Death near the shoreline, not life on land: Ordovician arthropod trackways in the Borrowdale Volcanic Group, UK

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ABSTRACT

The Borrowdale Volcanic Group of northern England hosts Late Ordovician arthropod trackways that are frequently cited as the earliest unequivocal evidence for animal life on land, and provides a key geological locality for our understanding of global myriapod evolution and terrestrialization. Original fieldwork at the trace fossil site has identified four additional bedding surfaces that yield 121 new trackways at the site (of a total 158 known individuals), and permit better sedimentological and paleoecological contextualization of the trackways. Contrary to published claims, none of the trackways occur in sandstones but are invariably preserved on bedding planes of dacitic tuffs. Trackway morphology comprises either short straight track segments with discernable footprint impressions (*Diplichnites*), long looping traces suggesting dragging and footprint amalgamation (*Diplopodichnus*), or transitional forms. Morphometric comparison of the *Diplopodichnus* with fossil and recent mortichnia (death traces) suggests they record immediate pre-mortem locomotion of dying myriapods, and modern analogue reveals mechanisms by which abundant volcanic ash within the environment would have elevated arthropod mortality rates. Sedimentary structures including wave ripples, bedding sags and detached large-scale ball-and-pillow structures, show that the tuffs were deposited subaqueously. One newly-discovered instance where trackways intermittently traverse 3–5 cm tracts of subaerially-exposed wave-ripple crestlines attests that the tracemakers were capable of surviving out of water over very short distances. However, the low diversity, semi-subaqueous ichnofauna has greater similarity with other Cambrian and Ordovician sites, recording pioneer tracemakers with limited tolerance of subaerial environments, than it does with the oldest preserved fully-terrestrial trace fossil communities from the Silurian and Devonian.

TRACKWAYS OF THE BORROWDALE VOLCANIC GROUP

The Borrowdale Volcanic Group (BVG) is a 6 km-thick Upper Ordovician (Sandbian-Katian) succession of volcanic and related rocks that crops out in Cumbria, NW England, and which accumulated in an arc setting associated with subduction of the Iapetus Ocean (Barnes et al., 2006). Trace fossils were first discovered within the group by Mitchell (1956, p. 434), who reported "animal-tracks" on bedding planes at Lum Pot; a 150 m-long outcrop along the River Lickle, which exposes a near-continuous 25 m-thick stratigraphic section from the upper BVG (likely within its constituent Wallowbarrow Tuff Formation (Fig. 1; see Appendix)). The trace fossils were later identified as *Diplichnites* and *Diplopodichnus* by Johnson et al. (1994), who described them on the basis of 34 trackways on a 1.9 m2 bedding plane at Lum Pot and 3 trackways on the 0.1 m2 surface of a loose clast from Sour Milk Gill, 19 km north of the original locality. Johnson et al. (1994) documented that the trackways occurred in sandstone, which they interpreted as having been deposited in a freshwater lacustrine environment. Subsequently, this report of Late Ordovician, fully non-marine arthropod trackways has had substantial influence on studies concerning the evolution of life on land. The BVG trackways are widely cited as the oldest unequivocal

ichnological evidence for established non-marine arthropod communities (e.g., Davies et al., 2010; Minter et al., 2016) and indirect evidence for the oldest terrestrial myriapods (e.g., Wilson, 2006).

LITHOLOGY OF THE TRACKWAY HORIZONS

In this study we have identified four new trackway-bearing bedding planes at Lum Pot (Surfaces A-D), bringing the total number of trackways recognized at the site to 158. There is no evidence to support previous assertions that they were deposited in a non-marine environment, which were based in part on the incorrect identification of their host lithology as fine-, medium- or coarse-grained sandstone (Johnson et al., 1994) (see Appendix). In actuality the trackways at Lum Pot are invariably cast in very fine dacitic tuff (Fig. 2). The thickness of individual tuff beds is commonly hard to discern due to weathered outcrop. However, the substrate revealed as Surface C (Fig. 2E) consists of amalgamated 1 cm-thick coarse-fine cycles, possibly recording discrete events, and elsewhere discrete tuff beds are recognized up to 30 cm thick. Locally the tuffs contain vesicular horizons (Fig. 2C) and < 3 cm-diameter clasts of pumice (or similar-sized weathered-out holes) (Fig. 2D) and petrographically each of the known trace fossil beds consists of a partially chloritized homogenous cryptocrystalline matrix with up to 30% opaque fragments (see Appendix). Isolated grains or more coarsely-crystalline bands permit the identification of subhedral alkali feldspar crystals (indicating a proximal source) and subhedral opaque oxide minerals (see Appendix), in addition to isolated lithic clasts, pumice, mica and calcite. There is a marked lack of (visible) quartz.

ENVIRONMENTAL SETTING

Johnson et al. (1994) considered the BVG trace fossils to be non-marine based on three lines of evidence: 1) At Sour Milk Gill, the loose block was found near bedrock outcrop of the Whorneyside Formation, which contains structures indicative of subaerial volcanism, and emergent volcanoclastic sedimentary substrates (Branney, 1991); 2) The 6 km BVG succession as a whole predominantly accumulated in non-marine environments (Branney, 1988) and contains few marine fossils; and 3) Modern isopods make trackways analogous to *Diplichnites*/*Diplopodichnus* in a drying mixture of very fine sand and clay.

The latter two lines of evidence are weak because the BVG is not necessarily exclusively non-marine (Branney, 1988), other Paleozoic clastic successions in the region can be poorly fossiliferous despite being deposited in marine settings (Rickards and Woodcock, 2005), and the Lum Pot trackways are preserved in materially-distinct ash and dust rather than sand and clay. Direct evidence for the trackways being non-marine rests on the Sour Milk Gill specimen having been derived from the local bedrock. However, it was recovered from the margin of a U-shaped valley, carved during Quaternary glaciations, and the local terrain is covered with extensive moraine, erratics and alluvium, the clasts of which consist of a range of regionally-derived lithologies (Wilson, 2004). As no in situ trace fossils are known from the Whorneyside Formation, despite concerted investigation and its good bedding plane exposure, the uncertain provenance of the loose block means it is unreliable as evidence for non-marine conditions.

The well-exposed Lum Pot section is more suited to confidently determining the tracemaker habitat. Here, a number of volcanic and sedimentary structures indicate that the trackway-bearing tuffs were deposited subaqueously: 1) Detached balls (Fig. 2J), imply emplacement onto a heated, fluidized wet substrate (Branney and Kokelaar, 2002); 2) Bifurcating wave ripples (Fig. 2B) attest to remobilization of

ash within shallow water, and climbing ripples indicate sustained sediment input into water (Fig. 2F); 3) Bedding sags (Fig. 2H) form when ejecta impacts wet, but not dry, sediment (Fisher and Schmincke, 1984); and 4) The association of vesicles with convolute lamination (Fig. 2C,I), suggests that the ash was water-rich at the time of deposition (Fisher and Schmincke, 1984). Further circumstantial evidence includes the lack of diagnostically subaerial structures common in many parts of the BVG (Branney, 1988) and the tuff's conformable stratigraphy above the lower Dunnerdale Sandstone Formation, which is composed of turbidite sandstones (Johnson et al., 2001). There is no diagnostic evidence to determine if the water in which the tuffs were deposited was freshwater or saline.

Ash can be variably consolidated after deposition, affecting its material properties and thus its likelihood of being indented with trackways. The Lum Pot succession contains evidence that both firm (Fig. 2G, 3G) and semi-firm (Fig. 2A) (i.e., cohesive media), and unconsolidated (Fig. 2B) (i.e., granular media) substrates were traversed by the tracemakers (Fig. 3). Trackways are most common on cohesive substrates, but on unconsolidated, wave-rippled substrates, they are preserved only on ripple crests, implying material differences to ripple troughs (Fig. 3B-C, Appendix). This was most likely due to standing water, with moisture impeding trackway emplacement when substrates were composed of granular media, and provides the first direct evidence from the BVG that the tracemakers were adapted to traverse subaerial surfaces for short distances. Conversely, where trackways are seen on firm and semi-firm substrates of cohesive media, trackways are pervasive across substrate topography (Fig. 3D-E) and must have been imparted when cohesive sediment was wholly wet or damp, so that it could plastically deform and retain footprint indents.

. The null hypothesis is that the trace fossils were made by subaqueously-dwelling animals, because: (1) all known trackways were emplaced onto subaqueously-deposited ash-fall substrates; (2) no trackways are known from demonstrably subaerial Borrowdale facies; and (3) evidence for established subaerial animal communities elsewhere in the world is lacking before the Silurian (Minter et al., 2016).

TRACEMAKER BEHAVIOR

The trackways at Lum Pot consist exclusively of *Diplichnites* (paired discrete footprint impressions, 40 instances) and *Diplopodichnus* (paired grooves, 106 instances) (Fig. 3). Both forms have a mean width of 6 mm (Fig. 3J)) and, in 12 instances, *Diplichnites* transitions to *Diplopodichnus* along its length (Fig. 3H), indicating the different ichnogenera had a shared tracemaker (as noted by Johnson et al., 1994). A significant difference is that *Diplichnites* are shorter (average 56 mm) and straighter (average sinuosity 1.02) than *Diplopodichnus* and transitional trackways (average 153 and 197 mm) which commonly occur in single or multiple, broadly or tightly arcuate and self-crossing loops (Fig. 3A, D, I). The most likely tracemaker remains a myriapod, as discussed by Johnson et al. (1994), who noted one instance of lateral probing on a trackway (evidenced by a short terminal 'branch' to the main trackway as it curved), implying a laterally-flexible tracemaker. In this study, a further instance of probing (Fig. 3F) in *Diplichnites* reveals 10 footfall impressions along one side of the length of the probing branch, indicating an organism with at least 20 legs, and confidently eliminating trilobites, chelicerates, crustaceans and hexapods as potential tracemakers.

Johnson et al. (1994) argued that the different forms resulted from the same tracemaker organism walking on wet (*Diplopodichnus*) or dry (*Diplichnites*) sediment, but this is unlikely as both forms occur on multiple substrates (i.e., firm, semi-firm, unconsolidated). Additionally, the presence of transitional forms on continuous surfaces which lack topography (e.g., depressions where water may have been

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retained) implies that a single tracemaker could create both ichnogenera during one traverse of a planar, materially-uniform substrate (Fig. 3H). Without a sedimentological cause, the preservation of both trackways must be due to behavioral variation from the tracemaker. Extant myriapods transition from making *Diplichnites-* to *Diplopodichnus*-like trackways as their walking speed decelerates (Wilson, 2006), and the occasional widening of *Diplopodichnus* trails indicates that the organism was also irregularly wobbling the axis of its body, as it moved in self-crossing concentric pathways. Such pathways of motion and trackways have been observed being made by a variety of dying arthropods, including myriapods (Gerdes et al., 1993; Martins-Neto and Gallego, 2006; Hegna, 2012; Martin, 2013; see Appendix). In the rock record, 'mortichnia' can only be conclusively identified by the rare fossilization of the tracemaker, but usually with no evidence for the cause of death. While no body fossils accompany the Lum Pot trackways, a mortichnial origin for the traces is supported by (1) morphometric similarity with unequivocal arthropod mortichnia (e.g., Barthel et al., 1990; Collette et al., 2010; Figure 3K, Appendix); and (2) direct sedimentary evidence for a known cause of arthropod death. Volcanic ash abrades and adheres to arthropod cuticles (causing desiccation and interfering with osmoregulation), enters articular membranes (increasing friction and restricting mobility), and acts as a highly inimical substrate on which to search for resources as its ingestion destroys arthropod digestive and breathing apparatus (Edwards, 2005; Miserendino et al., 2012; Elizalde, 2014). Further, subaqueously remobilized ash can increase arthropod mortality for years after an eruption (Miserendino et al., 2012). As the Lum Pot trackways occur within a sedimentary succession composed almost uniformly of < 0.01 mm ash, with evidence for post-settling remobilization of ash in the water column (i.e., wave ripples; re-entrainment of ash during the erosion of fluted surfaces), the potential for ash-induced mortality would have been severe.

The low ichnodiversity and ichnodisparity of the BVG trackways means that they share few similarities with the diverse trackways and infaunal traces known from Silurian-Devonian non-marine strata, and which record the major global onset of arthropod-sediment interactions on land (Minter et al., 2016; Shillito and Davies, 2017). Statistical comparison reveals stronger similarities with other Cambrian-Ordovician subaerial trace fossil sites (Fig. 3L), where low diversity arthropod trackways are seen in subaqueously deposited strata with evidence for intermittent emergence (e.g., adhesion marks, desiccation cracks) or fully subaerial strata deposited within a few meters the paleoshoreline (MacNaughton et al., 2002; Collette et al., 2010; Hagadorn et al., 2011).

CONCLUSIONS

Rather than providing a trace-fossil record of incipient fully non-marine animal communities, the BVG trackways likely provide one of few globally-distributed snapshots of littoral arthropod activity during the protracted Cambrian-Ordovician prelude to terrestrialization. However, their association with thick ash deposits, and apparent record of distressed behavior, renders them an exceptional fossilized record of organisms interacting with, and dying within, a marginal subaqueous volcanic environment in deep time, in part analogous to modern arthropod response to eruptions.

APPENDIX

Details of the local stratigraphy, further images of surfaces A-E, = thin sections, comparative images of arthropod mortichnia and details and data for the plots in Figure 3 are provided as an Appendix.

ACKNOWLEDGMENTS

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FIGURE CAPTIONS

Figure 1. Geological context of trackway bearing horizons in the BVG at Lum Pot. A) Map showing location of Lum Pot and Sour Milk Gill trackway localities. Inset shows current British Geological Survey (BGS) map for studied locality (see Appendix for discussion of Whorneyside/Dunnerdale boundary); B) Cross-section through the Duddon Basin, along line A-A' (Fig. 1A) showing regional stratigraphic relationships, after Millward (2004). Formations not mentioned in text referred to by BGS lexicon codes (see Millward, 2004); C) Measured stratigraphic log at Lum Pot showing trace-fossil surfaces (log location shown in 1A; base of log at 54° 18⬚ 12.08" N, 3° 12⬚ 18.63" W, top of log at 54° 18⬚ 15.21" N, 3° 12⬚ 13.36"; bedding dips ~20° toward the ESE).

Figure 2. Sedimentological characteristics of the trackway-bearing tuffs at Lum Pot [position on Figure 1C log or trackway surface in square brackets]. A) Furrowed grooves developed as overlying ash eroded down to a new semi-firm substrate, later traversed by *Diplichnites* and *Diplopodichnus* [Surface D]; B) Unconsolidated substrate revealed by reworking of tuff into bifurcating wave ripple marks. Surface hosts multiple short (<15 cm) trackways (not visible at this scale; locations starred) [Surface B]; C) Homogenous tuff with two vesicular horizons [20.7 m]; D) Pumice clasts (pink arrow) with similar-sized weathered out holes (yellow arrow), plan-view of exposed internal part of tuff bed [22.4 m]; E) Coarse layer of settled ash [1 cm below Surface C2]; F) Aggradational climbing wave ripples in cross section, indicating continuous ash deposition in agitated water [14.0 m]; G) Consolidated substrates revealed by vertical section through small brittle faults and fractures. Overlying 30 cm tuff bed has a horizontal upper bounding surface [21.1 m]; H) Bedding sags arising from impacting ejecta onto a wet substrate. Arrow points to *Diplichnites* (not visible at this scale) which descends over lip of crater and into sag [Surface C2]; I) Soft-sediment deformation arising from liquefaction of saturated, unconsolidated ash [13.6 m]; J) Banded tuff (B) passing vertically into large ball-and-pillow structures (BP) indicating instance of wholly unconsolidated and liquefied sediment [21.8 m]. Scale bars: 10 cm (black); 1 cm (red). See Appendix for larger photographs.

Figure 3. Distribution and form of trackways. A) Scaled sketch showing distribution of *Diplopodichnus* (pink) and *Diplichnites* (blue) on Surfaces C1 and D; B-C) *Diplichnites* restricted to ripple crests on Surface B, sketch shows measured transect of surface topography and distribution of trackways in pink; D-E) *Diplopodichnus* following microtopography of furrowed Surface D, with sketch as in Figure 3C; F) Evidence for probing behavior at a curve in a *Diplichnites* trackway [Surface D]; G) Planview of a microfault scarp (top and bottom highlighted in blue) showing *Diplichnites* passing over scarp lip from left, and rejoining lower foot of scarp at a distance as tracemaker stepped downwards [Surface D]; H) Transition from *Diplichnites* to *Diplopodichnus* along same trackway [Surface D]; I) Mean values for sinuosity (see Appendix) and length in the different trackway morphologies: *Diplopodichnus*, made by slower moving and wobbling tracemakers, are more likely to be seen looping; J) Mean values for width and length in different trackway morphologies: low standard deviation (2.04) of widths supports contention that they were made by the same type of animal; K) Histogram showing the distribution of loop diameter/trace width for all looped examples, and similar clustering of known mortichnia. Values

from known arthropod mortichnia (see Appendix) are marked as a – Silurian myriapod, b – Cambrian euthycarcinid, c – modern dipteran, d – modern apterygote, e – Jurassic xiphosuran; L) Multivariate cluster analysis showing similarity of trace fossil communities in coastal and alluvial settings from the Cambro-Ordovician (C-O), Silurian (S) and Devonian (D) (see Appendix). See Appendix for larger photographs.
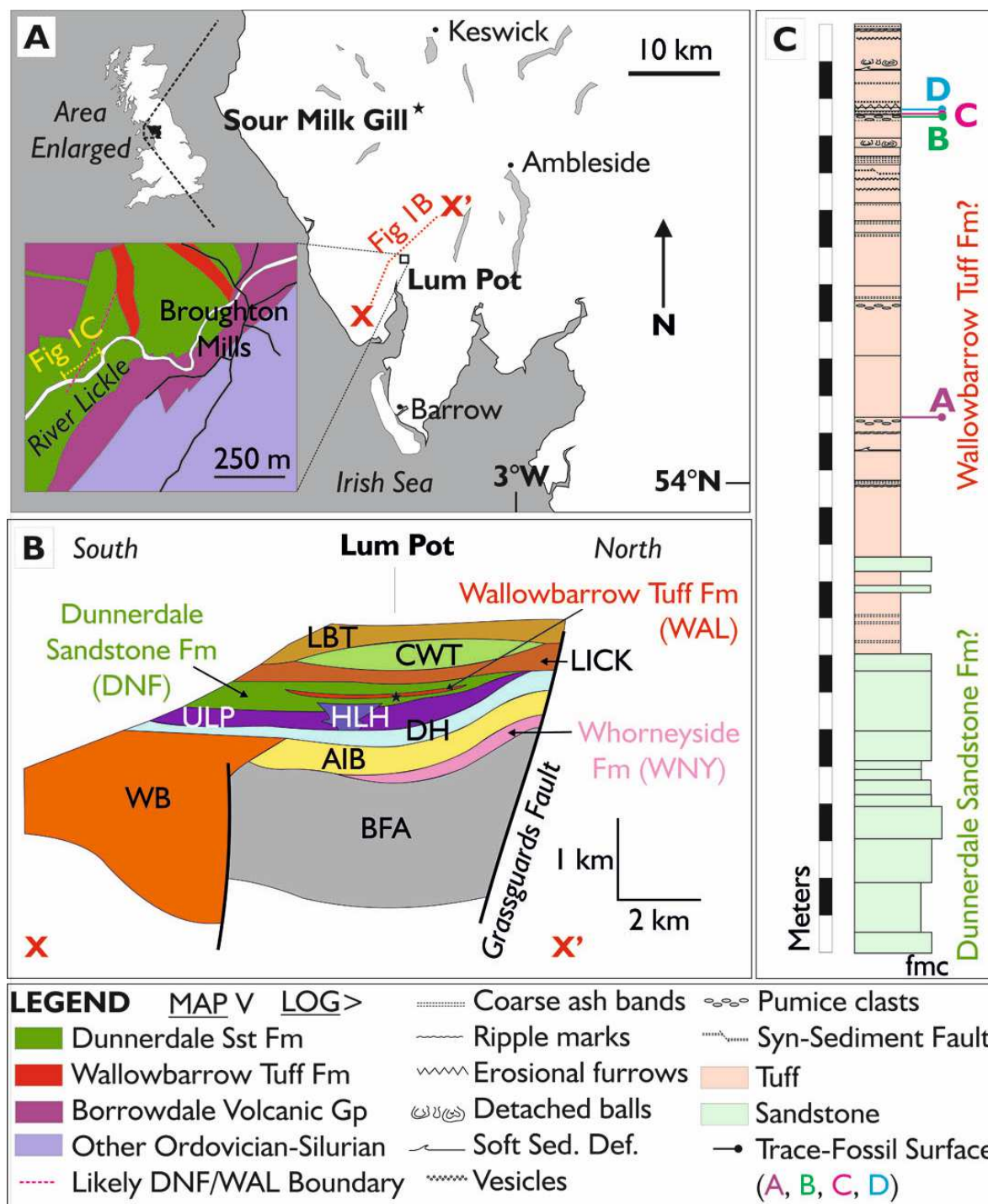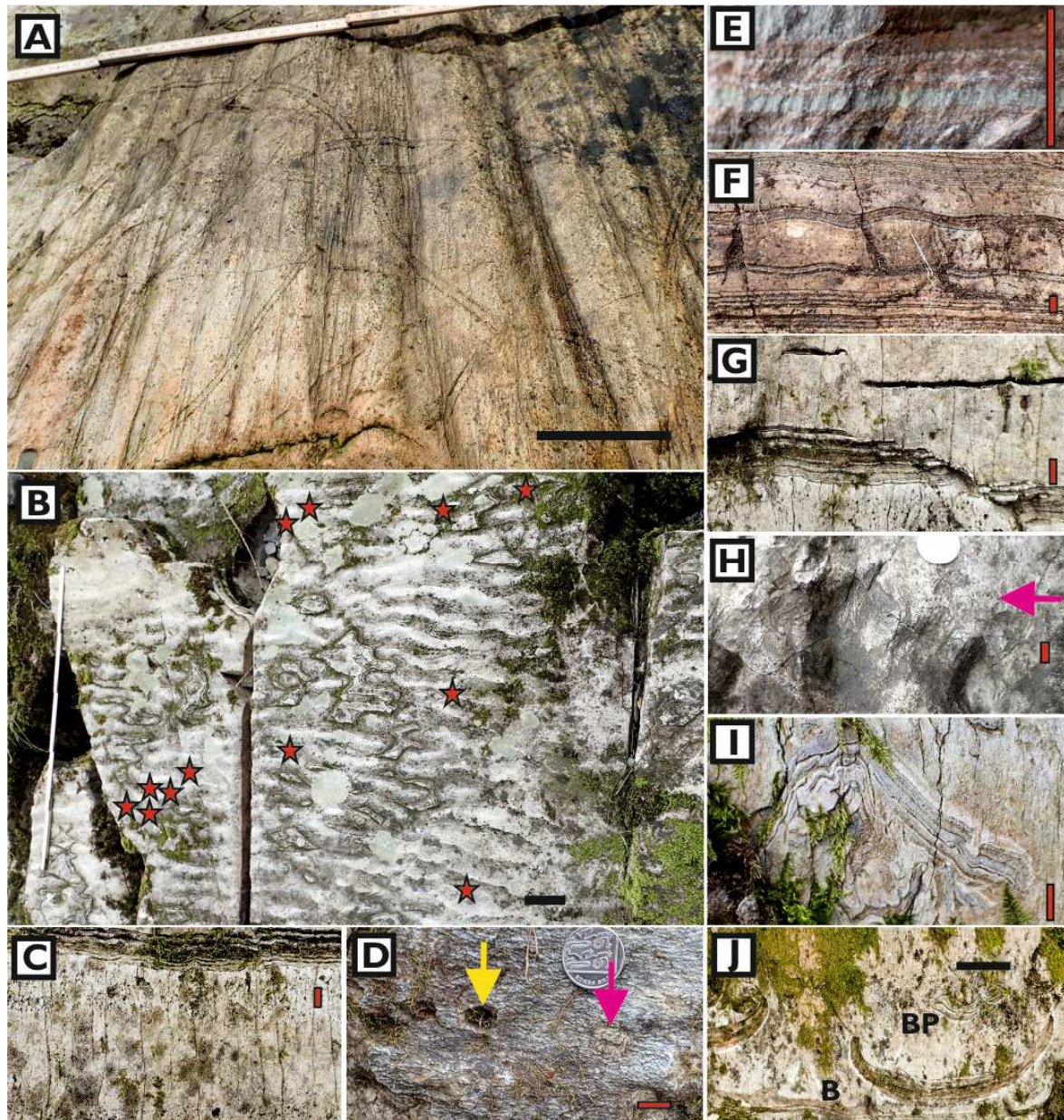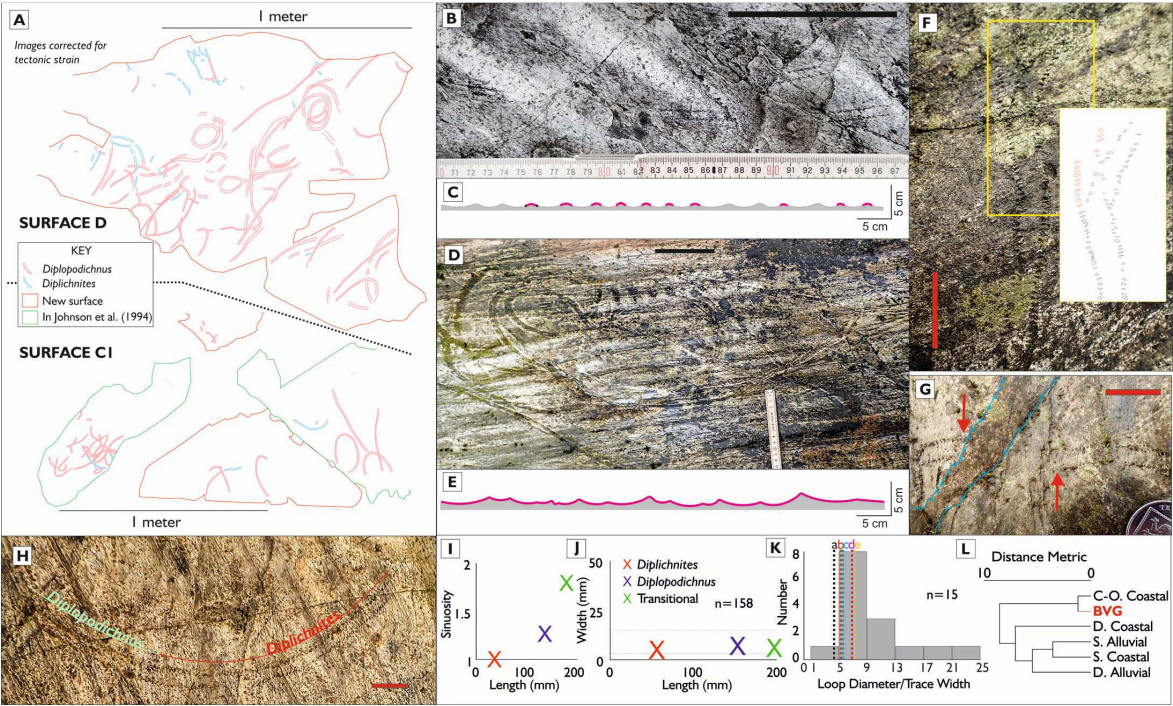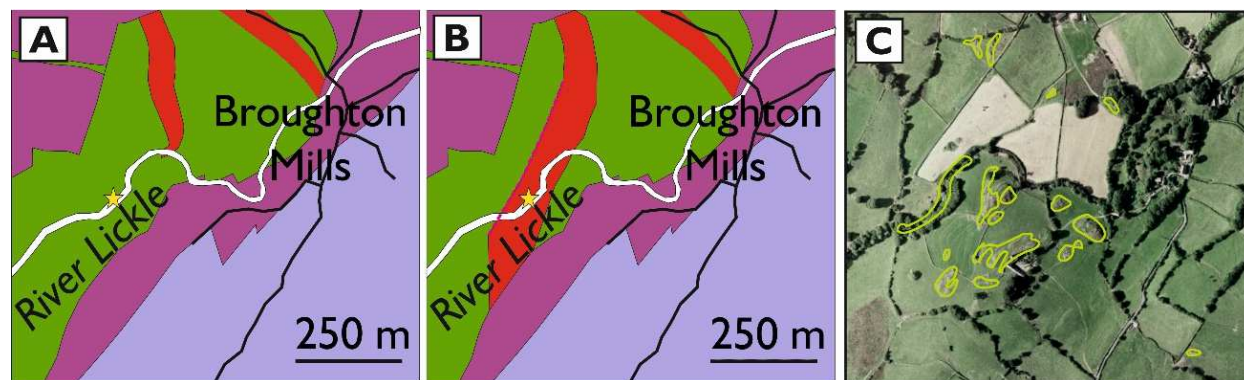
FIGURE 1

FIGURE 2

FIGURE 3

Supplementary Material: Death near the Shoreline, not Life on Land: Ordovician Arthropod Trackways in the Borrowdale Volcanic Group, UK Anthony P. Shillito and Neil S. Davies

STRATIGRAPHIC CONTEXT OF THE TRACKWAYS

The Lum Pot site, where the arthropod trackways occur, was described as being in the Dunnerdale Sandstone Formation (DNF) by Johnson et al. (1994), and is presently mapped as such by the British Geological Survey (BGS). In this paper we consider it more likely that the trackways are within the Wallowbarrow Tuff Formation (WAL), which is a localized stratigraphic unit bounded above and below by the DNF (Figure 1B). This conclusion is based on the fact that the lithology of the Lum Pot stream section consists of at least 14 meters of continuous tuff, whereas, by definition, the DNF consists entirely of volcanoclastic sandstones and breccia (Millward, 2004). The sandstone lithology of the trackway beds, as previously reported, was inconsistent and incorrect (described by Johnson et al. (1994) variably as fine-grained sandstone (p. 397, 404), fine- to medium-grained sandstone (p. 397) or medium- to coarse-grained sandstone (p. 398, 399)). Additionally, the presence of WAL at the locality is not surprising: whilst existing BGS bedrock maps show the predicted DNF/WAL boundary to be approximately 200 meters upstream on the River Lickle from Lum Pot, such a boundary is not exposed in the field. The drift cover, extensive faulting, and lack of continuous exposure in the area means that existing maps are, at least in part, conjectural but the re-identification of the Lum Pot rocks as tuff (as originally noted by Mitchell, 1956) identifies the WAL as the most likely host stratigraphic unit (Figure S1).

Figure S1. *Geological maps of the Lum Pot site, with trace-fossil site starred. WAL shown in red and DNF in green: see Figure 1 for full key. A) Current BGS map; B) Proposed map, based on tuff outcrop along the River Lickle; C) Limited outcrop exposure (highlighted in green) on which map in A was based. © 2018 Google Earth, Infoterra & Bluesky.*

TRACKWAY SURFACES

Johnson et al. (1994) recorded two trackway-bearing surfaces at Lum Pot: a bed with abundant trails on top (here, Surface C1), and a bed with sparse trails on a rippled surface (here, Surface B). In this study we identified three further surfaces bearing trackways, referring to them in stratigraphic order from oldest to youngest (A, B, C1, C2, and D, where C2 is a different surface of the same bed as C1, exposed on the south side of the River Lickle). A description of each of the trackway bearing surfaces, and their position in the local stratigraphy, is shown in Table S1. The outcrop of each surface is shown in Figures S2-S6, with trackways traced onto the photographs in pink (*Diplopodichnus*) and blue (*Diplichnites*).

Figure S2. *Surface A (ruler is 24 cm).*

Figure S3. *Surface B (ruler is 1 meter).*

Figure S4. *Surface C1 (ruler is 1 meter).*

Figure S5. *Surface C2 (ruler is 1 meter).*

Figure S6. *Surface D (ruler is 1 meter).*

Surface	Location	Local Strat (Fig 1C)	Regional Strat.	Latitude	Longitude	Lithology	Surface area	Primary Surface Features	Number of Traces		
									Diplichnites	*Diplopod.*	Transitional
A	Lum Pot, North Side of River Lickle	15.50 m	Wallowbarrow	54° 18' 12.16" N	3° 12' 16.65" W	Tuff	0.14 m^2	Brittle failure scarps? (may be secondary)	0	2	0
B	Lum Pot, North Side of River Lickle	22.56 m	Wallowbarrow	54° 18' 12.79" N	3° 12' 15.39" W	Tuff	2.86 m^2	Wave Ripples	8	10	1
C1	Lum Pot, North Side of River Lickle	22.61 m	Wallowbarrow	54° 18' 12.85" N	3° 12' 15.56" W	Tuff	1.96 m^2	Brittle failure scarps? (may be secondary)	4	24	3
C2	Lum Pot, South Side of River Lickle	22.61 m	Wallowbarrow	54° 18' 12.41" N	3° 12' 15.16" W	Tuff	1.11 m^2	Low amplitude ripples, Pumice, Bedding sags	3	4	1
D	Lum Pot, North Side of River Lickle	22.92 m	Wallowbarrow	54° 18' 13.45" N	3° 12' 14.41" W	Tuff	1.92 m^2	Erosional furrows, Brittle failure scarps	25	66	7
X	Sour Milk Gill, Seathwaite	Unknown	Unknown	54° 29' 57.30" N	3° 11' 36.66" W	Sandstone?	0.01 m^2	None	3	0	0

Table S1. Contextual information for trackway surfaces studied in this paper (A-D) and Johnson et al. (1994) (C1, X).

THIN SECTION IMAGES
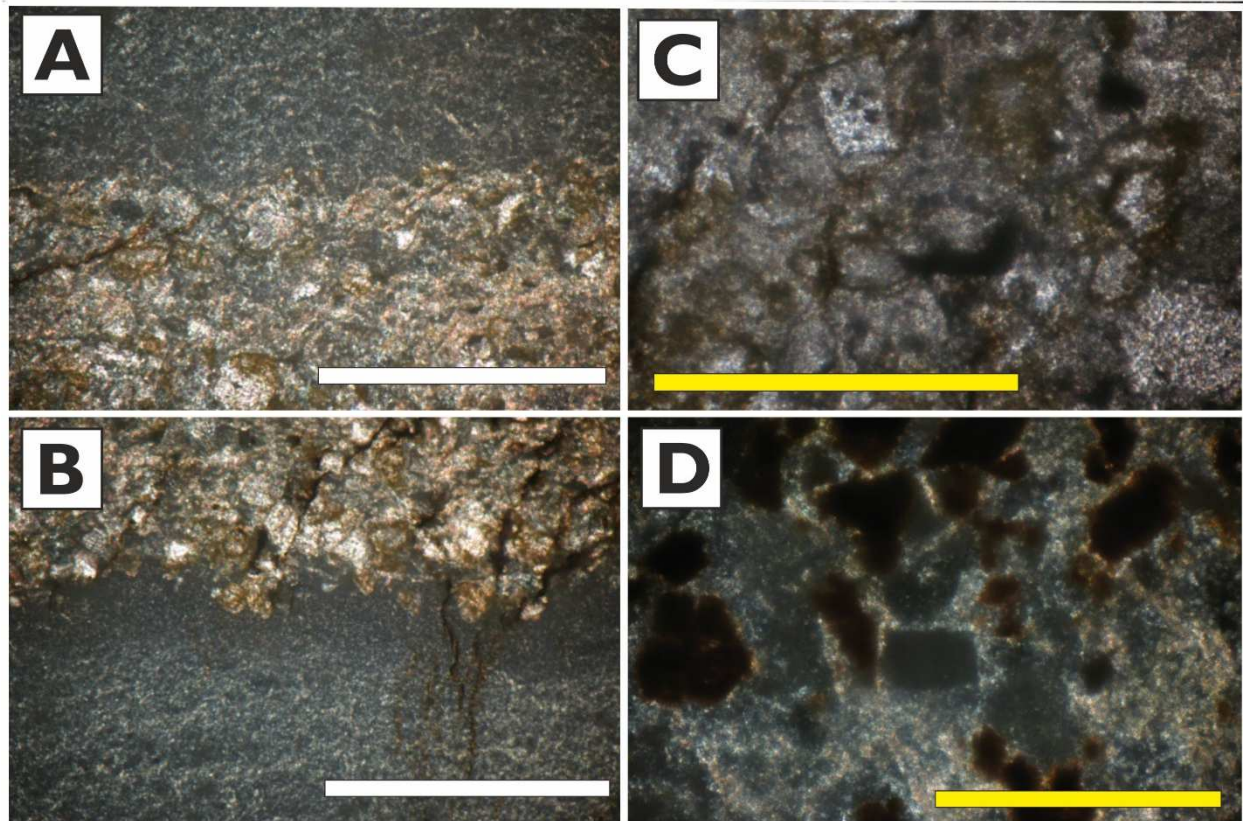
Figure S7. Images of tuff in thin section: A) Bottom of 3 mm-thick coarser ash fall layer (see Figure 2G), showing feldspar-dominated grains settling into cryptocrystalline ash [Surface C2]; B) top of same layer, succeeded by more fine ash [Surface C2]; C) subhedral alkali feldspar grains [Surface C2]; D) subhedral opaque oxides [8.1 m]. Scale bars 0.5 mm (white), 0.25 mm (yellow).

SUBSTRATE FIRMNESS

The Lum Pot succession contains evidence that the substrates traversed by the tracemakers had varying degrees of consolidation, irrespective of how wet they were (Table S2). The different material properties of these substrates placed a control on the potential for trackways to be emplaced. The table below shows the suspected likelihood of trackways on substrates of different firmness in different states of moistness, and instances where these were seen.

Substrate firmness	Examples (Figures)	Evidence	Potential Trackways		Seen Trackways	
			Wet	Dry	Wet	Dry
Unconsolidated (granular)	2F, 2H, 2I, 2J, 2K, 3B	Various soft-sediment deformation structures, ripple marks	N	Y	N	Y
Semi-firm (cohesive)	2A, 3D, 3F, 3H	Furrowed erosion surface indicating erosion down to a more cohesive layer within ash deposit	Y	?	Y	?
Firm (cohesive)	2N, 3G	Brittle syn-sedimentary deformation, fracture scarps	Y	N	Y	N

Table S2. Evidence for unconsolidated, semi-firm and firm ash substrates in the Lum Pot section and their propensity for being imparted with trackways when wet and dry.

TRACKWAY MORPHOLOGY

The plots shown in Figure 3I-K show the morphometric characteristics of the trackways (measurements in Tables S3-S5 at the end of this appendix). All trace fossil dimensions were corrected to account for a regional tectonic shortening of approximately 30%, with the direction of shortening determined from the cleavage in each trackway-hosting bed (Johnson et al., 1994). Figure 3J (shown in full as Figure S8, and including the three trackways from Sour

Milk Gill) shows how the width of the trackways is consistent regardless of length or ichnogenera, supporting the notion of a single type of tracemaker.
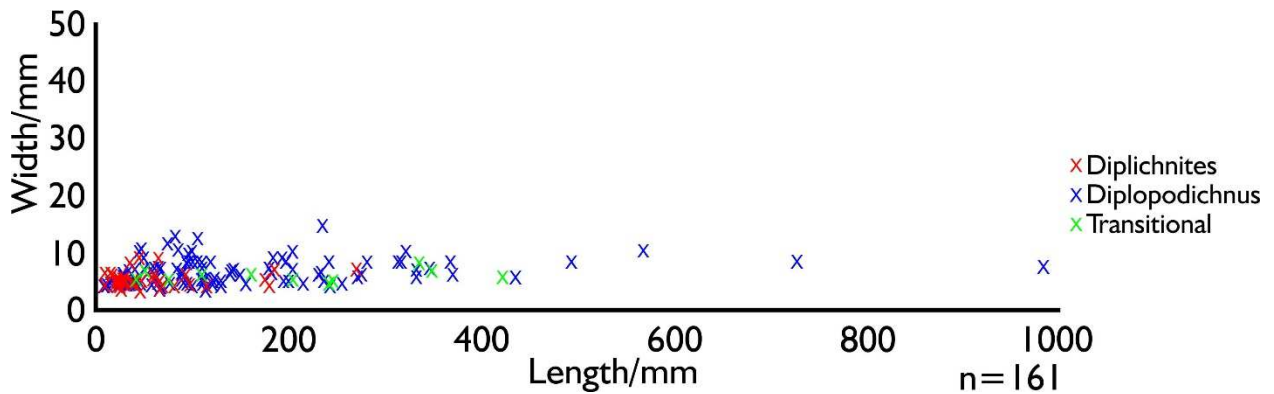
Figure S8. *Length-width graph shows that all traces are of similar width, fitting very closely to a normal distribution (standard deviation = 2.04). The lengths of the traces have a much greater range and far higher standard deviation (=135.93) highlighting the more variable nature of the values.*

The graph showing sinuosity against length (Figure 3I, S9) shows that *Diplopodichnus* tracks, reflecting slow moving and wobbling tracemakers, were more likely to be long and looping than the *Diplichnites* tracks. Looping, common in mortichnial trails, was approximated with a measurement of sinuosity: the ratio of the length of a trace to its distance, where "distance" records the minimum distance between the end points of a trace in a straight line, and "length" records the distance between the end points of a trace when following the path of the trace.
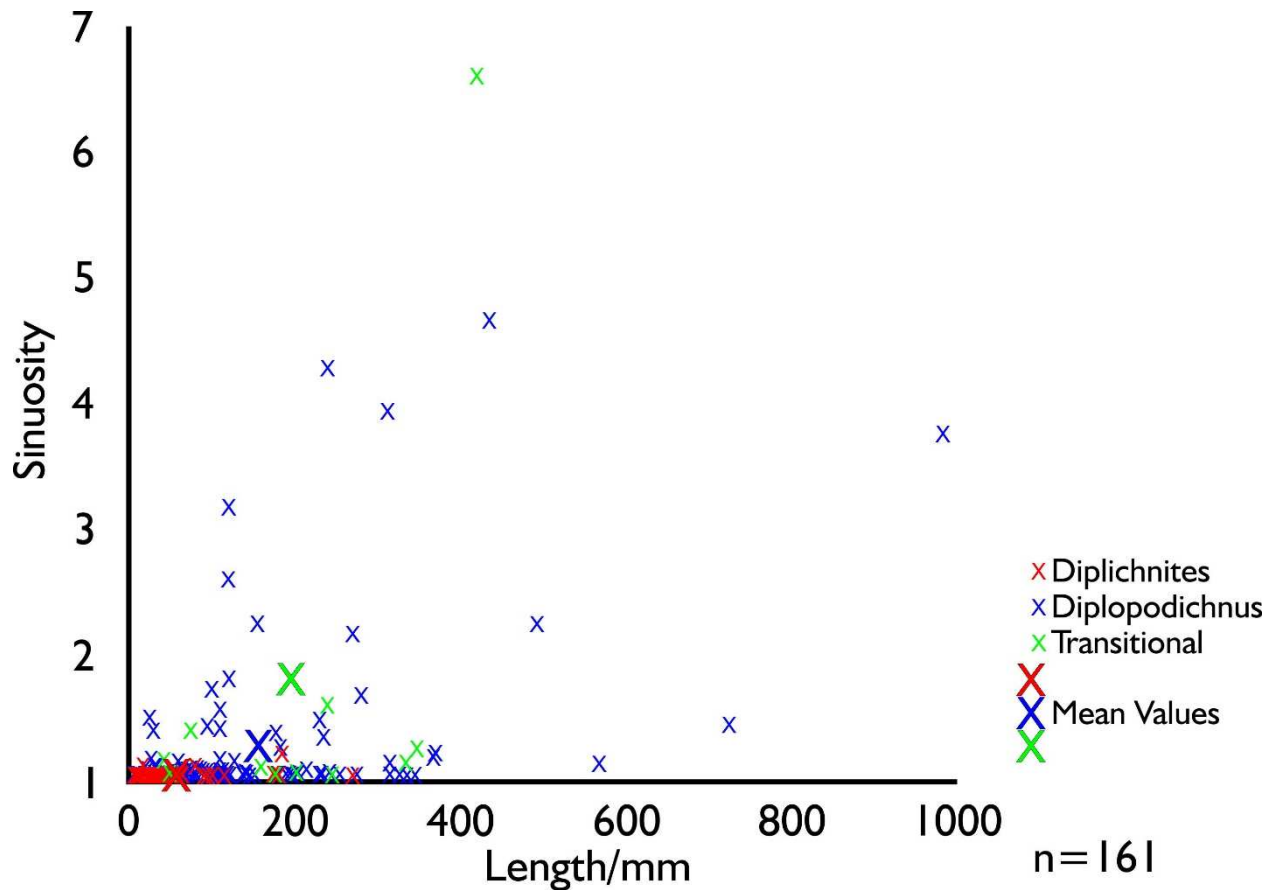
Figure S9. *Sinuosity-length graph shows that most of the observed traces have a sinuosity below 1.1, including all but 3 examples of Diplichnites. Diplopodichnus and transitional forms exhibit a much greater range of sinuosities, and higher mean values.*

Looping of the trackways was further quantified as a ratio of the diameter of the loop in the region of the tightest curvature to the mean width of the trace along its length (Figure 3K; Figure S10). The degree of shortening in the Lickle area is reported to be approximately 30% (Johnson et al., 1994). This was corrected for using photo manipulation to artificially adjust the traces to their original proportions. Diameter was divided by trace width to produce a ratio comparable with other global examples of known or suspected mortichnia independent of the size of the trace maker. This was then presented as a histogram with bin size 4, starting from the minimum possible ratio (1.0). Published examples of arthropod mortichnia that were measured for comparison included the death trail of a Jurassic xiphosauran (in Barthel et al., 1990; their Fig. 5.5; 'e' in Figure 3K) and Cambrian euthycarcinid (in Collette et al., 2010; their Fig. 3D; 'b' in Figure 3K). Unpublished instances are shown in Figures S11-15.

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Myriapod death trails illustrated by Martins-Neto and Gallego (2006) are omitted as no scale was shown with their image (their Fig. 4D).

Figure S10. *Measurements taken in the construction of Figure 3K (example is on Surface C1).*

Figure S11. *Self-crossing looping trail of a dying dipteran trapped on the surface of a pond. Murchison River, Western Australia ('c' in Fig. 3K).*

Figure S12. *Looping and self-crossing mortichnia of a dead silverfish (Zygentoma) observed on modern mudflat. Hastings, Sussex, UK ('d' in Fig. 3K).*
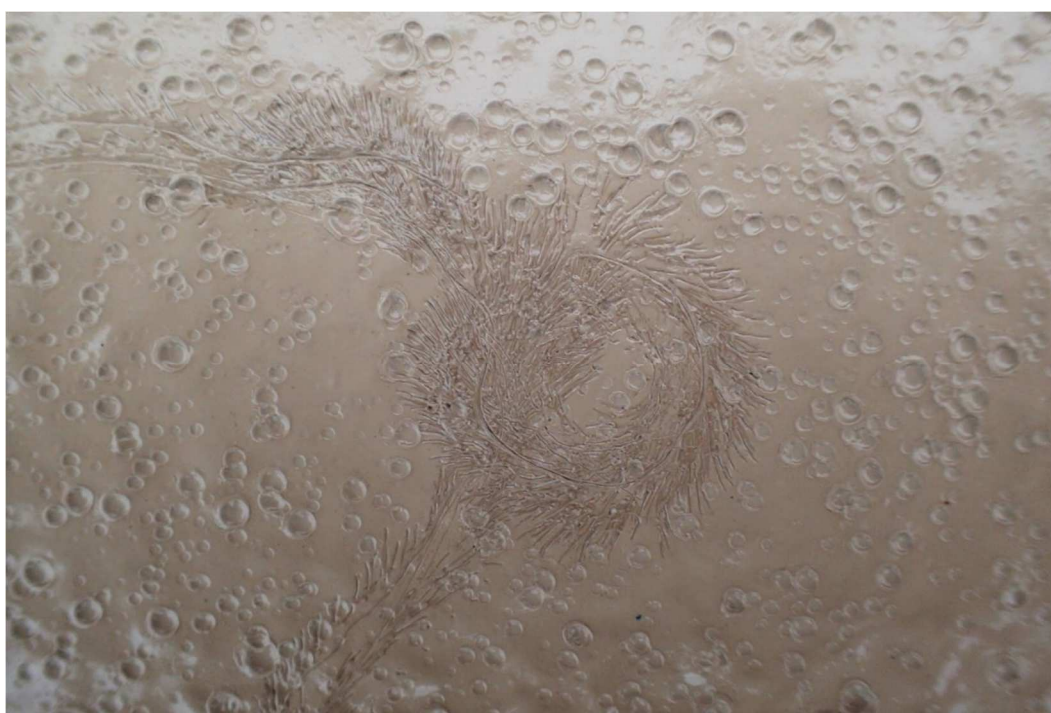
Figure S13. *Detail of Figure S12 showing irregular widening of trail as dying silverfish wobbling and walked in circles.*

Figure S14. *Detail of Figure S12 showing irregular widening of trail as dying silverfish wobbling and walked in circles.*

Figure S15. *Suspected but unconfirmed mortichnial trail of a myriapod in the Silurian Tumblagooda Sandstone, Western Australia. Facies Asssociation 2 of this formation contains hundreds of examples of Diplichnites but this is the only trail to show looping, suggesting a rarer form of behavior (i.e., suspected to be dying) than other trackways in the formation ('a' in Fig. 3K).*

OTHER COMPARATIVE NEOICHNOLOGY

Comparative neoichnology also provides analogues for instance where footprints are seen only on ripple crests (i.e., where dry granular sediment on ripple crestlines preserves footprint indents, but saturated granular sediment within troughs cannot retain such impressions). Figures S16-17 show examples of similar arthropod traces within damp fine-grained sands within an intertidal zone (Rainy Cove, Nova Scotia, Canada).

Figure S16. *Preservation of footprint indents on damp ripple crests, but absent in waterlogged ripple troughs. Intertidal sands at low tide, Rainy Cove, Bay of Fundy, Nova Scotia, Canada.*

Figure S17. *Preservation of footprint indents on damp ripple crests, but absent in waterlogged ripple troughs. Intertidal sands at low tide, Rainy Cove, Bay of Fundy, Nova Scotia, Canada.*

COMPARISON WITH OTHER PALAEOZOIC ICHNOFAUNAS

Classical multivariate cluster analysis was performed using Ward's method with a Euclidean similarity index in order to compare the ichnofaunal assemblage of the Wallowbarrow Tuff Formation with other Palaeozoic ichnofaunas. Analysis was performed using PAST (PAlaeontological STatistics) software (https://folk.uio.no/ohammer/past/). The known trace fossil assemblages from all formations grouped as Cambrian-Ordovician Coastal, Silurian Coastal, Silurian Alluvial and Lacustrine, Devonian Coastal and Devonian Alluvial and Lacustrine were used for comparison (utilizing ichnofaunal lists in Minter et al., 2016: see Table S6). While the Silurian and Devonian ichnofaunas grouped together in one cluster, the

Wallowbarrow assemblage is more similar in composition to the limited arthropod trackway ichnofaunas of other Cambrian and Ordovician littoral successions.

DATA TABLES

Table S3. Measurements of individual traces on each trackway surface (see Table S1) (trace fossil type shown as A = Diplichnites, B = Diplopodichnus, AB = Transitional forms).

Surface	Trace #	Distance	Length	Width	Sinuosity	A/B?
X	1	92	93	6	1.01	A
X	2	64	67	5	1.05	A
X	3	48	48	5	1.00	A
A	1	200	205	10	1.03	B
A	2	315	323	10	1.02	B
B	1	173	237	5	1.37	B
B	2	240	247	5	1.03	AB
B	3	113	113	3	1.00	B
B	4	63	67	3	1.05	B
B	5	25	25	4	1.00	A
B	6	20	20	4	1.00	A
B	7	270	270	7	1.00	A
B	8	30	30	5	1.00	A
B	9	45	45	9	1.00	A
B	10	100	100	4	1.00	B
B	11	50	50	9	1.00	B
B	12	200	200	5	1.00	B
B	13	40	40	5	1.00	B
B	14	35	35	8	1.00	A
B	15	40	40	5	1.00	A
B	16	30	30	5	1.00	A
B	17	130	130	4	1.00	B

B	18	195	195	5	1.00	B
B	19	300	370	6	1.23	B
C1	1	44	47	4	1.05	B
C1	2	18	27	4	1.50	B
C1	3	71	111	4	1.56	B
C1	4	27	27	4	1.00	B
C1	5	91	91	4	1.00	B
C1	6	40	42	4	1.06	B
C1	7	38	120	4	3.18	B
C1	8	18	18	4	1.00	B
C1	9	22	24	4	1.10	B
C1	10	62	64	6	1.04	B
C1	11	69	156	4	2.26	B
C1	12	24	29	4	1.18	B
C1	13	67	96	4	1.43	B
C1	14	64	64	4	1.00	B
C1	15	22	31	4	1.40	B
C1	16	44	44	4	1.00	B
C1	17	151	242	4	1.60	AB
C1	18	29	29	4	1.00	A
C1	19	196	216	4	1.10	B
C1	20	27	27	4	1.00	B
C1	21	38	120	4	3.18	AB
C1	22	93	436	6	4.67	B
C1	23	47	122	4	2.62	B
C1	24	33	33	4	1.00	B
C1	25	25	25	4	1.00	A
C1	26	153	186	7	1.22	A
C1	27	322	333	7	1.03	B
C1	28	64	422	6	6.61	AB

C1	29	125	272	6	2.18	B
C1	30	328	333	6	1.02	B
C1	31	39	39	4	1.00	A
C2	1	60	60	6	1.00	A
C2	2	150	150	6	1.00	B
C2	3	110	110	6	1.00	AB
C2	4	110	110	8	1.00	B
C2	5	115	115	4	1.00	A
C2	6	50	50	7	1.00	B
C2	7	65	65	9	1.00	A
C2	8	95	95	8	1.00	B
D	1	306	367	8	1.20	B
D	2	300	316	8	1.05	B
D	3	82	90	6	1.10	B
D	4	167	282	8	1.68	B
D	5	102	106	8	1.04	B
D	6	65	67	7	1.03	B
D	7	190	198	8	1.04	B
D	8	104	106	8	1.02	B
D	9	144	184	9	1.28	B
D	10	249	256	4	1.03	B
D	11	20	20	4	1.00	A
D	12	278	349	7	1.26	AB
D	13	58	58	7	1.00	B
D	14	49	51	7	1.05	AB
D	15	266	276	6	1.04	B
D	16	230	244	4	1.06	B
D	17	184	194	9	1.05	B
D	18	56	60	6	1.07	B
D	19	60	60	6	1.00	A

D	20	156	232	6	1.49	B
D	21	136	140	6	1.03	B
D	22	294	336	8	1.14	AB
D	23	196	204	7	1.04	B
D	24	85	91	6	1.08	B
D	25	121	123	5	1.02	B
D	26	96	96	10	1.00	B
D	27	230	234	6	1.02	B
D	28	96	98	4	1.02	A
D	29	30	30	5	1.00	A
D	30	13	13	4	1.00	B
D	31	31	31	5	1.00	A
D	32	62	68	4	1.09	B
D	33	64	67	4	1.05	A
D	34	41	43	4	1.07	B
D	35	90	90	5	1.00	B
D	36	31	34	7	1.11	B
D	37	498	568	10	1.14	B
D	38	59	59	6	1.00	B
D	39	54	76	5	1.41	AB
D	40	34	34	4	1.00	B
D	41	132	141	7	1.06	B
D	42	25	25	3	1.00	A
D	43	219	494	8	2.26	B
D	44	502	727	8	1.45	B
D	45	100	100	8	1.00	B
D	46	96	96	8	1.00	B
D	47	56	242	8	4.30	B
D	48	52	60	7	1.16	B
D	49	46	48	10	1.05	B

D	50	58	58	4	1.00	B
D	51	75	75	11	1.00	B
D	52	21	21	4	1.00	B
D	53	345	347	7	1.01	B
D	54	145	161	6	1.11	AB
D	55	78	110	7	1.42	B
D	56	106	106	12	1.00	B
D	57	8	8	4	1.00	B
D	58	104	113	5	1.08	B
D	59	29	29	6	1.00	B
D	60	233	235	15	1.01	B
D	61	177	183	6	1.04	B
D	62	21	21	5	1.00	A
D	63	112	129	5	1.16	B
D	64	82	84	7	1.02	B
D	65	75	82	13	1.11	B
D	66	39	41	7	1.05	B
D	67	84	86	10	1.02	B
D	68	94	110	5	1.17	B
D	69	278	316	8	1.14	B
D	70	16	18	6	1.13	A
D	71	20	20	4	1.00	A
D	72	192	204	5	1.06	AB
D	73	16	16	5	1.00	A
D	74	22	22	4	1.00	A
D	75	37	43	5	1.17	AB
D	76	10	10	4	1.00	A
D	77	63	65	7	1.03	B
D	78	129	180	7	1.40	B
D	79	80	314	8	3.95	B

D	80	73	82	4	1.11	A
D	81	59	59	5	1.00	A
D	82	69	69	4	1.00	A
D	83	176	180	4	1.02	A
D	84	167	176	5	1.05	A
D	85	15	15	6	1.00	A
D	86	46	46	3	1.00	A
D	87	10	10	6	1.00	A
D	88	17	17	5	1.00	A
D	89	25	25	5	1.00	A
D	90	58	100	10	1.74	B
D	91	45	45	10	1.00	B
D	92	48	48	5	1.00	A
D	93	119	119	8	1.00	B
D	94	260	983	7	3.78	B
D	95	67	121	5	1.81	B
D	96	25	25	4	1.00	A
D	97	70	77	4	1.10	B
D	98	144	144	7	1.00	B

Table S4. Measurements of looping in fully self-crossing Diplopidichnus trackways.

Surface	Loop diameter	Track width	D/W
C1	33	6	5.6
C1	44	6	7.4
C1	33	6	5.6
C1	16	6	2.6
C1	24	4	6.1
C1	29	4	7.2
C1	103	6	17.1

C1	128	6	21.3
D	69	8	8.6
D	96	8	12.0
D	65	8	8.2
D	102	8	12.8
D	71	7	10.1
D	56	7	8.0
D	92	7	13.1

Table S5. Average trackway dimensions.

		Av. Sinuosity	Av. Length	Av. Width	Number
Diplichnites	A	1.02	56	5	43
Diplopodichnus	B	1.28	153	7	106
Transitional	AB	1.80	197	6	12

Table S6. Data matrix compiled from Minter et al. (2016) and used for multivariate cluster analysis. 0 indicates absence and 1 indicates presence of a particular trace from the facies/age combination shown.

	C-O. Coastal	BVG	S. Coastal	S. Alluvial	D. Coastal	D. Alluvial
Diplichnites	1	1	1	1	1	1
Protichnites	1	0	1	0	0	1
Diplopodichnus	1	1	0	1	1	1
Palmichnium	1	0	1	1	1	1
Skolithos	0	0	1	1	1	1
Diplocraterion	0	0	1	0	1	1
Psammichnites	0	0	1	0	0	0
Daedalus	0	0	1	0	0	0
Palaeophycus	0	0	1	1	0	1

Arenicolites	1	0	1	1	1	1
Polarichnus	0	0	1	1	0	0
Arthraria	0	0	1	0	0	0
Bergaueria	0	0	1	0	0	0
Cochlichnus	0	0	1	1	0	1
Gordia	0	0	1	0	0	0
Cruziana	0	0	1	1	1	1
Monomorphichnus	0	0	1	1	1	0
Helicodromites	0	0	1	0	0	0
Chondrites	0	0	1	0	1	0
Protovirgularia	0	0	1	0	1	0
Petalichnus	0	0	1	0	1	0
Beaconites	0	0	1	1	1	1
Syncoprulus	0	0	1	0	0	0
Didymaulichnus	0	0	1	1	1	0
Rhizocorallium	0	0	1	0	0	0
Heimdallia	0	0	1	0	1	0
Didymauliponomos	0	0	1	0	1	0
Helminthopsis	0	0	1	0	1	0
Crescentichnus	0	0	1	0	1	1
Taenidium	0	0	1	0	1	1
Rusophycus	0	0	1	1	1	1
Tumblagoodichnus	0	0	1	0	0	1
Planolites	0	0	1	1	1	1
Paleohelcura	0	0	1	1	0	1
Siskemia	0	0	1	0	0	1
Merostomichnites	0	0	1	1	0	1
Oniscoidichnus	0	0	1	0	0	0
Stiaria	0	0	1	0	0	1
Steinsfjordichnus	0	0	1	0	0	0

Scoyenia	0	0	1	0	0	1
Striatichnium	0	0	1	0	0	0
Spirophyton	0	0	0	0	1	0
Teichichnus	0	0	0	0	1	0
Lockeia	0	0	0	0	1	0
Maculichna	0	0	0	0	1	0
Asterosoma	0	0	0	0	1	0
Lanicoidichna	0	0	0	0	1	0
Agrichnium	0	0	0	0	1	0
Treptichnus	0	0	0	0	1	1
Lophoctenium	0	0	0	0	1	0
Halopoa	0	0	0	0	1	1
Svalbardichnus	0	0	0	0	0	1
Striatichnium	0	0	0	0	0	1
Stiallia	0	0	0	0	0	1
Undichna	0	0	0	0	0	1
Danstairia	0	0	0	0	0	1
Keircallia	0	0	0	0	0	1
Mitchellichnus	0	0	0	0	0	1
Scolicia	0	0	0	0	0	1
Mermia	0	0	0	0	0	1
Asterichnus	0	0	0	0	0	1
Bifungites	0	0	0	0	1	0
Cylindricum	0	0	0	0	1	0
Thalassinoides	0	0	0	0	1	0
Gyrichnites	0	0	0	0	0	1
Pustulichnus	0	0	0	0	0	1
Entradichnus	0	0	0	0	0	1
Ancorichnus	0	0	0	0	0	1
Cornulatichnus	0	0	0	0	0	1

Kouphichnium	0	0	0	0	1	0
Nereites	0	0	0	0	1	0
Total	5	2	40	16	35	38

LARGER IMAGES OF PHOTOGRAPHS SHOWN IN FIGURES 2 AND 3

Figure 2. Sedimentological characteristics of the trackway-bearing tuffs at Lum Pot [position on Figure 1C log or trackway surface in square brackets]. A) Furrowed grooves developed as overlying ash eroded down to a new semi-firm substrate, later traversed by Diplichnites and Diplopodichnus [Surface D]; B) Unconsolidated substrate revealed by reworking of tuff into bifurcating wave ripple marks. Surface hosts multiple short (<15 cm) trackways (not visible at this scale; locations starred) [Surface B]; C) Homogenous tuff with two vesicular horizons [20.7 m]; D) Pumice clasts (pink arrow) with similar-sized weathered out holes (yellow arrow), plan-view of exposed internal part of tuff bed [22.4 m]; E) Coarse layer of settled ash [1 cm below Surface C2]; F) Aggradational climbing wave ripples in cross section, indicating continuous ash deposition in agitated water [14.0 m]; G) Consolidated substrates revealed by vertical section through small brittle faults and fractures. Overlying 30 cm tuff bed has a horizontal upper bounding surface [21.1 m]; H) Bedding sags arising from impacting ejecta onto a wet substrate. Arrow points to Diplichnites (not visible at this scale) which descends over lip of crater and into sag [Surface C2]; I) Soft-sediment deformation arising from liquefaction of saturated, unconsolidated ash [13.6 m]; J) Banded tuff (B) passing vertically into large ball-and-pillow structures (BP) indicating instance of wholly unconsolidated and liquefied sediment [21.8 m]. Scale bars: 10 cm (black); 1 cm (red). See Appendix for larger photographs.
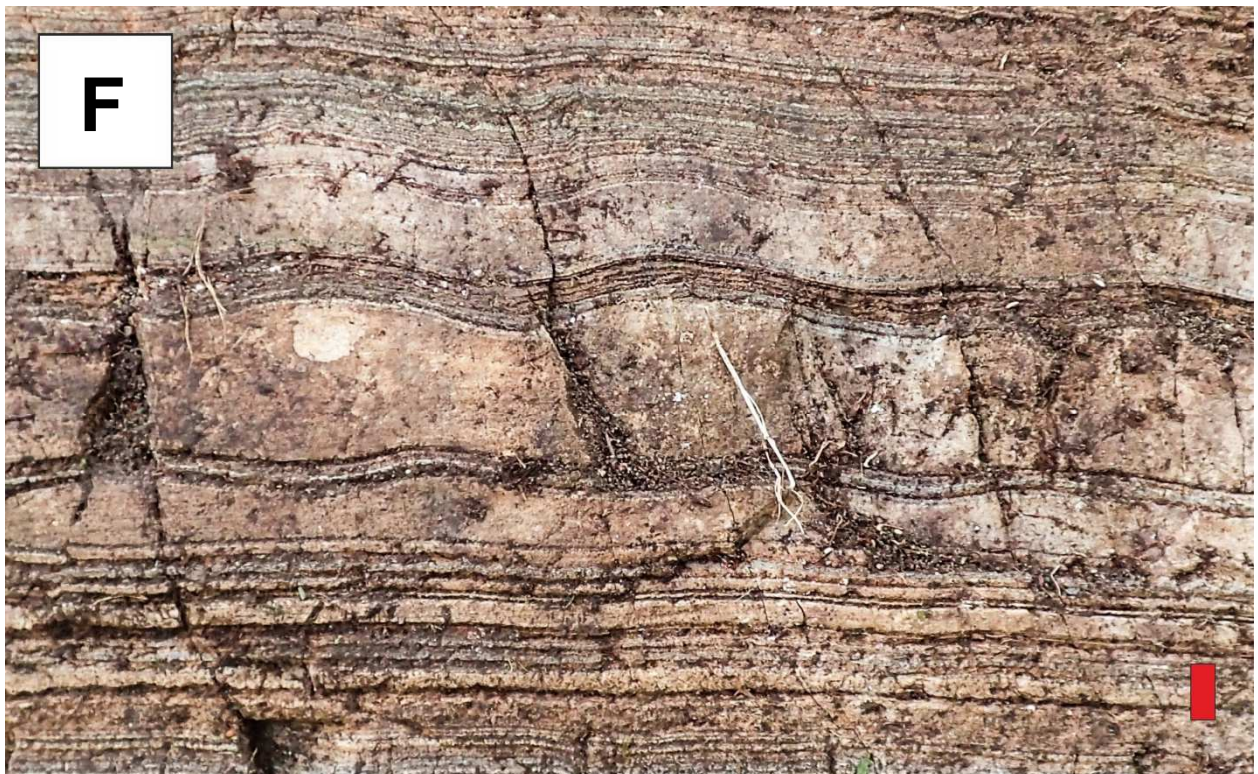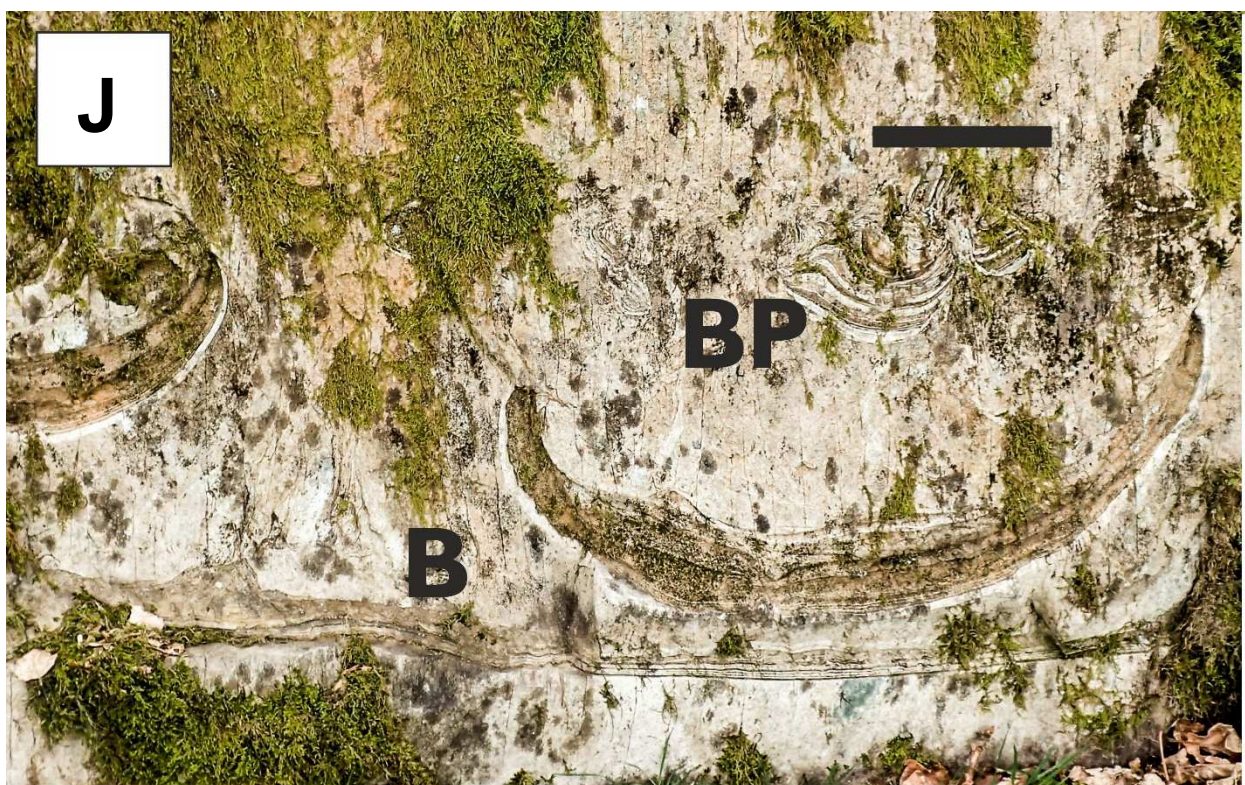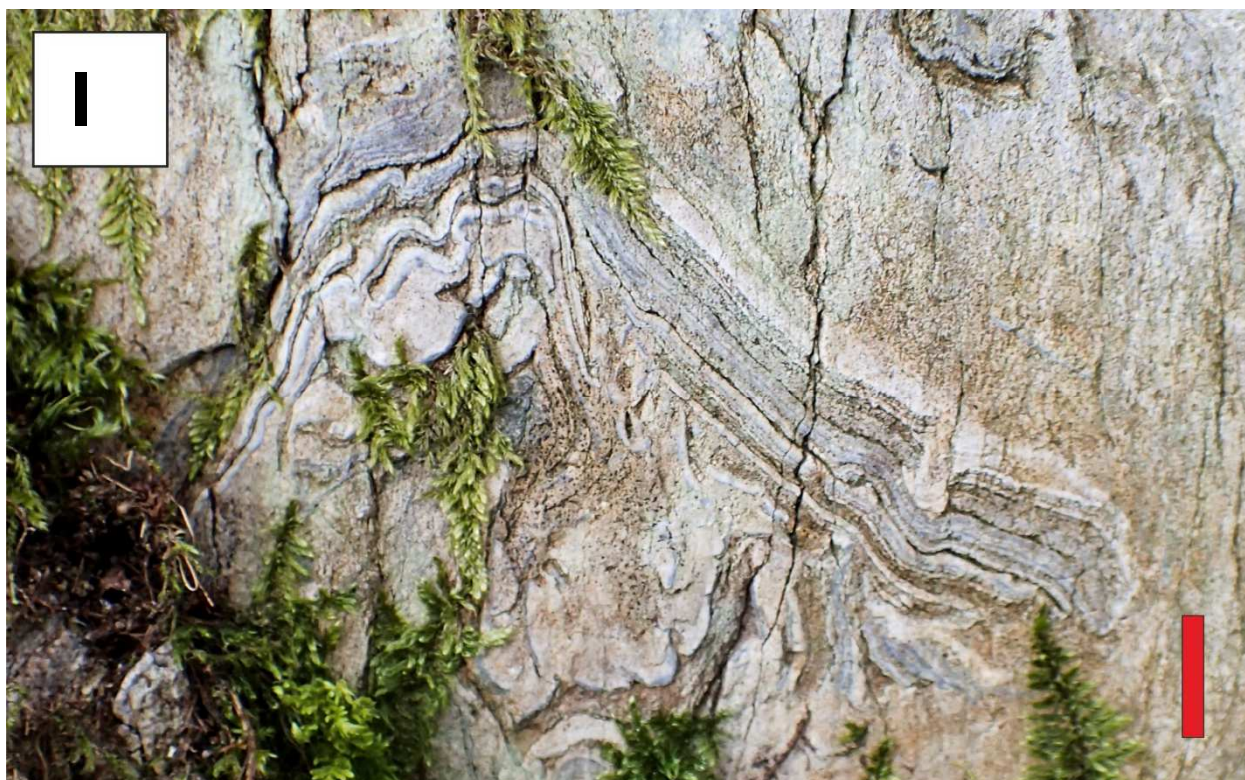
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Figure 3. Distribution and form of trackways. B) *Diplichnites* restricted to ripple crests on Surface B, sketch shows measured transect of surface topography and distribution of trackways

in pink; D) *Diplopodichnus* following microtopography of furrowed Surface D, with sketch as in Figure 3C; F) Evidence for probing behaviour at a curve in a *Diplichnites* trackway [Surface D]; G) Planview of a microfault scarp (top and bottom highlighted in blue) showing *Diplichnites* passing over scarp lip from left, and rejoining lower foot of scarp at a distance as tracemaker stepped downwards [Surface D]; H) Transition from *Diplichnites* to *Diplopodichnus* along same trackway [Surface D].