A GIANT MYRIAPOD TRAIL FROM THE NAMURIAN OF ARRAN, SCOTLAND

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ABSTRACT. A large trace fossil in the Limestone Coal Group of Arran is preserved in a deltaic, channel-fill sandstone from a cyclic sequence including coals. The trail, *Diplichnites cuithensis* ichnosp. nov., consists of two parallel series of closely spaced imprints, and is attributed to the giant Carboniferous myriapod *Arthropleura*, making this the earliest evidence for the genus. Analysis of the trail suggests the individual responsible was *c.* 1 m long, and had twenty-three pairs of appendages. Knowledge of modern myriapod gaits has been used to extrapolate a theoretical trail for *Arthropleura*, which compares well with the fossil trail. The trail suggests that a gait pattern of forestroke:backstroke of 5·5:4·5 was used in walking across the sand substrate. This contrasts with the previous estimated gait of 3:7 that *Arthropleura* might have used in pushing through coal-forest litter. Such a range of gaits is well within that recorded for individual Recent species of millipede. *Diplichnites* is emended to exclude most trilobite locomotion trails.

'As Professor Phillips has remarked, every geologist who visits Arran is tempted to write about it, and finds something new to add to what has been already put on record' (Bryce 1859, p. 61). It is therefore remarkable that the present large trail (Pl. 28), 6·25 m long and 0·36 m wide, has escaped previous attention, lying as it does on one of the popular geological excursion routes (south-east of locality 12 of Macgregor 1965, pp. 128-129) beside the footpath from Laggan to the Cock of Arran. The oversight is due to the trail's near invisibility on the dipping bedding plane, except under the raking light of early morning and evening. The trail was drawn to the attention of one author (D. E. G. B.) on a Cambridge University excursion in 1975. It will form a useful new locality on future itineraries (Macgregor 1965, p. 126, fig. 13), the usual conservation courtesies being observed. An exhibit of a replica of the trail is mounted in the Arran Nature Centre, near Brodick. Specimens referred to are held by the Hunterian Museum, University of Glasgow (prefixed HM).

GEOLOGICAL SETTING

Occurrence

The trail runs (vector 087°) across the south face of a small sandstone quarry (NR 9722 5112) which opens off the south shore of the salt pans harbour between Cock Farm and Laggan, 1·75 km south-east of the Cock of Arran. The bedding plane dips 32° at 358°. The quarry, which is flooded by the sea at high tide, was opened no later than the eighteenth century: it is quite likely that quarried blocks of the sandstone bearing the missing part of the trail are built into the walls of the ruined malt kiln, above the south-east corner of the quarry (at NR 9720 5111). A second trail (Pl. 29, fig. 3) 1·9 m long (lineation 167°-347°) is located on the slab, 2·32 m at 181° from a point on the main trail 5·5 m from the west face of the quarry.

Stratigraphy

The trail occurs on the bedding plane forming the south face of the quarry, *c.* 60 mm below the top of a 6 m thick white sandstone (text-fig. 1). This is sandstone unit 136 on the large-scale unpublished maps of the area by Dr. Grace Page, Bedford College, London University. The unit formed the roof of the coal seams (Ramsay 1841, p. 31) which ceased to be worked in the eighteenth century (Gunn *et al.* 1903, p. 146; Gunn *in* Tyrrell 1928, p. 268). The top of this sandstone is 42·6 m (dyke omitted) below the base of the limestone taken as the Index Limestone (Gunn *et al.* 1903, p. 49; Gunn and Lee *in* Tyrrell 1928, p. 60; Macgregor 1965, p. 32) and 92·7 m above the top of the supposed Hosie Limestone equivalent (Gunn *et al.* 1903, p. 48; Gunn and Lee *in* Tyrrell, 1928, p. 58). This places the trail in the Limestone Coal Group, of Namurian Series, Pendleian Stage (E_1—Ramsbottom 1978). The Limestone Coal Group section around Laggan was measured (text-fig. 1) and found to total 135·3 m. This is thicker than the whole of the Carboniferous Limestone Series of the Corrie section (*c.* 119 m according to Macgregor 1965, pp. 104–105) and emphasizes the southerly attenuation (George 1960, pp. 74–76) of the Limestone Coal Group (estimated to be 83 m thick at Corrie from George *et al.* 1976, p. 48, fig. 13: 2).

Sedimentary environment

The Limestone Coal Group (text-fig. 1) is predominantly composed of clastic sediments and is bounded above and below by limestones (Index and Hosie respectively) representing marine transgressions. The succession appears to have been deposited in a proximal deltaic environment (Frazier and Ozanik 1969), similar to that of the Midland Valley Limestone Coal Group (Moore 1959; Francis 1965, p. 352; Read and Dean 1976 and references therein). The trail is preserved on the surface of a bedding plane of heterogeneous sandstone. At the eastern end the sandstone is thicker, coarser, and purer (HM TS.17841—quartz arenite, McBride 1963) than elsewhere and it grades westwards into a finer sandstone (HM TS.17843—lithic arkose) containing discontinuous layers of shale.

Sections of the western slab (Pl. 28; Pl. 29, fig. 2) reveal small-scale ripples with silt drapes, a structure analogous to flaser bedding and indicating a variable low-velocity flow regime. Some of the ripples appear to be flat topped, although the evidence is equivocal, which may indicate planing in very shallow water. The coarser cross-bedding lower down in the sandstone unit indicates a higher current velocity and the accumulated evidence suggests that the unit may represent a channel which was gradually silted up. The surface of the slab preserves traces of roots to which biogenic disruption of the bedding structures may also be attributed. The material immediately overlying the trail lacks evidence of penetration by roots which suggests that the vegetation was penecontemporaneous with the formation of the trail and was not established subsequently. This is supported by the occurrence of a root apparently pulled into alignment by the arthropod (Pl. 29, fig. 1). The clarity of the imprints in such a coarse lithology (Pl. 30, figs. 5, 6) renders it unlikely that they were subaqueous in origin.

Roots occur at many horizons in the succession (text-fig. 1), as do *Lepidodendron* sp. (Gunn *et al.* 1903, pp. 49, 156, 166; Gunn *in* Tyrrell 1928, p. 60) and *Stigmaria* sp.

Abundant plants occur in a dark-grey micaceous siltstone 1·4 m above the trail horizon (text-fig. 1). These consist (Dr. A. C. Scott, pers. comm.) of fragmentary 'carbonized' compressions, stem and root fragments of which about half are unidentifiable, and include one piece of unidentified lycopod (HM Pb.4577). The most common plant is a pteridosperm, *Sphenopteris elegans* (Brongniart) Sternberg = *Heterangium grievii* (Williamson), represented mainly by ribbed stems (an up-to-date synonymy and description is given by Van Amerom 1975, pp. 9–14, pls. 1–3). Stratigraphically *S. elegans* is most widely recorded (Kidston 1923, pp. 242–248; Walton 1940, p. 124 as *Diplotmema adiantoides*) in the Scottish Upper Limestone and Limestone Coal Groups. Maceration of the siltstone yielded one unidentified *Lagenicula*-like megaspore.
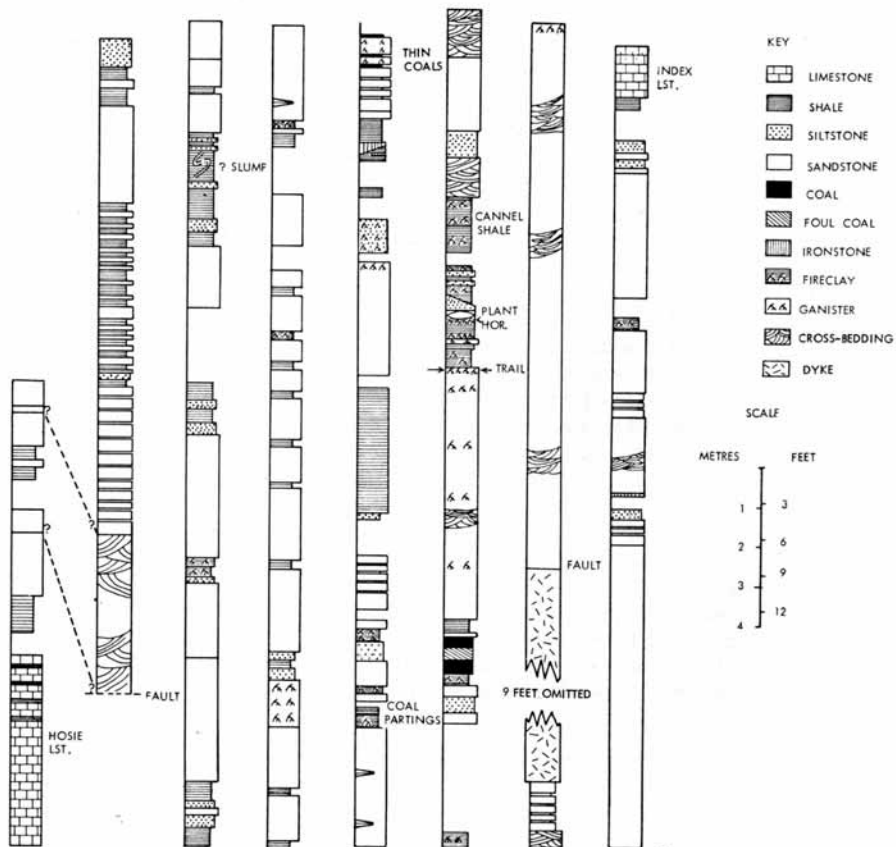
TEXT-FIG. 1. Measured section through the Limestone Coal Group north-west of Laggan, showing the position of the trace fossil and the overlying plant-rich horizon.

THE TRACE FOSSIL

Description

Both trails are somewhat indistinct from over two hundred years of weathering. The longer one (Pl. 28) is 36 cm wide, and extends some 6·25 m across the bedding plane. It may be considered, for descriptive purposes, to run east–west, although it curves gently southward at the western and northward at the eastern end of the exposure. A large slab removed from the central part of the trail (Pl. 28), presumably by the quarriers, divides it into two sections. The western end is thinner bedded and separated readily from the substrate, whereas the unit thickens to the east and becomes fused to the subjacent sandstone. The western section was collected by us (HM X.1041, Pl. 29, fig. 2), and reinforced latex peels taken of the eastern section (and shorter trail) were used to prepare fibreglass casts (HM X.1042).

The imprints of individual appendages are usually represented by a single depression oriented roughly normal to the axis of the trail (Pl. 29, fig. 1; Pl. 30, fig. 1). Each depression is generally deeper and wider at the end nearest the trail margin and shallows and tapers towards the axis. The appendages also pushed up mounds of sediment between the imprints which may be preserved raised slightly above the general level of the bed surface. The tracks become progressively more distinctly preserved towards the eastern end of the exposure, where sharper impressions were revealed by removal of overburden from the northern set in 1977, the width of the paired series of imprints increasing from about 5 cm to a maximum of 9 cm (Pl. 30, figs. 1–4). The footfalls of the shorter appendages, which occur inside the majority, are only evident at this end. This is thought to be due to a variation in the water content of the substrate when the track was formed; the sediment probably became wetter (or perhaps drier) and less cohesive, accounting for the poorer preservation westward (Pl. 29, fig. 2). The poorly defined prints appear to be different in character rather than the product of weathering; the entire slab is thought to have been exposed for the same length of time (*c.* 200 years). Only one series of imprints (Pl. 29, fig. 3) is preserved in the shorter trail, but the reason for this is not clear. During removal of overburden from the eastern section of the longer trail, a careful search was made to see if the previously exposed trail was only an undertrack (Goldring and Seilacher 1971, p. 424), the original being within the removed material. No tracks were found in the overlying sandstone even though it split along planes that might be expected to show them had they been present. The trail therefore appears to be a true surface feature, albeit modified by erosion; no loss by omission of track elements ('fallout' of Goldring and Seilacher 1971) has occurred. This is borne out by the imprints' general lack of sharpness (Goldring and Seilacher 1971, p. 428).

EXPLANATION OF PLATE 28

Diplichnites cuithensis sp. nov. View westward across the bedding plane bearing the trail as it was in 1975. The slab just in view at the western end, beyond the missing portion, has since been removed to constitute a holotype (HM X.1041, Pl. 29, fig. 2). The scale bar represents 10 cm.

PLATE 28

BRIGGS, ROLFE and BRANNAN, Myriapod trail

Individual imprints are spaced closely and fairly regularly at a linear density of about one per cm (Pl. 29, fig. 1; Pl. 30, fig. 1). A certain amount of interference occurs due to footfalls almost coinciding, but this can usually be identified except where the preservation is poor or the impressions have merged due to water in the substrate (Pl. 29, fig. 2). At the newly exposed eastern extremity the well-preserved imprint of a shorter appendage has survived apparently undistorted (Pl. 30, figs. 5, 6). It shows the distinct impression of three spines, the median one deepest and most distal with respect to the appendage which made the imprint, the other two shallower and flanking it symmetrically separated by a distance of about 14 mm. The imprints of the three spines are elongate and they shallow towards the axis of the trail. The individual traces produced by these three projections usually coalesce to form a single depression. The groove made by the largest median spine can sometimes be distinguished as an adaxially tapering extension of the imprint. The imprints of some of the shorter appendages which fall adaxial of the rest, are relatively narrow and shallow and may represent the median spine alone; these appendages may have supported less weight. Evidence for the direction of locomotion based on the orientation of the tracks to the axis of the trail and the mounds of sediment pushed up by the appendages is equivocal (cf. Hanken and Størmer 1975, pp. 262, 263; Goldring and Seilacher 1971, p. 426).

Interpretation

A number of factors indicate that the trail is that of *Arthropleura*, although body fossils of this giant myriapod have yet to be reported from Arran. The large number of regularly spaced imprints eliminates any vertebrate of equivalent size, and all but multipedal arthropods (on grounds partly discussed by Gevers *et al.* 1971, pp. 87-91). Eurypterids are heteropodous, and produce a series of distinctive tracks repeated *en échelon* (Hanken and Størmer 1975; Goldring and Seilacher 1971, p. 429; Waterston pers. comm. although cf. *Merostomichnites* trails), quite unlike the present trail. Eurypterid trails may also show a median longitudinal groove, made by the genital appendage, and such a feature is lacking. Scorpions, such as *Gigantoscorpio*, presumably left distinctive *Paleohelcura* trails, and individual tracks should show a characteristic trifid (or even pentadactyle) imprint from the plantigrade foot with its terminal claw (Størmer 1963, fig. 37). Such imprints are found in *Paleohelcura* (= *Beaconichnus*) *antarcticum* (Gevers), which might have been left by a large amphibious scorpion like *Gigantoscorpio*, rather than by the eurypterid suggested by Gevers *et al.* (1971, p. 90). A number of large, unusual, partially known chelicerates existed in the Carboniferous such as *Cyrtoctenus* Størmer and Waterston, 1968, but these would presumably also have produced trails with widely separated *en échelon*

PLATE 29
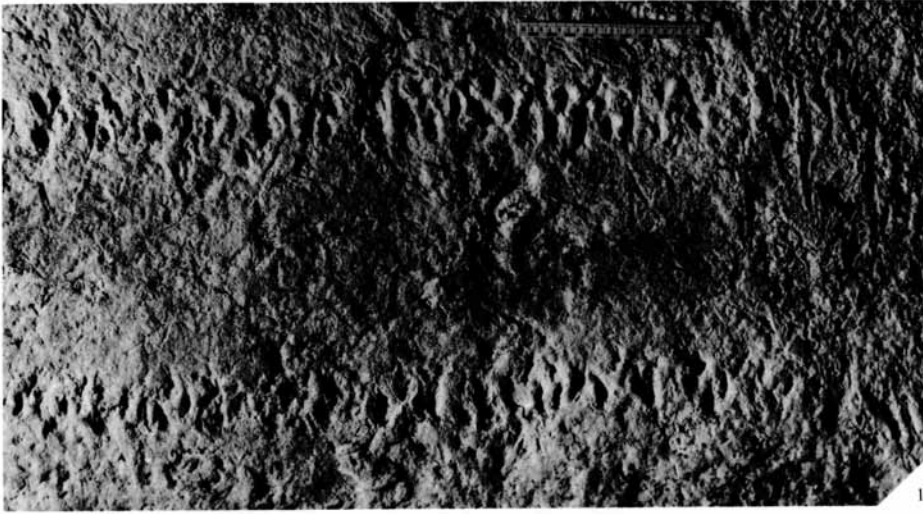
BRIGGS, ROLFE and BRANNAN, Myriapod trail

groups of heteropodous tracks. The large size of the Arran trail is consistent with *Arthropleura*, one of the largest arthropods known, which reaches lengths of up to 1·8 m. The individual making the trail would have measured only about 1 m. The sedimentary environment is similar to that in which the body fossils of *Arthropleura* occur, a cyclic sequence of sediments including coal, representing flood plain or deltaic swamp. In addition, the isolated imprint described above (Pl. 30, figs. 5, 6) conforms exactly to the distal extremity of the walking limbs which terminate in a single spine flanked by the paired spines of the preceding segment (Rolfe and Ingham 1967; Rolfe 1969, fig. 390).

Analysis

The trail produced by an arthropod may be envisaged as a 'set' of footprints (the imprints of three paired appendages in the case of a hexapod) repeated at an interval determined by the distance between successive footfalls of the same appendage, i.e. the stride length. The stride is made up of two elements, a propulsive backstroke when the appendage is in contact with the ground, and a recovery forward stroke. The distance travelled during the backstroke depends on the angle of swing of the limb and the dimensions of the arthropod. The distance travelled during the forward stroke depends on the relative durations of forward and backward strokes.

The size of the trail indicates an *Arthropleura* about 1 m long, assuming that Rolfe and Ingham (1967, fig. 1) have reconstructed the attitude of the appendages to the trunk correctly, and a study of the relative dimensions of their reconstruction shows that the appendages would have been about 10 cm long. Angle of swing varies with the rate of progress of the arthropod (Manton 1954, p. 335) but the large size of *Arthropleura* and simple appendage structure suggest a maximum value of about 60°. The base of an appendage 10 cm long swinging through an angle of 60° will travel

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Notes on the plates

Plate 29 and Plate 30, figs. 1, 5, and 6 were taken in low-angle incident light. Plate 30, figs. 2-4 were taken with the fibreglass replica illuminated from behind (in transmitted light). The deepest part of individual imprints is replicated in slightly thinner fibreglass than elsewhere, and therefore appears as lighter areas using this technique; the tracks are more easily identified as they are unobscured by shadows. The figures are arranged on the plates so that the trail is orientated as it is viewed *in situ*—the western end to the right or top of the plate. Directions of illumination are given in the explanations with reference to the margins of the plate and are bracketed with the magnification.

EXPLANATION OF PLATE 30

Figs. 1-6. *Diplichnites cuithensis* sp. nov. 1-4, HM X.1042/3, fibreglass replica of best-preserved portion of the trail exposed at the eastern end. 1, (north, ×0·15). 2, pair of closely spaced repeated imprints indicating stride length ringed, scale bar 10 cm (transmitted, ×0·15). 3, 4, northern set of imprints (on the right side in fig. 2) largely exposed by excavation in 1977 (transmitted, ×0·35); individual imprints outlined, closely spaced repeated imprints ringed, those flanking them marked by dots in fig. 4 to show evidence of stride length and twenty-three pairs of walking appendages. 5, 6, HM X.1045, latex of counterpart (X.1044) removed in 1977 showing detail of well-preserved imprint indicated *x* in fig. 4 (north-east, ×0·75).

PLATE 30
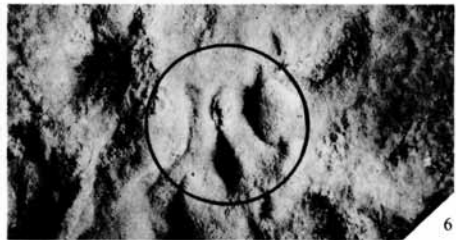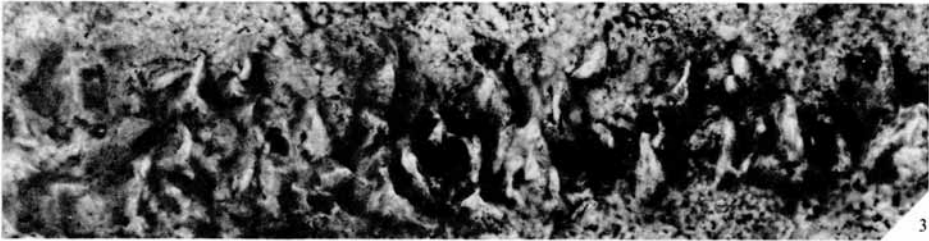
BRIGGS, ROLFE and BRANNAN, Myriapod trail

10 cm during the execution of the backstroke; this provides an *estimate* for this component of the stride length.

If the length of stride can be deduced from the trail, the pattern of gait (the ratio of time spent in the forward stroke to that in the backstroke; Manton 1950, p. 534; 1977, p. 298) can then be calculated using the distance travelled during the backstroke estimated above. The speed and power achieved by an arthropod depend on the relative duration of the forward and backstroke. More powerful gaits (such as those employed by polydesmoid millipedes pushing through leaf litter) at relatively slower speeds are the result of a longer backstroke and hence a larger number of appendages in contact with the ground at any given moment. Stride lengths are notoriously difficult to determine even in Recent millipedes (Manton 1954, p. 337). A large number of uniform appendages produces a dense trail of evenly spaced foot-falls and Manton (1954; 1977, p. 504) often found it necessary to place a 'boot' on one limb to determine the stride length. The smaller number of appendages may make the stride length easier to identify in the tracks of chilopods. Variations in limb length may ensure that the footfalls of some appendages occupy characteristic positions.

A rhythm or repetition in the track will not necessarily conform to stride length (cf. Manton 1952, p. 153, fig. 11; 1977, fig. 7.6c, d) but may represent imprints of intermediate appendages. This is the most likely explanation for the repetition of groups of footfalls at intervals of 6 cm, apparent in the most easterly part of the trail exposed (top section of series on the right of Pl. 30, fig. 1). 6 cm is an unlikely stride length as the distance travelled by the leg bases during the backstroke alone with an angle of 60° is 10 cm. More satisfactory evidence of the stride is provided by the individual imprints of the shorter appendages which plot adaxial of the majority, where they are not obscured by subsequent footfalls. At the eastern end of the northern series of imprints (Pl. 30, figs. 2–4) two closely spaced footfalls and one more widely spaced flanking them on either side are repeated at an interval of about 22 cm. The repeated pair is also evident, although poorly preserved, in equivalent positions in the southern series (Pl. 30, fig. 2) indicating that the left and right appendages were in phase. No satisfactory evidence for any other stride length has been observed.

The stride length of 22 cm evident in the trail combined with a backstroke estimated as 10 cm (assuming an angle of swing of 60°) gives a ratio of the duration of forward to backstroke of 12:10, i.e. a pattern of gait of 5·5:4·5 (diagrammatically represented in text-fig. 2). Thus approximately 45% of the walking appendages were in contact with the ground at any given time. The trail provides no satisfactory basis for deducing the angle of swing; it cannot be assumed, for example, that a relationship exists between this angle and that made by the elongate imprints with the axis of the trail. In places the latter approaches 90° suggesting an angle of swing of zero! It is quite possible, however, that the angle was less than 60° implying an even shorter back-stroke and correspondingly faster gait, assuming that the evidence for a stride length of 22 cm is reliable. The number of walking appendages is indicated by the number of footprints between two successive imprints of the same limb, i.e. within a stride length; there appears to have been about twenty-three pairs (Pl. 30, fig. 4). The number of appendages employed in a single metachronal cycle (executing various stages of the same stride) depends on the phase difference between them, i.e. the

TIME ———————→

APPENDAGES

n-1

n

n+1

pd   t
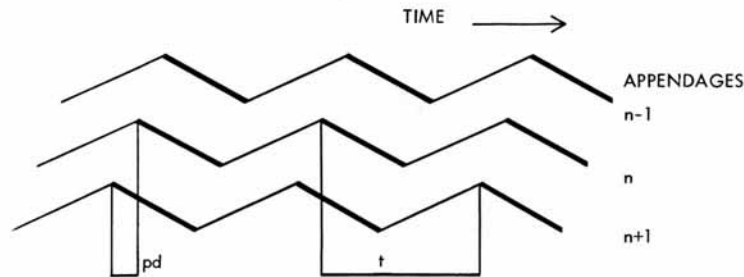
TEXT-FIG. 2. Diagrammatic representation of the gait of *Arthropleura* based on the trail. The movements of three successive appendages are shown, the forward swing by a thin upward-sloping line, the propulsive backstroke by a thicker downward-sloping line. The relative durations of the forward and backward strokes are 5·5:4·5 and the phase difference ($p\,d$) between successive appendages is 0·14. t is the time separating the footfalls of the two successive appendages. (Diagram constructed after Manton.)

fraction of the duration of a pace separating two successive limbs (the smaller the phase difference below 0·5 the greater the number per cycle). The phase difference is expressed as that proportion of a pace by which appendage $n+1$ is in advance of appendage n (text-fig. 2; cf. Manton 1950, fig. 1; 1977, fig. 7.1). Changes in the pattern of gait in Recent arthropods are always accompanied by alterations in the phase difference, but this relationship cannot be expressed as a formula which would allow phase difference to be calculated from the gait deduced above. However, Recent arthropods tend to space the propulsive limbs so that the distance between the footfall of the last of one metachronal wave and the first of the following approximately equals that between propulsive limbs within a wave (Manton 1954, pp. 329, 330, text-fig. 5; 1977, fig. 7.4). This factor can be used to assess the number of appendages in a wave, and hence the phase difference (text-fig. 3), assuming a pattern of 5·5:4·5 and an angle of swing of 60° (a value of less than 0·5 is indicated by the even spacing of the footprints in the trail and the fact that the left and right appendages were in phase). The most regular spacing is achieved with seven appendages in a wave, suggesting a phase difference of 0·14. Thus three metachronal waves would have been evident travelling forward along the length of the arthropod (a gait similar in most respects to that employed by *Polydesmus* running freely; Manton 1954, pl. 55, fig. 38; 1977, pl. 5, fig. *f*).

The data deduced above can be used to plot a theoretical trail (cf. Manton 1950). The stride length is known; the relative spacing of the imprints in a single set, however, must be determined. Distance from the axis of the trail depends mainly on the length of the appendages. Rolfe and Ingham's (1967, fig. 1) reconstructed individual has twenty-eight pairs, but the anamorphic ontogeny of *Arthropleura* suggests that the relative dimensions of an individual with only twenty-three may be assessed by removing five median somites and closing the gap. The footprints of shorter limbs at the anterior and posterior end will plot inside the rest, thus accounting for a maximum width of each series of imprints of about 9 cm (Pl. 30, figs. 1–4). The linear distance separating a footprint of limb n from the first subsequent footprint of limb $n+1$ (the
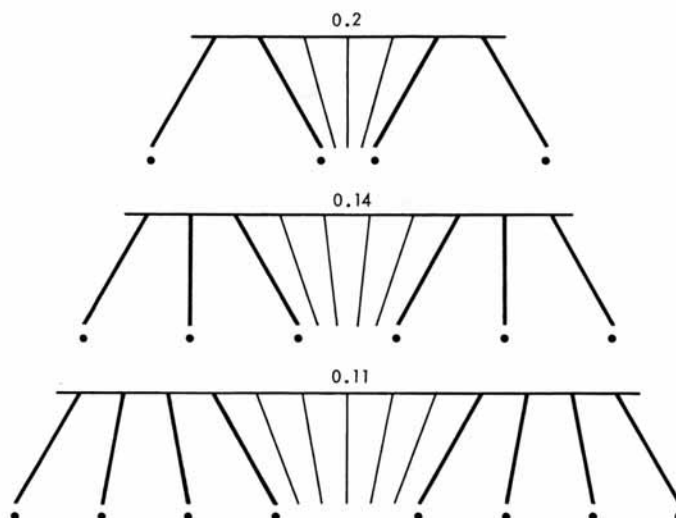
TEXT-FIG. 3. Diagram showing the effect of altering the phase difference between successive appendages on the spacing of the propulsive limbs. A relative duration of forward to backstroke of 5·5:4·5 (i.e. approximately 45% of the appendages in contact with the ground) and an angle of swing of 60° are assumed. Propulsive limbs (in contact with the substrate) are represented by thick lines, the dots emphasizing the spacing between them; legs performing the forward recovery stroke are shown as thin lines. (After Manton 1954.)

appendage behind n) is given as d (the distance travelled by the arthropod during the time between the footfalls of the two successive appendages) minus the exsagittal distance s separating the middle of the bases of the two limbs (Manton 1950, p. 537). d is the product of the time t (text-fig. 2) separating the footfalls of two successive appendages, and the speed y. t can be calculated from the duration of pace (stride length/speed, i.e. 22 cm/y unknown), if the phase difference (0·14) is known: thus $t = (22/y) - 0·14(22/y)$. Hence $d = y(0·86 \times 22)/y = 18·9$; the speed of progression y is eliminated and need not be known. The distance s between the bases of the appendages varies along the length of the arthropod and was estimated on the basis of Rolfe and Ingham's (1967, fig. 1) reconstruction. The resultant of $(d - s)$ is positive and therefore the footprint of $n + 1$ is plotted that distance anterior of the footprint of appendage n (Manton 1950, p. 537). The theoretical trail (text-fig. 4) is similar to the best-preserved section of the fossil trail. Individual footprints in the latter could even be attributed to particular appendages, but this is considered unwarranted on the available evidence. It is likely, however, that the two closely spaced imprints upon which the deduced stride length is largely based (Pl. 30, fig. 4) represent the shortest appendages, i.e. the first and last, which plot together in the theoretical trail (text-fig. 4). A theoretical
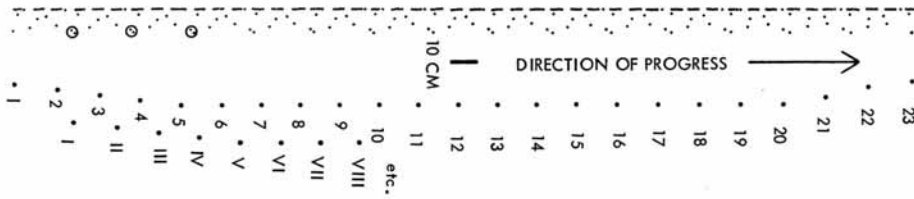
TEXT-FIG. 4. Theoretical trail of *Arthropleura* based on Rolfe and Ingham's (1967) reconstruction of the body, and the gait deduced from the trail (text-fig. 2). The arthropod is assumed to have had twenty-three pairs of walking appendages. Each dot represents the imprint of a single appendage. The right side of the trail represents a single set of imprints made by the right appendages (numbered in Arabic). Part of the next set is also shown (numbered in Roman) offset but separated by the stride length of 22 cm. The left side shows the trail generated when sets produced by the left appendages are superimposed overlapping as they would in life. Individual imprints tend to merge giving the impression of a dashed line along the outer margin. The imprints of appendages 1 and 23, which plot close together, are ringed at the beginning of the trail to show how they indicate the stride length.

trail could also be generated by constructing a series of 'gait diagrams' showing the positions which the appendages would occupy at equally spaced intervals of time. Such diagrams have been used by Manton (1977, pp. 503, 504) in the analysis of gaits of Recent uniramians, and have the advantage that the relationship between the gait and the imprints produced is instantly apparent; the approach cannot, however, be applied so readily to the trace fossil in question.

DISCUSSION

Rolfe and Ingham (1967, fig. 1) reconstructed *Arthropleura* employing a lower-geared gait than that deduced from the trail, in which nineteen of the twenty-eight pairs of walking appendages borne by the individual were included in a metachronal wave (i.e. a phase difference of *c.* 0·05). This corresponds to a pattern of about 3:7 (text-fig. 5) in which 70% of the appendages are in contact with the ground at any given time. If it is assumed that the distance travelled during the backstroke was not greater than the maximum 10 cm postulated for the gait which produced the trail (and it would likely have been reduced in a lower-geared pattern), the resultant stride would not have exceeded 14·3 cm. It might therefore be argued that Rolfe and Ingham's interpretation of the mode of life of *Arthropleura*—pushing through the debris on the swamp floor—is incorrect in the light of the trace fossil attributed to it, which shows evidence of a much higher geared gait. It is perfectly feasible, however, that both gaits were performed by the same arthropod. Manton (1954, pl. 55, figs. 39, 40) figured a female *Polydesmus angustus* running freely with a pattern of 5·9:4·1, and also harnessed to a 'sledge' (to simulate the effect of pushing through leaf litter) employing a pattern of 2·2:7·8. *P. angustus* thus displays a wider range of gaits than that separating Rolfe and Ingham's reconstruction of *Arthropleura* from the pattern that apparently produced the trail. The low-gear gait would only have been employed
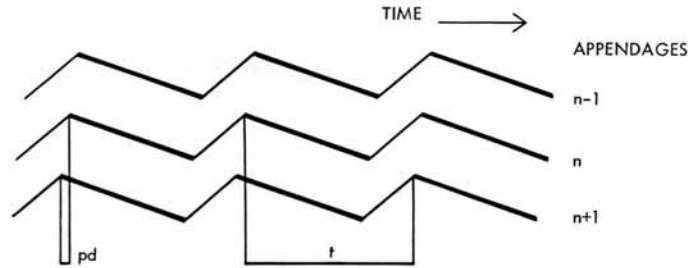
TEXT-FIG. 5. Diagrammatic representation of the gait of *Arthropleura* reconstructed by Rolfe and Ingham (1967, fig. 1). The relative durations of the forward and backward strokes are 3:7 and the phase difference between successive appendages is 0·05. (Symbols as on text-fig. 2.)

by *Arthropleura* when forcing its way through vegetation, an environment un-conducive to the preservation of tracks. The arthropod would have quickened its pace unimpeded by plant debris on more open ground, reducing the time spent on the propulsive backstroke. The nature and interpretation of the trail imply a greater flexibility of the appendages than that assumed by Manton (1977, pp. 234, 235). *Arthropleura* apparently walked on the three distalmost spines of the limb (Pl. 30, figs. 5, 6), suggesting that the paired spines on the more proximal podomeres only supported the appendage when walking over loose vegetation, for example. The simple, undifferentiated nature of the podomeres would have imposed limitations on flexibility, but this is compensated to an extent by the large number of podomeres (Manton 1973, p. 273). The poorer preservation of a triangular area of cuticle at the junction between the podomeres of some specimens (Rolfe and Ingham 1967, pl. 1, fig. 11; Rolfe 1969, fig. 389) may represent the less sclerotized arthrodial membrane of a simple hinge joint (cf. *Anomalocaris*, Briggs, in preparation).

The trail provides little basis for revising Rolfe's (1969) interpretation of the mode of life of *Arthropleura*, which was based on the occurrence of the body fossils, although it does indicate that the arthropod ventured out from the coal forest to cross abandoned distributary channel sands. The observation that one root seems to have been aligned (Pl. 29, fig. 1, top right) by a limb dactyl, if this is not merely coincidental, suggests that some vegetation had become established on the old channel fill.

A similar trace fossil to that on Arran, from the celebrated Joggins section (Westphalian B) in Nova Scotia, was reported and figured by Ferguson (1965, 1966, 1975). It occurs in a sheet sand thickening into a channel sand (bed 39/S2 of Ferguson 1975, p. 74; Duff and Walton 1973, p. 370) and the sedimentary sequence, albeit younger, represents a similar deltaic environment (Duff and Walton 1973; Way 1968). One of the three trails on the slab recovered (Ferguson 1975, fig. 4) was origin-ally attributed to an amphibian (Ferguson 1965, p. 13), but all are now considered to have been made by *Arthropleura* (Ferguson 1966, p. 128; 1975, p. 74, cf. fig. 4; Baird *in* Carroll *et al.* 1972, p. 75). When the Nova Scotia trail maker was identified, body fossils of the arthropod were not known from the Joggins section. Since then the

myriapod described as *Amynilyspes springhillensis* by Copeland (1957) from the same Cumberland Group facies B at Springhill, has been recognized as a juvenile *Arthropleura* (Rolfe 1969, p. R617). In addition, it is possible that the telson of the supposed *Hastimima*? sp. (Copeland and Bolton 1960, p. 43) from Joggins also belongs to *Arthropleura*. Similarly *Eurypterus*? *pulicaris* Salter from the Upper Carboniferous of New Brunswick and the spined 'supposed limbs of myriapods' from Joggins (Copeland 1957, p. 59, pl. 15, fig. 3) could be arthropleurid limbs: reinvestigation is needed. Large, poorly preserved trails from the Westphalian D north of Florence, Cape Breton County, Nova Scotia, have also been attributed to *Arthropleura* (Baird *in* Carroll *et al.* 1972, p. 54). Some of the large cuticle fragments from the Joggins hollow tree stumps previously thought to be tetrapod skin, then eurypterid, were referred by Carroll (1972, p. 71) to *Arthropleura*. However, Dr. C. D. Waterston (pers. comm.) has pointed out that all the material figured by Dawson in 1863, and most of that in 1882, is comparable with large eurypterids such as *Vernonopterus* and *Dunsopterus* (Waterston 1957, 1968). *Hibbertopterus* (= *Campylocephalus*) cf. *scouleri*, a similarly ornamented form, has been recorded from the Upper Carboniferous of Port Hood, Nova Scotia (Copeland and Bolton 1960). The Joggins trails are smaller than the Arran example, ranging in total width from 20 to 26 cm. The largest consists of a paired series of regularly spaced oval depressions, elongate normal to the axis, presumably representing groups of near coincident footfalls which cannot be distinguished. The smaller trails, which are better preserved (Ferguson 1966, fig. 2; 1975, fig. 4) show individual imprints apparently arranged in closely spaced diagonals. Ferguson (pers. comm.) ascribes the difference in preservation to a decrease in water content of the sediment, and presumably increased cohesiveness, when the smaller trails were formed. The trails are clearly those of a multipedal arthropod, and the paired limbs apparently moved in phase, indicating a phase difference between successive appendages of less than 0·5. Although Scudder (1891, pp. 10–18; 1895) reported eight millipedes from Joggins, one scorpion (?) (Scudder 1895, cf. Petrunkevitch 1913), and the crustacean *Pygocephalus*, to which may be added the eurypterid mentioned above, the trace fossil is attributed to *Arthropleura* as the only myriapod of sufficient size. It proved impossible to interpret the best-preserved example with confidence, although Dr. Ferguson kindly provided a cast of a 0·25 m length of the clearest imprints. The gait employed was probably similar to that which produced the Arran trail (a detailed study of the entire length of the smallest trail using the approach described above might confirm a stride of about 13 cm and approximately thirty pairs of limbs). The paired series of imprints, however, occupy a maximum of about 60% of the total width as compared to 50% in the Arran trail. Further they are not concentrated along the abaxial margins to the same extent as in the Arran example, but appear to show a more even density throughout the width of the paired series. This suggests a greater variation in appendage length and flexibility in the smaller Joggins arthropleurids.

The body fossil of *Arthropleura* has been recorded in sediments from Westphalian A to Stephanian C in age (Rolfe 1969). Other trace fossils attributed to this arthropod (Ferguson 1966, 1975; Baird *in* Carroll *et al.* 1972, p. 54) fall within this range and occur in a similar environment. The trail in the Namurian (E_1) Limestone Coal Group of Arran therefore represents the earliest evidence of *Arthropleura*; it probably

simply reflects the establishment of coal swamp conditions in Scotland sooner than elsewhere.

Størmer's (1976) description of a genus from Alken an der Mosel, Germany, extended the range of the arthropleurids to the Lower Devonian. He reconstructed *Eoarthropleura* (1976, figs. 45, 46) with the opposing limbs out of phase, the body undulating laterally as the propulsive limbs converged. Størmer justified this relatively rapid gait, leading to horizontal undulations, by the wide posterior doublure of the tergites which allowed considerable movement between them, and the over-all morphology which indicates that 'the Devonian form was more agile than the Carboniferous one' (1976, p. 43). It seems unlikely, however, that the gait reconstructed would have been suitable for the habitat envisaged by Størmer (p. 113), which is essentially similar to that of the Carboniferous genus. Body undulations occur in some myriapods when the two limbs of a pair are used in opposite phase. They are a hindrance to locomotion and are controlled as far as possible by a variety of adaptations (tergite heteronomy, segmental musculature), generally only appearing during fast running (in epimorphic chilopods). Størmer (1976, p. 95) draws an analogy between the trunk flexibility in *Eoarthropleura* and in the Recent Symphyla, which are adapted to follow the tortuous passages between soil particles. These myriapods, however, do not employ a gait with the opposing limbs out of phase (Manton 1977, fig. 7.8) and there is no tendency to produce body undulations; phase differences are less than 0·5. The relatively small *Eoarthropleura* (*c.* 11 cm), although lacking the extra tergites of the Symphyla (Manton 1977, pp. 373–375) may have twisted and turned its way through swamp vegetation rather than forcing a passage by pushing, as *Arthropleura* did. It is unlikely to have walked on open ground with the opposing appendages out of phase, because this, combined with the flexibility of the articulations, would have thrown the body into severe undulations. It presumably employed a similar range of gaits to that deduced for *Arthropleura*.

TAXONOMY

Many ichnogenera of myriapods have been described: *Acanthichnus, Acripes, Arthropodichnus, Beaconichnus, Diplichnites, Diplopodichnus, Diplopodomorpha, Hamipes, Harpepus, Merostomichnites, Myriapodites, Pterichnus, Tasmanadia, Umfolozia* are among those listed by Häntzschel (1975). To these may be added *Dunstairia* and *Stiaria* from the overlooked work by Smith (1909). The type specimens of *Diplichnites* and *Myriapodites* came from the Joggins section that has yielded the trail described by Ferguson. Indeed, the two distinct types of trails on Ferguson's (1975, fig. 4) slab could well be referred to those two genera. Unfortunately, *Diplichnites* has become firmly entrenched in recent literature as a trilobite locomotion trail, despite the fact that Dawson's holotype of his type species came from deltaic Westphalian, and comprised two rows of tracks six inches apart. This usage stems from Seilacher's (1955, pp. 342–343) suggestion that when a trilobite moves straight forward or backward, it will leave a trail that will be difficult to differentiate from trails of other arthropods. He 'provisionally' used Dawson's name *Diplichnites* for such trails of trilobites, as well as for those of trilobites moving obliquely forward. Since such trails were of rather generalized type, however, the actual omnibus name applied to them was felt

by Seilacher to be of secondary importance. Granted that trace fossil genera are liable to expansion with use (Häntzschel 1975, p. W35), this nevertheless seems an undue extension in meaning of the term, and it would be better to revive one of the undoubted trilobite ichnogenera (as by Osgood 1970; Anderson 1975) at present regarded as junior synonyms of *Diplichnites*. Most workers since Dawson have ignored the fact that he originally correctly deduced that his large trails 'were probably produced by a land or freshwater animal—possibly a large crustacean or gigantic annelid *or myriapod*' (1862, p. 7—our italics). Dawson (1891, p. 389) also noted that 'the space between the rows of marks is slightly depressed and smoothed, as if with a heavy body', a feature more likely in terrestrial myriapods than trilobite trails.

The holotype of the type species of *Diplichnites* has not yet been located. Baird (*in* Carroll *et al.* 1972, p. 54) has used the name *Duovestigia* Butts, 1891 for the arthropleurid trail from Florence, Nova Scotia. This genus (cf. Kuhn *in* Häntzschel 1975, p. W184) is based on small trails from the Upper Carboniferous of Missouri, and the name could equally be used for the Arran trail. Baird (letter to Ferguson, 1966) has also suggested that the Westphalian (*sic*) *Acripes* is a junior synonym, and that similar trails are figured by Abel (1935, figs. 222?, 238). The figured, but undescribed, *Beaconichnus giganteum* Gevers *in* Häntzschel, 1975, p. W45 should also be assigned to *Duovestigia*, thus extending the record to the Devonian of Antarctica. Clearly, much revision is required of myriapod ichnogenera, in the light of work on modern myriapod gaits, and with study of living myriapod trails. In the interim, *Duovestigia* may be regarded as a junior synonym of *Diplichnites* as emended below (cf. Häntzschel 1975, p. W61).

Ichnogenus DIPLICHNITES Dawson, 1873 (emend.)

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

Emended diagnosis. Morphologically simple trail, up to 36 cm wide, consisting of two parallel series of tracks (each up to 9 cm wide); individual tracks elongate roughly normal to trail axis, spaced closely and regularly at up to about one per cm.

Diplichnites cuithensis ichnosp. nov.

Plates 28–30

Derivation of name. From Cuithe (Gaelic: cattle-fold)—the name of the cleared clachan near the locality.

Holotype. Slab Hunterian Museum X.1041 (Pl. 29, fig. 2).

Paratypes. Four fibreglass replicas of trail, HM X.1042/1–3, X.1043; and small fragments of counterpart X.1044/1–3.

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

Horizon. Limestone Coal Group, Pendleian Stage, Namurian Series, Carboniferous.

Diagnosis. Very large *Diplichnites*, with rare trifid tracks shallowing towards axis of trail.

Description. See pp. 276–278 above.

Interpretation. Locomotion trail of large myriapod *Arthropleura*.

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