THE FIRST RECORD OF XIPHOSURID (ARTHROPOD) TRACKWAYS FROM THE SALTWICK FORMATION, MIDDLE JURASSIC OF THE CLEVELAND BASIN, YORKSHIRE

by MIKE ROMANO *and* MARTIN A. WHYTE

ABSTRACT. Trackways attributed to a xiphosurid (arthropod) maker are described for the first time from the Middle Jurassic Saltwick Formation, Ravenscar Group, of the Cleveland Basin, Yorkshire. The trackways are assigned to *Kouphichnium* aff. *variabilis* (Linck, 1949) and clearly demonstrate the heteropody and varied behaviour of the maker. Their occasional asymmetry indicates a slight rotation of the body relative to the direction of locomotion. The Saltwick Formation has generally been regarded as a coastal plain deposit, and the presence of xiphosurid tracks reinforces the suggestions of periodic marine influences.

KEY WORDS: Jurassic, Yorkshire, Saltwick Formation, xiphosurid trackways, *Kouphichnium*.

INVERTEBRATE trace fossils may provide invaluable evidence of the behaviour of the animal that left the trace, the sedimentological regime and occasionally the actual identity of the trace maker. Such trace fossils abound in the Jurassic of the Cleveland (Yorkshire) Basin and may provide the basis for distinguishing major facies types and palaeosalinities. However, despite their abundance in the Yorkshire sequences relatively little published work has concentrated on the detailed systematics of the ichnofaunas. Arkell (1947) frequently referred to these biogenic sedimentary structures as ‘fucoid beds’ while Wilson (1949) considered some of them to be of inorganic origin. It was not until Farrow (1966) described the general distribution of the Middle Jurassic traces, with a bathymetric zonation scheme based on those from the marine ‘Scarborough Beds’, that their potential as sedimentological facies indicators in the Yorkshire sequence was appreciated. Since Farrow’s work only Romano and Whyte (1987, 1990) and Powell (1992) have published exclusively on selected Yorkshire Jurassic invertebrate traces, although a field meeting was held on the Yorkshire coast during the Fifth International Ichnofabric Workshop (IIW5) in 1999 which indicated the abundance and importance of these traces.

The present paper describes, for the first time, arthropod trackways from the Middle Jurassic Saltwick Formation of Yorkshire. The Saltwick Formation, the lowest unit of the Ravenscar Group (Text-fig. 1), is generally regarded as non-marine and is probably of Aalenian age (Cope *et al.* 1980). The rocks of the Ravenscar Group are now usually accepted as representing a coastal plain and fluvial complex (Alexander 1989; Bradshaw *et al.* 1992) with occasional marine intercalations. The Saltwick Formation exhibits a variety of facies that indicate habitats representing river channels, flood plains and crevasse splays, lakes and marshes (see references in Alexander 1989 and Romano *et al.* 1999).

The single tracks and trackways described here were discovered in a landslip area approximately 100 m west of Maw Wyke Hole, Hawsker Bottoms, Whitby (Text-fig. 1); they occur on the base of a thick (*c.* 0·7 m) loose block of sandstone (1·1 × 0·8 m) (Text-fig. 2). Owing to the steepness of the cliffs in that area, it was not possible to determine the source horizon of the block. However, since the rocks exposed in the cliff face consist only of the Whitby Mudstone Formation and overlying Dogger and Saltwick formations, there is no doubt that the sandstone block was derived from the latter unit (Text-fig. 1). The inaccessibility of the block prevented any detailed sedimentological work being undertaken, but 30-mm-thick cross-laminated sets separated by thin carbonaceous laminae, appear to characterise much of the

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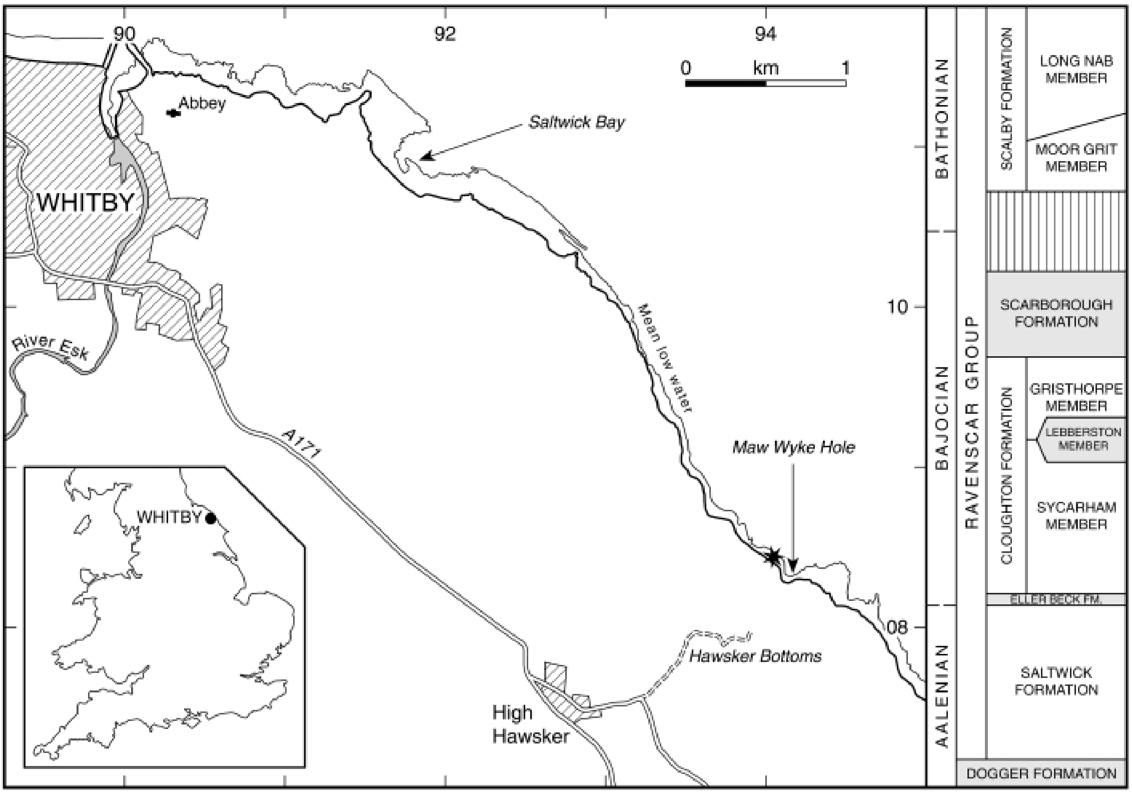


TEXT-FIG. 1. Map showing the location of the xiphosurid tracks (marked by an asterisk). The source formation of the tracks, the Saltwick Formation, is shown on the simplified stratigraphic log; marine units are shown in grey.

TEXT-FIG. 2. Photograph of surface of sandstone block, showing distribution of tracks. Scale bar represents 100 mm.

block. The sand at the true base of the block is more massive with indistinct bedding (Text-fig. 3). From our experience of the Saltwick Formation at Whitby the thickness and overall characteristics of the sandstone unit indicate that it is probably of a crevasse splay origin.

The trace fossils described below are assigned to *Kouphichnium* aff. *variabilis* (Linck, 1949). The

TEXT-FIG. 3. Photograph of side of sandstone block containing tracks, showing sedimentary features described in the text. The photograph shows the slab in its correct orientation (i.e. upside down from its position in the field). Vertical thickness of block in photograph is 193 mm.

morphology of the ichnite is described and its preservation, presumed maker, method of locomotion and habitat are discussed.

SYSTEMATIC PALAEONTOLOGY

Ichnogenus KOUPHICHNIUM Nopcsa, 1923

Type species. *Ichnites lithographicus* Oppel, 1862 from the Solnhofen Limestone, Jurassic, Bavaria.

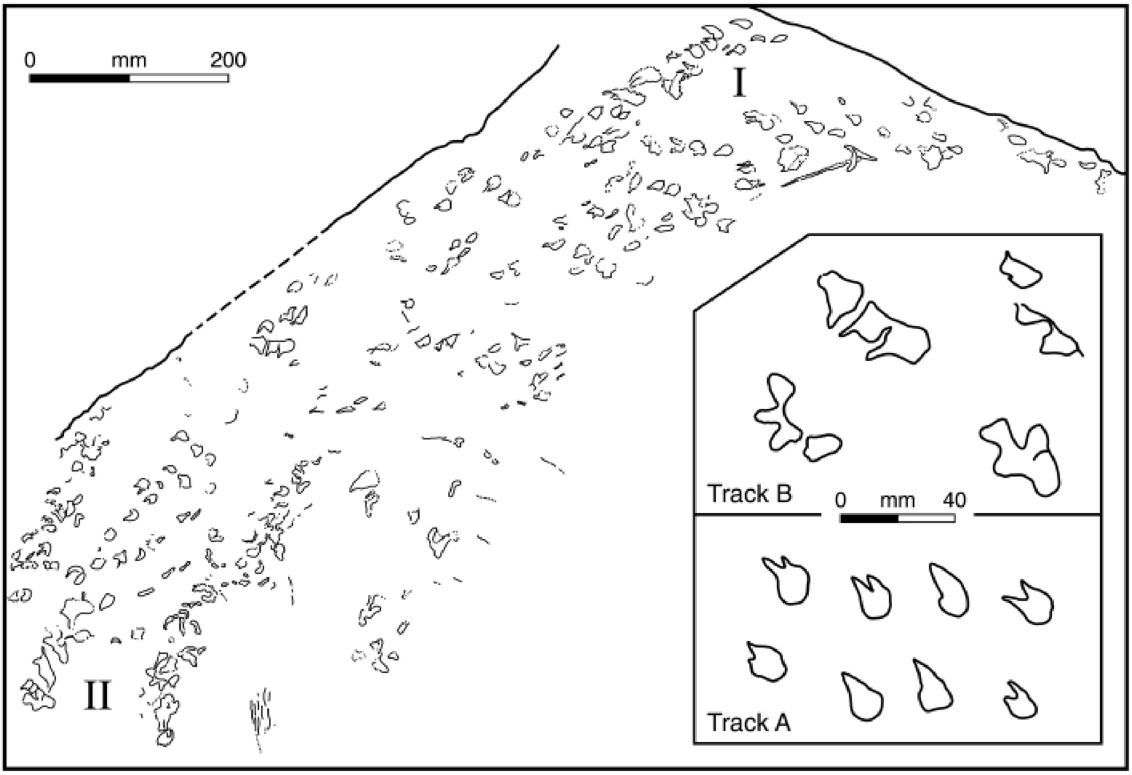
Diagnosis (following Häntzschel 1975, p. W75). Heteropodous tracks of great variability; complete track consisting of two kinds of imprints: (1) two chevron-like series each of four oval or round holes or bifid V-shaped impressions or scratches, forwardly directed [made by anterior four pairs of feet]; and (2) one pair of digitate or flabellar, toe-shaped or otherwise variable imprints [made by birdfoot-like 'pushers' of fifth pair of feet, with their four or five leaf-like movable blades]; track with or without median drag-mark.

Kouphichnium aff. *variabilis* (Linck, 1949)

Text-figures 2–8

Material. Tracks and trackways preserved as positive hypichnia on the lower surface of a loose sandstone block approximately 1·1 × 0·8 m and *c*. 0·7 m thick.

Horizon and locality. The sandstone block was found on the foreshore, near the cliff, approximately 100 m north-west of Maw Wyke Hole, Hawsker Bottoms, Whitby. The sandstone is from the Saltwick Formation (Aalenian, Middle Jurassic) but the exact horizon is unknown.



TEXT-FIG. 4. Drawing of tracks on surface of sandstone block. Trackways mentioned in the text are labelled I and II. Insets show drawings of examples of Track A and Track B types.

Description. A number of complete and incomplete trackways cover an area of sandstone approximately 0·74 m^2 (Text-figs 2, 4). Only in a few instances can discrete trackways be discerned, although superimposed trackways are common. Four discrete types of traces are associated on the block surface.

Tracks and imprints

Track A. Well over 100 individual tracks are represented by small (2·5–8·0 mm long; mean of 50, 5·7 mm) sub-oval mounds with rounded, pointed or bifid (two short, subparallel projections) ends (Text-fig. 4). The length:width ratio of these prints varies from 1·4–2·7.

Track B. This type is much less common than Track A and, owing to their irregular and variable preservation, only 15 have been definitely identified. They range from irregular prints up to approximately 30 mm wide, with no definite outline, to semicircular prints with 3–4 projections on the convex side (Text-fig. 4).

Imprint C. This type is represented by rare (< 10) thin, delicate subparallel ridges, less than 30 mm in length (Text-fig. 4). In the lower part of the block these imprints occur in two areas, each with four or five examples. In one of these areas the ridges are up to 30 mm long and 50 mm apart and offset from each other. In the second area the ridges are less than 12 mm long, much closer together (*c*. 10 mm), and not offset.

Imprint D. This is represented by a single straight ridge, asymmetric in cross-section, and thicker and longer (nearly 100 mm in length) than Imprint C (Text-figs 4–6).

TEXT-FIG. 5. Photograph of surface of sandstone block showing Trackway I in detail. Maximum width of surface of sandstone block in photograph is 0·45 m.

Trackways (this term is preferred to trails as used by Caster 1938, p. 5)

The tracks described above are occasionally recognised in well-ordered sequences which undoubtedly may be interpreted as part of a single trackway. The most clearly defined trackway is shown at the top right of Figure 4 (Trackway I). This trackway (Text-figs 4, 6) is approximately 170 mm wide and consists of two series of tracks exhibiting marked asymmetry.

Trackway I shows a regular, repeated, sequence of Track A prints on one side of the trackway (the lower side in Text-figs 5–6) that are arranged in rows of up to four prints, with the long axes of each print aligned oblique to the row and to the median axis of the trackway. Each row is up to 100 mm long and is 40–60 mm from adjacent rows. The prints in the rows generally point in the same direction with the pointed or bifid end directed 20–30 degrees towards the trackway midline. The rows of Track A prints are oblique (*c.* 50°) to the axis of the trackway. The Track A prints on the other side of the trackway show broadly similar, yet more irregular, arrangement. In particular, the rows are closer together and are arranged either transversely to the trackway length or aligned in the opposite direction to those on the other side.

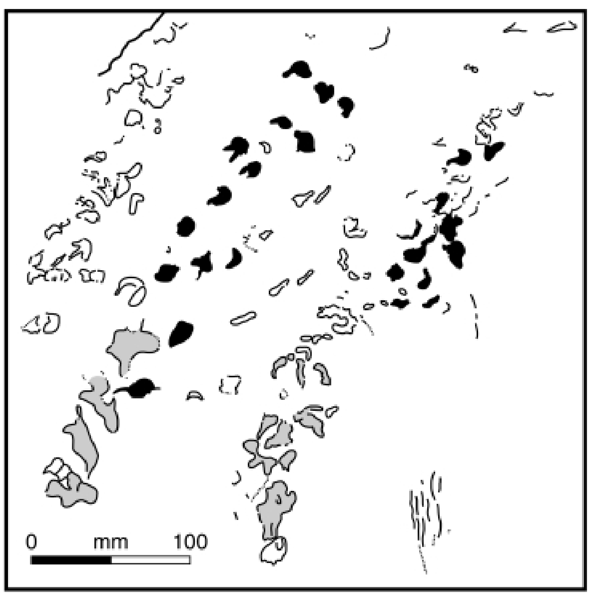
Single prints of Track B are present at the outer end of each row of Track A prints on the best defined (lower) side of Trackway I, sometimes overprinting the most distal Track A print. Although not well shown in this particular trackway, the projections on Track B are pointing in the same direction as the pointed/bifid ends of Track A. The one example of Imprint D occurs on the better preserved side of the trackway. It is aligned parallel to the midline of the trackway and is situated lateral to Track B prints. Although a possible Track B print abuts against the end of Imprint D, it is not possible to interpret cross-cutting relationships. No examples of Imprint C traces are present in this trackway.

On other areas of the sandstone surface are short sequences of rows of Track A, and in the bottom left hand corner of the slab (Text-figs 4, 7) at least four large paired prints of Track B are closely associated in two parallel rows, forming part of Trackway II. The remainder of this trackway is dominated by en-echelon rows of Track A traces. No traces of Imprint C type are associated with this trackway, although such imprints occur close by and apparently on the outer margin of poorly preserved trackways (Text-fig. 4).

Remarks

The overall morphology of the tracks and imprints and their spatial arrangement in the trackways leave little doubt that they may be assigned to the ichnogenus *Kouphichnium* Nopcsa, 1923 (Häntzschel 1975).

TEXT-FIG. 6. Drawing of tracks in Trackway I. Track A type in black; Track B type in grey.



TEXT-FIG. 7. Drawing of tracks in Trackway II. Track A type in black; Track B type in grey. Anastomosing lines in the bottom right-hand corner represent a plant impression.

Ichnospecies originally or subsequently assigned to this ichnogenus have been described from rocks of Devonian–early Tertiary age by Willard (1935), Caster (1938, 1939, 1940, 1944), Linck (1943, 1949), Malz (1964), Goldring and Seilacher (1971), Miller (1982), Chisholm (1983), Eagar *et al*. (1985), Miller and Knox (1985), Romano and Meléndez (1985) and Buatois *et al*. (1998).

Hardy (1970) erected the ichnospecies *Kouphichnium rossendalensis* for a series of lunate casts in the Upper Haslingden Flags, Carboniferous, of Lancashire. Miller (1982) included this ichnospecies in her new ichnogenus, *Limulicubichnus*, a practice followed by Chisholm (1986) and Eagar *et al*. (1985).

Romano and Whyte (1987) proposed a new ichnogenus, *Selenichnus*, later changed to *Selenichnites* (Romano and Whyte, 1990), in which they included '*K.*' *rossendalensis*. These authors also restricted the type species only, *Limulicubichnus serratus*, to Miller's ichnogenus.

As noted by Buatois *et al*. (1998), there is a need for a thorough taxonomic revision of *Kouphichnium* ichnospecies. Of the existing described ichnospecies of *Kouphichnium* [see listing in Buatois *et al*. (1998, p. 160) and also *K. fernandezi* (Romano and Meléndez 1985)], the present material is most similar to the Upper Triassic form *K. variabilis* (Linck 1949) from Germany, and also resembles the Upper Triassic ichnospecies *K. arizonae* (Caster 1944) from Arizona (USA). An unnamed trackway from the Triassic of East Greenland (Nielsen 1949, p. 30, fig. 21) bears a strong resemblance to Trackway I of the Yorkshire material.

K. arizonae differs from the Yorkshire material in possessing simple tracks that are 'mere slits' (Caster 1944, p. 81, pl. 1) and the chevron rows are much further apart. The trackway of *K. variabilis*, as first described by Linck (1949, text-fig. 2; pl. 5, fig. 1), do not show the outer, more complex tracks (Track B) of the Yorkshire species, but is similar in that it displays distinct asymmetry, and the simple prints (comparable to Track A) are represented as short, oval imprints. Both Triassic trackways exhibit telson drag marks, and are significantly narrower than the Yorkshire specimens; the average width of the American ichnospecies is 65 mm, while examples of the German form range from 70–120 mm. Chisholm (1983) described as *K.* aff. *variabilis* specimens from the Upper Haslingden Flags (Namurian) of Whitworth, Lancashire (material also figured in Collinson and Banks 1975, and Eagar *et al*. 1983). This ichnotaxon exhibits considerable variation in the six trackways figured by Chisholm but none of these shows the combination of features seen in the present material. The Lancashire specimens are preserved in laminated siltstones and, as stated by Chisholm, probably represent both surface and undertrack preservations as well as behavioural variants (see below). As in the specimens described by Linck, the Haslingden Flags trackways are considerably narrower (maximum width 30 mm) than those described here (170 mm).

Though we are provisionally assigning the present material to *K.* aff. *variabilis*, it is clear that the material currently associated with this ichnospecies encompasses a range of morphotypes, which reflect different behavioural patterns. In future some of these may be reassigned to separate ichnospecies.

Interpretation

The detailed trace fossil studies by Caster (1938, 1939, 1940, 1944), Linck (1943, 1949) and Goldring and Seilacher (1971) leave little doubt that the trackways in the Saltwick Formation were made by xiphosurid limulinids. Limulinids are heteropodous chelicerate arthropods. Their appendages surround the mouth and consist of small anterior chelicerae (or pincers) and five pairs of walking legs. The first four pairs (II–V) are chelate, while the posterior pair (VI, the pushers *sensu* Caster 1944) have 4–5 flat spines. The Saltwick trackways show evidence of the four pairs of chelate walking legs (Track A) and pushers (Track B), although the former tracks only occasionally exhibit bifid projections, and never the typically long, delicate bifid prints recorded by Caster (1938, pl. 1, figs 1–3; pl. 5, figs 1–2; pl. 8, fig. 4). The common sub-oval mounds of Track A may indicate a preservational, morphological or behavioural variant (see below).

The Track B prints similarly do not show the distinctive pusher imprints illustrated by Caster (1938, pl. 4, fig. 1; pl. 12, fig. 3) and Romano and Meléndez (1985, fig. 1, pl. 1), where the forward-directed blades and posterior-directed bifid spine are clearly displayed. They more closely resemble the incomplete semicircular imprints drawn by Caster (1944, fig. 2C), and probably represent a behavioural variant (see below). The Imprint D trace from the Saltwick Formation is taken to indicate the drag mark of the lateral margin/genal angle of the prosoma or telson as it made intermittent contact with the sediment surface during locomotion. Imprint C traces possibly represent short drag marks made by inwardly directed movement of the walking legs. These are comparable to the marks described by Romano and Meléndez (1985, fig. 1) and assigned by these authors to *Monomorphichnus* ichnosp.

Trace fossils assigned to *Kouphichnium* are very variable and range from relatively simple, straight-ahead trackways with discrete individual tracks to complex, sinuous trackways with numerous superimposed tracks. The best preserved Saltwick trackway is gently curved and asymmetric (Trackway I). It seems unlikely that the small, gradual change in direction (35°) can be sufficient to account for the marked dimorphism in the two sides of this trackway, since sigmoidal trackways figured by Caster (1938, pl. 4, fig. 5), with a similar 35 degree change in direction do not exhibit such asymmetry. In a study of Upper Ordovician arthropod (trilobite) tracks from Cincinnati, Ohio (USA), Osgood (1970) recognised straight-ahead, straight to slightly sinuous trackways with no dimorphism (pl. 75, fig. 2), to strongly dimorphic trackways (pl. 73, fig. 2; pl. 74, fig. 5 *pars*). Following Seilacher (1955), Osgood attributed the dimorphic trackways to oblique movement, whereby the median axis of the trilobite body was aligned at an angle to the direction of movement.

Limulinid and trilobite trackways were discussed by Osgood (1970, p. 351), who pointed out that they differed in that the angle of the prints produced by the limbs resulted in a 'V' which was backward pointing in trilobites and forward pointing in limulinids. The latter have been observed in modern limulid trackways. Fossil limulinid traces are also generally easier to interpret than those for arthropods with numerous appendages, and the direction of locomotion is normally more readily resolved for the former group, particularly when pusher tracks are well preserved. The well-preserved trackway (Trackway I) on the Saltwick slab shows a clear directional sense as evidenced by the walking leg and the pusher blade imprints on the lower part of the trackway (Text-fig. 6). The pattern of imprints on the upper part of Trackway I is less clear, but corresponding series are recognised aligned subparallel to the median line of the trackway, resulting in an asymmetric forward pointing 'V' arrangement.

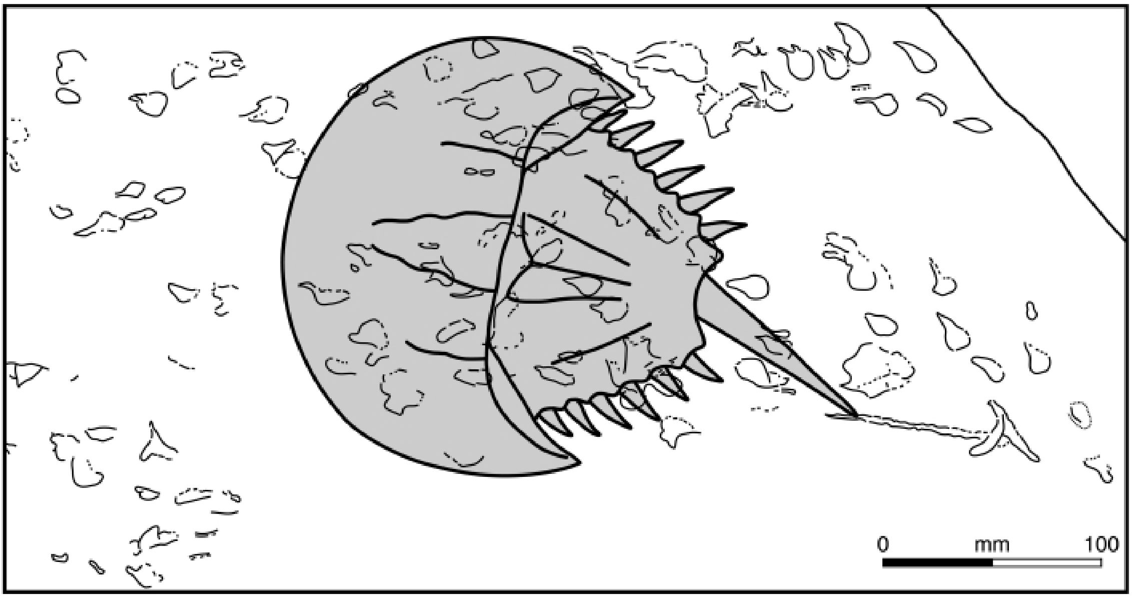
If asymmetry in trackways is the result of the animal walking crab-like (Osgood 1970, pp. 352–353, fig. 17) then the asymmetry of the Hawsker trackway may be explained if the body of the maker was rotated anticlockwise to the direction of movement (Text-fig. 8). If this was the scenario it remains to be discussed why the animal walked with its long axis at an angle to the direction of locomotion, since this does not appear to be the normal method of locomotion (see symmetrical tracks of Caster 1938, 1939, 1940, 1944, and Linck 1943, 1949). The most likely mechanical stimulation that may have influenced the orientation of the body is current direction. The overlying and casting medium (sand) was clearly transported by a unidirectional current (see above), which may have existed at the time the limulinid was traversing the substrate. If this was the case, the anticlockwise alignment of the body may have been an attempt to counteract the down-current drag of the water. If this interpretation is correct, then Imprint D may have been made by either (1) the right-hand side of the prosoma as it made contact with the sediment, perhaps as a result of the animal turning into the current to avoid being swept away, or (2) the drag of the telson as the animal attempted to retain contact with the sediment surface to prevent it being washed away down-current (Text-fig. 8). Unfortunately, it was not possible to measure the palaeocurrent directions from the cross-bedding in the sandstone, so the theory cannot be tested.

Another behavioural type may be represented by a less clear, and slightly narrower, trackway (Trackway II) towards the left-hand margin of the bedding surface (Text-figs 4, 7). If this assemblage of tracks does indeed represent a single trackway, then it consists initially of dominantly simple tracks (Track A) followed by mainly pusher tracks (Track B). This trackway may represent a sequence whereby the animal changed from a walking to swimming locomotion, the simple bifid tracks representing the former, while the closely spaced pusher tracks, exhibiting only the more deeply impressed, vertical flat spines, represent the latter. If the animal was attempting to take off and swim into the current, it is conceivable that the limited forward motion would result in closely spaced pusher prints, as seen in this trackway (Text-fig. 9).

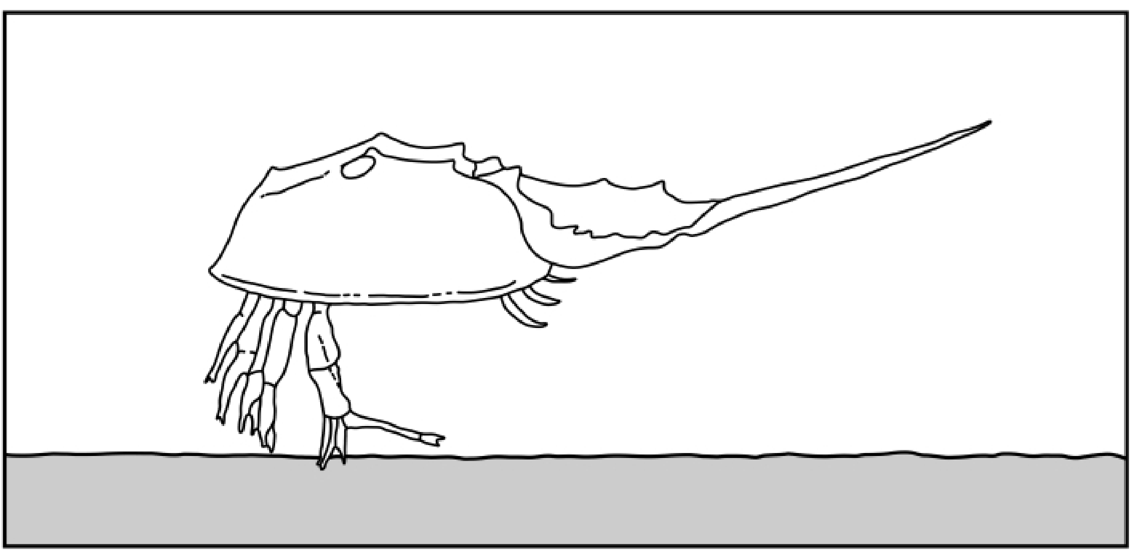
All the trackways may be assigned to the repichnia of Seilacher's (1953, 1964) ethological classification, since the animal(s) responsible has (have) left no obvious probing traces as may be expected from a feeding activity.

Producer of the traces

Within the Limulina, Jurassic forms are known only from the Palaeolimulidae (Carboniferous – Jurassic) and Limulidae (Jurassic – Recent), although in the former family the last record just extends into the



TEXT-FIG. 8. Drawing of Trackway I with superimposed *Mesolimulus*, as seen from the undersurface of the block.



TEXT-FIG. 9. Suggested life attitude of xiphosurid (based on modern limulid) to produce lower end of Trackway II in Text-figure 6.

lowermost (Hettangian) Jurassic (Selden 1993). Thus, from the current knowledge of limulinid body fossils the animal responsible for making the Hawsker tracks must belong within the limulids. Within the limulids only *Mesolimulus* Størmer (1952) is of comparable age. Fisher (1975, fig. 1) illustrated a transverse reconstruction through the prosoma of the Jurassic *Mesolimulus walchi*, based on material from the Solnhofen Limestone. His illustration shows that when the walking legs were fully extended the distance between the distal ends would approximate to the width of the prosoma. Using *M. walchi* as a model, this indicates that during walking the width of the trackway would be less than the prosomal width (the amount depending on the flexure of the legs). Thus the trackway from Hawsker would suggest an animal with a prosoma at least 170 mm wide. This compares very closely with the width (170 mm) of the prosomal trace in *Selenichnites hundalensis* (Romano and Whyte 1987, 1990), a resting (cubichnia, *sensu* Seilacher 1953, 1964) trace assigned to a limulid maker from the younger (Bajocian), marine Scarborough Formation. Thus, it is likely that the makers of the Saltwick and Scarborough traces were probably the same or similar species of the genus *Mesolimulus*. Though the single known specimen of *Mesolimulus*? *woodwardi* (the only known Aalenian limulinid body fossil) is smaller in prosomal width (*c*. 80 mm) than the form(s) that produced these traces, the body fossils of the Upper Jurassic *Mesolimulus walchi* are of comparable size (*c*. 130 mm) (Romano and Whyte 1987).

Surface tracks or undertracks?

The term undertrack is used in the sense of Goldring and Seilacher (1971, p. 424) for tracks that are 'duplicate imprints on lower surfaces'. These authors noted that surface tracks are often only faint impressions while those in the uppermost undertrack level 'combine sharpness with completeness'. Below this uppermost layer, Goldring and Seilacher noted that the fallout in detail preserves less with increasing depth; their observations were made on tracks preserved in mm-thick and evenly laminated siltstone. This medium is very different from the more massive, coarser grained sandstone which preserves the Saltwick example, so it is likely that the preservational features may be different from those observed by Goldring and Seilacher. However, as the stratigraphically higher beds above the surface on which the Saltwick tracks are preserved do not appear to contain tracks, conclusions concerning the level at which the maker moved must rely on other evidence.

Since both chelate (Track A prints) and pusher (Track B) tracks occur, it would indicate (following the argument of fallout by Goldring and Seilacher) that the tracks are either surface or high level undertracks. This would be supported by the presence of a possible prosomal/telson drag mark (Imprint D). Conversely, the short bifid Track A prints may represent the distal and deepest end of the stroke of the chelate appendage, and suggest a deeper level, as would the apparent absence of a median telson drag mark and the generally well-defined, sharp prints. Taken together the evidence is equivocal, particularly since it is unknown whether the surface on which the trackways were made may have undergone modification through scouring prior to deposition of the overlying (casting) sands.

Marine or non-marine?

From a consideration of the habitat of modern limulids and a survey of the record of fossil limulid tracks, Goldring and Seilacher (1971) concluded that the main habitats of limulids have always been in shallow marine environments. They suggested that the preponderance of fossil limulid tracks that occur in marginal and non-marine environments, is due to a fossilization bias. The presence of limulinid traces in the marine Scarborough Formation (Romano and Whyte 1987, 1990) indicates that Jurassic limulinids were able to tolerate shallow marine conditions.

The environment of deposition of the Saltwick Formation is generally regarded as non-marine, with the lithotypes representing such habitats as river channels, flood plains and crevasse splays, lakes and marshes. *Unio kendalli*, a non-marine bivalve, is the only invertebrate body fossil known from this unit. The limited sedimentary evidence available for the present material, together with not knowing the exact horizon from which it originated, prevents a realistic interpretation being made of the environment of deposition. However, although it is most likely that it was a fluvially-dominated environment with no clear evidence of marine influence, it is important to appreciate that probably throughout the time during which the sediments of the Saltwick Formation were accumulating, marginal marine conditions periodically existed. Occurrences of limulinid trace fossils in these sequences may thus be useful and highly significant indicators of very distal marine connections, and comparable to the penetration of the modern *Carcinoscorpius rotundicauda* up the Hooghly River, India, to a distance of some 150 km from the open sea (Annandale 1901, *fide* Shuster 1957). The authors have also recorded limulinid resting/burrowing traces from the non-marine Long Nab Member of the Scalby Formation at the top of the Ravenscar Group.

Apart from *Kouphichnium* aff. *variabilis* described here, only rather low diversity invertebrate trace fossil assemblages are known from the Saltwick Formation ('usual for non-marine ichnocoenoses'; Bromley 1990, fig. 11.16, but see Pickerill 1992, p. 21 and references therein). Although *Lockeia*, *Diplocraterion* (R. G. Bromley, pers. comm. 1999), ?*Taenidium* (*sensu* Keighley and Pickerill 1994; or possibly *Beaconites sensu* Goldring and Pollard 1995) and *Planolites s.l.* have been recorded from the Saltwick Formation, none of these ichnotaxa is particularly useful as a palaeosalinity indicator. Similar ichnofossil assemblages occur in the Silesian (mid-Carboniferous) rocks of the Central Pennine Basin (Eagar *et al.* 1985), where a *Pelecypodichnus* (= *Lockeia*)-*Kouphichnium*-*Arenicolites* assemblage has been recognised from Lower Westphalian arenaceous non-marine strata. Despite the similarity of this assemblage to that from the Saltwick Formation at ichnogeneric level, it is premature to imply a similar ichnofacies until a more thorough taxonomic study is undertaken and the stratigraphic locations and associations of the ichnofaunas of the Yorkshire sequence are known in more detail.

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MIKE ROMANO

MARTIN A. WHYTE

Environmental and Geological Sciences
[now Department of Geography]
University of Sheffield
Dainton Building
Brookhill
Sheffield, S3 7HF, UK
e-mail m.romano@sheffield.ac.uk
m.a.whyte@sheffield.ac.uk

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