

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

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We thank Briggs et al. (2019) for their Comment on our recent paper (Shillito and Davies, 2019). Our work reported a number of arthropod trackways from the Ordovician Borrowdale Volcanic Group (BVG), demonstrated that the trace fossils were hosted within very fine dacitic tuffs, and, coupling this with trackway morphology, proposed that the tracemakers had been lethally stressed by the presence of volcanic ash.

Our paper emphasized that there is no positive evidence for a freshwater lacustrine depositional setting, as proposed by Johnson et al. (1994). This matters because Johnson et al.'s assertion that BVG traces "probably record some of the earliest freshwater arthropods" has commonly been taken to imply that the trackways are a global first. The traces are often cited as such in studies as divergent as the characterization of the tangible ichnological-stratigraphic record (Minter et al., 2016) and the interpretation of molecular clock models (Fernández et al., 2018). Their significance has persisted because all other known Cambrian–Ordovician non-marine trackways (e.g., MacNaughton et al., 2002) were demonstrably imparted within meters of the shoreline. While these reflect sporadic subaerial excursions by marine organisms, the BVG alone is posited as evidence of freshwater lake-dwelling arthropods.

Our paper shows that the only sedimentological evidence at the BVG locality is for subaqueous deposition and, potentially, emergent substrates: not freshwater lacustrine conditions. Briggs et al. contend that a lacustrine environment 'remains likely' because other parts of the 6-km-thick BVG appear to be non-marine in origin (but see the discussion in Shillito and Davies [2019]). They imply that the global singularity of a trace fossil-bearing Ordovician lacustrine succession is not suspect because (1) there is a rarity of non-marine strata of this age globally, and (2) subaerial arthropod trackways have a very low preservation potential. However, the abundance of Ordovician non-marine strata is irrelevant, because trace fossils are an intensive lithological property of this extensively incomplete rock record. In other words, even though diminished in volume, many non-marine strata of Cambrian–Silurian age have been preserved and studied in detail (e.g., Davies and Gibling, 2010). Amongst these, only the BVG is inferred to contain freshwater trace fossils, rendering it unusual. The preservation potential of surface trackways is higher than Briggs et al. imply, illustrated by the fact that subaerial arthropod trackways are known from every period of the post-Silurian rock record (Minter et al., 2016). Further, the existence of traces on eroded bounding surfaces in the BVG (e.g., flute marks; our figure DR6 in the GSA Data Repository) proves that they had a high preservational potential, even within an erosive setting. This is not unexpected because, contrary to traditional models (e.g., Seilacher, 2008), trackway preservation is probable under many spatially heterogeneous, but otherwise mundane, sedimentary conditions (Davies and Shillito, 2018).

Our work shows that the trace fossil-bearing strata are composed of dacitic tuff, formed by the redistribution of volcanic ash by aqueous sedimentary processes. Johnson et al. (1994) variably described the lithology as fine-grained (p. 397, 404), fine- to medium-grained (p. 397) and medium- to coarse-grained sandstone (p. 398, 399). Briggs et al. defend the description of the local lithology as volcanogenic sandstone, but only a negligible fraction of its largest grains even reach very-fine-grained sand caliber. The maximum size of isolated grains is 0.1 mm in diameter, but they are usually much smaller (our figure DR7). The diminutive grain size of the trackway-bearing tuffs is crucial to interpreting the trace fossils because such ash particles are able to pass through gaps in modern arthropod exoskeletons, interfering with articular, digestive, and breathing apparatus (Elizalde, 2014). The inimical nature of the sediment explains why arthropod trace fossils are exceedingly rare

from tuff horizons worldwide (to our knowledge, there is only one other Paleozoic instance: e.g., Morrissey and Braddy, [2004]), and partly justifies our interpretation of these traces as mortichnia.

There are plural explanations for the morphological differences between the ichnotaxa *Diplopodichnus* and *Diplichnites*, which can be made by the same individual trace-maker. Either the latter may be imparted after the substrate dried, and the former when it was moister, or it can be due to the trace-maker moving at a slow speed and amalgamating imprints to create *Diplopodichnus*. Briggs et al. favor the first explanation for the BVG trackways because individual imprints are hard to discern in the *Diplopodichnus* specimens, and *Diplichnites* overlies *Diplopodichnus* in the few instances where they cross. However, our newly discovered trackways show how individual trackways may alternate between the two ichnotaxa morphologies along their length on planar bedding surfaces (our figure. 3H). It is implausible that the moisture of the ash varied laterally, on a flat substrate, at the spatial scale of individual tracks. It is also implausible that the ash was drying out at a faster rate than it took an individual trackway to be imparted. In short, in the particular case of the BVG examples, only changes in trace-maker walking speed remain as a viable explanation when the full ichnological and sedimentological evidence is considered.

Johnson et al.'s (1994) realization that the BVG trackways may provide some of the earliest evidence of myriapods remains a significant ichnological contribution. However, their suggestion that they may be freshwater lacustrine traces has no robust supporting evidence.

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