Trace fossils in the Permian rocks of South-West England

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Gallois, R.W. and Mather, J. D. 2016. Trace fossils in the Permian rocks of South-West England. *Geoscience in South-West England*, **14**, 20–28.

Trace fossils in the form of presumed annelid burrows have been known from the Permian rocks of the Devon coast for over 150 years. Notwithstanding the presence of almost continuous exposures of up to 1000 metres of Permian sediments on the coast between Torbay and the River Exe, indisputable trace fossils are only known from three localities where they are confined to narrow stratigraphical ranges: one in the Torbay Breccia Formation and two in the Watcombe Formation. The authors have looked at all the accessible coastal sections between Goodrington and Exmouth for the present review, but have not recorded any burrow localities other than those previously been mentioned in the literature. They have, however, recorded a greater variety of burrow forms together with additional localities that contain possible trace fossils. All the undoubted burrows recorded are morphologically similar endichnial meniscate backfilled forms that can be assigned to a single ichnogenus, either *Beaconites* or *Taenidium*. Their sizes range from 3 mm to 150 mm in diameter and the sediments in which they are preserved indicate that they were formed by a variety of animals that lived in the vadose zone in wet-desert environments.

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Keywords: Permian, trace fossils, burrows, reptile tracks, crustaceans, worms, Devon, desert environments

Introduction

A strict definition of a trace fossil is any disturbance of sediment caused by an animal. They range from the obvious such as borings in shells, reptile footprints and worm burrows to pervasive mottling as a result of the complete re-sorting of a sediment. In practice, the less obvious examples are commonly only identified as trace fossils on the grounds that they do not appear to have been caused by sedimentary processes such as scouring, slumping, loading, dewatering or fluid-escape. Trace fossils are classified as ichnogenera and ichnospecies following Linnaean taxonomy, but because they are morphological forms they can only rarely be linked to a specific animal, and in some cases apparently identical forms have been formed by different animals or mechanisms. The International Commission on Zoological Nomenclature (ICZN) adjudicates on the names of trace fossils, and although many ichnologists consider structures formed by plants as trace fossils and have given them names, these are not recognised as such by the International Code of Botanical Nomenclature (ICBN) which deals with plants, algae and fungi. Possible plant-related structures are included in this account for completeness as *incertae sedis*.

There are numerous published classifications of trace fossils, most of which are based on their presumed mode of formation or their assumed purpose. For example, *domichnia* and *repichnia* are dwelling burrows and footprint trails respectively (Seilacher, 1953). More elaborate classifications include

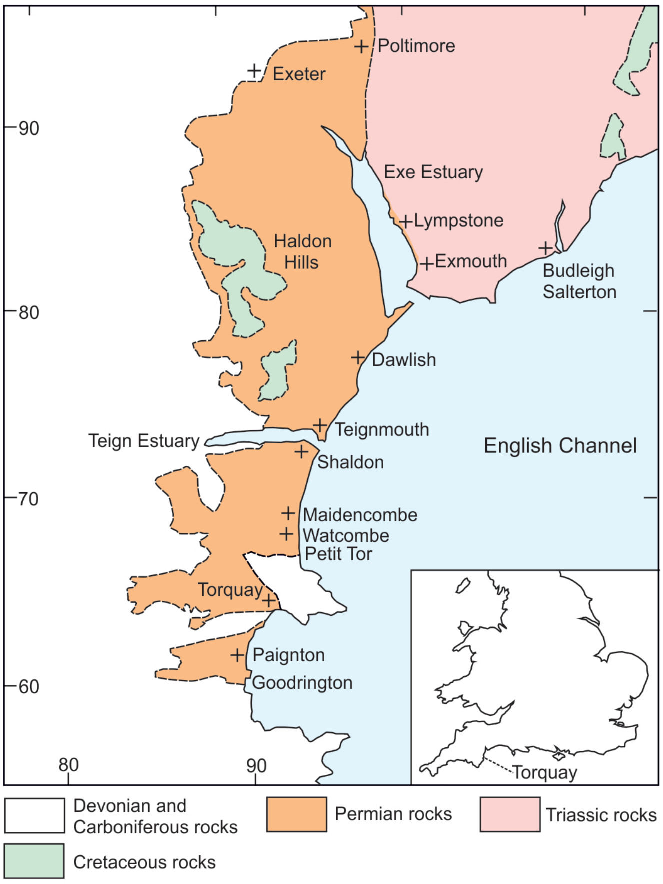

Figure 1. *Geological sketch map of south Devon coastal area showing the distribution of the Permian and Triassic rocks and localities referred to in the text.*

fugichnia (escape traces) and *agrichnia* (grazing traces). The simplest classification refers only to the morphology and does not imply any mode of formation or possible use. This has the advantage of limiting the number of available genera, but the disadvantage that the same genera are attributed to burrows made by a wide range of animals of markedly different ages that lived in a wide range of environments. All except two of the types of trace fossil recorded to date from the Permian rocks of Devon can be classified as *endichnial*, a structure preserved within the sediment. The exceptions are examples of *exichnial* traces, crustacean trails (Shapter, 1842) and reptile footprints (Clayden, 1902) preserved on the surfaces of Permian sandstones in inland quarries.

Presumed annelid burrows were recorded by Pengelly (1864) in the Torbay Breccia at Goodrington and Ussher (1877) noted "numerous annelid tracks" in sandrock in the Watcombe Formation in a quarry above Watcombe Cove. The Goodrington examples have been described by Laming (1969), Henson (1971) and in Selwood *et al*. (1984), Perkins (1971), Ridgeway (1974, 1976) and Pollard (1976). Henson (in Selwood *et al*., 1984) noted that "thin burrows were common" in the tops of graded sedimentation units in the Watcombe Formation in outcrops in the Watcombe valley.

As part of the present review, the authors have looked at all the accessible coastal sections in the Permian rocks exposed on the Devon coast between Goodrington and the River Exe (Fig. 1). This has not revealed any localities with unequivocal trace fossils that have not previously been referred to in the literature, but it has recorded a greater variety of burrow forms and additional localities that contain possible trace fossils. Notwithstanding the presence of extensive exposures of unweathered Permian rocks *in situ* and in fallen blocks in the intertidal zone, structures attributable to animal burrows are rare overall. However, they are abundant in a few thin (<0.5 m thick) beds close above the base of Torbay Breccia Formation near Waterside Cove, Goodrington [SX 896 587], and in the Watcombe Formation at Petit Tor Beach [SX 926 664] and Watcombe Cove [SX 926 763] (Fig. 2). Trace fossils are especially common in almost all the fallen blocks of this material at Petit Tor Beach and at Watcombe Cove. Those at Watcombe Cove include a wider range of morphological types than at other locality recorded to date in Permian rocks in Devon. A third occurrence, in the Dawlish Sandstone Formation in an inland quarry at Poltimore [SX 966 966] is no longer visible. Poorly preserved structures that might be attributable to animal burrows are recorded here in the Torbay Breccia at Paignton and in the Teignmouth Breccia at Maidencombe Beach [SX 928 684] and Ness Beach, Shaldon [SX 940 718]. Possible plant traces have been recorded in the Exe Breccia at Lympstone [SX 990 837].

Age	Formation	Thickness m	Predominant lithologies: depositional environments	Localities with trace fossils and *possible trace fossils*
early Triassic	Exmouth Mudstone and Sandstone	250	red-brown mudstone with lenticular sandstones: playa lakes crossed by braided streams	Sandy Bay, Exmouth
-?-?-?-?				
late Permian (Lopingian)	Dawlish Sandstone; Exe Breccia	> 150	sandstones and breccias: braided streams, sand dunes and fluvial fans	*Lympstone* Poltimore
	Teignmouth Breccia	120	breccias with minor sandstone interbeds: fluvial fans	*Ness Cove, Shaldon* *Maidencombe*
	Oddicombe Breccia	130	breccias and sandstones: braided streams and fluvial fans	not exposed on the coast
	Watcombe Formation	100	breccias (Watcombe Breccia) passing down into sandstones (Petit Tor Member): fluvial fans and braidplains	Watcombe Cove Petit Tor Beach
	unconformity		*c.* 12Ma erosional gap	
early Permian (Cisuralian)	Torbay Breccia	200	breccias and sandstones: debris flows, fluvial fans and braided streams	Waterside Bay *Paignton*
	unconformity			
Devonian	Torquay Limestone and Nordon Formation		complexly folded limestones, mudstones and tuffs	

Figure 2. *Generalised stratigraphy of the Permian rocks exposed on the south Devon coast between Torbay and Exmouth. All thicknesses and lithologies are, laterally, highly variable.*

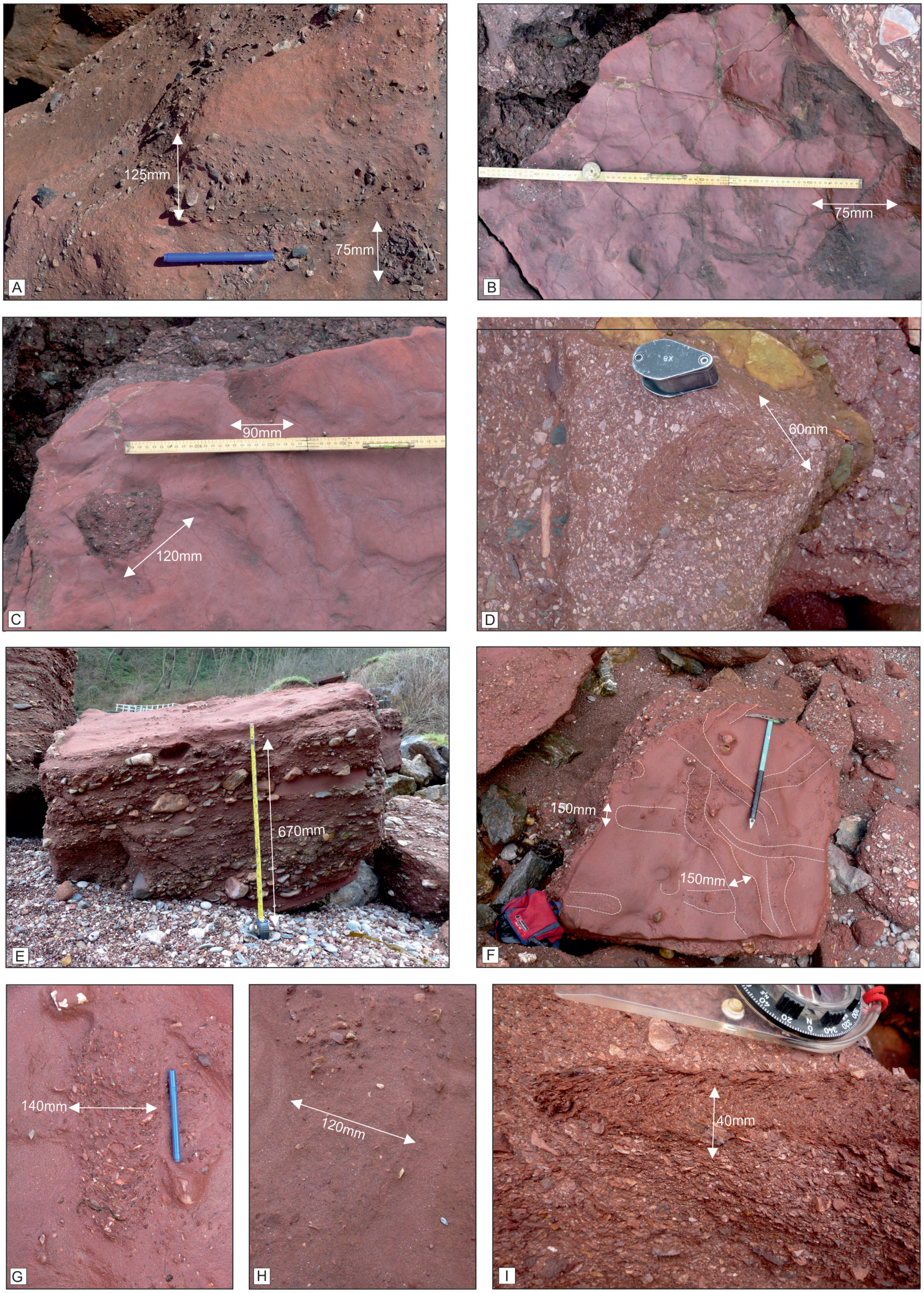

Figure 3. *Type 1 trace fossils: (**A**) to (**D**) horizontal to vertical meniscus-fill trace fossils in fine-grained sandstones and breccias, Torbay Breccia Formation, Waterside Cove, Goodrington. (**E**) and (**F**) Similar trace fossils in a sandstone bed in a fallen block of Watcombe Formation at Watcombe Cove. (**G**) to (**I**) detail of meniscus fills at Watcombe Cove (**G**) and Waterside Cove (**H** and **I**).*

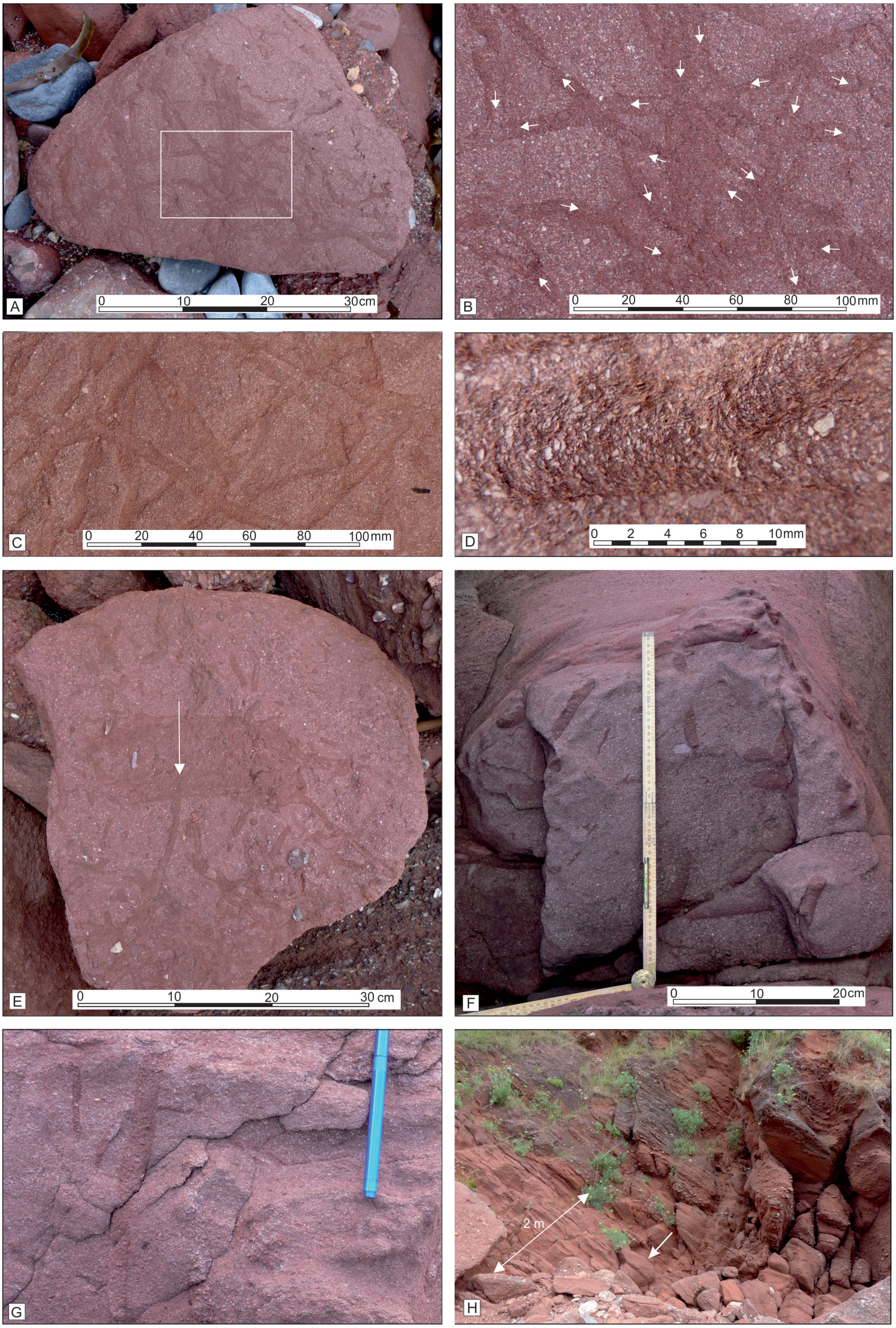

Figure 4. *Burrows in fine-grained sandstones in the Watcombe Formation at Watcombe Cove. (**A**) to (**E**) Type 2 trace fossils: almost all parallel and sub-parallel to bedding. (**B**) Detail of central part of (**A**); arrows indicate the presumed direction of movement of the burrower. (**C**) Detail of crossover of individual burrows, mostly at high angles. (**D**) Detail of meniscus fill. (**E**) Highly disturbed area 90 x 200 mm formed by coalescing Type 2 burrows: possible access to surface. (**F**) and (**G**) Type 3 with a few Type 2 burrows, all of which radiate downwards at high angles from a bedding plane. Pen is 137mm long. (**H**) Sandstone bed in the predominantly breccia succession: arrow indicates bedding surface with many Type 2 and Type 3 burrows.*

Figure 5. *(**A**) to (**C**) Type 3 and Type 4 burrows in sandstones in the Watcombe Formation at Watcombe Cove. (**A**) and (**C**) Type 4 burrows with well-developed curved menisci picked out by packeted layers of darker (muddy) and paler (sand-grade-clast rich) fine-grained sandstone infillings. (**B**) Top surface of block shown in (**A**) pervasively burrowed by Types 2 and 3 burrows mostly at low angles to bedding. (**D**) and (**E**) Type 3 burrows in relatively homogeneous fine-grained sandstone in the Watcombe Formation at Petit Tor Beach in which the menisci vary from well developed (**D**) to very weakly developed to absent (**E**). (**F**) Trackway of* Cheilichnus bucklandi *(Jardine). Royal Albert Memorial Museum and Art Gallery, Exeter specimen number EXEMS 287/1908 Slab A. Photographed by David Garner and reproduced courtesy of the museum.*

ENDICHNIAL TRACE FOSSILS

All the endichnial burrows recorded in the Permian rocks of the Devon coast are morphologically similar, straight to gently curved, unbranched, unlined, meniscus-fill burrows that can be divided into four broad groups based on size. They are interpreted here as possible species within a single ichnogenus. Although each group appears to represent a distinct population, there is some overlap between the groups with the result that there is an almost continuous range of diameters between 4 and 150 mm.

Type 1

Type 1 burrows are large (up to 150 mm diameter and commonly >1 m long) unbranched, straight and sinuous, ovoid to circular unlined tubes with well-developed meniscus fills (Fig. 3A, 3F). These are common at a few stratigraphical levels *in situ* and in fallen blocks in the lowest part of the Torbay Breccia near Waterside Cove, and in fallen blocks of Watcombe Formation at Watcombe Cove. They commonly occur in sandstone interbeds in predominantly breccia successions. Vertical and steeply inclined connecting burrows penetrate breccias that contain angular clasts of mudstone and sandstone up to several centimetres across. Examples exposed near Waterside Cove and at Watcombe Cove include breccia-filled and sand-filled tubes 40 to 150 mm in diameter with well-defined, crescent-shaped to parabolic meniscus fills. The fills are prominent in the breccias but less obvious in the sandstones where there are few grain-size differences between the burrow fills and the sandstone hosts. Most of the burrows follow bedding planes or are at low angles (< 10°) to the bedding, but vertical burrows are also relatively common. The latter are mostly circular in cross-section and 60 to 140 mm in diameter where vertical or steeply inclined (Fig. 3A, 3B, 3C, 3D), and ovoid (presumably due to compaction) 40 to 150 mm diameter where horizontal or at low angles to the bedding (Fig. 3A, 3F, 3G, 3I; see Ridgeway, 1974, fig. 1). In practice, the presence of extensive *in situ* bedding planes dipping at < 10° and numerous bedding-plane-bounded fallen blocks give the impression that low-angle burrows are the more numerous. No obvious burrow linings or walls were seen although sorting within the parabolic menisci such that the smaller clasts are aligned parallel to the edge of the burrows can give the impression of linings (Figs 3A, 3G, 3I).

The meniscus fills in the Waterside Cove trace fossils were illustrated by Laming (1969, fig. 3) and by Perkins (1971, fig. 38). The latter suggested that the burrows had been made by a worm-like creature that could ingest small pebbles. The first detailed description of the burrows was that of Henson (1971) who thought that they were most probably made by reptiles for occupation or in search of food. In the most complete description of the Waterside Cove burrows to date, Ridgeway (1974) recorded all the morphological features referred to above. She concluded that the trace fossils were made by primitive burrowing reptiles and that the variations in size were related to the sizes of the animals and the ages of the individuals. Pollard (1976) broadly agreed with this interpretation and suggested that the burrows might have been formed by limbed amphibians or reptiles during aestivation rather than as dwelling or feeding burrows. He concluded that the Waterside Cove examples could “probably be named” *Beaconites* cf. *antarcticus* Viavlov, 1962.

Type 2

Type 2 trace fossils are abundant in fallen blocks of breccia and fine-grained sandstone in the Watcombe Formation at Watcombe Cove and less common at Petit Tor Beach, in fine-grained clayey sandstones, clean fine-grained sandstone and fine- to medium-grained sandstones with small clasts up to 0.5 mm across. They comprise straight to gently curved, unbranched, meniscus-fill burrows mostly 4 to 8 mm in diameter with a maximum observed length of 400 mm. They are mostly sub-parallel to or at low angles to bedding (Fig. 4A, 4B, 4C), but with relatively common round, vertical examples. They form complex networks in which burrows made by individual animals travelling in opposing directions are superimposed on one another at angles of mostly 40° to 90° (Fig. 4C). Locally, many burrows coalesce to form irregular disturbed patches up to 90 x 200 mm which may have given access to the sediment-water interface (Fig. 4E). The burrow infillings are lithologically similar to the matrix with curved menisci picked out by grain-size variations in the sandstones or by clasts in the breccias. Wall linings are absent (Fig. 4D) although in some examples, where the ends of parabolic menisci are parallel to the burrow margin, they look similar to a lining.

Types 3 and 4

The Type 3 burrows are morphologically similar to the Type 1 and Type 2 burrows, but are mostly 10 to 18 mm in diameter. They are abundant at particular levels in the Watcombe Formation at Petit Tor Beach where they and Type 2 burrows pervasively penetrate loose blocks of fine-grained sandstones with and without small (< 5 mm diameter) clasts, mostly at low angles to the bedding (Fig. 5B). They are present, but less common, in sandstones in the same formation at Watcombe Cove where they mostly occur at high angles to the bedding (Fig. 4F, 4H). They occur *in situ* in cliff outcrops at both localities (Fig. 4G). At Petit Tor Beach, where the burrows are present in fine-grained muddy sandstones with abundant sand-grade angular clasts, the menisci are clearly visible as curved packets of paler and darker, finer and coarser sediment. Where the burrows are preserved in homogeneous fine-grained sandstone the menisci are weakly developed or not discernible.

Type 4 burrows have been recorded at Watcombe Cove (Fig. 5A, 5C) and Petit Tor Beach where they are mostly 22 to 30 mm in diameter. The menisci vary from well-developed curved packets in the sandstones with sand-grade-size clasts (Fig. 5C) to less obvious examples in the more homogeneous sandstones (Fig. 5D).

EXICHNIAL TRACE FOSSILS

The Dawlish Sandstone Formation contains rare trace fossils including crustacean trails (Shapter, 1842) and reptile footprints. Clayden (1902) reported that trackways of the mammal-like synapsid reptile *Cheilichnus bucklandi* (Jardine) were relatively common on some of the sandstone bedding planes in a quarry at Poltimore [SX 971 971] (Edwards and Scrivener, 1999, plate 3i; Fig. 5F). He concluded from the state of preservation of some of the footprints that the reptile was walking on loose, hot dry sand. The Dawlish Sandstone is well exposed in the Dawlish sea cliff and in former quarries in the Exeter area, but only in vertical faces that are not conducive to exposing trackways. The ichnogenus has been recorded in Permian dune sands from widely spaced localities throughout the former Pangaean supercontinent including Argentina, Germany, Scotland, South Africa and the USA (Gallois, 2014).

POSSIBLE TRACE FOSSILS

In contrast to the abundance of well-defined trace fossils at Waterside Cove, Petit Tor Beach and Watcombe Cove, structures that might be interpreted as trace fossils are rare in the Permian rocks of the Devon coast. Small (mostly 2 to 4 mm diameter) calcium- carbonate lined tubes and possible crushed tubes at various angles to the bedding were recorded at one locality in the Torbay Breccia at Livermead Head (Fig. 6C).

Small (2 mm diameter) cone shaped raised structures are present in fine-grained sandstones in the Teign Breccia at Maidencombe Beach (Fig. 5D). The same forms occur in the Teign Breccia at Ness Cove, Shaldon where they occur in positive relief (as here) and also as cone-shaped depressions that do not extend down into the sediment. They may be air or

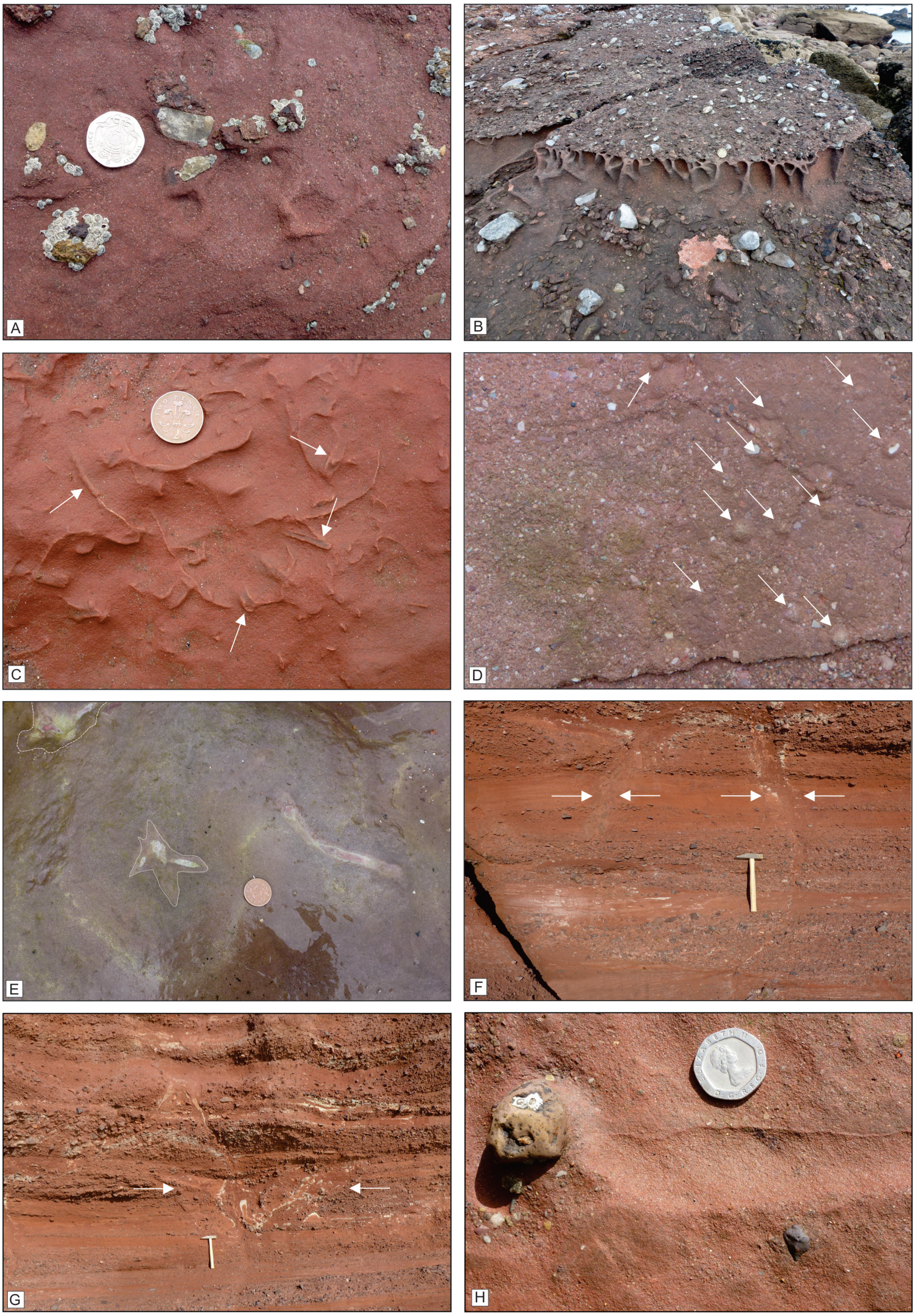

Figure 6. *Possible trace fossils and a pseudo trace fossil. (**A**) and (**B**) Honeycomb-like hexagonal structures in the Torbay Breccia at Herring Cove [SX 930 694]. Coin 21 mm diameter. (**C**) Lined tubes and possible crushed tubes 2 to 4 mm diameter in fine-grained sandstone in the Torquay Breccia at Livermead Head. Coin 25 mm diameter.(**D**) Small (2 to 3mm diameter) epichnial cones in the Teign Breccia at Maidencombe Beach. (**E**) Possible burrow or root traces in the Corbyn's Head Member at Corbyn's Head, Torbay. Coin is 22 mm diameter. (**F**) Possible root traces (arrowed) up to 1.5m long in the Exe Breccia at Lympstone. Hexagonal desiccation cracks and irregular syneresis structures are common in the breccias, but none of these appear to extend down more than 0.5 m. Hammer is 0.4 m long. (**G**) Irregular disturbed area in the Exe Breccia at, Lympstone that is not readily attributable to a sedimentary structure such as those formed by scour, slumping or dewatering. Hammer is 0.4 m long. (**H**) Burrow-like structure presumed to have been formed by a sliding pebble. Coin is 21 mm diameter.*

water escape structures or related to vertical burrows. An irregular, star-shaped disturbance with associated cementation and reduction in the Corbyn's Head Member of the Torquay Breccia at Corbyn's Head, Torbay (Fig. 5E) might be a partially lined trace fossil cf. *Heliophycus* Miller and Dyer, 1878, a burrow of unknown affinity or the result of plant action. Poorly preserved possibly root traces (Fig. 6F) are present in in the Exe Breccia Formation at Lympstone together with sediment disturbances of unknown origin that may be attributable to an animal (Fig. 6G). Bedding planes underlain by honeycomb-like hexagonal structures are relatively common in fine-grained sandstones in the Torbay Breccia, Watcombe Formation and Teign Breccia (Fig. 6A, 6B). These may be a salt-weathering feature or cf. *Palaedictyon* (Cambrian to Recent) which itself may or may not be a trace fossil.

Several examples of structures that might be mistaken for trace fossil when seen in isolation were noted at various stratigraphical levels throughout the Permian succession. These include structures made by modern grazing and boring animals, limpet holdfasts and a horizontal burrow-like groove formed by a sliding pebble (Fig. 6H).

INTERPRETATION AND PRESUMED PALAEOENVIRONMENTS

The classification and naming of trace fossils has been subject to numerous revisions since Seilacher (1953) proposed a system that was largely based on their presumed mode of formation. Most subsequent authors have only used morphological features to define ichnogenera and ichnospecies given that, except for modern examples, the originator of a burrow can rarely be identified with confidence, and that wholly unrelated animals can produce trace fossils that look closely similar. Different authors have placed different emphases on different morphological features when naming burrows with the result that the published literature contains numerous synonyms. The simplest classifications are based on overall shape (straight tubes, U-shaped tubes, complex networks, etc.), backfill structures (uniform, meniscus fills, spreiten, pelleted, etc.), surface features (walled or unwalled, lined or unlined). Most authors do not regard size as a distinguishing feature at the ichnogenus level, but some have used it to define ichnospecies.

Unlike conventional palaeontology in which holotypes provide the standard against which other fossils are compared, much of ichnology is based on incomplete or poorly described type specimens that are commonly only known from drawings or photographs. This has led to the common practice of emendation in which later researchers enhance the descriptions of the type specimens by adding diagnostic features or by placing an emphasis on particular features in the original description. This is a subjective process which depends to a large extent on those features that individual researchers regard as diagnostic. In the case of the endichnial trace fossils described here from the Permian rocks of Devon, all four types can be classified as the same ichnogenus, but it is not entirely clear what this should be called. Almost all unbranched meniscate burrows fall into one of five ichnogenera: *Anchorichnus, Beaconites, Naktodemasis, Taenidium and Scoyenia*. *Anchorichnus* Heinburg 1974, *Naktodemasis* Smith *et al.* 2008 and *Scoyenia* (White, 1929) can be excluded because of the nature of their infills and, additionally in the case of *Anchorichnus* and *Scoyenia*, the presence of wall linings.

Pollard (1976) named the Waterside Cove examples *Beaconites* based on a comparison with the type material (photographs, not rock specimens) of Vialov's (1962) *B. antarcticus* from the Devonian part of the Beacon Supergroup in Antarctica. The Type 1 burrows described here are much larger than those described by Vialov (1962), but occupy a similar range of sizes as those described by Bradshaw (1981) from Viavlov's type locality as *B. barretti*. Similar, meniscus-fill trace fossils were subsequently described as *Beaconites* from Devonian rocks in South Wales (Allen and Williams, 1981; Morrissey and Braddy, 2004) and from Carboniferous rocks in County Mayo, Ireland (Graham and Pollard, 1982). However, Bradshaw (1981), in an emendation of the type description of *B. antarcticus*, noted that in many cases the backfilling material had an irregular appearance and that a poorly developed sand lining was present. Similarly, in her description of *B. barretti* (Bradshaw, 1981) she noted that the burrow infills were composed of relatively thin menisci that met the burrow wall at an acute angle and could merge laterally to form a crude lining. D'Alessandro and Bromley (1987), in a comprehensive review of *Taenidium* and morphologically similar forms drew attention to the close similarity between *Beaconites* and *Taenidium*. They concluded that until the description of the former, which they regarded as "extremely weak", had been clarified unlined, unbranched meniscus fossils of the type in this account should be referred to as *Taenidium* (Heer, 1877). Keighley and Pickerell (1994) noted that *Beaconites* had been used to include burrows of a wide range of sizes, with and without linings or walls. They concluded that the type specimen of *Beaconites* was walled and that "the presence of a lined wall is a primary diagnostic criterion for the definition of this trace fossil" and re-named unlined examples of *Beaconites* as *Taenidium* (Heer, 1877). However, Hasiotis (2017) described *Taenidium* as thinly lined and D'Alessandro and Bromley (1987) had noted that although the original description of *Taenidium* stated that it was rarely branched, the name had generally been applied to branched or secondarily branched burrows that radiate downwards (e.g., Häntzschel, 1962), a morphology that differs from the proposed type specimen of *T. barretti* and the Permian trace fossils described here. In their emended description of *Taenidium*, Keighley and Pickerill (1994) included unbranched burrows at low angles and vertical to the bedding with diameters ranging from 5 mm to 450 mm. Of the three ichnospecies that they recognised, *T. cameronensis* Bradley, 1947 from the Permian of Arizona has parabolic menisci similar to those of some of the Devon specimens (Fig. 3D, 3G, 3I). *T. satanassi* D'Alessandro and Bromley, 1987 from the Eocene of Italy has menisci consisting of evenly spaced packets of two types of sediment of more or less equal thickness similar to that shown in Figure 5A and 5C. However, Souza *et al.* (2015, fig. 4) figured similar burrows with the same segmented menisci from the early Cretaceous of Brazil as *T. barretti*. *T. sepentinum* Heer, 1877 is markedly more sinuous that any of the recorded Devon specimens. If the Keighley and Pickerill (1994) emendations of the descriptions of *Beaconites* and *Taenidium* are accepted, then all the Permian endichnial burrows described here can be called *Taenidium*. However, if the downward radiating, branched nature of the type material is regarded as a diagnostic feature then they cannot. Alternatively, if *Beaconites* includes unlined forms then the Devon examples can be referred to that ichnogenus. The question as to whether *Beaconites* or *Taenidium*, or neither of these names, is appropriate for the Devon Permian examples depends on which definition or emended definition of the type material is used.

SUMMARY AND CONCLUSIONS

Trace fossils are abundant at three localities in the Permian sediments on the coast between Torbay and the River Exe where they are confined to narrow stratigraphical ranges, one in the Torbay Breccia Formation and two in the Watcombe Formation. All those recorded to date are unbranched, unlined meniscus backfilled burrows that form an almost continuous range of sizes from 2 mm to 150 mm in diameter. The smaller burrows are confined to sandstone interbeds in the predominantly breccia succession, the larger (> 50 mm diameter) occur at high angles to bedding in the coarser breccias and at low angles to bedding in the sandstones. They are presumed to represent access shafts and occupation/feeding burrows respectively. The sedimentology of the Permian rocks of the Devon Coast is indicative of deposition in a series of coalescing and overlapping fans in wet-desert environments that included debris flows, sediment-laden sheet floods, and planar to turbulent stream flows (Laming, 1966; Henson, 1971). The larger trace fossils were deposited in high-energy environments and the smaller examples, which are mostly confined to fine- and medium-grained sandstones and muddy sandstones, were deposited in ephemeral fluvial sand sheets and/or channels.

All the undoubted trace fossils recorded to date from the coastal exposures are meniscus-fill burrows that can be assigned to *Beaconites* or *Taenidium* depending upon which definition of these ichnogenera is followed. For convenience, they are all referred to as *Taenidium* here. The earlier researchers (e.g., Pengelly, 1864; Ussher, 1877) attributed the Type 1 burrows to an annelid, but subsequent authors (e.g. Ridgeway, 1974; Pollard, 1976; Henson in Sellwood *et al*., 1984) and those who have described *T. barretti* preserved in Devonian to Permian aeolian sediments elsewhere in Europe have suggested that they were made by reptiles, amphibians or myriapods for feeding and/or aestivation purposes. Morrissey *et al*. (2011, fig. 7G) published a rare example of the resting trace of an arthropod, the presumed producer of a *Taenidium* but adjacent to a *T. barretti* burrow. It should be noted, however, that *Taenidium barretti* has also been reported from Devonian shallow marine sandstones (Abbassi, 2007), and that *Taenidium* (Cambrian to Recent) must have had a wide range of producers. Some of the smaller Devon burrows (Fig. 5D, 5E), in which the structure of the infill material is less distinct, are similar to *Naktodemasis* Smith *et al*., 2008, which in Recent deposits has been observed to have been formed by insects. Given the wide range of burrow sizes recorded in the Devon examples, any or all of these might be represented in the burrow populations described here. In terrestrial environments meniscus-fill burrows are thought to be made by air-breathing animals and are therefore confined to the vadose zone with access to the surface (Hasiotis, 2007).

The question of why Permian trace fossils are abundant at three localities stratigraphically close above the basal Permian unconformity on the Devon coast, but are apparently very rare or absent in what appear to be the same lithofacies and depositional environments elsewhere in the extensive, well exposed sections, remains unexplained.

Acknowledgements

The authors are grateful to Professor Ken Higgs whose comments on an earlier draft of this account led to many improvements, and to Thomas Cadbury of the Royal Albert Memorial Museum and Art Gallery, Exeter for permission to publish Figure 5F.

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