ARTHROPLEURA TRAILS FROM THE WESTPHALIAN OF EASTERN CANADA

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ABSTRACT. The trace fossil *Diplichnites cuithensis* Briggs, Rolfe and Brannan, 1979 is described from the Tynemouth Creek Formation of southern New Brunswick, and is interpreted as a trail of the giant Carboniferous myriapod *Arthropleura*. The arthropod was weaving through a forest of calamites which formed a single species stand on a sheetflood deposit in an alluvial fan environment. Comparison with other *Arthropleura* trails suggests that, in this case, drier conditions prevailed, supporting the interpretation of an essentially terrestrial habit for the arthropod. This trail is the first of *Arthropleura* to be described in detail from North America, and provides evidence that the myriapod's mode of turning was similar to that of modern myriapods, and unlike trilobites. The ichnogenus *Diplichnites* should not be applied to trilobite trails.

TRACE fossils can rarely be ascribed with confidence to a particular organism, but when this is possible they provide otherwise unavailable evidence of its mode of life and habitat. They can prove particularly important in interpreting the degree of terrestrialization achieved by arthropods in transitional environments, such as eurypterids (Briggs and Rolfe 1983) and the giant Carboniferous myriapod *Arthropleura*, because, unlike body fossils, traces are not transported (Rolfe 1980, p. 131). The first trails attributed to *Arthropleura* were reported and figured by Ferguson (1966, 1975) from the celebrated Joggins section (Westphalian B) in Nova Scotia (text-fig. 1). An analysis of an older Namurian example from Arran, Scotland, by Briggs *et al.* (1979) revealed details of the morphology and locomotory capability of the arthropod. Smaller arthropleurid trails are known from the Stephanian of Montceau-les-Mines, France (Langiaux and Sotty 1977*a*; Rolfe *et al.* 1982). The new example described here, however, is the first to preserve evidence of the arthropod making a pronounced change in direction, its path being constrained by calamite 'trees' growing in sheetflood deposits near the margin of an alluvial fan. The resultant trail provides information on the mode of cornering employed by *Arthropleura*, and its habitat. It also extends the geographical range of the trace fossil to New Brunswick, where unequivocal body fossils of *Arthropleura* have yet to be reported (Briggs *et al.* 1979, p. 287).

The trace fossil locality was discovered by A.G.P. in 1981; he and R.K.P. made a latex cast of the best-preserved part of the trail in August 1982. Unfortunately, most of the bedding plane was buried by a landslip the following winter. The trail was mapped (text-fig. 3B) using both a mosaic of enlarged photographs (cf. text-fig. 3A), and the latex cast. The position of the calamite stems was also recorded in the field. The latex cast (GSC 76665) is housed in the Geological Survey of Canada, Ottawa; sets of photographs of the trace fossil are held by the Department of Geology, University of New Brunswick, and the Hunterian Museum, University of Glasgow.

GEOLOGICAL SETTING

The trace fossil occurs in the Tynemouth Creek Formation (Plint and Poll 1982) which outcrops in the area around Tynemouth Creek, on the south coast of New Brunswick (text-fig. 1). The locality is about 200 m south-west of Gardner Creek Bridge. The trail horizon lies 28·5 m above the base of the section exposed on the shore, immediately to the west of Gardner Creek (text-fig. 1; cf. Plint and Poll 1982, fig. 2). A less well-preserved example, about 1 m long, occurs at approximately the same horizon about 100 m along strike to the north-east. The succession shown in text-fig. 2A is approximately

equivalent (along strike) to the lowest 30 m shown by Plint and Poll (1982, fig. 3). Spore analysis (Barss *in* Plint and Poll 1982, p. 106) indicates a Westphalian A or B age for the trace fossil; poor preservation of the spores makes a more precise age determination impossible. Two similar poorly preserved trails occur in a cliff exposure 300 m east of Tynemouth Creek (text-fig. 1). Both lie at the top of channel sandbodies beneath overbank sediments, 75 m and 90 m respectively above the base of Section 2 of Plint and Poll (1982, fig. 18). The trail horizons at Gardner Creek and Tynemouth Creek cannot be accurately correlated, but it seems likely that they are approximately contemporaneous.
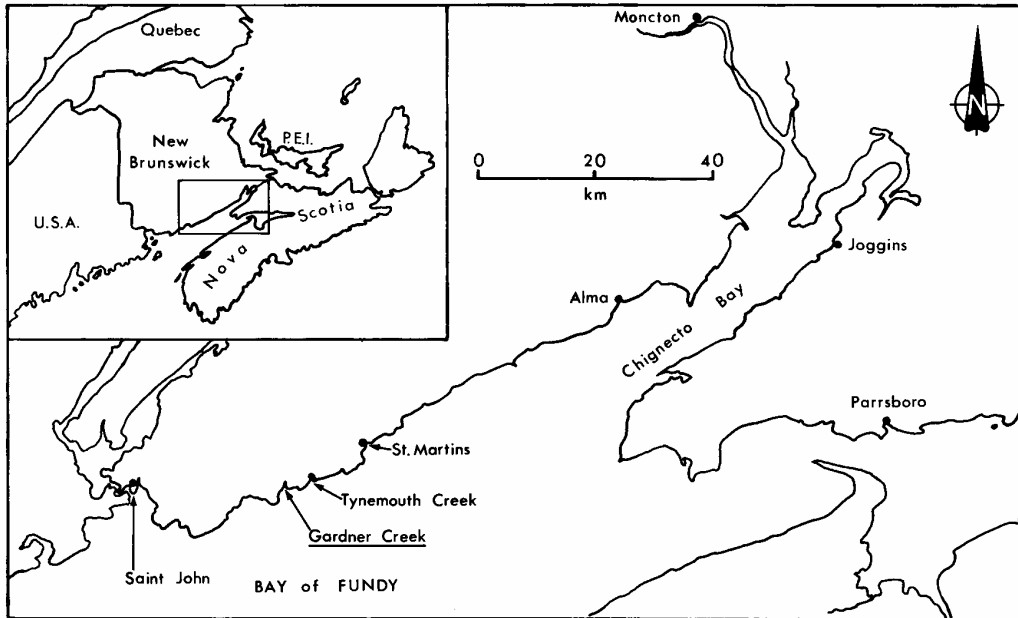
TEXT-FIG. 1. Location map.

The Tynemouth Creek Formation consists predominantly of red siltstones, red and grey sandstones, and coarse conglomerates, and shows an overall upward-coarsening. Rare freshwater limestones are locally present. The sequence containing the trace fossil consists of fine, red, slightly silty, tabular sandstones, interbedded with red and green siltstones (text-fig. 2A). The sandstones are dominantly massive, but include plane and cross-laminated units, and vary in thickness from thin laminae within siltstones to units up to 2 m thick. The thicker units are usually composed of several decimetre-thick sandstone beds, separated by silt laminae. The top 10–20 cm of the thicker sandstone units are usually mottled pale green and bioturbated. Both siltstone and, in particular, sandstone beds contain numerous upright and obviously *in situ* calamite stems, up to 10 cm in diameter.

The best-preserved myriapod tracks at Gardner Creek occur within a 1·5 m sandstone which rests on 40 cm of siltstone. Bed 1 (text-fig. 2B) comprises fine, grey sandstone, containing large calamite 'tree stumps' and *Stigmaria* (otherwise rare in the Tynemouth Creek Formation) which radiate to a distance of about 5 m. It was not possible to determine whether the *Stigmaria* trees project above this bed, due to insufficient exposure. Bed 1 is overlain by 12 cm of siltstone (Bed 2), and 40 cm of fine sandstone (Bed 3) with numerous *in situ* calamites rooted in Bed 2. The top of Bed 3 grades up into a few millimetres of siltstone, and it is on this surface that the trace fossil is preserved. The trail surface undulates slightly but shows no evidence of sedimentary structures (e.g. ripple marks) or other trace
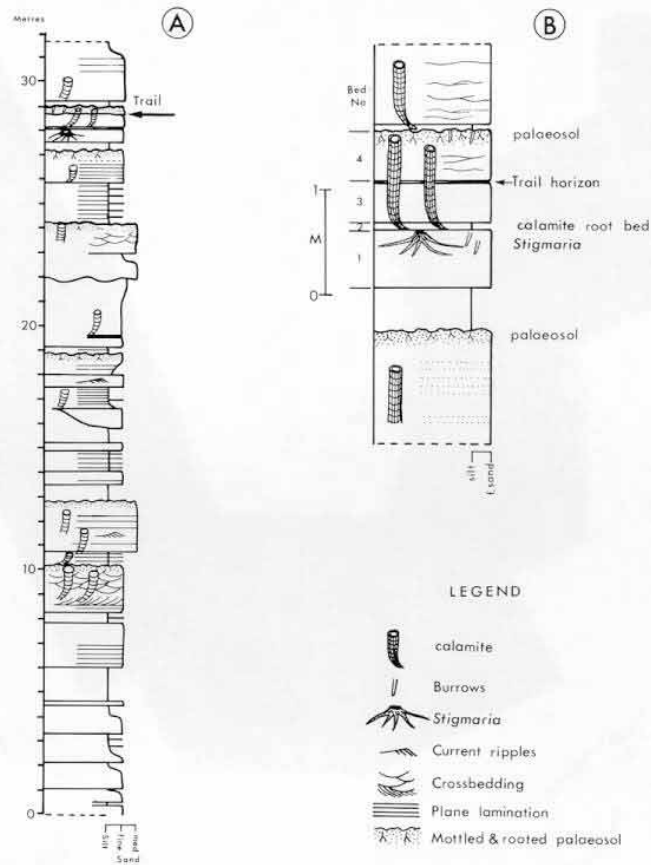
TEXT-FIG. 2. Stratigraphic sections: A, lowest 30 m immediately west of Gardner Creek, showing position of trail horizon; B, detail of beds including trail horizon.

fossils. Bed 4 comprises 50 cm of fine sandstone, at the top of which is a green-mottled palaeosol. The calamites in Bed 3 can be traced up *through* the trail horizon into Bed 4.

The sandstones are interpreted as the deposits of major sheet floods; palaeocurrents indicate a flow toward the north and north-west. The intervening siltstones were probably deposited during less vigorous floods. Thin sandstone laminae within the siltstones suggest a pulsatory flow. Green-mottled and bioturbated horizons at the top of sandstone units are interpreted as palaeosols which probably formed during prolonged breaks in sedimentation. The upper trail east of Tynemouth Creek occurs on the top of a highly bioturbated sandstone palaeosol which contains *Stigmaria* and locally displays low-amplitude, straight-crested ?wave ripples, suggesting periodic shallow immersion. The environment, therefore, appears to have been stable for relatively long periods, favouring colonization by plants, except for short intervals of very rapid sedimentation during major floods. The depositional area was of low relief and gradient, and lay towards the margin of a major alluvial fan that was prograding toward the north-west (Plint and Poll 1982).

The large numbers of calamites, and the apparent absence of other plants (except for rare
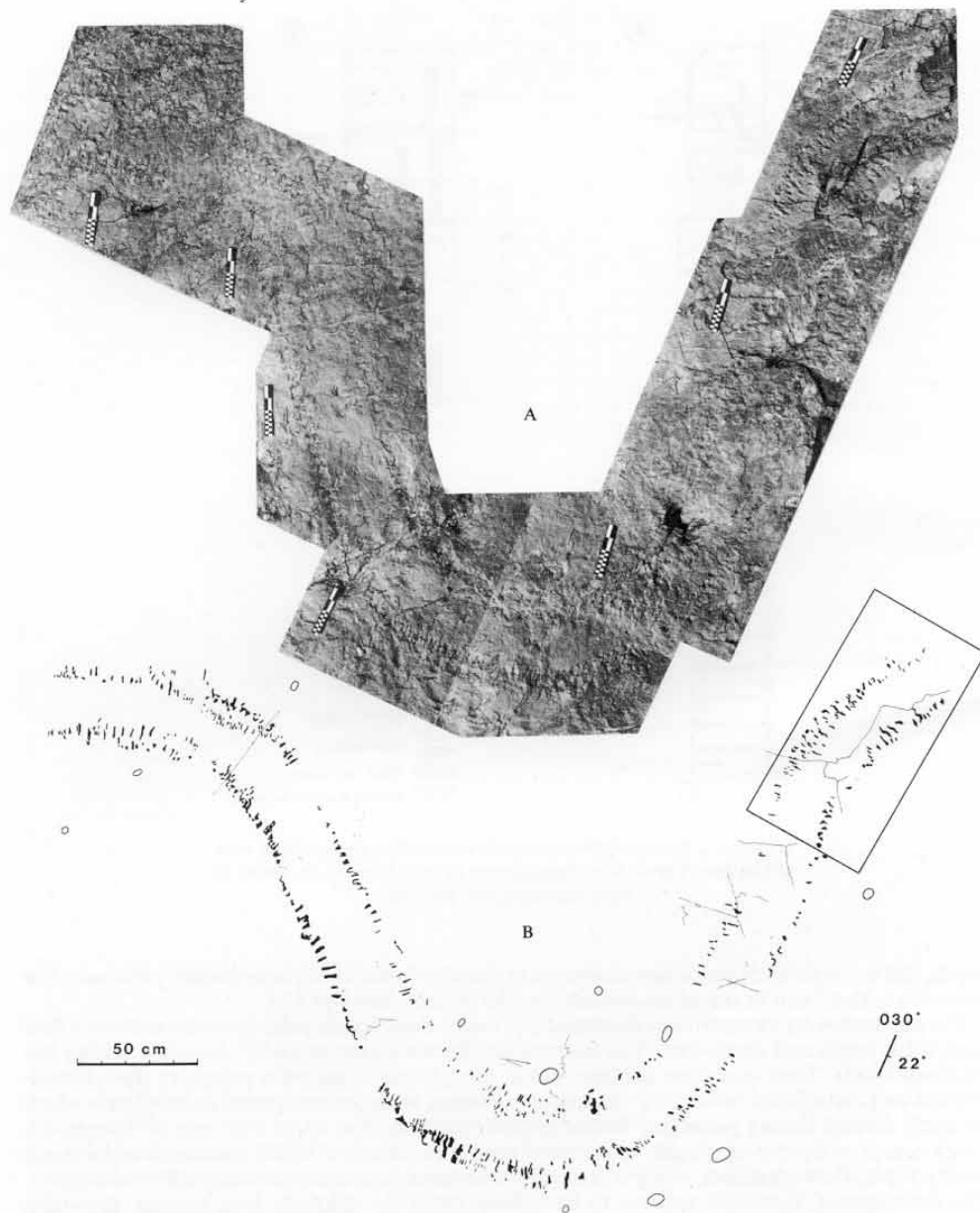
TEXT-FIG. 3. *Diplichnites cuithensis* Briggs, Rolfe and Brannan 1979, Tynemouth Creek Formation (Westphalian A or B), 200 m south-west of Gardner Creek Bridge, near Tynemouth Creek, New Brunswick. A, photomosaic of the trail as it was in 1982 (20 cm scale bar). B, plan of the trail to show the position of the preserved tracks and calamites (represented by subcircular outlines); box marks position of text-fig 4.

Stigmaria), suggest that calamites alone were well suited to colonizing this type of sedimentary environment, and formed essentially single species forests. Pfefferkorn and Zodrow (1982) recorded similar standing forests of calamites in the Pennsylvanian of Nova Scotia; they concluded that calamites and lycopods grew where sedimentation rates were high, in areas 'that were generally not occupied by other plant groups'.

DESCRIPTION OF THE TRACE FOSSIL

The most extensively exposed trail follows a sinuous course, over 5·5 m long, between calamite stems (text-fig. 3). The trail varies between 29·5 and 36·5 cm in total width (the trails at Tynemouth Creek are 30 and 27 cm wide), and is preserved in a layer of siltstone about 5 mm thick grading into the underlying sandstone (text-fig. 2B). The siltstone parts readily along planes parallel to the bedding, and the effects of differential erosion were quite evident even after one winter (1981–1982). Thus the majority, if not all, of the imprints are preserved as undertracks (Goldring and Seilacher 1971), and in places erosion has removed short sections of the trail completely. The detailed morphology of individual imprints is not preserved (contrast Briggs *et al.* 1979, pl. 30, figs. 5, 6), and the tracks vary in size and shape. This may result from: (1) the superimposition or coalescing of two or more footfalls; (2) the water content of the sediment; (3) slight erosion during deposition of the overlying fine sand.

The maximum width (normal to the axis) of both the entire trail (36·5 cm) and of the right and left rows of tracks (*c.* 11 cm) is reached roughly at the points of maximum curvature of the trail. Here the lateral spread of right or left tracks is over twice that in the straight sections of the trail (although the number of footfalls remains the same). Thus the proportion of the total width of the trail occupied by imprints increases from less than 50 to about 60 %. The curve at the bottom of text-fig. 3A, B displays a linear density of about twenty imprints in 20 cm, i.e. about 1 per cm (text-fig. 4). There appears to be a lower density in the straight sections of the trail, but this is due to the superimposition of a greater proportion of footfalls. The pronounced elongation of some of the tracks transverse to the trail is also due to the coalescing of adjacent footfalls. A deep depression hidden in shadow (text-fig. 3A, bottom right) marks the site of a calamite which appears to lie only just on the edge of the trail. There is some equivocal evidence that its close proximity to the course taken by the arthropod may have prompted slight 'side stepping' by the limbs on the side in question. The surface has been eroded in the vicinity of the depression, however, and the critical imprints either lost or impaired as a consequence. There is no reliable evidence for the direction of progress of the arthropod (cf. Briggs *et al.* 1979, p. 278).
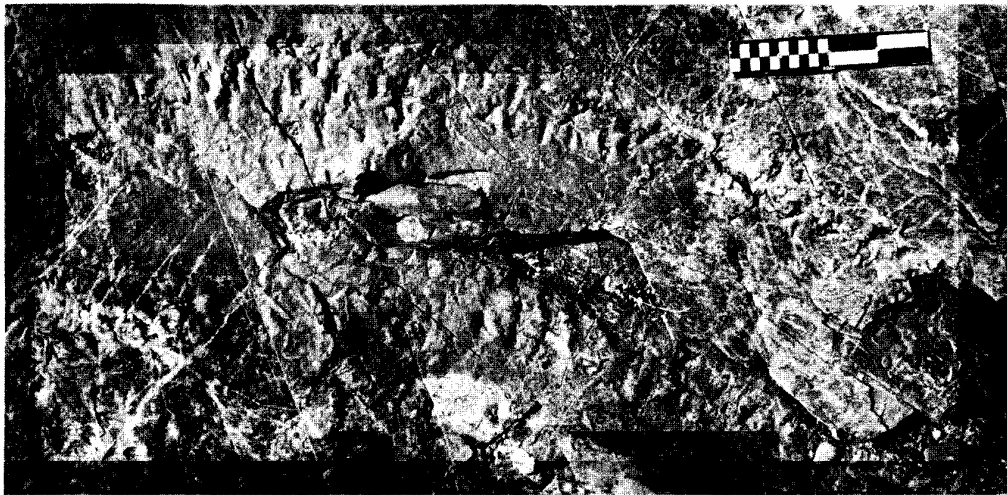
TEXT-FIG. 4. Well-preserved portion of the trail (down-dip; position marked on text-fig. 3B) showing increase in the lateral spread of tracks in curve (20 cm scale bar).

INTERPRETATION AND DISCUSSION

The trailmaker. The size of the trace fossil, the large number of regularly spaced tracks, and the sedimentary environment all indicate that the trail was made by *Arthropleura* (see Briggs *et al.* 1979, p. 278 for a fuller discussion).

Environmental setting. Following the deposition of Bed 1 (text-fig. 2B), probably by sheetflooding, a *Stigmaria* 'forest' was established. Low-energy floods deposited the siltstone of Bed 2 in which stands of calamites later rooted. A subsequent sheetflood deposited Bed 3, burying the lower parts of the calamites. A thin layer of silt accumulated on the top of Bed 3, probably during the waning phase of the flood. *Arthropleura* then walked through the area, following subaerial emergence, perhaps searching for food among the detritus carried in by the floodwaters. The cohesive nature of the mud was probably essential for preservation of the tracks which would have been easily eroded by the next flood had they been made in sand alone. Calamites in Bed 3 extend *through* the trail horizon into Bed 4. There is evidence of syndepositional scour of the sediment of the trail horizon around some of the stems. There is no sign of upward disruption of the bedding, such as would have occurred if the calamites had grown up through the trail horizon after it had been deposited. It is highly unlikely that the bed could have preserved the trail while remaining sufficiently wet to allow a large calamite to grow through it without causing disruption. It is also improbable that the calamites grew in positions flanking the trail by chance. The 'trees' were therefore standing when the trail was made. The sinuous course represents *Arthropleura* picking its way through this 'forest' of calamite stems.

Number of limbs and size. Due to the small number of complete specimens known, the ontogeny of *Arthropleura* is poorly understood. The apparent variation in the number of somites in near complete specimens (Rolfe 1969, p. 608) may indicate that development was partially anamorphic. If somites were indeed added during growth, estimating the dimensions of the trail-maker (apart from width) from the trace-fossil is not straightforward, particularly in the absence of evidence for the number of appendage-bearing somites. A reconstruction by Rolfe and Ingham (1967, p. 121, fig. 2) was based on the largest, most complete specimen known (Rolfe 1969, p. 607). Their reconstruction shows an individual 85 cm long with twenty-eight limb-bearing somites, which would produce a trail about 24·5 cm wide, assuming that Rolfe and Ingham have reconstructed the attitude of the appendages correctly (note that the magnification of × 0·2 given for the same figure reproduced in Rolfe 1969, p. 609, fig. 387, is extrapolated for an animal 1·8 m long). The *Arthropleura* trail from the Namurian of Arran (Briggs *et al.* 1979) was made by an individual with only twenty-three limb-bearing somites (assuming that all the limbs were used in walking) but is none the less much wider (36 cm) than predicted by Rolfe and Ingham's (1967) reconstruction. Reducing the length of the reconstruction by five somites (assuming anamorphic development) indicates that the Arran individual was about 105 cm long. The near-complete juvenile figured by Rolfe (1969, p. 608, fig. 386), however, has at least twenty-three postcephalic (and presumably limb-bearing) somites although it is only 65 mm long. The smallest *Arthropleura* known (Rolfe *et al.* 1982, p. 426) is 29 mm long and appears to have twenty to twenty-two somites (Secretan 1980, p. 32). The data available, although unsatisfactory, therefore suggest some variability in rates of development in different examples (or species) of *Arthropleura*. The number of body segments commonly varies in living adult myriapods with more than twenty (Lawrence 1952).

Preliminary observations by John Almond (pers. comm.) suggest that two rather than one pair of limbs correspond to each of the more posterior tergites (at least) of small *Arthropleura* from Montceau-les-Mines (see Secretan 1980). If true, this does not necessarily imply a return to Waterlot's (1934) interpretation of *Arthropleura* limbs as biramous (see discussion in Rolfe and Ingham 1967, p. 118); it may, however, indicate that each tergite of *Arthropleura* corresponds to some sort of diplosegment. If Almond's observation can be confirmed and shown to apply to large arthropleurids, the basis for the reconstruction in text-fig. 5 (Rolfe 1969, p. 609) will require revision. In addition, a reconsideration of the estimate of the number of tergites in the individual which made
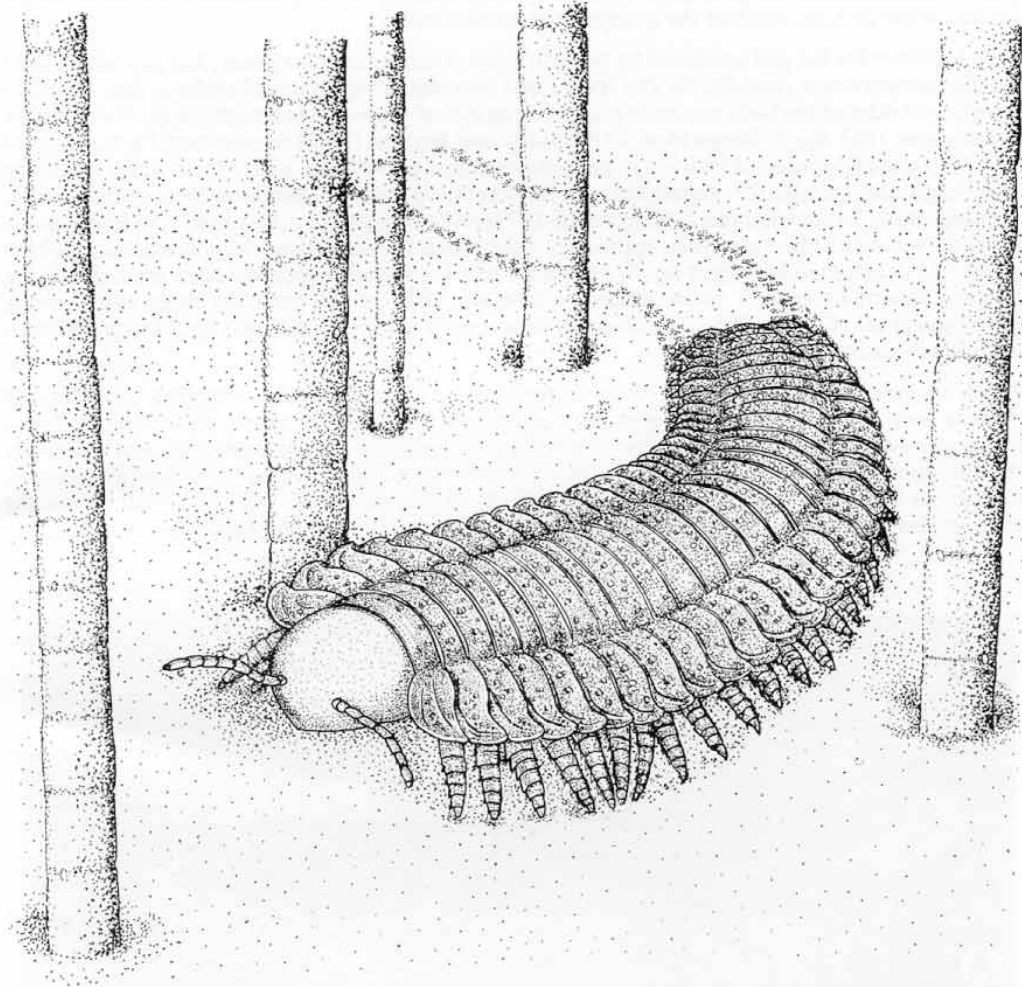
TEXT-FIG. 5. Reconstruction of *Arthropleura* making the trail. The detailed morphology of the head is unknown. The arthropod is depicted walking around the corner at the bottom of text-fig. 3A, B in a northerly direction (toward the left of the page). There is no evidence, however, to indicate that this was the more likely direction of progress. The position of the calamites is somewhat schematic; that in the left foreground has been displaced to one side to avoid concealing part of the arthropod. (For discussion see text; drawing by Annemarie Burzynski.)

the Arran trail (Briggs *et al*. 1979) will be necessary. Twenty-three pairs of walking limbs would then imply about half that number of tergites—an unlikely total for such a large individual.

Determination of the number of walking appendages from the trace-fossil depends on identifying two successive imprints of the same limb (i.e. evidence of a stride) and counting the number of footfalls between them (Briggs *et al*. 1979, p. 282). Unfortunately, the preservation of the present trail is inadequate to provide the necessary evidence. For the purpose of reconstruction (text-fig. 5) the number of walking limbs (twenty-eight pairs) and relative proportions of the Rolfe and Ingham

(1967) reconstruction are assumed; the arthropod is unlikely to have exceeded 102 cm in length (based on the 29·5 cm width of the straight sections of the trail).

Gait. Evidence for the gait employed by the arthropod is largely circumstantial, but provides a basis for the reconstruction (text-fig. 5). The trace-fossil provides no unequivocal evidence that the limbs on opposite sides of the body moved in phase, but an out-of-phase mode is highly improbable (Rolfe and Ingham 1967, fig. 2; Briggs *et al.* 1979). Rolfe and Ingham (1967) reconstructed a slow gait of 3·0 : 7·0 (ratio of duration of forward to backstroke; Manton 1977), i.e. with 70% of limbs in contact with the ground, suitable for pushing through the vegetation and plant debris on the coal-forest floor. Analysis of the Arran trace fossil (Briggs *et al.* 1979) revealed a gait of 5·5 : 4·5 (45% of limbs on the ground), when the arthropod was apparently unimpeded by vegetation. An intermediate pattern of 4·0 : 6·0 is adopted here (text-fig. 5) as a likely gait for the arthropod on open ground walking between calamite stems. A phase difference between limbs of 0·1 gives the most even spacing (cf. Briggs *et al.* 1979, pp. 283–284), hence *Arthropleura* is reconstructed (text-fig. 5) with ten limbs in a metachronal wave.

Mode of cornering. This trace fossil provides direct evidence for the cornering capability of *Arthropleura*. The configuration of imprints suggests that it changed direction in a fashion similar to living myriapods. The series of papers on arthropod locomotion by Manton (1977 and references therein) does not include a detailed discussion of cornering in the Myriapoda, but her observations on turning in the onychophoran *Peripatus* (1950, p. 561) explain how this is achieved. When the arthropod changes direction the body follows a turn of the head—'the legs of both sides are displaced
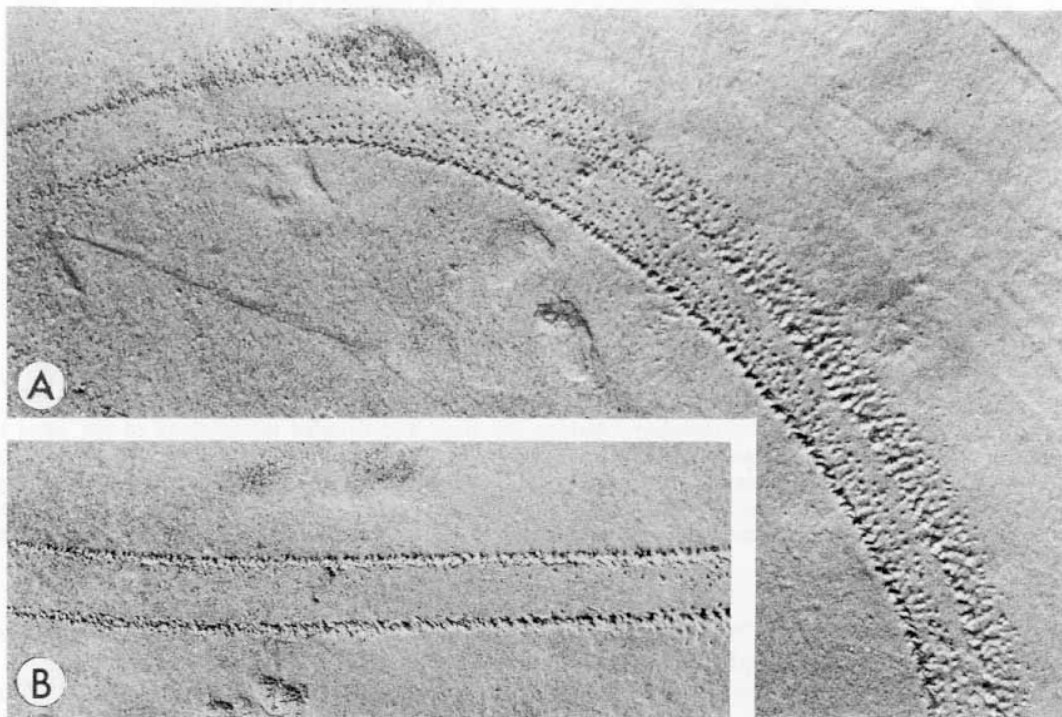

TEXT-FIG. 6. Trails of a recent millipede *Scaphiostreptus seychellarum* (130 mm long) made in wet mud, × 0·7. A, curved, to show the increase in the lateral spread of tracks. B, straight. (Research and photographs by E. F. Walker.)

laterally in the direction of the turn, and the angle of swing of the legs on the outer side is increased without alteration of the pattern of the gait. If the turn is acute . . . the posterior part of the body does not follow the path of the anterior end but becomes progressively displaced towards the side.'

Although Manton's studies of the locomotion of myriapods were based in part on records made by the arthropods walking on smoked paper, very little work has been done on the traces produced by living arthropods walking on soft substrates. Some preliminary work by Rolfe (1980, p. 135, fig. 5) and Elaine Walker (Manchester University) has emphasized what a range of trails an individual arthropod can produce. Walker has provided photographs (text-fig. 6) of trails produced by the millipede *Scaphiostreptus seychellarum* which, although made by an individual a mere 130 mm long with about one hundred pairs of limbs, provides a basis for comparison with *Arthropleura*. Walker describes (pers. comm.) how the less dense part of the curved trail (text-fig. 6A) is made by the anterior limbs of the millipede as it probes forward, while the more pronounced lineation is the product of the overlapping imprints of the posterior limbs. The apparent 'doubling' of the right and left rows of prints on the corners of the *Arthropleura* trail (text-fig. 3A, B, left curve) indicates that, in this case also, the posterior part of the body did not precisely follow the anterior as the arthropod probed ahead to find a course between the calamite stems.

Briggs *et al.* (1979, p. 287) noted that the Joggins *Arthropleura* trails (Ferguson 1966, 1975) showed a wider spacing of imprints across the width of the right and left rows than the Arran example, and they considered that this suggested 'a greater variation in appendage length and flexibility in the smaller Joggins arthropleurids'. It is perhaps more likely that this wider spacing is the result of the arthropod 'probing' forward with the anterior appendages, although the figured examples from Joggins (Ferguson 1966, fig. 2; 1975, fig. 4) do not show as pronounced a change of direction as the example described here.

Lateral flexure. The deduced length of the trailmaker indicates that significant lateral flexure of the body must have taken place. Størmer (1976, p. 111, fig. 43) figured a posterior axial doublure on the tergites of *Arthropleura* extending forward about 25% of the length of each somite (a length equivalent to the overlap between tergites reported and reconstructed by Rolfe 1969, p. 608, fig. 387). Lateral flexure of the trunk would have been limited by the length of this doublure, and by the pronounced anterior keel on the paratergal folds (cf. Richardson 1959, fig. 43). Text-fig. 7 shows that sufficient curvature could be achieved within these constraints to allow *Arthropleura* to produce the trace fossil.
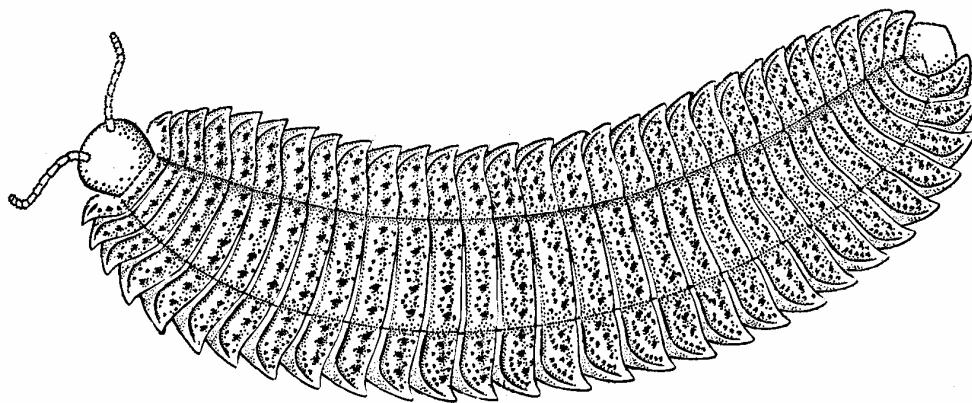
TEXT-FIG. 7. Reconstruction of *Arthropleura armata* displaying the lateral flexure required to produce the trail (after Rolfe and Ingham 1967, fig. 2), × 0·14. Both the telson and the detailed morphology of the head are unknown.

DISTRIBUTION OF ARTHROPLEURA TRAILS

Arthropleura trails have been reported from both North America and Europe, and range in age from Namurian (Pendleian) to Stephanian B (Table 1). In addition to those figured in the literature (Table 1), large, poorly preserved trails from the Westphalian D north of Florence, Cape Breton Island, Nova Scotia, have been attributed to *Arthropleura* (Baird *in* Carroll *et al.* 1972, p. 54). M. Gibling (pers. comm.) also reported an example from the upper Westphalian–Stephanian Morien Group in the Sydney Basin, Cape Breton Island.

TABLE 1. *Arthropleura* trails figured in the literature

Locality	Age	Width of trail	Source
Arran, Scotland	Namurian (Pendleian)	36 cm	Briggs *et al.* 1979
Gardner Creek, New Brunswick	Westphalian A or B	29·5–36·5 cm	This paper
Joggins, Nova Scotia	Westphalian B	Up to 26 cm	Ferguson 1966, 1975
Montceau-les-Mines, France	Stephanian B	Up to 10·8 cm	Langiaux and Sotty 1977*a* Rolfe *et al.* 1982

The sedimentary environment of the Montceau-les-Mines trails has yet to be described (Langiaux and Sotty 1977*b*; Rolfe *et al.* 1982), but they appear to occur in fluvial flood-plain overbank deposits (J. E. Pollard, pers. comm.). The environment of the New Brunswick locality described here and those at Joggins and in Scotland are similar, but the New Brunswick occurrence differs in detail. The specimens at Joggins occur in a sheet sandstone that thickens laterally into a channel-filling sandstone (Bed 39/S2 of Duff and Walton 1973). The sheet sandstone possibly represents a crevasse splay that was subaerial at the time the tracks were made. The overall sedimentary environment was interpreted by Duff and Walton (1973) as an upper delta plain, characterized by laterally migrating fluvial channels with intervening low-lying floodbasins, lakes, and coal-swamps. In Arran, the well-preserved trail also occurs in a proximal deltaic environment, near the top of a fluvial channel-fill, in rippled, flaser-bedded, and rooted sandstones that were probably deposited in shallow water, close to the channel margin. The relatively good preservation of the tracks suggests that they were made subaerially, after the water level in the channel had dropped (Briggs *et al.* 1979).

The Tynemouth Creek Formation (Plint and Poll 1982) contrasts with the previously described depositional settings in that it apparently represents a much drier alluvial fan environment characterized by periodic sheetfloods across an otherwise quiescent area of relatively slow deposition. Desiccation, bioturbation, and weathering considerably modified the sediments under these conditions of intermittent deposition. Although smaller *Arthropleura* may have sought the relatively humid environment provided by hollow trunks (Rolfe 1980, p. 149), this refuge was presumably not as readily available to larger individuals such as the trail-maker in this case. The occurrence of *Arthropleura* in this environment thus provides additional evidence for an essentially terrestrial rather than amphibious or aquatic habitat (Rolfe 1969; Briggs *et al.* 1979). A specimen of an *Arthropleura* limb with *Monoletes* pollen grains attached has recently been reported from the middle Pennsylvanian Mazon Creek biota (Richardson 1980). This suggests that the arthropod may have pollinated medullosan seed ferns while brushing flood-plain scrub (Scott and Taylor 1983; Taylor and Scott 1983), thus supporting a terrestrial habitat.

TAXONOMY

Briggs *et al.* (1979) referred the *Arthropleura* trail from Arran to *Diplichnites* Dawson, 1873, pointing out that this genus was originally described from a similar non-marine environment in the Westphalian at Joggins.

The holotype of the type species, *D. aenigma* Dawson, 1873, has not been located, and the details of the specimen are not clear on the original woodcut (Dawson 1873, fig. 3). Briggs *et al.* (1979) established a new species, *D. cuithensis* for the Arran example, in recognition of the morphology of the individual tracks, and the size attained by the trace. Although in agreement with the need to maintain a morphological rather than biological basis for trace fossil taxonomy, they (1979, pp. 288–289) argued against the current tendency to extend the concept of *Diplichnites* (Seilacher 1955) to include what are obviously *marine* trails and probably the work of trilobites. In doing so they pointed out that such a restriction would not necessitate the erection of new taxa for these marine trace fossils, as a number have long been available in the literature (see Osgood 1970; Anderson 1975).

The ichnogenus *Diplichnites* has been applied to non-marine traces made by animals other than arthropleurids and myriapods (Tevesz and McCall 1983). Savage (1971) described traces from later Carboniferous or early Permian periglacial lake sediments in Natal which he assigned to *Diplichnites* and interpreted as trails of syncarid or peracarid crustaceans. Bromley and Asgaard (1979, p. 64) referred traces from Triassic freshwater sediments in East Greenland to *D. triassicus* which they also considered to be the work of crustaceans (branchiopods). Detailed study of well-preserved examples of such traces should reveal the number of walking limbs employed by the animal. This would provide a means of distinguishing crustacean walking trails from those of the more numerous-limbed myriapods.

Dawson (1862), in his first report of the trails which he subsequently named *Diplichnites*, observed that 'their direction curves abruptly'; the original concept for the ichnogenus therefore included curved trails. The straight portions of the trail described here widen gradually into the curved portions which are characterized by a greater width of the rows of tracks (text-figs. 3, 4). In part of the trail (text-fig. 3A, B, left curve) the lateral spread of imprints in the opposing rows of tracks appears to divide for a short distance where the posterior end of the arthropod has not precisely followed the anterior. Examples of arthropod trace-fossils are known where different sections are referable to different ichnotaxa; Crimes (1970, pl. 12, figs. *a, b*), for example, figured specimens of *Rusophycus* continuous with *Cruziana*. These traces normally occur separately, however, are clearly distinct morphologically, and represent different behaviour patterns. In the present example it would seem unnecessary and counterproductive to assign the curved portions of the trail to a new ichnogenus, separate from the straight portions. It would be impossible to decide exactly where one taxon ends and the next begins! Thus the diagnosis of *Diplichnites* is emended below, as Dawson (1862, 1873) presumably intended, to include the curved parts of trails. The trail described here is referred to *D. cuithensis* Briggs, Rolfe and Brannan, 1979.

This more complete diagnosis of *Diplichnites* reinforces the observation of Briggs *et al.* (1979) that the ichnogenus should not be applied to traces attributed to trilobites. The opposing rows of imprints in trilobite traces differ in showing no obvious tendency to expand in width on corners (see Osgood 1970, for example). The articulation of the trilobite thorax does not permit significant lateral flexure. Thus unlike myriapods, including *Arthropleura* (as evidenced by this trail), the anterior of trilobites could not 'probe' forward and follow a slightly different line to the posterior.

SYSTEMATIC PALAEONTOLOGY

Ichnogenus DIPLICHNITES Dawson, 1873 (emended)

Type ichnospecies. D. aenigma Dawson, 1873, by original monotypy.

Emended diagnosis. Morphologically simple trail, up to 37 cm wide, consisting of two parallel rows of tracks (each up to 11 cm wide); width of opposed rows increasing on curves corresponding to greater lateral separation of individual tracks; each row may divide into two on acute curves; individual tracks elongate roughly normal to trail axis, spaced closely and regularly at as few as one per cm in large examples.

Diplichnites cuithensis Briggs, Rolfe and Brannan, 1979

Text-fig. 3

Type locality. Salt Pans harbour quarry, Laggan, Arran, Scotland.

Additional localities. Gardner Creek, Tynemouth Creek, southern New Brunswick, Canada.

Horizon. Carboniferous. Namurian, Pendleian Stage (E_1) to Westphalian A or B.

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