

# Arthropod trackways from the Early Devonian of South Wales: a functional analysis of producers and their behaviour

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**Abstract** – Abundant arthropod trackways, assigned to *Diplichnites gouldi*, are described from the Lower Old Red Sandstone (Early Devonian; Lochkovian) of Pant-y-Maes quarry, Brecon Beacons, South Wales. The trackways are preserved on bedding planes of finely laminated planar and rippled siltstones. The sedimentology of the succession indicates that these units represent bar top and marginal deposits in a braided fluvial setting. Two trackway types are recognized (Type A and B); comparisons with contemporaneous myriapodous producers favour kampecarid and earthropleurid myriapods, respectively. Functional analysis of the trackways indicates that the producers were not using the most efficient, stable, walking techniques, but instead utilized in-phase 'swimming stroke'-like gaits. Together with their occurrence on rippled surfaces, and lateral displacement of some trackways (attributed to currents), this indicates that they were produced sub-aqueously.

Keywords: trace fossils, Arthropoda, Devonian, biomechanics, fluvial, Wales.

## 1. Introduction

Our understanding of the stages involved in the colonization of land by arthropods has been improved by the study of Palaeozoic trace fossils; these allow us to analyse the diversity and palaeoenvironmental distribution of early terrestrial arthropods (Pollard, 1985). Through an understanding of how these traces formed, they can even reveal information on the behaviour, biomechanical limitations, and life habits of particular producers.

Myriapod-produced trackways have a wide temporal and spatial distribution. Some of the earliest fully terrestrial trackways and trails, from the Middle Ordovician of Cumbria, England, were produced by myriapodous arthropods (Johnson *et al.* 1994). Sub-aerial *Diplichnites* trackways were reported from the late Silurian of Newfoundland (Wright *et al.* 1995). Diverse freshwater trackway-dominated ichnofaunas (including *Diplichnites*) were described from the ?late Silurian (or earlier: Iasky *et al.* 1998) of Western Australia (Trewin & McNamara, 1995), and similar Early Devonian terrestrial ichnofaunas (including *Diplichnites*) are also known from Antarctica (Gevers *et al.* 1971; Bradshaw, 1981) and northern India (Draganits, Grasemann & Braddy, 1998; Draganits, Braddy & Briggs, 2001), indicating a recurrent terrestrial ichnofauna on the margins of Gondwana (Draganits, Braddy & Briggs, 2001). Diverse ichnofaunas (including myriapod-produced trackways) have also been described from the Early Devonian of the

Midland Valley of Scotland (Smith, 1909; Walker, 1985; Trewin & Davidson, 1996) and the Orcadian Basin (Trewin & Kneller, 1987, p. 119). In the Carboniferous, some *Diplichnites* are extremely large and record the activities of the giant arthropleurids (e.g. from the Namurian of Arran: Briggs, Rolfe & Brannan, 1979; Westphalian of Canada: Briggs, Plint & Pickerill, 1984; and Viséan of Fife: Pearson, 1992).

Here, we report on a new arthropod ichnofauna from the Early Devonian of the Welsh basin, and investigate the probable producers and their behaviour by way of comparisons with contemporaneous arthropods and a functional analysis of the trackways. Similar paired sinuous trackways were reported from the Lower Old Red Sandstone of Krokws quarry, on the outskirts of Brecon, and attributed to a scorpion or scorpion-like arthropod (Bassett & Owens, 1974, p. 13). However, series of at least seven tracks are apparent in places, and the trackways are very similar to the myriapod-produced *Diplichnites* (Type A) described here. Similar trackways also occur in the Early Devonian Rat Island Mudstone (Freshwater West Formation) of Pembrokeshire (B. P. J. Williams, pers. comm.). Thus, it appears that myriapodous arthropod trackways are far more widespread in the Devonian of the Welsh basin than has previously been reported.

## 2. The occurrence of the trace fossils

### 2.a. Locality

The Pant-y-Maes quarry, a 275 m long east-facing exposure, is situated 3 km south of Sennybridge, in

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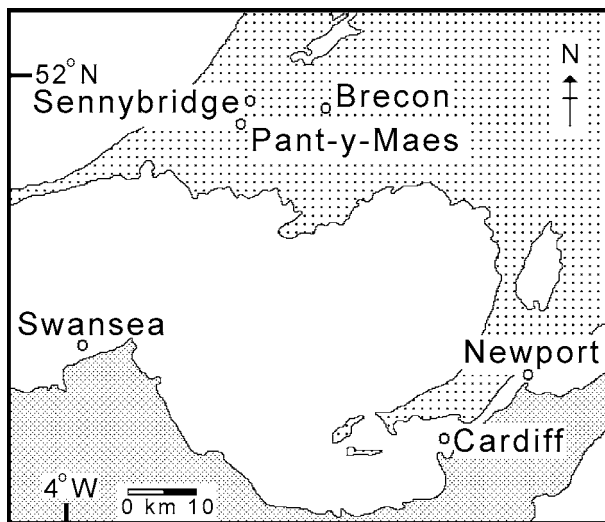


Figure 1. Location of Pant-y-Maes quarry in South Wales (SN 913 264), showing outcrop area of Old Red Sandstone (stippled).

Powys, South Wales (SN 913 264) (Fig. 1). Around 25 m of vertical exposure is present in the quarry, although scree covers much of the lower units. The trace fossils described here occur within a 5 m long, 3 m high, west-facing exposure of siltstones, which surrounds a pool in the centre of the quarry.

### 2.b. Stratigraphy, sedimentology and palaeoenvironmental setting

The strata were assigned to the Upper Red Marl Group of the Lower Old Red Sandstone on the basis of evidence from miospores and palynomorphs (A. Hassan, unpub. Ph.D. thesis, Univ. London, 1982). The Red Marl Group is placed within the Dittonian chronostratigraphic stage of South Wales and the Welsh Borders (House *et al.* 1977). The local stage names persist in this region because of a lack of biostratigraphically informative fossils that would enable use of the internationally defined system. However, the occurrence of *Parka decipiens* (Hemsley, 1990) at the locality allows a tentative link to the Lochkovian stage.

Two main sedimentary facies are present in the quarry (Fig. 2a): a lower unit about 15 m thick that is comprised of interbedded intraformational conglomerates, grey/green micaceous sandstones and grey siltstones (Sandstone Facies Association of Owen & Hawley, 2000); and an erosively-based upper red mudstone unit about 10 m thick (Mudstone Facies Association of Owen & Hawley, 2000). The sandstones and intraformational conglomerates in the Sandstone Facies Association form interlocking sequences with major bounding surfaces. Many of the contacts are erosional and define stacked channel sequences. It is suggested that these sand bodies represent sand or sand and gravel bars and sand sheets within a sand-bed braided stream

system (Owen & Hawley, 2000), since Allen (1983) interpreted a similar sequence of sandstone bodies and intraformational conglomerates from the Brownstones (Pragian–Emsian, Early Devonian) of the Welsh Borders, as representing this type of depositional setting.

The change to red beds at the top of the sequence marks a change in depositional environment. The Mudstone Facies Association comprises tabular-bedded, bioturbated red siltstones and fine sandstones. The siltstones contain horizons rich in pedogenic calcrete nodules, weakly defined pseudoanticlinal structures and desiccation cracks. This facies association represents overbank floodplain deposits probably associated with a meandering fluvial system (Owen & Hawley, 2000).

The exposure containing the majority of the arthropod trackways described here consists of planar-laminated and ripple-laminated micaceous fine sandstones and siltstones (Fig. 2b), which correspond approximately to section D in the main quarry face (Fig. 2a). These overlie a cross-bedded coarse sandstone channel unit that wedges out laterally. Beneath this is a massive sandstone at least 1 m thick, containing occasional rip-up mudstone clasts (Fig. 2b). The beds bearing most of the trackways are only 50 cm thick and are overlain by further cross-bedded medium- to coarse-grained channel sandstones. These occasionally show trackways on bed tops and on cross-laminated channel margin sediments (Fig. 2b). Rare trackways have been reported from higher in the exposed sequence in thin, weakly cross-laminated micaceous siltstones within the uppermost Mudstone Facies (Owen & Hawley, 2000; Fig. 2a, Section A). No infaunal traces were recorded in any part of the lower sandstone units, though vertical burrows (*Skolithos*-type) are reported from some horizons in the red beds (Owen & Hawley, 2000).

The trackways were found in the laminated fine sands and siltstones at the tops of fining-upwards sequences. These are made up of intraformational conglomerates and sandstones that exhibit compound cross-bedding and planar laminations. These sandstone units are superseded in places by inclined heterolithic beds of alternating sandstone and grey siltstone (Fig. 2a), which could be accretionary deposits on channel-margin benches (Gibling, Nanson & Maroulis, 1998; Marriott, Wright & Williams, 2003), and in other areas by fine sandstones and siltstones in straightforward fining-upwards units which probably represent mid-channel bars in a low-sinuosity braided system.

The discharge regimes would appear to have been highly variable with periods of high, possibly flood, flow resulting in ripping-up and incorporation of mud and pedogenic calcrete clasts from adjacent floodplain regions. There is also evidence of upper flow regime fluvial hummocky cross-stratification in some of the

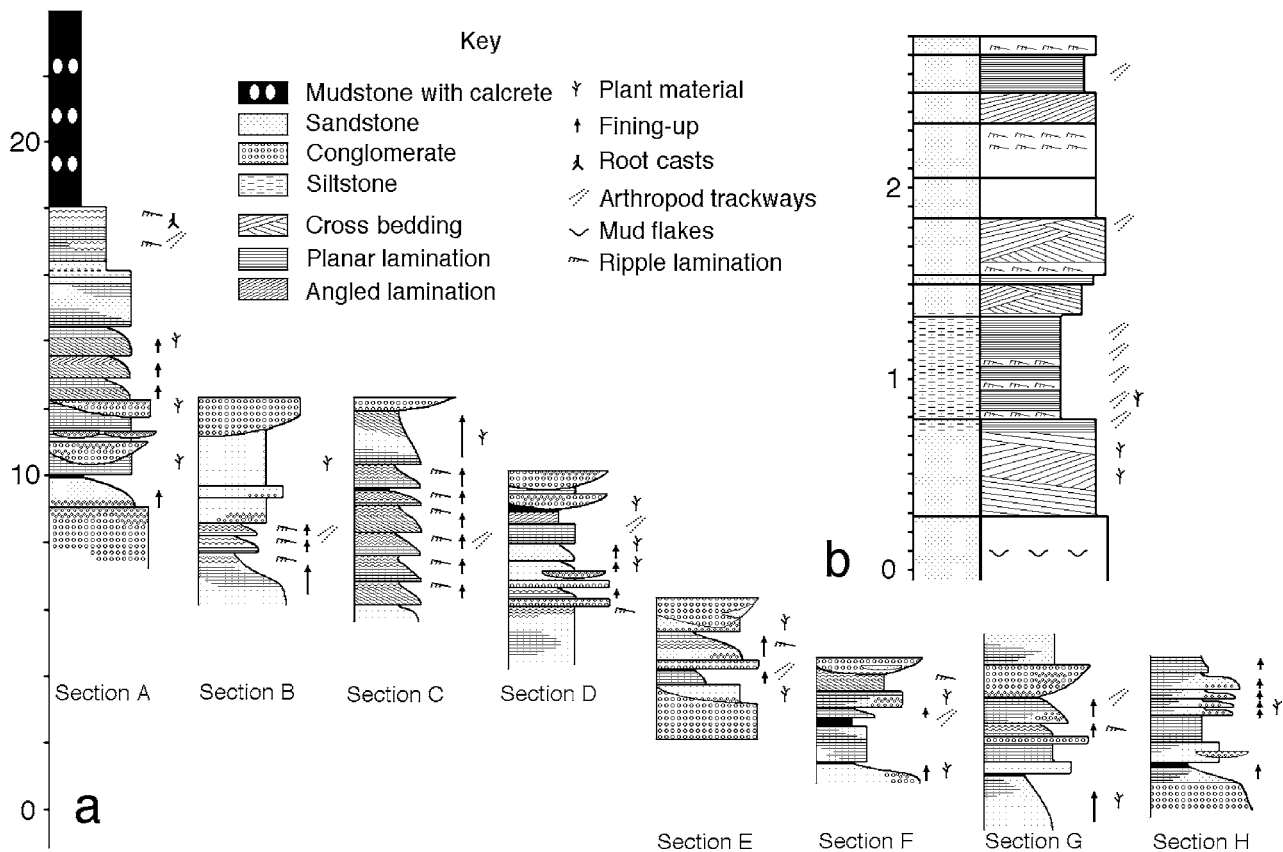


Figure 2. Sedimentary logs of the Pant-y-Maes succession. (a) Eight vertical transects (Section A furthest south, Section H furthest north) of the main (east-facing) quarry exposure. (b) Detailed sedimentary log of small (west-facing) exposure in the centre of the quarry, from which most of the material, described herein, was collected. Scale in metres.

sandstones. Waning flow and shallowing resulted in the fining-upwards grading, and possible exposure of bar tops and channel margins for short periods. Exposure was not persistent as there is no evidence of desiccation or pedogenesis in the Sandstone Facies at the quarry, although the incorporation of reworked calcrete clasts in the channel lags indicates that pedogenic processes were operating elsewhere in the system.

### 3. Palaeontology

The ichnological data described here are based on material collected from Pant-y-Maes quarry by R. M. Owens, D. Edwards, A. J. Boucot and L. Voronova in 1985, SBM in 1989, and AS and SJB in 2000.

The morphology of well-preserved trackways was recorded by tracing them onto acetate sheets, before morphological measurements were taken, following Trewin (1994). The orientation (direction of converging series) of trackways collected in the field was measured (where possible) to determine their relationship to the sedimentary fabric. A fine scale sedimentary log of the trackway-bearing horizon (Fig. 2b) was produced to determine the distribution of trackway layers.

#### 3.a. Systematics

Two trackway morphologies, both assignable to *Diplichnites gouldi*, are recognized: Type A (external width 10 to 28 mm, with up to nine variably shaped tracks per series), and Type B (external width 38 to 102 mm, with 16 to 20 spindle-shaped tracks per series (frequently overprinted)). This distinction is reflected in a histogram of the external widths (Fig. 3a), showing a bimodal distribution, and a bivariate plot of external width against the number of tracks per series (Fig. 3b).

Ichnogenus *Diplichnites* Dawson, 1873 (emend. Briggs, Rolfe & Brannan, 1979); Ichnospecies *Diplichnites gouldi* Gevers (in Gevers *et al.*), 1971

For full synonymy see Trewin & McNamara (1995) and Buatois *et al.* (1998).

1990. *Diplichnites* isp. C, Fillion & Pickerill, p. 97, pl. 7, fig. 4.

1995. *Diplichnites gouldi* Form A, Trewin & McNamara, p. 194, figs 18a, b, 19a.

1995. *Diplichnites*, Wright *et al.*, p. 307, figs 5, 6, 8.

1998. *Diplichnites gouldi*, Buatois *et al.*, figs 3A, B, D, 4A, 5A, B.

*Material.* National Museum of Wales, Cardiff (NMW): repository numbers 86.10G.1a, b; 2a, b; 3; 4a, b; 5a, b;

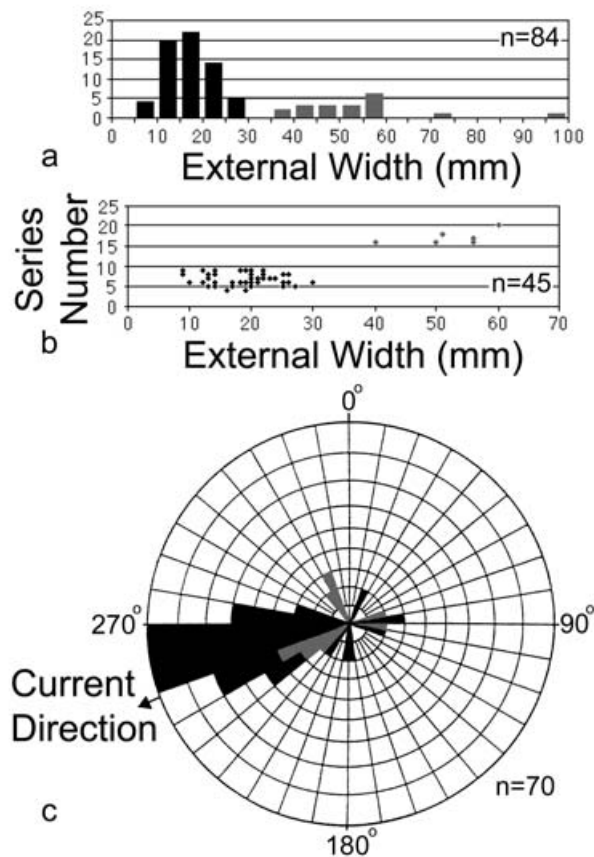


Figure 3. (a) Histogram of the external width of *Diplichnites gouldi* trackways showing bimodal distribution (Black, Type 1; Grey, Type 2). (b) Bivariate plot (number of tracks per series vs external width) of *D. gouldi* Type 1 (Black) and Type 2 (Grey). (c) Rose diagram of trackway orientations of *D. gouldi* Type 1 (Black) and Type 2 (Grey), showing sub-parallel alignment with the current direction.

7; 9. 89.31G.10a, b; 11a, b. 2002.45G (separate slabs, trackways occur on top and base of slabs). Individual trackways are denoted by lower Roman numerals following the slab number, as several may occur on the same slab. Type A is represented by 42 trackways, and Type B by 9 trackways, in the earlier deposited material (NMW 86.10G and 89.31G). Additional data derived from material (NMW 2002.45.G) collected by AS and SJB in 2000: 52 of Type A, and 10 of Type B.

**Horizon.** Lower Old Red Sandstone (upper Red Marl Group), Dittonian stage, Lochkovian (upper Gedinian).

**Description.** Trackways follow a straight to gently curved course, and consist of two, roughly parallel rows of overlapping straight to slightly curved series, showing no internal or external markings (Fig. 4). *D. gouldi* Type A is made up of series of six to nine evenly spaced tracks, arranged opposite, either parallel, or oblique (up to 60°) to the mid-line on one (that is, asymmetric) or both sides; series overlap each other by 20 to 40% (Figs 4, 5a–d). The shape of the tracks varies: punc-

tate, elongate, spindle-shaped or tapered (either internally and externally). External width varies from 10 to 28 mm.

*D. gouldi* Type B consists of series of 16 to 20 evenly-spaced tracks, arranged at a low angle to the mid-line, which may overlap each other by 40 to 60% (Figs 4, 5e). The tracks are elongate, crescentic or tapering, generally perpendicular to, and deepening away from, the mid-line. Tracks tend to be larger in the central portion of the series and consistently show a small back-push mound. Tracks may overprint, due to near-parallel series orientation, masking the true series number in places. In gently curved trackways (or on sloping surfaces) the tracks tend to spread out and the series number becomes apparent. External width varies from 38 to 102 mm. In some smaller preservational variants these trackways become more trail-like (cf. *Diplopodichnus*, Johnson *et al.* 1994).

**Remarks.** The classification of *Diplichnites*-like trackways has a long and complex history. *Diplichnites aenigma* was originally described by Dawson (1873), but the type material was subsequently lost and the original illustrations are insufficient to identify the features clearly (Briggs, Rolfe & Brannan, 1979; Briggs, Plint, & Pickerill, 1984). Numerous ichnotaxa have been attributed to myriapods (Briggs, Rolfe & Brannan, 1979) or are similar in their overall morphology to *Diplichnites* (Buatois *et al.* 1998; Keighley & Pickerill, 1998). Many of these have been reassigned, or synonymized with other ichnogenera. The issue is further complicated by the ‘provisional’ use by Seilacher (1955) of *Diplichnites* to denote straight trilobite trails (Briggs, Rolfe & Brannan, 1979; Briggs, Plint, & Pickerill, 1984).

The ichnogenus *Arthropodichnus* was erected by Gevers *et al.* (1971) to include *A. darwinum*, *A. gouldi* and *A. antarcticum*. *Arthropodichnus* was renamed to *Beaconichnus* (Gevers, 1973) due to prior use, and a further ichnospecies (*B. giganteum*) added. However, these ichnospecies are too disparate and their producer-defined status is not a valid ichnotaxobase; *Beaconichnus* was considered ‘best disregarded’ by Buatois *et al.* (1998). Buatois *et al.* (1998) synonymized *B. darwinum* with *Diplopodichnus biformis* Brady, 1947 (emended to include grooves containing track series) and Braddy & Milner (1998) referred *B. antarcticum* to *Palmichnium* Richter, 1954. Bradshaw (1981) identified *B. giganteum* as the junior synonym of *B. gouldi* having found an ‘almost complete gradation in [external] width between 10 and 200 mm’, contrasting with the limited size range identified by Gevers *et al.* (1971). Absolute trackway width is not a valid ichnotaxobase. Bradshaw (1981) further synonymized these ichnospecies within *Diplichnites* based on similarity with *D. cuithensis* Briggs, Rolfe & Brannan, 1979, distinguishing the two forms on the basis that *D. gouldi*





Figure 4. *Diplichnites gouldi* Types A (three examples) and B (one example), from Pant-y-Maes quarry, South Wales (SN 913 264). NMW 86.10G.1.i–iv (left to right along the bottom margin).  $\times 0.84$ .

has ‘fewer [tracks per series] than *D. cuithensis* and each [track] lacks the slight transverse element of the Scottish form’. Bradshaw considered that ‘fresh’ (that is, undeformed by currents) specimens of *D. gouldi* resembled *Duovestigia scala* Butts, 1891 (= *Diplichnites*, Briggs, Rolfe & Brannan, 1979). Some forms of *D. gouldi*, reported by Bradshaw (1981) as 40–90 mm in external width (larger than the original ‘*B. gouldi*’ size range of Gevers *et al.* 1971), display a medial ‘tail’ impression as in *Protichnites sensu lato* of Seilacher (1955). These trackways were probably produced by a euthycarcinoid-like arthropod (see Section 4.a).

Trewin & McNamara (1995) divided *D. gouldi* from the Tumblagooda ichnofauna into three ‘broad-end-member types’, Forms A, B and C, but stressed these were not separate ichnospecies, rather part of a continuum. *D. gouldi* Form A (10–40 mm wide, with series of 5 tracks) compares with our Type A, herein, although it has fewer tracks. *D. gouldi* Forms B (50–200 mm wide, with series of 10–11 tracks) and C (200–300 mm wide, with series of 16 tracks), however, are somewhat larger with less tracks than our Type B, herein, but overall are broadly comparable. Trewin & McNamara also recognized a gradation between their *D. gouldi* Form A and *Diplopodichnus bififormis*, which consists of a trail

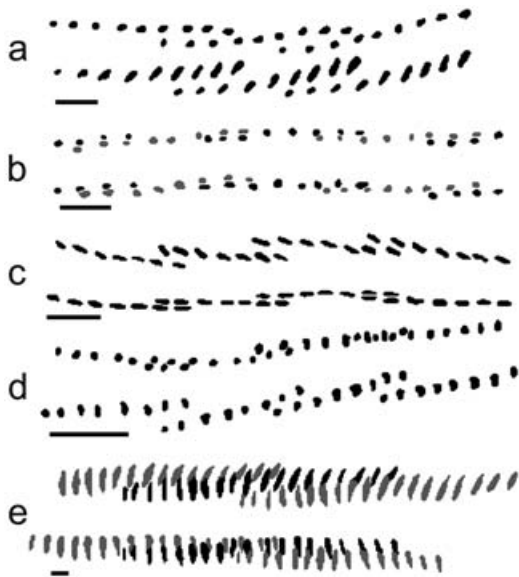


Figure 5. Generalized trackway forms of *Diplichnites gouldi* Type A (a–d) and Type B (e), from Pant-y-Maes quarry. (a) NMW 86.10G.1a.iii; (b) NMW 86.10G.9; (c) NMW 86.10G.3.i; (d) NMW 86.10G.1a.ii; (e) NMW 86.10G.3.ii. Scale bar = 1 cm.

composed of two parallel grooves, the result of the producer walking over wet sand. Buatois *et al.* (1998) referred *D. gouldi* Form A *sensu* Trewin & McNamara (1995) to *Umfolozia* Savage, 1971, based on the presence of series of five tracks in both. However, no internal sinuous row of imprints, as described by Savage (1971), is present in *D. gouldi* Form A, and it is here retained in *D. gouldi*.

The ichnotaxonomy of *Diplichnites* has been emended by Briggs, Rolfe & Brannan (1979), Briggs, Plint & Pickerill (1984), Fillion & Pickerill (1990) and Keighley & Pickerill (1998), so far without consensus. Keighley & Pickerill (1998, p. 90) noted that ‘at least four ichnospecies of *Diplichnites* have been named, with several other ichnospecies having ... been transferred to this ichnogenus, for example: *D. aenigma* Dawson, *D. incertipes* (Matthew), *D. minor* (Matthew), *D. triassicus* (Linck), *D. gouldi* (Gevers *et al.*), *D. govenderi* Savage, *D. cuithensis* Briggs, Rolfe & Brannan, and *D. binatus* Webby’. *D. minimus* Walter & Gaitzsch, 1988 may be added to this list. Pending an ichnotaxonomic review of *Diplichnites* and related ichnotaxa, we assign this Welsh material to two different ‘types’ of *D. gouldi*, similar to Trewin & McNamara’s (1995) use of ‘forms’ to denote their Tumbagoooda material.

**Interpretation and discussion.** The variation in trackway morphology (external width, series number, series length and angle, and track morphology) is considered insufficient to assign the two types to separate ichnospecies. The two types (A and B) are themselves morphologically discrete, although slight variation within one trackway may occur; this is attributed

to undertrack preservation, sediment consistency, and rheotaxis. The variation between the two types is attributed to producer morphology (see Section 4.a).

The trackways frequently cross each other, but there is no evidence of interactions between the arthropods (e.g. one changing direction to avoid another). Neither type of *D. gouldi* consistently overprints the other, indicating that both were produced contemporaneously. A single specimen of *D. gouldi* Type A stops abruptly, suggesting that the arthropod was lifted off the substrate by the current and carried away; the series in this trackway, up to that point, converge in the direction of travel. This termination is not the result of undertracking as a significant depth of tracks is present initially. Likewise, no scouring structures are evident, indicating that the trackway was not eroded by a current.

The trackways were produced on flat-laminated or long-wavelength rippled surfaces, indicating a low-velocity current, and occasionally on surfaces sloping at up to 15°. The orientation of the trackways (measured as the direction of ‘V’ing) shows a clear sub-parallel alignment with the current direction, determined by ripple crest orientation and ripple laminations (Fig. 3c).

The effects of current action (e.g. lateral shifts) can often be useful in determining the number of tracks per series (Trewin & McNamara, 1995). Currents generally produce asymmetry; *D. gouldi* Type A is more influenced by currents than the larger Type B trackways, indicating that smaller arthropods were more affected by the currents (Fig. 5).

The sediment mounds associated with each track were probably produced by the leg pushing the sediment backwards, although Hanken & Størmer (1975) and Wright *et al.* (1995) suggested that thrusting of legs into sediment, or dragging on withdrawal, may generate mounds in front of a track.

The presence of these trackways on rippled surfaces, generally parallel to the palaeocurrent (Fig. 3c), supports a subaqueous production of these trackways. This is further evidenced by the terminated Type A trackway (see above), the effects of current on the arthropods, and the in-phase walking technique (that is, swimming stroke-like) of the producers (see Section 4.b). Although it is possible that some of the trackways were produced under emergent conditions, on the damp rippled margins of the river channel, their opposite symmetry (that is, an in-phase walking technique) implies that the producers were not well-adapted for terrestrial locomotion.

#### 4. Analysis of trackways (producers and biomechanics)

Manton’s (1954, 1977) studies of arthropod locomotion have been applied to functional analyses of extinct myriapodous arthropods (Briggs, Rolfe & Brannan, 1979; Briggs, Plint & Pickerill, 1984; Wright *et al.* 1995; A. Smith, unpub. M.Sc. thesis, Univ.



Bristol, 2000), eurypterids (Selden, 1981; S. J. Braddy, unpub. Ph.D thesis, Univ. Manchester, 1996, including computer modelling; Braddy & Almond, 1999), and Burgess Shale arthropods (A. Lane, unpub. M.Sc. thesis, Univ. Bristol, 1999). Here we apply similar methods to the myriapodous arthropod producers of the Pant-y-Maes trackways.

#### 4.a. Producers

The trackways described here are compared with the morphology of four contemporaneous myriapodous arthropods, selected to represent the range of morphologies present in the Early Devonian: *Eoarthropleura*, *Kampecaris*, *Kalbarria* (a euthycarcinoid), and a scutigermorph centipede.

*Eoarthropleura* is known from the Early Devonian of Alken-an-der-Mosel, Germany (Størmer, 1976), and South Mountain, USA, and the late Silurian of the Welsh borders (Shear & Selden, 1995). *Eoarthropleura* is distinguished from *Arthropleura* by its smaller size, tergite ornamentation and morphology of the ventral B and K plates associated with each appendage (Størmer, 1976). Shear & Selden (1995) interpreted *Eoarthropleura* as diplopodous based on its similarity with *Arthropleura*. Wright *et al.* (1995) retained Størmer's original body plan but added four segments to account for trackways from the late Silurian of Newfoundland. Briggs & Almond (1994) suggested that the most posterior appendages would have been ineffective in walking. According to Størmer's (1976) reconstruction, and allowing for diplopody, *Eoarthropleura* had 26 appendage pairs.

*Kampecaris*, known only from the late Silurian to Early Devonian of the Welsh borders and Midland Valley of Scotland, was reconstructed by Shear (1997, based on A. Almond, unpub. Ph.D thesis, Univ. Cambridge, 1986) as diplopodous. As the appendages of this form are scarce, a complete kampecarid found by A.S. from Carmyllie Quarry, Angus, Scotland (Department of Geology and Petroleum Geology, Aberdeen University: AUGD12249a, b (part and counterpart)), was used to determine the appendage and body morphology, taking into consideration the fact that this specimen has one diplotergite fewer than usual, suggesting that it is an instar (that is, only 13 appendage pairs).

*Kalbarria*, from the ?late Silurian Tumblagooda Sandstone of Western Australia (McNamara & Trewin, 1993), is the earliest known euthycarcinoid. This form is interpreted as having 11 appendage pairs (based on tagmosis pattern), although unlike the myriapods, the euthycarcinoids possessed a postabdomen and tail spine that could produce a medial impression.

Scutigermorph centipede legs were reported from the Silurian of the Welsh borders and the Early Devonian of Rhynie, Scotland, and Gilboa, USA (Shear, Jeram & Selden, 1998), although complete body fos-

sils of this age have not been identified. The pattern of their leg construction is reportedly conserved over their 415 million year history (Shear, Jeram & Selden, 1998), so the body plan of the modern form *Scutigera* (from Manton, 1977, fig. 5.2) was used for comparison (that is, 14 appendage pairs).

Based on comparisons between the Pant-y-Maes trackways and these four potential producers, *D. gouldi* Type A was most likely produced by kampecarid myriapods, given that the trackways are of appropriate size, and have series of six to nine tracks, although this requires that some of the kampecarids' appendage imprints were lost due to undertracking. A euthycarcinoid producer cannot be ruled out, however, although there is no evidence of a medial impression in any of the Pant-y-Maes material. We note, however, that some similar trackways from the undescribed ichnofauna at Manorbier, Pembrokeshire, are associated with a tail trace (B. P. J. Williams, pers. comm.).

The trackway size and number of tracks per series in *D. gouldi* Type B discount the smaller arthropods. *Eoarthropleura* is considered the probable producer of these trackways. The 20 tracks per series found in the largest trackways from Pant-y-Maes would therefore correspond to ten diplopodous segments in the main trunk, excluding the posterior and anterior appendage pairs.

#### 4.b. Walking techniques

The determination of the gait ratio used by fossil arthropods from fossil trackway data is reliant on identifying an accurate backstroke distance in the presumed producer, and determining the stride, as recorded in the trackway (Braddy, 2001, p. 390). In addition, a number of practical considerations may be used to constrain the opposite and successive phase differences of the producer.

First, the feasible phase differences are reduced as the gait increases, according to stability constraints. Therefore, in lower-gear gaits stability is not the main control on locomotion as a large range of phase differences are feasible. As the gait becomes higher-gear, stability becomes increasingly important in determining optimal gaits. In-phase gaits are less stable than out-of-phase gaits; an opposite phase difference of 0.5 (leg pairs half a step cycle out of phase) is most advantageous in terms of stability.

Second, a low variation in the number of propulsive legs is advantageous as constant thrust is provided for the body; at low-gear gaits this is less important, but at higher-gear gaits fewer legs are in contact with the ground, and the importance of having a constant number of propulsive legs is increased. Long metachronal waves tend to produce low variations in the number of propulsive legs, whereas short waves induce more variation. Assuming a constant gait ratio, the length of the metachronal wave and its apparent direction of

movement are dependent on the successive phase difference (suc.); the number of legs in a wave equals  $1/\text{suc.}$  (if suc. is less than 0.5, waves appear to travel forward), or  $1/(1-\text{suc.})$  (if suc. is greater than 0.5, waves appear to travel backward). Thus, particularly high or low successive phase differences produce long metachronal waves. During walking it is advantageous for an arthropod to space its legs evenly to provide even support for the body; equal spacing occurs when the successive phase difference equals  $1/\text{the number of legs}$  in the metachronal wave (e.g. an arthropod with five limbs in a metachronal wave has a phase difference of 0.2).

Third, the range of gaits is limited by the ability of a leg to complete a step cycle in spatial relation to other legs. Legs of similar structure cannot cross each other, particularly in the propulsive phase. Some crossing is possible on the recovery phase of the step cycle (whilst the leg is not in contact with the substrate) as the leg can be contorted to avoid interference. At higher-gear gaits there is less constraint on leg crossing as each leg spends less time in contact with the substrate.

Therefore, in lower-gear gaits the variation in the number of propulsive legs and the effects of leg crossing are the most important parameters controlling optimal walking. In higher-gear gaits stability becomes increasingly important in determining optimal gaits. The most advantageous walking technique tends to 'drift' towards lower successive phase difference values as the gait becomes higher-gear, and generally follows the pattern 'optimal successive phase difference equals  $r/10$ ' (Braddy, 2001), that is, an increase in gait is balanced by a corresponding (one-tenth) decrease in the successive phase difference.

According to these considerations, the four *D. gouldi* Type A trackways illustrated in Figure 5, representative of the overall behavioural variability, were produced by a kampecarid myriapod (Fig. 6) using the following gait parameters: NMW 86.10G.1a.iii (Fig. 5a), Gait 8 : 2, Opp. 0, Suc. 0.2; NMW 86.10G.9 (Fig. 5b), Gait 6.9 : 3.1, Opp. 0, Suc. 0.31; NMW 86.10G.3.i (Fig. 5c) and 86.10G.1a.ii (Fig. 5d), Gait 7.8 : 2.2, Opp. 0, Suc. 0.22. All trackways have an opposite phase difference of zero, indicating in-phase movement of op-

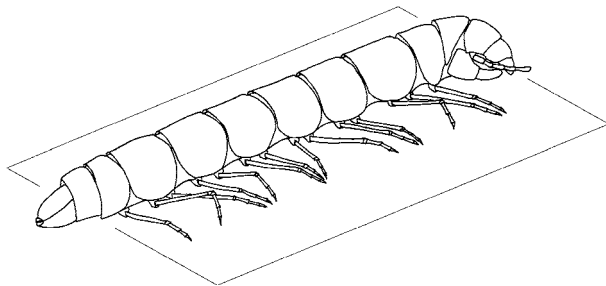


Figure 6. Suggested producer of the *D. gouldi* Type A trackways, a kampecarid myriapod, reconstructed here using a gait of 6.9 : 3.1, Opp. N/A, Suc. 0.3.

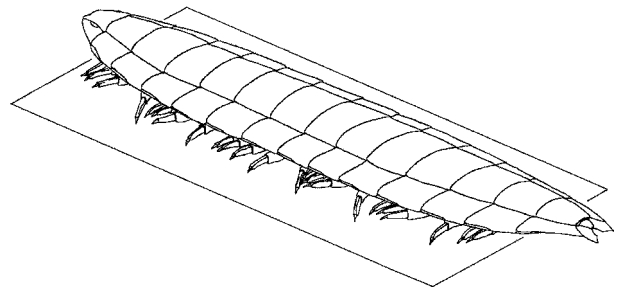


Figure 7. Suggested producer of the *D. gouldi* Type B trackways, an eoarthropleurid myriapod, reconstructed here using a gait of 7.7 : 2.3, Opp. N/A, Suc. 0.23.

posing limbs (see below). NMW 86.10G.9 is straight, with a lower gait ratio than the others (produced under 'normal' conditions); current probably affected the other trackways more, causing them to become skewed, influencing the gait pattern used.

The gait pattern of *Eoarthropleura*, based on the trackway NMW 86.10G.3.ii (Fig. 5e) was Gait 7.7 : 2.3, Opp. 0, Suc. 0.23 (Fig. 7). Six legs were almost constantly propulsive. Diplopods tend to vary the length of the step cycle to increase speed, rather than change the gait pattern (Manton, 1977). Trackways attributed to *Eoarthropleura* from the late Silurian of Newfoundland (Wright *et al.* 1995) also show a gait ratio of 7.7 : 2.3. The similarity of these Silurian trackways to those described here suggests that *Eoarthropleura* typically used a high-gear gait of 7.7 : 2.3; this gait enabled three or more legs on each side to support the body at all times.

None of these myriapods was using the most suitable gait pattern for terrestrial locomotion (that is, out-of-phase gaits). They were using a swimming-stroke, as indicated by the opposite phase difference; the functional requirements of in-phase appendage movements (to reduce yawing) was evidently more important than stability, as expected if they were walking underwater. This functional evidence correlates with the sedimentological and orientation evidence (see Section 3.a) for subaqueous production of these trackways.

## 5. Conclusion

The use of trace fossils as proxies for the presence of animals allows palaeoecological data to be gathered in the absence of body fossils. Understanding the typical trackways produced by arthropods can help our understanding of faunas that occupied Palaeozoic terrestrial settings. The abundant but low diversity ichnofauna (dominated by two types of *Diplichnites gouldi* trackways, distinguished on series number and external width) described from this Early Devonian fluvial sequence, at Pant-y-Maes quarry, south Wales, adds to these data, and indicates the presence of eoarthropleurids and kampecarids in south Wales during the Early Devonian.



Functional analysis of Early Devonian myriapodous arthropods enables the trackway producers and their behaviour to be constrained. Not all stable gaits are optimal due to the constraints of minimizing variation in the number of propulsive legs and leg crossing; the best constrained gait patterns occur where successive phase difference equals  $\pi/10$ . The opposite symmetry of these fossil trackways shows that the producer used in-phase walking; functional analysis of the trackways (together with sedimentological evidence) indicates that these kampecarids and eoarthropleurids were aquatic, possibly amphibious (no evidence of their respiratory system is known). The *D. gouldi* Type A trackways were probably produced by kampecarids using high-g geared gaits, but their walking techniques were affected by walking in currents. Eoarthropleurids, the producers of *D. gouldi* Type B, like many extant diplopods, preferred one gait ratio (7.7 : 2.3); their speed was probably controlled by changing the duration of their step cycle. Continued study of fossil arthropod trackways, and their locomotory capabilities, will help to trace further the conquest of land by the arthropods.

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