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PROTICHNITES EREMITA UNSHELLED? EXPERIMENTAL MODEL-BASED NEOICHNOLOGY AND NEW EVIDENCE FOR A EUTHYCARCINOID AFFINITY FOR THIS ICHNOSPECIES

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ABSTRACT—*Protichnites eremita* from the Cambrian Elk Mound Group of Wisconsin is reinterpreted based on new material and trackway experiments. Two new forms of *P. eremita* suggest that the discrete medial imprints of these traces could be produced by the segmented postabdomen of euthycarcinoids from the same deposit. Form 1 could have been produced by a pair of euthycarcinoids traveling together, like in limulid amplexus, where both individuals made imprints with their postabdomens. In this scenario, if one individual held its postabdomen to the left side, it is possible to produce left-handed shingling in trackways and angled segmentation of each medial imprint. Form 2 could have been produced by a single animal traveling in arcing or tightly looping paths. Experimentally-produced medial imprints yield morphologies that are consistent with both trackway forms. Thus, it seems more likely that *P. eremita* was produced directly by the animal's body (alone or paired) rather than by employing hermit-like behavior.

INTRODUCTION

PROTICHNITES TRACKWAYS are a ubiquitous component of many sandy coastal lithofacies in middle and late Cambrian epicratonic strata of North America. Although the identity(ies) of their producers remain enigmatic, morphological details from Cambrian and younger specimens indicate a possible euthycarcinoid tracemaker (Trewin and McNamara, 1995; MacNaughton et al., 2002; Morissey and Braddy, 2004; Collette et al., 2010). The Cambrian Elk Mound and Potsdam Groups of Wisconsin, New York, Ontario and Quebec contain spectacularly well-preserved examples of these trace fossils (Logan, 1851; Owen, 1852; MacNaughton and Hagadorn, 2007; Hagadorn and Seilacher, 2009; Hagadorn et al., 2011). Co-occurring in these strata are the euthycarcinoid arthropods *Mosineia macnaughtoni* and *Mictomerus melochevillensis*, each of which have body sizes, appendage sizes, and postabdominal widths which plausibly could have produced many of the *Protichnites* in these deposits (Collette et al., 2010).

This study focuses on *Protichnites eremita*, which has been hypothesized to reflect the hermit-like behavior of an unknown eurypterid-like stem arthropod (Seilacher, 2007; Hagadorn and Seilacher, 2009). The hermit interpretation was based on looping *Protichnites* in which segmented, regularly-spaced and consistently left-offset impressions occur between two lateral track rows. It was hypothesized that these consistently offset impressions were produced by the ambulation of an arthropod that was utilizing a dextrally coiled (right-coiled) shell held with a dorsally-curled abdomen to cover its caudal region (Hagadorn and Seilacher, 2009). Based on new material and experimental work utilizing a model of a co-occurring euthycarcinoid arthropod, we hypothesize that *Protichnites eremita* were produced by euthycarcinoids that 1) traveled in pairs, and whose forward movements produced shingled, composite imprints; and/or 2) produced deep, sweeping medial imprints with their postabdomens while making tight turns.

PRESERVATION AND ENVIRONMENTAL CONTEXT

Studied *P. eremita* traces occur only in strata deposited in intertidal to supratidal facies of the Elk Mound Group (PRI Station 3421; Hagadorn et al., 2002b; Hagadorn and Seilacher, 2009). Bedding planes from these facies contain a variety of microbial sedimentary structures (Bottjer and Hagadorn, 2007; Dornbos et al., 2007; Hagadorn and McDowell, in press), indicating that a wide spectrum of siliciclastic microbial fabrics was present (Seilacher and Pflüger, 1994; Seilacher, 2008), ranging from unbound sand to cohesive, well-developed biomats. Similarly, primary sedimentary structures and bedforms indicate that grains on bed surfaces in these settings had a variety of moisture contents, from completely dry to moist to completely saturated due to submergence (Hagadorn et al., 2002a, 2002b; Hagadorn and McDowell, in press).

Given this context, trackways preserved in this deposit were produced on bed surfaces that were completely dry, completely wet, or damp. Similarly, trackways could have been produced on bed surfaces that had labile grains, on surfaces where grains were held together by weak interstitial extracellular polysaccharide substances (EPS or ''bioglue'' of Seilacher, 2008), on surfaces held together by thin biofilms, or on surfaces that had thicker microbial mats (Hagadorn and McDowell, in press). For example, one of the slabs described below (PRI 10143) contains unbioturbated patches of microbially mediated wrinkle texture. Considered together with the abundant clustered sand stromatolites found on other *P. eremita* surfaces (e.g., figs 1, DR2 of Hagadorn and Seilacher, 2009), these features suggest that the bed surface was bound by a biofilm before arthropods moved over it, and that mobile but pliable sand clasts may have existed in the environment inhabited by the trace-makers. Other *P. eremita*-bearing surfaces (e.g., figs. 2, DR4, Hagadorn and Seilacher, 2009) indicate that mats existed on bed surfaces prior to bioturbation, these surfaces were intermittently subaerially exposed, and that microbial growth continued after tracemaking occurred. Such microbial binding can facilitate preservation of bioturbated bed surfaces, because it reduces or inhibits the erosion potential of medium-grained bed surfaces by at least 50 percent (Hagadorn and McDowell, in press).

It is possible that the adhesive properties of EPS and interstitial pore water may also affect the sharpness or blurring of limb and abdomen imprints. Circumstantial evidence to suggest this comes from the size-independent differences in depth and sharpness of medial imprints and lateral impressions at this site. For example, trackways on the slabs described below tend to be very deep (1.2 to 4.3 mm) and rather sharp (Fig. 1.1, 1.3) relative to other *Protichnites eremita* documented from this site (Hagadorn and Seilacher, 2009).

Form 2 material described herein was collected as quarried float blocks from PRI Station 3421. New trackways (except for the Form 1 specimen, PRI 8466) are preserved in concave epirelief on bed tops in tan to orange, cross-bedded to planar laminated quartz arenites. Sandstone beds are planar laminated for approximately the upper half of their 8–10 cm thickness. Planar laminae and stratification range from 3 mm to approximately 2 cm in thickness; individual laminae vary from very fine- to medium-grained, well-rounded to subangular sand. Lower cross-beds are inclined approximately 19° from the upper laminated bed, and are truncated by a horizontal bed at their base. Individual lee surfaces are straight, with no curvature at their lower truncation, and a possible slight curvature at their upper truncation; individual cross-beds are up to 5.3 cm thick, and are >24 cm long. Adjacent cross-beds vary substantially in grain size, but grain size within each cross-bed is fairly uniform; grain size ranges from coarse to fine sand within beds; occasionally, coarser-grained lags are evident at the bottom of individual cross beds.

Material described herein is reposited as PRI 10143, 11040 and 11041 in the collections of the Paleontological Research Institution (PRI), Ithaca, New York. Other examined materials are at Yale Peabody Museum (YPM) and PRI.

SYSTEMATIC PALEONTOLOGY

Ichnogenus PROTICHNITES Owen, 1852

Ichnospecies PROTICHNITES EREMITA Hagadorn and Seilacher, 2009

Figures 1–2.1, 2.4–2.6

Diagnosis.—*Protichnites* with distinct or indistinct, broad, subcircular to ovate tracks, and segmented medial imprints. Tracks may or may not be arranged in broad, shallow, trough-like lateral channels. Segmented medial imprints may be present or absent from straight or gently curving trackways but are expressed in the vicinity of sharp turns; where present in straight or curving trackways, segmented medial imprints may consistently offset to one side. A second set of smaller, discrete medial imprints (="groove" or "notch" of Hagadorn and Seilacher, 2009) may be present. Emended after Hagadorn and Seilacher, 2009.

PROTICHNITES EREMITA Form 1

Figure 2.4–2.6

Protichnites sp., HOXIE, 2005, figs. 6B, 22A–D.

Hermit *Protichnites*, SEILACHER, 2007, p. 24, 28, pl. 10, fig. E.

Protichnites, SEILACHER, 2008, fig. 6B.

Protichnites eremita HAGADORN AND SEILACHER, 2009, p. 295, fig. 1, 2A–2C.

Description.—Medial imprints consistently shingled to the left regardless of trackway looping direction. Each medial imprint segment is tilted to the right. A second, smaller, set of medial imprints (c.f., the "grooves" or "notches" of those authors) is usually present. Its tracks are variously distinct and arranged in trough-like lateral channels. Abridged from Hagadorn and Seilacher, 2009.

PROTICHNITES EREMITA Form 2

Figures 1–2.1

Description.—Known specimens of Form 2 (Figs. 1, 2.1) preserved as straight to sharply curved trackways on bed surfaces of three slabs. Medial furrow of all but one trackway (Trackway A, Fig. 1.1, 1.2, PRI-10143) divided into discrete, elongate-ovoidal sections (i.e., medial imprints), each showing some degree of segmentation. Each trackway bears distinct, discrete, ovate to subcircular tracks. No discernible track sets are present. Trackway length up to 58.4 cm; width 6.8 to 7.5 cm. Medial imprint length 3.2 to 6.9 cm; width 9.9 to 19.8 mm; depth 1.2 to 4.3 mm at straight regions, up to 4.9 mm at sharp turns. Shingling of medial imprints present only in vicinity of sharp turns (Trackway B, Fig. 1.1, 1.2, PRI-10143). Trackway A consists of a C-shaped *Protichnites* with a deep (up to 4.3 mm), continuous medial furrow (12.8 to 17.3 mm wide) bearing occasional segmentation perpendicular to its axis (s in Fig. 1.2). Individual tracks ovate, track long axes oriented approximately 120° and 210° relative to trackway axis; arranged in distinct, lateral track rows. Trackway B (Fig. 1.1, 1.2, PRI-10143) partially encircled by Trackway A; consists of a tightly curved *P. eremita* with six elongate medial imprints located axially or at an angle with axial portion of trackway (pB in Fig. 1.2). Each medial imprint divided into 3 to 5 distinct segments. Trackway external width unknown; exposed length approximately 29.5 cm. Medial imprints approximately equal in width to medial furrow of Trackway A (9.9 to 19.8 mm wide, 2.2 to 4.3 mm deep) except those at turn apex of Trackway B, where they are wider (up to 23.2 mm wide) and 4.9 mm deep from lowest point of imprint to highest point of pushback hill. Medial imprints become increasingly offset from trackway axis near turn apex. Segmentation in two medial imprints prior to turn apex, and one imprint at turn apex (Trackway B) not perpendicular to axes of respective medial imprints; segment impressions in this area of trackway diagonally elongated (NW:SE) relative to the axis of medial imprint in which they occur. Tracks ovate; long axes forming a similar angle to those in Trackway A. Spacing between discrete tracks slightly more irregular than in Trackway A. Tracks not arranged in rows, except in relatively straight portions of trackway; no discernible sets present. Trackways C (Fig. 1.3, PRI-11040), D (Fig. 1.3, PRI-11040), and E (Fig. 2.1, PRI-11041) are straighter and less deep than Trackways A and B, but include 3 to 5 (possibly 6 in Trackway C) forwardly-arched segments in their medial imprints. At least four other trackways with individual tracks similar to those of Trackways C and D are present on the surface of PRI-11040. Medial imprints are only occasionally discernible in these trackways. Length:width ratios of medial imprints 3:1 to 4:1 for Trackways C, D and E; 2:1 for Trackway B.

Discussion.—The discrete medial imprints of Trackways B–E were probably produced by a segmented apodous arthropod abdomen or postabdomen, as suggested by their relatively uniform shape (elongate-ovoidal), presence of up to five (possibly six) segments, and their medial position between rows of tracks. The association of Trackways A and B on the same slab, their orientation relative to each other, and the similarities noted above suggest they could have been produced by the same individual as it executed an ever-smaller loop that eventually crossed itself (Fig. 1.2). The offset placement of the medial imprints in the vicinity of the sharp turn suggests that the animal did not appreciably flex its postabdomen laterally (Figs. 1.1, 1.2, 3), instead keeping it in

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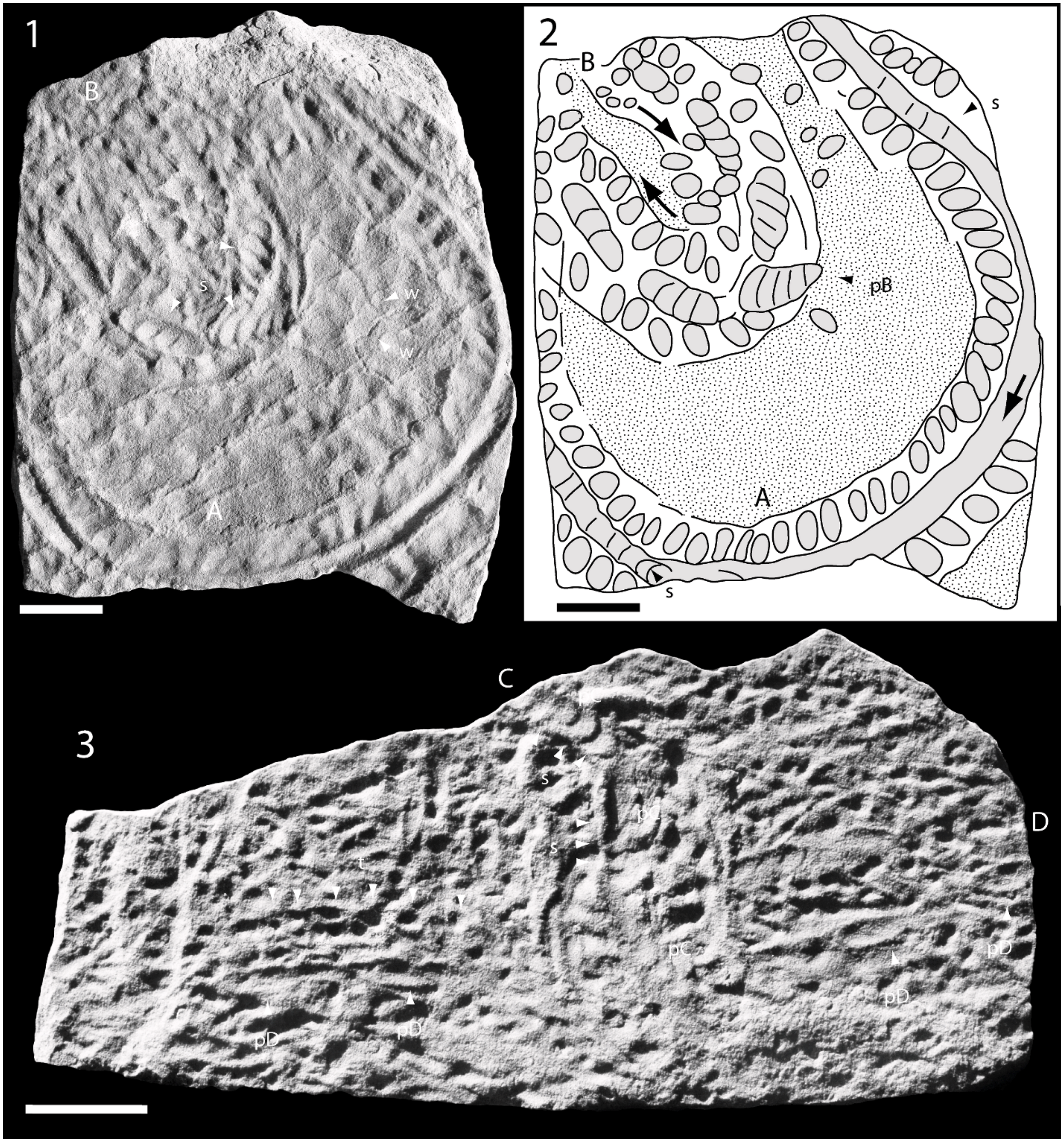


FIGURE *1*—*Protichnites eremita* Form 2, Trackways A and B, Elk Mound Group, Blackberry Hill, Wisconsin, PRI Station 3421. *1*, PRI 10143, both trackways shown, Trackway B exhibits a sharp right turn whereas Trackway A exhibits a gentle turn; segmentation present in the intermittent medial impressions (*Fig. 1.1*, arrowed s; *Fig. 1.2*) is well-defined, as is the microbially mediated wrinkle texture (arrowed w); *2*, line drawing of PRI 10143 showing morphology of trackways A and B in *Figure 1.1*; segmented intermittent medial impressions (arrowed p), interpreted as representing impressions of an apodous postabdomen of at least five somites; arrows point in the direction of travel; tracks and imprints of Trackways A and B are shaded gray for clarity; *3*, PRI 11040, *Protichnites eremita* Form 2, Trackways C and D. Abbreviations: p=postabdominal imprint, s=segment, t=track. Photos lit from top-left. Scale bars=4 cm.

line with its body while turning. However, the consistent left-offset medial impressions in *P. eremita* Form 1 that do not turn demonstrate the tracemaker's ability to flex its postabdomen laterally as a unit, indicating lateral flexibility at the junction between its walking and apodous tagmata.

Trackway A, with its continuous, weakly segmented medial furrow, was likely produced as the arthropod intermittently stopped as it dragged its postabdomen on the substrate. Similar segmented medial drag marks are produced by limulids ambulating across moist, subaerial sand (Fig. 4.1).

However, limulid medial drag marks are produced by the interaction of the relatively wide telson head and the sediment surface as the animal moves forward utilizing a pulse-like style of ambulation.

Euthycarcinoid Resting Trace

Figure 2.4, 2.5

Description.—Horseshoe- to ovate-shaped impression on one slab of *P. eremita* Form 1 (Fig. 2.4, 2.5). Impression centered between two lateral margins of a *P. eremita*, approximately equal in width to the external trackway width. Impression slightly more negative in relief than surrounding trackway; a slightly raised sediment ridge is positioned along anterior margin of impression. A left-offset medial impression occurs at the posterior margin of the main impression.

Discussion.—This impression is interpreted to represent a resting trace of the arthropod responsible for making *P. eremita* (Fig. 2.5). The sediment ridge along the anterior part of the impression indicates that the arthropod lowered itself onto the sediment surface as it moved forward; in this respect, this horseshoe-shaped resting trace is similar to those made by modern limulids while moving across the beach (Fig. 4.2). Although imbricated lateral features (which would represent impressions of the dorsal tergites) are not apparent along the lateral margins of the body impression, the overall gross morphology is similar to Cambrian euthycarcinoid body fossils from both Wisconsin and Quebec. Given these similarities, this impression is interpreted as a euthycarcinoid resting trace.

EXPERIMENTAL MODEL-BASED NEOICHNOLOGY

Based on the trackways, behaviors and body fossils described above, it seems plausible to link *P. eremita* to a euthycarcinoid tracemaker. Trackway experiments can further constrain the range of conditions under which a euthycarcinoid might produce *Protichnites*, and can determine if/how these conditions and resulting traces match the fossil record.

Methods.—A scale model of the postabdomen of the euthycarcinoid arthropod, *M. macnaughtoni* from the Elk Mound Group was constructed of Primo! Sculpey brand heat-hardening polymer modeling clay (Fig. 5.1). This fossil was chosen because it possesses a six-segmented postabdomen that matches the gross morphology of the imbricated, left-offset medial impressions of *P. eremita*. In order to facilitate manipulation of the model by hand, the model was constructed to approximately two times the dimensions of the best preserved specimen of *M. macnaughtoni* (holotype, PRI 10144, Collette and Hagadorn, 2010, fig. 7.1, 7.2). Each postabdominal 'segment' was modeled in polymer clay, placed in an oven and allowed to harden at 350°F for 30 minutes. Segments were shaped to mimic the shape and proportions of the holotype, but because the holotype is somewhat flattened, the dorsal-ventral segment thickness was inflated to approximate the uncompacted height of the animal by scaling dimensions to that of a similar unflattened euthycarcinoid, *Mictomerus melochevillensis*. Segments were then assembled into a rigid postabdominal model by adhering them together with Loctite gel superglue (thickened cyanoacrylate). A rigid model was the logical choice because both body and trace fossil evidence indicates limited lateral flexibility of the postabdomen except at its junction with the thorax/preabdomen.

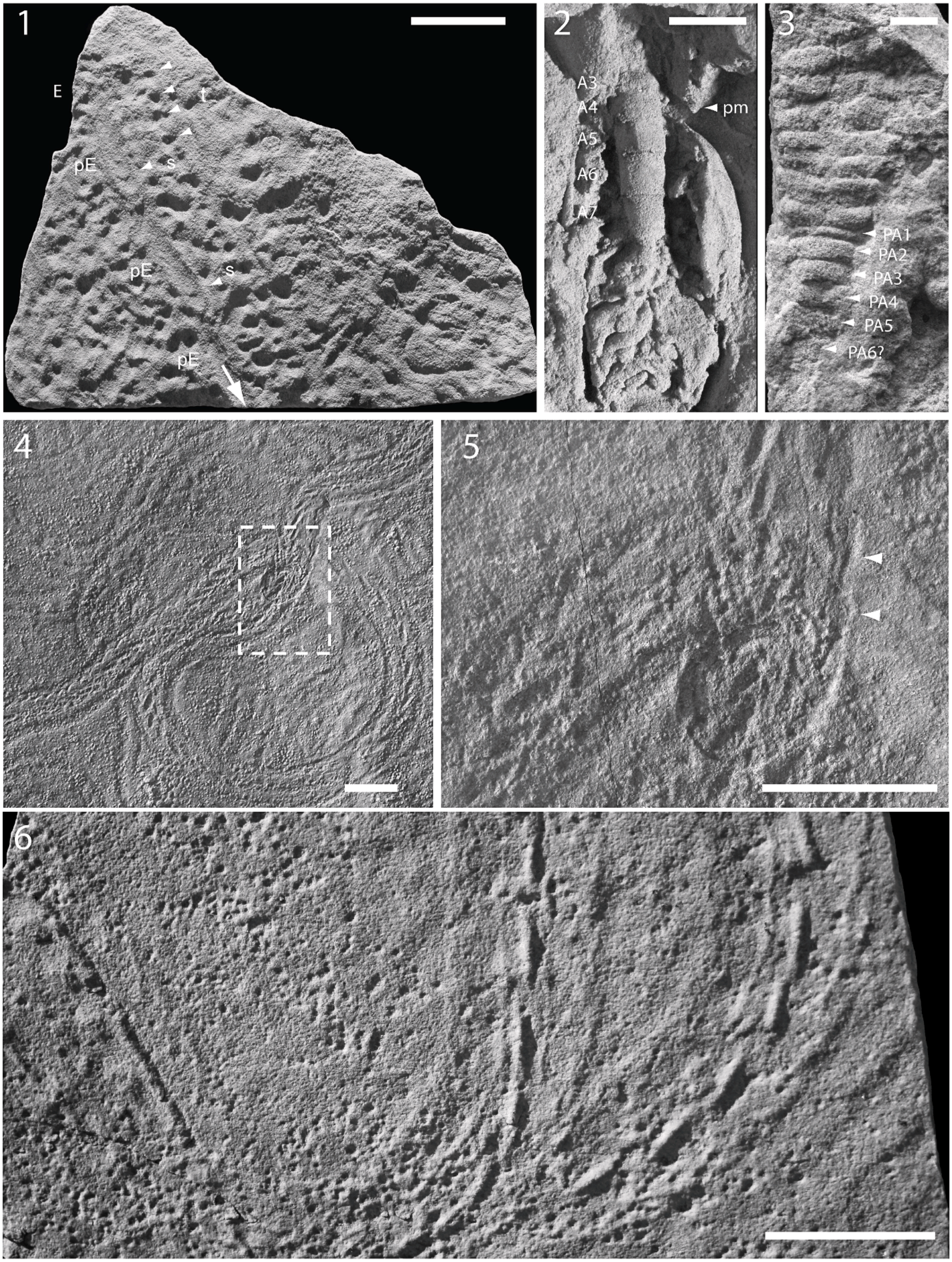
Carmeuse Industrial Sand (Orange County Silica Sand) was used for 'ichnological' experiments; two different grain sizes were used, '20 grit', and '30 grit'. The finer grained 30 grit sand was fine- to medium-grained, well-sorted, subangular to subrounded quartz sand with <10 percent angular quartz grains and <1 percent opaque grains. The coarser 20 grit material was coarse-grained with minor (<5 percent) fine grains, well-sorted, subangular to subrounded quartz sand.

A 6-cm thick bed of each size class of sand was poured into a separate 58.5 × 39.0 × 15.6 cm high clear plastic storage container. Each experiment consisted of a single grain size sand, and was divided into three trials: dry, damp, and water-saturated sand. Sand was smoothed between individual trials by using the straight edge of an acrylic drafting triangle. For each dry trial, sand was poured directly out of the bags of sand and experiments were undertaken with no additional preparation other than initial leveling of the surface. For each damp trial, sand was misted with approximately 2.5 to 3.0 ounces of water from a spray bottle. The mist penetrated approximately 1 to 2 cm into the sediment as viewed through the clear sides of the plastic storage container. For the saturated trials, enough water was slowly added to each plastic storage container so that the 'water table' was just below or nearly at the surface of the sand. A photograph of each trial in each of the six experiments was taken for later comparative analysis.

In each of the three trials, thirteen individual 'trackways' were produced (Fig. 5.2–5.14 for diagrammatic representations of each experimental trackway). The dry trial was done first, followed by the damp trial, and finally the saturated trial. The same procedure was then followed for the other grain size sand. Each neoichnology experiment consisted of attempting to approximate the method of locomotion required by an arthropod to produce medial impressions seen in looping fossil examples of *P. eremita*. In an attempt to replicate different distinct morphological variants of *P. eremita*, thirteen different trackways were produced under three substrate moisture regimes (sand completely dry, moist, and completely saturated) for each grain size. These thirteen experimental trackways included simulations of a: 1) resting trace, 2) continuous linear trace, 3) intermittent linear trace, 4) continuous arcuate trace, 5) intermittent arcuate trace, 6) continuous U-shaped trace, 7) intermittent U-shaped trace, 8) continuous left-offset linear trace, 9) intermittent left-offset linear trace, 10) continuous left-offset arcuate trace, 11) intermittent left-offset arcuate trace, 12) continuous left-offset U-shaped trace, and 13) intermittent left-offset U-shaped trace.

Discussion.—These experiments are valuable because they demonstrate that the key features of the medial imprints of *Protichnites eremita* Form 1 and 2 can be replicated under conditions known to exist at the time of Elk Mound deposition, by an object approximating the postabdominal morphology of the euthycarcinoid *Mosineia macnaughtoni*. The experimental trackway(s) that replicate each form and morphological variant and the key features which they replicate are indicated in Table 1. Nearly all morphological variants of the medial impressions of *P. eremita* Forms 1 and 2 were replicated by using the postabdominal model of *Mosineia macnaughtoni*.

Whereas sand particle size did not cause great variations in the results, water content did. Experimental trackways that most closely matched the fossil medial imprints were those that utilized dry sand (compare Fig. 6 [dry] with Fig. 7 [damp, saturated]). The damp and wet sand trials produced imprints that were appreciably shallower than those in dry sand and those observed in the fossil imprints (Fig. 7). The rigidity of the damp sand limited imprint depth, resulting in very shallow trackways lacking significant detail (Fig. 7.1, 7.2). Trackways produced in saturated sand tended to slump, leveling trackway



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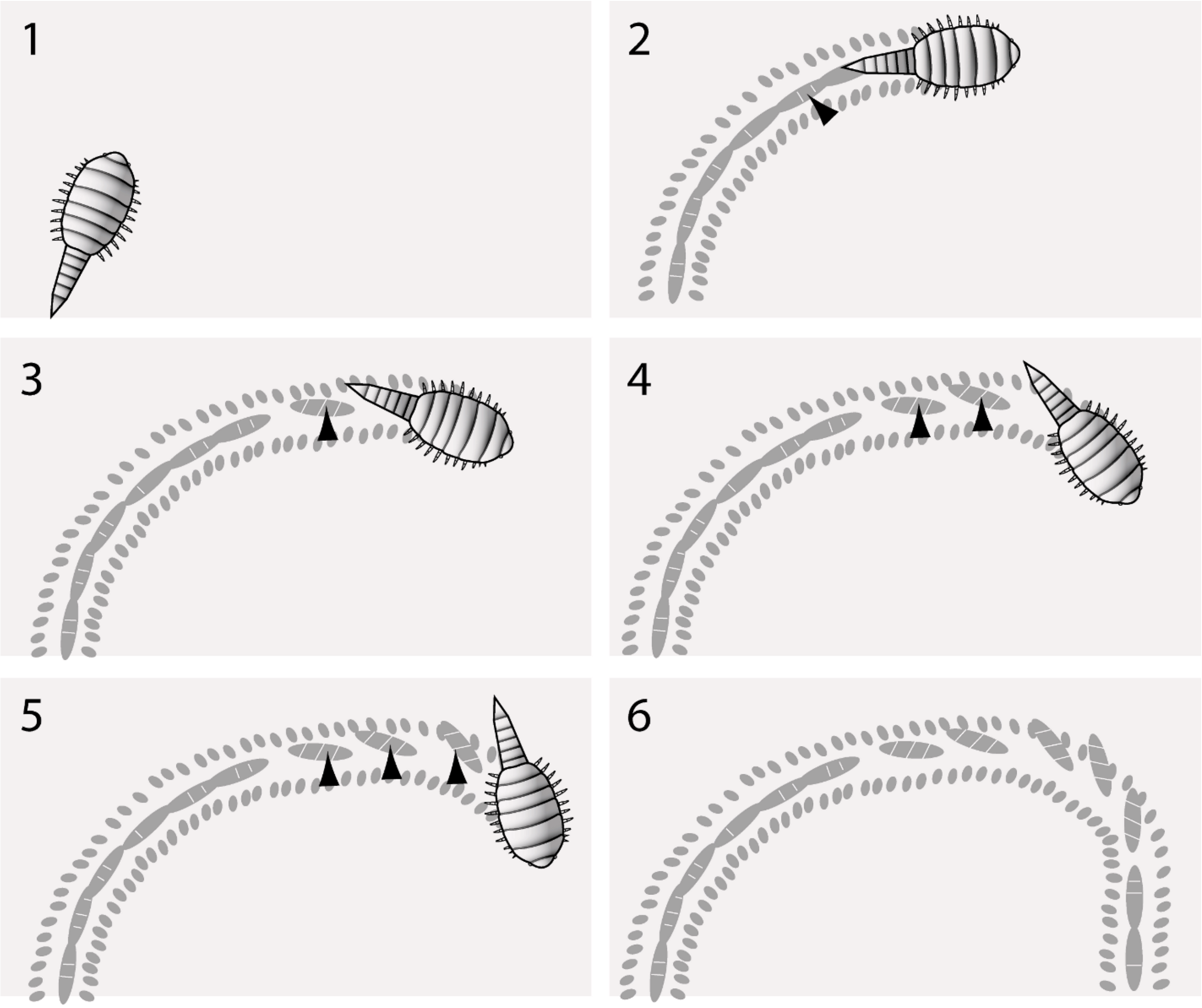

FIGURE *3*—Hypothetical model of *Protichnites eremita* Form 2 production by the euthycarcinoid arthropod *Mosineia macnaughtoni*. *1*, euthycarcinoid travelling in an arcuate pathway; *2*, continuing on arcuate path, impressions produced by the animal's postabdomen are confined to the medial portion of the trackway (arrowhead); *3–5*, continued forward motion, combined with an increasing turn radius, pulse-like locomotion, and little to no lateral flexibility in the postabdomen of the producer begin to produce outward-swinging postabdominal imprints (arrowed), such as those observed in Trackway B (*Fig. 1*); *6*, turn completed, the producer resumes a straight path.

features, and resulting in trackways with depth, but little detail (Fig. 7.3, 7.4). Obtaining more depth in the damp sand required a degree of downward force unlikely to be within the capacity of the animal and bulldozed the sand in ways not observed in the fossils (Fig. 7.1, 7.2). Because it is unlikely that biomats and biofilms on *P. eremita*-bearing surfaces existed on dry sand, it is likely that factors other than water content, probably the biomats and biofilms themselves, contributed to the sharpness of the fossil traces.

Distinct angling of the medial impression segments, as seen in Trackway B of Form 2 and in Form 1, was replicated in experimental trackways 8–13 (Fig. 6.3–6.6). This tilt of the segment impressions to either side is a function of the tilt of the model axis relative to the direction of movement of the model, combined with the forward motion of the model. These experiments falsify the notion that transversely-segmented arthropods could not have produced angled impressions of their segments; carrying a coiled shell is not required.

←

FIGURE *2*—Elk Mound Group fossils, Blackberry Hill, Wisconsin, PRI Station 3421. *1*, PRI 11041, *Protichnites eremita* Form 2, Trackway E, (p=postabdominal imprint, s=segment, t=track); arrow indicates likely direction of travel; *2*, *Arenosicaris inflata* (phyllocarid crustacean), showing two partial arthropods, five abdominal somites are exposed in this specimen (seven total) but only four of these protrude past the posterior carapace margin (pm); *3*, *Mosineia macnaughtoni* (euthycarcinoid); in this incomplete example, at least five postabdominal somites are preserved, (A3–A7=abdominal somites three to seven, PA1–PA6?=postabdominal somites one to six?, pm=posterior carapace margin); *4*, *Protichnites eremita* Form 1, a resting trace (in box), holotype, YPM 204961; *5*, close-up of area in *Fig. 2.4*; *6*, PRI 8466, *Protichnites eremita* Form 1, convex hyporelief, showing multiple grooves in the medial imprint region on two of three trackway sections. Scale bars: 1=4 cm, 2, 3=1 cm, 4–6=10 cm.

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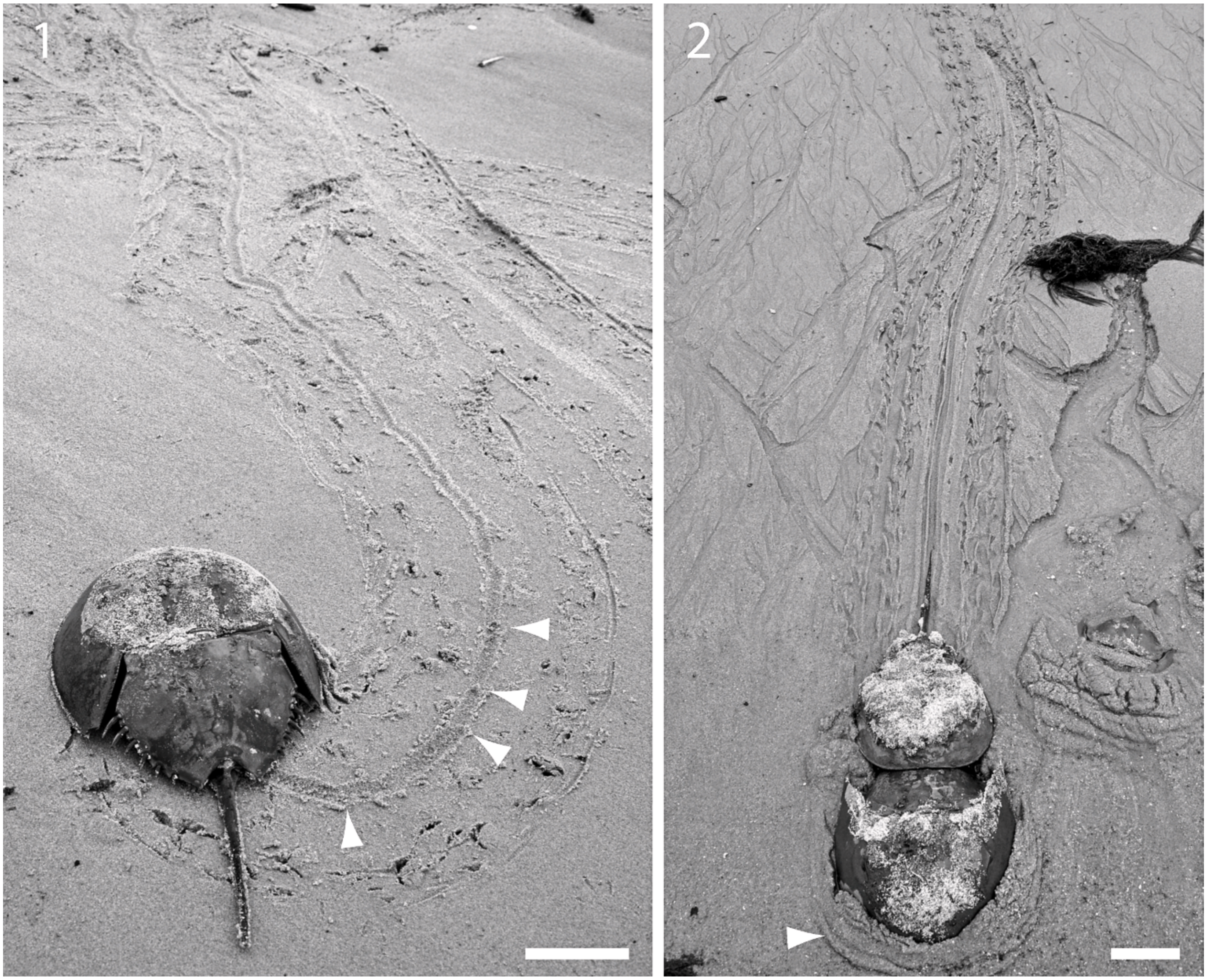

FIGURE 4—*Limulus polyphemus*. *1*, solitary animal and its trackway after making a sharp turn, the medial drag made by its telson exhibits weak segmentation (arrowheads); *2*, pair in amplexus showing a combined trackway, note sediment accumulation at the anterior of the female's carapace (arrowhead) that has been 'plowed' forward by the motion of the paired animals. Scale bar=10 cm. Images from G. Gauvry.

Medial impressions of Form 2 trackways are frequently composed of imbricated individual segment impressions that are often convex or U-shaped, with the cup- or U-shaped opening facing in the direction of travel (pC, top middle, Fig. 1.3). This feature was replicated in neoichnology experiments (Fig. 6.1) and indicates an intermittent, start-stop-start mode of locomotion in which the postabdomen moved both forward and upward concurrently. While at rest, the rearward-narrowing postabdomen may have rested on the substrate surface at the end of a locomotive 'push.' As the next locomotive pulse began, the postabdomen moved forward as it simultaneously moved upward off of the sediment surface. As the anterior shoulders of each postabdominal somite moved forward and upward, the width of their contact patch with the sediment gradually decreased, so that an ever-decreasing sliver of the ventral shoulder and anteroventral portion of the postabdominal somites made contact with the sediment. This forward and upward motion thus created a concave, U-shaped depression that swept some sediment forward with it, creating a raised, U-shape. Each somite that made contact with the sediment could create a similar concave, U-shaped structure, and because each sweeps a bit of sediment forward with it as it is made, the entire structure could have a topography that is ripple- or saw tooth-like. Similar U-shaped troughs can be created by pressing a coin into loose sand and carefully moving it forward and upward concurrently.

ADDITIONAL EVIDENCE FOR A EUTHYCARCINOID AFFINITY

Two macroscopic arthropods co-occur in the same outcrops as these trackways: the phyllocarid crustacean *Arenosicaris inflata* (Fig. 2.2), and the euthycarcinoid *Mosineia macnaughtoni* (Fig. 2.3) (Collette and Hagadorn, 2010). Whereas both of these arthropods possess an apodous abdomen or postabdomen respectively, a number of morphological details exclude phyllocarids as potential producers of the trackways described herein. For example, all known specimens of *A. inflata* are too small to have produced these trackways (widest, splayed open carapaces of *A. inflata* are only 3.6 cm wide); they possessed slender, gracile appendages; they had seven abdominal somites, of which only three or four protruded past the posterior carapace margin (A3 to A7 in Fig. 2.2); and they likely produced trackways of substantially different morphol-

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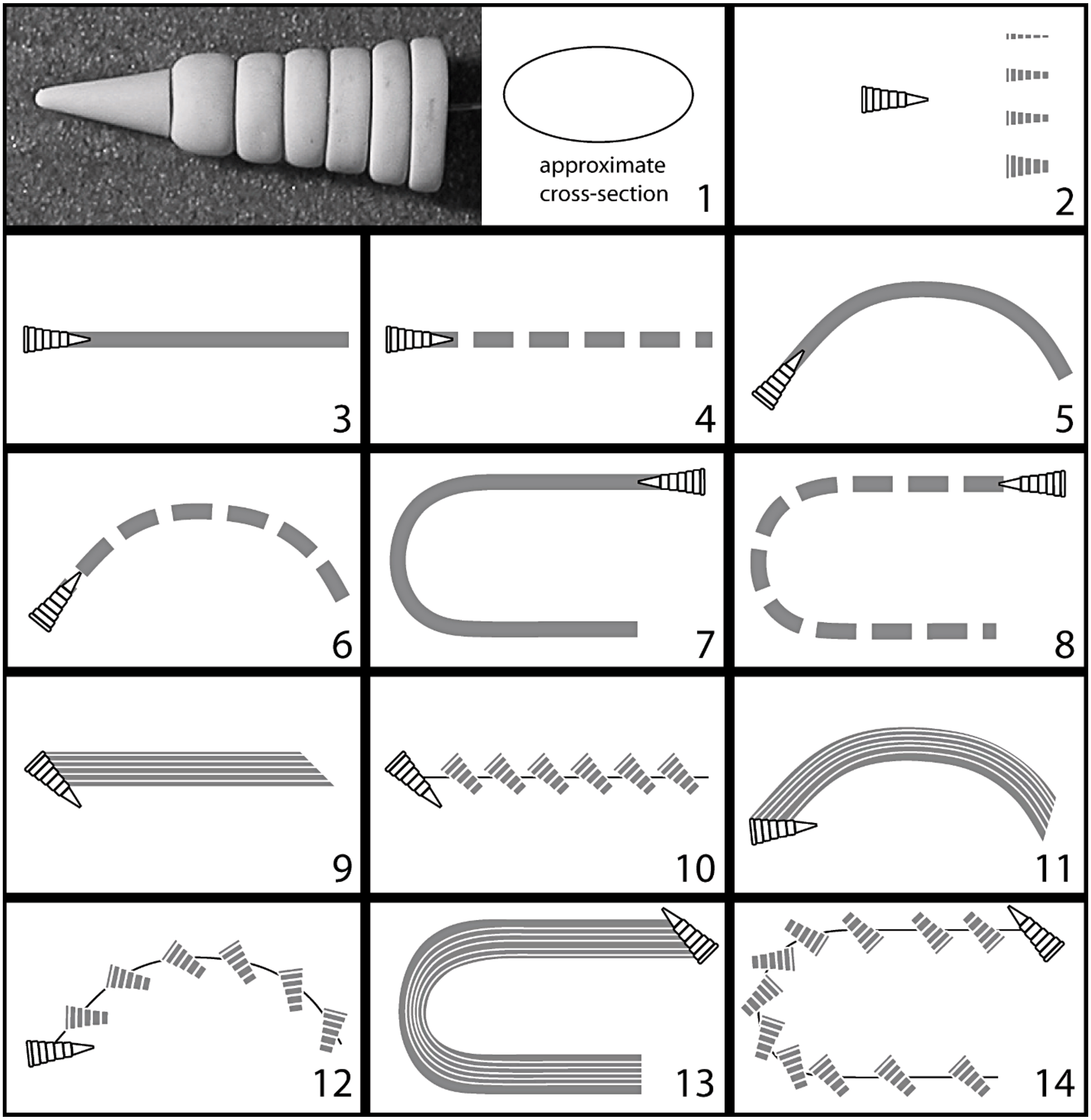

FIGURE 5—Euthycarcinoid abdomen model and pathways for trackway experiments. *1*, photograph of model and approximate cross section of model at anterior end; *2–14*, drawings of experimental trackways representing: *2*, resting traces (trackway 1 in text) made from gently placing the model on the sand (top drawing), dropping the model from 2 cm (second-from-top), 4 cm (third), and 8 cm (bottom drawing); *3*, continuous linear trace (trackway 2 in text); *4*, intermittent linear trace (trackway 3 in text); *5*, continuous arcuate trace (trackway 4 in text); *6*, intermittent arcuate trace (trackway 5 in text); *7*, continuous U-shaped trace (trackway 6 in text); *8*, intermittent U-shaped trace (trackway 7 in text); *9*, continuous left-offset linear trace (trackway 8 in text); *10*, intermittent left-offset linear trace (trackway 9 in text); *11*, continuous left-offset arcuate trace (trackway 10 in text); *12*, intermittent left-offset arcuate trace (trackway 11 in text); *13*, continuous left-offset U-shaped trace (trackway 12 in text); *14*, intermittent left-offset U-shaped trace (trackway 13 in text).

ogy (for comparison, probable phyllocarid-produced trackways from the Elk Mound Group are described in Collette et al., 2010). By contrast, *M. macnaughtoni* had more robust appendages and a postabdomen of six somites (five somites of quasi-equal length and a sixth, anteriorly located, somite of reduced length; PA1 to PA6? in Fig. 2.3). Additionally, specimens of *M. macnaughtoni* (maximum width = 5.1 to 6.7 cm) are nearly as wide as external trackway dimensions of *Protichnites eremita* Form 2 described here (6.8 to 7.5 cm). Postabdomens (minus telsons) of *M. macnaughtoni* specimens are 2.6 to 3.2 cm long; segmented medial imprints of *P. eremita* Form 2 are 4.0 to 5.1 cm long. Individual somites of

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TABLE 1—Experiment(s) and sediment conditions that produced morphological variants and key features of *P. eremita* Forms 1 and 2.

Form	Key features[1]	Morphological variant	Experiment(s) that replicate the key features	Sediment conditions	Figure
1	Trackway shape varied Medial imprint discrete Medial imprint always offset	All	9, 11, 13	Dry	6.4, 6.5, 6.6
2	Trackway shape arcuate Medial imprint continuous Medial imprint not offset Segmentation perpendicular to path, weak	Trackway A	Limited replication, 3	Dry	6.1
	Trackway U-shaped Medial imprint discrete Medial imprint offset only at turns Segmentation diagonal, strong	Trackway B	7	Dry	6.3
	Trackway shape straight to sinuous Medial imprint discrete Medial imprint not offset Segmentation perpendicular to path or diagonal	Trackways C, D, E	3, 5	Dry	6.1, 6.2

[1] Replicating tracks and a bifid medial imprint was not attempted.

M. macnaughtoni are 3.6 to 4.9 mm long; individual segments in medial imprints of *P. eremita* in Figures 1–5 are 6.9 to 13.7 mm long. The greater lengths of medial imprints of *Protichnites eremita* Form 2 relative to somites of *M. macnaughtoni* can be explained by the forward motion of the trace-maker exaggerating or smearing the imprints left by its postabdomen.

Trackway B was probably made by a euthycarcinoid arthropod making a sharp right turn, while alternately lifting and touching its postabdomen to the substrate (Figs. 2, 3). The laterally extended or 'smeared' appearance of the postabdominal imprints at and near the turn apex of Trackway B (Fig. 1.1), together with a prominent raised sediment ridge along the outside margin of the medial postabdominal imprints, suggest that the animal making this tight-radius turn did not significantly deflect its postabdomen laterally. The offset of the postabdominal imprints is analogous to the offset telson imprints made by limulids executing sharp turns (Boucot, 1990, fig. 255). In both cases, the end of the respective caudal appendage/postabdominal imprint extends beyond the paths made by the pairs of walking legs (Boucot, 1990).

The five segments in the postabdominal imprints of Trackway B are interpreted as imprints of five of the postabdominal somites of the trace-maker (Fig. 3). *Mosineia macnaughtoni* has a morphologically very similar postabdomen with five prominent postabdominal somites—a sixth, anteriorly situated somite, was much shorter in length and may not have often made contact with the substrate (PA1 in Fig. 2.3). The ovate shape of the tracks of Trackways A and B further constrain the morphology of the trace-maker. These elongate tracks could be produced by the rear appendages as the animal moved over unconsolidated sediment. In loose, unconsolidated sand, the oar-like motion of the appendages could create analogous trackway structures. In this scenario, each limb would initially point forward as it makes contact with the sediment, but as the animal moves forward, each appendage rotates as it is used during ambulation, and finally leaves the sediment in a rear-facing orientation. This is akin to the action of a swimmer using the butterfly stroke. In most euthycarcinoids there are eleven pairs of limbs (e.g., Gall and Grauvogel, 1964; Schram and Rolfe, 1982; Edgecombe and Morgan, 2001), but in dry, unconsolidated sand, each successive posterior limb pair might overprint and/or partially destroy tracks produced by the more anterior limb pairs. Such limb-produced disruption might not destroy the medial imprints if the producer lifted its postabdomen as it moved forward. Similarly, if the substrate was bound by microbial mats prior to production of the trackways, the repetitive setting down of limbs or a large arthropod exerting its weight could have locally damaged or destroyed the mats. In such localized 'punctured' areas, a loss of cohesion, or an increase in erosion potential caused by local mat damage might also help to explain the exaggerated, paddle-like appearance of the limb imprints, especially if this damage were combined with oar-like limb motion as discussed previously. Alternatively, there is tentative evidence that suggests *M. macnaughtoni* may have had broad, paddle-like preabdominal appendages (Collette and Hagadorn, 2010, figs. 6.3, 6.4; Fig. 2.3).

Based on similarities in both overall size and morphological detail between *M. macnaughtoni* and *P. eremita* presented herein, as well as the co-occurrence of *M. macnaughtoni* and *P. eremita* in the same outcrop, a linkage between trace-maker and trace species is well-supported.

Moreover, the multi-segmented imprints of *Protichnites eremita* could not have been produced by abdominal or postabdominal structures of Cambrian Aglaspidida, Chasmataspida or other basal arachnomorphs. Aglaspidids, such as *Aglaspis spinifer*, had a relatively wide, short region, largely undifferentiated from the trunk and composed of only three or four apodous trunk somites (Briggs et al., 1979). *Chasmataspis*-like body impressions from the Cambrian Hickory Sandstone of Texas had very elongate opisthosomas of as many as 13 apodous somites (Dunlop et al., 2004). Finally, *Paleomerus hamiltoni* had a wide, gradually tapering, aglaspidid-like abdomen of 11 segments, a wide terminal telson, and lacked a clearly-defined abdomen or postabdomen (Dunlop and Selden, 1997). Rather, *P. eremita* exhibit features that closely match the postabdominal morphology of an animal like *M. macnaughtoni*, which possessed a narrow (relative to preabdomen/thorax), multi-segmented postabdomen of at least five somites (Fig. 2.3). To explain these trackway morphologies, especially the deep and distinct margins of the tracks and medial imprints of Trackways A and B, one cannot invoke leveling/enlarging of small tracks. Yet it is difficult to constrain whether the differences in the shape and size of the tracks of these trackways (i.e., large and ovate in Trackways A and B; relatively small and sub-circular in Trackways C, D and E) are related to preservation, ambulation or limb posture, presence/absence of lateral movement of appendages against the

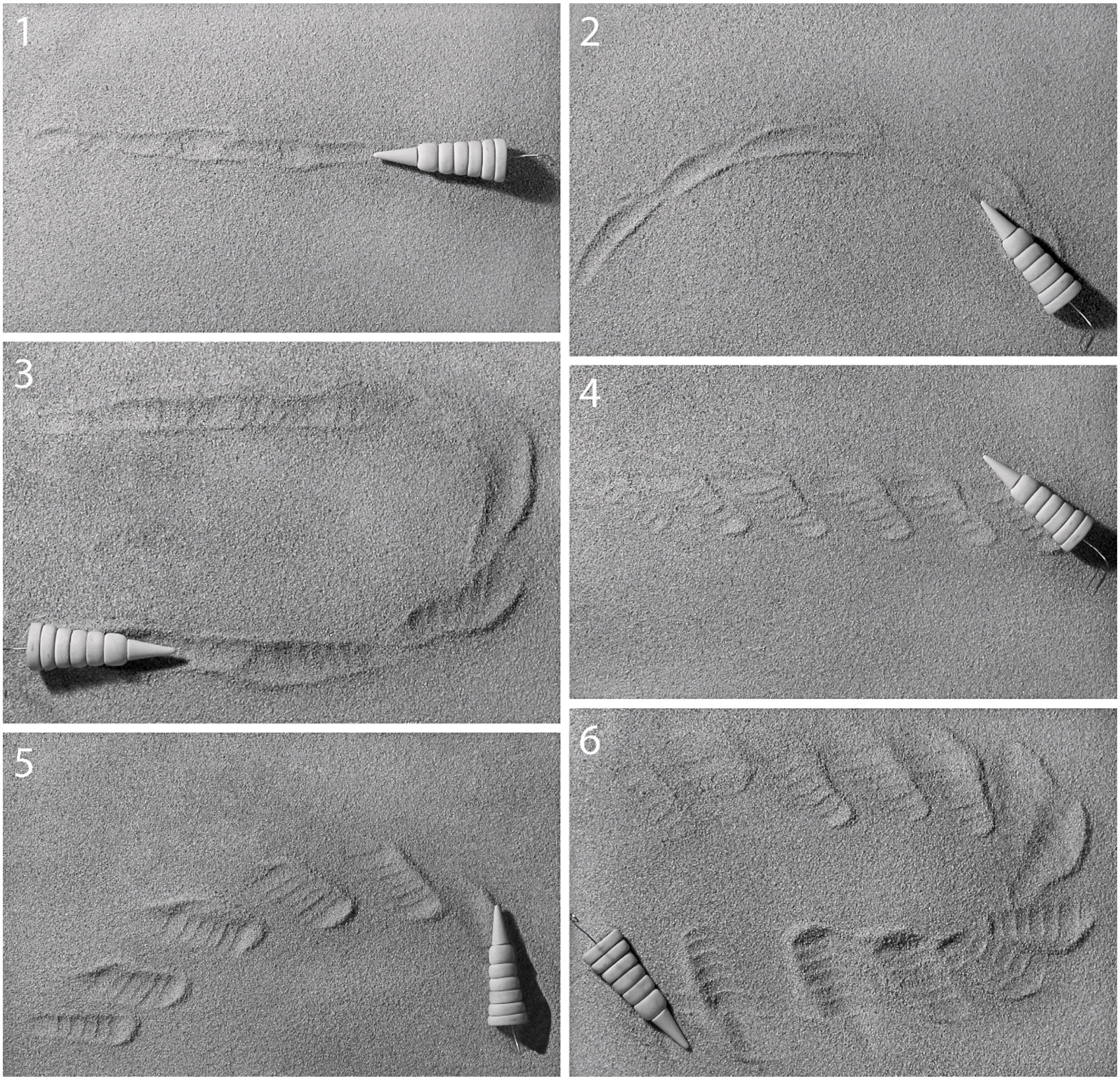

FIGURE 6—Impressions produced during the experimental trials that successfully replicated medial imprints analogous to those of *Protichnites eremita*. *1*, trackway 3 in text, compare with *Fig. 5.4*; *2*, trackway 5, compare with *Fig. 5.6*; *3*, trackway 7, compare with *Fig. 5.8*; *4*, trackway 9, compare with *Fig. 5.10*; *5*, trackway 11, compare with *Fig. 5.12*; *6*, trackway 13, compare with *Fig. 5.14*. All trackways produced in dry, medium-grained quartz sand; euthycarcinoid abdomen model was moved along sediment surface using a wire, visible at the widest end of the model in each photograph.

substrate, superposition of tracks, taxonomic distinction, or a combination of these factors.

The reason for the exclusively left-oriented impression of the postabdomen in *P. eremita* Form 1 remains uncertain. There is at least one example of “left-handedness” among the Arthropoda. Buthid scorpions, such as *Centruroides*, are known to rest their upwardly-curved caudal appendage laterally on the substrate while at rest and while walking slowly (Stahnke, 1966; D. Sissom, personal commun., 2010). Where known among buthids, there is a tendency for the left side to be chosen (Stahnke, 1966, fig. 6).

Form 1: Hermit behavior or Amplexus?—Hagadorn and Seilacher (2009) hypothesized that the peculiarities of *P. eremita* were produced by a eurypterid-like stem arthropod that used a high spired, dextrally coiled shell to reduce desiccation of its abdominal gills. The left-pointing medial impressions were thought to be produced as the animal touched the shell to the substrate while holding it with its presumed upwardly bending tail. This hermit hypothesis accounts for three features of trackway medial impressions: 1) impressions are always shingled to the left side; 2) impression segments are always angled to the right side; 3) each impression includes a deep notch. The trackways' lack of pushback hills prohibited interpretation of shingled postabdominal impressions as being produced by a tail bent to the left side during locomotion. Right-tilt of the segments in the medial impressions also

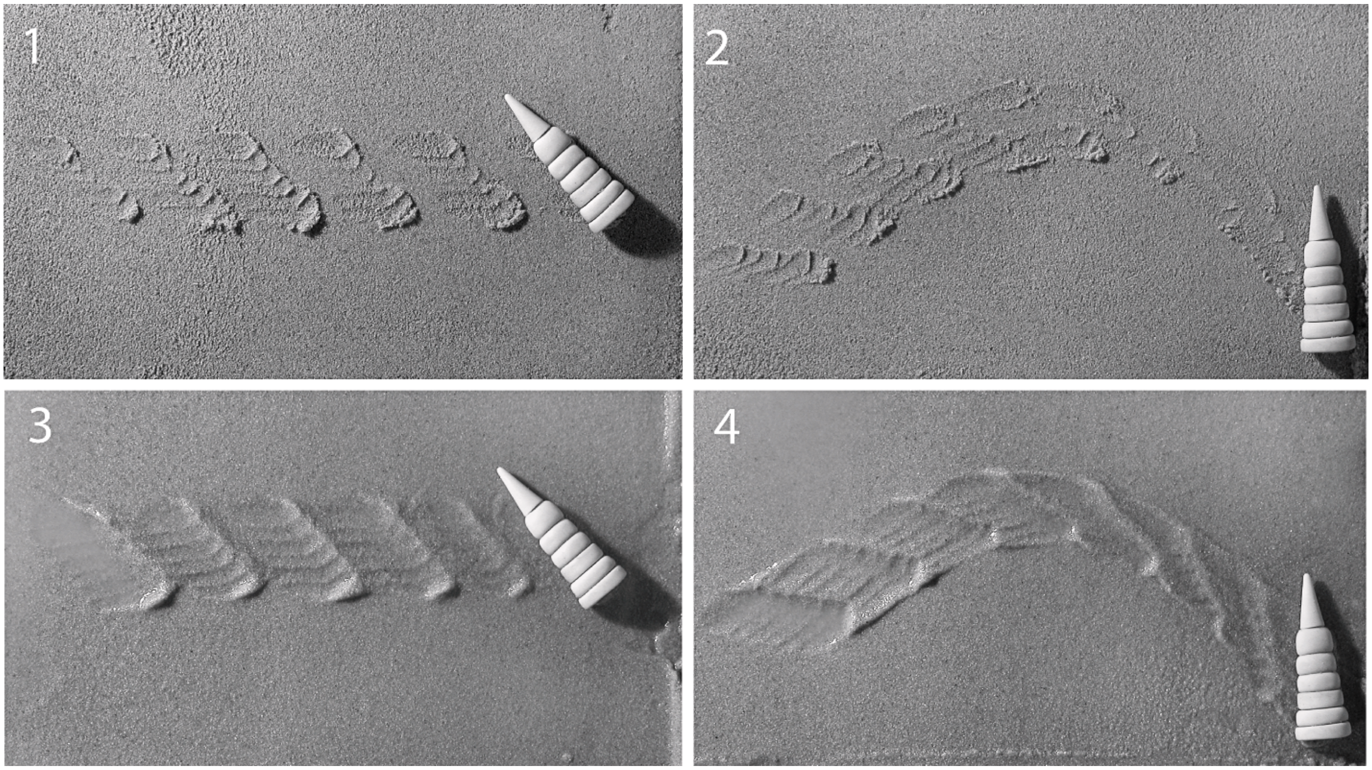

FIGURE 7—Impressions produced during the experimental trials that incompletely replicated medial imprints analogous to those of *Protichnites eremita*. *1, 2*, examples of trackways produced in moist or damp sand, note the shallow trackway depth; *3, 4*, examples of trackways produced in saturated sand, note the general lack of detail: *3*, trackway 9, compare with *Figs. 5.10* and *6.4*; *4*, trackway 11, compare with *Figs. 5.12* and *6.5*.

contrasted with the transverse segmentation of arthropod tails. However, our experiments demonstrate that a transversely segmented tail held at less than a 90° angle can leave segment impressions that are similarly tilted. Most Cambrian high-spired mollusks, univalved mollusks, and coiled serpulids were small and had poorly developed spirals (see summary in Hagadorn and Seilacher, 2009) and members of these groups could not have made the larger Form 1 *P. eremita* medial impressions, which reach a length of 7 cm. The deep medial notch/groove of *P. eremita* sometimes disappears within the same trackway (compare imprints at the center of Hagadorn and Seilacher, 2009, figs. 2B and 2C, with those at the bottom of the same figures), which is inconsistent with impressions that would be caused by a fixed spire and aperture lip of a rigid shell. Also perplexing is the rarity of *P. eremita* Form 1; it only occurs on a few of the dozens of beds on which *Protichnites* occur (Hagadorn and Seilacher, 2009, fig. D1), including other bedding planes representing the same depositional environments and taphonomic conditions.

Based on these considerations, the unusual morphologies of Form 1 could have been the result of euthycarcinoid-like arthropods ambulating while conjoined, such as in inguinal or abdominal limulid amplexus. This interpretation explains all of the Form 1 peculiarities, with none of the difficulties inherent in the hermit hypothesis, and does so utilizing only evidence which co-occurs in the outcrop in question.

Although modern limulids are poor morphological analogues for the hypothesized euthycarcinoid trace-makers interpreted to make *P. eremita*, their reproductive strategies provide insights into how the *P. eremita* trace-maker might have produced offset, shingled and grooved medial imprints. Limulids mate by external fertilization, with the male attached to the female while submerged and as the pair leaves the water and crawls along the beach during the mating process. Resulting trackways are often composite traces which include an intermittent medial imprint made by the telson of the male (Fig 4.2). Nearly all of the eggs of *Limulus polyphemus* become fertilized (Brockmann, 2003, p. 53), indicating that the narrow telson of the female does not significantly interfere with the fertilization process; thus, the female *L. polyphemus* does not need to hold her telson to the side during amplexus (H. Brockmann, personal commun., 2010).

If euthycarcinoids also moved in a manner similar to mating xiphosurans, the male could have made imprints from the posterior region of its body in proximity to those of the female, and the male's imprints could have manifested themselves as the deeper grooves and notches of *P. eremita* Form 1. The relatively wide postabdomen of the female euthycarcinoid (by contrast to the narrow telson of limulids) could have had a greater tendency to interfere with fertilization if not moved out of the way. Displacement of the female's postabdomen to the side might therefore provide a reproductive advantage. Holding the postabdomen to the side during ambulation would also account for the diagonal orientation of the postabdominal impression segments, as demonstrated in our experimental trackways. If such behavior was stereotypical, it would also explain why the shingled medial markings are repeatedly aligned to one side of the animal regardless of the turning or looping direction.

Linear troughs along the trackway margins might also be produced, analogous to those in *Protichnites eremita* Form 1. For example, the additional weight of the male in amplexus would tend to push the female down slightly into the sediment, thus causing the lateral margins of her carapace to drag along the sediment. Dragging of the carapace margins while in

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subaerial environments commonly occurs with modern limulids, even when a male is not attached (Shuster and Anderson, 2003, fig. 7.17; Fig. 4.1).

The offset imprint being from the male and the groove being from the female is an alternate scenario to consider when interpreting *P. eremita* Form 1; however, the observed depth of the groove is more consistent with an object pointing slightly downward into the sediment, as would be expected from a male whose body is inclined downward posteriorly due to its anterior end being off of the substrate. Furthermore, the generally smaller dimensions of the grooves as compared to those of the offset postabdominal imprints are indicative of the groove-maker being relatively small.

It is possible that *P. eremita* Form 1 may be a trace fossil produced in a mass-mating congregation (Erickson, 2004). Other marine arthropods practice synchronized mating behavior in emergent environments, such as the extant horseshoe crab, *Limulus polyphemus*. Eurypterids are also thought to have come ashore en-masse, mated, and then molted before returning to deeper water (Braddy, 2001; Vrazo and Braddy, 2011). Some euthycarcinoids may have also intermittently come ashore and died in emergent nearshore environments (Collette and Hagadorn, 2010).

Although this might be the first report of trackways hypothesized to be made by such tandem or chain-like pairs of arthropods (Erickson, 2004 hypothesizes a 'dismount' in a composite trackway), our trackway evidence is consistent with the body fossil record, in which chain-like aggregations of trilobites, phyllocarids, and waptiids are known (Chatterton and Fortey, 2008; Hou et al., 2008; Gutiérrez-Marco et al., 2009; Collette and Hagadorn, 2010; Fig. 2.2).

CONCLUSIONS

New *P. eremita* Form 2 trace fossils, the *P. eremita* resting trace, and neoichnology experiments expand our understanding of the preservation of *Protichnites*, one of the most common trace fossils in Cambrian epicratonic strata of North America. The well-preserved, segmented medial imprints, together with a euthycarcinoid-like resting trace both suggest that *Protichnites eremita* was likely produced by a euthycarcinoid-like arthropod such as *Mosineia macnaughtoni*, and that the medial imprints of *P. eremita* are likely serial impressions of its apodous postabdomen. This work illustrates how variations in animal behavior and substrate characteristics yield different trackways (e.g., Minter et al., 2007). Considered together, this experimental work and these fossils offer the best explanation for the asymmetrical morphological characteristics of *P. eremita*; rather than being produced by the hermit-like behavior of arthropods, they can be produced by stereotypical behaviors of euthycarcinoid-shaped arthropods. One type of *P. eremita* might even be produced by ambulating pairs of individuals.

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