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

by

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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. A similar site near Kingston, Ontario, has been described as the first evidence of land animals. 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 arranged in a chevron pattern. The organism was traveling in the direction of the convergence of the chevron pattern.

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 cannot be recognized on any digit. Variable preservation probably 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 in the Potsdam (=Nepean) Sandstone by

Logan (1851, 1852) in southern Quebec (Figure 1). Plaster casts were shipped from

Canada to London, where they were formally described by Owen (1852). Additional

original sections of trackway beds were also distributed. 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 (e.g., *Climactichnites*

(Yochelson and Fedonkin, 1993) 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 behavior, in the interaction implied by

two *Protichnites* trackways (Erickson 2004). This paper examines more completely the

trackways discussed by Erickson as well as presenting the results of an extensive

literature search to determine the characteristics commonly attributed to the ichnogenus.

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 likely track-maker; d) remark upon the interaction seen between the

trackways (Figure 2; and e) redefine the ichnogenus *Protichnites* so that it may have

more precise taxonomic usage in the future.
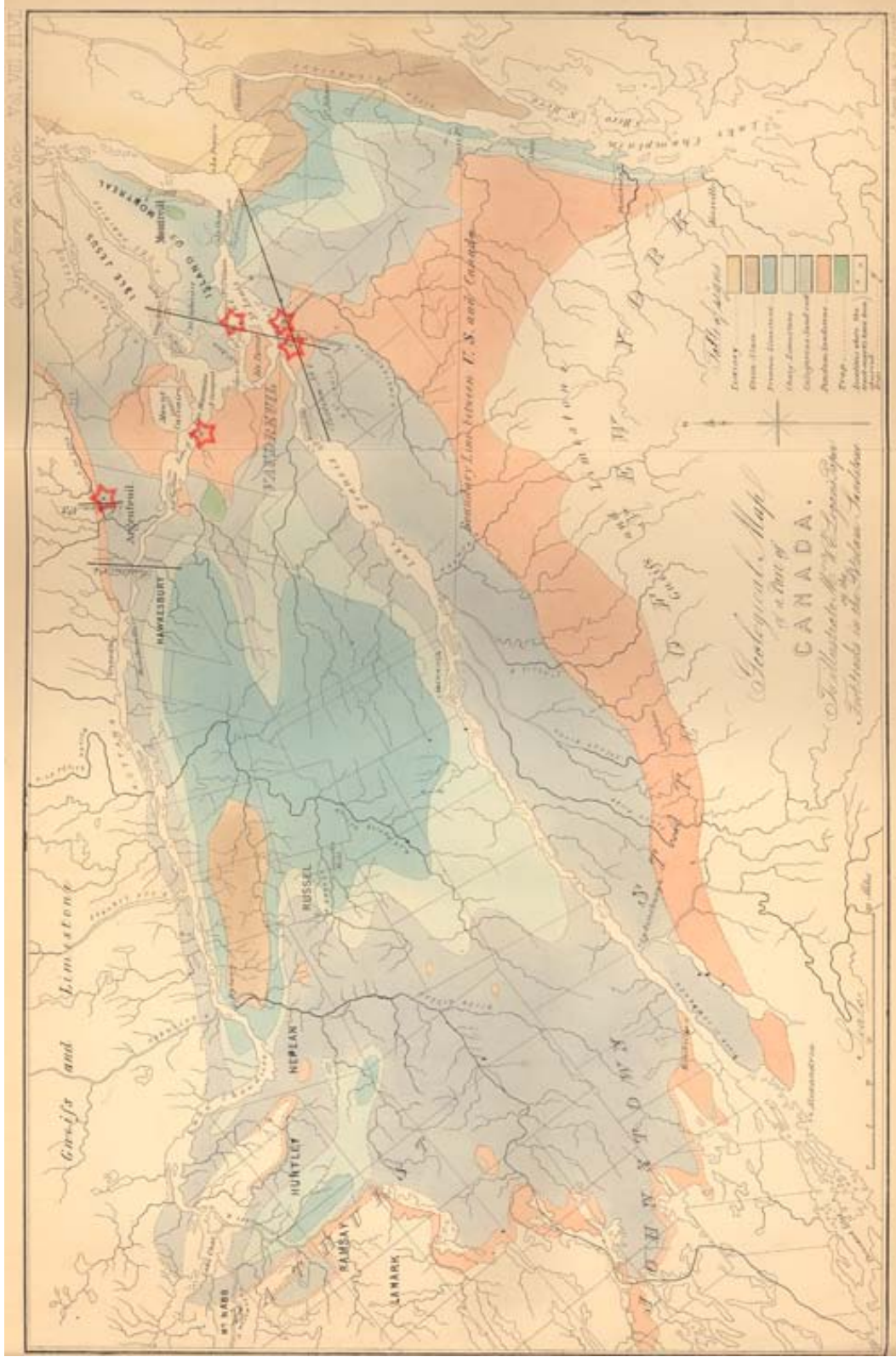
Figure 1. Regional bedrock map of southern Canada near Quebec, from Logan (1852, Plate VI). Stars added to more clearly show five trackway localities in the Potsdam Sandstone described by Logan and by Owen (1852).
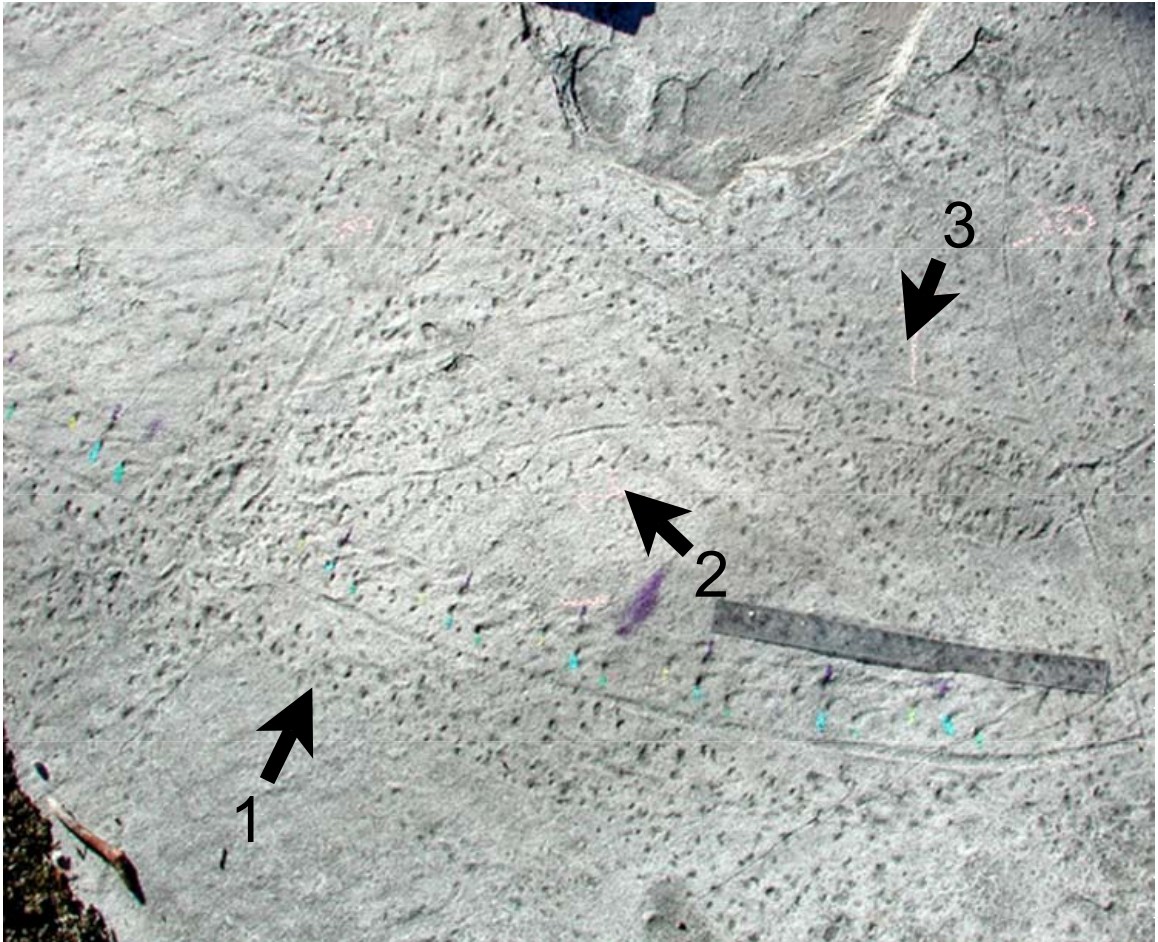
Figure 2. Bedding-plane exposure showing at least 11 trackways. Trackways examined by the current study are indicated by arrows. Ruler is 35 cm in length. Photograph by J.M.E.

Historical review

Trackways assigned to the ichnogenus *Protichnites* were first noted in the Potsdam (=Nepean) Sandstone in the *Montreal Gazette* in 1847 (Walcott, 1912) and later described by Sir Richard Owen (1851) as tracks belonging to "a species of Terrapene or Emydian Tortoise." The following year, apparently after further study, he emended his interpretation to describe the producers as arthropods and defined *Protichnites* (Owen 1852). Owen designated six species (scanned images of his plates follow as Figures 3-8): *P. septem-notatus*, *P. octo-notatus*, *P. latus*, *P. multinotatus*, *P. lineatus* and *P. alternans*. The description and plates given show a superficial resemblance to the trackways discussed below, which crop out of the Potsdam Sandstone in northern New York State rather than in southern Quebec and Ontario; it will be shown later that these trackways are comparable enough with Owen's to be identified to the species level.

In the remainder of the 19th century similar trackways were described and assigned to *Protichnites*, adding two more species to Owen's original six: *P. logananus* Marsh, 1869 and *P. carbonarius* Dawson, 1873. *P. carbonarius* was reassigned by Packard (1900) to *Ostrakichnites* after he found Dawson's description to be insufficient. Caster (1938) also remarked upon the poor quality of the specimens Dawson was working with. Hitchcock (1858) worked to standardize Owen's (1852) description by listing *Protichnites* according to the following criteria, possessing: a) a medial groove, b) tracksets of five or more, c) variable track morphologies, d) variable size and e) not limited to any single producer (Keighley and Pickerill, 1998). This designation was little used to identify trackways, and was effectively nullified when Seilacher (1955) suggested

Figure 3. Plaster cast of *Protichnites septem-notatus*. (Owen, 1852; Plate IX). Scale bar 5 cm with 1 cm subintervals.
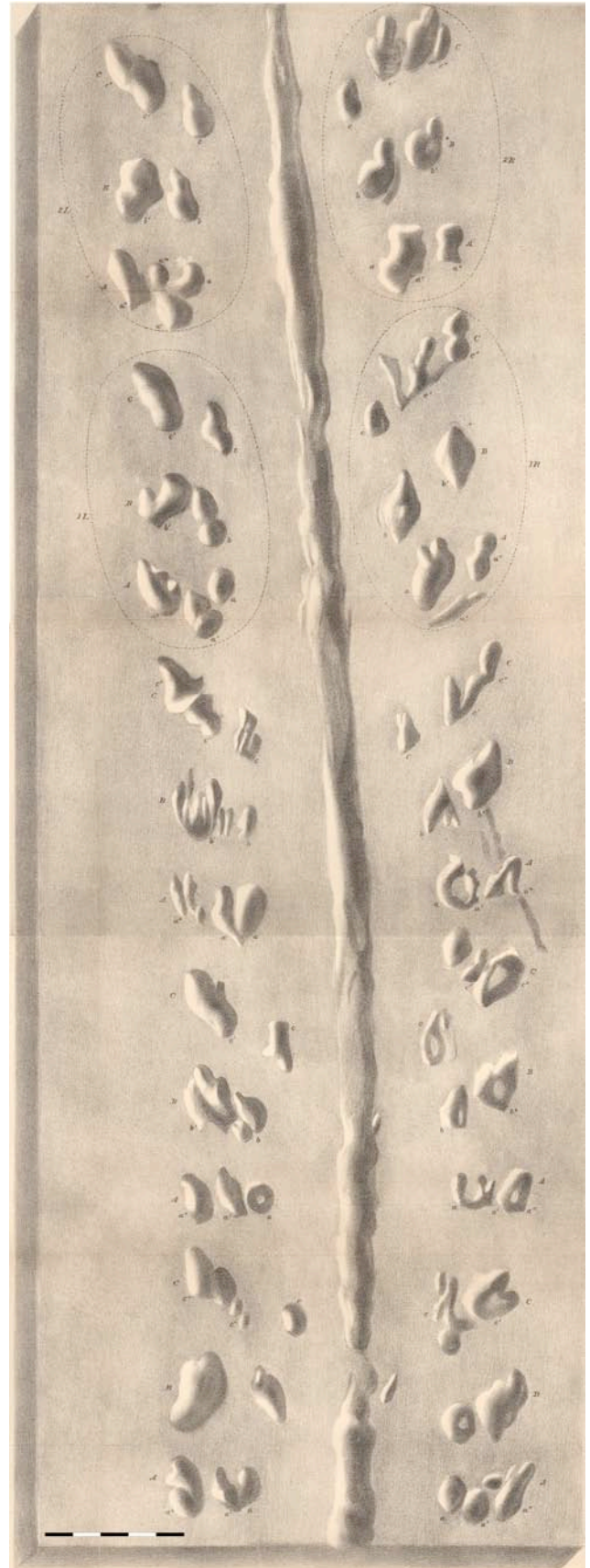
Figure 4. Plaster cast of *Protichnites octo-notatus*. (Owen, 1852; Plate X). Scale bar 5 cm with 1 cm subintervals.
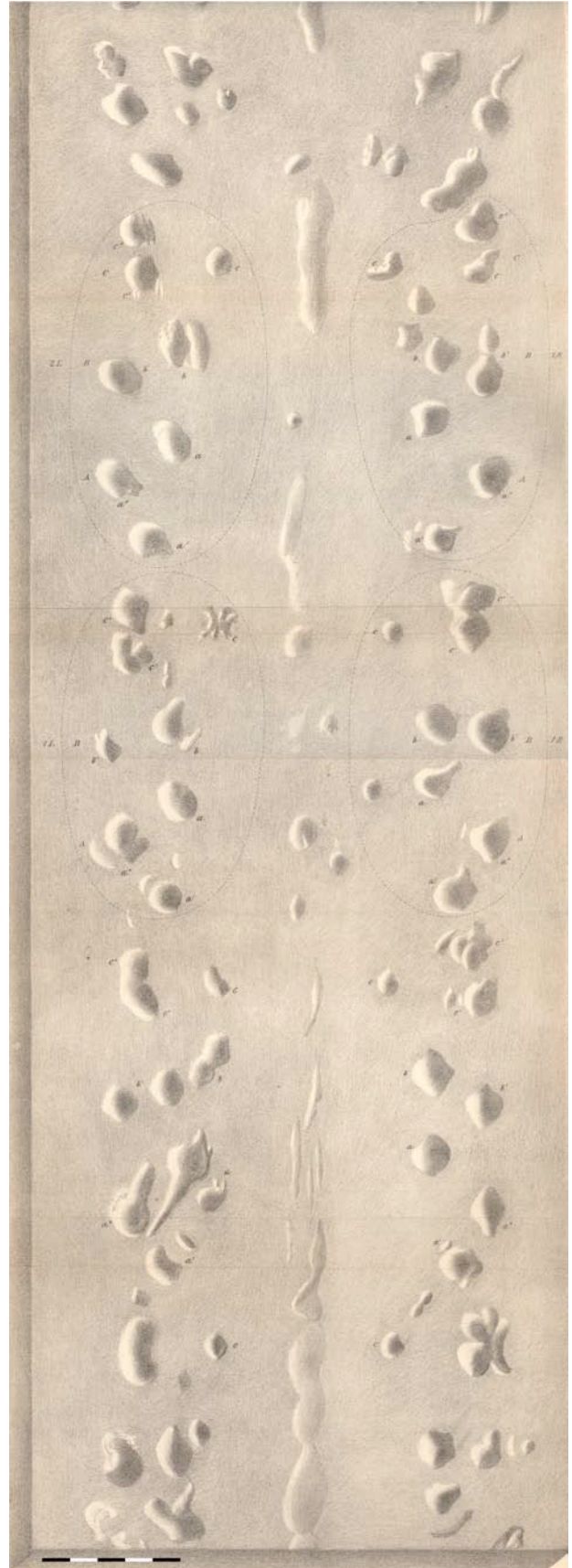
Figure 5. Plaster cast of *Protichnites latus*. (Owen, 1852; Plate XI). Scale bar 5 cm with 1 cm subintervals.
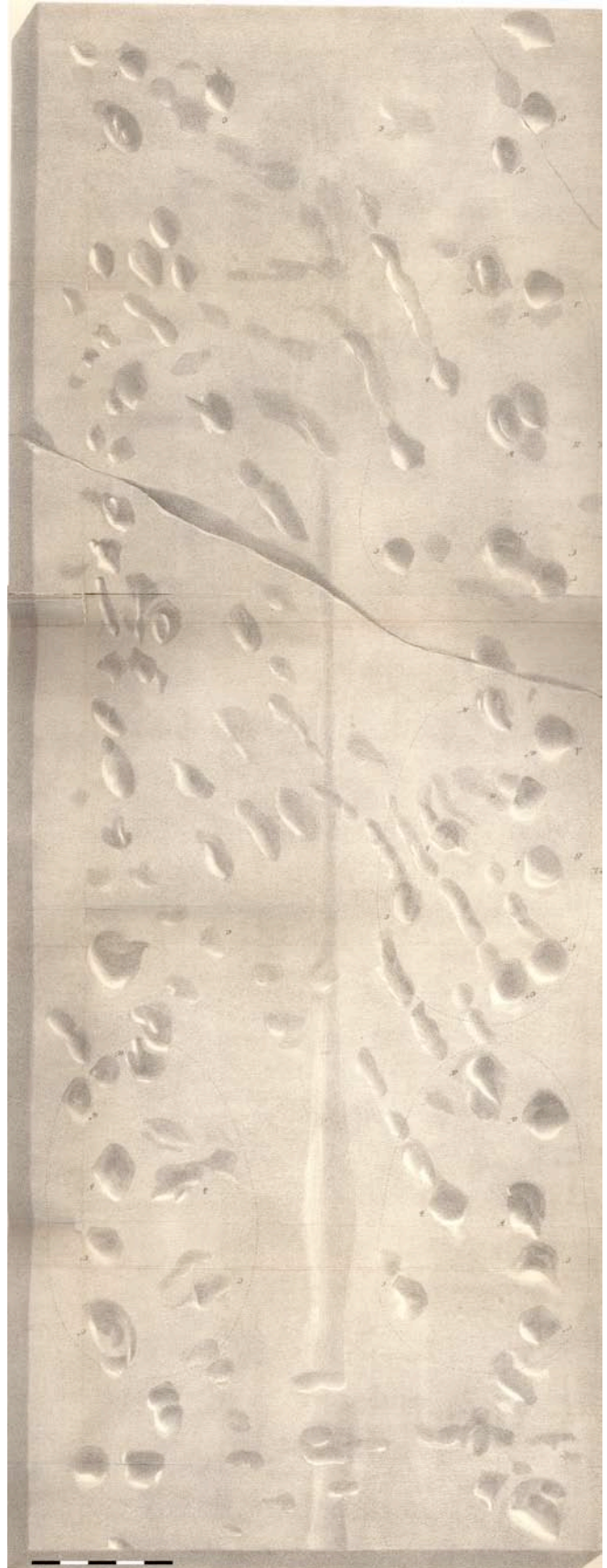
Figure 6. Plaster cast of *P. multinotatus* (Owen, 1852; Plate XII). Scale bar 5 cm with 1 cm subintervals.
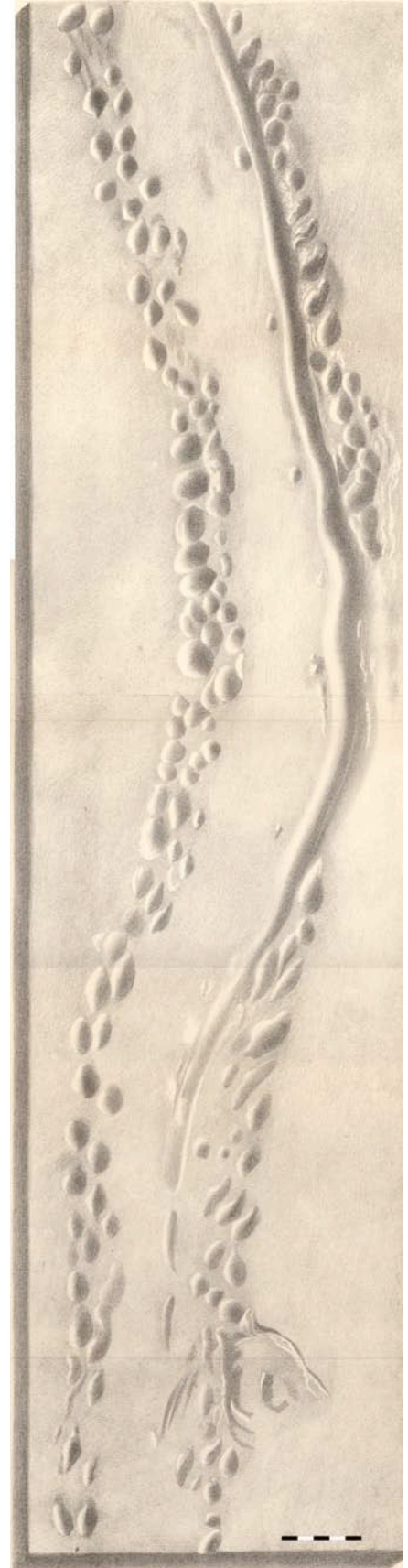
Figure 7. Plaster cast of *Protichnites lineatus* (Owen, 1852, Plate IX). Scale bar 5 cm with 1 cm subintervals.

Figure 8. Plaster cast of *Protichnites alternans* (Owen, 1852, Plate XIV). Scale bar 5 cm with 1 cm subintervals.

that *Protichnites* be applied to trackways with a medial groove and *Diplichnites* to those without one. Hantzschel (1962, 1975) later designated *P. septemnotatus* the type species for the genus. Trewin and McNamara (1995) discussed some inconsistencies in Hantzschel's description. His illustrations show two trackways possessing different features and his description seems to have little basis on published work.

SYSTEMATIC PALEONTOLOGY

The *Protichnites* material described here remains *in situ* in an exposure located in the St. Lawrence Valley, northern New York state, USA, at the time of publication. Exact coordinates are available on request to qualified researchers who give assurance that they will not be revealed.

As most of the work involving *Protichnites* identifies specimens only to the generic level, it seems cumbersome here to discuss the material on a species-by-species basis. Therefore, all instances of *Protichnites* will be introduced *en masse* first in hope that some better sense can be made of how the genus has been identified in the past and how it should be interpreted in the future. Published works describing a new occurrence of *Protichnites* rather than a discussion are indicated with an asterisk (*). Where a new species is introduced the author indicated is the author of that species.

Ichnogenus *Protichnites* Owen 1852

Type species: Protichnites septem-notatus Owen, 1852 (=*P. septemnotatus* SD Hantzschel (1975))

Included species: P. septemnotatus Owen, 1852. *P. octo-notatus* Owen, 1852. *P. latus* Owen, 1852. *P. acadicus* Dawson, 1873. *P. narragansettensis* Packard, 1900.

> *1847 "tortoise tracks," Mr. Abraham, editor *Montreal Gazette* (Logan, 1851).
> 1851 "foot-prints of an animal," Logan, pp. 247-250.
> *1851 "tortoise tracks," Owen, pp. 250-252.
> *1852 *Protichnites septem-notatus* Owen, pp. 214-217, pl. IX.
> *1852 *Protichnites octo-notatus* Owen, pp. 217-218, pl. X.

*1852 *Protichnites latus* Owen, pp. 218-219, pl. XI.
 1852 *Protichnites* Owen; Logan, pp. 210-213.
 1857 *Protichnites* Owen; Billings, pp. 35-39.
 1860 *Protichnites* Owen; Logan, p. 280.
 1862 *Protichnites* Owen; Dawson, pp. 271-277.
 1870 *Protichnites* Owen; Billings, pp. 484-485.
 1877 *Protichnides* Owen; Chapman, pp. 486-490. (*nom. null.*)
 1890 *Protichnites davisi* Owen; Dawson, pp. 599-601.
 1890 *Protichnites* Owen; Dawson, pp. 599-601, fig. 4.
 1900 *Protichnites narragansettensis* Packard, p. 402.
 1900b *Protichnites* Owen; Packard, pp. 63-71.
 1912 *Protichnites septemnotatus* Owen; Walcott, pp. 278-279, pls. 46
          and 47.
 1917 *Protichnites logananus* Marsh; Burling, pp.387-390, fig. 1.
          (assignment to this ichnospecies does not agree with Marsh's
          designation).
 1955 *Protichnites* Owen; Seilacher.
 1962 unidentified arthropod trackway; Taljaard, pp. 25-27, fig. 1, pls.
          1,2.
 1970 *Protichnites* Owen; Osgood.
*1971 *Protichnites* sp. B Savage, p. 227, fig. 11.
 1975 *Protichnites* Owen; Anderson, p. 40.
 1998 *Protichnites* Owen; Shah et al,, p. 780, pl. 1*f*, fig. 2*b*.
 2001 *Protichnites* Owen; Sudan and Sharma, p. 166, pl. 1*d*.
*2002 *Protichnites* Owen; MacNaughton *et al.*, p. 393, fig. 4*a,b* but not *c*.
 2004 *Protichnites* Owen; Braddy, p. 137-138.
*2004 *Protichnites* Owen; Morrissey *et al.*, p. 352, fig. 8*b*.

Emended Diagnosis

Opposite, symmetric trackway consisting of two rows of tracks in chevron formation

with a single narrow medial discontinuous or continuous incised impression parallel to

the general trend of the trackway. Individual tracks vary in distance from the midline and

in morphology, including but not limited to unifid, bifid, and trifid imprints. Most

complete compliments of tracks consisting of seven or eight tracks arranged at low angle

to the midline. Trackset overlap along trackway is variable, meaning that comparative

unit distances over the course of the trackway may include more or fewer tracksets.

Medial impression typically equal distance from opposite tracks and, if discontinuous, remains linear rather than becoming steeply angled to the trend of the trackway.

Discussion

The ichnogenus *Protichnites* is currently commonly paired with *Diplichnites* Dawson as a sort of dichotomous key to arthropod trackways: i.e., *Protichnites* includes a medial groove, and *Diplichnites* does not. This was suggested provisionally by Seilacher (1955) as a means to simplify invertebrate ichnotaxonomy by defining a medial impression as the defining characteristic of a trackway (Keighley and Pickerill, 1998). It has been suggested (Keighley and Pickerill, 1998) that *Protichnites* include trackways with any number of medial grooves, but this does not agree with Owen's (1852) original description of the members of the ichnogenus, which only had a single medial impression. It is the hope of the author that the characters listed in the above diagnosis lead to a more definitive approach than this. The following specimens identified in the literature as *Protichnites* do not fall under the emended diagnosis presented above. This tighter designation serves to eliminate three of the species Owen described concurrently with the ichnogenus, *P. multinotatus*, *P. lineatus*, and *P. alternans*. It is the opinion of the author that the ichnofossils these names represent would be better placed under other genera. In any case no published work (barring Owen (1852)) has identified trackways as any of the three species listed.

*1852 *Protichnites multinotatus* Owen, pp. 219-220, pl. XII.

P. multinotatus under this emended diagnosis could be loosely included, however the

number of tracks per track set cannot be resolved from Owen's description or illustration.

Since *P. septem-notatus* and *P. octo-notatus* were described first as having a defined

number of tracks per series it seems inappropriate to include *P. multinotatus* since it could

be better placed in one of various other genera with more similar characteristics.

*1852 *Protichnites lineatus* Owen, pp. 220-221, pl. XIII.

P. lineatus lacks discrete repeating tracks and displays more than one continuous

impression within the bounds of the trackway. Owen (1852) suggested that this type of

trackway is a disturbed and badly-preserved version of other *Protichnites* produced by

the same animal, and stated that the name (*P. lineatus*) "is one of convenience only, and is

not to be regarded as the sign of a species recognized as actually distinct from the

differently-marked and better-defined impressions of the same size and breadth." It is the

opinion of the author that *P. lineatus* should not belong to this ichnogenus because of its

dissimilarity.

*1852 *Protichnites alternans* Owen, pp. 221-222, pls. VIII and XIV.

P. alternans, if interpreted correctly and illustrated accurately by Owen seems to show

alternating tracksets rather than opposite tracks. Although it seems improbable that such

a trackway was produced by an arthropod similar to the probable producer of other

species of *Protichnites* (e.g., *P. septemnotatus*, this paper), this should not affect an

ichnogenus designation. *P. alternans* should not be included in the ichnogenus under the

diagnosis presented above, which does not include trackways with non-opposite tracks.

1867 *Protichnites scoticus* Salter (in Murchison), p. 151.
1890 *Protichnites scoticus* Salter; Dawson, pp. 599-601.

*1998 *Protichnites scoticus* Salter; Keighley and Pickerill, p. 97, fig. 5*e.*

Although this trace possesses a medial groove, it has only six pairs of tracks per track set

rather than seven or eight, arranged at first glance in sets of three at a high angle to the

midline.

*1869 *Protichnites logananus* Marsh, pp. 322-324. (=*Diplichnites*
      logananus, *nom. trans*. Keighley and Pickerill, 1998)
*1912 *Protichnites logananus* Marsh; Walcott, p. 279, pls. 48 and 49.
      (=*Diplichnites logananus*, *nom. trans*. Keighley and Pickerill,
      1998)
 1962 *Protichnites logananus* Marsh; Hantzschel, p. W210, fig. 131,*4*.e
 1975 *Protichnites logananus* Marsh; Hantzschel, p. W97, fig. 61,1c.
 1998 *Protichnites logananus* Marsh; Keighley and Pickerill, p. 95.

Marsh's description of the trackway includes noting the "absence of a medial trail or tail-

mark," (p. 323) and as such cannot be included in *Protichnites*. Keighley and Pickerill

(1998) note that this ichnospecies is more appropriately assigned to *Diplichnites* Dawson,

1873. Walcott's description is similar to Marsh's designation of *P. logananus*, but also

incorporates trackways possessing a medial groove under the same designation. No

mention of the number of tracks per set is made.

*1873 *Protichnites acadicus* Dawson p. 18, fig. 3.
 1890 *Protichnites acadicus* Owen; Dawson, pp. 599-601.

The structure of this trackway is dissimilar to all known *Protichnites* to this time. It

consists of a series of long parallel slashes at a moderate angle to the midline. Dawson's

figure 3 suggests a medial groove.

*1873 *Protichnites carbonarius* Dawson
?1878 *Protichnites carbonarius* Dawson
*1900 *Protichnites carbonarius* Dawson; (=*Ostrakichnites carbonarius*)
      Packard, p. 403-404.
*1998 *Protichnites carbonarius* Dawson; Keighley and Pickerill, p. 95-
      96, fig. 3*c*, 5*a-c.*

Individual tracks are arranged in grouped rhomboidal patterns of four rather than

chevrons paired across the midline (Keighley and Pickerill, 1998). Reassigned to

Ostrakichnites by Packard (1900); reassigned again to *Protichnites* by Keighley and

Pickerill (1998).

> *1885 *Protichnites davisi* Williamson, p. 19-23, pl. 1,*4*.

The markings described by Williamson (1885) consist "of four pairs of slightly curved

indentations" opposite across a slightly raised medial ridge. This agrees neither with

Owen's (1852) nor any subsequent author's description of *Protichnites*.

> *1932 *Protichnites gallowayi* Sharpe, p. 357, figs. 1 and 2. (="
> *Palmichnium,*" cf. Braddy, 2004)
> 1938 *Protichnites gallowayi* Sharpe; Caster, pp. 28-30. (=*Palmichnium*).

Too few tracks per trackset (4), angle to midline too high, and the presence of large

imprint out of line with the other tracks. Braddy (2004) suggested that this trackway be

assigned to *Palmichnium* rather than *Protichnites* based on form. It can be noted that

Sharpe and Braddy agreed on the trackway producer. Caster (1938) discusses the

questionable assignment of *P. gallowayi* to *Protichnites* due to the form differences

between Sharpe's description and the original description of the ichnogenus by Owen

(1852).

> *1959 *Protichnites sp.T* Oepik, p. 9, figs. 2,3,5.

Possesses a flattened area between paired tracksets rather than a medial groove: "None of

the described *Protichnites* trails has such a wide median drag trail; its width is here one

third of the width of the trackway, whereas in the others it is a sixth or even less" (p. 9).

All tracks are equidistant from the medial line.

1962 *Protichnites* isp. Owen; Hantzschel, p. W97, fig. 129,*5.*
1975 *Protichnites septemnotatus* Owen; Hantzschel, p. W97, fig. 61,*1a.*

The trackway figured possesses a single medial groove flanked by rows of tracks, but there do not appear to be any more than five tracks per track set as illustrated.

1962 *Protichnites septemnotatus* Owen; Hantzschel, p. W210, fig. 131.
1975 *Protichnites* isp. Owen; Hantzschel, p. W97, fig. 61,*1b,c.*

Two longitudinal grooves present between tracksets; *Protichnites* has only one.

*1971 *Protichnites* sp. A Savage, p. 226, fig. 10.

This specimen includes two medial grooves.

*1995 *Protichnites* isp. Owen; Trewin and McNamara, p. 183-184, 200-201, fig. 29.

Similar to trackways described by Oepik (1959) in having flattened area between tracksets rather than a medial groove, and in having no discernible angle of tracksets to the midline.

*1998 *Protichnites kennediea* Smith (as *Danstairia kennediea*); Keighley and Pickerill, p. 97, fig. 5*d.*

Keighley and Pickerill (1998) reassign *D. kennediea* to *Protichnites*, however their specimen does not exhibit the double medial groove as in Smith's (1909) original description. Although the "two shallow but sharply cut gutters placed close together" (Smith, 1909, p. 12) could in some cases mimic a single groove, calling this trace *Danstairia* prior to assigning it to *Protichnites* seems improper. The number of tracks per set in *P. kennediea* is currently inconclusive according to the information presented by Keighley and Pickerill (1998).

1998 *Protichnites variabilis* Keighley and Pickerill, p. 98, fig. 3*d.*

Due to poor preservation, Keighley and Pickerill (1998) were unable to provide much descriptive information, but after examination of their figure it seems doubtful that this specimen be diagnosed as *Protichnites* of any sort, although they stated that it seems similar to *Kouphichium variabilis* and went on to classify it as *Protichnites*.

> *1998 *Protichnites* isp., types A, B, C, D Keighley and Pickerill, p. 98,
> figs. 5*d*, 3*e-g*,

Keighley and Pickerill (1998) were not able to make a distinction between these types of trackway due to their poor preservation. The common factor between them is that they possess medial grooves, but there is not enough information preserved to be able to assign them to *Protichnites*.

Similar ichnofauna

A complete list of ichnogenera similar to *Protichnites* (having two rows of tracks and a medial groove) would be prohibitive to include at this point. Examples of similar ichnogenera from the same literature as (but not always associated with) *Protichnites* include *Mesichnium* (Braddy, 1995), *Paleohelcura* (Briggs *et al.*, 1979; Braddy, 1995; Morrissey and Braddy, 2004), *Stiallia* Smith, 1909 (Buatois *et al.*, 1998), *Palmichnium* Gevers *et al.*, 1971 (Braddy and Milner, 1998; Braddy and Almond, 1999)*, Petalichnus* Miller, 1880 (Anderson, 1975), *Siskemia* (Walker, 1985)*, Stiaria* Smith, 1909 (Buatois *et al.*, 1998; Walker, 1985)*,* and *Triavestigia* (Braddy, 1995), to name only a few authors.

ARTHROPOD TERRESTRIALIZATION

Although the trackways described here show only (at most) partial terrestrialization of a group of arthropods, it seems appropriate at this time to discuss the problem of arthropod terrestrialization during the early Paleozoic. Evidence from different assemblages can be combined to model generally what problems had to be overcome, and how specific groups of arthropods reacted to the stresses of living in a terrestrial environment.

The evidence for the first terrestrial organisms is fairly sparse, and the time frame is often debated. It is no surprise that the terms "invading" (Shear, 1990; Trewin and McNamara 1995) and "conquering" the land are used so often: the transition from a wholly aquatic lifestyle to one that was fully terrestrial did not occur overnight and is a good deal less simple than it first appears.

Since fully terrestrial forms have been found in the Middle Silurian of Scotland, the transition must have begun quite a bit earlier (Braddy 2004). The body fossil record is limited during this period, so behaviour and therefore functional morphology must be examined through trace fossils. Braddy (2004) offered a good summary of trace fossils of the Lower Paleozoic; the mere presence of ichnofossil evidence in what is definitely a terrestrial environment would be exemplary of a variety of adaptations. Shear (1990) listed seven areas of adaptation that would have to be addressed before a taxon could be fully terrestrial: 1) desiccation and wetting, 2) air-breathing, 3)locomotion, behaviour and mating, 4) sense organs, 5) feeding, 6) temperature control and 7) developmental constraints.

Seldon (2001) added comments on structural support, internal fertilization, and excretion and ion balance regulation. Desiccation is one of the most obvious problems with attempting to live subaerially, especially as the water supply is typically seasonal (Selden, 2001), but the hard shells of arthropods make retaining moisture a much easier task than that of most soft-bodied animals. Transfer of oxygen is not necessarily as great a problem as it would seem; since there is more oxygen available (a diffusion coefficient of 11.0 rather than 0.000034) an organism with a small cross-section could easily diffuse enough air through its skin (Selden, 2001). Book lungs are first seen in Devonian chelicerates and are still seen in extant *Limulus polyphemus* (Shear, 1990). Locomotion is tied to structural support because, not only did the organisms have to be able to move, they had to survive the effects of gravity in a less viscous medium than sea- or freshwater. Shear (1990) cites the development of plantigrade locomotion as an indicator of terrestriality, in opposition to legs ending in a single point which were likely to be aquatic. He goes on to show that historically the presence of trichobothria (sensory hairs) is also indicative of subaerial habitat. Selden (2001) suggests that the difference in refraction index between water and air would potentially cause problems for organisms during the transition from the sea to the land, although sight distance could be increased exponentially. Feeding strategies would have to change prior to an arthropod group taking advantage of terrestrial food sources due to the lack of a preoral cavity as proposed by Stormer (1976), but the move to capitalize on underutilized ecospace is one theory for early forays onto the land (Buatois and Mangano, 1993). Braddy (2004) discounted this as a possibility for eurypterids because they did not possess advanced mouthparts.

Detritus from land plants would have been a great source of nutrition for organisms attempting survive on land, where locomotion was more difficult.

Excretory practices would also have to be adapted to retain moisture and nutrients (Selden, 2001). Internal fertilization is also a result of the effort to retain water and increase the chances of successful mating and survival of fertilized eggs. Methods of temperature control will likely remain a mystery as they are either physiological (something not evident in the fossil record) or behavioral (which would be difficult to assume with any degree of certainty).

The terrestrialization of certain arthropod groups is dependent on certain biological factors, and all of these adaptations had not occurred by the Late Cambrian, making it improbable that the trackways discussed here are representative of fully terrestrial organisms which happened to be present in a tidal flat environment.

TERMINOLOGY

Notation

Notation used for describing arthropod trackways is variable. Discussion here will be limited to certain features, so it is unnecessary to define terminology that was not applied to these trackways. Terminology used here is after Braddy (1995), Braddy and Briggs (2002) and Trewin (1994). In this study, an *impression* is defined as any mark that appears to be associated with the presence of an organism. An *imprint* is a discrete impression that was produced by a walking limb, and a *track* is an imprint that repeats at regular intervals and can therefore be identified throughout as having been made by the same walking limb. *Trails* are continuous impressions over any distance. A *trackway* is any combination of impressions, imprints, or trails proceeding in a recognizable manner across the substrate. The *midline* represents a line parallel to the path of the trackway and equally distanced from rows of tracks on either side, whereas *medial* refers only to marks located anywhere between the greatest lateral extent of the trackway. When referring to individual imprints, *stride* is the distance between the same location on the two most adjacent tracks made by the same walking limb (parallel to and on the same side of the medial line). *Width* is the distance from exterior edge to exterior edge of opposite tracks, measured perpendicular to the path of the trackway. A track *set* (or *trackset*)is a group of tracks including one track made by each walking leg before repetition, and can be applied to either or both sides of the midline.

Identifying tracks

The outcrop was visited first in the Spring of 2002 and on two other 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 author. 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.

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 model arranged tracks in "paired chevrons" across the midline (Figure 9*a*). It was rejected because the arrangement of tracks shows no overlap (i.e. a set overlap of zero or less than zero) implying an organism making neat "jumps" or, if floating, "strokes" to end up in precisely the same relative position as the previous tracks. Chapman (1877) argued for *Protichnites* and *Climactichnites* to be deemed "fucoidal" (resulting from algal or microbial growth) in origin using the argument above.

A second hypothesis showed more overlap but less linearity of the series of tracks on either side of the midline (Figure 9*b*). The consistency of both the tracks and the medial drag line show that these hypotheses were in error for reasons described below
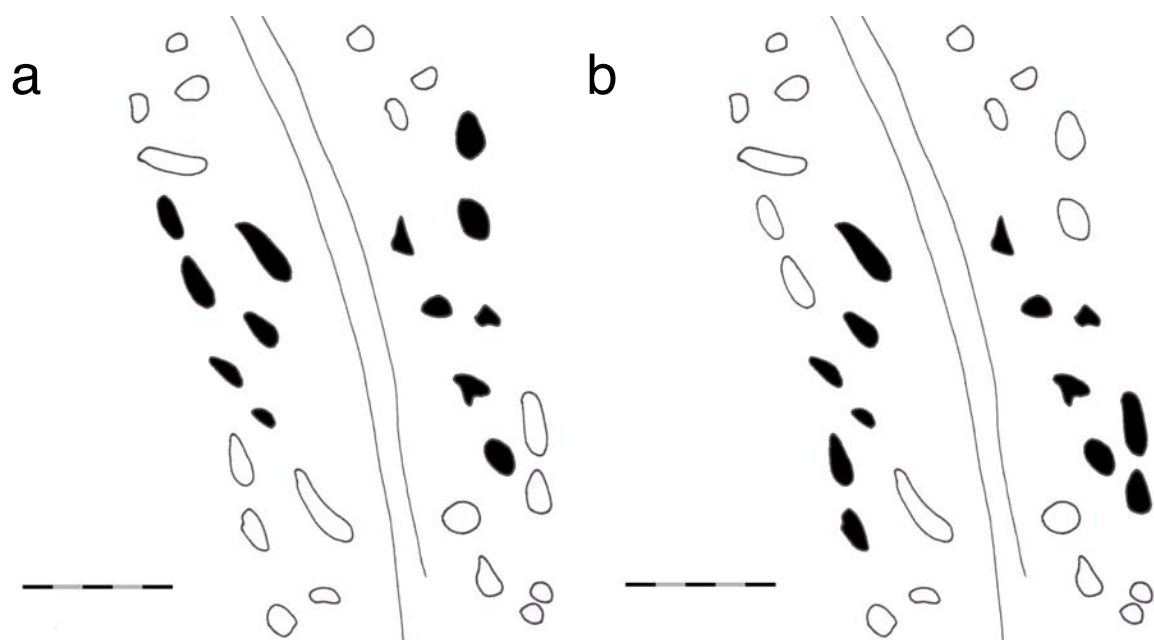
Figure 9. Two ways of grouping individual tracks into tracksets in trackway 1, darkened areas represent tracks within sets. a) "Paired chevron" grouping. b) a more linear arrangement with more overlap between sets. Scale bars, 5 cm

and in discussions of similar trackways by Anderson (1975), Braddy & Briggs (2000), Braddy & Almond (1999), Briggs and Rolfe (1983), Owen (1852) and Trewin (1994).

Tracksets were designated by locating similar tracks at set intervals along the length of the trackway. This was accomplished using the tracings on acetate by choosing adjacent tracks and overlaying them upon other sections of the trackway to find repetition. Similar tracks in different tracksets (each imprint 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 on Plates II-IV.

The imprints making up the trackways were designated as such 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**, *et cetera*. 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 had been designated by a letter. This resulted in eight sets of tracks per side in each trackway.

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. Two other exposures containing similar trackways are located nearby; one 3 meters to the west and the other ~500 m to the northeast, both on different bedding planes. 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-to-crest distance of 20-30 mm (mean 23 mm) and ripple crests trend roughly northeast/southwest. At least 11 trackways are visible, three of which are described in detail here (Plate I, Figure 2). They do not seem to have a preferred orientation. Most of the trackways are too poorly preserved to distinguish series order. Many scattered impressions are present that cannot be resolved into organized trackways, however all stride lengths and relative track positions are very consistent along the length of each trackway. 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 are in-phase across the medial line.

Trackway 1 (Figure 10; Plate II)

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 walking limb marks. Some individual tracks appear to be bifid or trifid in form. This trackway is the large (11.6 cm) trackway interpreted as having been made by a female examined by Erickson (2004).

Figure 10. Schematic diagram of trackway 1. Shaded areas represent identified tracks, open areas show imprints that have not been associated with a specific trackset. Arrow indicates interpreted direction of travel. Scale bar, 5 cm.
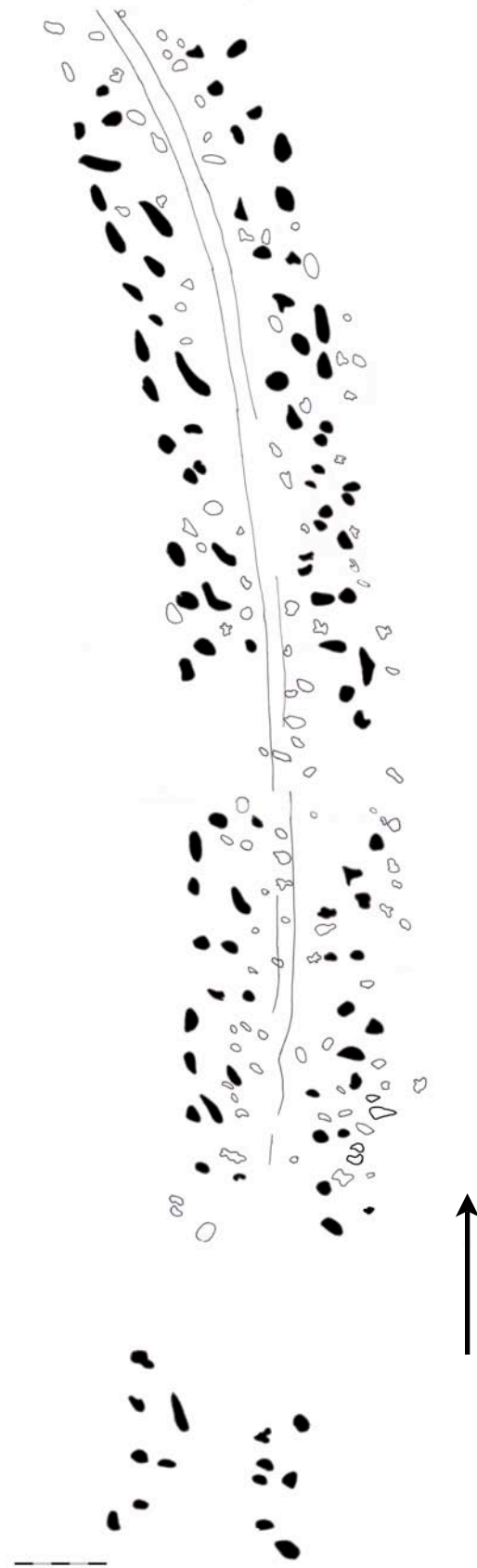
Tracks from 10 sets are apparent. The medial groove is continuous and remains in the middle of the paired tracksets, although some unassociated impressions are located in the groove. Its width is between 7 and 9 mm throughout. Tracks on the right side of the trackway were labeled A-G and tracks on the left side, A'-G' as described under "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 G) 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, and Table 2 compares the mean

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

| Series | Right side of trackway – Stride (mm) | | | | | | | Left side of trackway – Stride (mm) | | | | | | | External width (mm) |
	A	B	C	D	E	F	G	A'	B'	C'	D'	E'	F'	G'	
I-II	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
II-III	--	--	--	--	--	--	--	--	--	--	--	--	--	98	115
III-IV	105	105	105	101	--	--	--	102	95	101	--	--	--	--	--
IV-V	105	109	111	105	107	105	108	102	104	102	--	103	105	--	--
V-VI	100	102	102	104	104	105	109	102	100	102	--	98	105	101	117
VI-VII	108	107	103	100	104	104	104	105	100	100	--	98	104	103	114
VII-VIII	103	99	100	107	103	99	101	95	98	94	--	99	96	--	114
VIII-IX	95	100	102	--	101	100	100	81	90	97	--	89	103	--	--
IX-X	--	--	--	--	93	89	107	--	--	--	--	--	89	91	116
X															121
Average	102.8	103.7	104.2	103.5	102.0	100.6	104.7	97.9	97.9	99.7	--	97.5	100.6	98.5	116.2

stride and standard deviation of every track. There is no change in stride length or width through the area where this trackway intersects with trackway 2.

Table 2. Mean stride and standard deviation of paired tracks in trackways 1, 2 and 3. Tracks C and C' combined preserved only one measurable stride.

| Track | Trackway 1 | | Trackway 2 | | Trackway 3 | |
	Mean stride (mm)	St. Dev.	Mean stride (mm)	St. Dev.	Mean stride (mm)	St. Dev.
A, A'	100.3	7.4	80.1	3.6	85.0	2.2
B, B'	100.8	5.1	77.7	2.8	83.7	2.8
C, C'	102.0	4.2	76.6	2.7	81.4	~
D, D'	103.5	2.8	77.2	3.2	82.1	3.7
E, E'	99.8	5.3	78.4	4.0	83.0	3.4
F, F'	100.6	6.1	77.1	4.1	85.0	3.8
G, G'	101.6	5.1	77.3	3.6	83.7	2.8
Average	101.2		77.8		83.4	

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.

Trackway 2 (Figure 11; Plate III)

Trackway 2 may be identified as the narrower (6.5 cm) trackway Erickson (2004) interpreted as that of a male. It consists of a discontinuous medial groove flanked by repeated series of seven imprints of varying morphology. The portion that is preserved in enough detail to study contains 112 imprints and 74 identified tracks in a 42 cm distance. The trackway curves very gently to its left.

Tracks representing 6 sets are apparent. The medial groove is discontinuous and varies in proximity to each row of tracks. The length of the medial groove where it is present ranges from 1.5 to 5 cm (mean 4.2) with an intermediary distance ranging from 0.5 to 3.5 cm (mean 2.1 cm). In one instance (sets IV-V) the medial drag becomes erratic. The average external width of the trackway at its widest point (track F) 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 3. The trackway is

Table 3. Stride length and external width of trackway 2. (after Braddy and 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	79	81	--	--	--	80	76	79	79	81		--	70
III-IV	75	82	80	79	82	82	82	--	76	73	74	79	77	80	65
IV-V	84	79	79	79	81	82	80	--	74	73	72	71	76	73	66
V-VI	--	--	76	81	80	73	79	--	--	--	74	74	72	72	67
VI-VII	--	--	--	--	--	--	79	--	--	--	--	--	--	--	--
VI															--
Average	78.9	80.0	78.3	79.6	80.7	78.9	79.6	81.2	75.3	75.0	74.8	76.1	75.3	75.0	66.7

not visible past its intersection with trackway 1 (Figure 2).

Figure 11. Schematic diagram of trackway 2. Shaded areas represent identified tracks, open areas show imprints that have not been associated with a specific trackset. Arrow indicates interpreted direction of travel. Scale bar, 5 cm.
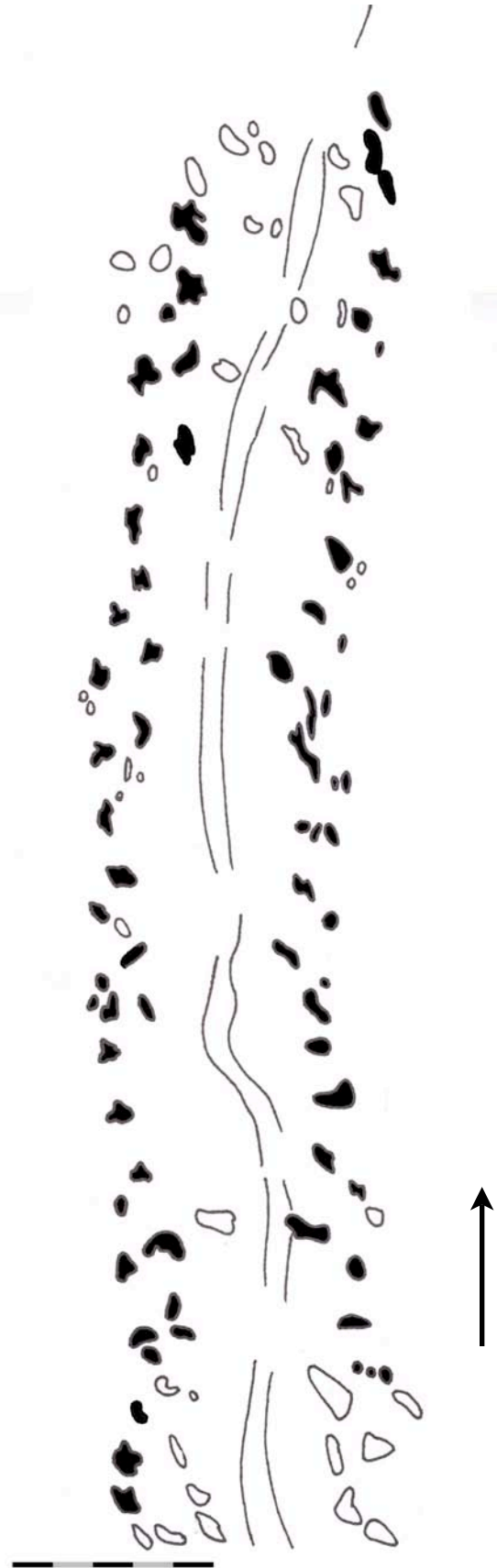
Most tracks are roughly sub-circular or sub-oval with long axes parallel to the axis of the trackway. Track identifications were also assigned to more linear features in some cases (e.g., Plate II, set IV, track F).

<p align="center">Trackway 3 (Figure 12; Plate IV)</p>

This trackway exhibits many characteristics similar to trackways 1 and 2. The medial groove is discontinuous and 8-11 mm wide. Medial groove segments are 3 to 5.5 cm long (mean 3.8 cm) with a distance between from 1 to 4 cm (mean 2.8 cm). 77 cm of the trackway are visible enough to be examined, but tracks could only be resolved over 48 cm. This distance includes 127 imprints, 56 of which 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 4.

Table 4. Stride length and external width of trackway 3. (after Braddy and Milner, 1998)

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

Tracks from seven sets are present, with the same structure as described above. The external width of the trackway averages 72 mm (track F). Track is straight along section analyzed. Average stride length on the right is 82 mm and on the left is 84 mm.

Figure 12. Schematic diagram of trackway 3. Shaded areas represent identified tracks, open areas show imprints that have not been associated with a specific trackset. Arrow indicates interpreted direction of travel. Scale bar, 5 cm.

DISCUSSION

Ichnotaxonomy

The trackways described here are designated as *Protichnites septemnotatus* based on the

emended diagnosis presented above. They are very similar in arrangement and angle to

midline according to Owen's (1852) illustrations (Figures 3-5). Figure 13 correlates

Owen's *Protichnites septem-notatus* tracksets with the tracksets described here; the colors

used to designate tracks produced by the same limb are the same as those used in Plates

II-IV. Although the trackways he described seem to have preserved some small-scale

features better, those features can also be found in the trackways described here (see

below). Opposite tracks in the same set are in-phase, implying that the organism was

adapted for swimming rather than terrestrial life (Braddy and Almond, 1999). While he

found it most likely that the animal producing the tracks was hexapodous with bifurcate

or trifurcate legs, Owen 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 and 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 organism defined as the producer of

these particular trackways has no effect on their designation as *P. septemnotatus*.

Keighley and Pickerill (1998) summarize very well the criteria upon which a named

ichnotaxon must be based. Trewin (1994) added that interpreted direction of movement

should also be disregarded when defining traces. Were direction of movement an

applicable diagnostic tool, new ichnotaxa could be generated from the same trackways simply by interpreting the direction of movement differently.

Trackways denoted 1, 2 and 3 are made up of tracksets which are 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 ichnospecies 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.

<p style="text-align:center">Organisms responsible</p>

I am suggesting an invertebrate 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 their geologic age, rules out most organisms, leaving arthropods as the most likely producers (Briggs *et al.*, 1979; see similarity to crab trackways in Curran, 1984). Although Walcott (1912) attributed *Protichnites* trackways to *Dikelocephalus,* a trilobite, it seems unlikely that a trilobite of this size would have produced such well-defined trackways with no extraneous continuous impressions (e.g., gill marks) in an intertidal pool. Osgood (1970) offers good examples of trilobite trackways from the Ordovician of Cincinnati (notably Plates 73-75).

MacNaughton *et al.* (2002) and Braddy (2004) attributed similar trackways to members of the Euthycarcinoidea (Figure 14*a*) possessing 11? pairs of limbs and ranging from the Late Cambrian to Middle Triassic (Vaccari, *et al.*, 2004). Other Cambrian-age arthropods with similar body plans include the strabopids, once

associated with aglaspids but now of indeterminate phylogenetic position, due mostly to

the lack of material that includes ventral structures and appendages (Tetlie and Moors,

2004). Figure 14 (*b,c*) illustrates two such organisms, *Strabops thacheri* and *Paleomerus*

hamiltoni. Arrangement of these tracks is reminiscent of those made by Braddy and

Almond's (1999) reconstruction of the walking pattern of the eurypterid *Onychopterella*

augusti, but the Eurypterida are limited to 3 or 4 pairs of limbs. Braddy and Almond

(1999) suggested that xiphosurans (e.g., modern *Limulus polyphemus*) possessing 10

limbs would not have been able to produce tracks similar to eurypterids due to

differences in morphology (number of legs), size, and the fact that, "xiphosurans are

infaunal burrowers, whereas the ichnological evidence indicates that eurypterids were

mostly hexapodous or octopodous animals" (p. 172). In spite of these facts, a *Limulus*-

like xiphosuran with fewer than 10 walking limbs could very well have produced these

tracks. 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, however the

combination of the cephalon and thorax into a prosoma reduces the "number of ventral

appendages available for locomotion" (Gevers *et al.*, 1971). There is at least one

example in every type of track (A, B, C, etc.) in each trackway that indicates a trackway

producer with bifid or trifid limbs (e.g., Plate I, set I, track B, set VI, track A, set V, track

D; Plate II, set III, track E', set IV, track F', set V, track C; Plate IV set V, track G).

Because it is unlikely that a limb would reduce its apparent morphology between

tracksets, any apparent reduction from bifid or trifid tracks must be a result of poor

preservation. Unfortunately, no described organism fits the description expressed above.

Figure 13. Plaster cast of *Protichnites septem-notatus* (Owen, 1852; Plate IX) with identified tracks and tracksets. Colors correspond with Plates II-IV: Tracks A=blue, B=red, C=orange, D=brown, E=green, F=light blue, and G=yellow. Compare with Figure 3 (Owen's unalterered Plate IX) and Plates II-IV. Scale bar, 5 cm.
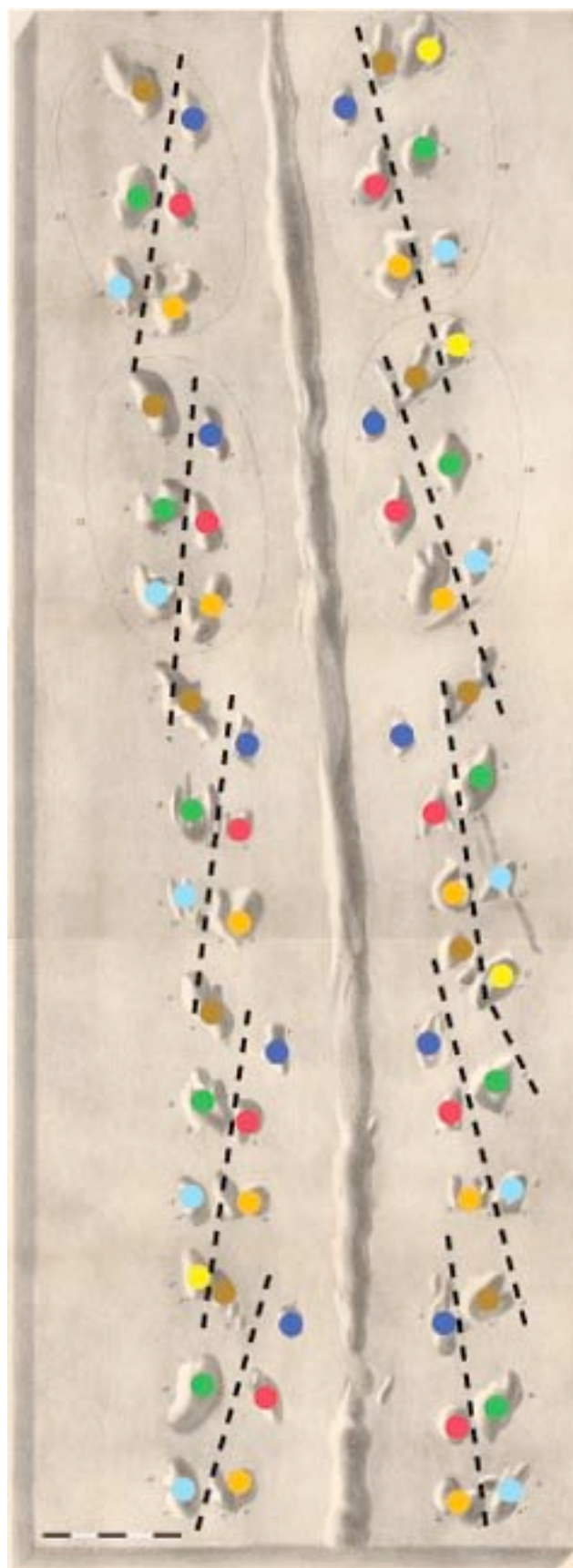
Other organisms with similar postulated morphology include *Chasmataspis laurencii* (Figure 15*a*) and *Stylonurus longicaudatus* (Figure 15*b*), which displays effectively uni-, bi-, and triramous appendages.

Functional morphology

Owen reported that in some cases his specimens exhibited intermittent tail drags. He associated each interval where the tail drag was present with a specific trackset, implying that the presence or absence of a tail drag was related to the walking cycle of the animal. Anderson (1975) made this association with *Petalichnus*.

The specimens described here 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 flexing or repositioning its legs, while the telson would react independently (see medial groove data in "Description"). It is unlikely that the skips represent substrate ripple crests that have been lost due to erosion because the locations of tail skips seem distributed in a random fashion unrelated to preserved ripple marks (Figure 16). Whether the ripples were formed before or after the formation of a microbial mat cannot be determined. If the ripples were formed before both the algal mat and the trackways, it is unlikely that the orientation of the ripples that are preserved would have an effect on the size of the tail skips or that these skips would be variable according to the orientation of the trackways.
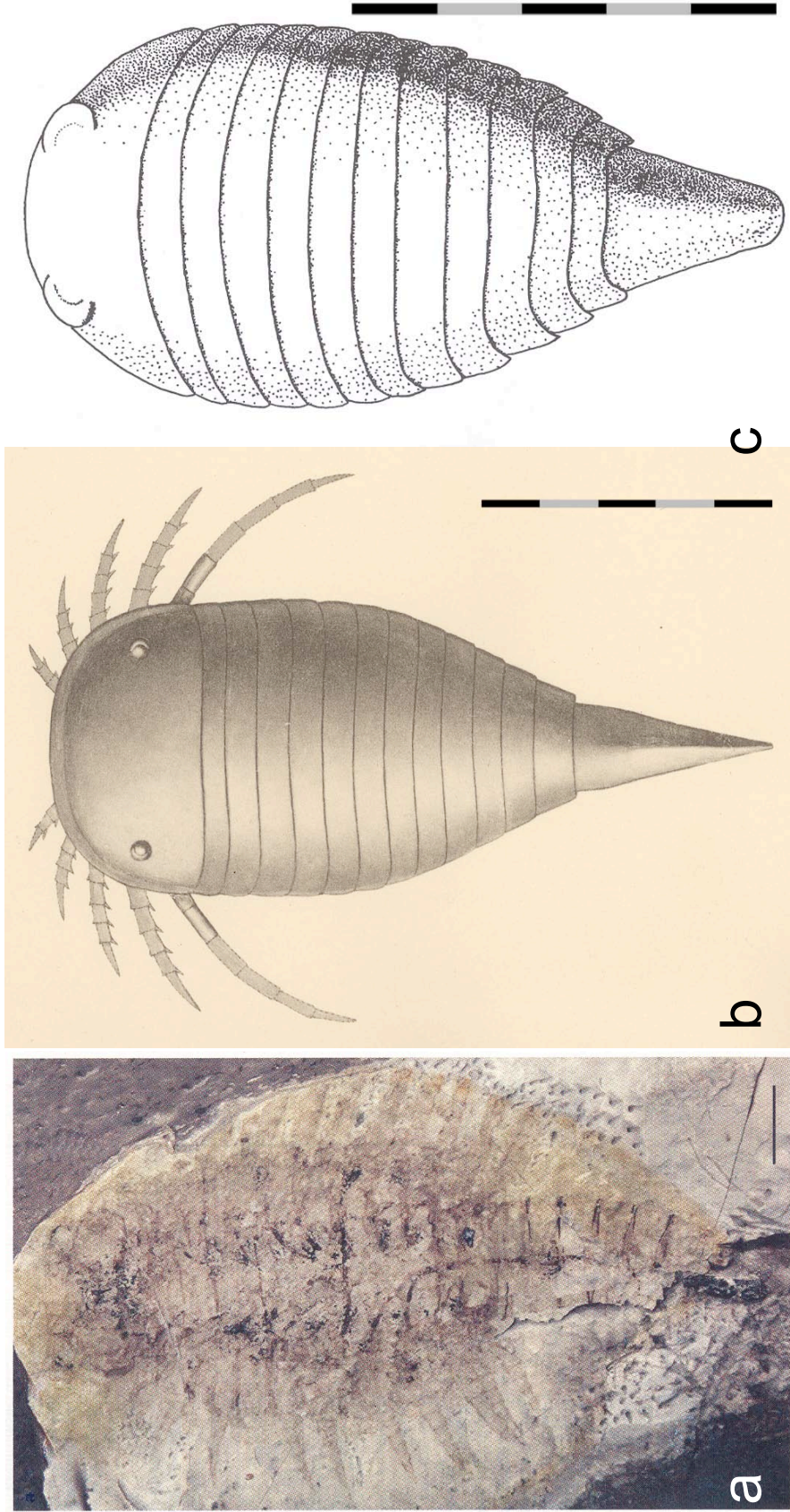
Figure 14. Cambrian arthropods, not to scale. a) Body fossil of euthycarcinoid *Apankura machu*, possessing 11? pairs of uniramous limbs. Scale bar, 5 mm. (From Vaccari *et al.*, 2004, p. 555.) b) Reconstruction by Clarke and Ruedemann (1912, pl. 1) of *Strabops thacheri*; includes interpretation of possible limb structure. Scale bar, 5 cm. c) Tetlie and Moore's (2004, p. 197) reconstruction of *Paleomerus hamiltoni*. Scale bar, 5 cm.

Telson skips were therefore caused by water waves of some type.

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 10; Plate II). The deepest part of these tracks is to the rear (bottom of figure), tapering and shallowing to the front. This was most likely caused by a limb dragging through the sediment at the beginning of another step. This evidence supports a converging-forward series direction of travel as suggested by Braddy and Almond's (1999, p. 175) "tear-shaped morphology of some of the tracks, the more angular end of the track pointing in the direction of travel."

Braddy and Milner (1998, p. 1121) suggested that a "discrete mark within the medial impression" suggested that the organism "inclined its body away from the substrate" in preparation for swimming rather than walking on the substrate. Impressions such as this are present in the medial grooves of trackways 1, 2, and 3, either as a named track or an associated imprint (Figures 10-12). The above hypothesis does not seem a likely scenario for the trackways illustrated herein because they lack the linear scratches attributed to a "launching" motion off the substrate, and so these marks are probably attributable to something else. These trackways were also produced in water which was probably too shallow for the organisms to have been able to swim.

Paleoecology

Trackways at this site appear to show bimodality in width and stride length (Tables 1-3). Larger trackways (including those not explicitly discussed here) are about 115 mm in width, and smaller ones are around 70 mm. A range of sizes exposed at this site would
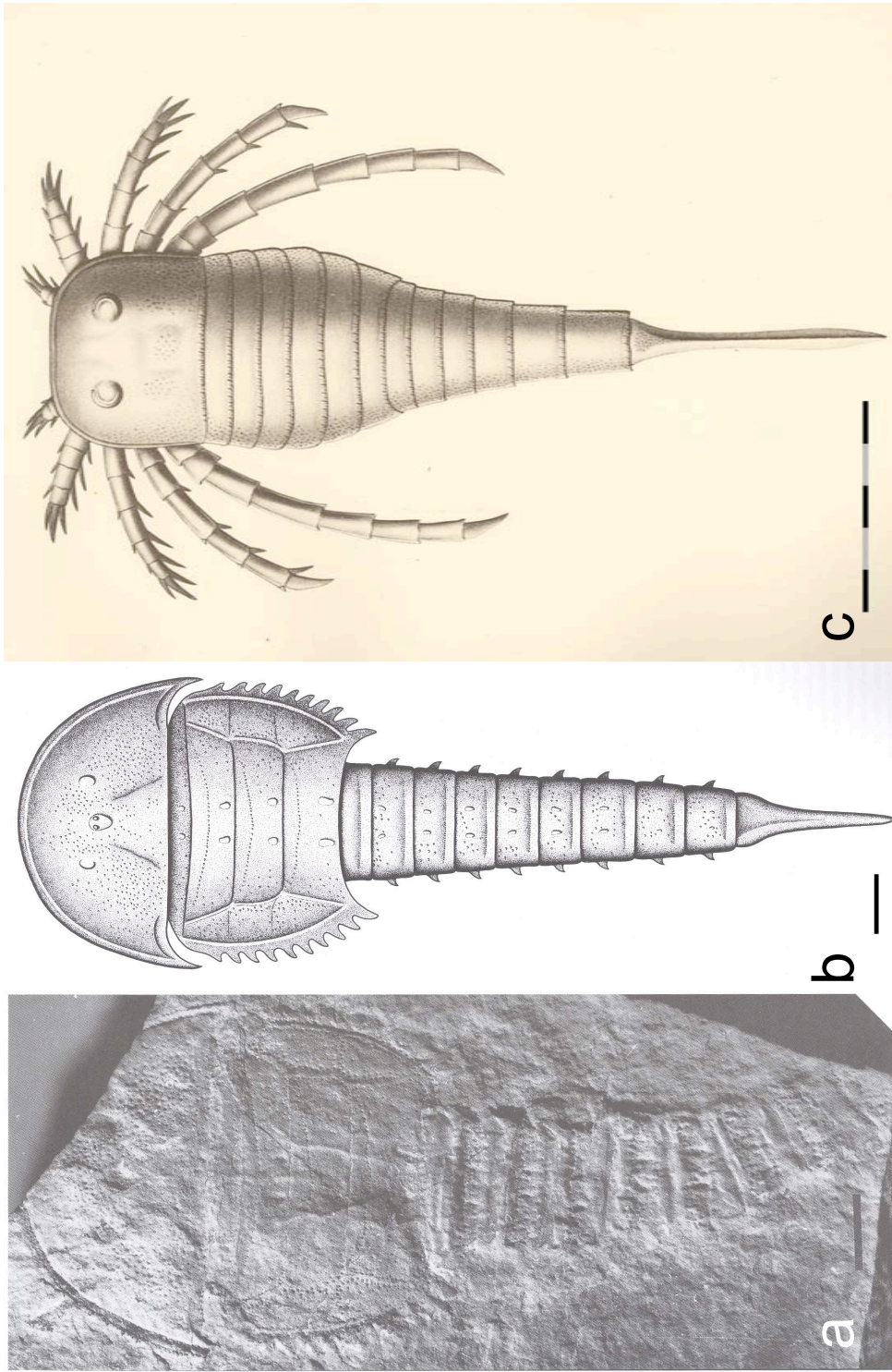
Figure 15. Later forms possessing morphologies that are probably similar to the trackway-producing organisms. a) Ordovician chelicerate *Chasmataspis laurencii* body fossil and b) dorsal-view reconstruction (from Dunlop *et al.*, 2004, p. p. 210, 218). Scale bars, 5 mm. c) Reconstruction of Silurian eurypterid *Stylonurus longicaudatus* expressing uni-, bi- and triramous limbs (from Clarke and Ruedemann, 1912, pl. 54). Scale bar, 5 cm.

suggest a population consisting of adults and juveniles of varying ages. 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).

Braddy discussed the probability of near-shore eurypterid assemblages being the result of a migration in order to increase chances of reproduction as well as of survival rates in juveniles. Living in the near-shore environment would have been advantageous for survival due to the lack of terrestrial predators and would have kept juveniles segregated from cannibalistic adults. It is because of the interaction seen between these trackways, as well as the fact that they were formed on a single bedding plane, that I add my support to Erickson (2004) in suggesting a sexual dimorphism (smaller males and large females, to draw from many modern analogues) rather than a residing juvenile population. Assuming Braddy's eurypterid mass-mate hypothesis, if the juveniles lived in this marginal environment to avoid adult predators, why are they present together as seen in this exposure? The trackways here may not be indicative of the average size difference, however. It is suspected that these trackways were produced in a more landward section (inundated only at spring tides) than Braddy's "marginal environment" juvenile eurypterid habitat extends. Assuming that a mass-mate strategy can be applied to these trackway-producing organisms, Braddy (2001, p. 126) suggested that "individuals who were not yet fully grown could attempt mating although the males, with their smaller size and less developed claspers, probably had less success". Applying a mass-mate reproductive strategy to this trackway assemblage has the potential to explain

Figure 16. Bedding plane surface including arthropod trackways. Black lines represent the presence of medial grooves associated with trackways; red lines show trend of ripple crests in the substrate, formed before the trackways. Ripple crests trend northest/ southwest; there is no recognizable trend among trackways.

some of the interactions going on, however proving this behavior becomes very difficult without a fully identified trackway producer. Absence of a juvenile population suggests that these organisms were not adapted to survive for long periods of time in a terrestrial environment. Braddy (2001, p. 124) reported that, "these migrations were undertaken by entire populations of eurypterids".

The interaction noted between trackways 1 and 2 has been interpreted as evidence of mating behavior similar to that of the modern horseshoe crab, *Limulus polyphemus* (Figure 17) by Erickson (2004). A variety of observations support this hypothesis, the first being the direction of travel as indicated above. If the organism that produced the smaller trackway 2 was male, the interaction may have played out thus (Erickson, pers. comm.): At the point where trackway 2 becomes visible in Figure 2, traveling from the upper right to lower left, the organism was oriented toward the bottom of the photograph. Some stimuli (probably visual) alerted the organism to the presence of the larger female producing trackway 1, at that point to the middle left edge of the photograph. The change in direction of the male was abrupt and marked by the sharp change in direction of the medial drag. Both organisms continued their trajectories, until the male was near enough to "charge" the female, evidenced by the erratic s-curves in the telson mark near the left end of trackway 2. The male proceeded to mount the female, in a manner similar to that of modern *Limulus*, leaving a sharp "hook" in the medial groove caused by his 180º turn, while she continued at the same pace as before. The mounting procedure may have been imperfect, as one-half of a trackway similar to trackway 2 is preserved next to and overlying the right (bottommost) side of trackway 1. If the male organism was hanging

off the side of the female, a trackway such as this would be produced. Unfortunately, evidence of any further interaction was not preserved, nor was a dismount. In any case, trackway 2, produced by the male, does not continue past its intersection with trackway 1.

The presence of a single row of tracks (similar to trackway 2) associated with trackway 1 after the disappearance of trackway 2 is very suggestive of this hypothesis. Alternatively, the organism that produced trackway 1 could have eaten and eliminated the originator of trackway 2. This is unlikely because the interpreted direction of movement shows the narrower trackway moving toward the larger rather than away, as would be expected if the larger was a potential predator. Most notable, however, is the fact that the producer of trackway 1 has a consistent stride throughout the exposed surface, and this would not be the case had it stopped to prey upon the producer of trackway 2.

Preservation

This surface exhibits textures such as "elephant skin" (Gerdes *et al.*, 2000) (Figure 18*a,d*) and erosional pockets characteristic of microbial mats (Noffke, 1998; Gerdes *et al.*, 2000). Ripple marks (Figure 18*b,c*) have been cut through by tracks and associated imprints, and apparently underlay and therefore were generated prior to, the microbial mat surface. 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. Tidal evidence in the Potsdam in association with arthropod trackways was first noted by Logan (1860, p. 280):

The surface on which the tracks are impressed and the one immediately beneath, shew ripple-mark; the next in succession which is about an eighth of an inch be low, shews wind-mark, in a number of sharp and straight parallel ridges from two to four inches long and an eight or a quarter of an inch wide. These characterize a considerable surface, and are precisely similar to the marks so familiar to every person who has examined blown sand. The surface must thus have been alternately wet and dry, and the organic remains of the formation being marine, we have thus a pretty clear evidence of a tide.

The organisms were present at the same, or very nearly the same, time. Ripple marks were produced by wind that created small waves in a tidal pool. The track producers were probably only partially supported by water, as postulated by Sharpe (1932, pp. 360 -361):

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.

The presence of the microbial mat texture suggests that these impressions are not undertracks (produced in layers of sediment below the exposed surface upon which the organism was actually walking). Although the mat may have formed and then have been subsequently inundated and buried, the presence and depth of a large number of impressions and the medial groove show that any sediment overlaying the now-exposed bedding plane could not have been very thick. Eventual covering of the bedding plane may have been accomplished by eolian processes, which has been suggested by Taljaard (1962), who also tested the preservation potential of arthropod trackways under wind-

Figure 17. *Limulus polyphemus* male mounting a female in an intertidal zone, eastern North America. This represents the closest modern analogue to the mating behavior hypothesized by Erickson (2004) to explain the interaction seen between trackways 1 and 2, although the organisms involved were structurally different. (photograph from Lohmann and Lohmann, 2001)

rippled water and found it insufficient for most trackways to be preserved. However, the

presence at this site of trackways associated with microbial mats suggests that the

preservation potential was increased a great deal by this association.
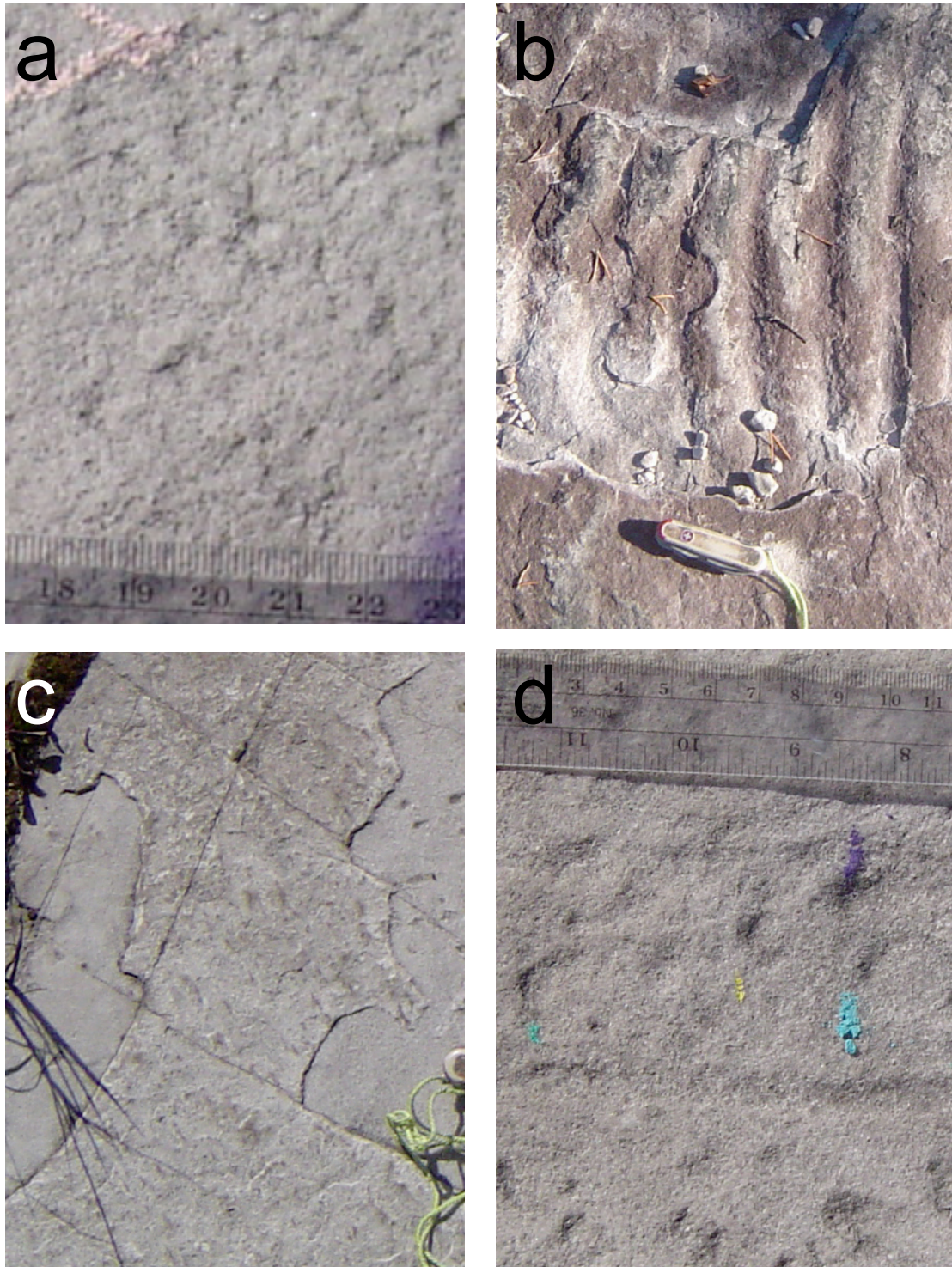
Figure 18. Exposed bedding-plane surfaces at trackway locality: a) microbial mat "elephant skin" texture adjacent to trackway 1, b) nearby preserved ripple marks, c) laminar bedding at a nearby trackway site showing microbial mat texture, d) a portion of trackway 1 showing preservation of tracks. Colored chalk was used to analyze trackways while on the outcrop.

CONCLUSIONS

Following the methods outlined above in reference to the trackways described, the following conclusions were reached concerning these specific trackways and the ichnogenus *Protichnites*:

1. The ichnogenus *Protichnites* Owen, 1852 has been historically problematic for trackway workers. It serves little purpose to represent all trackways with medial tail drags as belonging to the same ichnogenus because there are a number of other criteria that can be used to distinguish trackways.

2. The ichnogenus *Protichnites* Owen, 1852 is here redefined (see Systematic Paleontology) in order to make identification easier and to remove confusion: "Opposite, symmetric trackway consisting of two rows of tracks in chevron formation with a single narrow medial discontinuous or continuous incised impression parallel to the general trend of the trackway. Individual tracks vary in distance from the midline and in morphology, including but not limited to unifid, bifid, and trifid imprints. Most complete compliments of tracks consisting of seven or eight tracks arranged at low angle to the midline. Trackset overlap along trackway is variable, meaning that comparative unit distances over the course of the trackway may include more or fewer tracksets. Medial impression typically equal distance from opposite tracks and, if discontinuous, remains linear rather than becoming steeply angled to the trend of the trackway."

3. All trackways described here are examples of the same ichnogenus *Protichnites* Owen, 1852, according to the above emended diagnosis. It is likely that they were all

produced by organisms of belonging to the same species due to the similarity between trackways and the interaction noted above (see Discussion).

4. The trackways represent examples of the ichnospecies *Protichnites septemnotatus* Owen, 1852 because they possess repeated tracksets of seven tracks per set and agree with the emended diagnosis given above for the ichnogenus *Protichnites*.

5. The presence of oscillation rippled sand and microbial mat surface shows that these trackways were most likely produced in a shallow-water (~3 to 7 cm) tidal pool in the high-intertidal or low-supratidal zone of the beachfront.

6. Bimodality of width among trackway producers suggests organisms were sexually dimorphic and were present in an intertidal   environment for short periods of time (e.g., for breeding purposes) rather than having been adapted for terrestrial life. No confirmed fully-terrestrial arthropods of the type that produced these tracks have been found in sediments of a similar age.

7. The interaction between trackways 1 and 2 seems more likely to have been an example of mating behavior than of predation. The direction of travel and the bimodal distribution of the trackway-producing organisms supports Erickson's (2004) hypothesis concerning mating behavior.

Although three trackways have been described here already, this research is ongoing. In the interest of future researchers, more descriptive work of individual trackways beyond identification needs to be done. This project could obviously have been more quantitative, and ideas and suggestions for methods of quantification that can be applied across a wide variety of trackways are welcome.

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