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A new reconstruction of continental *Treptichnus* based on exceptionally preserved material from the Jurassic of Massachusetts

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Abstract.—Continental deposits of the Early Jurassic East Berlin Formation in Holyoke, Massachusetts, have yielded an exceptional occurrence of the ichnogenus *Treptichnus*. Here, burrows are preserved in full relief within thin mud laminae between layers of fine-grained, cross-bedded sandstone. We studied these burrows to evaluate whether earlier explanations of burrow morphology are applicable to all *Treptichnus*. Our research focused on three questions. (1) Do the Holyoke *Treptichnus* have significant vertical relief? (2) Does the lack of projections in some of the Holyoke *Treptichnus* result from stratinomic sectioning through the bottom of the burrow? (3) Do expanded, bulbous ends of burrow segments result from sediment compaction? While addressing these questions, the Holyoke fossils were compared to syntype and topotype material of *Treptichnus* from the Carboniferous of Indiana. The Holyoke *Treptichnus* did not exhibit significant vertical relief, and the presence and absence of projections is explained by the positioning of new segments at different points along older ones. The bulbous ends of burrow segments resulted from trace-maker behavior, not sediment compaction. Drawing on the analysis of the Holyoke material, a new reconstruction is proposed that presents continental *Treptichnus* as a shallow mole-tunnel-like burrow produced just below the sediment surface. This reconstruction is consistent with the morphology of Recent *Treptichnus*-like burrows produced by fly (dipteran) larvae, which are considered the most likely makers of the Holyoke *Treptichnus*.

Introduction

Miller (1889) established the ichnogenus *Treptichnus* for trace fossils that were collected from continental deposits of the Mississippian Mansfield Formation of Indiana. These traces are composed of a series of zigzagging, interconnected segments exhibiting projections at most of the segment junctions (Fig. 1.1, 1.2). *Treptichnus* is among the most widely known of trace fossils today, which resulted from the inclusion of marine forms within the ichnogenus nearly a century after its initial description (e.g., Häntzschel, 1975; Palij, 1976; Pacześna, 1986; Orłowski and Żylińska, 1996; Jensen, 1997; Uchman et al., 1998; MacNaughton and Narbonne, 1999). Most important was Jensen's (1997) proposed synonymy of *Phycodes pedum*, which had been described by Seilacher (1955) and was subsequently chosen as a biostratigraphic marker to define one of the major milestones in Earth history, the Precambrian–Cambrian boundary (Crimes and Anderson, 1985; Narbonne et al., 1987; Brasier et al., 1994; Landing, 1994). Thus, the first occurrence of *T. pedum* Seilacher, 1955 at the global stratotype ushered in the beginning of the Phanerozoic Eon. Considering its broad environmental distribution and stratigraphic range, different trace makers are likely responsible for the different occurrences of this ichnogenus. For example, continental specimens are typically considered the result of larval insects (Miller, 1889; Bajard, 1966; Uchman, 2005; Muñiz Guinea et al., 2014), whereas marine forms are attributed to priapulid worms or similar animals (Vannier et al., 2010).

Miller (1889) considered *Treptichnus* to be a surface trail. Later, Archer and Maples (1984) and Maples and Archer (1987) reevaluated *Treptichnus* by reexamining Miller's type specimens along with additional material that they collected. From this additional material (e.g., Fig. 1.2, 1.3), Archer and Maples (1984) noted that *Treptichnus* was in fact a subsurface burrow. Following Seilacher and Hemleben's (1966, fig. 4c) reconstruction of a Lower Devonian marine burrow system, Archer and Maples (1984) proposed a three-dimensional reconstruction in which *Treptichnus* was composed of a series of interconnected J- or U-shaped segments whose distal ends arced upward and reached the sediment surface (Fig. 1.4, left side).

Archer and Maples (1984) also argued that, due to the burrow's three-dimensionality, *Treptichnus* exhibits different morphologies depending on the horizontal plane through which it is sectioned (Fig. 1.4a–c). In particular, sections through the middle of the burrow yield the typical *T. bifurcus* Miller, 1889 morphology with projections (Fig. 1.4b), whereas sections at the bottom of the burrow yield simple, zigzag traces without projections (Fig. 1.4c). This reconstruction has gained

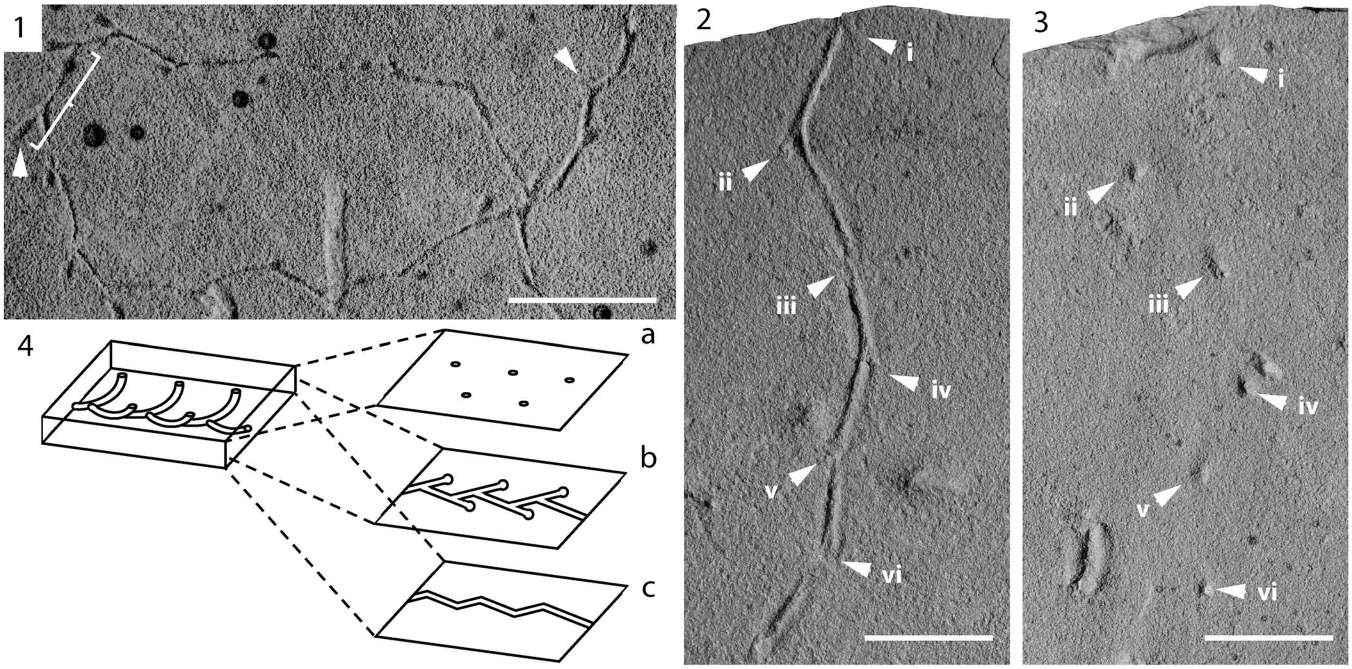

Figure 1. *Treptichnus bifurcus* from the Pennsylvanian Mansfield Formation of Indiana; specimens are housed at the Field Museum (UC) and the Indiana University Paleontological Collection (IU). (**1**) Close-up of *T. bifurcus* syntype 1 on UC 54099 with an individual segment on the left indicated by a bracket and an expanded, bulbous projection by an arrowhead. The arrowhead on the right points to a segment junction lacking a projection. (**2, 3**) Bed bottom and top views, respectively, of a *T. bifurcus* topotype on IU 16063-2. Ends of segments are labeled in (**2**) and their corresponding pits on the bed top are numbered the same in (**3**). (**4**) Three-dimensional reconstruction of *T. bifurcus* by Archer and Maples (1984) showing proposed changes in burrow morphology resulting from differences in plane of sectioning. Scale bars = 10 mm.

widespread acceptance among researchers (e.g., Metz, 1992, 1996, 2007; Buatois and Mángano, 1993; Buatois et al., 1998; Uchman et al., 1998; Jensen et al., 2000; Rindsberg and Kopaska-Merkel, 2005; Carbone and Narbonne, 2014), and has implications for the taxonomic status of other taxa Miller (1889) established. For example, Buatois and Mángano (1993) argued that *Plangtichnus* should be synonymized with *Treptichnus* because the former is simply a bottom view of the latter burrow.

Despite the notoriety of *Treptichnus*, various aspects of this ichnogenus are in need of further evaluation. In particular, there is still disagreement among researchers as to which traces belong within the ichnogenus, how many species there are, and whether Miller's other taxa represent junior synonyms of *Treptichnus* (e.g., Buatois and Mángano, 1993; Archer et al., 1995; Jensen, 1997; Schlirf, 2000; Dzik, 2005; Rindsberg and Kopaska-Merkel, 2005). Furthermore, *Treptichnus* exhibits considerable morphological variability, not all aspects of which have been fully explored. For example, it is unclear whether other factors besides stratinomic sectioning result in the presence or absence of projections at the ends of burrow segments. In addition, various hypotheses such as sediment compaction (Jensen, 1997; Wilson et al., 2012) and differences in plane of section (Metz, 2007) have been proposed to explain why some burrow segments show bulb-like expansions of different shapes at their ends.

In this paper, we examine a suite of well-preserved *Treptichnus* from Early Jurassic continental deposits in Holyoke, Massachusetts, to determine whether previously proposed explanations for the presence or absence of projections and bulbous terminations apply to those fossils. In particular, we evaluate whether the Holyoke *Treptichnus* exhibit significant vertical relief and whether the stratinomic reconstruction proposed by Archer and Maples (1984) explains the presence or absence of segment projections in the burrows examined. Finally, we evaluate the origins of the expanded, bulbous ends of individual burrow segments seen in many of the specimens.

Geological and paleontological context

The burrows evaluated herein were collected from a small outcrop on a residential lot known locally as the Gary Gaulin track site, which is located in Holyoke, Massachusetts (42°11'51.74"N, 72°38'41.16"W, Fig. 2). This outcrop exposes approximately 2 m of mudstone and fine-grained sandstone of the East Berlin Formation. These rocks are part of the Late Triassic through Early Jurassic Newark Supergroup strata within the Hartford Basin, and along with basaltic lava flows, filled a half graben that formed as Pangea pulled apart during the opening of the Atlantic Ocean (Olsen, 1997).

The East Berlin Formation is 145–450 m thick (Hubert et al., 1976) and is considered of Early Jurassic age due to its position above the Late Triassic or Early Jurassic Shuttle Meadow Formation (Cornet et al., 1973). The strata that make up the East Berlin Formation consist of cycles of playa lake red mudstones and sandstones between which are gray to black shales produced in perennial, oligomictic, alkaline lakes, some of which were 10s of meters deep and extended over 4,700 km^2 (Hubert et al., 1976, 1992). The cyclic changes from playa to perennial lake deposition, called Van Houten cycles, are the consequence of climatic changes resulting from Milankovich cycling (Olsen, 1986).

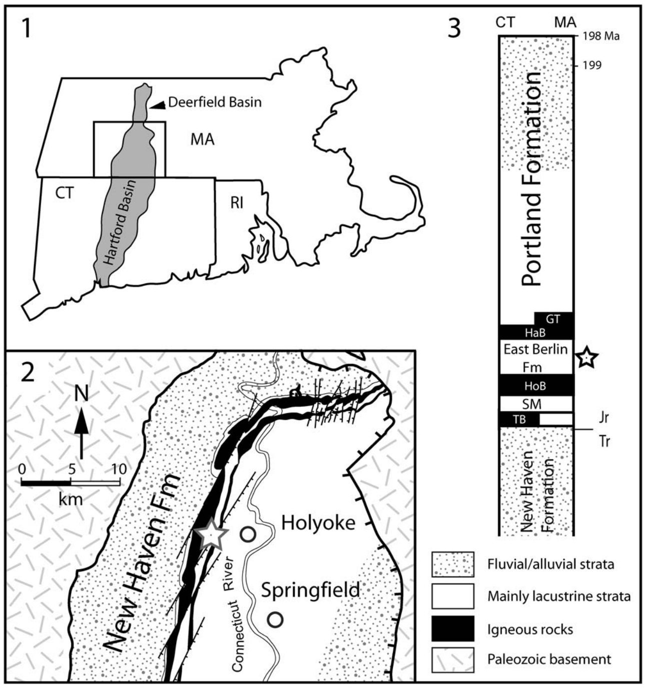

Figure 2. Geography and stratigraphy of the study area. (**1**) Map of southern New England showing Newark Supergroup Mesozoic rocks in gray. (**2**) Bedrock geologic map of the boxed area in (**1**). The star indicates the location from which the *Treptichnus* described herein were collected. (**3**) Stratigraphic column of the Hartford Basin with a star indicating the approximate position of the field site. (**2**) and (**3**) are modified from Collette et al. (2011) and used with permission from Atlantic Geology. CT = Connecticut; MA = Massachusetts; RI = Rhode Island; GT = Granby Tuff; HaB = Hampden Basalt; HoB = Holyoke Basalt; SM = Shuttle Meadow Formation; TB = Talcott Basalt; Jr = Jurassic; Tr = Triassic.

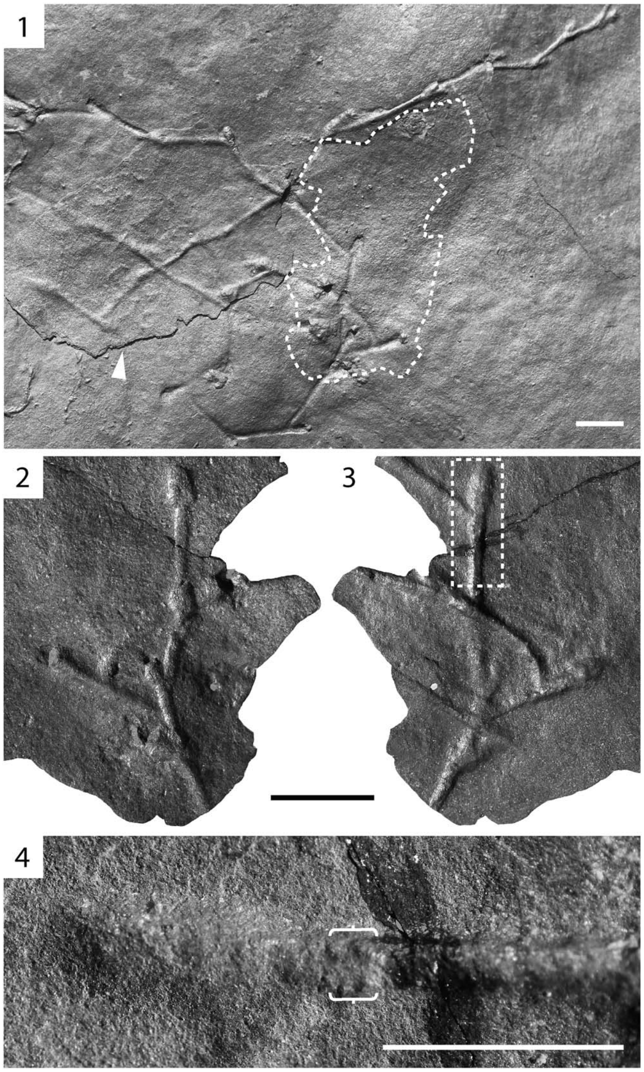

Figure 3. *Treptichnus bifurcus* from Holyoke, Massachusetts, preserved within thin mud laminae; specimens are housed at the Springfield Science Museum. (**1**) Part of 2013/4-03, a bed sole from which the lamina (arrowed) is exfoliating; the dashed outline indicates the position of a flake from the lamina shown in (**2**) and (**3**). (**2, 3**) Top and bottom views, respectively, of the flake (2013/4-04), showing burrows preserved in full relief. (**4**) Close-up of the boxed area in (**3**) showing, between the two brackets, two series of paired ovate imprints preserved on the burrow floor. (**1–3**) Scale bars = 10 mm; (**4**) scale bar = 5 mm.

At the Gary Gaulin track site, *Treptichnus* are restricted to the southern portion of the outcrop, where they are preserved in full relief within thin mud drapes between muddy, fine-grained, cross-laminated sandstone beds that are up to 3 cm thick (Fig. 3.1). The mud drapes sometimes spall away from the overlying and underlying sandstone layers such that both the top and bottom of the burrows are visible (Fig. 3.2, 3.3). More often, however, the mud drapes adhere to the overlying layer to produce concave epireliefs and convex hyporeliefs, or to the underlying layer to produce convex epireliefs and concave hyporeliefs. Some of these burrows are well enough preserved to reveal two parallel rows of raised structures on opposite sides of the bottom of the burrow segments (Fig. 3.4), which are here inferred to have been made by the body (legs?) of the trace maker.

The burrows exhibit a patchy distribution, and the disruption of bedding ranges from 2 (little disruption) to 4 (zones of generalized disruption) on the scale proposed by Miller and Smail (1997). Sedimentary structures on these beds include oscillation ripple marks and desiccation cracks, indicating deposition in shallow water followed by drying of the surface. Similar beds in the East Berlin Formation are interpreted as ephemeral lake deposits (e.g., Drzewiecki and Zuidema, 2007), and we infer the same origin for the *Treptichnus*-bearing beds at the Gaulin track site. Additional trace fossils associated with the *Treptichnus* include abundant vertical *Skolithos* isp., which are common in the East Berlin Formation as a whole (Gierlowski-Kordesch, 1991; Getty, 2005), as well as occasional horizontal trails resembling *Cochlichnus anguineus* Hitchcock, 1858 and *Helminthoidichnites tenuis* Fitch, 1850 (unpublished data, Getty, 2013). Dalman and Weems (2013) reported that vertebrate tracks, such as *Anchisauripus* isp. and *Anomoepus lacertoideus* Hitchcock, 1858, are found associated with *T. bifurcus*. These tracks are made by theropods and basal ornithischians, respectively (Olsen et al., 1998; Olsen and Rainforth, 2003; Dalman and Weems, 2013). In addition, Dalman and Lucas (2015) reported an arthropod body imprint from the site, which they named *Cheliceratichnus lockleyi* and attributed to a solifugan-like chelicerate.

Beds overlying those preserving the *Treptichnus* exhibit abundant *Skolithos* isp. and occasional *Planolites* isp. that crosscut ripple marks, as well as medium-sized theropod tracks assigned to *Anchisauripus* isp. One bed preserves a large theropod trackway assigned to *Eubrontes giganteus* Hitchcock, 1836 (Getty and Fox, 2015). These higher beds exhibit multiple generations of desiccation cracks that are irregularly sinuous in both cross-sectional and bedding plane parallel view and were likely produced in pedogenically altered playa mudflats (Demicco and Gierlowski-Kordesch, 1986; Gierlowski-Kordesch and Rust, 1994). Trace fossils on the playa mudflats are poorly preserved, in contrast to the excellent preservation on the *Treptichnus*-bearing shallow lacustrine deposits. The trace fossil assemblage and associated sedimentary structures found at the locality share features of both the *Scoyenia* (e.g., low diversity, presence of vertebrate tracks, and desiccation features) and *Mermia* (dominance of horizontal trails and shallow-tier burrows) ichnofacies (Buatois and Mángano, 2011).

Materials and methods

The Holyoke burrows were uncovered in the year 2000 while the owner was excavating the outcrop for dinosaur tracks (Dalman and Weems, 2013; Getty and Fox, 2015). During this excavation, rock slabs, some of which contained the *Treptichnus*, were removed from approximately 32 m^2 of the southern part of the site. The excavation process resulted in the loss of some stratigraphic control on the distribution of the burrows; however, they all came from a few beds and occurred within approximately 3–5 cm above the dinosaur-footprint-bearing slabs described by Dalman and Weems (2013). The Holyoke slabs described herein are housed at the Springfield Science Museum (SSM) in Springfield, Massachusetts.

The Holyoke *Treptichnus* were photographed for comparison with each other and with syntype and topotype material from Indiana. Dimensions such as segment length, projection length, and angle between segments were recorded for a subset of 92 well-preserved burrows following the guidelines presented by Archer and Maples (1984, fig. 3.2). The measurements were recorded from photographs using ImageJ software. A further subset of nine burrows was sectioned in order to observe their three-dimensional morphology. The sections were made by cutting either parallel or perpendicular to the burrow segment using a tile saw and then polishing the cut surface until the burrow segment was penetrated to the desired depth. Cut and polished sections were photographed and compared to each other and to the reconstruction of Archer and Maples (1984).

The two syntype and 12 topotype *T. bifurcus* were examined in detail for comparison with each other and with the Holyoke material. The syntypes are housed at the Field Museum in Chicago (UC) and are preserved on a slab labeled UC 54099. The syntypes are hereafter called *T. bifurcus* syntype 1 (Fig. 1.1) and 2, respectively. The topotype material is housed within the Indiana University (IU) Paleontology Collection.

Observations

Morphological variability.—There is considerable morphological variability in the Holyoke burrows (Figs. 4–7). The simplest morphology is composed of isolated segments scattered about the bedding surface (Fig. 4.1). This morphology cannot be assigned to *Treptichnus* and is instead similar to *Arenicolites*. In other examples, the burrow segments, although unconnected, are aligned and close together, suggesting that the same animal made them (Fig. 4.2). Some of these unconnected, aligned burrow segments grade into *T. bifurcus*. For example, one burrow begins as a looping series of unconnected segments on the right side of the image and then transitions to *T. bifurcus* on the left (Fig. 4.3).

The *T. bifurcus* morphology is itself highly variable. In some burrows, individual segments are long and thin; the projections are short and approximately the same width as the rest of the segment; and the angle between successive segments is relatively high (e.g., Fig. 3.1). By contrast, other *T. bifurcus* have relatively short burrow segments that diverge at low angles and show long, often bulbous, projections. In some of these latter specimens, the segments on either side are tightly packed, giving the burrow a rather congested, bushy appearance (Fig. 4.4, right side of image).

As will be discussed in more detail in the following, some *Treptichnus* lack projections entirely or exhibit them only in some portions of the trace (Fig. 4.5–4.8). Some of these (e.g., Fig. 4.6) resemble *Treptichnus pollardi* Buatois and Mángano, 1993. Segments in these burrows may be short and relatively thick (Fig. 4.5) or long and thin (Fig. 4.6–4.8). Projections, where present, are either the same width as the rest of the segment (Fig. 4.8) or exhibit bulbous terminations. Some of these burrows resemble a string of beads when segments are arranged end to end (Fig. 4.5).

When seen in bedding parallel view, most burrows have straight or approximately straight segments, although in some burrows the segments are curved (Fig. 4.8). The burrow course is often gently curving to meandering, but one burrow (Fig. 4.9) is tightly looped and resembles *T. coronatus* Crimes and Anderson, 1985. Finally, some burrows are composed of a thick central tunnel from which thinner projections radiate in a dense, fan-like pattern as the burrow turns (e.g., Fig. 4.10). These last burrows do not fit well into *T. bifurcus* but instead bear some resemblance to Cambrian forms.

Occurrence of projections.—Of the 92 Holyoke *Treptichnus* that were examined, 28 (30%) have projections at all segment junctions; 56 (61%) exhibit projections at some junctions but lack them at others; and eight (9%) lack projections entirely. Four burrows with intermittent projections are illustrated in Figure 5, where arrowheads point out segment junctions lacking projections. A short looping burrow (Fig. 5.1) consists of eight segments and has projections at four of the seven junctions. The projections range 18%–43% (averaging 31%) of the segment length. Figure 5.2 illustrates another short burrow consisting of seven segments with six junctions, five of which exhibit projections of different lengths (14%–43% of segment length, average 22%). Figure 5.3 shows a burrow consisting of five segments with bulbous terminations. The first junction lacks a projection, whereas the other four exhibit projections ranging from 16% to 47% (average 35%) of segment length. Finally, Figure 5.4 shows an eight-segment, seven-junction burrow. Four junctions have projections between 10% and 31% (average 20%) of segment length. In this last burrow, the junctions that lack projections exhibit round, bulbous expansions in between segments arranged end to end.

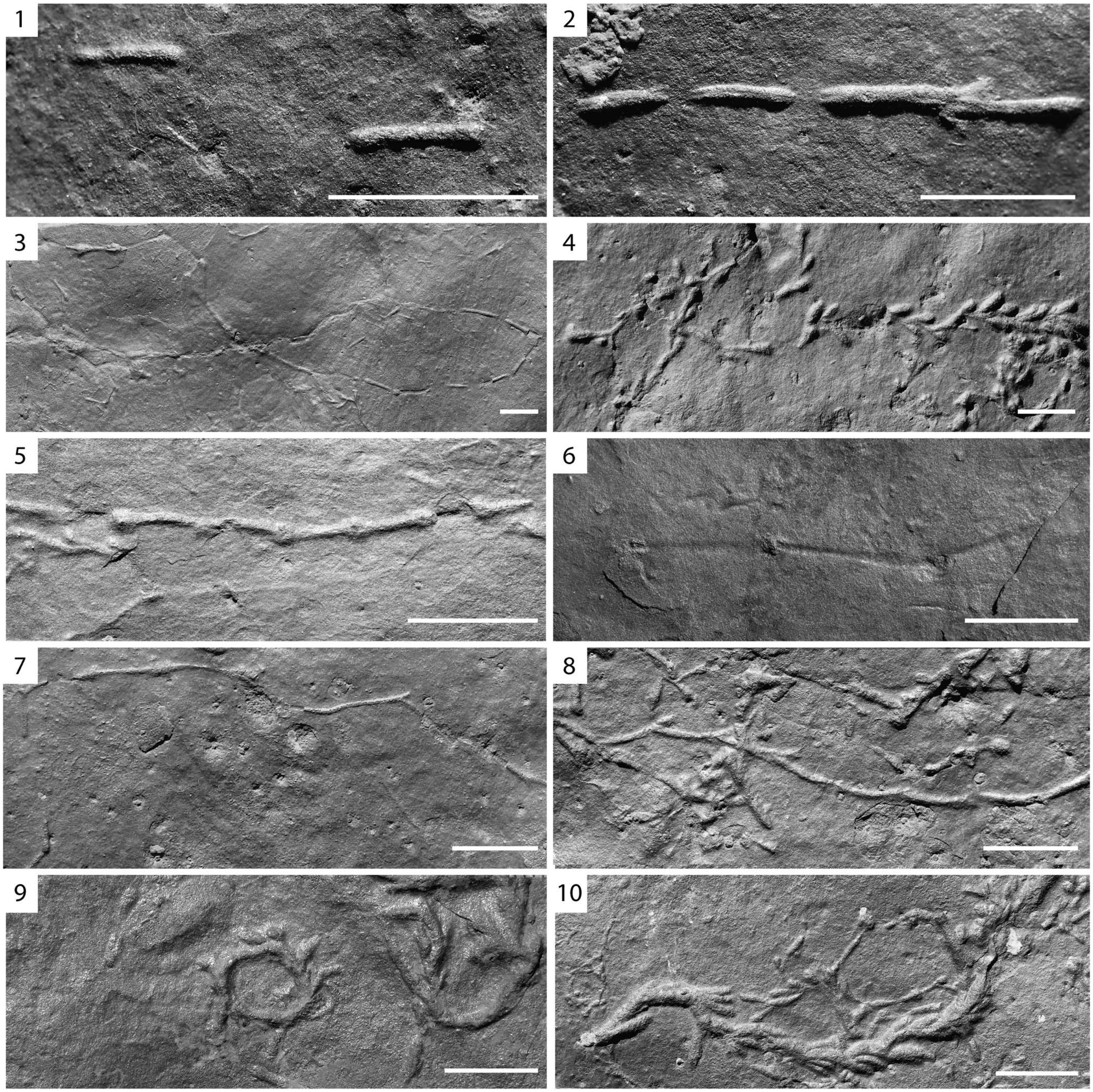

Figure 4. Morphological variability in burrows from Holyoke, Massachusetts; specimens are housed at the Springfield Science Museum. (**1**) SSM 2014/4-11, showing isolated burrow segments; (**2**) SSM 2014/4-23, showing a burrow composed of aligned but unjoined segments; (**3**) SSM 2014/1-10, showing a burrow starting as unjoined segments that grades into *T. bifurcus*; (**4**) SSM 2014/4-24, a slab on which is preserved a burrow with densely packed burrow segments that have bulbous ends; (**5**) SSM 2014/1-7, a slab exhibiting a burrow with segments aligned end to end and exhibiting bulbous projections; (**6**) SSM 2014/4-26, a slab on which is preserved a burrow with segments arranged end to end and lacking bulbous terminations; (**7**) SSM 2014/1-5, a slab on which is preserved a more sinuous burrow with expanded nodes and short projections; (**8**) SSM 2013/4-10, a slab on which a burrow with curved segments is preserved; (**9**) SSM 2014/4-13, a slab preserving a tightly looping burrow; (**10**) SSM 2014/1-8, a slab preserving a burrow with fanning projections. Scale bars = 10 mm.

Projections are also variably present within syntypes and topotypes of the Indiana taxa (Fig. 1.1–1.3). In *T. bifurcus* syntype 1, projections occur in 40 of 45 (89%) segments, where they range from 17% to 46% (average 28%) of segment length. In syntype 2, projections occur in 39 of 41 (95%) segments, where they range from 10% to 36% (average 24%) of segment length. One topotype (Fig. 1.2) is composed of seven segments with six junctions, three of which (Roman numerals ii, iv, and vi) exhibit short, straight projections ranging from 9% to 20% of segment length.

Bulbous ends of segments.—Twenty-eight (30%) of the 92 Holyoke *Treptichnus* had segments that were the same width along their entire length. The remaining 64 burrows (71%) exhibited bulbous ends on at least some of the burrow segments (Fig. 6). Figure 6.1 illustrates a burrow that has bulbs near the end

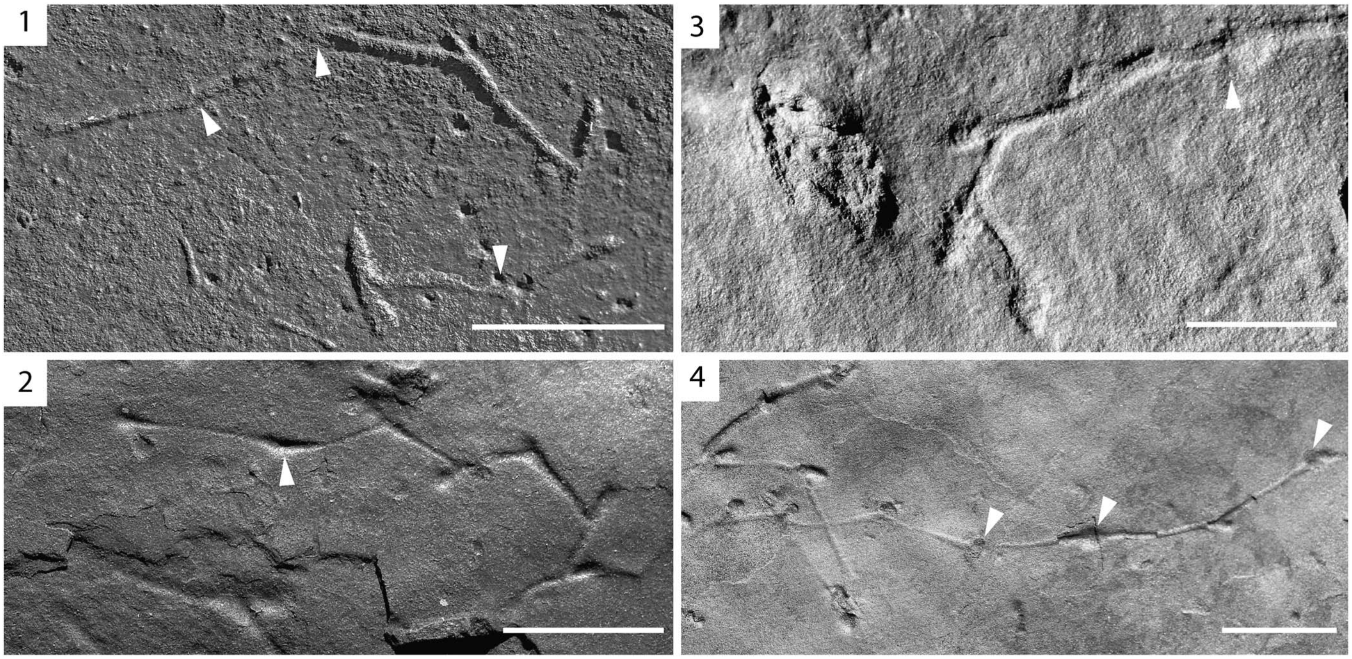

Figure 5. *Treptichnus bifurcus* showing variation in projection presence and length within individual burrows; specimens are housed at the Springfield Science Museum. (**1**) Burrow on SSM 2013/4-2 preserved in convex hyporelief; (**2**) burrow preserved in concave epirelief on SSM 2014/4-6; (**3**) a burrow exhibiting bulbous segment terminations preserved as a convex epirelief on SSM 2014/1-9; (**4**) a burrow preserved variably as a concave and convex epirelief on SSM 2014/4-25. Scale bars = 10 mm.

of the trace (one is arrowed) but lacks them at the ends of segments that were produced earlier. By contrast, burrows in Figure 6.2–6.6 exhibit bulbs at the end of each segment. The segments within a burrow may gradually widen along their length to produce the bulbous expansion, or the bulbs may occur as an abrupt widening of the segment near its end. The presence of bulbs does not correlate with the arrangement of the segments within a burrow as traces with zigzagging, straight, or curved courses have them. Most bulbs have well-defined boundaries, although in some burrows the boundaries are indistinct and grade into bedding.

Bulbs are round or ovate in bedding-plane-parallel view and are typically less than twice (~1.3–1.8 times) the width of the remainder of the segment. In rare examples, however, they are over three times segment width, and in one burrow they reach 5.6 times the width of the segments, giving the burrow the appearance of a bouquet of balloons on a string (Fig. 6.2). In one burrow, the walls of the bulbs are rugose (Fig. 6.3), whereas in all others they are smooth. In some examples where the burrow is preserved as a concave epirelief, the bulbs are deeper than the remainder of the burrow segment to which they belong (e.g., Fig. 5.4, see arrow). A burrow preserved on the edge of an exfoliating mud lamina confirms this last observation, since the undertrace preserved in the sandstone below the lamina shows a more strongly defined bulb relative to the rest of the segment (Fig. 6.5, see arrow). In some burrows, new segments were observed to begin beneath the bulb of the previous segment (Fig. 6.6, see arrow).

Among the Indiana material, bulbous projections were observed only in *T. bifurcus* syntype 1. Only 12 of the 40 projection-bearing segments (30%) within the burrow exhibited bulbs. The expansions, which are ovate, teardrop shaped, or triangular in shape, reach a maximum of 2.9 times segment width, although most are narrower.

Cross-sectional profiles.—Thirteen burrow segments were cross-sectioned longitudinally, and five of them are illustrated in Figure 7. The burrows from which the sections were made are shown in Figure 7.1, 7.4, 7.6, 7.8. Superimposed on the burrows are labeled dashed lines indicating the position and orientation of the cross sections. The cross sections themselves are shown in the panels below each of the burrows from which they were cut.

The cross sections show that, like *Treptichnus* from other localities, the ends of the segments exhibit openings that communicate with the sediment surface (e.g., Fig. 7.2, 7.3, 7.5, 7.7, 7.9). The segments themselves, however, do not always show the U or J shape for which *T. bifurcus* is generally known. For example, the burrow segment illustrated in Figure 7.2 is horizontal along its length, with the opening at its end being in the same plane as the remainder of the burrow roof. The bottom of this burrow segment is also horizontal until it reaches the bulb, at which point the burrow floor dips downward into the underlying sandstone layer. The segment in Figure 7.3, which is from the same burrow, shows a similar pattern of being horizontal along most of its length and exhibiting a slight downward deflection of the burrow floor at the bulb. It is different from the previous segment in that it takes a slight upward turn at its end. Thus, the overall pattern of this burrow is a straight top and slightly sinuous bottom.

Two additional burrow segments (Fig. 7.5, 7.7) also have slightly upturned ends, but both the top and bottom of previous portions of the segment are concave downward such that the segments are slightly sinuous in profile view. Of the remaining segments that were sectioned, only one (Fig. 7.9) showed the typical U-shaped profile, and this burrow was extremely shallow.

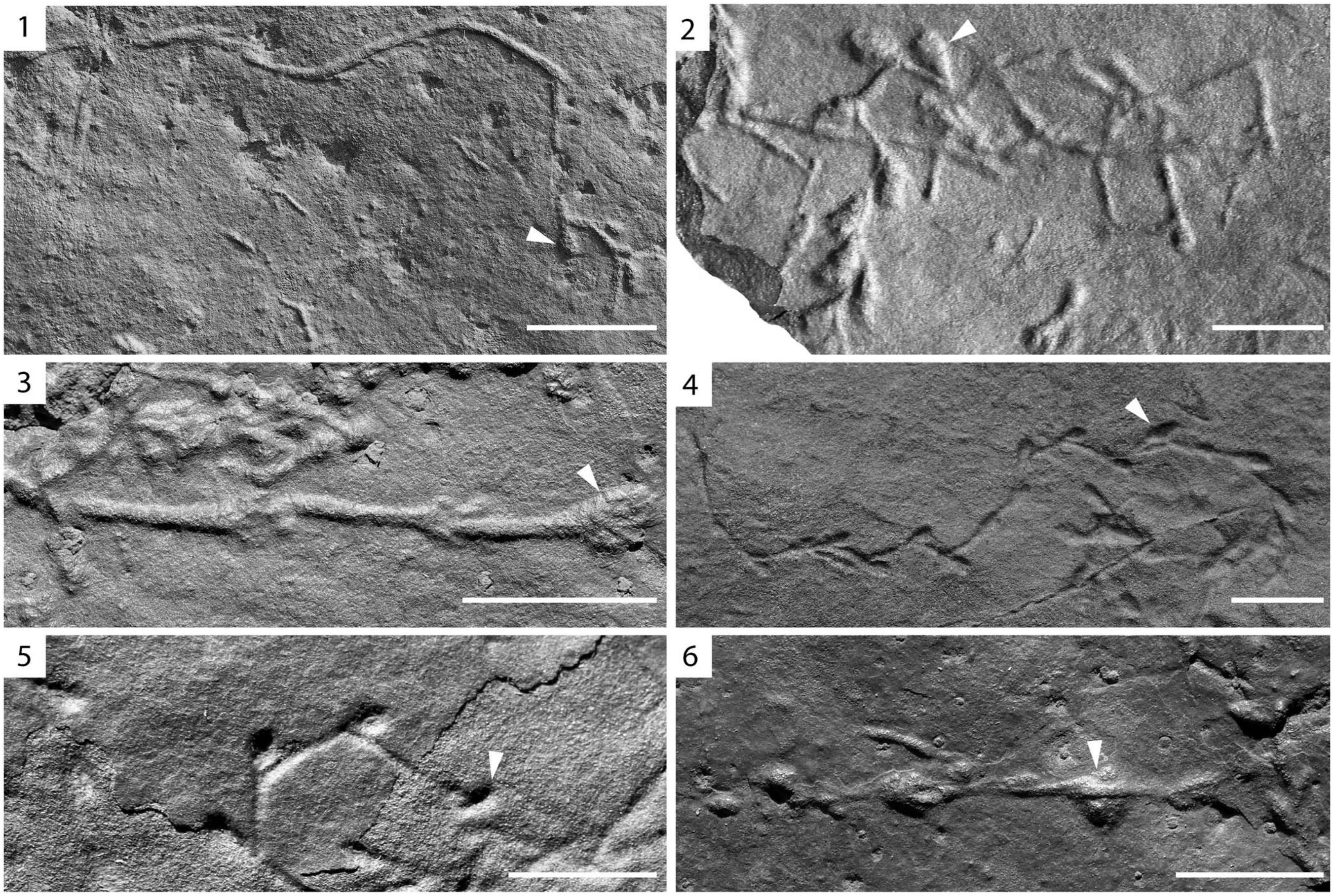

Figure 6. *Treptichnus bifurcus* with expanded, bulbous distal portions of burrow segments; specimens are housed at the Springfield Science Museum. (**1**) Part of 2013/4-2, showing a burrow lacking bulbous projections in the segments to the left but exhibiting them in the segments on the right; (**2**) burrow on SSM 2013/4-6 preserved as a convex epirelief and exhibiting significantly expanded distal portions of segments (arrowed); (**3**) burrow on SSM 2013/4-10 preserved as a convex hyporelief and exhibiting lines (see arrow) on the bulbs; (**4**) a burrow preserved on SSM 2013/4-7 (counterpart is SSM 2014/1-6) as a convex epirelief and exhibiting bulbous terminations that are deeper than the rest of the burrow segments to which they belong; (**5**) part of 2013/4-09, a bed top, showing a burrow preserved as a concave epirelief and as an undertrace below the lamina (note that in the undertrace the bulb is deeper than the rest of the burrow segment); (**6**) burrow on SSM 2014/4-24, a bed bottom, preserved as a convex hyporelief and exhibiting an unexpanded proximal portion of a segment below the bulbous distal portion of the preceding segment (arrowed). Scale bars = 10 mm.

Discussion

Presence or absence of projections.—Five observations of the Holyoke *Treptichnus* suggest that the presence or absence of projections at segment junctions is not simply the result of stratinomic sectioning of the burrows. First, cross sections show that the burrows are primarily horizontal in nature and do not have long, arcuate projections that penetrate thick layers of sediment (Fig. 7). Second, burrows preserved on a single plane exhibit projections at some junctions but lack them at others (Fig. 5). Third, when projections are present within a single burrow, they are often of different lengths at different junctions, even when the bedding plane is relatively flat. Fourth, in some burrows where the segments arc slightly downward and are deepest at their end, the following segment is connected to the termination of the preceding segment. Fifth, longitudinal cross sections (e.g., Fig. 7.2) show unequivocally that the burrow segments are sometimes constructed near or at the end of previous segments, which results in short projections or none at all. These observations indicate that the presence or absence of projections in the Holyoke material results from differences in the placement of newly constructed burrow segments relative to the ends of the previous segments, rather than stratinomic sectioning. Where projections are present, the animal backed into the previously made segment, changed directions, and excavated a new segment. The length of the projection depended on how much the trace maker backed up; short projections resulted from a short retrograde movement whereas long projections resulted from long retrograde movement. By contrast, burrows that lack projections resulted from the animal constructing the new segment directly at the end of a previously made one.

The presence or absence of projections in the Indiana material may be the result of a combination of factors, however. The syntypes of *T. bifurcus* are preserved as concave epireliefs on single bedding planes and have projections of different lengths at the different junctions, which suggests that, like their counterparts from Holyoke, their variability results from changes in horizontal placement of new segments relative to previous ones. By contrast, the *T. bifurcus* topotype illustrated in Figure 1.2 and 1.3 closely matches the stratinomic reconstruction of Archer and Maples (1984; Fig. 1.4) in that the burrow was excavated relatively deeply below the surface and had longer shafts that intersected the overlying bedding plane as a series of pits. If the lamina in which this specimen is preserved were split,

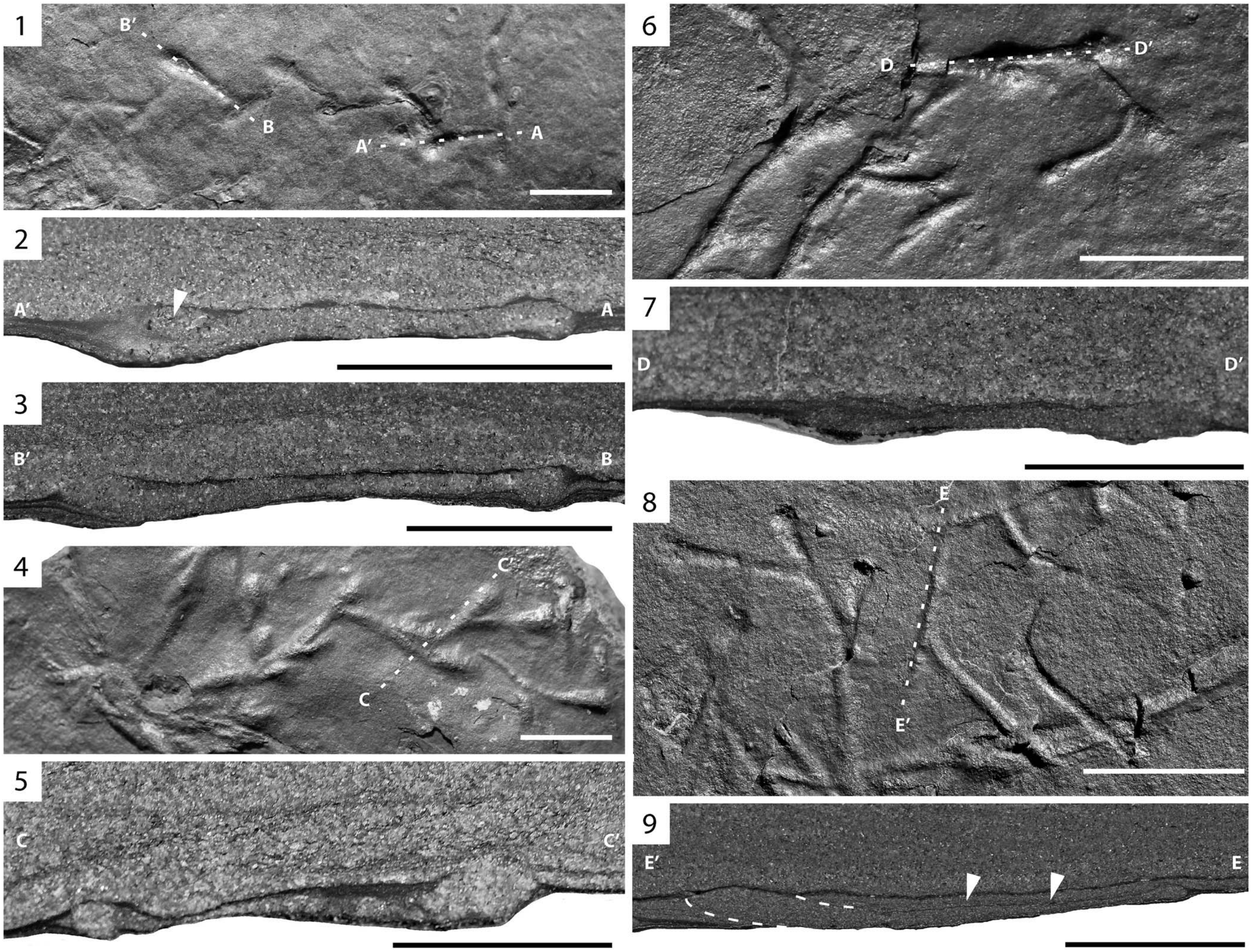

Figure 7. Longitudinally sectioned *T. bifurcus* from Holyoke, Massachusetts; all are preserved as convex hyporeliefs and are housed at the Springfield Science Museum. (**1, 2, 3**) Overview showing the location of two cuts on 2013/4-12, one on each side of a burrow with expanded projections, and views of the cross sections themselves. Arrowhead in (**2**) points to the beginning of the following segment, which can be seen as a small ovate structure at the top of the projection. (**4, 5**) Overview showing the location of a cut on 2013/4-13 through a burrow with bulbous projections, and the cross section itself. (**6, 7**) Overview showing the location of a cut along of 2013/4-14 through a burrow with bulbous projections, and the cross section of the segment, respectively. (**8, 9**) Overview showing the location of a cut through part of 2013/4-11 parallel to a burrow lacking bulbous projections, and the cross section of the segment, respectively. Arrowheads in (**9**) point to the faint burrow roof proximally, and dashed lines distally indicate the position of the roof and floor of the burrow where they become thin. (**1, 4, 6, 8**) Scale bars = 10 mm; (**2, 3, 5, 7, 9**) scale bars = 5 mm.

it is likely that the projections would appear longer than they do in the bottom view of the specimen.

Ultimately, it is likely that either or both factors—the horizontal placement of burrow segments relative to preexisting ones and the stratinomic sectioning of the burrow—will affect the presence or absence of projections, depending on the geometry of the specimen at hand. For more horizontal burrows, such as those from Holyoke, lateral placement of burrow segments will be a primary controlling factor in the presence of projections, whereas in burrows with more vertically oriented terminal shafts, stratinomic sectioning will play a more important role.

Origin of the bulbous ends of burrow segments.—Burrow segments seen in transverse section, such as those at the beginnings and ends of the longitudinally sectioned segments in Figure 7, are often ovate in outline, indicating that the burrows experienced compaction. Various lines of evidence, however, indicate that this compaction did not produce (although it probably enhanced) the wide, bulbous ends seen in the burrow segments of the Holyoke fossils. For example, some burrows exhibit bulbous, expanded ends on some segments but lack them on others (Fig. 7.1). Furthermore, burrows exhibiting bulbs on the ends of their segments occur next to burrows lacking bulbs (Fig. 6.2). Finally, in burrows where the successive segments were excavated underneath the bulbous ends of the preexisting segments (e.g., Fig. 6.6, see arrow), the portion of the next segment underneath the bulb is not wider than the rest of the segment, which would be the case if a long, sand-filled burrow were compressed atop it. These observations suggest that, rather than being the result of compaction, bulbs are the result of trace-maker behavior. This hypothesis is further supported by the rugose texture of the bulbs in one burrow, which we infer to be the result of scratching during the construction of the bulb (Fig. 6.3), and the greater depth of the bulbs relative to the rest of their associated segments (Fig. 6.4, 6.5). As with the Holyoke material, we propose that the slight expansions of the ends of the segments in the Indiana burrows are the result of animal behavior.

Trace-maker identity.—Miller (1889) suggested that the *Treptichnus* he described were produced by larval insects. His hypothesis has since been supported by field and laboratory observations that modern fly (Diptera) larvae, including midges (Chironomidae), horse flies (Tabanidae), and crane flies (Tipulidae), produce *Treptichnus*-like traces in both naturalistic and lab settings (Seilacher, 1955; Bajard, 1966; Tessier et al., 1995; Uchman, 2005; Martin, 2009; Muñiz Guinea et al., 2014). These modern burrows are shallow, mole-tunnel-like excavations that deflect upward and crack only the upper few millimeters of the sediment (Bajard, 1966; Uchman, 2005; Muñiz Guinea et al., 2014). Many of these modern burrows show a striking similarity to the Holyoke *Treptichnus*. For example, Uchman (2005, figs. 1, 2) illustrated modern burrows that resemble the fossils in Figures 4.6 and 5.4 in having bulbous expansions within the burrow and occasional short projections.

The earliest known definitive dipteran body fossils are mid-Triassic in age (Krzemiński et al., 1994), and dipterans are known from Late Triassic portions of the Newark Supergroup (Fraser et al., 1996; Blagoderov et al., 2007). Considering that the first occurrence of dipterans predates the Holyoke *Treptichnus*, and that recent fly burrows and their fossil counterparts are remarkably similar, we consider the Holyoke *Treptichnus* to be the work of larval dipterans. The long stratigraphic range of *Treptichnus* in continental deposits, however, means that the ichnogenus predates dipterans and earlier occurrences are likely attributable to other insects (Miller, 1889; Muñiz Guinea et al., 2014).

Burrow reconstruction.—The Holyoke *Treptichnus* are preserved in mud laminae atop thicker sandy layers and are primarily horizontal. Since the presence or absence of projections results from changes in position of newly constructed segments along the length of preexisting ones, the Archer and Maples (1984) reconstruction does not work well for these fossils. Consequently, in Figure 8 we provide a new *Treptichnus* reconstruction that is more consistent with what was observed in the Jurassic continental fossils. As with modern dipteran burrows, the Holyoke *Treptichnus* are subhorizontal mole-tunnel-like structures excavated just below the surface, the roofs of which protruded slightly above ground level. Individual segments had at least one opening to the surface, as is indicated by the black ovals at the end of each segment. As one follows the top burrow from left to right, the projections get progressively shorter as the new segments are constructed closer to the ends of the preexisting segments. The last two segments lack projections due to the construction of new segments at the ends of the earlier ones. A single, bulbous terminal chamber is shown in each burrow.

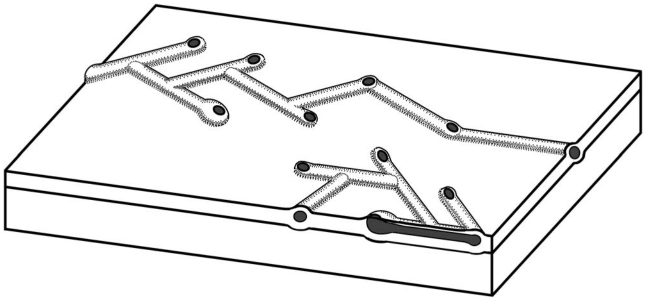

Figure 8. Reconstruction of the Holyoke, Massachusetts, *Treptichnus bifurcus* emphasizing the burrow's shallowness and the horizontal positioning of subsequent burrow segments relative to the ends of previous ones in determining the presence or absence of projections.

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