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Trace fossils of the arthropod *Camptophyllia* from the Westphalian (Carboniferous) rocks of Lancashire, UK and their palaeoenvironmental context

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ABSTRACT

Two arthropod trace fossils are described and analysed from the Carboniferous Lower Westphalian (*C. communis* and basal *A. modiolaris* chronozones) coal-bearing strata of Lancashire. The biserial trackway *Diplichnites triassicus* consists of five overlapping en echelon sets of 7–9 tracks preserved as epichnia and hypichnia in lacustrine siltstones. The trackway suggests subaqueous in-phase walking by a multi-segmented producer with a body length of 35–40 mm, width 17–22 mm, and 7–9 appendages. Curved, clustered, or laterally repeated, hypichnial lobes with transverse striations on the base of ripple cross-laminated sandstone are identified as *Rusophycus versans*. This trace fossil is interpreted as shallow resting or furrowing burrows of a homopodous arthropod, 30–60 mm long, 15–30 mm wide, and probably the same kind of arthropod as produced *D. triassicus*.

A review of contemporary arthropod body fossils from *Lagerstätten* in Lancashire favours the onisciform, or *Arthropleura* like arthropod *Camptophyllia* as a potential producer of both of these trace fossils in a lacustrine palaeoenvironment.

This study integrates the analysis of sediments, trace fossils and body fossils for reconstructing the arthropod biota and ecology in Westphalian lacustrine and crevasse splay fluvial palaeoenvironments.

1. Introduction

The contributions of Roland Goldring to our knowledge of arthropod trace fossils expanded our understanding of both the sedimentological significance of undertracking in the preservation of trackways (Goldring, 1969; Goldring and Seilacher, 1971) and the endogenic versus exogenic origin of such burrows as *Cruziana* and *Rusophycus* (Goldring, 1985). The study of two new arthropod trace fossils described here from coal-bearing strata of Lancashire addresses both of these issues.

Trace fossils are recorded only rarely from Westphalian rocks of Lancashire, particularly since the cessation of exploration and production of the coalfield several decades ago. Re-examination of undescribed specimens and recent collection at classic localities (e.g. Bickershaw colliery tip, Leigh (Anderson et al., 1997) and Glodwick brickpit, Oldham (Broadhurst, 1989)), however, have led to the recognition of the specimens described here.

The arthropod trackway was discovered in an exploration borehole near Culcheth by National Coal Board geologist A.A. France in the late 1970s. It was partially analysed by one of us (J.E.P) and exhibited at the Palaeontological Association's annual meeting at Sheffield in 1982. The trackway was referred to as an undescribed specimen of *Diplichnites* in a review of Westphalian ichnofaunas by Eagar et al. (1985, p.133). Subsequently it was included as *Acripes* isp. as a component of the lacustrine ichnofauna typical of British Westphalian coal-measures by Pollard (1988, Fig. 1, association 6a). The analysis and description presented here was delayed until arthropod trackways were understood better and the discovery of body fossils of possible arthropod producers (Anderson et al., 1997, 1999; Braddy, 2001; Nudds, 2005).

The structures described below as arthropod resting traces were first discovered as loose material from Bickershaw colliery tip heap in mid 1990s. Their true nature, however, was not recognised until better preserved specimens were found at Glodwick by S. Watts, P.A. Selden and F.M. Broadhurst in 2003.

The present interpretation of these trace fossils, their relationship to one another and contemporaneous arthropod body fossils, results from a comparison with similar ichnofossils of other ages and locations such as Triassic of Germany (Schlirf et al., 2001) and new discoveries in the Lancashire coal measures (Anderson et al., 1997, 1999).

2. Stratigraphical and sedimentological context of the trace fossils

2.1. Arthropod trackway

This specimen consists of a double row of arthropod appendage imprints, preserved in both negative and positive (= cleavage) relief on

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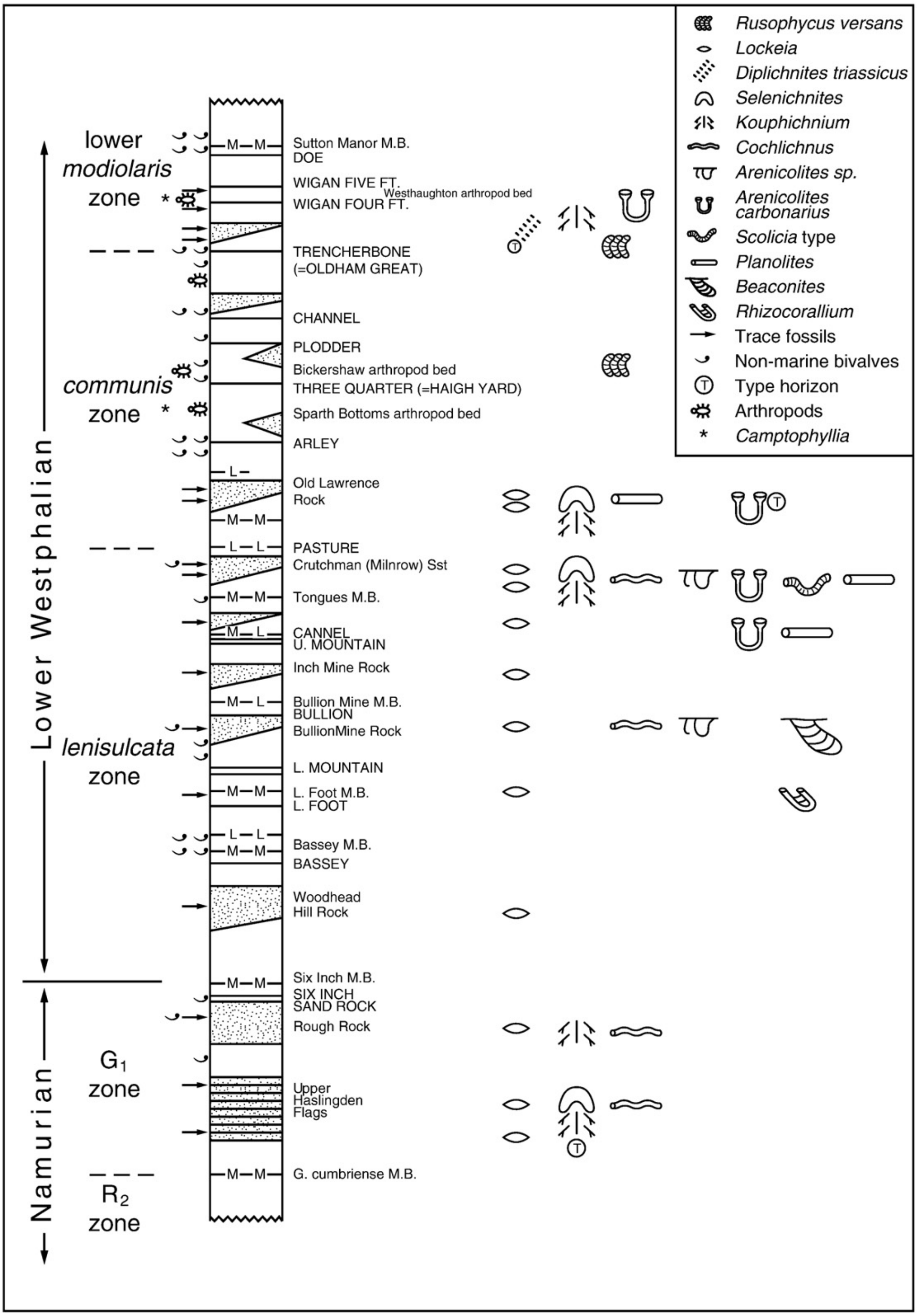

Fig. 1. Stratigraphical position of the new records of *Diplichnites triassicus* and *Rusophycus versans*, other trace fossils and arthropod *Lagerstätten* in Lower Westphalian and uppermost Namurian rocks of Lancashire (stippled units are sandstones, MM = marine bands, LL = *Lingula* bands).

the parting surface of a dark grey, micaceous siltstone sectioned in a borehole core. The borehole, NCB Larkhill Borehole was drilled east of Light Oaks Moss Farm, Culcheth (SD 36903968) (A.A. France, pers. comm. 1982). The stratigraphical horizon of the specimen is about 18 m above the Trencherbone-Peacock Seam and 13 m below the Wigan Two Foot Seam in the cristagalli bivalve faunal belt, at the base of the *A. modiolaris* chronozone, Upper Westphalian A (Langsettian), Carboniferous (Magraw, 1960; Ramsbottom et al., 1978; Fig. 1).

The associated strata consist of thin, ripple cross-laminated sandstones and interbedded siltstones and mudstones indicative of fluvial crevasse splay and lacustrine environments (Pollard, 1988, Fig. 1). Although no other identifiable body fossils or trace fossils were

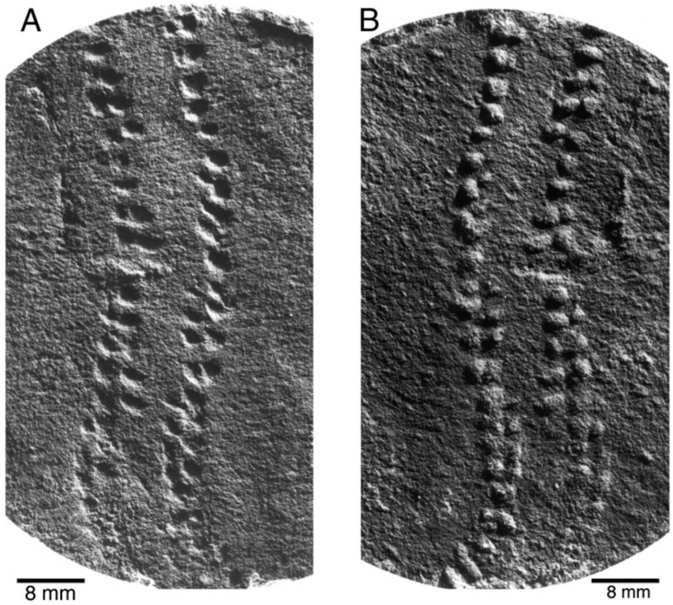

Fig. 2. *Diplichnites triassicus* trackway in borehole core from Culcheth, Lancashire. (A) Negative epichnia (part), (B) positive hypichnia (counterpart) Manchester Museum LL. 15800 a–b.

associated with the trackway, the thinly laminated muddy siltstone matrix suggests deposition in a lacustrine environment.

2.2. Arthropod burrows and resting traces

These trace fossils were first recognised as curved and lobed structures with transverse markings preserved on the muddy base of a grey, fine-grained sandstone. They were found at two localities, Bickershaw colliery, Leigh and Glodwick brickpit, Oldham.

The stratigraphical horizon from which the Bickershaw specimens came is probably above the Haigh Yard Seam, in the *pseudorobusta* faunal belt of *C. communis* chronozone (Anderson et al., 1997). At Glodwick the strata are between the Oldham Great Mine (= Trencherbone Seam) and the Blenfire Seam (Tonks et al., 1931; Broadhurst, 1989) in the cristagalli faunal belt, at the base of the *A. modiolaris* chronozone, Westphalian A, close to the horizon of the arthropod trackway from Culcheth (Fig. 1). The trace fossils at Glodwick are preserved on the base of a composite sandstone bed overlying shales containing non-marine bivalves and fish remains. The basal surface of this sandstone also preserves hierarchical mudcracks suggesting a break in sedimentation. The basal unit of the sandstone is ripple cross-bedded, consistent with being the toe of a crevasse splay sand sheet advancing into a lake. Higher units of the sandstone body are tabular cross-bedded, possibly indicating migration of a crevasse channel. The occurrence of the trace fossils at this interface suggests that the arthropods were active on the coherent mud-floor of a lake and were overcome by the advancing crevasse splay sand.

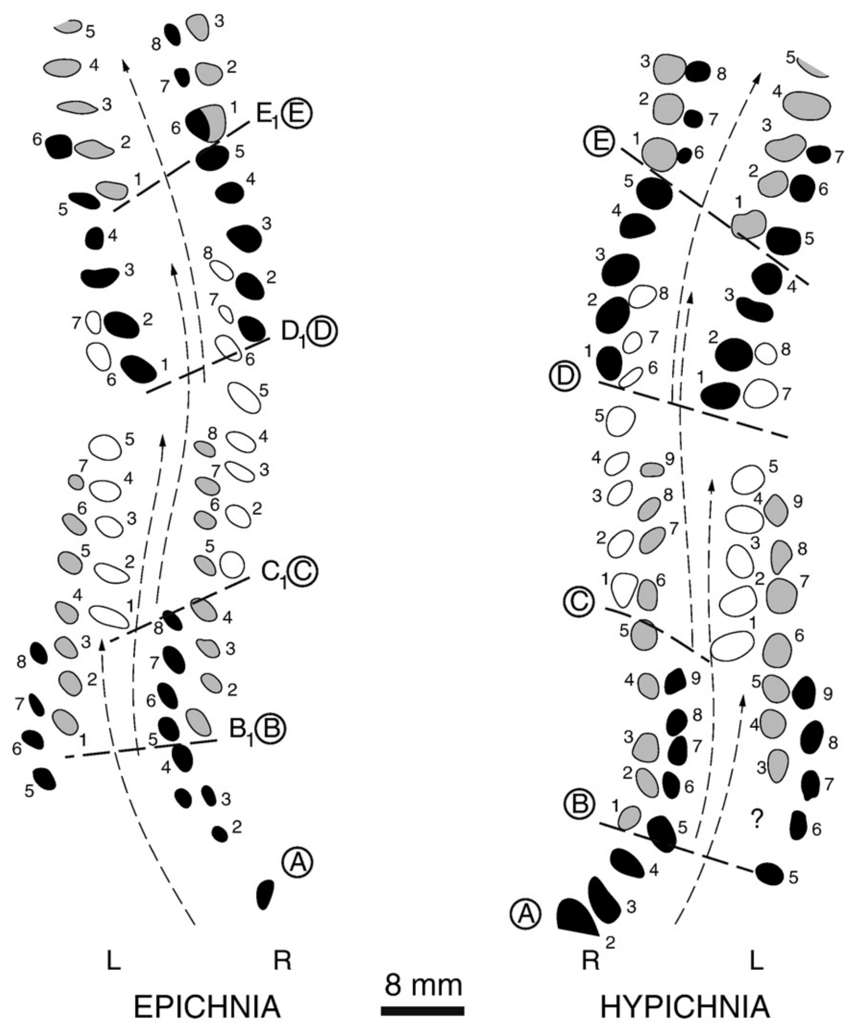

Fig. 3. Analysis of series and sets in *Diplichnites triassicus* trackway shown in Fig. 2. Part (epichnia) (left), counterpart (hypichnia) (right). Sets indexed A–E blocked in; arrows showing centre line and % overlap.

Similar situations have been recorded from Triassic fluvial–lacustrine deposits where the resting traces *Rusophycus eutendorfensis* are found commonly on the base of fluvial sandstones, for example in the St Bees Sandstone, Corsehill Quarry, Annan, Scotland (Pollard, 1985) and in the Hasseberge Formation, Franconia, Germany (Schlirf et al., 2001).

It is apparent from the distribution of trace fossils known from the Westphalian rocks of Lancashire and Cheshire (Fig. 1) that these new specimens add to the diversity of invertebrate trace fossils and also extend upwards their stratigraphical range.

3. Systematic description of the trace fossils

3.1. Arthropod trackway

3.1.1. *Diplichnites triassicus* (LINCK, 1943)

3.1.1.1. Diagnosis. Two parallel rows of multiple circular, appendage imprints composed of overlapping en echelon series of 6–9 tracks. Preserved in both positive and negative semirelief.

3.1.1.2. Material. One specimen, part and counterpart. Manchester Museum LL. 15800 a and b.

3.1.1.3. Description. The trackway is about 90 mm in preserved length, 15–19 mm in external width and crosses the core slab in a slightly sinuous fashion (Fig. 2). It is composed of two parallel rows of single or duplicate tracks or appendage imprints, 35/36 tracks in right hand row, 33/30 tracks in left hand row of the part and counterpart, respectively. The single or double nature of the tracks results from the overlap of five sets (opposed series) of 6–9 tracks (Fig. 3; Table 1). The inner width (straddle) of the trackway is about 5–10 mm (mean = 8 mm), although the inner width of each set is about 10 mm and external width 16–18 mm. The length of a complete set varies from 34–40 mm, depending on the number of imprints and their spacing (pace), which is mainly 4–5 mm. The repeat length of the first track in each set (stride) varies from 17–22 mm (Table 1) (see Trewin 1994 for terminology). The individual tracks vary in size and shape in each series, the largest being circular or pointed and 3–4 mm in transverse dimension and 2 mm in longitudinal direction. Smaller tracks are circular or triangular, about 2 mm in longest dimension and alternate with larger tracks of the adjacent series. Some tracks are obliquely pointed in the same direction (Figs. 2 and 3), indicating the likely withdrawal direction of the appendage (Osgood, 1970, text — Fig. 18; Trewin, 1994) and, therefore, the progress direction of the track maker (Fig. 3 sets A–E). On this basis, the smaller tracks are at the anterior (forward) end of each set. None of the individual tracks show any surface sculpture that can be directly linked to morphologic features of the producer's appendage (Seilacher, 1962; Anderson, 1981, pl. 2, Fig. 2). Only three sets of tracks are completely represented in the trackway (Fig. 3, B–D), and they show an offset angle of 5–20°and an overlap of 30–50% between sets. As the curvature of the trackway (offset angle of sets), increases so the en-echelon nature of the series becomes apparent, especially in left hand series of sets D–E (Fig. 3) (cf. Osgood, 1970, text — Fig. 22a, pl.75, Fig. 4).

Table 1
Analysis of Westphalian trackway *Diplichnites triassicus* LL. 15800 a and b

(a) Counterpart (hypichnia = h)

Set index	Number of appendages		Set length (mm)	Set width (mm)	
	Left	Right		External	Internal
E	5	3	>17	16	9–11
D	6	8	34.5	17.5	8–12
C	7	8	36.5	16.5	8–11
B	7	9	39.5	16.5	9–11
A	5	8	>27	15.5	9–12

(b) Part (epichnia = e)

Set index	Number of appendages		Repeat length (=stride) (mm)	Imprint spacing (=pace) (mm)	Offset angle set midline	
	Left	Right			(h)	(e)
E	5	3		4–5		
			20–22		3°	5°
D	7	8		3–5		
			20–22		10°	20°
C	7	8		4–5		
			17–18		10°	20°
B	8	9		4–6		
			20–22		20°	15°
A	6	7		3–5		

3.1.1.4. Remarks. The ichnotaxonomy of simple biserial arthropod trackways has been a subject of controversy in recent decades. There are two broad schools of thought, the lumpers who include all variants as ichnospecies of *Diplichnites* Dawson (e.g. Bromley and Asgaard, 1979; Pickerill, 1992, 1994; Buatois et al., 1998) and the splitters who place distinct variants in separate ichnogenera. (e.g. Walter, 1983; Pollard, 1985). Although no general consensus has been reached, recent taxonomic practice tends to the use of various ichnospecies of *Diplichnites* for such trackways (Pickerill, 1992, 1994; Buatois et al., 1998; Keighley and Pickerill, 1998; Smith et al., 2003).

The most distinctive character of the trackway described here is the clear recognition of the series of 7–9 tracks within the track rows. This character is diagnostic of the ichnospecies *Diplichnites* [*Acripes*] *triassicus* (Linck) (Pollard, 1985; Buatois et al., 1998), although 9 imprints per series also may occur in *D. gouldi* assigned to such myriapodous producers as arthropleurids (Smith et al., 2003). This trackway should be named *Diplichnites triassicus*, an ichnospecies which has been recorded also from Carboniferous rocks of eastern Canada (Pickerill, 1992; Keighley and Pickerill, 1998).

From the above description this trace fossil is interpreted as the walking trackway of a homopodous multilimbed arthropod using 7–9 appendages in locomotion. The set length (one complete metachronal wave) suggests a body length of 35–40 mm and body width 17–22 mm. The track spacing (= pace) is about 5 mm and repeat distance of same track (stride) is 17–22 mm (Trewin, 1994). The trackway appears to show opposite arrangement of tracks in a set, suggesting opposite phase difference of zero, and in-phase movement of opposite limbs (Braddy, 2001; Smith et al., 2003). By comparison with the similar, but larger trackways of *Diplichnites gouldi* type A from the Old Red Sandstone of South Wales, which show equivalent 40% series overlap, *D. triassicus* suggests a walking pattern with a gait of 8:2, an opposite phase difference of 0 and a successive phase difference of 0.2 (Smith et al., 2003, pp. 69–70). In-phase limb movement suggests that the producer is more likely to have been walking subaqueously rather than performing terrestrial locomotion.

3.2. Arthropod resting or feeding traces

3.2.1. *Rusophycus versans* SCHLIRF et al., 2001

3.2.1.1. Diagnosis. Curved, clustered, or laterally repeated hypichnial lobes, commonly displaying transverse striations or ridges.

3.2.1.2. Material. Glodwick brickpit, Oldham. Manchester Museum LL. 15801-2.
Bickershaw colliery, Leigh. Manchester Museum LL. 15803-4.

3.2.1.3. Description. Hypichnial mounds on base of a fine-grained sandstone with a variable arrangement of mud-draped lobes with transverse striations or annulations. The quality of preservation varies

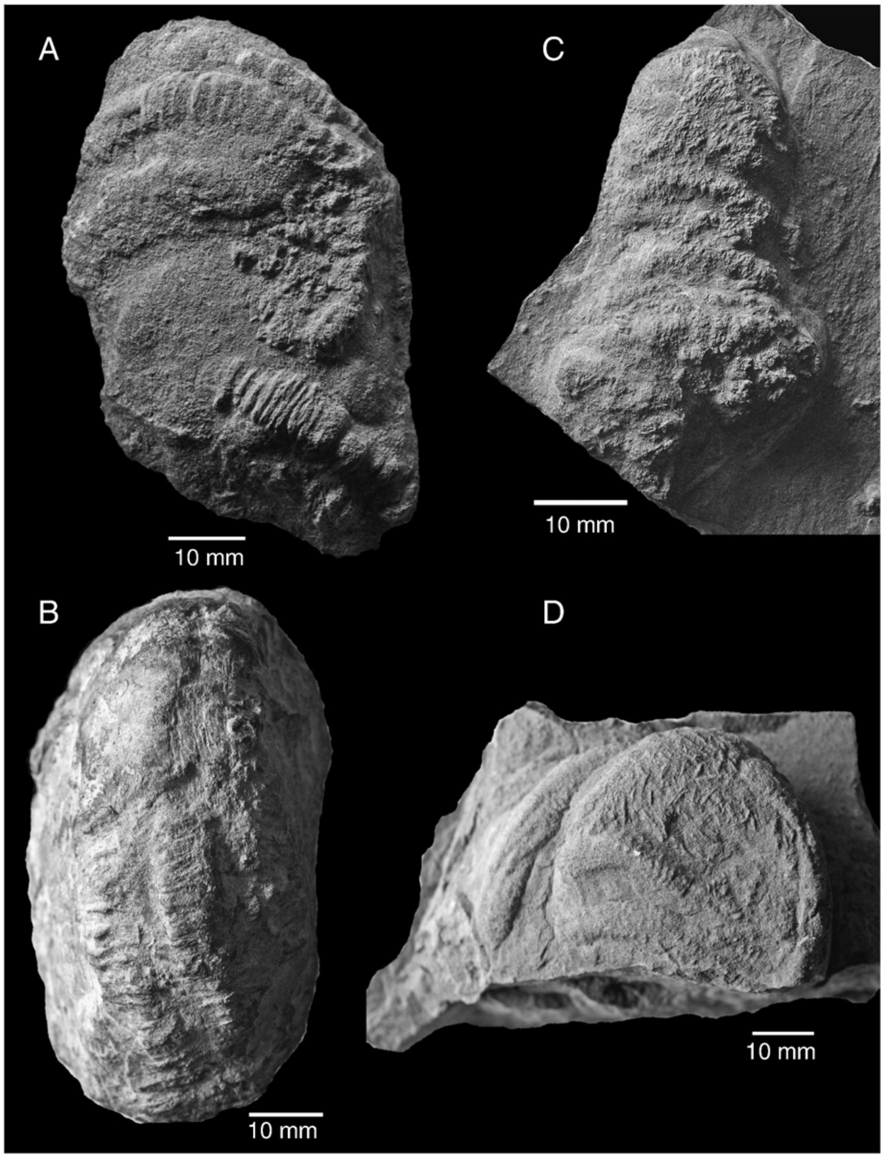

Fig. 4. A, B, *Rusophycus versans* from Low Side brickpit, Glodwick, Oldham, Lancashire. (A) form with isolate curved striated lobes (LL. 15801), (B) oval hypichnial mound with three parallel striated lobes, resembling a trilobite exoskeleton (LL. 15802), C, D, *Rusophycus versans* from Bickershaw colliery, Leigh, Lancashire. (C) Deeply incised hypichnial striated lobes showing strong curvature, overlap and lateral repetition (LL. 15803), (D) semicircular hypichnial mound on base of a sandstone composed of curved overlapping and cross-cutting striated lobes up to 12 mm in height (= incised depth) (LL. 15804).

considerably which affects the shape of hypichnial mounds, the number, form and arrangement of the component striated lobes.

The simplest form of the trace fossil consists of isolate curved crescentic lobes up to 30 mm long by 7 mm wide and 2 mm deep, with transverse striations or fine ridges, sometimes resembling annulations (Fig. 4A). Rarely the mound is oval in shape, up to 60 mm long by 35 mm wide, composed of three parallel striated lobes, each about 30 mm long, 7 mm wide, and 3 mm deep, resembling the axial and pleural regions of the dorsal exoskeleton of a trilobite (Fig. 4B). A more complex form shows overlapping crescentic striated lobes, repeated laterally up to ten times (Fig. 4C). The lobes of these specimens from Bickershaw are 25–30 mm long, about 5 mm wide, and up to 8 mm in depth. The most complex specimen recovered is semicircular in shape 60 mm by 40 mm, composed of multi-depth, cross-cutting and overlapping striated lobes 5–7 mm wide, incised to a depth of 12 mm below the base of the overlying casting sandstone (Fig. 4D). The sculpture on these lobes is highly variable, ranging from striations 3 mm by 0.5 mm, to strongly curved ridges 5 mm long by 1 mm wide, 1–2 mm deep (Fig. 4A), mostly parallel to each other, and transverse to the long direction of the lobes. In more complex specimens striations are shorter, more frequent and varied in direction, frequently cross-cutting (Fig. 4C, D). Frequency of striations on specimens from Glodwick varies; 11 striations in a 17 mm lobe, 15 striations in a 30 mm lobe, 20 striations in a 35 mm lobe (Fig. 4A, B).

3.2.1.4. Remarks. The lobate shape of this trace fossil with lateral repetition and transverse striations resembles closely *Rusophycus versans* described from Triassic rocks of Germany by Schlirf et al. (2001). The trilobite like resemblance of some of the specimens (Fig. 4B) suggests the basic shape of this multi-lobed form of *Rusophycus* (Schlirf et al., 2001, Fig. 9). Likewise, the strong annular-like striations (Fig. 4A), which can be preserved without the lobes, and high burrow density and overlap, are all features described for this ichnospecies (Schlirf et al., 2001, Figs. 9 and 10). The more complex expressions of the ichnofossil with laterally repeated curved lobes, cross-cutting and deeply incised into the substrate, show some resemblance to *Fuersichnus* Bromley and Asgaard 1979, although the transverse sculpture is different.

This trace fossil is interpreted as a semi-relief, hypichnial burrow preserved on the base of a fine-grained sandstone. The burrows were excavated by a multi-limbed organism with rotational and lateral movement to varying depths in a cohesive mud, probably below a thin sand sheet. The deeply incised burrows from Bickershaw are preserved on the base of a ripple cross-laminated, fine-grained sandstone, and were undercut to depth of 12 mm (Fig. 4D), presumably in cohesive mud. The forms of the trace fossil suggest both a resting or more complex deposit-feeding behaviour of the trace maker (Schlirf et al., 2001), especially in the varied expressions of the burrows from Bickershaw.

The characters of this trace fossil and its ichnospecific assignment suggest that its producer most likely was a homopodous benthic arthropod. If so, the ovoid and discrete lobate forms of this trace fossil from Glodwick indicate that the body may have been 30–60 mm long and 15–30 mm wide. The more variable burrows from Bickershaw, however, suggest a smaller more active producer, perhaps about 30 mm long and 15 mm wide.

4. Producers of the trace fossils

The characters of the trace fossils described here, and their similarity to conspecific Triassic trackways and burrows, suggest that they both may have been made by the same kind of arthropod. This suggestion is reinforced by the restricted stratigraphical occurrence of these ichnofossils and the variety of possible arthropods known as body fossils in associated ironstone nodule *Lagerstätten* (Anderson et al., 1997, 1999).

The trace maker suggested for comparable Triassic trackways of *D. triassicus* and burrows of *Rusophycus* from Britain, Germany and Greenland are deposit-feeding notostracan crustaceans (Bromley and Asgaard, 1979; Pollard, 1985; Schlirf et al., 2001). These arthropods, however, have not been recorded from Westphalian arthropod *Lagerstätten* in Britain (Schram, 1981; Anderson et al., 1997, 1999).

The aquatic arthropod groups recorded from the approximately contemporaneous *Lagerstätten* in Lancashire are crustaceans (*Palaeocaris*, *Pleurocaris*, *Pygocephalus*, *Anthracaris*), xiphosurans (*Bellinurus*, *Euproops*, *Liomesaspis*, *Valloisella*), and the possibly amphibious forms *Arthropleura* and *Camptophyllia* (Anderson et al., 1997, 1999). Walking trackways and burrows have not been recognised for the crustaceans, possibly because they were predominantly necto-benthic swimming forms. Trace fossils produced by the heteropodous xiphosurans are well known as *Kouphichnium* (walking trackways), *Selenichnites* [*Limulicubichnus*] *rossendalensis* (resting traces) and *Aulichnites bradfordensis* (furrowing traces) (Hardy, 1970; Chisholm, 1983, 1985; Eagar et al., 1985; Pollard, 1988, Fig. 1), all distinctly different from the trace fossils analysed here. *Arthropleura* and probably *Camptophyllia*, however, were homopodous multi-limbed arthropods that could have created traces like those described here.

Trackways of arthropleurids are known as ichnospecies of *Diplichnites* from Westphalian rocks of Canada (Briggs et al., 1984), the Bristol area (Pollard and Hardy, 1991; Proctor, 1998) and Stephanian faunas of Montceau les Mines, France (Briggs 1986). These trackways are usually of giant size with 20 or more tracks per series. Some small specimens of *Arthropleura*, possibly juveniles 30–40 mm long are known from Britain (Calman, 1914; Anderson et al., 1997), but there are no comparable size trackways. Neither resting traces nor burrows have been attributed to Carboniferous arthropleurids, although the meniscate burrow *Beaconites* which commonly occurs in Devonian fluvial deposits, has been assigned to an arthropleurid-like producer (Morrisey and Braddy, 2004). Also Falcon-Lang et al. (2006) recorded meniscate *Taenidium barratti* in the same facies association as *Diplichnites cuithensis* in the Joggins Formation of Nova Scotia, Canada.

Table 2
Comparison of data from trace fossils and *Camptophyllia*

Data	*Diplichnites*	*Rusophycus*	*Camptophyllia*[a,b]
Body length (mm)	35–40	30–60	25–40+
Body width (mm)	17–22	14–20	14–20
Form ratio (*L*/*W*)	2:1	2:1	2:1
Leg pairs/segments	7–9 legs	?	8–10 segments
Appendage type	Homopodous	Homopodous (paired scratches)	Homopodous (paired leg bases?[a])
Mode of life	Benthic walker	Benthic burrower	Benthic
Feeding type	?	Deposit feeder? (digging scratches)	Deposit feeder? (sediment in gut?[b])

Sources of data: [a]Gill, 1924; [b]Anderson et al., 1999.

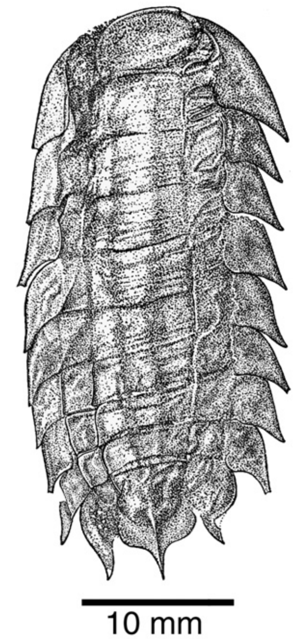

Fig. 5. Reconstruction of the Carboniferous arthropod *Camptophyllia* (from Gill, 1924). (Dorsal view with anterior end up).

A possible trace maker could be the enigmatic fossil arthropod *Camptophyllia*. This is an onisciform arthropod with 10 tergites, probably at least 7 pairs of thoracic walking legs, body length 25–40 mm and 14–20 mm in width, deduced from known body fossils (Gill, 1924; Rolfe, 1969; Hansman, 1972; Anderson et al., 1999). The affinities of this arthropod are uncertain and it has been allied to either isopod crustaceans (Gill, 1924) or arthropleurids (Brooks, 1962). Despite uncertainties of affinity and mode of life, this genus does possess several characters similar to the potential producer of this trace including body size and form ratio (*L*/*W*) 2:1, probably 7–10 pairs of homopodous limbs, and benthic habit (Table 2). Furthermore, if a reconstruction of the exoskeleton of *Camptophyllia* (Fig. 5) at the same scale as the *D. triassicus* trackway is placed over the tracing of the trackway (Fig. 3), the opposed appendage tracks lie under the lateral regions of each body segment. This corresponds well with the reconstructions of the locomotion and burrowing behaviour of Devonian fluvial arthropleurids shown by Smith et al. (2003, Fig. 7) and Morrisey and Braddy (2004, Fig. 8).

Body fossils of this genus have been recorded in Westphalian arthropod *Lagerstätten* in Lancashire, namely at Sparth Bottoms, Rochdale (Hansman, 1972) (pseudorobusta faunal belt, *C. communis* chronozone) (Tonks et al., 1931) and Westhaughton (regularis faunal belt, Lower *A. modiolaris* chronozone) (Anderson et al., 1999), occurring stratigraphically below and above the horizons of the trace fossils described here.

5. Palaeoenvironmental context of the trace fossils

Since the arthropod tracks *D. triassicus* were first recorded and assigned to a palaeoenvironment (Eagar et al., 1985; Pollard, 1988), there have been major advances in the documentation and palaeoenvironmental analysis of fluvial and lacustrine ichnofaunas, recently reviewed by Buatois and Mangano (2004, 2007). It is therefore appropriate to reconsider this aspect of these trace fossils.

In Eagar et al. (1985, p.133) *Diplichnites* isp. was assigned to a lacustrine or lagoonal environment, whilst Pollard (1988, Figs. 1 and 5) included these small forms as *Acripes* in an aquatic arthropod trace fossil association (6a), typical of flood basin lakes or crevasse splays. He contrasted these trackways with the larger form *D. cuithensis* (association 6b), produced by arthropleurids in sheet flood sands, sometimes forested, in a more terrestrial alluvial plain situation.

Studies of fluvial and lacustrine ichnofaunas and sediments in eastern Canada of Lower Carboniferous age (Pickerill, 1992) and Westphalian age (Briggs et al., 1984; Falcon-Lang et al., 2006) have confirmed these distinctions. Pickerill (1992) records a *D. triassicus* and *Rusophycus carbonarius* association, or *Rusophycus* ichnocoenosis, as indicating diverse subaqueous arthropod behaviour (shallow burrowing, scavenging, deposit-feeding, resting, walking) in the ponded uppermost part of fluvial channel-fill sequences. In their comprehensive review of the sediments, floras and faunas of the classic Joggins Formation (Langsettian = Westphalian A) Falcon-Lang et al. (2006) confirmed the assignment of aquatic arthropod traces to an open water assemblage and *D. cuithensis* to a poorly drained coastal plain association.

The trace fossil/sediment relations in this study suggest that *D. triassicus* was formed on siliciclastic substrate on the floor of a shallow lake. The mode of preservation of *R. versans*, with detailed scratch marks and the undercut nature of some of the lobes, supports an endogenic interface origin with rapid infilling by overlying sand in the manner of the formation of *Cruziana* described by Goldring (1985). There is no evidence for the erosion or exposure of the burrows prior to their moulding by basal sand of the overlying ripple cross-bedded sandstone. These observations reinforce the interpretation that these burrows were made in a shallow lake floor below a thin covering of sand from the toe of the advancing crevasse-splay.

Body fossils of *Camptophyllia* from Lancashire are preserved in ironstone nodules in lacustrine mudstones or siltstones. One specimen appears to have a mineral filled gut cast (Anderson et al., 1999, p. 327) possibly indicating that the animal was a deposit feeder, as is suggested from the trace fossils.

These sediments and trace fossils appear to belong to the Scoyenia Ichnofacies, characterised by arthropod tracks and burrows in fluvial-lacustrine transitional environments (Buatois and Mangano, 2007). This reassessment of the trace fossils and their enclosing sediments confirms their palaeoenvironmental context as being lacustrine, possibly with input from fluvial crevasse splay sedimentation.

6. Conclusions

1) Two newly described trace fossils from the Lower Westphalian (*C. communis* and basal *A. modiolaris* chronozones) Carboniferous rocks of Lancashire represent behavioural and taphonomic variations of structures produced by the same homopodous, multi-limbed arthropod.
2) The walking trackway, *Diplichnites triassicus*, was produced and preserved in siltstones deposited in a lacustrine environment.
3) The trace fossil *Rusophycus versans* suggests shallow burrowing for resting, shelter or feeding in a lake floor just below the sediment–water interface, possibly under a thin covering of rippled sand, reflecting the advance of the toe of a crevasse splay into a lake.
4) A review of the appropriate sizes, body forms, inferred leg numbers, modes of benthic life, and locomotion of contemporaneous arthropod body fossils, suggests that the onisciform arthropod *Camptophyllia* may have been the producer of both of these trace fossils.
5) Comparison of these sediments and trace fossils with similar contemporaneous relationships in other localities, particularly from eastern Canada, confirms the distinction of this lacustrine association from the more alluvial plain arthropleurid association. This association is assigned to the Scoyenia Ichnofacies.
6) The integration of the analyses of deposits and taphonomy and morphology of trace fossils and body fossils in this study reflects the reward of the biotic–sediment interaction approach, which was so well developed in the work of Roland Goldring.

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