction of a 3D digital model. When the two models are aligned and overlain, the extent of loss of the surface is immediately apparent. In little over a decade, the originally exposed surface has been reduced in size by c. 50% (Fig. 2), and the remaining portion of the surface has suffered significant erosion and weathering of track morphology to the point that previously present anatomical detail (i.e. digit impressions) have almost completely disappeared. Unlike body fossils, collection of tracks – and particularly tracksites – can be difficult or even impossible, and they are usually left in situ. Conservation of such fossil resources is difficult, however, particularly in localities such as this where wave action and public access can rapidly degrade the fossils. A partial solution to this lies in modern 3D digital documentation, either through photogrammetry or laser scanning (Bates et al. 2009a, b, 2008; Breithaupt & Matthews, 2001; Breithaupt et al. 2004, 2006; Falkingham, 2012; Farlow et al. 2012; Bennett et al. 2013; Matthews et al. 2016; Falkingham et al. 2018). Regular digital documentation of sites such as this will enable monitoring of degradation rates and capture of 3D morphology soon after first exposure, maximizing the information recorded. In this case, alignment of the two digital models was difficult because the surfaces had changed so much. If regular 3D mapping of the site is to be carried out in the future, reference positions should be established to facilitate easier, and more accurate, alignment and comparisons of models made at different times.

7. Conclusions

Large impressions in sediments of the Blue Anchor Formation located on the beach near Penarth, south Wales are interpreted as tetrapod tracks. Although it is difficult to identify individual trackways, the high density of impressions suggests that the area was a trample ground that might have been visited by many individuals. Although the number of taxa making these impressions cannot be reliably inferred because of their poor preservation, based on their large size, round shape and digit impressions, we consider it likely that they were made by large sauropodomorph dinosaurs and refer them tentatively to the ichnogenus *Eosauporus*, although other unidentified taxa might also have been present. This provides an important additional datapoint for documenting Late Triassic terrestrial tetrapod faunas in the UK, where the remains of large-bodied taxa are otherwise rare. Although abiotic processes might have contributed to the formation of other

Fig. 6. (Colour online) Cow tracks left in soft mud beside a stream, from north Wales. Cows of a similar size (i.e. members of the herd were of approximately equal size) were the only possible trackmakers. Tracks near and under the water are much larger (2–3 times the diameter) than tracks formed in much firmer mud further away from the water’s edge. Tracks display prominent displacement rims, even in collapsed, submerged tracks. Overprinting is present in some impressions. General morphology of the submerged tracks is very similar to the Penarth tracks. Scale bar: 7 cm.
similar features nearby, the track morphology, overprinting, rim displacement and the lack of a residual gypsum infill suggest that these are biogenic structures.

The track-bearing surface extends for an unknown distance beneath the overlying strata and loose pebbles and boulders. However, because it is below the high-tide line, excavations are problematic and would risk destroying the tracks. Until a major endeavour can be undertaken to expose and conserve more of the surface, the tracks are best protected by remaining buried. Regular 3D documentation of the site is the best way to map the surface as it becomes further exposed naturally. Future exposures of this surface will enable additional testing of our hypothesis and, hopefully, will reveal new, better-preserved examples of these features. Photogrammetry represents an excellent tool for archiving and comparing these data and we advocate its habitual use alongside traditional trackway study methods (such as conventional photography, outline tracing, measurements and moulding/casting) in order to maximize data collection potential.

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