Xiphosurid traces, Kouphichnium aff. variabilis (Linck), from the Namurian Upper Haslingden Flags of Whitworth, Lancashire

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CHISHOLM, J. I. 1983. Xiphosurid traces, Kouphichnium aff. variabilis (Linck), from the Namurian Upper Haslingden Flags of Whitworth, Lancashire, Rep. Inst. Geol. Sci., No. 83/10. pp. 37-44

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SUMMARY

An assemblage of trackways and trails on the base of a siltstone near the top of the Upper Haslingden Flags is attributed to the activities of Carboniferous xiphosurids. Walking traces can be distinguished from half-swimming traces by the relative lengths of the paces: the difference is believed to reflect that between air-supported and watersupported locomotion. Most of the traces are probably undertracks, impressed through thin layers of sediment, rather than surface markings. The whole assemblage is assigned to a single taxon in the belief that the combination of behaviour patterns represented by the traces may indicate a particular depositional environment; the assemblage more closely resembles that of *Kouphichnium* variabilis (Linck) than any other so far described, and is named accordingly.

INTRODUCTION

The two specimens described here were found by the author during an excursion led by Dr J. D. Collinson to Hey's Britannia Quarries, Whitworth, in 1972. The larger specimen has twice been figured (Collinson and Banks, 1975, pl. 26: Eagar and others, 1983, pl. 11E), but without detailed description.

The specimens were found lying loose among other fallen debris on a ledge in the quarry face, and were clearly not far out of place, having been derived from the top part of bed 2 of the following section (located at British National Grid Reference SD 8713 2031):

metres

		meente
4	Sandstone, very coarse-grained, feldspathic	
	pale brown; erosional base	1.5 +
3	Mudstone and siltstone, dark grey, fissile	2.5
2	Siltstone and fine-grained sandstone with	
	silty mudstone bands, all greenish grey; a	
	few bivalve escape-shafts	5.0
1	Sandstone, fine-grained, with a few silt-	
	stone bands; all greenish-grey	10.0 +

The section is similar to those seen in the nearby boreholes 3 and 7 illustrated by Collinson and Banks (1975, pl. 29), bed 1 being the Upper Haslingden Flags and bed 4 the Rough Rock. Both sandstones lie within a single late-Namurian cyclothem, that with the *Gastrioceras cumbriense* Marine Band at its base. The Upper Haslingden Flags are thought to represent the mouth-bar deposits of a delta-lobe that advanced into an area of open water from the west (Collinson and Banks, 1975, pp. 448-451) The Rough Rock, by contrast, is believed to represent the channel deposits of a vigorous river system that flowed generally from north-east to south-west across the central Pennine region (Shackleton, 1962, pl. 7).

The specimens are numbered LZA 8874-5 in the Palaeontology Collections of the Institute of Geological Sciences. The better preserved specimen, 8874, is shown



Plate 1 Under-surface of specimen LZA 8874 *Ever*, part of trace A lit from another angle to show details of outer tracks, scale at side in millimetres

in Plate 1: if e tainter specimen, 8875, in Plate 2. Figure 1 shows how the two fit together and identifies the individual traces. A to G, described below. All are preserved as positive reliefs on the base of a bed of laminated pale greenish grey quartz-siltstone. Following the usage recommended by Frey (1972), and Simpson (1975), the term 'track' is used to denote an impression made by an individual appendage and the term 'trackway' is applied to a succession of tracks. A 'trail' is a more continuous trace. In description the traces are treated as positive features (mounds, ridges), as they appear on the specimens, but are interpreted in terms of the negative teatures (pits, hollows, scratches) produced by the animal

The traces include heteropodous limb and ressions the





outermost pair being different from the inner pairs), as well as tail traces, and are sufficiently like those made by the modern *Limulus* (Caster, 1938) to suggest that they were produced by xiphosurids. All are believed to have been made while the animals were walking on the sediment surface or swimming close above it. Caster (1938, pp. 15-22) states that the present-day *Limulus* (king crab) or horseshoe crab) will normally burrow into the sediment if fully submerged; it will swim only if the water becomes very shallow, and will walk only when exposed to air. On this basis the Haslingden traces suggest very shallow conditions, with subaerial emergence at times, and this was the interpretation placed on them by Collinson and Banks (1975, p. 451). A shallow-water origin is consistent with a notable difference of pace length between two kinds of trackway preserved on the specimens; longer paces suggest that the body was partly supported by water, and are taken to denote a half-walking, half-swimming mode of locomotion, whereas shorter paces suggest more laborious walking, perhaps on a surface exposed briefly to the air. The difference is conveniently expressed by the pace ratio, defined here as the repeat interval of the outermost limb impressions divided by the width between the centres of each pair of these; this figure gives a rough measure of relative length of paces, and is independent of the size of the animal. Trackways A and B, with pace ratios of 0.44 and 0.35, are interpreted as true walking traces, and trackway C, with pace ratio of 1.2, as a half-swimming trace. Trackways E and F show relatively long repeat intervals (but no outer limb impressions) and are also interpreted as half-swimming traces.

The shallow-water interpretation is not the only possibility, however, for the behaviour of recent *Limulus* is not necessarily a guide to the behaviour of ancient forms, and Goldring and Seilacher (1971) have described fossil xiphosurid walking trails from a variety of formations, some of them supposedly deposited in water of moderate depth.

Tracks showing fine detail, like those described here, are unlikely to be true surface traces; they are more likely to be undertracks (Goldring and Seilacher, 1971, p. 428) that have been impressed through a thin layer or layers of sediment on to the surface where they are preserved. The trackways are of different ages, as shown by cross-cutting relationships, and it is likely, therefore, that the surface of the specimen harbours an accumulation of undertracks impressed at different times from slightly different overlying levels. Some true surface traces may also be included.

DESCRIPTION AND INTERPRETATION OF TRACES

Formal nomenclature of xiphosurid traces is unusually difficult, for almost every trail or trackway is morphologically distinct. The approach favoured by Häntzschel (1975, p. W75) has been to group all heteropodous traces that show evidence of xiphosurid origin in one ichnogenus, *Kouphichnium*, a practice which has been employed in the present case, with slight modification, in that here an entire assemblage of tracks is assigned to a single species of *Kouphichnium*. Individual traces, whether heteropodous or not, are regarded as variants of the species and are distinguished by letters. The alternative, to give each trace a separate name, is not necessary for present purposes.

Ichnogenus KOUPHICHNIUM Nopsca 1923 Kouphichnium aff. variabilis (Linck) 1949 Plates 1-2

1949 Limuludichnus variabilis Linck, pp. 46-57; figs. 2, 3; pl. 5, figs. 1, 2; pl. 7, fig. 1. 1983 Kouphichnium sp. Eagar and others, pl. 11E.

DIAGNOSIS

An assemblage of locomotion traces, some of which are heteropodous and show evidence of xiphosurid origin in the roughly triangular shape of the outermost limb impressions and the presence of a telson (tail) trace. Others consist of a single type of limb impression or of a tail trace alone.

REMARKS

The assemblage broadly resembles K. variabilis from the Triassic of Germany in containing a variety of walking and swimming traces; both assemblages include a heteropodous walking trace with a tail mark, some swimming traces composed of grouped scratch- and prodmarks, and isolated tail traces. The Triassic trackways are wider than the present examples, however, with maximum width 63 mm (Linck, 1949, p. 47), as against 30 mm.

TRACE A

The trackway extends across both specimens for a total

distance of 35 cm (Plates 1, 2; Figure 1). The width is 20 mm throughout. It is a heteropodous trace with an outer set of regularly spaced paired tracks enclosing fainter marks spaced at roughly the same intervals. There is a well marked median ridge. The trackway closely resembles the walking traces of fossil and present-day xiphosurids described by Caster (1938; 1939) and by Goldring and Seilacher (1971). It is interpreted mainly by comparison with these.

The outer paired tracks repeat on average at intervals of 7 mm, and the width between the centres of most pairs is 16 mm: the pace ratio is thus 0.44. The long axes of the elongate-triangular tracks lie oblique to the axis of the trackway in a pigeon-toed arrangement, with the broad ends facing inwards; this can be seen clearly (Plate 1, inset) in only a few places because of poor preservation of the left series of tracks. The tracks were probably made by the outermost pair of appendages, which are distinguished from the inner pairs by the presence of forwardpointing 'pushers' (Caster, 1938, fig. 2). The pigeon-toed arrangement allows the direction of movement to be inferred (Goldring and Seilacher, 1971, p. 426), which in this case was from bottom to top of Figure 1.

The tracks made by the inner pairs of appendages are fainter than those of the outer pair and have probably also been in part overprinted by them, but one or two series are visible in places on the left side of the trackway, the best preserved being small elongate marks, sharp at the anterior ends but blunt behind. They are regularly spaced, like the outer tracks, about 7 mm apart. The sharp ends are interpreted as drag-marks made by the pointed ends of the appendages as they were withdrawn from the sediment and are well matched, both in shape and orien tation, among the medium-level undertracks described by Goldring and Seilacher (1971, fig. 2,A) from the Carboniferous Parrsboro Formation.

The right side of the trackway differs markedly from the left side, for instead of the distinct prod-marks of the inner appendages it shows up to four evenly spaced parallel lines. These are thought to represent dragging traces made by abdominal spines at the rear of the animal (Caster, 1938, fig. 2), which have erased the tracks made by the right series of inner appendages. Traces of the spines were not noted in the material described by Caster, but have been illustrated by Goldring and Seilacher (1971, fig. 7) in surface traces from the Carboniferous Bude Sandstones.

The median trace is clearly that of the tail, and slight rhythmic variations in depth, which are spaced at the same intervals as the tracks, can be explained by a bracing action exerted by the tail during walking (Caster, 1938, p. 18). Two marked gaps in the trace were probably produced by sudden changes in the direction of movement, which are indicated by bends in the course of the outer tracks some 2 to 3 cm beyond. If so, the direction of movement was from bottom to top (Figure 1), as already inferred from the orientation of the outer tracks.

There is an unexplained discrepancy between the details preserved in this trackway and those predicted by the undertrack model of Goldring and Seilacher (1971, fig. 2), for the limb impressions match those of medium-level undertracks, whereas the tail and spine traces would be more appropriate to surface or shallow undertrack interpretation.

TRACE B

The trackway consists of two series of small faint tracks, roughly paired, and a median trace (Plate 2). The width is





between 8 and 9 mm, and the median trace can be recognised over a distance, including gaps, of about 20 cm (Figure 1). Individual tracks are poorly preserved: some are slightly elongate and lie oblique to the axis of the trackway. They are generally spaced about 3 mm apart, giving an approximate pace ratio of 0.35. Analogy with trackway A suggests that it is the walking trace of a small xiphosurid, probably a juvenile of the same species as made the other traces.

TRACE C

The trackway is 15 cm long (Plate 2). The tracks are paired, and arranged in repeating sets of four (i, ii, iii) and iv in Figure 2), all markedly oblique to the axis. One of the individual tracks of pair iii cuts the tail mark of trackway A, which is therefore older.

It seems likely, in view of its close association with trackways A and B, that trackway C is also that of a xiphosurid. The longer paces, expressed by the greater pace ratio (*see below*) suggest that the weight of the animal was supported by water, however, and that it was swimming as much as walking. This type of movement was described by Caster (1938, p. 16) but there is no similar trace among the material he described. The body was aligned obliquely to the direction of movement, as if the animal was working across a current.

Pair *i* are wider apart than the other tracks, and were probably made by the outermost pair of appendages. The broader side of such tracks is likely to be the anterior (Caster, 1944, fig. 2) and if so the animal moved from left to right of Figure 1 (bottom to top of Figure 2). Of the other three pairs of tracks, pairs *iii* and *iv* are interpreted as scratch marks made by swimming movements of the inner appendages. Pair *iii* are closest together and probably represent the most anterior appendages. The most likely order of impression is thus *iii*, *ii*, *iv*, with pair *i* overprinted on or close to pair *ii* at the start of the next forward movement. The width between centres of pair *i* averages 30 mm, the repeat interval is 35 mm, and the pace ratio is 1.17.

If correctly interpreted as a half-swimming trace, it is likely that surface tracks or near-surface undertracks are represented here.

TRACE D

A group, about 3 cm long, of narrow arcuate ridges (Figure 1; Plate 1) probably represents scratch marks made by xiphosurid appendages. The scratches are arranged at angles between 45 and 90° to the axis of the trackway, which is identified by a discontinuous median ridge, the trace of the tail. The sharpness of the marks indicates undertrack preservation. The trackway is taken to represent swimming or half-swimming movements in which the appendages raked the sediment laterally; but the tracks are not so regularly spaced as those of trackway C, and the pace ratio cannot be determined.

TRACE E

The trackway consists of groups of six tracks, each group containing three pairs of low rounded mounds 1 to 2 mm in diameter and arranged in a V shape (Plate 1). The repeat interval is about 26 mm. Some of the tracks (notably those to left of trace A; orientation as in Figure 1) show a small sharp projection pointing to the right.

The tracks are probably xiphosurid undertracks (compare with Goldring and Seilacher, 1971, fig. 2) and as in trace F the absence of pusher impressions does not prove that none was made; however the relatively long repeat



Figure 2 Outline drawing of trackway C, based on a tracing from Plate 2, to identify track-pairs i-iv

interval suggests that this is a swimming or halfswimming trace, in which three pairs of inner limbs were being used either to probe the sediment or for support. The xiphosurid arrangement of limbs, in which the front pair are closest together (Caster, 1938, fig. 2), would under the circumstances described produce tracks in V-shaped groups pointing forwards, so that movement from right to left can be inferred. The pointed projections are on this basis interpreted as the points of entry of the sharp extremities of the limbs and there is in this respect a similarity with trace F.

TRACE F

The trackway extends for 19 cm (Plate 1). Where it crosses trackway A it appears to be the younger, for it is more delicate and would probably have been obliterated if it had been impressed first. At the bottom end (orientation as in Figure 1) there are up to six fine parallel ridges which are almost continuous, but higher up the specimen the trace consists of up to four parallel marks in groups separated by wide gaps, the repeat interval being about 19 mm. In isolation the trace would not necessarily have been interpreted as that of a xiphosurid but in the present context is reasonably regarded as such.

There are no impressions of the 'pushers', and the

parallel ridges are interpreted as scratch marks by the inner appendages. Such delicate impressions are likely to be undertracks, so that pusher impressions, if produced at all, may have been present only at higher levels; their absence does not mean that none was made. However, absence or faintness are both consistent with the watersupported (swimming) movement that is suggested by the relatively long repeat interval.

At the top end of the trace, where the scratches are in groups of four, their upper ends are sharp, and staggered so that the outer pair overlaps the inner pair by a few millimetres. The lower ends are broad and vague. The sharp ends probably show where the points of the limbs first penetrated the sediment after a swimming stroke, and the broader ends were produced when the limbs dragged clear of the sediment during the next stroke; the impetus came presumably not from the inner limbs, which made the scratches, but from movements of the body and outer limbs (Caster, 1938, p. 16). The direction of movement thus inferred is from top to bottom of Figure 1. The same direction is suggested by the staggered arrangement of the sharp ends of the scratches, for this is the pattern that would be expected from the xiphosurid array of limbs, in which the innermost pair is the most anterior (Caster, 1938, fig. 2).

At the lower end of the trace the animal was probably closer to the sediment surface, and gliding rather than swimming, for the groups of four scratches give way here to a more continuous series of six. The extra pair are at the outside of the trace, and the spacing of the scratches presumably reflects the spacing of the limbs; the innermost pair are 3 mm apart, the second pair 5 to 6 mm apart and the third pair 8 to 9 mm apart.

TRACE G

An irregular pattern of low ridges can be seen to the right of trackway A (orientation as in Figure 1) in specimen 8874 (Plate 1). One ridge, straighter than the others, extends roughly parallel to trackway A for about 14 cm. The ridges are up to about 1 mm wide and most show periodic emphasis, where the ridge is slightly sharper and higher, at intervals of 5 to 13 mm. The pattern is irregular and varies from zig-zag to sinuous, with bends generally less than 90° but locally up to 180°. Collinson and Banks (1975, p. 439) referred to these traces as Cochlichnus and interpreted them as annelid trails but they are not sinsuoidal and cannot, therefore, be assigned to that ichnogenus. In view of their association with undoubted xiphosurid traces they are interpreted here as the marks made by the tail of a xiphosurid as it swam about close to the sediment surface. Similar trails were recorded by Caster (1938, fig. 1, e; pl. 11, fig. 7) among Devonian traces and correlated (Caster, 1938, p. 9) with recorded behaviour of the present-day Limulus. The periodic emphases mark the places where the tail was pressed against the substratum at each forward stroke.

Some irregularly sinuous linear traces are found with the K. variabilis assemblage described by Linck (1949, p. 72; pl. 5) and were tentatively interpreted by that author as crawling traces or faecal strings comparable with Lumbricaria or Tomaculum. They are similar to trail G in their irregular overall pattern and in the presence of periodic projections, but differ in that the projections are more rounded and more closely spaced. They may be xiphosurid tail traces, by analogy with trail G, but an unrelated faecal or burrowing origin is at least as likely, in view of the differences noted above.

DISCUSSION

TYPES OF LOCOMOTION

Three types of movement are recorded in these traces. Walking produced trackways with relatively short repeat intervals expressed, in the case of the well preserved heteropodous trackway A, by a pace ratio of 0.44. Trackway B may also be of this type. Swimming and halfswimming movements of a directed kind produced a variety of traces consisting of limb impressions with relatively long repeat intervals which, in the case of the heteropodous trackway C, is expressed as a pace ratio of 1.17. Trackways D, E and F also fall into the swimming category. The third type of movement was an irregular form of swimming, largely non-directed, in which only the tail touched the bottom: trail G is the only example. There is no evidence, in any of the traces, that the animal swam upside down, as *Limulus* can (Vosatka, 1970).

There is no common direction of movement among the traces (Figure 1), perhaps because they represent an accumulation of markings that were formed over a period of time. The cross-cutting relationships suggest that the swimming traces C and F are younger than the walking trace A.

CARBONIFEROUS XIPHOSURID TRACES

Walking traces from the Upper Carboniferous of the Canadian Maritime Provinces, illustrated by Copeland (1957, pl. 20) include examples that resemble traces A and B of the present assemblage. The best preserved are heteropodous, with the tracks of the last pair of appendages overprinting those of the inner pairs, and a central telson mark. They range in width from 7 to 10 mm and the pace ratios vary from 0.46 to 0.93. A somewhat similar trackway from the same region was named Protichnites carbonarius by Dawson (1873). Examples illustrated more recently from the Maritime Provinces (Goldring and Seilacher, 1971, fig. 1) also have several features in common with trace A and range in width from 20 to 30 mm. The most complete has a pace ratio of 0.61. The same authors (1971, fig. 7) also illustrate some similar trackways from the Upper Carboniferous Bude Sandstones of Cornwall; the best preserved has a pace ratio of 0.44 and is 12 mm wide. Other examples from this formation were assigned by King (1965, p. 162) to Kouphichnium; they include a sinuous double tail trace attributed to the movement of a mating pair. The inferred width of the animals responsible is about 20 mm. Some traces of supposed xiphosurid origin were illustrated by Bandel (1967) from an Upper Carboniferous siltstone in Kansas. They include complex and irregular walking traces up to 55 mm across, some of them apparently of two trackways superimposed, and feather-like traces up to about 17 mm wide. These last are quite unlike any of the present examples and were interpreted as drag marks made by the tail and appendages of swimming and halfswimming xiphosurids. Resting or nestling traces of xiphosurids are now assigned to the ichnogenus Limulicubichnus Miller. One form, L. rossendalensis (Hardy, 1970a), shows impressions about 15 mm wide of headshield, limbs and tail. It records a style of locomotion where nestling alternated with short forward movements and is quite unlike any of the elements of the K. aff. variabilis assemblage, although it was found in the same quarry as the specimens described in the present paper (Hardy, 1970b, p. 45). Another xiphosurid resting trace, L. serratus, has been described by Miller (1982) from the