XIPHOSURID TRACE FOSSILS FROM THE WESTBURY FORMATION (RHAETIAN) OF SOUTHWEST BRITAIN

by GUANZHONG WANG

ABSTRACT. The abundant and diverse trace fossils attributed to xiphosurid activity on sandstone soles at Westbury on Severn are described and interpreted. The xiphosurids seem to have been active in this area mainly after major storm event sedimentation. Two patterns of scratches, three types of lunate marks, and a bilobate furrow assignable to *Cruziana perucca* are distinguished. The lunate marks and one pattern of the scratch marks are assigned to *Selenichnites* isp. The marks were produced either during carnivorous feeding or burrowing for concealment. Variation in the traces is attributed to variable formation and preservation, sediment grain size, mud cohesiveness, as well as sediment thickness above the trace-taking sole surface, which modified the behavioural activity of the trace maker.

THE fossils believed to have been formed by xiphosurid arthropods have long been known from the Westbury Formation (Upper Triassic, Rhaetian) at the much frequented section at Westbury Garden Cliff (SO 717132), located on the north bank of the River Severn, 13 km (8 miles) west-southwest of Gloucester (Text-fig. 1). The section, described in detail by Richardson (1905, 1911), is readily accessible and displays the upper part of the late Triassic Mercia Mudstone Group, which dips gently towards the southeast. This contrasts with the more or less horizontal (though faulted) attitude of the better-known section at Aust Cliff (Savage 1977). The xiphosurid marks are associated with the upper of two sandstones in the section, blocks of which litter the beach. Recognition of the traces has been only by brief mention (Magor 1978; Ager and Edwards 1986).

Traces interpreted as those produced by xiphosurids are not rare in the geological record, especially those included in the ichnogenus *Kouphichnium* (Caster 1938, 1944; King 1965; Bandel 1967; Goldring and Seilacher 1971; Wright and Benton 1987); they are xiphosurid walking tracks, often accompanied by telson or genal spine marks. Traces attributed to xiphosurid resting burrows have been reported by Hardy (1970), Fisher (1975), Miller (1982) and Romano and Whyte (1987). Chisholm (1986) described a xiphosurid burrow which he interpreted as the product of intrastratal feeding activity. The present material, however, records a more complex relation of the animals with the substrate in what must have been a marginal marine environment.

The object of this paper is to document the traces found at Westbury Garden Cliff and to discuss problems related to the formation and interpretation of the traces. Material illustrated is deposited in the PRIS (University of Reading) Archive Collection. A specimen in the National Museum of Wales, Cardiff is numbered 88.72G.

STRATIGRAPHY AND SEDIMENTOLOGY

The Westbury Formation at Westbury Garden Cliff rests directly on the mudstones and thin sandstones of the Mercia Mudstone Group (Text-fig. 2). As is generally the case, some 4 m of greenish mudstones are present below the base of the Westbury Formation. This base is an almost planar erosion surface, except for local elevations of a few centimetres, perforated by *Diplocraterion parallelum* filled with black mud or pebbly clasts and indicating firmground colonization (Text-fig. 2). A thin layer of small rounded, pebble-sized clasts derived from the underlying mudstone and some

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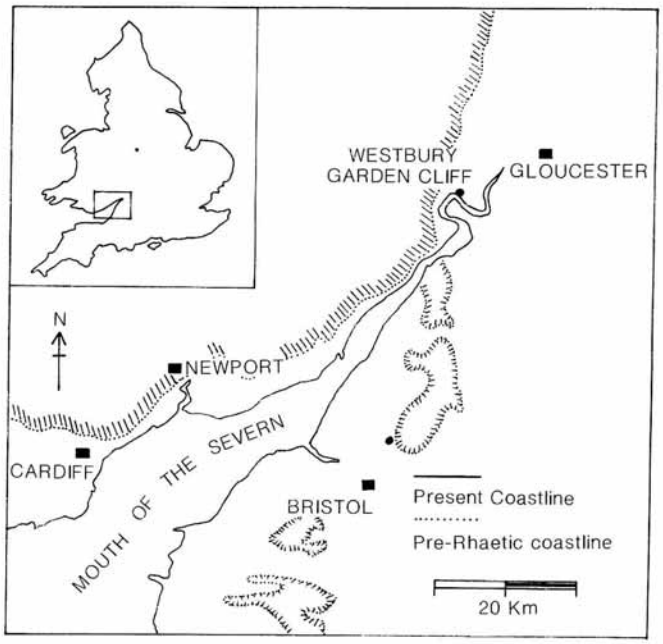


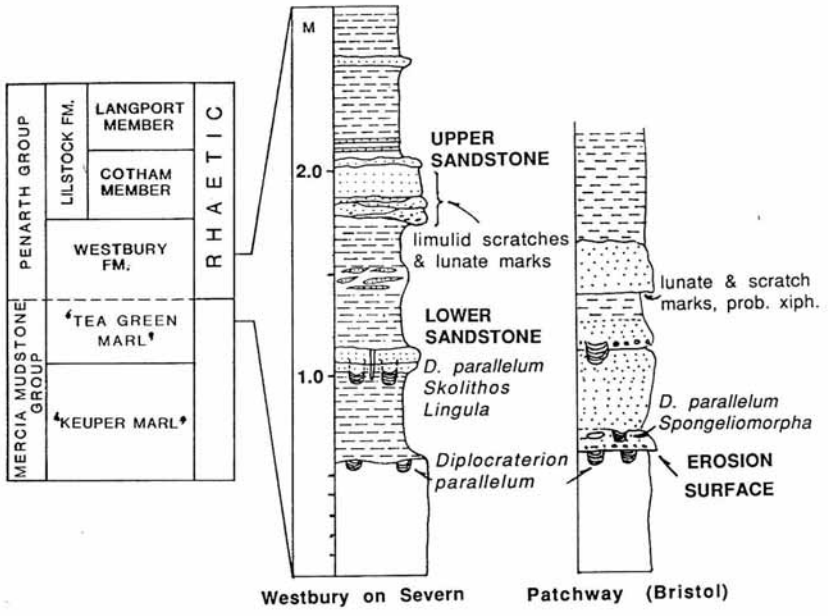
TEXT-FIG. 1. Location map of Westbury Garden Cliff with pre-Rhaetic coastline (from Audley-Charles 1970). Dot in the centre of inset indicates location of Needwood Basin, Staffordshire (Wright and Benton 1987) and the dot north of Bristol, the location of Patchway.

bone fragments mark the base. A black, finely laminated shale, some 0·4 m thick follows, from which no fossils have been recorded.

The black shale is terminated by a 10–25 mm thick, poorly cemented siltstone, above which is a 90 mm sandstone. The siltstone contains fragmental bivalve shells, fish teeth and scales, and well-preserved *Lingula*. The sandstone generally splits into two layers. The lower layer (20–30 mm thick) contains small bivalves, bones and teeth (including teeth of the lungfish *Ceratodus latissimus* and plesiosaur vertebrae) and the trace fossil *Diplocraterion*, which extends into the underlying siltstone. The upper layer is thicker (50–60 mm) and more fossiliferous, with numerous fish scales and teeth as well as spines. The upper surface of the unit is slightly undulose and bears a shell pavement of convex, dissociated bivalves including *Rhaetavicula contorta*, *Protocardia rhaetica* and *Schizodus* sp. Both sandstones have been extensively bioturbated. But the only recognizable traces are *D. parallelum*, and simple vertical and oblique burrows (*Skolithos*) filled with clean sand.

Above the Lower Sandstone is another unit (0·58 m) of black shale, the basal 10–20 mm of which is a silt containing small pieces of broken shell. Individual laminae in the shale are thicker than in the lower shale and the unit includes thin, wavy to lenticularly bedded, fine-grained sand, with opposed current directions suggesting tidal influence.

The Upper Sandstone (about 0·2 m thick) rests sharply on black shale. Bone material and bivalve shells are abundant. It is compound, with a few interbedded impersistent muddy seams and partly amalgamated units of sand that individually fine upwards and frequently have a rippled upper surface. The several leaves are markedly impersistent and separated by distinct erosion surfaces. The sandstone is calcareous and well sorted. Clasts range from coarse bone material (average 2–4 mm)



TEXT-FIG. 2. Stratigraphy (Penarth Group after Warrington *et al.* 1980) and summary logs of the sections at Westbury Garden Cliff and Patchway (Bristol) with occurrence of trace fossils indicated.

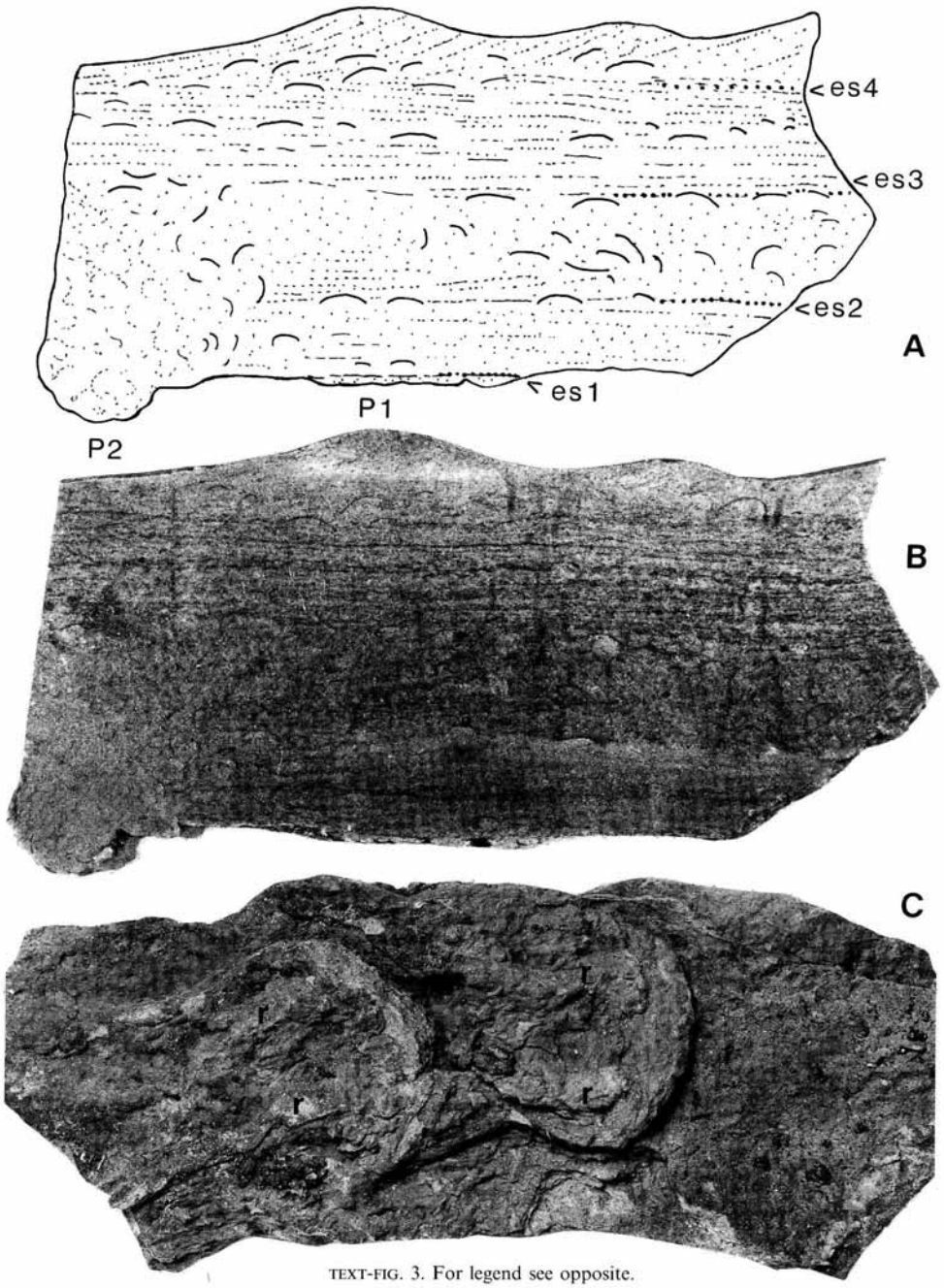
and intraformational mud chips, to very fine to fine-grained sand. Dissociated bivalves of small size, usually pyritized, occur throughout, with a notably higher concentration on each of the upper rippled surfaces. The patterns of ripple are variable, ranging from symmetrical or nearly so, to straight or sinuous, but usually low-crested with ripple crests peaked or rounded or of spill-over form.

In a representative section, the Upper Sandstone can be divided into three parts. The lower part (40–60 mm) is composed of four layers of sandstone containing abundant coarse bone debris, that laterally change in thickness and are separated by muddy drapes or leaves. Scratch marks can be seen on each lower interface, and especially on the lowest sole surface where the bone bed is in contact with the underlying black shale.

The middle part is a thicker (0·12–0·16 m), fine- to coarse-grained sandstone, which is harder and more compact and has less vertebrate debris. Slabs seen in section show at least four sedimentation events (Text-figs 3, 5D). Scratch marks are less abundant and not as sharp as seen on the sole of the lower part, but sharply outlined lunate marks are more common.

The upper part comprises two to three thin fine-grained sandstones with mud partings and includes occasional lunate marks of type *c*. The sandstone was locally highly biotubated, but only as a result of xiphosurid activity, except for occasional *Lockeia* and some small unidentified traces, identical to, but less abundant than, those described from the Needwood Basin (Wright and Benton 1987).

The sharp contact with the underlying shales, graded bedding, spill-over ripples (Seilacher 1982), and the mud-filled scours, suggest a storm-event origin for each unit of the Upper Sandstone.



TEXT-FIG. 3. For legend see opposite.

DESCRIPTION OF TRACE FOSSILS

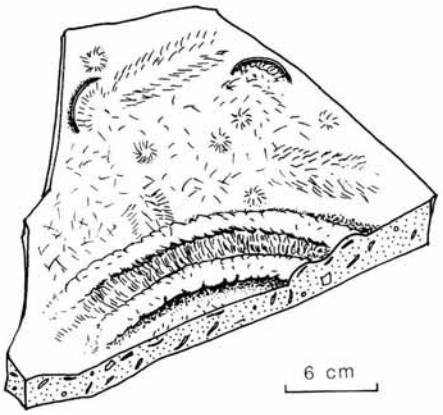
The trace fossils are all positive hypichnia and include two patterns of scratch marks, three types of lunate marks and a bilobate ridge.

Scratch marks. Distinct scratch marks are of only one kind: they are sharp, up to 15 mm in length and V-shaped, and may bifurcate towards the outer end. The latter feature indicates a bifid claw. Scratch marks show two patterns of arrangement and stratigraphical distribution in the Westbury Formation. The first pattern is found on the sole of the Upper Sandstone. The second is present on soles within this sandstone, following a thin mud interface.

Pattern 1 (Pl. 1, figs 2–3; Text-fig. 5A) are sharp scratches, randomly arranged or in paired rows which cover extensive areas of the sole of the Upper Sandstone. The paired scratches have a V-arrangement: the low relief of each row being separated by a wide and shallow furrow. The scratches tend to bifurcate laterally and diverge posteriorly (in contrast to the posteriorly converging scratches of most *Cruziana*).

Pattern 2 (Pl. 1, figs 4, 7; Text-fig. 5C) are ovoid to subtriangular outlines with a low relief, and short scratches on lower surfaces within the Upper Sandstone. Some show a superficial resemblance to *Rusophycus* but there is no median groove. They resemble Miller's (1982) *Limulicubichnus* but lack posterior ridges. Others recall Seilacher's model (1985, p. 233, figs 2*g*, 3*b*) where *Rusophycus* was formed below an appreciable thickness of sand cover.

Bilobate furrow. A bilobate positive hypichnial ridge (Pl. 1, fig. 2; Text-fig. 4) found on the sole of the Upper Sandstone, associated with pattern 1 scratch marks. The two broad and relatively smooth ridges (each 20 mm wide) are separated by a broad furrow (20 mm wide) with sharper scratches. The two ridges were probably produced by modification by the appendages of a groove cut by the prosoma, as illustrated by the ridges (*r*) in Text-fig. 3C. The measurable length of the whole trace is 200 mm.



TEXT-FIG. 4. Sketch of sole of upper sandstone showing a bilobate positive hypichnion (bottom) resembling *Cruziana perucca* (see Pl. 1, fig. 2), pattern 1 scratch marks, and mounds which may represent the feeding activity of the trace-maker. The layer is composed of pebble-size fish bones, teeth and spines, and fine-grained sand.

TEXT-FIG. 3. A, B. Sketch and vertical section (×1) through middle part of the Upper Sandstone showing amalgamation of event layers each separated by an erosional surface. Prosoma mark P1 (type *b*) was truncated by erosion surface (es) 1. Erosion surfaces 2 and 3 record the truncation of two subsequent units. Erosion surface 4 may represent a change in hydraulic regime. It is uncertain when prosoma mark P2 (type *a*) was emplaced, possibly prior to erosion surface 3 or even higher. (Specimen number PRIS. S33820). C, Positive hypichnia from high in Upper Sandstone with two prosoma marks (type *c*) probably made by a single individual twisting somewhat over substrate surface. Paired ridges (*r*) cast grooves formed by appendages. Genal spines have not left any appreciable groove, ×0·5. (PRIS. S33821).

The trace recalls *Arthrophycus*, but the latter has a smooth surface. A cruzianiform furrow thought to have been produced by xiphosurans was reported from the Rhaetic Sandstone of Pfrondorf near Tübingen (Seilacher 1985, p. 233, fig. 2*i*). There the high relief of the two lobes is separated by a narrower and deeper furrow and the trace shows head shield impressions. The leg scratch marks are less distinct but clearly diverge posteriorly. The bilobate trace described here, however, is much like *Cruziana perucca* Seilacher (1970, p. 469, figs 10*d–e*). Seilacher (1970) attributed this ichnospecies in trinucleid trilobites though later (Seilacher 1985, p. 234) commented on the possibility of xiphosurans producing similar traces.

Lunate (prosoma) marks and associated burrows. Three types of lunate mark are present.

Type a (Pl. 1, figs 1, 5; Text-fig. 5D (3)) is a crescent-shaped prosoma mark formed by the anterior part of the prosoma, forming a smoother band without enclosing scratches. Typically the mark exhibits several ridges parallel to the margin, which may be interpreted as repeated thrusts of the animal to push into a cohesive substrate. The area enclosed varies from smooth to rough. This kind of mark is found on lower surfaces, within the Upper Sandstone, specially of the sole of the middle part of the Upper Sandstone, sometimes at intervals in a linear sequence (Ager and Edwards 1986, fig. 4), similar to those illustrated by Hardy (1970). The sole surfaces follow mud drapes over rippled surfaces with convex-up dissociated bivalves.

Type b (Pl. 1, figs 1, 6; Text-fig. 5D, (1–2)) is a prosoma mark which is an almost complete impression of the doublure, with a median carina often evident. The prosoma mark encloses scratch marks and a telson mark may be evident. This trace closely resembles *Selenichnites hundalensis* (Romano and Whyte 1987), and is found mainly on the sole of the middle part of the Upper Sandstone and within the sandstone.

Type c (Text-figs 3C, 5B) is a lunate sole mark corresponding in outline with a limulid prosoma; it occurs mostly widely separated and without preferred orientation. The anterior margin is deep (15 mm) but seldom sharply defined. The mark is prolonged and shallows towards the marks of the genal spines. This mark may or may not enclose an area of rather obscure scratches. In section (Text-fig. 5B) the mark passes upwards into a broad asymmetrical burrow, posteriorly sloping upwards at about 10° with a relatively sharp margin. The anterior slope is sharper and steeper (approx. 50°). The bioturbated sediment of the burrow fill often carries mud flakes at the base, and abuts against bioturbated sand.

This mark is found on soles within the middle part of the Upper Sandstone, where the bone layer covers fine-grained, laminated sandstone (Text-fig. 5D) and in the upper part of the Upper Sandstone.

Dimensions. Most specimens are between 70 and 80 mm in width, and length including telson mark, 110 mm. An exceptionally large specimen (130 mm width) was recorded by D. V. Ager (personal communication).

The palaeolimulid responsible for the various marks at Westbury on Severn was probably *Limulitella* which has a prosomal outline and size in agreement with the trace fossils. *Limulitella* is well known from the Late Triassic (Størmer 1952).

FORMATION AND PRESERVATION

There has been considerable discussion on the origin of *Cruziana* and *Rusophycus*, as to whether they were formed epigenically, or endogenically and intrastratally. While Seilacher (1955, 1970,

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EXPLANATION OF PLATE 1

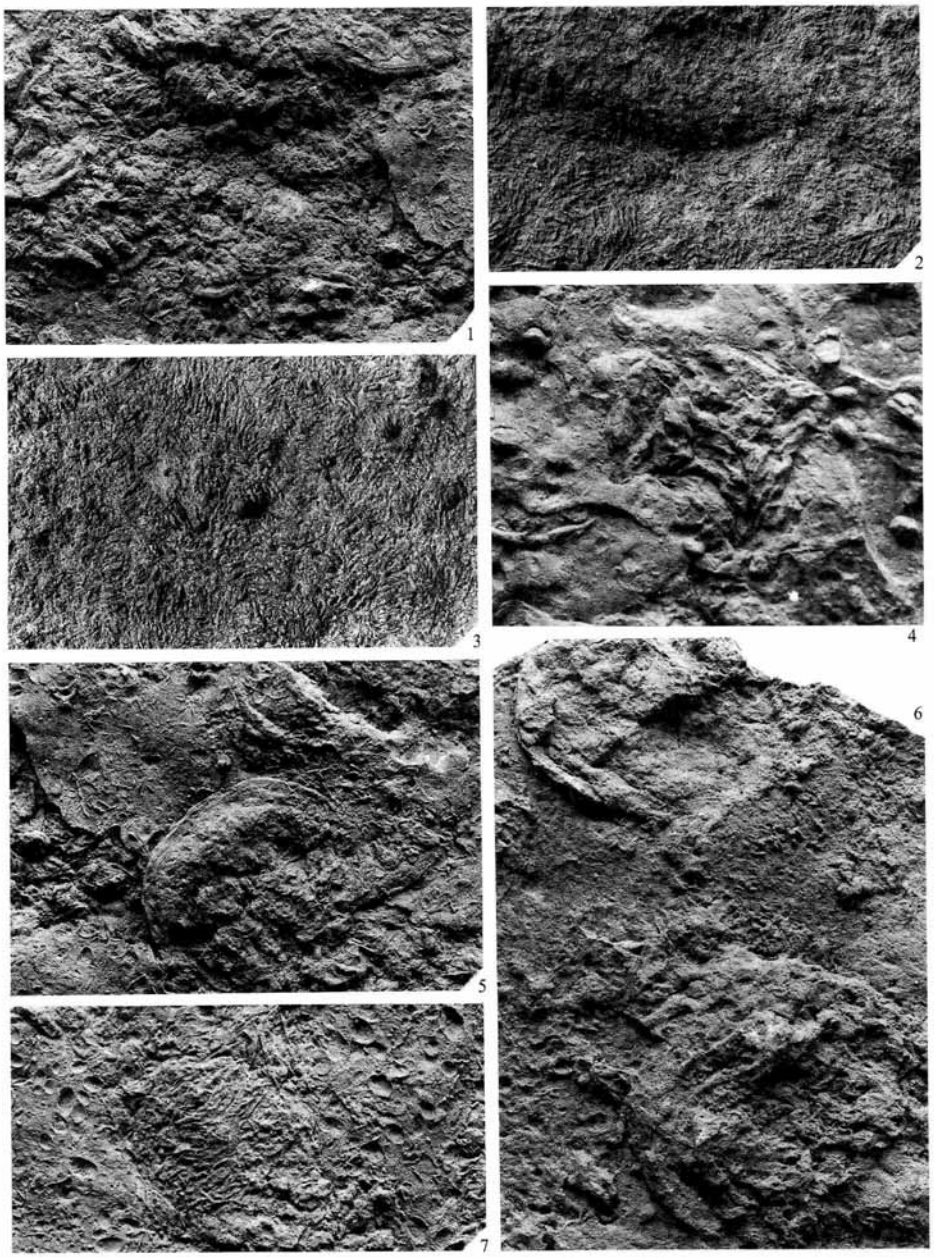
All specimens were collected from the Rhaetian of Westbury Garden Cliff.

Figs 1, 4–7. *Selenichnites* isp. 1; PRIS. S33815; lunate mark type *a* (upper right) on a rippled lower surface and lunate mark type *b* (left) on a split lower surface of a sandstone block. The split surface was extensively scratched, ×0·4. 4, PRIS. S33819; converging scratch marks of pattern 2 within a diamond-shaped outline, ×0·5. 5, lunate mark type *a* on a rippled surface on the same block as shown in fig. 1. This surface has abundant external moulds of convex-up bivalves, ×0·5. 6, PRIS. S33818; lunate marks of type *b* on the lower surface of a sandstone block from the middle part of the Upper Sandstone, showing scratches, marks of prosoma and telson (below), ×0·6. 7, scratch marks of pattern 2, also on same block, within an ovoid-shaped outline, ×0·4.

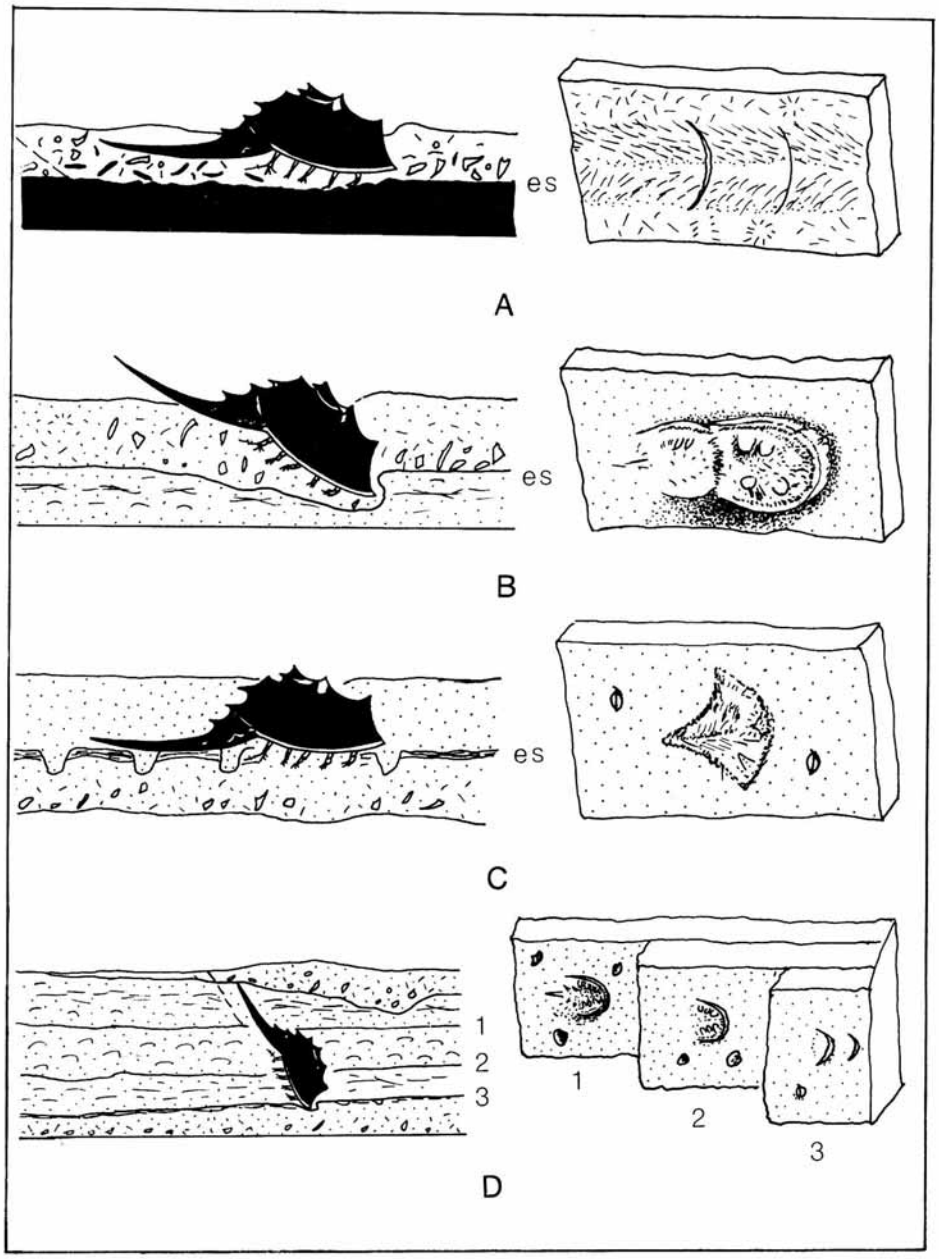
Fig. 2. *Cruziana perucca* Seilacher, 1970. PRIS. S33817; bilobate furrow and scratch marks on the sole of the Upper Sandstone, ×0·4.

Fig. 3. *Selenichnites*? isp.; PRIS. S33816; scratch marks of pattern 1 on the sole surface of the Upper Sandstone, ×0·35.

PLATE 1



WANG, *Selenichnites*



TEXT-FIG. 5. For legend see opposite.

1985) has maintained that *Cruziana* was cut intrastratally, Crimes (1975) and Baldwin (1977) presented evidence in support of an epigenic mode of formation, whereby the mark was cut at the sediment–water interface and then cast by a subsequently deposited sand. Sectioning material firmly demonstrates an interstratal mode of formation for *Cruziana* (Goldring 1985), though he was not able to determine the thickness of the sand layer and Seilacher (1970) only presented a rough model for variation in *Cruziana* reflecting bed thickness.

Only by sectioning the rock, therefore, is it possible to understand the way in which the hypichnial traces were formed and preserved, and to interpret the behavioural activity of the animals responsible. Each trace reflects the relationships between the type of behavioural activity, the depth of the mud–sand interface below the original sediment–water interface, any lateral variation in this depth (as between ripple crest and trough), the cohesiveness of the mud below the sand, and the grain size and texture of the sand. Scratch mark of pattern 1 (Pl. 1, figs 2–3; Text-fig. 5A) and the bilobate furrow (Pl. 1, fig. 2; Text-fig. 4) were formed when the animal could move freely through the coarse-grained, loose sand trying to locate food. Where the sand was fine and cohesive, the activity of the animal was restricted and only scratch mark type of pattern 2 could form. Lunate mark type *b* (Pl. 1, figs 1, 6; Text-fig. 5D (1–2) and lunate mark type *c* were possibly produced at different levels by limulids burrowing down from the same sediment–water interface (Text-fig. 5D).

Where the trace is a sole mark directly above mud it is evident that degradation of the mud had taken place before sand deposition was initiated so that the mud was relatively firm. Evidence for this is the common occurrence of mud flakes ripped up by the animal in the bottom of the burrows (Text-fig. 5A). No tool marks have been observed at any level of the sandstone, though it is possible that any present were subsequently obscured by scratches. The nature of the mud also seems to have controlled the sharpness of the scratches. The silty mud below the main sandstone unit favoured the formation of sharper, higher relief scratches compared with scratches associated with the mud leaves within the sandstone bed.

This mode of formation contrasts with *Kouphichnium* resulting from undertrack fallout through laminated siltstone (Goldring and Seilacher 1971). *Kouphichnium* reflects the relationship between the animal's activity and the fall-out principle enunciated by Seilacher (in Goldring and Seilacher 1971). The trace was formed by the animal moving over laminated sediment so that the fossil trace firstly reflects the particular lamina along which the rock has split. Occasionally traces may have been cut exogenically into a sandy substrate without a thin mud drape (Wright and Benton 1987).

ETHOLOGY OF TRACES

Limulids have been filmed during concealment when the animal pushes into loose sediment at a low angle, using a backward movement of its pushers with spread dactyli to effect. Some of the Westbury marks might be expected to result from this movement, with the prosoma impacting on the cohesive mud. In other instances the prosoma mark is repeated at intervals as in *Selenichnites rossendalensis*. But this type of trace is only present where the mark appears to have been formed below a thin layer of sand. No pusher marks have been observed. The reason is almost certainly because the pushers did not normally reach the sand/mud interface. On extensively scratched surfaces the pushers may not have splayed to give digitate impressions. In thicker layers (Text-fig. 5D) the prosoma impinged on the mud layer at a high angle. This trace probably represents activity

TEXT-FIG. 5. Interpretation of formation of different limulid traces. A, sharp scratch marks. The xiphosurid dug into the coarse sand and readily moved along the sand/mud interface, perhaps in search for food. The underlying mud was firm due to degradation, resulting in deep and sharp scratches. B, as in A, erosion surface (es) cuts fine-grained sand which was loose when intruded by limulid. The traces (type *c* lunate mark) are of high and rough relief. Associated scratches are not as sharp as in A. C, formation of type 2 scratches. Here the variation is largely due to body attitude, but consistency of the underlying sediment probably also exerted an influence. The thin mud between the two sandstones was readily disrupted. D, the animal dug down steeply from a high level and left, on split surfaces, lunate marks with different details.

in locating food. On the same sole surface where abundant scratches and a bilobate furrow appear, small hollows with scratch marks (Text-fig. 4; Pl. 1, fig. 2) are better interpreted as feeding traces.

TAXONOMY

Although xiphosurid trace fossils are well represented in the fossil record the nomenclature has grown in a haphazard way following individual discoveries. Like trilobites, xiphosurids must have performed a variety of activities (as limulids do today), generating a range of different types of trace. Further diversification of the marks is due to toponomic and preservational processes: amount of penecontemporaneous erosion and extent of bed amalgamation, grain size variation, bed thickness, and diagenesis. These factors are not nowadays accepted as having taxonomic significance (Bromley 1990).

It is these factors, however, that seem to have determined the main differences between the traces described here and have indeed influenced the form of the traces to an extent greater than that exerted by purely ethological influences. Seilacher (1970, p. 449, fig. 1; p. 451, fig. 3; 1985, p. 233, fig. 3) discussed the variation in *Cruziana* associated with bed thickness. The scratch marks described here are somewhat analogous to the traces *Rusophycus* and *Diplichnites* and to some extent also to *Cruziana*. The grain size of the sediment or the thickness of the mark-forming layers have never been considered aspects that might serve to differentiate between *Rusophycus* and *Diplichnites*. The Westbury marks appear to represent only two types of activity, either to burrow into the sediment, most likely for feeding on the abundant small bivalves or annelid or annelid-like animals, or for concealment.

Kouphichnium is typically applied to a series of appendage marks that are clearly heteropodous and also commonly include the telson mark and occasionally marks of genal spines. Higgs (1988) has shown that the supposed genal spine marks, without tenson or appendage marks, described by King (1965) are attributable to fish activity. *Koupichnium* does not display scratch marks and only minimal sideways movement of each appendage in the sediment is indicated.

Cruziana and *Rusophycus* have been used to include traces left by trilobites and xiphosurids (Seilacher 1970, 1985; Shone 1978; Wright and Benton 1987). They are somewhat similar to some of the scratch marks described here but the differences in overall morphology are against assigning the marks to either ichnogenus. However, the cruzianiform furrow (Pl. 1; fig. 2, Text-fig. 4) described here may be assigned to *Cruziana perucca* Seilacher, 1970 unless the posterior divergence of the appendage marks is given greater weight to warrant a separate ichnogenus.

Selenichnites was proposed by Romano and Whyte (1990) as a new name for *Selenichnus* Romano and Whyte (1987), *Selenichnus* being pre-occupied by a vertebrate footprint. The diagnosis for *Selenichnites* (as given in Romano and Whyte 1987) emphasizes the mark of the prosoma but also indicates that scratch marks and a posterior ridge may or may not be present. Romano and Whyte (1987) considered the mark to have been formed at the sediment–water interface rather than interstratally. The single specimen (not found *in situ*) was not slabbed to prove this. Romano and Whyte (1987) considered the object of the animal in making the trace was in burrowing into a resting position. They also included *K. rossendalensis* (Hardy 1970) and *K. cordiformis* (Fisher 1975) in their ichnogenus.

The most suitable name for the lunate marks is *Selenichnites* isp. Because of the close relation with the lunate marks, scratch mark pattern 2 may also be assigned to *Selenichnites*. Other marks are best left in open nomenclature.

ENVIRONMENTAL SIGNIFICANCE

Triassic xiphosurid traces in the UK are known from Westbury on Severn and from the Needwood Basin of Staffordshire (Wright and Benton 1987). The author has also found scratch and lunate marks in the Westbury Formation at Patchway (ST 587815), near Bristol (Text-figs 1–2), also on the sole of the second sandstone above the base of the formation, though the scratches are finer. They may be expected to be present in the Westbury Formation at other localities. But considering their abundance, diversity and preservation, their occurrence at Westbury Garden Cliff is unique. *Kouphichnium* and *Rusophycus* of probably limulid origin from the Needwood Basin (Wright and Benton 1987) are rare and of small size (19–21 mm wide) compared with the lunate marks at Westbury Garden Cliff. No limulid body fossils have been recorded from the Rhaetic in the Bristol area. There are three possible interpretations for this unusual distribution: environmental factors, toponomic and preservational factors, or a combination of these.

Sedimentologically and ichnologically, the sections at Westbury on Severn, Patchway and the Needwood Basin, differ in several aspects. The sandstones from the Needlewood Basin are similar to those at Westbury, but thicker (more than 0·35 m thick) and rest directly on the mudstone of the Blue Anchor Formation (Wright and Benton 1987). Apart from the limulid trace fossils, other traces are similar to those found at Westbury on Severn. The rarity of limulid scratch and lunate marks in the Needwood Basin may be due to the thickness of the sandstone and lack of mud layers, though slabbing may reveal similar bioturbation. Indeed, in Wright and Benton's figure (1987, pl. 49, fig. 1), the asymmetrical area of the bioturbated sediment, lower left, is close to the area depicted in Text-figure 3.

At Westbury on Severn, it seems that only after periods of storm-event sedimentation is there evidence of limulid benthic activity, which only temporarily provided suitable conditions, including appreciable organic material and enough oxygen to the bottom waters. The underlying and overlying mud indicates a quiet and probably anoxic environment (indicated by the fine lamination, large amount of pyrite, absence of bioturbation) with sediments that would not readily preserve traces. The Lower Sandstone from which no limulid traces were recorded, however, was deposited in a relatively more stable, shallow, frequently reworked and well oxygenated environment as indicated by the U-shaped spreiten burrow *Diplocraterion* and the extensive bioturbation. Besides, compared with the sediments near Bristol, which contain more and larger *Diplocraterion* at the base of the formation and on the sole of the Lower Sandstone (which also exhibits common *Spongeliomorpha*), the salinity at Westbury on Severn could have been much reduced, possibly due to its location near the palaeocoast (Text-fig. 1). *Diplocraterion* is normally regarded as a marine trace fossil, though xiphosurid traces have been frequently reported from marginal brackish marine environments (Størmer 1952; Hardy 1970; Goldring and Seilacher 1971; Chisholm 1983, 1986; Eagar *et al.* 1985).

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REFERENCES

AGER, D. V. and EDWARDS, D. 1986. The fauna and flora of the Rhaetian of the South Wales and adjacent areas. *Nature in Wales*, **4**, 71–79.

AUDLEY-CHARLES, M. G. 1970. Triassic palaeogeography of the British Isles. *Quarterly Journal of the Geological Society, London*, **126**, 49–89.

BALDWIN, C. T. 1977. Internal structures of trilobite trace fossils indicative of an open surface furrow origin. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **21**, 273–284.

BANDEL, K. 1967. Isopod and limulid marks and trails in Tonganoxie Sandstone (Upper Pennsylvanian) of Kansas. *Paleontological Contributions, the University of Kansas*, Article 19, 1–10.

BROMLEY, R. G. 1990. *Trace fossils: biology and taphonomy*. Unwin Hyman, London, 280 pp.

CASTER, K. E. 1938. A restudy of the tracks of *Paramphibius*. *Journal of Paleontology*, **12**, 3–60.

—— 1944. Limuloid trails from the Upper Triassic (Chinle) of the Petrified Forest National Monument, Arizona. *American Journal of Science*, **242**, 74–84.

CHISHOLM, J. I. 1983. Xiphosurid traces, *Kouphichnium* aff. *variabilis* (Linck), from the Namurian Upper Haslingden Flags of Whitworth, Lancashire. *Report of the Institute of Geological Sciences*, **83/10**, 37–44.

—— 1986. Xiphosurid burrows from the Lower Coal Measures (Westphalian A) of West Yorkshire. *Palaeontology*, **28**, 619–628.

CRIMES, T. P. 1975. The production and preservation of trilobite resting and furrowing traces. *Lethaia*, **8**, 35–48.

EAGAR, R. M. C., BAINES, J. G., COLLINSON, J. D., HARDY, P. G., OKOLO, S. A. and POLLARD, J. E. 1985. Trace fossil assemblages and their occurrence in Silesian (Mid-Carboniferous) deltaic sediments of the Central Pennine Basin, England. 99–149. *In* CURRAN, H. A. (ed.). *Biogenic sedimentary structures*. Society of Economic Paleontologists and Mineralogists Special Publication, **35**, 347 pp.

FISHER, D. C. 1975. Swimming and burrowing in *Limulus* and *Mesolimulus*. *Fossils and Strata*, **4**, 281–290.

GOLDRING, R. 1985. The formation of the trace fossil *Cruziana*. *Geological Magazine*, **122**, 65–72.

—— and SEILACHER, A. 1971. Limulid undertracks and their sedimentological implications. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **137**, 422–442.

HARDY, P. G. 1970. New xiphosurid trails from the Upper Carboniferous of northern England. *Palaeontology*, **13**, 188–190.

HIGGS, R. 1988. Fish trails in the Upper Carboniferous of southwest England. *Palaeontology*, **31**, 255–272.

KING, A. F. 1965. Xiphosurid trails from the Upper Carboniferous of Bude. *Proceedings of the Geological Society, London*, **1626**, 162–165.

MAGOR, P. M. 1978. Rhaetic trace fossils attributable to the ichnogenus *Kouphichnium* Nopsca. *Circular of the Palaeontological Association*, **94a**, 7 (Abstract).

MILLER, M. F. 1982. *Limulicubichnus*: a new ichnogenus of limulid resting traces. *Journal of Paleontology*, **56**, 429–433.

RICHARDSON, L. 1905. The Rhaetic and contiguous deposits of Glamorganshire. *Quarterly Journal of the Geological Society, London*, **61**, 385–424.

—— 1911. The Rhaetic and contiguous deposits of Westmid and parts of East Somersetshire. *Quarterly Journal of the Geological Society, London*, **67**, 1–74.

ROMANO, M. and WHYTE, M. A. 1987. A limulid trace fossil from the Scarborough formation (Jurassic) of Yorkshire: its occurrence, taxonomy and interpretation. *Proceedings of the Yorkshire Geological Society*, **46**, 85–95.

—— —— 1990. *Selenichnites*, a new name for the ichnogenus *Selenichnus* Romano & Whyte, 1987. *Proceedings of the Yorkshire Geological Society*, **48**, 221.

SAVAGE, R. J. G. 1977. *Geological excursions in the Bristol district*. The University of Bristol Printing Unit, Bristol, 196 pp.

SEILACHER, A. 1955. Spuren und Lebensweise der Trilobiten. 86–116. *In* SCHINDEWOLF, O. H. and SEILACHER, A. (eds). *Beiträge zur Kenntnis des Kambriums in der Salt Range (Pakistan)*. Akademie der Wissenschaften und der Literatur in Mainz, Abhandlungen der Mathematisch-Naturwissenschaftlichen Klasse Jahrgang, No. **10**.

—— 1970. *Cruziana* stratigraphy of 'non-fossiliferous' Palaeozoic sandstones. 447–476. *In* CRIMES, T. P. and HARPER, J. C. (eds). *Trace fossils*. Seel House Press, Liverpool, 547 pp.

—— 1982. Distinctive features of sandy tempestites. 333–349. *In* EINSELE, G. and SEILACHER, A. (eds). *Cyclic and event stratification*. Springer, Berlin and Heidelberg, xiv + 536 pp.

—— 1985. Trilobite palaeobiology and substrate relationships. *Transactions of the Royal Society of Edinburgh, Earth Sciences*, **76**, 231–237.

SHONE, R. W. 1978. Giant *Cruziana* from the Beaufort Group. *Transactions of the Geological Society of South Africa*, **81**, 327–329.

STØRMER, L. 1952. Phylogeny and taxonomy of fossil horseshoe crabs. *Journal of Paleontology*, **26**, 630–639.

WARRINGTON, G., AUDLEY-CHARLES, M. G., EVANS, W. B., IVIMEY-COOK, H. C., KENT, P. E., ROBINSON, P. L., SHOTTON, F. W. and TAYLOR, F. M. 1980. A correlation of Triassic rocks in the British Isles. *Special Report of the Geological Society, London*, **13**, 1–78.

WRIGHT, A. D. and BENTON, M. J. 1987. Trace fossils from Rhaetian shoreface deposits of Staffordshire. *Palaeontology*, **30**, 407–428.

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