POSSIBLE TETRAPOD BURROWS IN THE MID TRIASSIC OTTER SANDSTONE FORMATION AT SIDMOUTH, DEVON, UK

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Trace fossils interpreted as tetrapod burrows have been reported from fluvial Triassic deposits in geographically widely separated parts of the former Pangea supercontinent, including Morocco, South Africa, the USA and Antarctica. The burrows at most of these localities are hosted in deposits of ephemeral braided rivers that formed in arid to semi-arid settings. Vertebrate fossils have been recorded from all the burrowed formations, and in some examples vertebrate skeletons have been found in the burrows. Evidence of periods when the climate was sufficiently wet to support mature vegetation is present in the form of rhizocretions and caliche deposits that are associated with all the burrowed horizons. The depositional environments at all these localities, as evidenced by their sedimentology and faunas, are closely similar to those of the Mid Triassic Otter Sandstone Formation of South-West England. The *c.* 200 m thick formation is almost wholly exposed on the east Devon coast, but no trace fossil other than rhizocretions and a single reptile footprint has previously been recorded from the Otter Sandstone Formation. The sizes and shapes of some of the trace fossils described in the present account are similar to Triassic burrows in Antarctica, Morocco and South Africa that have been attributed to the access tunnels and resting chambers of small therapsid reptiles. Other, less well defined, structures in the Otter Sandstone Formation that disturb bedding features may represent the resting places or egg-laying sites of tetrapods. The small number of possible tetrapod burrows recorded and the sparse and fragmentary nature of vertebrate fossil occurrences in the Otter Sandstone Formation mean that it is not possible at the present time to determine which tetrapods might have made the burrows.

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INTRODUCTION

An almost complete section through the Otter Sandstone Formation (OSF) is exposed on the Devon coast in sea-cliffs up to 160 m high between Budleigh Salterton [SY 062 817] and Sidmouth [SY 130 873] (Benton *et al.*, 1994). The coastal outcrop exposes about 150 m of strata in which an unknown thickness of beds is cut out by faulting where the outcrop is broken by the valley of the River Otter. Up to 210 m of OSF has been proved nearby in inland boreholes (Edwards and Gallois, 2005). The formation consists of yellow- and orange-brown, cross-bedded, fine- and medium-grained sandstones with a few lenticular beds of conglomerate (channel-lag deposits) up to 0.5 m thick and lenticular red-brown mudstones up to 2 m thick. In the coastal exposures the unbroken succession east of the Otter Valley can be divided on the basis of sedimentary structures into three members (Figure 1) that approximately correlate with Units B to D of Hounslow and Macintosh (2003). A sharp lithological change at the base of each member probably represents an upward change to a different rainfall pattern and a climate that was drier overall (McKie *et al.*, 1998). At Budleigh Salterton the OSF rests with sharp lithological contrast on a reddish brown, silty clay palaeosol which rests on the Budleigh Salterton Pebble Beds Formation. The palaeosol was interpreted by (Wright *et al.*, 1991) as representing a major break in sedimentation of uncertain duration.

At Steamer Steps [SY 0632 8176] on the west side of the Otter Valley, the lowest part of the formation comprises aeolian sandstones overlain by fluvial, cross-bedded, fine-grained sandstones with small (up to 50 mm) angular mudstone clasts (Unit A of Hounslow and Mackintosh, 1993). Within the valley, a degraded sea cliff [SY 0703 8200] exposes a stratigraphically higher level with calcretes and associated calcareous rhizocretions. On the east side of the River Otter, lithologically similar cross-bedded sandstones with calcrete sheets and rhizocretions in the Otterton Point Sandstone Member are exposed in the sea cliff [SY 0774 8192] together with lenses of channel-lag gravel that contain calcrete debris and far-travelled rock clasts. The lithologies and sedimentary structures indicate that there is no overlap between the youngest beds at Steamer Steps and the promenade section, and between there and the sea cliff (Figure 1). North eastwards from the River Otter, the Otterton Point Sandstone Member is wholly exposed in continuous cliffs as far as Ladram Bay [SY 097 851] where a low easterly dip brings the junction with the Ladram Bay Sandstone Member down to beach level. The outcrop of the junction is repeated by faulting eastwards from there with the result that it is well exposed between Big Picket Rock and Sidmouth (Figure 2). The base of the Ladram Bay Sandstone Member is taken at a sudden upward change (Figure 3b) from sandstones with relatively narrow (up to 10 m wide) channels with numerous caliche beds and rhizocretions to sandstones with broad channels up to 100 m wide with pebbly basal-lag deposits that contain angular and rounded rip-up clasts of sandstone, caliche and red mudstone. The youngest part of the formation, the Pennington Point Member, comprises red playa-lake mudstones cut by a succession of up to eight sand-filled channels that were deposited by flash floods which became progressively weaker with time (Gallois, 2004). The last of the sandstones marks the

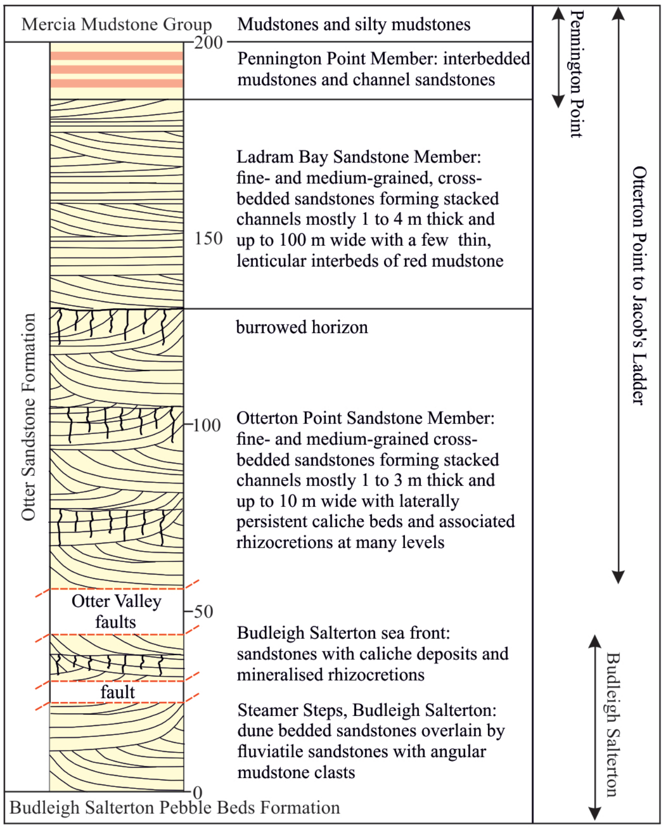

Figure 1. *Simplified generalised succession for the Otter Sandstone Formation exposed on the east Devon coast.*

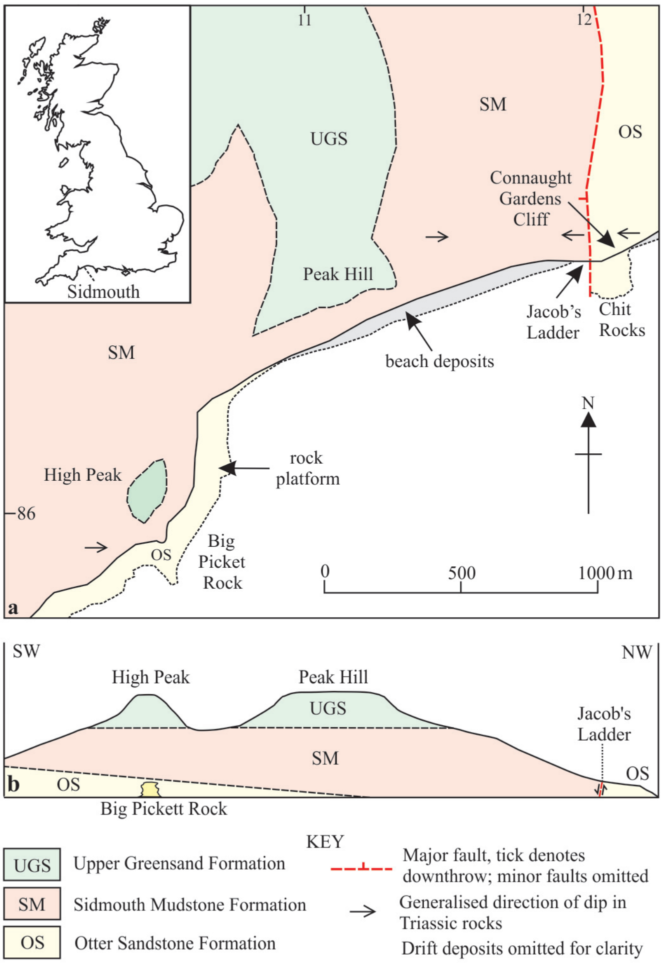

Figure 2. *Geological sketch map of the Otter Sandstone Formation outcrop between High Peak and Sidmouth showing the positions of sections referred to in the text.*

junction of the Otter Sandstone Formation/Sherwood Sandstone Group and the Mercia Mudstone Group, and the incoming of a drier climate that gave rise to muddy playa-lake environments that lasted for several million years.

The coastal exposures of the OSF in Devon are the most prolific source of Triassic vertebrates in Britain. The assemblages include archosaur and rhynchosaur reptiles (Benton, 1997; Benton and Spencer, 1995), amphibians and fishes. Most of the fish remains occur as scales or loose teeth, but some of the mudstone lenses have yielded more complete specimens (Milner *et al.*, 1990). The first published account of vertebrate remains in the OSF is that of Whitaker (1869) who described part of the skeleton of a rhynchosaur in a fallen block adjacent to the mouth of the River Otter at Otterton Point [SY 0773 8191]. Other 19th Century finds include bones and teeth from outcrops adjacent to Sidmouth (Cook, 1876; Irving,1888; Metcalfe, 1884) where Johnston-Lavis (1876) recorded vertebrate material in the youngest part of the formation (now the Pennington Point Member) in such profusion *in situ* and in fallen blocks below Peak Hill that he referred to the horizon as the "*Ossiferous Bed*". More recent collecting, in particular from channel-lag deposits in the Pennington Point Member at Pennington Point [SY 1296 7833], has yielded a vertebrate assemblage that is more diverse than that from any other part of the coastal exposures in the OSF (Spencer and Isaac, 1983; Spencer and Storrs, 2002). The assemblage includes the fragmentary remains of archosaurs with estimated body lengths ranging from 0.8 m to 3 m (Benton, 2011).

The vertebrate fossils in the OSF have mostly come from Otterton Point, Ladram Bay, beneath Peak Hill and at Pennington Point. The material almost certainly reflects an element of collection bias because these are the most readily accessible sections on the coast. The cliff and intertidal outcrops between Otterton Point and Ladram Bay can only be safely accessed by boat, and those between Ladram Bay and Peak Hill require a low tide. An artistic reconstruction by Pam Baldaro of the environment at the time of deposition of the OSF which includes all the key elements of the fauna and flora was reproduced in Benton (1997, figure 10). Taken together the sedimentary and palaeontological features show that the bulk of the OSF (the Otterton Point Sandstone Member) was deposited in deserts that were at times crossed by fertile river valleys. Cross-bedding directions in the coastal exposures in Devon indicate that the sandstones were mostly deposited in braided and meandering streams that flowed from south to north (Benton *et al.*, 1994). The caliche deposits represent cementation in zones of water-table fluctuation associated with rhizocretions that formed around rootlets and around the deep tap roots of trees that were adapted to survival in a semi-arid or arid environment with infrequent rain (Purvis and Wright, 1991).

The faunal assemblages indicate an Anisian age for much of the OSF. Hounslow and Mackintosh (2003) dated the base of the formation at Budleigh Salterton as Early Anisian, and the junction with the overlying Mercia Mudstone Group at Sidmouth as latest Anisian based on a study of the magnetostratigraphy of the Budleigh Salterton Pebble Beds Formation and the OSF. This is in agreement with the suggestion by Geluk (2005) that the sedimentary break at the base of the OSF is the probable correlative of the Hardegsen Unconformity of the Germanic Province.

Few trace fossils have been recorded from the 3000+ m thick Permo-Triassic red-bed succession that is almost wholly exposed on the Devon coast between Torbay and Seaton. The reported trace fossils include the burrow-like *Beaconites* cf. *antarcticus* (Viavlov) in the Early Permian Torbay Breccia Formation at Paignton (Ridgeway, 1974), rare reptile tracks in the Late Permian Dawlish Sandstone Formation (Clayden, 1908), abundant plant rhizocretions at numerous levels in the OSF (Purvis and Wright, 1991), a single reptile footprint in the OSF (Coram and Radley, 2013), and small freshwater burrows in sandstones in the Late Triassic Dunscombe Mudstone Formation (Porter, 2006).

Trace fossils in the Otter Sandstone

Rhizocretions

The most obvious and abundant trace fossils in the OSF are vertical and sub-horizontal calcareous concretions around the trunks, stems and root systems of plants. These are especially abundant in the Otterton Point Sandstone Member where they occur in association with caliche sheets and cross-bedded channel-lag accumulations composed largely of caliche debris (Figures 3a to d). The sedimentology and flora were described by Purvis and Wright (1991) who recorded fragments of horsetails and conifers as well as the spores of conifers, cycads and ginkgos. Many of the roots traces descend up to 2 m from caliche horizons.

Possible tetrapod burrows

Notwithstanding the abundance of vertebrate remains that have been recorded from a relatively small stratigraphical interval in the highest part of the OSF at Sidmouth (the Ossiferous Beds of Johnston-Lavis, 1876) and scattered occurrences throughout the rest of the formation, there is only one published record of a trace fossil that has been attributed to an animal. Coram and Radley (2013) described the cast of a single footprint on the upper surface of one of the channel sandstones in the Pennington Point Member on the foreshore below Peak Hill. The taxonomic identity is uncertain: they suggested that it might be that of an archosaur (chirothere).

Disruption of cross bedding and other sedimentary structures that does not appear to be attributable to plant action, desiccation, the dissolution of evaporites or sedimentary features such as slumping or dewatering has been recorded in the cliffs at two localities in the present study, at Connaught Gardens Cliff and below High Peak (Figure 2). Both groups of trace fossils occur at the same stratigraphical level in rhizocretion-rich sandstones in the youngest 2 to 5 m of the Otterton Point Sandstone Member. The best examples, those that contain the most convincing evidence of animal activity, occur in Connaught Gardens Cliff [SY 1215 8697] at Sidmouth (Figure 4a). They include moderately inclined (10° to 25° to the horizontal) parallel-sided structures that descend up to 2 m below a caliche surface together with associated ovoid structures (Figure 4a). The better preserved of these trace fossils are similar in size and shape to some of the trace fossils described from Antarctica, Morocco, South Africa and the USA that have been interpreted as the access tunnels and resting/shelter chambers of one or more types of tetrapod, mostly small therapsid reptiles (see below).

Figure 3. *Rhizocretions in the Otter Sandstone Formation at Big Picket Rock. (**a**) West face of the 25-m high Big Picket Rock showing sandstones with caliche surfaces and abundant rhizocretions. Horizon A marks a sudden upward change from sandstones with numerous caliche beds and rhizocretions (Otterton Point Sandstone Member) and sandstones with few such beds (Ladram Bay Sandstone Member) accompanied by an upward change from stacks of relatively narrow (up to 10 m wide) channels to broad channels up to 100 m wide. (**b**) Detail of rhizocretions-rich beds in Figure 3a. (**c**) Calcareous cementation around the vertical trunk of a small tree. (**d**) Subhorizontal nodular casts around plant roots.*

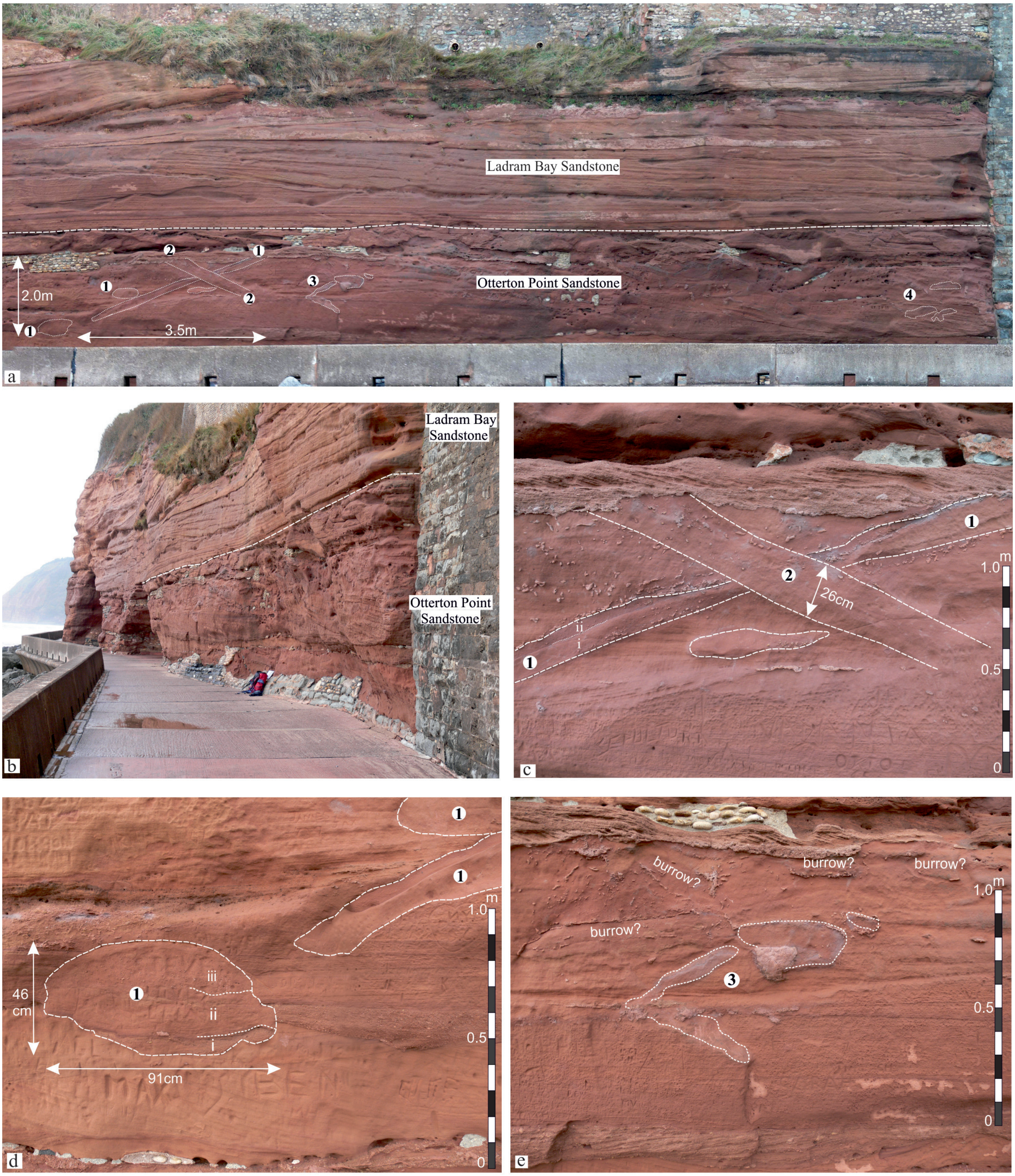

Figure 4. *Possible reptile burrows at Connaught Gardens Cliff [SY 1215 8697] Sidmouth: photographs uncorrected for parallax.* ***(a)*** *The burrows occur close below the junction of the Otterton Point and Ladram Bay Sandstone Members immediately below an erosion surface marked by a channel-lag deposit composed of caliche debris.* ***(b)*** *View west along the Millennium Walkway (opened 1999) which allows the sandstones to be examined in detail. In contrast to the low regional easterly dip of the OSF on the east Devon coast, the formation dips west in Connaught Gardens Cliff towards the fault at Jacob's Ladder.* ***(c)*** *Intersection of the access tunnels of Burrows 1 and 2 and associated chamber. The infill of Burrow 1 throughout its length comprises a lower fill of relatively clean sand and an upper fill of muddy sand. Burrow 2 is filled with relatively homogeneous sand with some faint lamination parallel to the burrow walls. Both tunnels appear in part to be lined with caliche debris.* ***(d)*** *The lower part of the access tunnel of Burrow 1 and its probable terminal chamber. The infill sediment comprises three 'layers': a lower sand with abundant caliche debris, a middle laminated sand, and an upper sand with scattered small caliche clasts.* ***(e)*** *Burrow complex 3 comprising poorly preserved possible resting chambers linked by access tunnels.*

Trace Fossil 1 (Figures 4a, c and d) comprises a parallel-sided, 3.7 m long structure inclined at 20º to the horizontal which cuts across sedimentary features in the sandstone host rock. The infilling sediment comprises a 'lower' structureless fine-grained sand overlain by an 'upper' muddy sand (i and ii in Figure 4c) with a sharp boundary that is picked out by iron-staining at the change in permeability. The upper margin of the structure is locally undulating and is marked in part by small angular fragments of caliche deposit which may have formed a lining. At its lower end, the structure is underlain by undisturbed sediment where it is presumed to have moved into or out of the plane of the cliff. An ovoid structure 0.3 m below the inclined structure is presumed to be part of the same trace fossil. The ovoid has well-defined boundaries that cut across the bedding in the sandstone and across a lenticular channel-lag deposit composed of caliche debris. The infill of the structure comprises a basal layer rich in caliche debris, a middle layer of laminated sand and an upper layer with scattered caliche debris (i, ii and iii in Figure 4d). The infill is capped by a thin (1 to 4 mm thick) layer of clean, coarse-grained sand. A similar infilled ovoid adjacent to the parallel sided structure higher in the cliff may be part of the same or a similar trace-fossil complex.

Trace Fossil 2 consists of a 20 to 30 mm wide roughly parallel-sided structure which is terminated at its upper end by a channel-lag deposit (Figure 4c). It descends at 25º to the horizontal for *c.* 2 m to an indistinct and poorly preserved lower margin that may have been connected to a wider structure. The infill material is a relatively homogeneous sand with traces of lamination parallel to the walls. The structure cuts across and therefore postdates Trace Fossil 1. Trace Fossils 3 and 4 (Figures 4a and e) comprise roughly parallel-sided structures at 20º to 30º to the horizontal and irregular shaped infillings which may be poorly preserved examples of Trace Fossils 1 and 2. An example of an ovoid structure (Figure 5a) which cuts across a bed of red overbank mudstone is preserved in the same cliff 50 m west of Trace Fossil 1.

A wide variety of bedding disturbances is present in the top 5 m of the Otterton Point Sandstone Member in the cliff [SY 1027 8577 to 1045 8585] below High Peak. They include large scale (>2 m across) collapse structures (Figure 5b) that might represent tetrapod resting places or nesting sites, and ovoid (Figure 5c) and parallel-sided structures infilled with relatively uniform sand (Figure 5d), both of which are similar in size and form to those at Connaught Gardens Cliff.

Other trace fossils

Two well preserved morphologically distinctive trace fossils were noted in sandstones in the Pennington Point Member in the foreshore exposures below High Peak during the present study. An unidentified trace fossil in a sandstone bed consists of a dense, sub horizontal network of circular casts 8 to 10 mm in diameter that radiate out from vertical circular tubes of similar diameter (Figure 5e). The uniform shape and diameter of the casts throughout their length and the absence of calcareous cement or nodules suggests that these are the access and dwelling/feeding traces of a deposit-feeding organism rather than plant roots. The trace maker was possibly an insect or a crustacean. Small (1-2 mm) diameter, unlined meniscus-fill burrows of *Taenidium* occur in a red mudstone in association with vertical green reduction patches that are probable root traces (Figure 5f). It has been suggested (Gregory *et al.*, 2004) that Quaternary examples of *Taenidium* associated with plant roots were formed by sap-sucking deposit-feeding insects.

Discussion

Triassic trace fossils that have been interpreted as tetrapod burrows have been recorded in sandstones of similar age and deposited in similar continental environments to those of the OSF from widely spaced present-day localities that were formerly part of the Pangean supercontinent (Table 1). Hasiotis *et al.* (2004) described a wide range of burrow sizes and architectural morphologies which they referred to as tunnels (horizontal and low angle tubes), shafts (vertical tubes), spiral shafts, resting chambers and nesting sites (shallow hollows). The better preserved examples, those that can be examined in more than one plane, show the tunnels and shafts to range from circular to ovoid in cross section, uniform diameter or tapering downward, and with surficial bioglyphs including scratch marks and grooves. Burrows can be isolated and simple, or complex with intersecting burrows indicative of colonial occupation. Tunnel and shaft sizes vary greatly with diameters of <20 mm to >350 mm and lengths ranging from a few centimetres to >3 m.

Smith (1987) described casts of burrows comprising helical ramps and terminal chambers in Late Permian sandstones in the Permo-Triassic Beaufort Group of the Karoo Basin in South Africa, some of which contained articulated skeletons of small theraspids (dicynodonts). Subsequent records of reptile burrows in the Beaufort Group include Early Triassic burrows (Groenewald *et al.*, 2001; Bordy *et al.*, 2009, 2011) and an injured amphibian sheltering in a burrow occupied by an aestivating theraspid (Fernandez *et al.*, 2013). In the Early Triassic Fremouw Formation in Antarctica, Hasiotis *et al.* (2004) and Hasiotis and Flaig (2013) recorded subhorizontal elliptical burrows ranging from 20 mm to 0.3 m in diameter in channel-form sandstones which contain archosaur and theraspid trails, and abundant rhizoliths. They concluded that the burrows were mostly formed by theraspids. In Morocco, Voigt *et al.* (2011) described a complex assemblage of burrow systems in Mid Triassic red-bed sandstones and mudstones (Timezgadiouine Formation) in the Argana Basin in the channel and overbank deposits of ephemeral braided streams.

Only the better preserved structures exposed in the OSF, those exposed in Connaught Gardens Cliff (1 and 2 in Figure 4a), are sufficiently complete for comparison to be made with Triassic vertebrate burrows described elsewhere. Assuming that they are vertebrate burrows, one can only speculate on what type of animal might have made them based on a comparison of the sizes and shapes of burrows of a similar Triassic age, and on the vertebrate fossils recorded from the OSF. The morphologically closest examples of published trace fossils to those exposed in Connaught Gardens Cliff are low-angle tunnels (10º to 40º to the horizontal) with diameters of 200 to 300 mm in the Early Triassic Katberg Formation in South Africa which have been attributed to theraspids (Bordy *et al.*, 2011). The formation contains theraspid (cynodont and dicyodont) fossils, but these have not been recorded in the burrows. The burrows differ from the Connaught Gardens Cliff examples in that the tunnels are terminated by rounded ends that are not associated with resting traces.

The vertebrate remains reported from the OSF in Devon include bones and/or teeth of archosaurs, rhynchosaurs, temnospondyls and procolophonids (Benton, 1997). Of these, the procolophonids were too small to have made the Connaught Gardens Cliff tunnels. The size ranges of the archosaurs and rhynchosaurs is too poorly understood from the limited amount of fossil evidence available to know if they might or might not have been the burrower. Some, such as a *c.* 3-m long archosaur described by Benton (2011) from the OSF at Sidmouth were probably too large, but forms recorded elsewhere in the world range from too small to a suitable size. A temnospondyl amphibian was recorded fitting neatly into a resting chamber in the Beaufort Group, but the burrow had been made by a therapsid (Fernandez *et al.*, 2013). To date, there is no published record of a theraspid in the OSF (Benton pers. comm.).

Burrows attributed to the lungfish *Ceratodus* have been described from the Late Triassic Chinle and Dolores Formations in the USA (Dubiel *et al.*, 1987). *Ceratodus* has been recorded in the Bromsgrove Sandstone Formation (Woodward, 1893), the correlative of the OSF in the English Midlands. However, the USA examples are closely spaced, vertical or steeply sloping shafts with rounded or flask-shaped terminations which are morphologically markedly different from the possible burrows

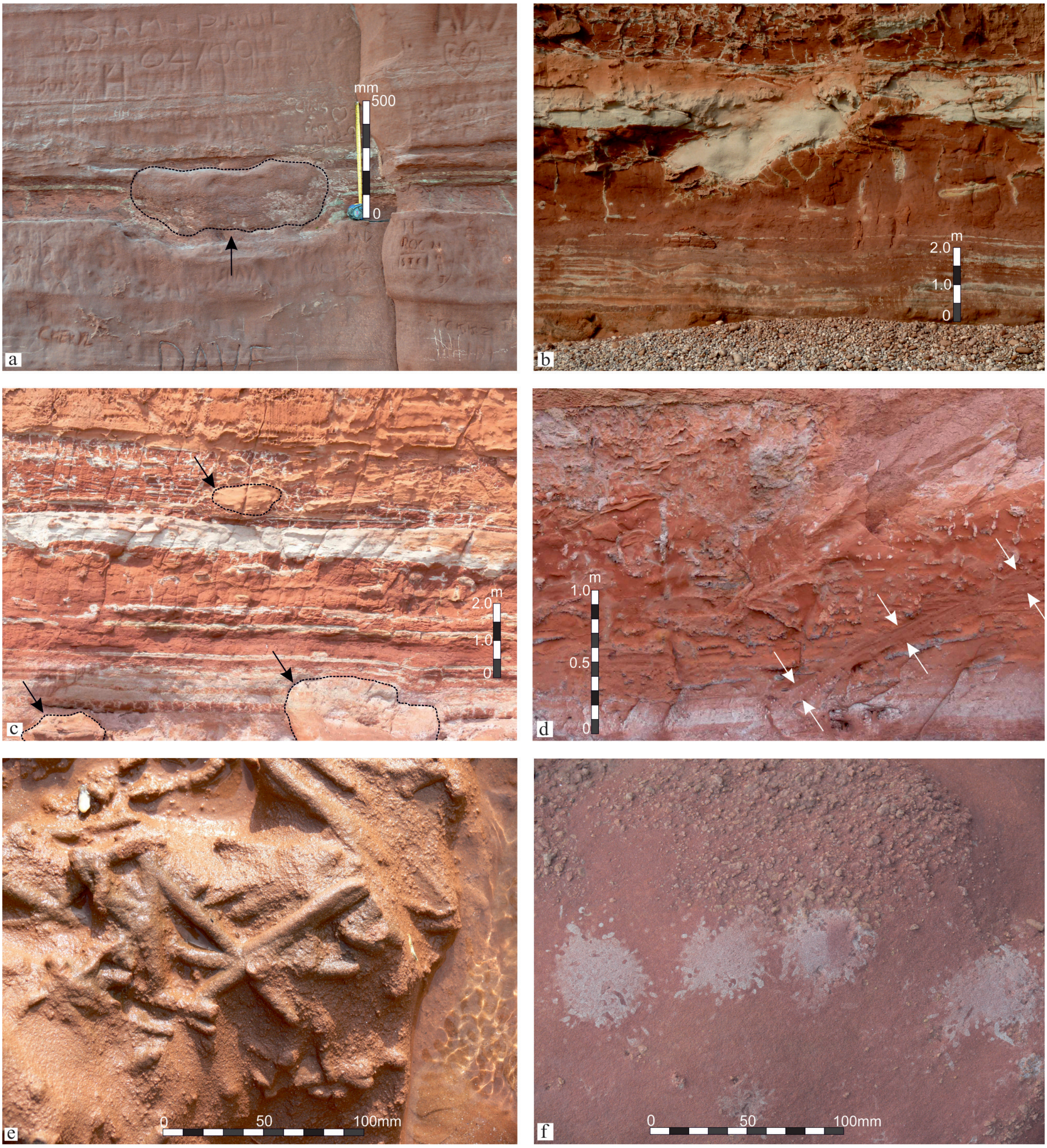

Figure 5. *(**a**) Possible resting chamber displacing a thin bed of red overbank mudstone. Connaught Gardens Cliff, 50 m west of Figure 4. (**b**) Large collapse structure of clean sand into muddy sand with plant rootlets which is morphologically similar to some of the tetrapod resting traces and/or egg-laying sites described from the Chinle Formation in Arizona. Highest part of the Otterton Point Sandstone, cliff below High Peak. (**c**) Possible resting chambers and (**d**) access tunnel. Location as in Figure 5b. (**e**) Unidentified trace fossil in sandstone in the Pennington Point Member, foreshore below High Peak, Sidmouth. Possibly formed by deposit-feeding insect or crustacean. (**f**) Small (1-2 mm diameter), unlined meniscus-fill burrows of Taenidium isp. associated with probable root traces in mudstone in the Pennington Point Member. Foreshore below High Peak, Sidmouth.*

described in this account. An alternative explanation for some of the trace fossils in the OSF might be that they are collapse structures that had formed around decaying logs. Odier *et al.* (2004) noted that in the Late Triassic?-Early Jurassic Navajo Sandstone Formation plant remains are distinguishable from the reptilian burrows by their mostly vertical orientation, branching, small diameters (<0.1 m) and knobbly surface textures (*cf.* Figure 3d). The same criteria can be applied to the OSF. All of the large number of rhizocretions visible in the cliffs and intertidal areas below High Peak formed either around horizontal/sub horizontal roots or vertical stems: none of the rhizocretions is at angles of 10° to 25° to the horizontal.

	OS	AB	BG	CF	FF	NS
Part of Pangaea	✓	✓	✓	✓	✓	✓
Arid/semi-arid environments	✓	✓	✓	✓	✓	✓
Fluvial channel sandstones	✓	✓	✓	✓	✓	✓
Overbank (mudstone) deposits	✓	✓	✓	✓	✓	✓
Caliche deposits	✓	✓	✓	✓	✓	✓
Rhizocretions	✓	✓	✓	✓	✓	✓
Tetrapod skeletal remains	✓	✓	✓	✓	✓	✓
Tetrapod footprints/tracks	✓	✓	✓	✓	✓	✓
Scratch marks in burrows			✓		✓	✓
Reptile remains in burrows			✓		✓	✓

***Table 1**. Features common to the burrowed formations referred to in the text. OS = Otter Sandstone Formation, Devon, UK (this account); AB = Argana Basin, Morocco (Voigt et al. 2011); BG = Beaufort Group, Karoo Basin, South Africa (Smith, 1987; Groenewald et al., 2001; Gastaldo and Robertson, 2008; Bordy et al., 2009, 2011); CF = Chinle Formation, Arizona, USA (Dubiel et al., 1987; Hasiotis, et al., 2004); FF = Fremouw Formation, Central Transantarctic Mountains (Hasiotis et al., 2004; Hasiotis and Flaig, 2013.); NS = Navajo Sandstone Formation, Utah, USA (Odier et al., 2004; Lucas et al., 2006; Riese, 2011; Riese et al., 2011).*

SUMMARY AND CONCLUSIONS

The OSF Sandstone Formation exposed on the east Devon coast was deposited in a variety of fluvial settings in semi-arid and arid environments. Much of the youngest part of the OSF, the Ladram Bay Sandstone Member, is composed of stacked, broad, shallow sandstone channels indicative of deposition in networks of fast-flowing ephemeral braided streams that were not conducive to the preservation of burrow systems. In contrast, the Otterton Point Sandstone Member is made up of sandstones with extensive caliche deposits and rhizocretion horizons which indicate that the water-table was at times sufficiently high and stable for long enough periods to support mature vegetation and their attendant faunas. Fossils occur sparingly in the OSF, but the faunal assemblage includes reptiles, amphibians, fishes, insects, scorpions and brine shrimps (Benton, 1997). Despite this there is no published record of trace fossils in the formation other than rhizocretions and a single reptile footprint.

Published accounts of trace fossils, other than rhizocretions, were similarly lacking for the extensively exposed 700-m thick Navajo Sandstone of Arizona, Colorado and Utah until 2004 when Odier described trace fossils at four stratigraphical levels that he interpreted as tetrapod burrows. These were associated with rhizocretions and bedding features indicative of fluvial periods in the predominantly aeolian formation. Subsequent research has shown such trace fossils to be relatively common at some stratigraphical levels and to represent complex animal communities in what had formerly been thought of as arid dune fields. The burrows were divided by Riese *et al.* (2011) into two broad types: those produced by multiple individuals living in social groups and single burrows produced by solitary animals.

In contrast to the almost wholly 2D outcrops of the OSF Sandstone exposures on the east Devon coast, localities with confirmed tetrapod burrows, notably those in Antarctica, South Africa and the USA, have extensive deeply dissected inland outcrops in which the sediments can be examined in 3D. In the coastal cliffs of Devon, weathering processes and natural disruptions to bedding and other sedimentary features can combine to produce structures that superficially resemble burrows. For example, cross bedding at similar angles (10º to 30º) to access tunnels can weather out to look like burrow walls. In the absence of fossil remains in the form of teeth, bones, coprolites or scratch marks within the presumed burrows, the principal feature that distinguishes the better preserved examples from plant-related or sedimentary structures is the infilling sediment. Multilayered infills indicate that the structure was an open void for a period of time and was not therefore a collapse structure that formed around a rotting log or an evaporite solution cavity.

The more complete examples of trace fossils in the OSF, for example those exposed in Connaught Gardens Cliff, are similar in size and form to some of the burrows described elsewhere from the former Pangean supercontinent which have been attributed to therapsid reptiles. However, there is to date no published record of a therapsid in the OSF. Better preserved examples of the possible burrows and a more detailed knowledge of the vertebrate fauna will be needed before the burrows can be attributed to a particular animal.

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