

This article was downloaded by: [Dean Lomax]

On: 29 August 2012, At: 10:40

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



## Ichnos: An International Journal for Plant and Animal Traces

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/gich20>

### A Long Mortichnial Trackway of *Mesolimulus walchi* from the Upper Jurassic Solnhofen Lithographic Limestone near Wintershof, Germany

Dean R. Lomax<sup>a</sup> & Christopher A. Racay<sup>b</sup>

<sup>a</sup> Doncaster Museum & Art Gallery, Doncaster, UK

<sup>b</sup> Wyoming Dinosaur Center, Big Horn Basin Foundation, Thermopolis, Wyoming, USA

Version of record first published: 29 Aug 2012

To cite this article: Dean R. Lomax & Christopher A. Racay (2012): A Long Mortichnial Trackway of *Mesolimulus walchi* from the Upper Jurassic Solnhofen Lithographic Limestone near Wintershof, Germany, *Ichnos: An International Journal for Plant and Animal Traces*, 19:3, 175-183

To link to this article: <http://dx.doi.org/10.1080/10420940.2012.702704>

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.tandfonline.com/page/terms-and-conditions>

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae, and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand, or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

# A Long Mortichnial Trackway of *Mesolimulus walchi* from the Upper Jurassic Solnhofen Lithographic Limestone near Wintershof, Germany

Dean R. Lomax<sup>1</sup> and Christopher A. Racay<sup>2</sup>

<sup>1</sup>Doncaster Museum & Art Gallery, Doncaster, UK

<sup>2</sup>Wyoming Dinosaur Center, Big Horn Basin Foundation, Thermopolis, Wyoming, USA

A 9.7 m long trackway was discovered in a plattenkalk quarry near the village of Wintershof, Bavaria, Germany, in 2002. The huge ichnofossil derives from the Lower Tithonian, Upper Jurassic Solnhofen Lithographic Limestone. The trackway is complete from beginning to end and consists of footprints, telson drag impressions, prosoma imprints and is identified as the ichnotaxon *Kouphichnium* isp. Preserved at the very end of the trackway is a complete specimen of *Mesolimulus walchi* confirming the trackway as a mortichnia (death march). Trackways and trace makers preserved together in the fossil record are rare and such specimens allow unique insights into behavior and ecology. The events that led to *M. walchi* preserved in this sediment are unknown; however, a most likely scenario is that the limulid was washed into the lagoonal environment during a harsh storm.

**Keywords** Mortichnia, Horseshoe crab, Large trace fossil, Upper Jurassic, Solnhofen Lithographic Limestone, *Mesolimulus walchi*, *Kouphichnium*

## INTRODUCTION

Fossil trackways are found worldwide, they are commonly found in rocks within the Palaeozoic (Collette et al., 2010; Gibb et al., 2009), Mesozoic (Fernandes and Carvalho, 2006; Zonneveld et al., 2010), and Cenozoic Eras (Donovan et al., 2005; Huddart et al., 2008). Examples of both body and trace fossils found together within the same sediments are rare in the fossil record; rarer still are trace fossils such as that described here, where the trace maker is found at the end of its trackway (e.g., Caster, 1940; Fortey and Seilacher, 1997; Collette et al., 2010). Such specimens are rare due to the preservation potential of the trace maker, trace and environment (Collette et al., 2010; Fatka and Szabad, 2011). Although in comparison, somewhat common and famous ichnofossil specimens have

been documented in the Upper Jurassic lithographic limestones; found within the Solnhofen plattenkalks in southern Germany, here they are exceptionally preserved (Seilacher, 2007, 2008; Barthel et al., 1990). The ichnofossils belong to arthropods that leave their tracks, and in some rare cases even the body behind; such trackmakers include: *Mesolimulus*, *Eryma*, *Mecochirus*, *Eryon*, and *Antrimpos* (Seilacher, 2007). These types of locomotion are known as mortichnia (death) trackways, or death marches (Seilacher, 2008). Other notable examples of mortichnia include Cambrian trilobites (Fortey and Seilacher, 1997; Ou et al., 2009; Fatka and Szabad, 2011), a polychaete annelid (Pickerill and Forbes, 1978), and a euthycarcinoid arthropod (Collette et al., 2010). This paper describes and interprets the mortichnial trackway of WDC CSG-233 (Wyoming Dinosaur Center, Thermopolis, Wyoming, USA) which belongs to the marine horseshoe crab, *Mesolimulus walchi* (Fig. 1). Horseshoe crabs (phylum: Arthropoda; class: Merostomata; subclass: Xiphosura) have retained a similar body plan since their first appearance within the fossil record during the Late Ordovician and are in turn often referred to as living fossils (Rudkin et al., 2008; Metz, 2009). The tracemaker of the studied specimen likely suffocated under the anoxic conditions present within a lagoon, a common perception of mortichnial trackways associated with horseshoe crabs and others (Viohl, 1990). Mortichnial trackways of several genera and species of arthropod bear similar characteristics in the structure and detail of how the tracks are formed. Trackways record the behavioral patterns of the tracemaker at their time of formation (Trewin, 1994). This is a strong character of WDC CSG-233, which displays a struggle throughout. This manuscript describes the mortichnial trackway of the horseshoe crab *Mesolimulus walchi*. It discusses the behavior of the trace maker as it made the trackway and the circumstances of its demise.

## GEOLOGICAL SETTING

WDC CSG-233 was found in 2002 and excavated from a plattenkalk quarry near the village of Wintershof, north

Address correspondence to Dean R. Lomax, Palaeontology Department, Doncaster Museum & Art Gallery, South Yorkshire, Doncaster, DN1 2AE, UK. E-mail: skalidis7@hotmail.com

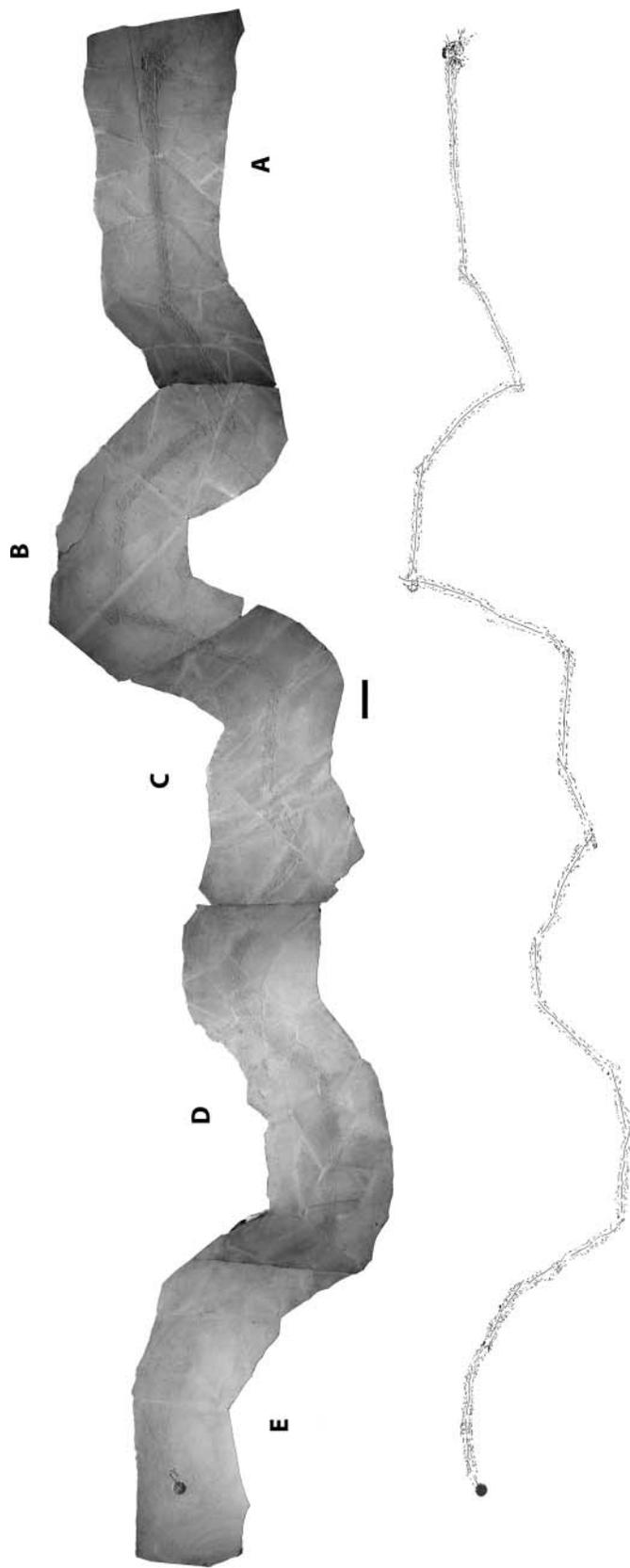


FIG. 1. WDC CSG-233, the entire trackway of the limulid (original specimen and interpretive illustration). Each slab section has been placed together and individually labeled (A–E). The lighting of the specimen has been modified slightly so that the track is more visible. Note, on the illustration black equals trackway and grey equals body fossil. Scale bar = 20 cm. (See Color Plate IV.)

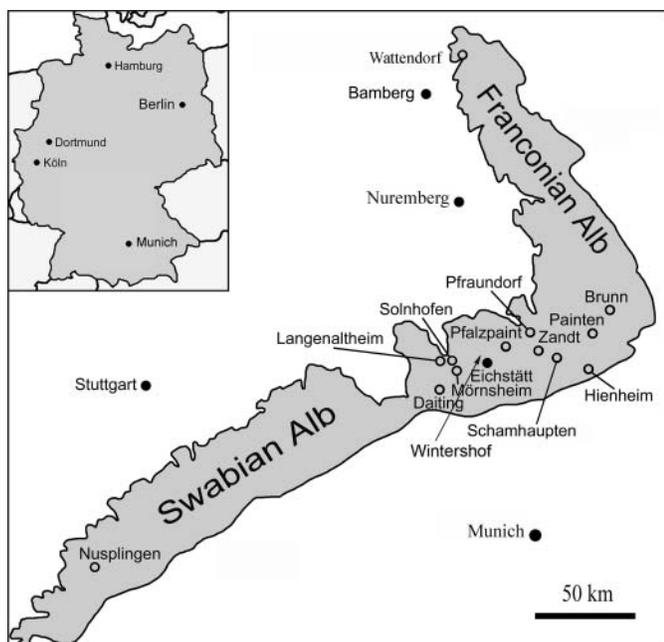


FIG. 2. Location of the fossil bearing localities pertaining to the Solnhofen area; note the areas of Eichstätt and Wintershof (modified very slightly after Schweigert, 2011).

of the town of Eichstätt in Bavaria, Southern Germany (Fig. 2). The specimen derives from the Upper Jurassic (Tithonian) Solnhofen Lithographic Limestones, Eichstätt Formation (Solnhofen Group), Hybonotum Zone, Riedense Subzone (former: Malm zeta 2 b), after Schweigert (2007) and Zeiss (1977). Unfortunately, the precise stratigraphic location of the specimen in question was not recorded when it was removed from the limestone quarry; however, the excavation process and retrieval of the specimen was documented. WDC CSG-233 was carefully removed in many separate slabs; each section was given an individual number that enabled the correct reconstruction of the specimen. The many separate slabs were placed back together using epoxy resin, of which numerous epoxied lines can be seen throughout the trackway. A soluble varnish was used to protect the imprints and the slabs were washed with a soft acid fluid making the slabs slightly lighter and the track darker. Two sections of the trackway were broken during excavation, which meant that perhaps a few centimetres were lost, although the entire trackway is original.

The Solnhofen-Eichstätt area is renowned for its extremely well-preserved fossil specimens (Barthel et al., 1990), which have included world famous fossils such as *Archaeopteryx* (Wellnhofer, 2009). The quarries of Wintershof have yielded a huge number and variety of fossils from this famous Lagerstätte. The Solnhofen lithographic limestones include, among other fossils, the remains of numerous arthropods such as the specimen studied (Barthel et al., 1990; Viohl, 1998). Plattenkalks of the Solnhofen-type were quarried in a region of around

80 × 30 km in the Southern Franconian Alb. Only few active quarries are in operation near the town of Eichstätt and the villages of Solnhofen and Langenaltheim (Keupp et al., 2007; Munnecke et al., 2008; Wellnhofer, 2009). The Solnhofen limestone was deposited on a sea floor with strong relief due to an abundance of algal-sponge reefs (Viohl, 1990; Wellnhofer, 2009). Originally, calcareous mud provided the material of Solnhofen's lithographic limestone. This mud was deposited on the floors of basins, layer after layer, with the result being almost pure calcium carbonate (Wellnhofer, 2009). The lithographic limestone is composed of pure limestones called Flinze with shaly calcareous marls called Fäulen. The almost complete lack of bioturbation, which is a strong characteristic of plattenkalks, indicates a hostile environment with no or relatively few organisms living in or near the sea floor (Keupp et al., 2007). The homogeneous fine bedding and abundance of load-sedimentation marks are indicative of stagnant bottom water and an extremely low energy environment (Keupp et al., 2007; Wellnhofer, 2009). The paleontological data point to a depositional environment, here the basins became stagnant with hypersaline brines that derived from inflowing seawater (Keupp et al., 2007). Differences within the saline layers inhibited water circulation, which resulted in a hypersaline, anaerobic, and stagnant environment near the bottom, which is said to be responsible for the excellent beddings and preservation of fossils (Barthel et al., 1990; Keupp et al., 2007; Wellnhofer, 2009).

## DESCRIPTION AND IDENTIFICATION OF THE TRACEMAKER

The tracemaker of WDC CSG-233 is preserved at the end of the trackway on slab E (Fig. 3) and is identified as belonging to the horseshoe crab *Mesolimulus walchi* (Desmarest, 1817, 1822). Isolated specimens of the genus *Mesolimulus* are relatively common in the Solnhofen limestone (Frickhinger, 1994). *Mesolimulus* has a rounded shield-like shape that narrows

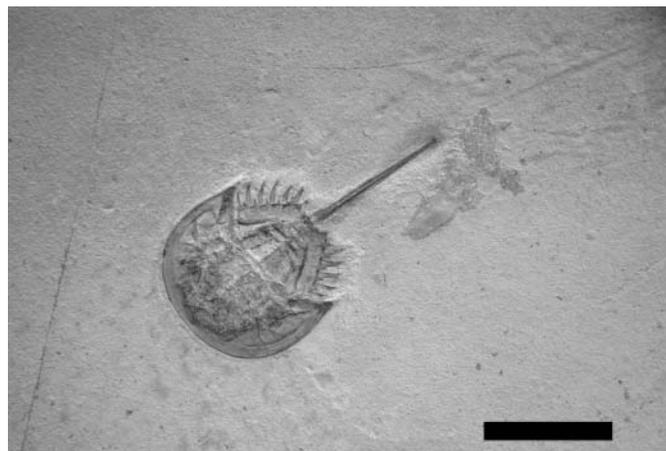


FIG. 3. Preserved *Mesolimulus walchi* (see Fig. 1, slab E). Specimen measures total length: 12.7 cm and width 6.9 cm. Scale bar = 5 cm. (See Color Plate V.)

to a trapezoid, finally narrowing to a long, pointed telson. The posterior of the body is lined with lateral spines protruding from the carapace (Frickhinger, 1994). The prosoma (6.9 cm wide) has undergone mineral replacement with calcite crystals replacing the original shell material. The mineral displacement of the prosoma ends at the boundary of the opisthosoma.

Horseshoe crabs found in the Solnhofen-Eichstätt area are all considered to be juveniles, although adult specimens have also been discovered in large numbers in the Lithographic limestones at such locations as Painten, where the water was better mixed and more hospitable (Barthel et al., 1990). Juvenile *M. walchi* specimens have been identified by size, and the size of the studied specimen is 12.7 cm in total length (measured from tip of prosoma to end of telson). Large specimens, likely adults, have been documented up to 53 cm in length (Frickhinger, 1999, fig. 52). Based upon the evidence presented above, we identify the limulid as a juvenile.

### ICHNOTAXONOMY

*Kouphichnium* is the name given to limulid tracks where the tracemaker is not available for true determination and is the most widely used ichnotaxon with great variability (Gaillard, 2011). Many species have been attributed to the ichnogenus *Kouphichnium*, and to an extent the ichnogenus has become a somewhat “wastebasket ichnotaxon.” Specimens identified as mainly related to this ichnogenus have been recorded from the Upper Palaeozoic through to the Oligocene Epoch (see discussion in Gaillard, 2011). The ichnogenus is in need of revision, but this is beyond the scope of this manuscript. This ichnotaxon is relatively complex and difficult to characterize as it corresponds to complete and incomplete traces which are made by different appendages and two types of legs, and telson (Gaillard, 2011). The difficulty of identifying a species to which an ichnotaxon belongs is difficult for those points outlined. Here we discuss the two ichnotaxa described from the Solnhofen areas which are of relevance to WDC CSG-233. Originally *Kouphichnium lithographicum* (Oppel, 1862) was described for simple straight locomotion traces discovered in the Solnhofen area. The type specimen exhibits a median groove with repeated series of imprints, including a trifold imprint on either side with only one simple imprint (Oppel, 1862, as cited in Gaillard, 2011). However, in some mortichnial trackways where the tracemaker *M. walchi* is present, they have been assigned their own ichnospecies as *Kouphichnium walchi* (Malz, 1964; Groiss, 1975). As an ichnotaxon without the preserved tracemaker the name *K. lithographicum* should be used as this would have priority over *K. walchi*. However, *K. lithographicum* was described for a particular type of track locomotion, and as discussed in Gaillard (2011) four types of limulid locomotion are known. They include walking, crawling, dying, and ploughing, of which the first three are specifically known from the Solnhofen Group, each of which are not attributed to a separate species if found without the tracemaker. In spite of this, as

mentioned above when the tracemaker is found preserved with the track; they have been identified as *K. walchi* which has more significance to the identification of the trace maker *Mesolimulus walchi*. The type of trackway seen in Groiss (1975, fig. 1a) is similar to WDC CSG-233 in the track morphology, as it shows the consistent use of legs and telson throughout. We feel that isolated limulid traces from the Solnhofen areas should be identified as *K. lithographicum*; as originally described. Despite this, both *K. lithographicum* and *K. walchi* are in need of revision, and it is probable that *K. walchi* is a synonym of *K. lithographicum*; and to reframe from any further confusion we identify the trackway as the ichnogenus *Kouphichnium* isp.

### DESCRIPTION OF THE TRACKWAY

The chance of finding tracks along with the maker, as seen in the specimen discussed, are extremely rare, they are important in the ability to identify the trace maker to species level and also look at the consequent paleobiological and paleoecological insights that can be inferred from such remarkable specimens. The well-preserved trackway of the studied specimen consists of 5 slabs (labeled individually A-E as seen in Fig. 1), with the first introducing the crab into the lagoon, and the last preserving the limulid after it had succumbed. The track has a total length of 9.7 m and a mean external width of 4.25 cm. The appendages of the limulid have been dragged through a soft surface leaving imprints, they occur irregularly in discontinuous marks, common in arthropod trackways (Trewin, 1994).

At the beginning of the trackway, on slab A, a disturbed surface (reminiscent of trampling) about 23.2 cm wide includes numerous pedal imprints and telson marks, along with two circular depressions, which could be presumed to be the area where the limulid landed dorsally on the substrate (Fig. 4).

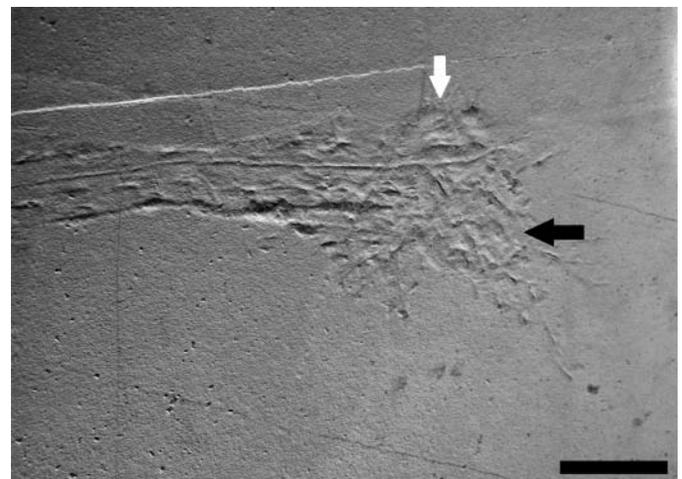


FIG. 4. Landing position of the horseshoe crab with start of track (see Fig. 1, slab A). Arrows indicate the circular depressions where the limulid may have landed dorsally on its carapace. Note the impressions of legs and use of the telson. Also note the start of the track with the strong indentation of the telson. Scale bar = 10 cm. (See Color Plate VI.)

The top depression (white arrow) measures approximately 5 cm wide by 7 cm long while the lower depression (black arrow) measures 9 cm wide by 10 cm long. The exact location of where the limulid first lands is difficult to discern; therefore, the two probable landing positions are given. However, on the basis of positioning, we suspect the lowermost depression to be the most likely candidate. Where the trackway begins, the imprints are long and are not identifiable of leg VI (pushers). The pushers, tetradactyl and didactyl imprints, are not distinguishable from the preserved pedal prints, making them absent on the trackway. The telson is also used at the beginning to correct its positioning after the fall into the lagoon, seen through the drag marks in the uppermost section of the landing position. However, the telson is then firmly placed onto the substrate (Fig. 4) and is preserved throughout as a fine continuous line, with lifts in areas of change in direction.

The preserved style of the prints and telson drag marks of the studied specimen are found in other trackways pertaining to *Mesolimulus* (Malz, 1964; Groiss, 1975; Seilacher, 2008). The walking style of the limulid alternates throughout the trackway. A mixture of styles are seen inconsistently throughout and they include curved, straight, and turning (see Fig. 1). The gentle meandering curves are quickly changed with sudden angular turns that result in either a straight track, or total body turn (as seen in Figs. 5A and 5B), which change the direction and orientation of the trackway. Breaks in the telson drag marks indicate the limulid has changed direction and the telson has been lifted, thus beginning the drag marks at a separate angle for the track to continue. On slab B, in two instances the limulid turns its entire body 90°, thus changing the direction of the trackway significantly; here the crab reverts and completes a small partial spiral, the prosoma is clearly used. In fact, apart from the landing position and isolated imprint towards the end

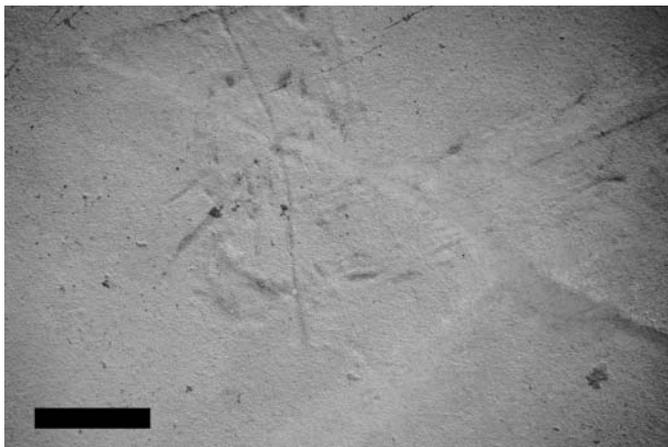


FIG. 5A. The first prosoma imprint with a spiral resulting in a change of direction (see Fig. 1, slab B): Note the acute 90° angle from where the trackway direction changes from almost horizontal to vertical. Scale bar = 5 cm. (See Color Plate VII.)

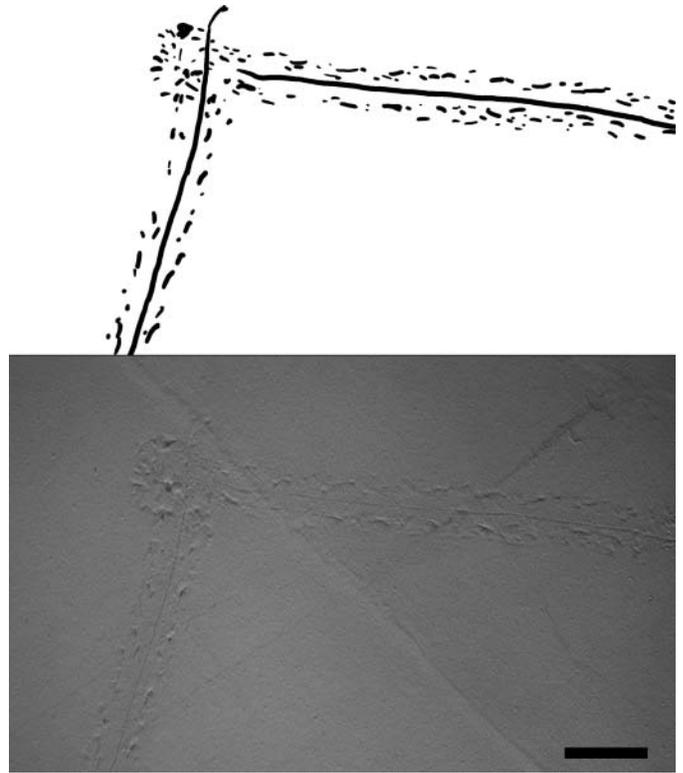


FIG. 5B. The second spiral (see Fig. 1, slab B): A schematic has been included to help interpret the image, it shows the strong use of the telson (seen through the drag marks), use of legs and change in direction, the prosoma depression is also evident. Note the similarities with Figure 5A including the acute 90° angle from where the telson is lifted and placed down. Scale bar = 10 cm. (See Color Plate VIII.)

of the track, the use of the prosoma is only seen at the two 90° turns. The 90° spirals occur only on slab B; the first spiral occurs 55 cm from the end of slab A (Fig. 5A). The second occurs an estimated 136 cm from the first and again displays the 90° turn, thus performing the second spiral (Fig. 5B). Both slab C and the majority of slab D display the continued walking style with the strong, consistent use of the telson. However, at certain points of the track as the limulid progresses, the telson drag marks become much shorter, erratic, and discontinuous. This can be seen midway through slab D and all the way until the end of the track on slab E (Fig. 6), and it shows the limulid changes direction numerous times. An estimated 88 cm from the end of the trackway an impression of what appear to be the genital spines from the opisthosoma are evident (note black arrows in Fig. 6). Despite this, there appears to be no prosoma indentation directly associated with the impressions; however, the length between the two impressions measures 5 cm, matching the opisthosoma of the limulid. According to Gaillard (2011) the consistent presence of the telson and short/long leg imprints is suggestive of a crawling or dying limulid, which complies with WDC CSG-233.

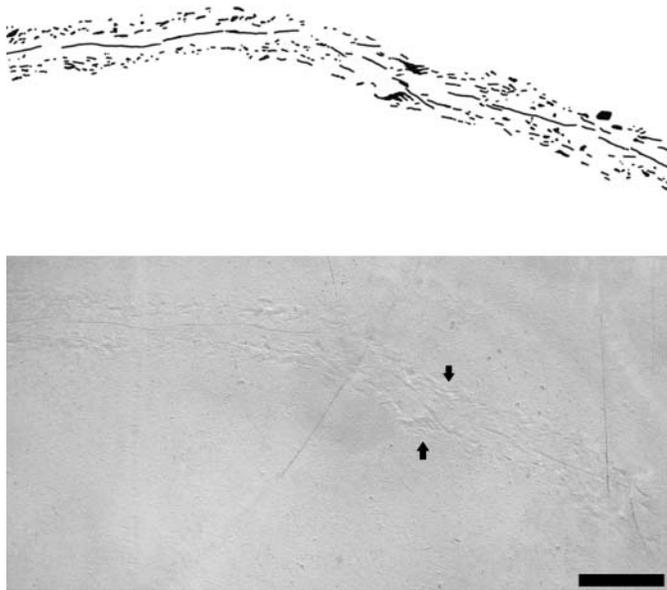


FIG. 6. Preserved section of the track revealing the changes of direction of the limulid (see Fig. 1, slab E). Note the uneven and discontinuous telson drag marks, they stop as the crab changes direction, indicative of the strong indentations of the legs. The two black arrows indicate the impressions of the genial spines. Scale bar = 10 cm. (See Color Plate IX.)

## DISCUSSION

Gaillard (2011) described a large 3 m track from Cerin, France. He compared the trackway from France with several types of limulid trackways, including the mortichnial trackways of Solnhofen; he determined the specimen from France differs from the mortichnia of Solnhofen. Gaillard (2011) also concludes that the strong meandering sinuous shape of a trackway (as opposed to an almost entirely straight trackway), well-marked telson impressions, occasional prosoma impressions and poorly preserved leg imprints (notably lack of pushers) are all strong characters of mortichnial trackways. The appendages are used heavily to support the limulid, although the last pair of legs, the “pushers,” are not distinguishable or identifiable. Random orientation of appendage and telson marks may exhibit the struggle of the limulid to gain stability before starting its long trackway. The characteristics mentioned by Gaillard (2011) pertain to WDC CSG-233; however, the imprint of the prosoma is slight and only visible when the limulid sharply changes direction (as in Figs. 5A and 5B) or at the beginning to perhaps aid with righting. The imprints of the legs, specifically the walking legs, are clearly used and are visible throughout the trackway, although poorly defined (Fig. 1). Deep impressions of the appendages are represented throughout the trackway, especially towards the end; here it appears the limulid has begun to struggle intensely from the toxic bottom waters. A similar trackway discussed in Malz (1964, fig. 15) depicts a short trackway preserved with a limulid, *M. walchi*. The track left behind is similar to that seen at the end of WDC CSG-233 (on slab E) with the strong erratic use of the legs,

and discontinuous use of the telson. Perhaps more erratic and deeper impressions of the appendages imply the limulid has attempted to lift off the substrate leaving only a few appendages placing pressure on the lagoon’s soft bottom. This is specifically seen towards the final resting place of the limulid, although deep impressions are also preserved at the beginning, again probably to aid with righting (Fig. 4). The pointed tips of limulid legs pierced the lagoon’s floor, penetration differed between the telson and legs, the shallowest undertracks show the most complete pattern (Seilacher, 2008). Another trackway, described from the lower Moenkopi Formation (Lower Triassic) of the Grand Staircase-Escalante National Monument in South-Central Utah, is comparable with the studied specimen with the strong consistent use of the telson, although the pushers are well marked (Hamblin and Foster, 2000, fig. 2b); this trackway follows the crawling style discussed in Gaillard (2011). With regard to WDC CSG-233, it bears all the characteristics of mortichnia trackways as suggested by Gaillard. Despite this, the studied trackway appears to have a combination of both Gaillard’s crawling and dying style of trackway present. The crawling style is present throughout with the continuous use of the telson (although there are breaks) and use of legs; however, the trackway is not straight throughout, there is a complete lack of pusher prints, the walking leg imprints are long, and the prosoma is placed on the substrate at least twice, not absent. As for the dying style, the trackway is sinuous throughout (apart from the very beginning on part of slab A), prosoma imprints are slight, the telson imprints are continuous but interrupted, and walking leg imprints are primarily long. However, the prosoma is not used consistently as seen in Gaillard (2011, fig. 10); it is only used when there is a sharp change of direction and the pushers are not slight but indistinguishable. In the specimen described by Gaillard, he determines that with the heavy use of the pushers, absence of contact with the telson to the soft sediment, and large repeat distance of the specimen, it points towards a normal but fast locomotion of a limulid. Contrastingly, both styles of crawling and dying traces are found within WDC CSG-233. It shows the imprints of legs, slight use of prosoma, and heavy use of the telson, all of which confirm a much more slowly moving limulid which characterizes the slow, last locomotion of the limulid before death (Gaillard, 2011), most probably from asphyxiation due to the anoxic environment and hypersalinity of the lagoon.

WDC CSG-233 derives from an area that has yielded numerous trackways of limulids, including mortichnial tracks (Barthel et al., 1990). The remains of mortichnial tracks pertaining to *Mesolimulus* have been discovered across several areas within the Solnhofen limestone of Bavaria (Caster, 1940; Leich, 1965, 1996; Groiss, 1975; Seilacher, 2008). All of the mortichnial trackways discovered around the locations of Solnhofen have been considered to be undertracks (Seilacher, 2008). Similar limulid mortichnial trackways involve either the meandering walk or a large death spiral, which concludes with the body of the individual at the end (Barthel et al., 1990).

The discussed specimen displays only the meandering walk throughout; however, it does display the 90° spirals that sharply change the direction of the trackway. In other specimens the death spiral is much larger than a 90° turn and consists of the trackmaker circling around itself, as illustrated in Barthel et al. (1990, fig. 5.5), and a large spiral track illustrated in Groiss (1975, fig. 1a). With comparison to the death spirals seen in Barthel et al. (1990) and Groiss, there is no such complete death spiral preserved in WDC CSG-233.

## INTERPRETATION

The horseshoe crab fell victim into a hypersaline lagoonal environment. The most likely scenario is that the horseshoe crab was washed into this environment where it was rapidly asphyxiated (Barthel et al., 1990; Collette et al., 2010). Several organisms including crustaceans were thrust into the lagoons of the Solnhofen limestone during harsh storms; only the hardiest of animals including horseshoe crabs such as *Mesolimulus* were still alive on reaching the bottom and thus left their tracks, although after entering a lagoon the individuals did not live long (Viohl, 1990; Wellnhofer, 2009; Lockwood, 1870). Variations in the lengths of the trackways suggest differences in the ability of the individual species to withstand asphyxiation by the toxic bottom waters (Viohl, 1990; Seilacher, 2008). Genera such as *Mesolimulus* continued for meters, crustaceans lasted for decimeters, and small bivalves identified as *Solemya* continued for only few centimeters (Seilacher, 2008; Viohl, 1990). A trackway similar to WDC CSG-233 produced by the decapod crustacean *Mecochirus longimanatus* was described by Viohl (1998). This specimen consists of a landing mark, short trackway, and the preserved tracemaker, although this crustacean only lasted for a short time before succumbing. In WDC CSG-233, on the final slab, slab E—resting place of the limulid—the telson drag marks and imprints become less uniform and more erratic; this may show evidence the limulid has become distressed and disorientated due to the toxic environment of the lagoon as it tries to escape (Barthel et al., 1990; Seilacher, 2008).

Initially, the limulid may have landed dorsally, characterized by the circular depressions preserved in the sediment (Fig. 4). To concur, in the lowermost section of the landing position a large amount of scattered appendage and telson marks are spread apart; perhaps here the limulid has struggled to right itself. It has been established that the specimen is a juvenile based on size (Frickhinger, 1999) and locality (Barthel et al., 1990). When compared with living limulids, the habits of juveniles and adults differ. Juveniles, unlike adults, swim up into the water column when disturbed and were therefore probably more susceptible to being washed away (Barthel et al., 1990). This could potentially allow the horseshoe crab to be carried into a restricted lagoonal environment through harsh storms (Viohl, 1990), floods, or possibly even turbidity currents (Seilacher, 2008; Keupp et al., 2007). Fisher (1975) determined that *M. walchi* swam dorsally in a general manner similar to that of the

extant horseshoe crab *Limulus polyphemus*. However, in this case, as the limulid has been washed into this environment, probably during a storm event, it is unlikely that it will be able to gain stability and swim comfortably. When dropped into this environment, the limulid most probably started in a random orientation but rotated (turning upside down) while falling through the water, as this is the most hydrodynamically stable orientation. Thus the juvenile limulid is most likely to land on its back when dropped into the lagoon. This is also seen in the study by Vosatka (1970), who observed the swimming styles (among other things) of 12 juvenile *Limulus* specimens. While swimming, the limulids finally came to a rest, landing dorsally on their carapace (with body doubled up at the cephalothorax-abdominal joint and telson positioned horizontally), and then began attempting to right themselves through a process of body arching and leg, gill, and tail movements, which in effect, rocked the inverted body sideways until the legs gained a firm hold on the substrate. This resting and righting action seen in Vosatka's (1970, fig. 1) study may explain the circular depression (of perhaps the carapace) and scattered appendage and telson marks seen at the beginning of the trackway as the limulid struggled to right itself (Fig. 4). It is known that limulids are hardy and can tolerate inhospitable environments (including changes in water temperature and salinity), enabling them to have a greater chance of survival in poor conditions. In the case of Solnhofen mortichnia, it allows their tracks to be preserved for up to several meters before they succumb (Barthel et al., 1990; Viohl, 1990; Frickhinger, 1994; McManus, 1969; Lockwood, 1870). A more unlikely, speculative scenario infers that perhaps the horseshoe crab was dropped into the lagoon via a predator. Remains of pterosaurs have been discovered within the Solnhofen limestones, including the first scientifically described pterosaur, *Pterodactylus antiquus* (Wellnhofer, 1983; Bennett, 1995; Frey and Martill, 1998). However, lack of predation marks on the exoskeleton of the crab eliminates this hypothesis. No tracks or imprints were found leading away from the crab which therefore determines the specimen is not a moult (Milsom and Sharpe, 1995).

## CONCLUSIONS

Long mortichnial trackways are rare. WDC CSG-233 is a 9.7 m long trackway that has the entire end-of-life processes of a mortichnial trackway, elaborating the story of a horseshoe crab's locomotion before succumbing. An interesting factor of the discussed specimen is the process in which the limulid travels with a combination of both the crawling and dying style of trackway preserved, showing the change in locomotion of the limulid. The death of *M. walchi* is attributed to asphyxiation in the hypersaline, anoxic bottom environment of the lagoon. The nature of this lagoonal environment prevented scavenging (Barthel et al., 1990) and resulted in the fine preservation of the limulid and undisturbed trackway.

## ACKNOWLEDGMENTS

We would like to thank the Wyoming Dinosaur Center and Burkhard Pohl for allowing the study of this specimen, whom without the permission this paper would not have been possible. A big thanks to Helmut Tischlinger for consistent help, advice, and early revisions of this manuscript. We are grateful to both Nicholas Minter and Christian Gaillard for critically reviewing this manuscript and suggesting some excellent revisions and additional information. Thanks also go to both William Wahl and Tristan Birkemeier for advice, assistance with photography and supplying helpful comments in order to progress this paper. Additionally, we thank Levi Shinkle and Bryan Miazga for their assistance with images and help physically constructing the specimen in order to photograph. Other thanks go to Raimund Albersdörfer for discussing the original discovery of the described specimen, and supplying important information that otherwise would have been lost. Finally, we are eternally grateful to Adam Smith for creating the entire schematic and thanks to Nobumichi Tamura for constructing parts of the other schematics used; plus the kind help of James Lamsdell and Simon Conway Morris for identifying some relevant papers for this study.

## REFERENCES

- Barthel, K. W., Swinburne, N. H. M., and Conway Morris, S. 1990. Solnhofen A Study in Mesozoic Palaeontology. Cambridge University Press, Cambridge, 236.
- Bennett, S. C. 1995. A statistical study of *Rhamphorhynchus* from the Solnhofen Limestone of Germany: Year-classes of a single large species. *Journal of Paleontology*, 69: 569–580.
- Caster, K. E. 1940. Die sogenannten 'Wierbeltierspuren' und die *Limulus*-Fahrten der Solnhofener Plattenkalke. *Palaontologische Zeitschrift*, 22: 12–29.
- Collette, J. H., Hagadorn, J. W., and Lacelle, M. A. 2010. Dead in their tracks—Cambrian arthropods and their traces from intertidal sandstones of Quebec and Wisconsin. *Palaos*, 25: 475–486.
- Desmarest, A. G. 1817. Crustacés fossiles. In Société de Naturalistes et d'Agriculteurs (eds.), *Nouveau Dictionnaire d'Histoire Naturelle, Appliquée aux Arts, à l'Agriculture, à l'Économie Rurale et Domestique, à la Médecine, etc. Tome 7*. Déterville, Paris, 495–519.
- Desmarest, A. G. 1822. Les Crustacés proprement dits. In Brongniart, A. and Desmarest, A. G. (eds.), *Histoire Naturelle des Crustacés Fossiles*. F.G. Levrault, Paris, 154.
- Donovan, S. K., Renema, W., and Pickerill, R. K. 2005. The ichnofossil *Scolicia prisca* de Quatrefages from the Paleogene of eastern Jamaica and fossil echinoids of the Richmond Formation. *Caribbean Journal of Science*, 41: 876–881.
- Fatka, O. and Szabad, M. 2011. Burrowing trilobite caught in the act. *Palaontologische Zeitschrift*, 85: 465–470.
- Fernandes, A. C. S. and Carvalho, I. D. S. 2006. Invertebrate ichnofossils from the Adamantina Formation (Bauru Basin, Late Cretaceous), Brazil. *Sociedade Brasileira de Paleontologia*, 9: 211–220.
- Fisher, D. C. 1975. Swimming and burrowing in *Limulus* and *Mesolimulus*. *Fossils and Strata*, 4: 281–290.
- Fortey, R. A. and Seilacher, A. 1997. The trace fossil *Cruziana semiplicata* and the trilobite that made it. *Lethaia*, 30: 105–112.
- Frey, E. and Martill, D. M. 1998. Soft tissue preservation in a specimen of *Pterodactylus kochi* (Wagner) from the Upper Jurassic of Germany. *Neues Jahrbuch für Geologie und Paläontologie*, 21: 421–444.
- Frickhinger, K. A. 1994. Die Fossilien von Solnhofen – The Fossils of Solnhofen; Crustaceans Their Relatives. Goldschneck-V, Korb, Germany, 336.
- Frickhinger, K. A. 1999. Die Fossilien von Solnhofen 2. Neue Funde, Neue Details, Neue Erkenntnisse – The Fossils of Solnhofen - A Documentation of Fauna and Flora of the Solnhofen Formation - 2. New Specimens, New Details, New Results. Goldschneck, Korb, Germany, 190.
- Gaillard, C. 2011. A giant limulid trackway (*Kouphichnium lithographicum*) from the Lithographic Limestones of Cerin (Upper Kimmeridgian, France): Ethological and environmental implications. *Swiss Journal of Geosciences*, 104: 57–72.
- Gibb, S., Chatterton, B. D. E., and Pemberton, S. G. 2009. Arthropod ichnofossils from the Ordovician Stairway Sandstone of central Australia. *Memoirs of the Association of Australasian Palaeontologists*, 37: 695–716.
- Groiss, Von J. T. 1975. Eine Spurenplatte mit *Kouphichnium* (*Mesolimulus*) *walchi* (Desmarest, 1822) aus Solnhofen. *Geologische Blätter für Nordost-Bayern*, 25: 80–95.
- Hamblin, A. H. and Foster, J. R. 2000. Ancient animal footprints and traces in the Grand Staircase-Escalante National Monument, South-Central Utah. In Sprinkel, D. A., Chidsey, T. C., Jr., and Anderson, P. B. (eds.), *Geology of Utah's Parks and Monuments*. Utah Geological Association Publication, 28: 557–568.
- Huddart, D., Bennett, M. R., Gonzalez, S., and Velay, X. 2008. Analysis and preservation of Pleistocene human and animal footprints: An example from Toluquilla, Valsequillo basin (Central Mexico). *Ichnos*, 15: 232–245.
- Keupp, H., Koch, R., Schweigert, G., and Viohl, G. 2007. Geological history of the Southern Franconian Alb – the area of the Solnhofen Lithographic Limestone. Stuttgart. *Neues Jahrbuch für Geologie und Paläontologie*, 245: 3–21.
- Leich, H. 1965. Ein neue Lebensspur von *Mesolimulus walchi* und ihre Deutung. *Aufschluss*, 15: 5–76.
- Leich, H. 1996. Vor 150 Millionen Jahren – Die Fossilienammlung H. Leich im Fossilium des Tierparks Bochum, 45.
- Lockwood, S. 1870. The horse foot crab. *American Naturalist*, 4: 257–274.
- Malz, H. 1964. *Kouphichnium walchi*, die Geschichte einer Fährte und ihres Tieres. *Natur und Museum*, 94: 81–97.
- McManus, J. J. 1969. Osmotic relations in the horseshoe crab, *Limulus polyphemus*. *American Midland Naturalist*, 81: 569–573.
- Metz, R. 2009. First record of a horseshoe crab trackway from the Bloomsburg Red Beds (Silurian: Ludlow Series) of New Jersey. *Bulletin of the New Jersey Academy of Science*, 54: 1–3.
- Milson, C. and Sharpe, T. 1995. Jurassic lagoon: salt or soup? *Geology Today*, 11: 22–26.
- Munnecke, A., Westphal, H., and Kölbl-Ebert, M. 2008. Diagenesis of plattenkalk: Examples from the Solnhofen area (Upper Jurassic, S-Germany). *Sedimentology*, 55: 1931–1946.
- Oppel, A. 1862. Über ber Fahrten im lithographischen Schiefer (*Ichnites lithographicus*). Paläontologische Mitteilungen aus dem Museum des Königlichen Bayerischen Staates, Stuttgart, 1: 121–125.
- Ou, Q., Shu, D. G., Han, J., Zhang, X. L., Zhang, Z. F., and Liu, J. N. 2009. A juvenile redlichiid trilobite caught on the move: Evidence from the Cambrian (Series 2) Chengjiang Lagerstätte, southwestern China. *Palaos*, 24: 473–477.
- Pickerill, R. K. and Forbes, W. H. 1978. A trace fossil preserving its producer (*Trentonia shegiriana*) from the Trenton limestone of the Quebec City area. *Canadian Journal of Earth Sciences*, 15: 659–664.
- Rudkin, D. M., Young, G. A., and Nowlan, G. S. 2008. The oldest horseshoe crab: A new xiphosurid from Late Ordovician konservat-lagerstätten deposits, Manitoba, Canada. *Palaontologia*, 51: 1–9.
- Schweigert, G. 2007. Ammonite biostratigraphy as a tool for dating Upper Jurassic lithographic limestones from South Germany – first results and open questions. *Neues Jahrbuch für Geologie und Paläontologie*, 245: 117–125.

- Schweigert, G. 2011. The decapod crustaceans of the Upper Jurassic Solnhofen Limestones: A historical review and some recent discoveries. *Neues Jahrbuch für Geologie und Paläontologie*, 260: 131–140.
- Seilacher, A. 2007. Trace Fossil Analysis. Springer Verlag, Heidelberg, 226.
- Seilacher, A. 2008. Biomats, biofilms, and biogluce as preservational agents for arthropod trackways. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 270: 252–257.
- Trewin, N. H. 1994. A draft system for the identification and description of arthropod trackways. *Palaeontology*, 37: 811–823.
- Viohl, G. 1990. Taphonomy of fossil-lagerstätten. Solnhofen lithographic limestones. In Briggs, D. E. G. and Crowther, P. R. (eds.), *Paleobiology: A synthesis*. Blackwell Science, Oxford, 285–289.
- Viohl, G. 1998. Die Solnhofener Plattenkalke – Entstehung und Lebensräume. *Archaeopteryx*, 16: 37–68.
- Vosatka, E. D. 1970. Observations on the swimming, righting, and burrowing movements of young horseshoe crabs. *Limulus polyphemus*. *Ohio Journal of Science*, 70: 276–283.
- Wellnhofer, P. 1983. Cuvier and his influence on the interpretation of the first known pterosaur. In Buffetaut, E., Mazin, J. M., and Salmon, E. (eds.), *Montbéliard. Actes du symposium paléontologique G. Cuvier*, 8: 525–538.
- Wellnhofer, P. 2009. *Archaeopteryx: The Icon of Evolution*. Verlag Dr. Friedrich Pfeil, München, 208.
- Zeiss, A. 1977. Jurassic stratigraphy of Franconia. *Stuttgarter Beiträge zur Naturkunde, Serie B*, 31: 1–32.
- Zonneveld, J., Gingras, M. K., and Beatty, T. W. 2010. Diverse ichnofossil assemblages following the P-T mass extinction, Lower Triassic, Alberta and British Columbia, Canada: Evidence for shallow marine refugia on the northwestern coast of Pangaea. *Palaios*, 25: 368–392.