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Evidence and significance of limulid instars from trackways in the Bude Formation (Westphalian), south-west England

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A previously unreported locality in the Bude Formation has yielded xiphosurid trackways varying in width from 3mm to 20mm. Over eighty measurements have been made relating the track set width to the distance between successive pusher marks. The data suggests that probably five instars were present in the xiphosurid population producing the ichnocoenosis. It is suggested that the depositional environment was actually hostile to the survival of limulids and that they were "washed-out" of their normal living environments and swept into a sedimentary basin.

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Introduction

Limulid trackways in the Bude Formation were first discovered by King (1965). His geological maps and composite section are reproduced by Freshney *et al.* (1972) and the xiphosurid horizons are identified in an excursion guide (Dearman *et al.* 1970). A number of inland localities were also listed (Freshney *et al.* 1979a), together with the only record of a xiphosurid body impression in the Bude Formation. Other investigations of the trackways have focused on the mode of preservation (undertracking) and sedimentological aspects (Goldring 1969; Goldring and Seilacher 1971). From the time of their discovery, these trackways have been recognised as providing an important constraint on depositional models of the laminated siltstones containing the tracks and of the Bude Formation itself. Conclusions arising from the present study provide additional constraints on depositional models and bear on ontogenetic aspects of limulid growth.

Stratigraphy and lithology of the xiphosurid horizons

King's detailed mapping of the coastal section from Widmouth Bay to Maer High Cliff has yielded eleven xiphosurid horizons, several of which are repeated by folding. These lie both above and below two major nodular shales: Tom's Cove Shale and Saturday's Pit Shale.

Three new xiphosurid horizons are located north of King's section, at Sandymouth Bay (SS 20180988). The new trackways are stratigraphically higher in the Bude Formation, but still between the biostratigraphical markers of the `*Anthracoceras' aegiranum*` horizon and the *Gastrioceras amaliae* horizon (Freshney *et al.* 1979b). The horizon yielding the trackways reported here is about 80cm thick, containing over a dozen laminae surfaces with a low density of trackways. The second horizon is greatly affected by shear movements, and the trackways that have been found are not suitable for removal and study. The third horizon is about 10cm thick, but the trackways are too profuse for reliable measurements to be made.

The rocks containing the trackways are difficult to relate to the published sequence (Freshney *et al.* 1979b). At Sandymouth, the Sandymouth Shale is repeated three times: at northing (1009) it is its normal thickness of 6-7m; at northing (1000) it has a structurally expanded thickness of around 17m; at northing (0988) much of the shale sequence has been sheared out. At this last locality, a 1.8m sheared shale has been tentatively identified as the Sandymouth Shale (E.C. Freshney, personal communication, August 1987). The first xiphosurid horizon is approximately 4m below the 1.8m sheared shale tentatively mapped as the Sandymouth Shale. The laminated siltstones belong to lithofacies 2 of Melvin (1986) and Facies Association 2 of Higgs (1986).

Observations of the siltstones by Goldring and Seilacher (1971), with additional points by the writer, are summarised below.

1. The siltstones have parallel laminations with varying thicknesses up to about 2mm.
2. Some grading is present in most laminae.
3. The laminae contain carbonaceous debris, which can be dense in places, but are not markedly pyritic.
4. Thin sandstones are often interbedded with the siltstones.
5. Low velocity currents are suggested by the lack of sedimentary indicators and the absence of trackway deflections.
6. Intervals of non-deposition must be invoked to account for the lateral persistence (several metres) of individual trackways.
7. Evidences of bioturbation of the siltstones are lacking. This observation is relevant to both the lack of feeding by the limulids and to the food resources available to them. Higgs (1986) states that these rocks, in thin section, show a disturbed horizontal lamination, suggestive of disruption by upward-migrating gas bubbles (presumably methane).
8. Body fossils of limulids, of molluscs, or of any other organisms are absent.

The trackways

Over a period of four years, about 30 slabs containing over 80 measurable trackways of varying length have been collected.

Feet and pusher marks are normally present in the Sandymouth trackways. Less well preserved specimens have pusher impressions but lose the feet markings. Telson impressions are common: sometimes continuous, but often intermittent as illustrated. The marks are generally found in the middle of the track set, although a number of samples show the telson displaced to one side (hence demonstrating a mobile telson). Genal spine impressions are rare, and opisthosomal spine traces have been observed on only one occasion.

All the traces observed are walking traces *(Kouphichnium),* comparable to Chisholm's Trace A (1983). Infilled resting traces *(Limulicuhichnus),* as defined by Miller (1982), shallow burrowing traces *(Selenichnus),* as defined by Romano and Whyte (1987), and deeper burrowing traces *(Aulichnites),* as defined by Chisholm (1985), have not been observed.

Measurements between pusher marks of track set width and step length (Fig. 1) were made on original specimens using dividers, as these provided the best preserved and most easily measured

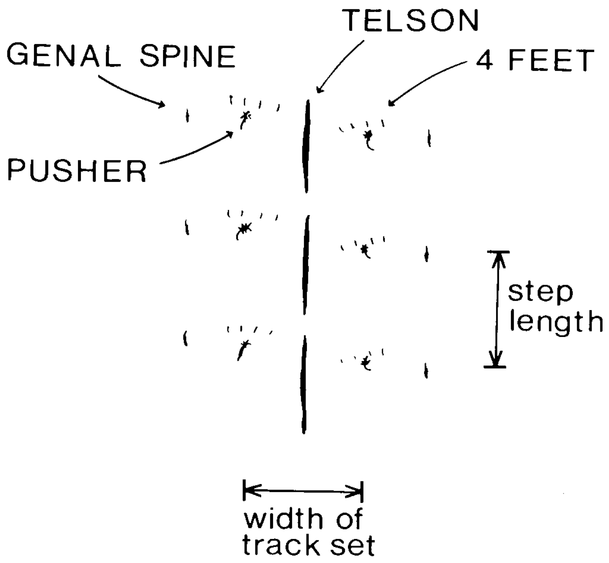

Figure 1. Representation of a limulid trackway showing the measurements taken.

feature. A series of measurements were made along each trackway, and the recorded figures are considered to have an accuracy of ± 0.5mm. Step lengths were measured over several steps: normally 10. Although individual steps vary in length, the average of 10 measurements effectively conceals random fluctuations.

Track set widths are here considered to be the most direct measure of the size and age of the organisms. During locomotion, the legs touch the ground in an orderly time sequence, and then the weight of the animal is transferred to the pusher, enabling the organism to move forward and repeat the cycle (Goldring and Seilacher 1971). The movements of the legs and the length of step are influenced by behavioural factors, and so are less reliable indicators of body size. Insofar as they carry the weight of the body and are responsible for moving the animal forward, the pushers are less influenced by behaviour, and so provide a suitable means of determining body size.

Fig. 2 summarises data on track set width obtained from 86 trackways. The range of widths is 3mm to 19.5mm. Trackways with a width of 6.5-7.5mm are absent, as are also widths of 10.511.5mm. Despite limited data, it is noted that there is a lack of trackways with a width of 17.5 - 18.5mm (see below). Thus, a cursory examination of the data suggests that there is not a continuum of body sizes, but that the limulids show an incremental pattern of growth.

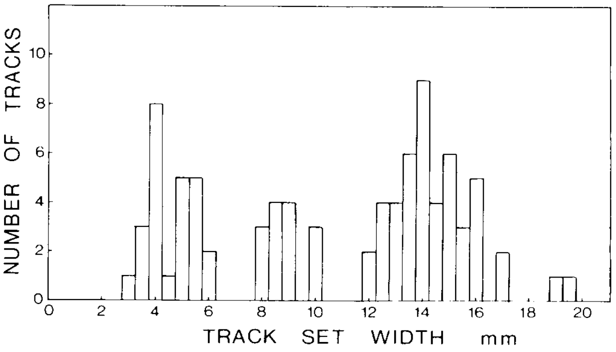

Figure 2. Analysis of track set width variations.

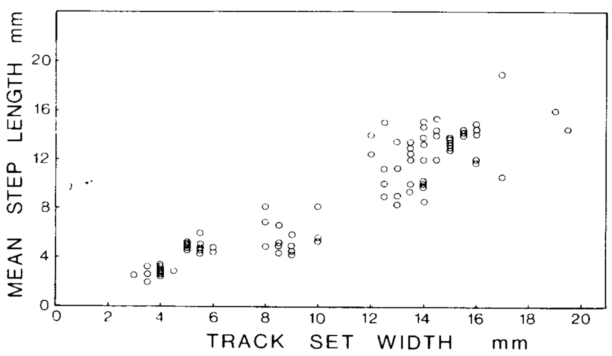

Figure 3. Variation of track set width with step length.

The smaller trackways are worthy of additional comment. The coarse scale of Fig. 2 conceals differences between the 3-4mm widths and the 5-6mm widths, which are apparent under visual inspection. By incorporating step length into the data plot, the differences are more clearly brought out.

Fig. 3 plots track set width against step length, with each track plotted as a separate data point. Tracks of the same width are found to have a range of step lengths, reflecting minor behavioural changes. Of particular interest are the trackways with widths from 3 to 6mm. The data points form two distinct clusters, with the larger track set widths associated with longer step lengths. There is actually no overlap of step length dimensions between the two clusters, which makes it difficult to argue that they may be explained by behavioural factors. The observation of an incremental increase in track set width associated with an incremental increase in step length leads to the conclusion that the larger cluster represents a separate instar.

It is well established that the dimensions of instars of similar body form change by a constant proportion at each ecdysis (Clarke 1973). This fact has been used here to analyse the data plotted in Fig. 3. Mean track set widths and standard deviations have been determined for each instar, and are tabulated in Table 1. The two largest width measurements have been tentatively assigned to a fifth instar although, as indicated below, the bracketed figures are obtained, not from the two measurements, but by extrapolating the patterns that emerge for the smaller instars. The ratio between the step length and the centres of paired tracks is defined as the pace ratio and a value for each trackway has been determined. Table 1 records the mean pace ratio for each instar, together with the standard deviation.

The `increase in size' factor shows that systematic increases in size occur, which strengthens this interpretation of the data. The figure of x 1.4 for the earliest ecdysis may reflect difficulties in measuring the small track dimensions, or may be associated with

Table l. Statistical analysis of instar dimensions.

Instar Number	Number of data points	Mean Track Set Width (mm)	St Deviation x2 (mm)	Increase in size at ecdysis	Mean Pace Ratio	Standard Deviation
1	13	3.9	0.8		0.75	0.1
				x 1.4		
2	12	5.4	0.8		0.95	0.1
				x 1.6		
3	14	8.9	1.4		0.67	0.16
				x 1.6		
4	45	14.3	2.5		0.88	0.15
				x (1.6)		
5	2	(22.9)	(4.0)		0.79	0.07

a change in body form. Assuming an increase in size of x 1.6 for the fourth ecdysis, a mean track set width of 22.9mm is calculated for the fifth instar. A spread of data around the mean has been estimated by making comparisons with observed variations for the smaller instars. Allowing these figures, it is defensible to allocate the two largest width track sets to the fifth instar. The mean pace ratio has an overall average of 0.83, and the means for each instar are close to this figure. The relative constancy of these means further supports the case for systematic increases in body size with each ecdysis.

Limulid trackways collected by King during his field research activities are in store at Reading University, and the writer was able to make measurements of them in September 1987. Three of the trackways measured belong to instar 3, and twenty-five belong to instar 4. No traces were found of instars 1 and 2. Narrow trackways have not been previously reported from the Bude Formation, although Goldring and Seilacher (1971) state that narrow xiphosurid tracks have been recovered from the associated Abbotsham Formation. Chisholm (1983) has reported *Kouphichnium* trackway widths of approximately 16mm for Trace A (instar 4) and approximately 3mm for Trace B (instar 1). Widths of burrows and of resting traces are related to the prosoma widths of the animals, and are slightly wider than the equivalent track set widths. Burrows described by Chisholm (1985) are from 10mm to 25mm in width, representing instars 3, 4 and 5. Hardy (1970) described resting traces with a width of 1617mm, which can be associated with xiphosurids belonging to instar 4.

In the Bude Formation, tracks have been observed to persist over several metres of a bedding plane. Although there are indications of a preferred direction, trackways frequently cross one another at a wide range of angles. Larger trackways show few rapid changes of direction and are typically linear or gently sinusoidal. The smaller width trackways, on the other hand, are characterised by changes of direction, with individuals repeatedly crossing over their own tracks. Although behavioural analysis of the trackways is not a topic developed in this paper, these particular observations are considered significant for the interpretation of the trackways which follows.

Environmental considerations and trackway interpretations

The Bude Formation exhibits many different sedimentological and palaeontological characteristics and its depositional environment has been the subject of much debate. Three models of importance are the fluviodeltaic model of Freshney et al. (1979b), the delta-fed sub-sea fan model of Melvin (1986), and the nonmarine shallow-shelf model of Goldring and Seilacher (1971) and Higgs (1986).

The xiphosurid trackways have acted as a constraint on these models, as Carboniferous limulid trace fossils are elsewhere found in association with nonmarine fluviatile and lacustrine environments. Eagar et al. (1985) describe a *Pelecypodichnus* - *Kouphichnium* - *Arenicolites* assemblage associated with mud banks in a shallow water nonmarine sedimentary basin, possibly controlled by seasonal climatic changes, with flooding a regular phenomenon. These xiphosurids lived in association with other organisms and they exhibited a variety of behavioural characteristics: walking, swimming, resting and burrowing (Chisholm 1983, 1985).

By contrast, in the Bude Formation, at the Sandymouth localities, limulid traces are limited to walking. This is particularly curious with the smallest instars, as small organisms are expected to spend more time below the sediment surface hiding from predators. A comparison may be made with early trilobite instars, which are suggested by Crimes (1970) to have this behaviour. Organisms commonly associated with limulids are absent: there are no bivalve fossils or traces, and there are no evidences of filter feeders or substrate feeders burrowing into the siltstones. The only traces of other living things associated with these siltstones are those of fish. Goldring (1978) has reconstructed an environment, calling it a Carboniferous Sea Level Lake Community. However, it is argued here that the evidences are against a living environment for the limulids.

In their 1971 paper, Goldring and Seilacher commented: "The depositional environment was not necessarily the optimal life environment for the xiphosurids." (p. 434). Indications that the xiphosurids were not normal inhabitants of the environment represented by the siltstones is shown by their restricted behaviour patterns, the lack of food in the sediments, and the lack of body fossils such as exoskeletons from ecdysis. These limulids appear to be transient occupants only.

King's (1965) analysis of the xiphosurid trackways has dominated their understanding, particularly his interpretation of out-of-phase sinuous trails as the result of a nuptial embrace. Since modern king crabs walk extensively only during the short mating season, the trackways and trails were associated with breeding behaviour. King commented on the "set course" of individual trails and suggested that the organism had a purpose in moving, "perhaps migratory". However, this analysis is no longer tenable. More recent work on the out-of-phase sinuous trails by Higgs (1988) has shown them to be fish trails assigned to the ichnogenus *Undichna*. The results reported here demonstrate the existence of probably five instars in one xiphosurid locality, and it may reasonably be deduced that the smaller instars are not engaged in breeding behaviour.

It is here proposed that the xiphosurid trackways in the Bude Formation are not in their normal environment. The turbid river waters described by Higgs (1986) not only carried sand, silt and mud into the sedimentary basin, but also limulid populations washed out of their living environment. As current velocities waned and sediments dropped out of suspension, so also were the limulids able to control their own movements. In an alien environment, the animals did not settle, and their purposeful migrations to find a place of refuge began. The tracked siltstones record temporary occupation only. The winding, backtracking, directionless movements of smaller instars is here interpreted as a distress behaviour arising from transportation to the unfamiliar environment.

It is now recognised that conditions of rapid sedimentation characterised much of the Westphalian (Broadhurst 1984; Broadhurst and France 1986). The evidences provided by patterns of sedimentation, sedimentary structures, patterns of fossilisation, polystrate trees, extensive upward escape of *Pelecypodichnus* bivalve traces, and major sheet sandstones, document an environment of instability with the rapid accumulation of sedimentary sequences. It is here suggested that the Bude Formation represents a distal extension of the same phenomena and that the presence of limulids serves to link patterns of sedimentation in apparently contrasting facies. Higgs (1986) describes turbid river waters from catastrophic stormfloods carrying fine-grained sands and muds into "Lake Bude", to be subsequently reworked by storm-generated waves.

Since Carboniferous xiphosurid traces are associated with nonmarine fluviatile and lacustrine environments, it has been natural to deduce a related model for the Bude Formation siltstones. However, accepting this alternative interpretation, such a direct association need not be made. For example, deeper water environments for the deposition of the siltstones may be investigated without being unduly constrained by the presence of a shallow water species.

Summary and conclusions

Three new xiphosurid horizons in the Bude Formation are reported, one of which has yielded trackways suitable for measurement and analysis. The trace fossils occur in the typical laminated siltstone facies previously described as carrying limulid tracks.

Measurements of track set width and step length are reported and discussed. Evidence is presented to show that at least four and probably five instars are present in the limulid population.

The limulid trackways have provided important constraints on models of the depositional environment of the Bude Formation. The presence of several instars in one siltstone horizon places additional constraints on interpretations of limulid behaviour. Evidences relevant to the ecology of the tracked siltstones are discussed, and it is concluded that the limulids represent a transported fauna.

This interpretation of the trackways links patterns of sedimentation associated with the Coal Measures of Central and Northern England with sedimentological characteristics of the Bude Formation. This dynamic overview may assist the resolution of problems evident in the conflicting models of its depositional environment.

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