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Evidence from trace fossils

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I wish to emphasize the importance of trace fossil evidence in studying the terrestrialization of invertebrates. Associations of trace fossils of arthropod origin are known from the late Silurian and Devonian non-marine sediments in the Welsh Borders, Scotland (Midland Valley and Orcadian basins), Norway (Ringerike and Hornelen basins), Spitzbergen, Appalachians of North America and Antarctica (Pollard *et al.* 1982, figure 15; Pollard & Walker 1984, figure 3). These ichnocoenoses occur in fluvial and lacustrine sequences and they confirm the diversity of fresh water arthropods, the existence of possible amphibious forms, eurypterids–scorpionids and probable myriapods, but are somewhat ambiguous about the nature of truly terrestrial trackway producers. Trace fossils are virtually unknown from Devonian aeolian sediments and the overall diversity of arthropod tracks in the playa environment is very much lower than that seen in comparable facies in the Rotliegend (Lower Permian) (Walter 1983) following the evolutionary radiation of terrestrial insects.

In our recent analysis of the trace fossils of the supposed ‘upland fauna’ (Smith 1909) of the Lower Old Red Sandstone of Dunure, Ayrshire, we adopted another approach to this problem by examining the intimate relationships between arthropod trackways and inorganic sedimentary structures preserved on bedding planes (table 1). The results suggest that the

TABLE 1. BEDDING PLANE ASSOCIATION OF TRACE FOSSILS AND SEDIMENTARY STRUCTURES FROM LOWER OLD RED SANDSTONE OF DUNURE, Ayrshire, AND THEIR INTERPRETATION

(Adapted from Pollard & Walker 1984.)

trace fossils Ichnogenus or spp.	number of specimens	sedimentary structures		foam marks†	environment or activity	possible producer
		unrippled surface	rippled surface			
<i>Siskemia elegans</i>	(66)	44 %	56 %	32 %	subaqueous walking	crustacean?
<i>S. bipedculus</i>	(16)	56 %	44 %	18 %	subaqueous walking	crustacean?
<i>S. lata-via</i>	(3)	67 %	33 %	—	subaqueous walking	crustacean?
<i>Stiallia</i>	(45)	62 %	38 %	15 %	subaqueous swimming	crustacean?
cf. <i>Merostomichnites</i>	(7)	—	100 %	—	subaqueous walking	crustacean?
<i>Isopodichmus</i>	(10)	90 %	10 %	—	subaqueous resting-furrowing	branchiopod crustacean?
<i>Stiaria</i>	(41)	80 %	20 %	2 %	pre/post emergent walking	eurypterid- scorpionid?
<i>Danstaria</i>	(10)	100 %	—	—	? walking	myriapod?
<i>Keircalia</i>	(3)	100 %	—	—	? walking	myriapod?
<i>Mermia</i>	(20)	45 %	55 %	35 %	post-emergent crawling	small arthropod
‘ <i>Scolicia</i> ’	(10)	60 %	40 %	20 %	pre/post-emergent crawling	worm or arthropod?

† May occur on either a rippled or unrippled surface.

majority of tracks were produced underwater, some showing behavioural modification related to ripple topography, others being made on the strand-line, both predating and postdating foam marks that record emergence of sediment surface. Unfortunately the evidence about the degree of subaerial activity of possible chelicerates or myriapods, which may have been undergoing terrestrialization at this time, is somewhat inconclusive. Overall the environment here appears to have been lacustrine rather than terrestrial. No trackway in the ichnofauna can be assigned with certainty to the millepede body fossil also known from this locality (Almond, this symposium).

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