AN ANALYSIS OF MULTIPLE TRACKWAYS OF *PROTICHNITES* OWEN, 1852, FROM THE POTSDAM SANDSTONE (LATE CAMBRIAN), ST. LAWRENCE VALLEY, NY

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ABSTRACT

Late Cambrian arthropod trackways from the Potsdam Sandstone have been known since the 1850's. A site in northern New York is an outcrop of fine-grained, quartz-rich, rippled, micro-laminated Potsdam Sandstone. Our study area includes evidence of microbial mat growth on the original surface on which the trackways were produced. Ripple marks presumably underlay and therefore were generated prior to the microbial mat. Preservation of these trackways is variable over the outcrop and is indicative of a high intertidal or low supratidal environment with microbial growth.

At least eleven distinctive trackways of multi-legged telson-bearing individuals are present with a roughly bimodal size distribution (widths of 11.6 cm, 6.5 cm, 10 cm and 7.2 cm). A disturbance at the intersection of trackways 1 and 2 has been interpreted to show the earliest evidence of invertebrate mating activity (Erickson, 2004). Trackway 1 (11.6 cm wide) consists of repeated series of seven pairs of imprints (labeled A-G and A'-G') with a continuous medial telson drag. Imprints are arranged in a chevron pattern with track A being proximal to the medial line and F and G distal. An eighth imprint, H, is present only in the left series of tracks in the absence of E' so it is likely that they are a result of the same limb. The organism was traveling in the direction of the convergence of the chevron pattern.

Average stride distance in cm (distance between the same imprints in adjacent series) over seven iterations of tracks on the right side is as follows: A-10.3, B-10.4, C-10.1, D-10.1, E-10.4, F-10.5 and G-10.2. The mean stride for the tracks on this side of the medial line (the outside of a shallow curve) is 10.3 cm. Stride distance on the opposite side of the medial line is: A'-9.8, B'-9.8 , C'-9.7, D'-10.0, F'-9.8, G'- 9.7 and H'-10.3. The mean stride for tracks on the inside of the curve is 9.9 cm, and the overall mean stride for this trackway is 10.1 cm. The narrower trackway (2) (width 6.5 cm) does not preserve as complete a series of imprints and has a discontinuous medial telson drag.

The trackways are consistent in number of imprints per series (leg number?) and stride lengths with members of the original descriptions of *Protichnites* Owen, 1852, although a tridactyl condition can not be recognized on any digit. Variable preservation was probably a resulted from varying thickness of the microbial mat and/or varying water depth or wind and wave action in an intertidal pool.

INTRODUCTION

Specimens of *Protichnites* were first observed the Potsdam (=Nepean) Sandstone by Logan (1852) in southern Quebec (Figure 1) and described by he and Owen (1852). Owen designated six species, *P. septemnotatus, P. octo-notatus, P. latus, P. multinotatus, P. lineatus* and *P. alternans*. Hantzschel (1975) later designated *P. septemnotatus* the type species for the genus. Although Owen's description was detailed given the material he had to work with, the genus seems to have become a catch-all to describe any arthropod trackway with a single continuous or discontinuous medial telson mark (e.g., Braddy, 2004). Due to the apparent lack of body fossils in the Potsdam Sandstone, it falls to these and other types of traces to elucidate the paleoecology of the Cambro-Ordovician beachfront. The presence of *Protichnites* in intertidal, low supratidal, and dune sand beds of the Potsdam seems to show some of the first terrestrialization efforts of arthropods (MacNaughton et al. 2002; Braddy 2004) in the Late Cambrian (Figure 2). The Potsdam may also hold the first evidence of animal mating behaviour, in the interaction between two Protichnites trackways (Erickson 2004). We have examined more completely the trackways discussed by Erickson. It is the aim of this study to a) describe these trackways in enough detail that they may be compared carefully with others; b) determine their legitimacy as *Protichnites*; c) determine a track-maker; and d) remark upon the interaction seen between the trackways (Figure 2).

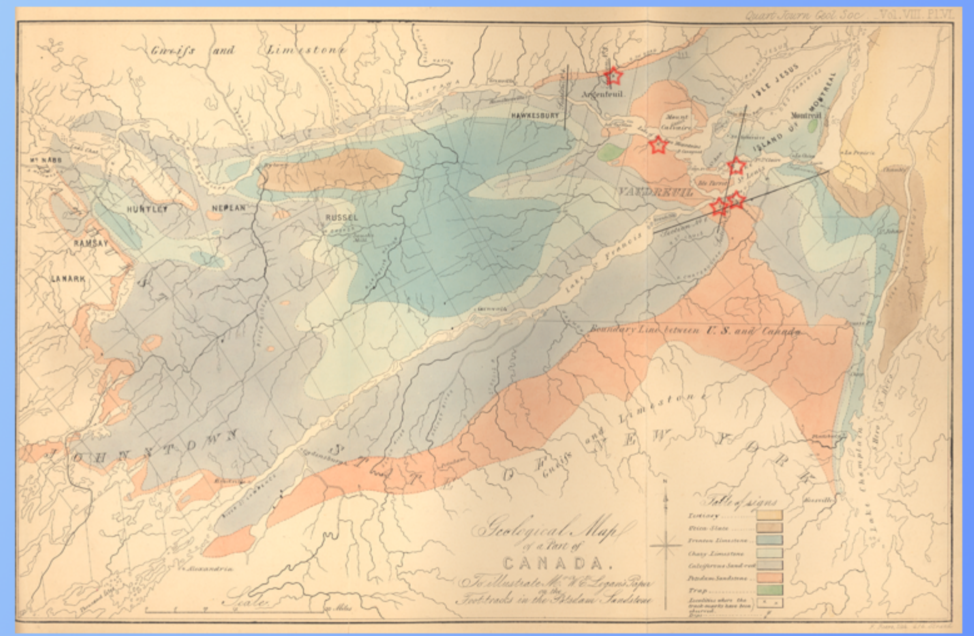

Figure 1. Regional bedrock map of southern Canada near Quebec, from Logan (1852, Plate VI). Stars added to more clearly show five trackway localities in the Potsdam Sandstone described by Logan and by Owen (1852).

Figure 2. Bedding-plane exposure showing at least 11 trackways. Trackways examined by the current study are indicated by arrows. Ruler is 35 cm in length. Photograph by J.M.E.

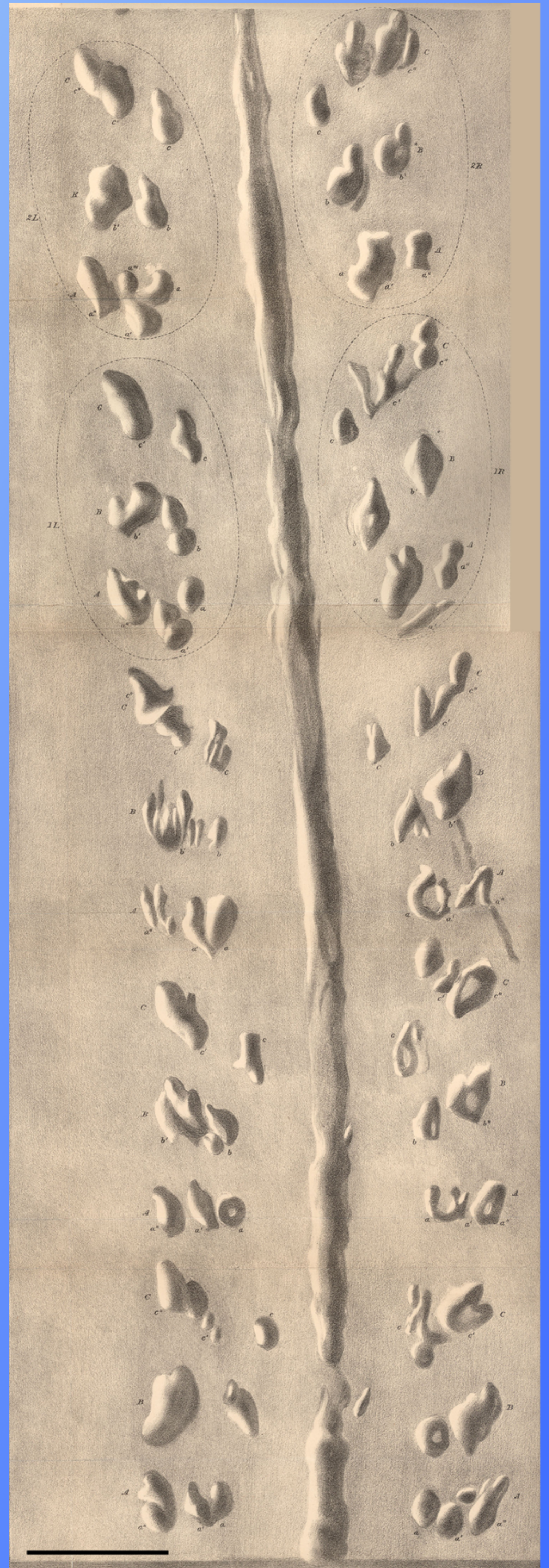

Figure 3. *Protichnites septem-notatus* as illustrated in Owen (1852) showing repeated groups of seven imprints on each side of a medial groove. Scale bar represents 5 cm.

METHODS

The outcrop was visited first in the Spring of 2002 and on two more occasions in Fall 2004 to begin direct measurements. Since snowfall and trackway access were early problems, a good deal of the data collection and interpretation relied on photographs taken by the authors. Digital photographs were high quality (greater than 3.0 megapixels) and directly vertical to the bedding plane being photographed. Two photographs were printed at near life size; measurements made from these photographs were scaled accordingly. Individual impressions and medial telson drags were traced onto clear acetate, from whence a series of tracings or copies could be made. All impressions were given the same weight without regard for preservation or depth (Figure 4)

Tracksets were designated by locating similar tracks at set intervals along the length of the trackway. This was accomplished by choosing adjacent tracks and overlaying them upon other sections of the trackway to find repetition. Similar tracks in different tracksets (each impression representing the same limb striking the sediment at different points) were marked with the same letter arbitrarily. These methods were used until the unassociated tracks were exhausted, or until no spatial relationship could be found between any of the remaining unassociated impressions. Each group of adjacent arbitrary letters (later re-labeled according to the methods below) was designated a trackset which repeated throughout the length of the trackway. These methods were used to resolve trackways 1, 2 and 3 and to correlate between the related tracks. Correlated impressions are designated by the same letter and color.

The impressions making up trackway 1 were designated as because of the relative spatial arrangement of the individual impressions. For the sake of consistency, paired tracks nearest the midline (i.e. having the smallest distance between internal edges) in all trackways were labeled "A." The impressions second-nearest to the midline and closest (along the length of the trackway) to tracks A were marked as "B." In order to keep each side of the trackway distinct, tracks on one side of the midline were arbitrarily labeled normally (e.g., "A") while their counterparts were labeled prime (e.g., " A' "). This type of track designation was continued in the same direction along the path of the trackway until the next track A was reached and all of the associated impressions designated by a letter.

There are a variety of ways in which these impressions can be divided into tracksets, but not all of them could have been produced by a living organism (Owen, 1852; Anderson, 1975; Trewin, 1994). The first easily understandable arrangement during the early stages of this study was the "double chevron" pattern shown in Figure 3. It was rejected in favor of the current model because it shows no overlap, implying an organism making neat "jumps" or, if floating, "strokes" to end up in precisely the same relative position. Chapman (1877) argued for Protichnites and Climactichnites to be deemed "fucoidal" (resulting from algal or microbial growth) in origin due to a variation of the former interpretation. The consistency of both the tracks and the medial drag line clearly show that this hypothesis was in error, and is remedied by the letter designations described above and in discussions of similar trackways by Anderson (1975), Braddy & Milner (2000), Braddy & Almond (1999), Briggs and Rolfe (1983), Owen (1852) and Trewin (1994).

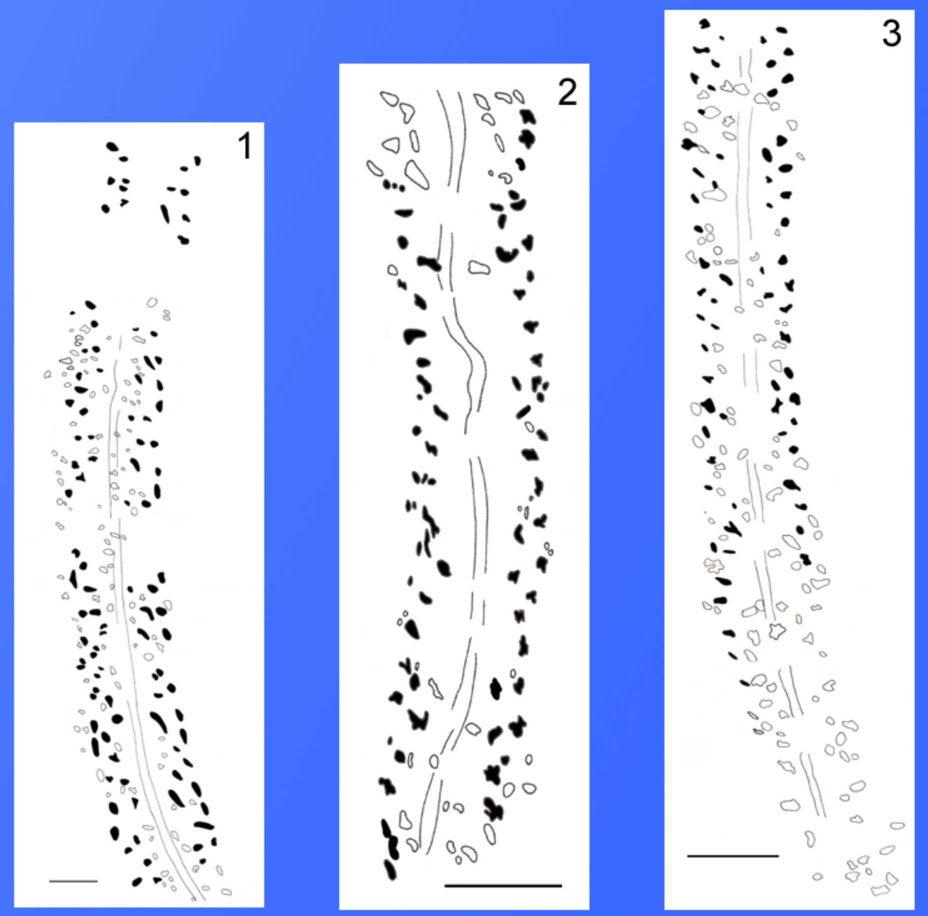

Figure 4. Schematic diagrams of trackways 1, 2, and 3. Scale bar in each is 5 cm. Shaded areas represent identified tracks; open areas show associated but unreconciled imprints.

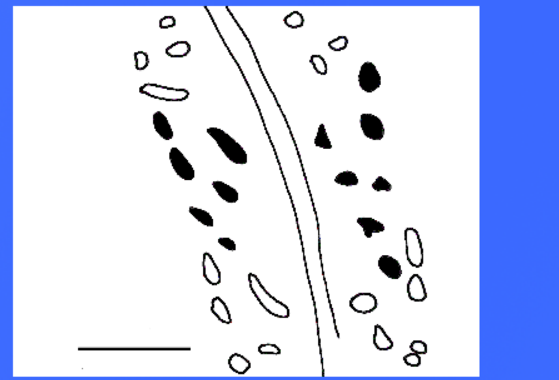

Figure 5. An alternative track series designation that was found to be unreasonable for reasons described above.

DESCRIPTION

The current study focused on a single bedding-plane exposure of flat-lying, thinly-bedded, fine-grained Potsdam Sandstone in Franklin County, New York state. Two other exposures containing trackways are located nearby; one within 3 meters to the west and the other ~500m to the northeast. The outcrop studied is the same as Erickson's (2004) Site A. It exhibits oscillation ripples, microbial mat textures (Gerdes et al., 2000; Noffke, 1999), and mudcracks. Oscillation ripples are sinuous with crest-crest distance of 20-25 mm. At least 11 trackways are visible, three of which are described in detail here. Most of the trackways are too poorly preserved to distinguish series order. Many scattered impressions are present that cannot be resolved into organized trackways. Trackways described below are labeled 1, 2 and 3 according to state of preservation seen in the outcrop (Figure 2). Trackways 1 and 2 intersect with each other; trackway 3 seems to be independent. All tracks were found to be in-phase across the medial line.

DESCRIPTION (continued)

Trackway 1 (Figure 6)

The trackway consists of a repeated series of seven oval or longitudinally tapered tracks on each side of a medial groove 1.5 meters in length. Over the course of 92 cm there are 152 imprints of which 110 have been confirmed as foot marks. 14 imprints make up seven pairs of what appear to be bifurcate tracks. This trackway is the large trackway interpreted as female examined by Erickson (2004).

Tracks from 10 sets are apparent. The medial groove is continuous and remains in the middle of the paired tracksets, although some unassociated impressions are located in the groove. Its width is between 7 and 9 mm throughout. Tracks on the right side of the trackway were labeled A-G and tracks on the left side, A'-G' (see Methods). An eighth imprint, H', is present only in the left series of tracks in the absence of E'. The average external width of the track farthest from the midline (track F) is 116 mm. The average stride length on the right side of the trackway (outside of gentle curve) is 103 mm. Stride lengths on the left side of the track average 99 mm. Track morphology on the left side of the medial line seems to be significantly different from that on the right, the tracks most proximal to the medial line being longer and more tapered. Trackway proportions can be seen in Table 1.

Individual tracks are oval (long axis parallel to trackway axis) or tapered (shallow-and-narrow end in direction of travel). Some tracks appear to be bifurcate, although these imprints are inconsistent.

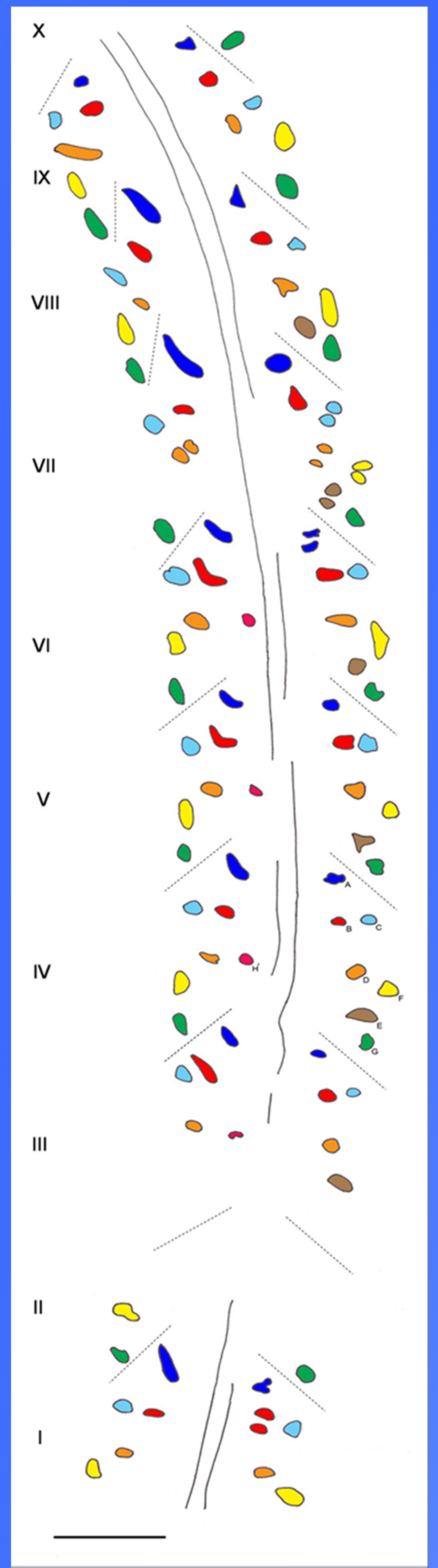

Figure 6. Schematic diagram of trackway 1. Dashed lines separate adjacent tracksets (labeled I-X). Colors indicate tracks in the same position in each trackset: dark blue = A, red = B, light blue = C, orange = D, brown = E, yellow = F, green = G, Pink = H Scale bar is 5 cm. Direction of movement is toward the top of figure.

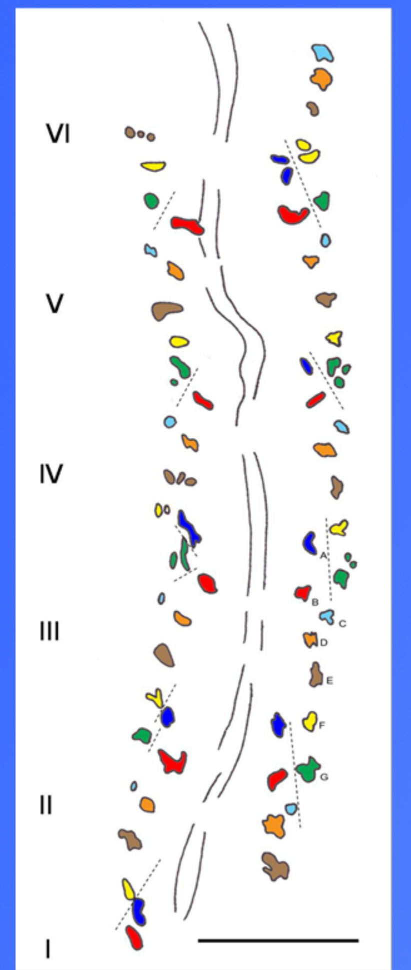

Figure 7. Schematic diagram of trackway 2. Dashed lines separate adjacent tracksets (labeled I-VI). See Figure 6 legend for key. Scale bar is 5 cm. Direction of movement is toward the top of figure.

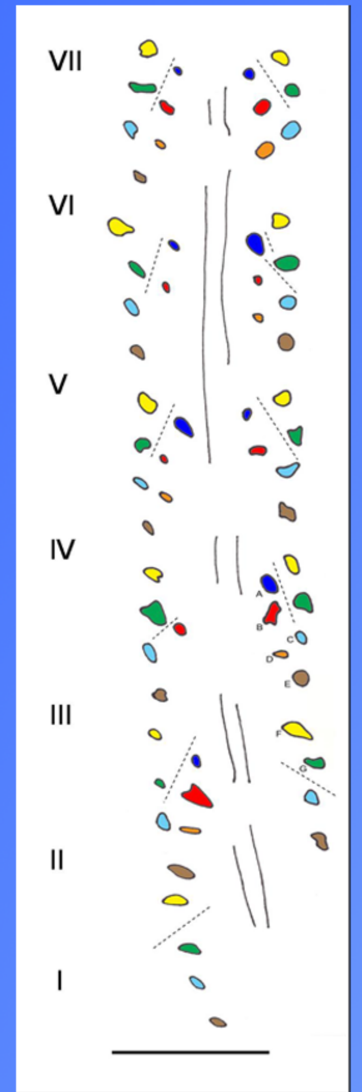

Figure 8. Schematic diagram of trackway 3. Dashed lines separate adjacent tracksets (labeled I-VII). See Figure 6 legend for key. Scale bar is 5 cm. Direction of movement is toward the top of figure.

DESCRIPTION (continued)

Trackway 2 (Figure 7)

Trackway 2 may be identified as the narrower trackway Erickson (2004) interpreted as male. It consists of a discontinuous medial groove flanked by repeated series of seven imprints of varying morphology. The portion preserved in enough detail to study contains 112 imprints and 74 identified tracks in 42 cm. Five tracks appear to have been produced by bifurcate and four by trifurcate limbs, although these are inconsistent. The trackway curves very gently to the left.

Tracks representing 6 sets are apparent. The medial groove is discontinuous continuous and varies in proximity to each row of tracks. In one instance (set V) the medial drag becomes erratic. The average external width of the trackway at its widest point (track G) is 67 mm. Stride lengths on the right side of the trackway average 79 mm. The average stride length on the left side is 76 mm. Trackway proportions can be seen in Table 2.

Most tracks are roughly sub-circular or sub-oval with long axes parallel to the axis of the trackway. Track identifications were also assigned to more linear features in some cases (e.g., Figure 7, set IV, track G).

Trackway 3 (Figure 8)

This trackway exhibits many similar characteristics to trackways 1 and 2. The medial groove is discontinuous and 8-11 mm wide. 77 cm of the trackway is visible enough to be examined but tracks could only be resolved over 48 cm. This distance includes 127 imprints including 56 that have been associated with repeated tracks. Tracks are sub-circular or oval with varying angle of long axis to the trackway. Trackway curves slightly to the right. Trackway proportions can be seen in Table 3.

Tracks from seven sets are present. A single series consists of eight tracks (C, E, F, G & C', E', F', G'), approximately the same distance from the midline, with the remaining tracks (A, B, D & A', B', C') internal to and between the external tracks along the trackway axis. The external width of the trackway averages 72 mm (track G). Track is straight along section analyzed. Average stride length on the right is 82 mm and on the left is 84 mm.

BIMODALITY

Trackways at this site appear to show bimodality in width and stride length. Larger trackways are about 115 mm in width, and smaller ones are around 70 mm. A range of sizes exposed at this site would suggest a population consisting of adults and juveniles of varying ages. As it stands, the apparent bimodality of the population of organisms that made these trackways suggests a mass-mate event as described by Braddy (2001) and discussed in reference to these trackways by Erickson (2004). Absence of a juvenile population suggests that these organisms were not adapted to survive for long periods of time in a terrestrial environment.

Tracks separated by a greater stride length typically appear on the outside of curves in the trackway. The disparity between the two sides is most visible in tracks A and B in trackway 1 (Figure 6). The deepest part of these tracks is to the rear (bottom of figure), tapering and shallowing to the front. We are interpreting this as a limb drag as the limb was raised out of the sediment for another step.

Table 1. Stride length and external width of trackway 1. (After Braddy & Milner, 1998)

	Right side of trackway – Stride (mm)							Left side of trackway – Stride (mm)							
Series	A	B	C	D	E	F	G	A'	B'	C'	D'	E'	F'	G'	External width (mm)
I-II	--	--	--	--	--	--	--	--	--	--	--	--	98	--	115
II-III	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
III-IV	105	105	105	105	101	108	--	102	95	105	101	--	--	--	--
IV-V	105	109	105	111	105	109	107	102	104	105	102	--	101	103	117
V-VI	100	102	104	102	104	104	104	102	100	104	102	--	103	98	114
VI-VII	108	107	96	100	103	101	104	105	100	96	104	--	--	98	114
VII-VIII	103	99	103	104	103	100	103	95	98	103	91	--	--	99	--
VIII-IX	95	100	89	102	--	107	101	81	90	89	97	--	91	89	116
IX-X	--	--	--	--	--	--	93	--	--	--	--	--	--	--	121
X															--
Average	102.8	103.7	100.6	104.2	103.5	104.7	102.0	97.9	97.9	100.6	99.7	--	98.5	97.5	116.2

Table 2. Stride length and external width of trackway 2. (After Braddy & Milner, 1998)

	Right side of trackway – Stride (mm)							Left side of trackway – Stride (mm)							
Series	A	B	C	D	E	F	G	A'	B'	C'	D'	E'	F'	G'	External width (mm)
I-II	--	--	--	--	--	--	--	83	74	--	--	--	--	--	--
II-III	77	80	82	79	81	--	--	80	76	80	79	79	81		70
III-IV	75	82	80	80	79	82	82	--	76	73	73	74	79	77	65
IV-V	84	79	79	79	79	81	82	--	74	72	73	72	71	76	66
V-VI	--	--	79	76	81	80	73	--	--	--	--	74	74	72	67
VI															--
Average	78.9	80.0	79.6	78.3	79.6	80.7	78.9	81.2	75.3	75.0	75.0	74.8	76.1	75.3	66.7

Table 3. Stride length and external width of trackway 3. (After Braddy & Milner, 1998)

	Right side of trackway – Stride (mm)							Left side of trackway – Stride (mm)							
Series	A	B	C	D	E	F	G	A'	B'	C'	D'	E'	F'	G'	External width (mm)
I-II	--	--	--	--	--	--	--	--	--	79	--	75	--	--	--
II-III	--	--	85	--	--	--	--	--	87	87	--	85	86	--	--
III-IV	84	79	81	--	81	81	78	--	83	83	--	81	78	--	72
IV-V	84	84	81	--	83	80	81	88	84	85		85	84	--	72
V-VI	83	84	85	81	--	86	84	85	87	87	--	85	86	--	71
VI-VII	--	--	--	--	--	79	84	--	--	--	--	--	87	88	72
VII															72
Average	83.3	82.2	83.2	81.4	82.0	81.7	81.7	86.6	85.2	84.2	--	82.1	84.2	88.3	72

INTERPRETATION & DISCUSSION

The trackways described here are designated as *Protichnites septemnotatus* after Owen's original description of repeated series of seven imprints. Opposite tracks in the same set are in-phase, showing that the organism was adapted for swimming rather than terrestrial life (Braddy & Almond, 1999). While he found it most likely that the animal producing the tracks was hexapodous with bifid or trifid legs, he did recognize that the association between what he considered trifurcate tracks was not proven and that an animal with any number of legs between six and fourteen could have produced these trackways. As stated by Braddy & Briggs (2002), "ichnotaxa are form taxa, and should be based on the morphology of well-preserved material, not on assumptions regarding the producer." Therefore it should be noted that the taxon defined as the producer of these particular trackways has no causal relationship with their designation as *P. septemnotatus*.

Trackways denoted 1, 2 and 4 are made up of tracks which are very similar in order and position. All figures use the same notation (A, B, C, etc.) to demonstrate the similarity. These trackways are therefore assigned to the same ichnotaxon and are likely to have been made by the same type of organism. Variation in substrate or preservation of the exposed bedding plane is minimal, making it improbable that these factors have contributed to making these trackways more similar than they actually are.

We suggest an animal with seven pairs of walking legs, with the possibility of additional limbs held out of contact with the substrate. The regularity and large number of tracks, in addition to the age rules out most organisms, leaving arthropods as the most likely producers (Briggs et al. 1979). Xiphosurans (e.g., modern Limulus polyphemus) possessing 10 limbs are probably ruled out (Braddy & Almond, 1999). MacNaughton et al. (2002) and Braddy (2004) attribute similar trackways to members of the Euthycarcinoidea (Late Cambrian to Middle Triassic). We were unable to reconcile these trackways with organisms having 11 pairs of limbs (Vaccari et al., 2004). Based on the estimated number of limbs and the presence of a medial telson drag, members of the Eurypterida (usually with 6 or 8 pairs of legs) are found to have been the most likely producers. Arrangement of these tracks is reminiscent of those made by Braddy & Almond's reconstruction of the eurypterid *Onychopterella augusti*, although no such specific name is being applied here. Tracks, while diverging to the front in trilobite and other trackways, diverge to the rear in merostomes due to the increasing length of limbs rearward (Gevers et al., 1971). This is apparent in our trackways and supports previous hypotheses concerning direction of travel. Direction of travel was toward the top in all schematic diagrams (Figures 4-8).

INTERPRETATION & DISCUSSION (continued)

Ripple marks have been cut through by tracks and associated imprints, and apparently underlay and therefore were generated prior to the microbial mat surface. This surface exhibits textures and erosional pockets characteristic of microbial mats (Noffke, 1998). The bedding plane on which the trackways are preserved was part of a high-intertidal or low-supratidal environment, possibly inundated only at spring-tide like intervals. The organisms were present at the same or very nearly the same time. Ripple marks were produced by wind creating small waves in a tidal pool. This is suggested by the good preservation and clarity of the imprints. The track producers were probably only partially supported by water, as postulated by Sharpe (1932):

> *It seems unlikely that an animal of the broad build of a eurypterid could walk across a soft mud flat without leaving blurred impressions due to the dragging of the legs and body, the weight of which could hardly be carried clear of the ground.. Probably in this case the animal happened to cross a small enclosed depression in a mud flat which held a few inches of water. The water though of sufficient depth to carry much of the animal's weight was shallow enough to allow [. . .] the walking legs to touch the soft muddy bottom where they left clear, regular impressions. The evaporation of the water in the pool then continued without further disturbance.*

Owen reported that in some cases his specimens exhibited intermittent tail drags. He associated each interval where the tail drag is present with a specific trackset, implying that the presence or absence of a tail drag is related to the walking cycle of the animal. Our specimens do not exhibit this association. It seems unlikely from a functional view that vertical movement of the telson with enough displacement to clear the substrate would be a beneficial adaptation if associated with each walking cycle. It is suggested that the incontinuity of the telson drag results from the effect of wind ripples or small waves upon the organism in the tidal pool already postulated. The organism could accommodate the change in water depth by bending or repositioning its legs, while the telson would react independently.

Braddy & Milner (1998) suggested that a "discrete mark within the medial impression" was suggestive if the organism "inclined its body away from the substrate" in preparation for swimming rather than walking on the substrate. This type of impression is apparent in all three trackways discussed either as a named track or associated imprint (Figure 4). This does not seem a likely scenario for the trackways illustrated here because they lack the linear scratches described by Braddy and Milner. These trackways were also produced in water which was probably too shallow for the organisms to have been able to swim.

The interaction noted between trackways 1 and 2 has been interpreted as evidence of mating behaviour similar to that of the modern horseshoe crab, Limulus polyphemus by Erickson (2004). The direction of movement as described here supports this hypothesis. In Figure 2, the organism producing trackway 2 moved from the upper right to the lower left, and the organism producing trackway 1 moved from the left to the right.

CONCLUSIONS

A variety of conclusions were reached about these trackways, following the methods described above:

1. All trackways observed are examples of the same ichnogenus *Protichnites* and were produced by the same type of organism.
2. The trackways represent examples of the ichnospecies *Protichnites septemnotatus* Owen, 1852.
3. These trackways were most likely produced in a shallow-water tidal pool.
4. Bimodality among trackmakers suggests organisms present in an intertidal environment for short periods of time (e.g., for breeding purposes) rather than being adapted for terrestrial life.
5. The direction of travel and the bimodal distribution of the trackway-producing organisms supports Erickson's (2004) hypothesis concerning mating behaviour.
6. Due to number of imprints and presence of a medial telson drag, the most likely producers of these trackways were eurypterids (6-8 limbs) rather than xiphosurans with 10 limbs or euthycarcinoids (11? pairs of limbs).

ACKNOWLEDGMENTS

I would like to thank Dr. J. Mark Erickson for his ongoing support, guidance and encouragement in this endeavor and in others. Jim Dawson provided vital insight into the nature of these trackways. Special thanks go to Joanne Cavallerano, Camille Partin, and Trisha Smrecak without whose continual presence this study would not have been possible.

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