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TREPTICHNUS AND *ARENICOLITES* FROM THE STEVEN C. MINKIN PALEOZOIC FOOTPRINT SITE (LANGSETTIAN, ALABAMA, USA)

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ABSTRACT: U-shaped burrows (Arenicolitidae: *Arenicolites longistriatus* n.isp.) and connected series of similar U-shaped burrows (*Treptichnus apsorum* n.isp.) are common at the Steven C. Minkin Paleozoic Footprint Site near Union Chapel, Alabama. Both kinds of burrows share a similar *bioprint* (new term), that is, characters that allow recognition of the maker. In this case, shallow U-shaped burrows and longitudinal striation comprise the bioprint of larval insects, or possibly other arthropods, having similar behavior and growth patterns to that of modern dipteran (fly) larvae. *Haplotichnus*, including *H. ornatus* n.isp., may have been made by very small insect larvae and other arthropods.

Ichnogenus *Treptichnus* is confined to *T. bifurcus* (the type ichnospecies), *T. apsorum*, and *T. pollardi*. Ichnofamily Arenicolitidae is revised.

INTRODUCTION

The most abundant trace fossils of the Steven C. Minkin Paleozoic Footprint Site near Union Chapel, Alabama, are insect burrows: zigzag burrows *Treptichnus apsorum* n.isp. and shallow U-shaped burrows *Arenicolites longistriatus* n.isp. Many slabs are covered on both sides with these trace fossils, which are commonly preserved in exquisite detail. These trace fossils are valuable keys to the paleoenvironment of the Steven C. Minkin Site. *Arenicolites* and *Treptichnus* are considered together here because they have similar size range and morphologic features. As will be shown, *Treptichnus* can be considered as a string of *Arenicolites* connected together in a particular pattern. Intergradational trace fossils consisting of only a few connected *Arenicolites* are considered to be incipient *Treptichnus*.

Setting

More than 25 m of Lower Pennsylvanian strata are exposed at the Steven C. Minkin Paleozoic Footprint Site near Carbon Hill, Walker County, Alabama, and about 7 m consist of the abundantly ichnofossiliferous *Cincosaurus* beds (Pashin, 2005). The site, about 13.4 hectares (33 acres) in area, is a small part of the Union Chapel Mine operated by the New Acton Coal Mining Company. Beginning in December 1999, amateur paleontologists conducted an extensive weekend salvage operation with the cooperation of coal company and state officials. In 2004, the site was acquired by the Alabama Department of Conservation and Natural Resources, and on March 12, 2005, the site was dedicated to the memory of deceased collector Steven C. Minkin.

The Steven C. Minkin Site has yielded a spectacular abundance of well-preserved tetrapod trackways (Haubold et al., 2005; Martin and Pyenson, 2005). Similar trace fossils occur elsewhere in the Black Warrior basin, though in smaller numbers (Rindsberg, 1990). Hundreds of slabs have been recovered from the spoil piles at the Steven C. Minkin Site, especially from the *Cincosaurus* beds underlying the Newcastle coal seam.

Paleoenvironment

Although previous workers suggested a floodplain to lacustrine environment for the Indiana *Treptichnus* (Archer and Maples, 1984), and a brackish tidal-flat environment for Alabama *Treptichnus* (Rindsberg, 1990), in both cases these are now recognized as freshwater tidal-flat environments (Kvale et al., 1989; Archer, 1998; Pashin, 2005). This is the result of a rapid and exciting increase in knowledge about such systems. *Treptichnus* has also been reported from marine paleoenvironments, but, as will be shown, these examples are morphologically distinct from the type species, tending to have relatively short segments and a relatively regular pattern (Buatois and Mángano, 1993a).

The *Cincosaurus* beds were deposited as silty mud in a freshwater tidal setting, evidently at the head of an estuary near a delta (Pashin, 2005). As shown by Pashin, the evidence for very rapid tidal deposition includes couplets of laminae up to 0.5 cm thick, each representing one diurnal tidal cycle. Freshwater conditions are suggested by the presence of amphibian trace fossils, as well as the absence of brackish and marine indicators such as siderite or stenohaline fauna. However, J. Clack (personal commun., 2005) indicates that some Carboniferous temnospondyls may have tolerated brackish water. There is no evidence of desiccation; mudcracks and rainprints are absent. Gas-escape structures are very common, suggesting, along with the dark color of the shale and the preservation of plant debris, that the organic content of the mud was very high (Rindsberg, 2005).

The shale has probably been compacted to some

FIGURE 1. Tetrapod trackway with *Treptichnus apsorum* and gas-escape structures. UCM 788, lower surface. The scale in all figures is in centimeters.

degree, perhaps to one-third of the original thickness (J. C. Pashin, personal commun., 2005).

In slabs from the Union Chapel *Cincosaurus* beds, *Treptichnus* and U-burrows may occur alone or together, and may also accompany any of the other ichnotaxa known from the same beds, including tetrapod trackways. In contrast, at Galloway Mine no. 11, from which Aldrich's (1930) specimens were collected, slabs with tetrapod trackways generally lack invertebrate burrows, though the horseshoe crab trackway *Kouphichnium aspodon* (Aldrich, 1930) is present. The reasons for this difference are unknown, but it is clear that the Union Chapel Mine represents only one snapshot from a whole album of paleoenvironments represented in other exposures within the Black Warrior Basin, for the ranges of ichnotaxa overlap in a gradient from freshwater to quiet-water marine shelf deposits (Rindsberg, 1990). Tetrapod trackways, *Treptichnus*, and *Undichna* are characteristic of the freshwater end of this continuum.

Trace fossil assemblage of the *Cincosaurus* beds

Trace fossils in the *Cincosaurus* beds are primarily preserved in full relief within laminated shale, and are exposed on laminar surfaces as hypichnia and epichnia. Most are very shallow and not clearly visible in cross section. Among the most common ichnotaxa from the *Cincosaurus* beds, other than tetrapod trackways, are *Treptichnus, Arenicolites, Kouphichnium,* and *Undichna* (Rindsberg et al., 2001, 2004; Rindsberg and Kopaska-Merkel, 2003). Surfaces having tetrapod trackways at Union Chapel generally also contain invertebrate traces (Fig. 1). Because the field relations must be deduced from broken spoil, it is important to note that each pair of these ichnotaxa has been found in close association on single slabs, confirming that they belong to one assemblage.

Bioprint

The characters that allow recognition of the maker are called a trace's *signature* or *bioprint*. The Union Chapel *Arenicolites* has a distinctive bioprint that is shared with the local *Treptichnus,* with which it occurs. Both are evidently the burrows of the same or similar animals.

In the following sections, the focus is on the ethology and possible makers of *Arenicolites* and *Treptichnus.*

The formal, morphologically-based classification of *Arenicolites, Treptichnus,* and similar trace fossils is dealt with under "Systematic Ichnology."

ARENICOLITES
The Alabama *Arenicolites*

Arenicolites Salter, 1857 consists of simple, vertical, U-shaped, open holes with distinct walls; the burrows extend upward to two apertures at the surface of the substrate. In modern examples, the tracemaker generally lives within the U-burrow, rarely leaving it; feeding is accomplished by circulating water through the burrow (a process called irrigation or bioirrigation) and filtering particles from the water. This dwelling-burrow (domichnial) strategy favors animals that live in water having a high flux of food particles, for example, in intertidal and nearshore environments having reliably strong currents. Dense populations of filter-feeders are possible in such environments, which are unsuitable for most other species.

Many kinds of living animals can excavate vertical dwelling burrows of various kinds; certain polychaete worms, amphipod crustaceans, and insects are among those that make modern examples of *Arenicolites* (Chamberlain, 1977). In contrast, the makers of most fossil *Arenicolites* are unknown because the burrows lack sufficiently diagnostic characters, or because the significance of those characters is not understood. However, the makers of *Arenicolites* from the Steven C. Minkin Site have a distinctive bioprint.

The Union Chapel U-burrows, *Arenicolites longistriatus* n.isp., are shallow, 2.5 to 11 mm wide at the ends and 11 to 84 mm long, but generally less than 8 mm deep (Fig. 2). Compaction of shale has probably flattened the traces somewhat, possibly to a fraction of the original depth. Some are simple, but others have a shallow spreite consisting of only a few laminae (Figs. 2, 3), which can be discounted for the purposes of classification. The U-burrows' most distinctive feature is their longitudinal striation, with striae scored into the floor of the burrow (Figs. 2, 3). As shown by Uchman (2005), this bioprint makes it possible to relate the burrows to those of the larvae of modern dipterans (true flies), including chironomids (midges) and tipulids (craneflies), in fresh water.

Arenicolites longistriatus as an insect burrow

Chironomids are abundant in modern freshwater to brackish aquatic environments; some species are even marine. Their habits are as diverse as their habitats. The larvae generally build silken tubes on or within the substrate, and in some species the tube is modified as a case that protects the larva as it travels on the substrate. Some forms spin silken nets to use as filters for gathering food particles; others graze on the substrate or burrow within it; still others are carnivorous. The group includes many species that are tolerant of low-oxygen and high-organic conditions.

Tipulids occur in moist to wet terrestrial, freshwater and brackish environments, where the larvae eat roots or organic debris such as leaf litter. Unlike the chironomids, they have a rather low tolerance of high-organic conditions.

It should be noted that the fossil record of the Diptera goes back only to the Late Triassic (Evenhuis, 2004). Although Pennsylvanian trace fossils that appear to be made by dipterans may in fact have been made by otherwise unrecorded, early dipterans, it is also possible that the burrows were made by other insects, or possibly other arthropods, having similar behavior.

TREPTICHNUS
The Alabama *Treptichnus*

Treptichnus Miller, 1889 is a burrow consisting of segments connected at their ends, each one to the next, characteristically but not invariably in a zigzag pattern. The Alabama ichnospecies, *T. apsorum* n.isp., is similar to Miller's type ichnospecies, *T. bifurcus*, but, like *Arenicolites longistriatus*, is longitudinally striate (Fig. 4). Several other zigzag burrows have been included in *Treptichnus*, but represent such different behavior that they are considered here as belonging to other ichnogenera, as suggested by Buatois and Mángano (1993a) and discussed further in "Systematic Ichnology."

The Alabama *Treptichnus* consists of shallow U-shaped segments of similar dimensions and sculpture to the U-burrows described here, but connected in a zigzag pattern (Figs. 4-9), suggesting that they were made by the same or similar species. The U-shaped components can be arranged in any pattern from a regular zigzag to an irregular zigzag to a nearly straight line, though most are irregularly zigzag (Figs. 5, 7). The U's are branched not at their ends, but just before (Fig. 8), so that at the original sediment surface, only a series of alternating apertures would have been visible. Each U-shaped segment within a specimen has a relatively constant width, ranging overall from 1 to 3.5 mm, but segment length may vary threefold within a specimen, from 2.5 to 60 mm overall. At depth within the substrate, the zigzag pattern in some cases is smoothed out to form a gently curved to nearly straight *Planolites*-like burrow (Fig. 9).

The burrows are longitudinally striate, a bioprint that points to an arthropod maker. More than one lamina of mud may be preserved within a burrow, and each can be striate, suggesting that the maker could adjust the burrow upward to some degree as a response to partial filling of the burrow owing to rapid deposition. The burrows show no sign of having been filled by the maker after use, but instead were allowed to collapse. As will be shown, these features, which are significant in interpreting the makers of these burrows, are different from those of burrows ascribed to *Treptichnus* from truly marine settings.

Treptichnus bifurcus and *T. apsorum* as insect burrows

Miller (1889) based *Treptichnus* and two similar trace fossils, *Plangtichnus* and *Haplotichnus,* on specimens he found in the Lower Pennsylvanian Hindostan

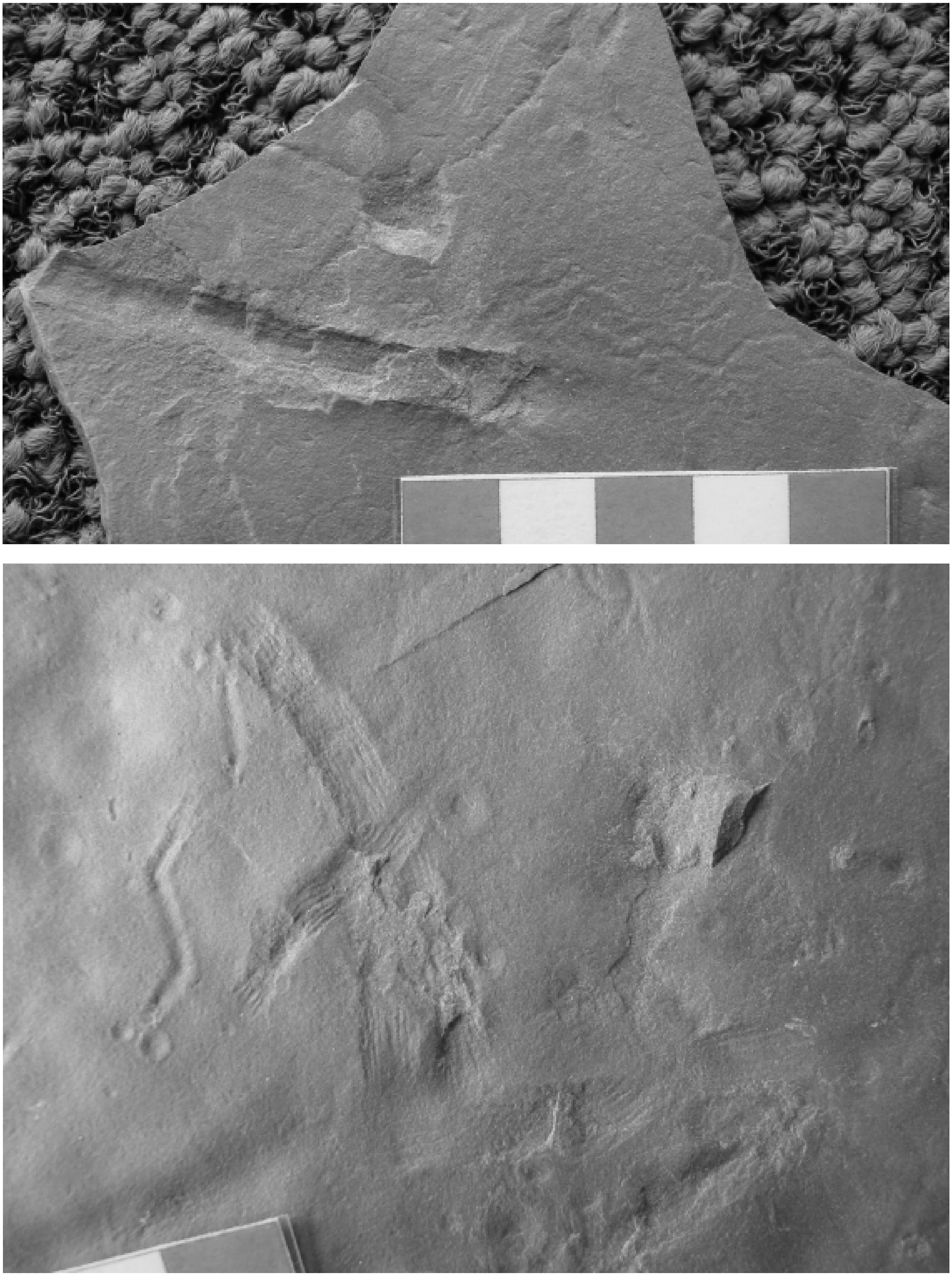

FIGURE 2. *Arenicolites longistriatus* showing the longitudinal striation for which it is named, scored into the floor of the burrow. Striation is evident in four different laminae within a rudimentary spreite. A (Top): Holotype, UCM 2038, upper surface. B (Bottom): Upper surface.

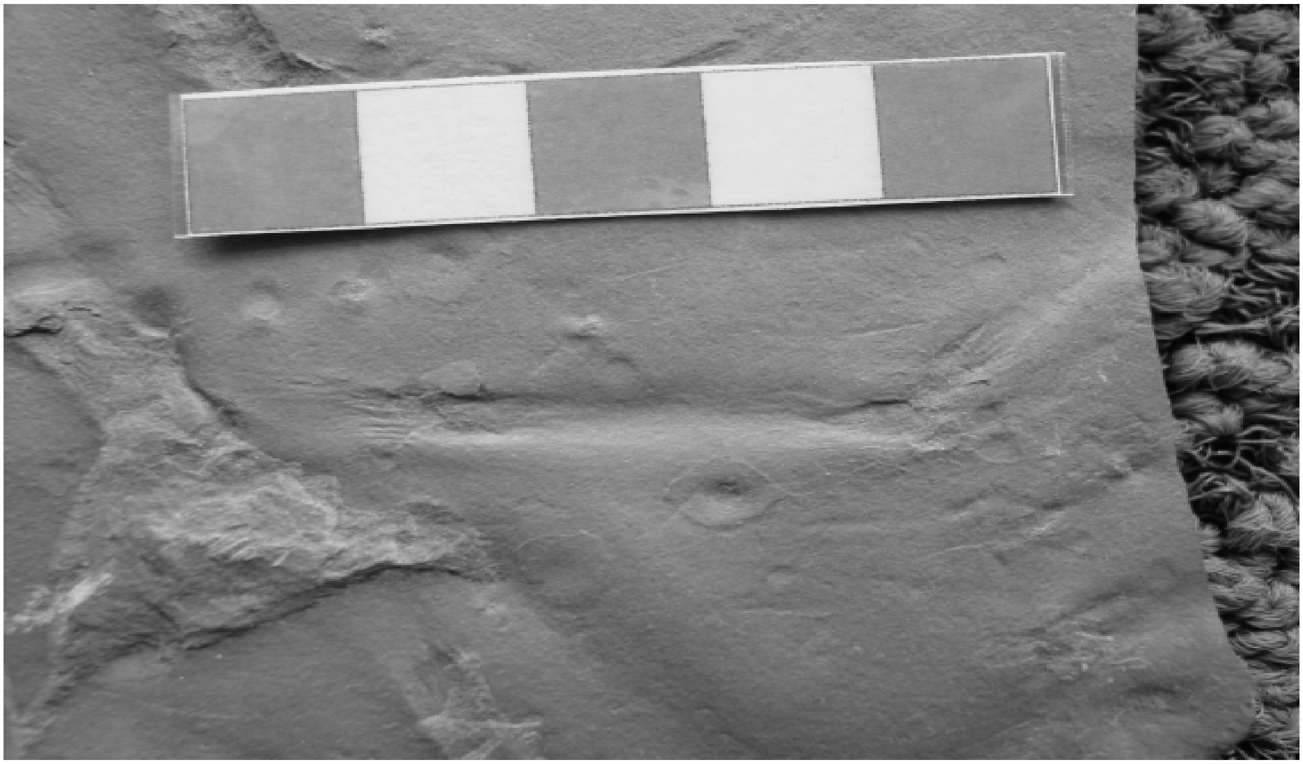

FIGURE 3. *Arenicolites longistriatus* showing collapse of sediment over shallow gallery. Upper surface. The shallow spreite can be discounted for the purposes of classification.

whetstone beds (Mansfield Formation) of Orange County, Indiana (Figs. 10-12). The original descriptions were embedded and forgotten in the section on fossil insects in a book-sized catalog of all the North American Paleozoic fossils known at that time, but the ichnogenera were rediscovered by Häntzschel (1975) and revised by Maples and Archer (1987) and Buatois and Mángano (1993a).

Miller (1889) attributed the burrows to insect larvae, and guessed that they might be the larvae of palaeodictyopterans, which were similar to dragonflies (Atkinson, 2005) and occur in both the Hindostan beds of Indiana and the *Cincosaurus* beds of Alabama. Although there is no need to read the Hindostan rock record so literally, Miller's attribution of the burrows to insect larvae was sound. If he had documented the modern analogs, it would have left a firm basis for recognition of *Treptichnus* elsewhere, but he did not. Eventually, however, *Treptichnus* of probable insect origin was discovered in Carboniferous strata in much of the Americas (Table 1). Tessier et al. (1995) and Archer et al. (1995) reported similar insect burrows on freshwater to brackish fluviotidal flats on the coast of northern France. Recent work by Uchman (2005) confirms that dipteran fly larvae are at least one of the makers of striate zigzag burrows in modern alluvial mud in Poland.

Ontogeny of the makers of *Treptichnus*

Evidence is seen for the ontogeny (growth) of the tracemakers of *Treptichnus*. In his Indiana specimens, which are of nearly the same age as the Alabama specimens and are found in similar kinds of rocks, Miller (1889) distinguished very small zigzags as *Haplotichnus*, medium ones as *Treptichnus*, and large ones as *Plangtichnus*, and some morphologic differences can be picked out between these forms. Because intermediate forms exist from *Haplotichnus* to *Treptichnus* to *Plangtichnus*, it seems possible that Miller named three stages in the behavior of one species as it progressed through life.

As shown in "Systematic Ichnology," *Haplotichnus indianensis* may be the work of very young larvae of the same species as made *Treptichnus bifurcus*, but their morphology is different enough to inspire caution about synonymizing these ichnotaxa.

In Alabama, similar relationships hold, except that *Haplotichnus* is present only at other Pottsville sites and not at Union Chapel. At any one horizon on a piece of broken spoil, each population of *Treptichnus* generally ranges only narrowly in size (Fig. 5), suggesting that tracemaker populations consisted of cohorts of the same age. However, the overall size range shows no clear evidence for separation into instars.

At some horizons, the size range is bimodal (Fig. 1). In this case, traces made at different times may be superposed, apparently accounting for the bimodality at least of U-shaped burrows and *Treptichnus*. The great overall size range suggests that deposition of the *Cincosaurus* beds encompassed at least one season, during which insect larvae had time to grow to maturity.

FIGURE 4. Longitudinal striation in a short but well-preserved specimen of *Treptichnus apsorum.* Upper surface.

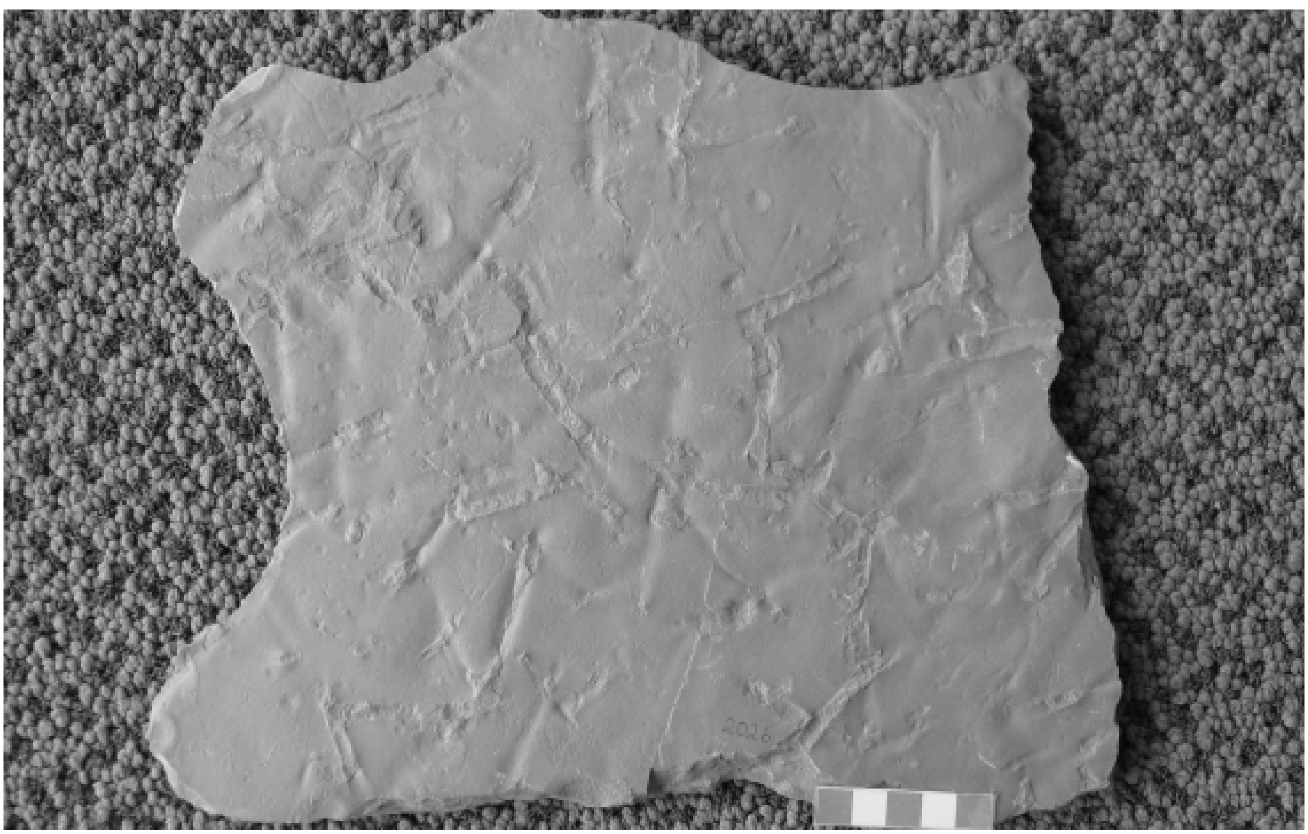

FIGURE 5. *Treptichnus apsorum* consisting of shallow, U-shaped segments of similar dimensions and sculpture to *Arenicolites longistriatus* (also present) but connected in a zigzag pattern. UCM 2026, upper surface. For closer view of holotype, see Fig. 6.

TABLE 1. Distribution of *Treptichnus bifurcus* and similar forms.

Age	Location	Ichnospecies	Reference
Oligocene	Switzerland	*T. pollardi*	Uchman et al., 2004
Late Triassic	Pennsylvania, USA	*T. pollardi*	Metz, 2000
Late Pennsylvanian-Early Permian	Santa Catarina, Brazil	*T. pollardi*	Balistieri et al., 2002
Late Pennsylvanian	Kansas, USA	*T. bifurcus* *T. pollardi*	Buatois et al., 1998a,b
Pennsylvanian	Catamarca, Argentina	*T. pollardi*	Buatois & Mángano, 1993b
Early Pennsylvanian	Alabama, USA	*T. apsorum*	this study
Early Pennsylvanian	Alabama, USA	*T. bifurcus*	Rindsberg, 1990
Early Pennsylvanian	Indiana, USA	*T. bifurcus*	Miller, 1889 Archer & Maples, 1984 Maples & Archer, 1987
Early Pennsylvanian	Nova Scotia, Canada	*T. pollardi*	Archer et al., 1995
Middle Pennsylvanian	Oklahoma, USA	*T. bifurcus*	Lucas et al., 2004
Late Mississippian	Alabama, USA	*T. bifurcus*	Rindsberg, 1991

RELATIONSHIP BETWEEN *ARENICOLITES* AND *TREPTICHNUS* IN ALABAMA

Burrows assigned to these ichnogenera are among the most common at Union Chapel. They occur on the same slabs as tetrapod trackways and the swimming trace *Undichna*, so their makers are all presumed to have lived together. Although they appear at first glance to be distinct, it is likely that *Arenicolites longistriatus* and *Treptichnus apsorum* were made by one species or at least a group of species of insect, as will be shown.

Arenicolites and *Treptichnus* from Union Chapel occur together (Fig. 5) and are built of similar U-shaped components: one in *Arenicolites*, two or more in *Treptichnus*. Segment width is 2.5 to 11 mm in *Arenicolites* and 1 to 3.5 mm in *Treptichnus;* segment length is 11 to 84 mm in *Arenicolites* and 2.5 to 60 mm in *Treptichnus*. Both are shallow U-burrows, with the greatest observed depth being 8 mm in a single specimen of *Arenicolites* in relatively coarse-grained, hence probably uncompressed, sediment. Tellingly, parallel longitudinal striation is found in both the Alabama forms despite this feature being rarely reported in either ichnogenus elsewhere. These similarities are so close, and so unusual, that they probably indicate that both types of burrows were made by the same kind of animals — possibly different species, but very likely belonging to the same group of insects or other arthropods. In more technical terms, similarities in bioprint (size and sculpture of components) as well as co-occurrence are evidence for a similar or identical maker (Rindsberg and Martin, 2003).

SYSTEMATIC ICHNOLOGY

Because the taxonomy of *Arenicolites* and *Treptichnus* is bound to that of other ichnogenera, the systematic ichnology includes discussion of some trace fossils that are not found at the Steven C. Minkin Site, especially *Treptichnus bifurcus* and *Haplotichnus indianensis*. These are based on examination of Miller's Indiana holotypes as well as observations on hundreds of specimens from the Steven C. Minkin Paleozoic Footprint Site.

Ichnofamily Arenicolitidae Richter, 1926

* 1926 Arenicolitidae Richter, p. 212.
1929 Arenicolitidae, Bentz, p. 1180-1181.
1932 Arenicolitidae, Mägdefrau, p. 158.
1941 Arenicolitidae, Hundt, p. 63.
1956 Arenicolitidae, Lessertisseur, p. 61.
1961 Arenicolitidae, Vialov, Table 1.
1975 Arenicolitidae, Häntzschel, p. *W*17.

Original diagnosis. "U-Röhre ohne Spreite. [Nicht "U in U"]." (U-tubes without spreite. [Not "U-in-U.]") (Richter, 1926, p. 212).

Emended diagnosis. Simple, unspiraled, U-shaped burrows without spreite, and systems consisting of J-shaped burrow segments with only one topologic U open at a time; plane of U normal or oblique to bedding; U oriented upward to include two apertures.

Type genus. Arenicolites Salter, 1857 by original designation.

Remarks. Richter (1926) contrasted U-shaped burrows with and without spreite, naming the U-burrows with spreite as Rhizocorallidae (properly Rhizocoralliidae, *nom. correct.*) and the U-burrows without spreite as Arenicolitidae. Believing that *Diplocraterion* lacks a

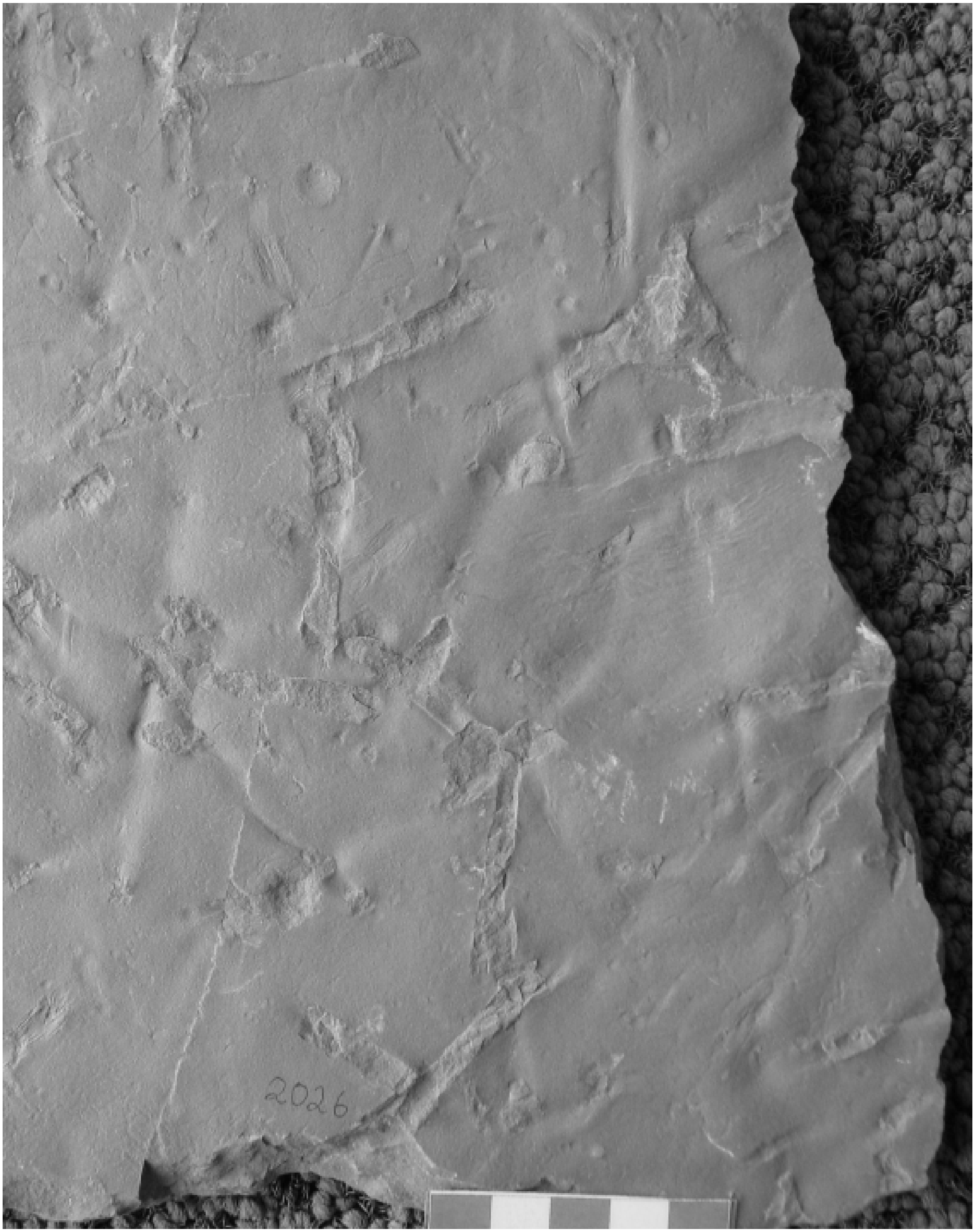

FIGURE 6. Holotype of *Treptichnus apsorum*. UCM 2026, upper surface.

spreite, Richter (1926) included it together with *Arenicolites* and perhaps *Arthraria* in Arenicolitidae. The Rhizocoralliidae included the spreite-bearing U-burrows *Rhizocorallium* and *Corophioides* (now considered to be a junior synonym of *Diplocraterion;* Fürsich, 1974). Bentz (1929) added his new ichnogenus, *Cavernaecola,* which is now considered as a synonym of *Rhizocorallium* with an obscure spreite (Häntzschel, 1975). Later revisions of ichnogenera make it necessary to rearrange the ichnogenera but not the basic diagnoses of the ichnofamilies.

As currently defined, arenicolitids include *Tisoa* Serres, 1840, *Arthraria* Billings, 1872, and perhaps *Lanicoidichna* Chamberlain, 1971 as well as *Arenicolites.*

Palaeophycus Hall, 1847 is currently rather broadly defined (Pemberton and Frey, 1982), and includes some species of U-burrows such as *P. triadicus* (Fliche, 1906), and *P. alternatus* Pemberton and Frey, 1982. As described by Pollard (1981, p. 573) based on specimens from the Triassic of England, *Palaeophycus triadicus* consists of short, subhorizontal, fusiform burrows having a sculpture of anastomosing longitudinal striae. *P. alternatus,* from the Upper Ordovician of the Cincinnati Arch, consists of short, subhorizontal burrows having a sculpture of both longitidunal and transverse striae (Osgood, 1970, pl. 76, fig. 9; Pemberton and Frey, 1982). *P. striatus* might be added to this list, as Hall (1852) emphasized its originally open character and lack of branching, but the types are incomplete so the full burrow morphology is unknown (Osgood, 1970; Pemberton and Frey, 1982). U-shaped burrows described from modern sediments may have long horizontal components compared to gallery width (e.g., MacGinitie and MacGinitie, 1968). The simple, U-shaped forms of *Palaeophycus* should be reassigned to another ichnogenus such as *Arenicolites;* further work on topotypes is needed before *P. striatus* can be understood.

Trichophycus Miller and Dyer, 1878 is another ichnogenus that includes simple, branched, and even spreite-bearing U-burrows and networks made of such components. Osgood (1970, p. 347) suspected that the simple form "*Palaeophycus*" *virgatus* Hall, 1847 is an older synonym of *Trichophycus venosus* Miller, 1879, and he was probably correct. In the best preserved specimens of *Trichophycus venosus*, the bioprint includes the inconstant diameter of the gallery, which has nodes that bear biradial sets of striae that are consistent with a trilobite maker (Seilacher and Meischner, 1964). The type species, *T. lanosus* Miller and Dyer, 1878, is more irregular than most and shows the striate pattern well (Osgood, 1970, pl. 68, figs. 2, 8). These features are more important to the taxonomy of *Trichophycus* than the branching pattern, which is labile. *Trichophycus* can thus be diagnosed as a mainly subhorizontal burrow or burrow system composed of one or more broad, originally open, U-shaped burrows, characteristically having a nodose gallery, and in exceptionally well preserved cases, with biradial striation on the walls of nodes. These features distinguish *Trichophycus* from *Treptichnus*.

In classifying U-burrows, one should keep in mind that the burrow must accommodate the growth of the animal that lives within it. For example, the spreite of *Diplocraterion* is a way of increasing the length and diameter of the burrow while utilizing part of it. The U can also be lengthened in other ways. In the simplest case, the tracemaker can abandon the burrow and dig a new one, but this leads to waste and the risk of predation.

The marine polychaete *Chaetopterus variopedatus* lives in a U-burrow with a tough, parchment-like lining; the animal's body occupies only about a third of the burrow (Enders, 1908). To enlarge its burrow, the worm cuts through the lining, digs a new burrow segment to the surface, and blocks off the old passage. For practical purposes such as bioirrigation, the resulting burrow is still U-shaped and oriented in one vertical plane to take advantage of prevailing currents. However, a fossilized example including the whole history of the burrow would be W-shaped, and the Carboniferous type species of *Arenicolites, A. carbonarius* Salter, 1856, is now recognized as having this pattern (Pollard, 1999). The key to recognition is the maker's preference for keeping all the burrow segments in one plane; systems that are built of J-shaped segments in different planes are not *Arenicolites.*

Ichnogenus *Arenicolites* Salter, 1857

* 1857 *Arenicolites* Salter, p. 204.
1977 *Arenicolites*, Chamberlain, p. 8.

Original diagnosis. "*Arenicolites* might stand for all worm-burrows with double openings" (Salter, 1857, p. 204).

Emended diagnosis. Simple, vertical U-shaped burrows with two apertures above.

Type ichnospecies. *Arenicola carbonaria* Binney, 1852, p. 192, by subsequent designation of Richter (1924, p. 137).

Remarks. Chamberlain (1977, p. 8) briefly delineated the differences of several ichnospecies of *Arenicolites,* only some of which are mentioned here. The ichnogenus has an unresolved taxonomic problem: The type ichnospecies, *A. carbonarius*, is now known to be branched (Pollard, 1999), though probably only two apertures were open at any one time. The most characteristic species is *A. sparsus* Salter, 1856, a simple, regular U-shaped burrow having vertical limbs and lacking a thick lining. *A. curvatus* Goldring, 1962 has inclined limbs. The new ichnospecies, *A. longistriatus*, is subhorizontal, at least after compaction, and is longitudinally striate.

Makers of modern *Arenicolites* include polychaetes, crustaceans, and insects (Chamberlain, 1977).

Arenicolites longistriatus n.isp.
Figs. 2, 3, 5

Etymology. Latin *longus*, long, and *striatus*, furrowed, striate.

Description. Unbranched, subhorizontal U-shaped burrows with parallel longitudinal striae all of approximately even depth.

Remarks. Comparisons to other species of *Arenicolites* are given under the ichnogenus. In addition, *Palaeophycus* includes ichnospecies with very shallow, originally open U-shaped burrows. *P. striatus* Hall, 1852 has parallel longitudinal striae, commonly with the median stria particularly deep; its complete burrow morphology is unknown (Osgood, 1970; Pemberton and Frey, 1982). *P. triadicus* (Fliche, 1906) is similar to *P. striatus*, but has a fusiform outline and anastomosing striae (Pollard, 1981, p. 573). *P. alternatus* Pemberton and Frey, 1982 has transverse as well as longitudinal striation.

Holotype. Geological Survey of Alabama Paleontological Collection, UCM 2038.

Ichnofamily *incertae sedis*
Ichnogenus *Treptichnus* Miller, 1889

*	1889	*Plangtichnus* Miller, p. 580.
*	1889	*Treptichnus* Miller, p. 581.
non	1948	Feather-stitch trail, Wilson, p. 57.
	1975	*Plangtichnus*, Häntzschel, p. *W*95.
partim	1975	*Treptichnus*, Häntzschel, p. *W*117-118, figs. 68(5a-c).
	1984	*Trepticynus*, Archer and Maples, p. 455 [*nom. null*.].
partim	1993a	*Treptichnus*, Buatois and Mángano, p. 220-221.
non	1997	*Treptichnus*, Wetzel and Uchman, p. 151 [cf. *Belorhaphe*].
partim	1998	*Treptichnus*, Uchman et al., p. 272-273.
partim	1998b	*Treptichnus*, Buatois et al., p. 157-158.
non	2000	*Treptichnus*, Schlirf, 2000, p. 156-157 [cf. *Belorhaphe*].
	2002	*Treptichnus*, Balistieri et al., p. 20.

Type species. *Treptichnus bifurcus* Miller, 1889 by original diagnosis.

Original diagnoses. *Treptichnus:* "A zigzag, half-cylindrical, continuous trail, forked at each angle, and running in any direction; each line is prolonged in the direction in which the animal moved, at the angle, so as to form a short fork or projection" (Miller, 1889, p. 581).

Plangtichnus: "A zigzag, half-cylindrical, broken trail, running in any and every direction; sometimes dotted or sunk deeper at the angles than at other places, or most depressed between the angles in some cases" (Miller, 1889, p. 580).

Emended diagnosis. Subhorizontal burrow consisting of one series of downbowed or J- to U-shaped segments joined near or at their ends in a uniserial pattern that may be irregular, zigzag, or arcuate. Segments extending to sediment-water interface with at least one aperture originally open; very gently downbowed or nearly straight; fill passive, commonly by collapse.

Remarks. Not all zigzag burrows were made by the same animals or in the same way. In ichnotaxonomy, behavior is the basis of classification. Each trace represents major and minor modes of behavior, but usually one can be recognized as the major function of the trace, such as locomotion, resting or hiding, deposit-feeding, grazing, or dwelling (Seilacher, 1953). If the zigzag burrows from different times and places represent fundamentally different behaviors as recognized morphologically, then they should be separated into distinct ichnogenera, as previously suggested by Buatois and Mángano (1993a).

The history of ichnogenus *Treptichnus* has so far been one of including more and more kinds of zigzag burrows, three of whose strategies are described here: (1) deposit-feeding, with narrow older segments abandoned to collapse (*Treptichnus* in a strict sense), (2) farming with all segments in simultaneous use (cf. *Belorhaphe*), and (3) deposit-feeding with older segments backfilled (unnamed ichnogenus). Each of these requires a separate ichnogeneric name — a position that may seem radical, but was previously articulated in very similar form by Buatois and Mángano (1993a).

Treptichnus and *Plangtichnus* consist of zigzag burrows that were originally described by Miller (1889) from Lower Pennsylvanian freshwater tidal flat deposits in Indiana. *Haplotichnus* Miller, 1889 is a smaller burrow having a rather angular path within a looping or wandering course. In their revision of Miller's Hindostan ichnogenera based on type and new material, Maples and Archer (1987) showed that *Plangtichnus* is a preservational aspect of *Treptichnus* in which the uppermost part of the burrow system is absent, but left the question open whether *Plangtichnus* should be maintained as a separate ichnogenus. Buatois and Mángano (1993b) formally placed *Plangtichnus* as a synonym of *Treptichnus*, and most subsequent workers have accepted this (though not all; Archer et al., 1995).

Miller's *Treptichnus bifurcus* and similar Carboniferous forms were poorly understood until Archer and Maples (1984) and Maples and Archer (1987) reinvestigated the Hindostan beds and their trace fossils. Buatois and Mángano (1993a) revised ichnogenus *Treptichnus* further. Figures of modern insect-made analogs were published in the paleontologic literature even later (Uchman, 2005; Rindsberg et al., 2004). It is now clear that these burrows represent deposit-feeding in a zigzag or other segmented, serial pattern, with older segments abandoned after use. Segments extended to the sediment-water interface but only one or two may have been open at any one time, the others probably being allowed to collapse.

Häntzschel (1975) broadened the concept of *Treptichnus* to include the zigzag or "feather-stitch trails" described by Wilson (1948) and Seilacher and Hemleben (1966) from Ordovician and Devonian strata. Häntzschel illustrated Paleozoic marine examples that differ from the type species in having relatively thin and deep galleries, which branched at a relatively deep level and apparently were all open at the same time (Schlirf, 2000).

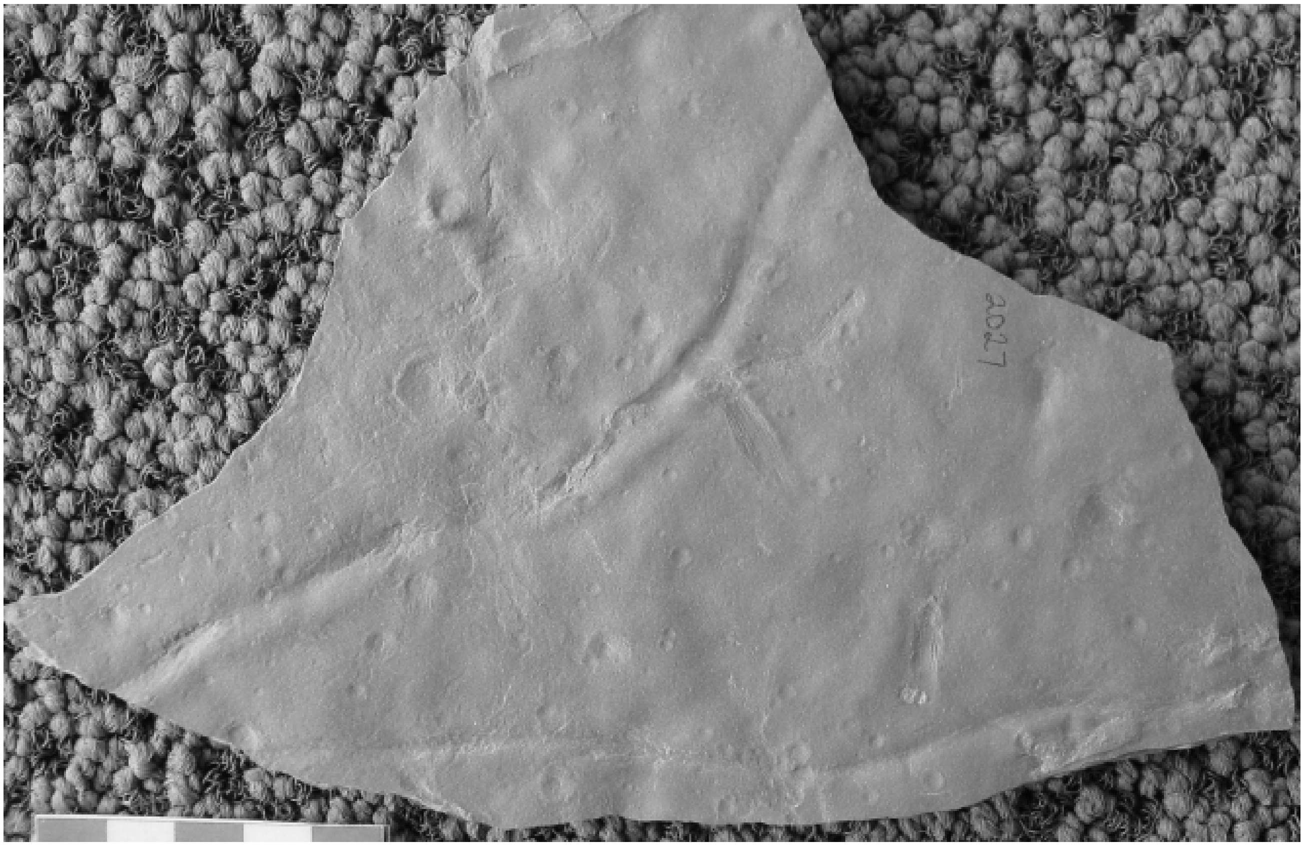

FIGURE 7. Obscure *Treptichnus apsorum* with nearly straight pattern. UCM 2027, upper surface. (For a closer view of the striate *Treptichnus* near the center, see Fig. 4.)

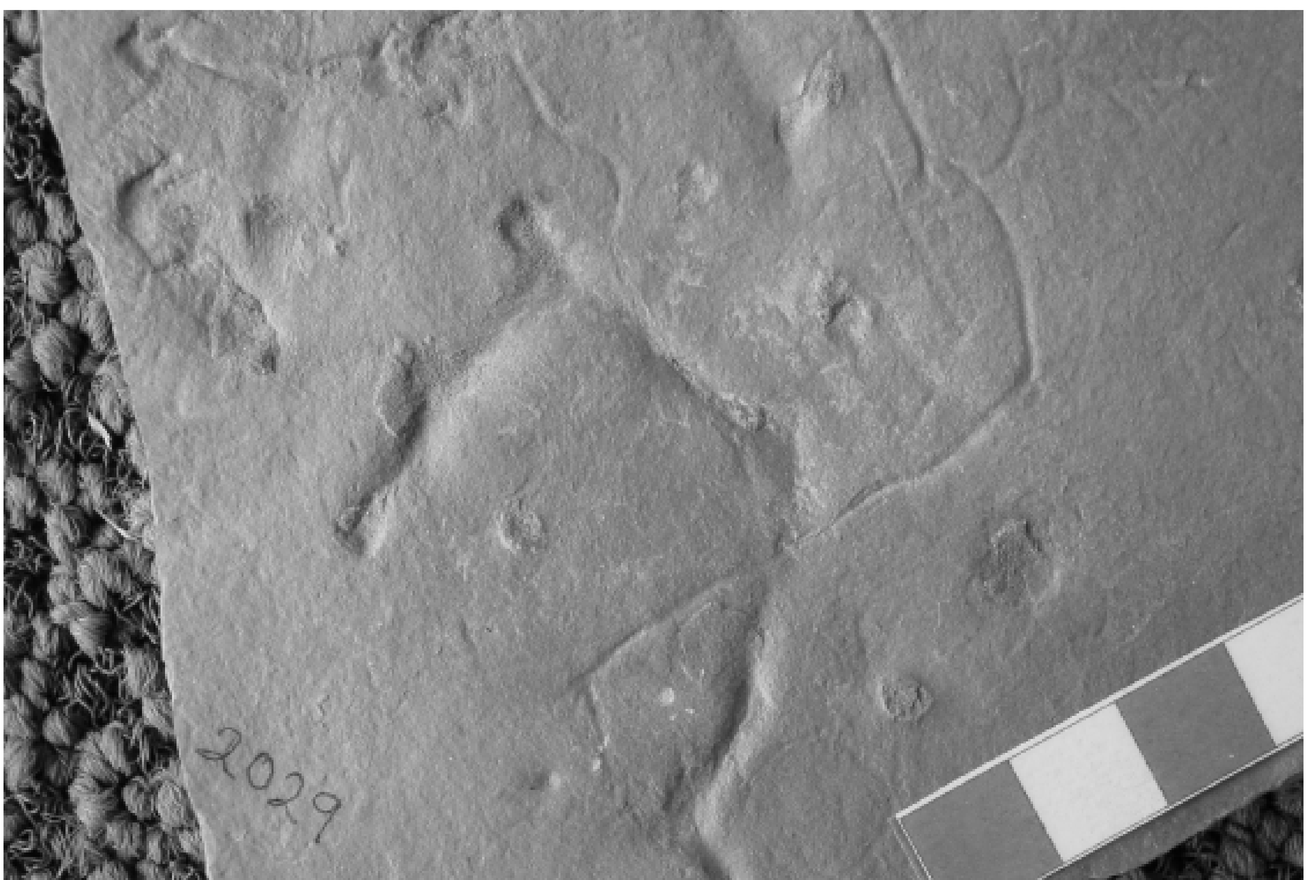

FIGURE 8. *Treptichnus apsorum* showing branching near ends of segments. UCM 2029, upper surface.

Häntzschel thus presented a misleading search image. Similar forms were later found in the Eocene flysch of Poland (Uchman et al., 1998) and in other deposits scattered through the Phanerozoic (Schlirf, 2000). These burrows were originally open, with several apertures and no backfill, characteristics more consistent with an agrichnial interpretation than with a deposit-feeding interpretation (Schlirf, 2000); Buatois and Mángano (1993a) questioned whether these burrows belonged in *Treptichnus*, and they are rejected here. The "featherstitch" *Treptichnus* shows similarities with *Belorhaphe*, as pointed out by Buatois and Mángano (1993a).

Jensen (1997, p. 91), and other researchers expanded the concept of *Treptichnus* still further to include the Lower Cambrian trace fossil that Seilacher (1955) named *Phycodes pedum*. Because "*Treptichnus*" *pedum* is now used to define the Precambrian-Cambrian boundary (Brasier et al., 1994), its taxonomy, paleoecology, and stratigraphy are matters of broad interest. *T. pedum* and similar ichnospecies differ from *T. bifurcus* in several respects. This "*pedum* group" has much thicker and more irregular branches whose ends are blunt, although they apparently did extend to the surface as in *T. bifurcus*, as shown in Seilacher's reconstruction (1955, fig. 4b). In well-preserved examples such as those described by Jensen (1997, fig. 62B), branches were evidently filled passively rather than allowed to collapse as in Carboniferous examples. This is clearly the work of deposit-feeders, but the makers are unknown.

Devonian specimens attributed to *Treptichnus pedum* from the Wapske Formation of New Brunswick have a distinctive bioprint. The tips of the branches are smooth and conical, distinctly separate from the main part of the branches, which have an annulate sculpture (Han and Pickerill, 1995). These specimens may be better placed in still a fourth ichnogenus and species.

Thus, if the overall zigzag shape is set aside, then nearly all the forms attributed to *Treptichnus* fall into three groups (Table 2): (1) *T. pedum* and similar forms that branch irregularly and have relatively broad branches (latest Precambrian to Cambrian, shallow marine); (2) *Belorhaphe*-like "feather-stitch" burrows that branch regularly deep in the sediment and whose branches are relatively narrow and constant in diameter, but with extensions that probably reached the surface (Phanerozoic, shallow to deep marine); and (3) *T. bifurcus* and similar forms that branch irregularly just below the sediment-water interface, at or near apertures, and have relatively narrow branches of fairly constant diameter (Carboniferous and recent, freshwater to brackish). Groups 1 and 2 have unknown makers but group 3 is made by insect larvae today. In such cases, it is preferable to choose morphologic criteria that shed light on the maker, behavior, paleoenvironment, or stratigraphy of the trace fossils, rather than adhere to a strictly geometric approach that groups all zigzag burrows together based on a single feature that is conspicuous to the human eye.

The zigzag configuration supports either a deposit-feeding (fodinichnial) or a farming and trapping (agrichnial) life strategy. In the fodinichnial strategy, an animal shifts from one segment to the next as it feeds on the sediment, perhaps maintaining the last segment as a bioirrigated open hole. In the agrichnial strategy, the animal keeps all the segments open as a trap to catch meiofauna, or alternatively as a farm for microbes that are periodically scraped from the walls. Because behavior, not a human geometric ideal, is the touchstone of ichnotaxonomy, it is desirable to distinguish these very different strategies at the ichnogeneric level despite their superficial similarity in form. In principle, fodinichial zigzag burrows should have relatively indistinct walls compared to agrichnial ones, because deposit-feeding would have been followed by only a brief period of dwelling before older segments filled or collapsed, whereas farming or trapping would have required maintenance of an open hole for a long time. However, this aspect has not yet been investigated for the marine examples.

Treptichnus apsorum **n.isp.**
Figs. 1, 4-8

Etymology. The name honors the collective effort of the Alabama Paleontological Society (APS), and accordingly is given a plural genitive suffix in the masculine (general) gender. It should be pronounced in three syllables as *ap-sorum*, not as *A-P-S-orum*.

Diagnosis. *Treptichnus* consisting of shallow, U-shaped segments serially connected in a zigzag, irregular, or other pattern near their ends, and, where well preserved, having longitudinal striae on at least the lower surface of the burrow, or on each of several laminae flooring the burrow, or in some cases on the sediment beyond the apertures.

Description. Subhorizontal burrow consisting of uniserial segments arranged in zigzag or irregular fashion, with shallow, U-shaped segments curving upward into shafts near junctions; parallel longitudinal striation on floor of well-preserved galleries; some galleries with a minimal spreite of a few laminae. Preservation as full-relief epichnia and hypichnia. Longitudinal sections may show anything from the zigzag lower portion to a series of dots for the upper portion. Measurements: gallery width, 1 to 3.5 mm, nearly constant in individual; segment length ranging as much as threefold within an individual, 2.5 to 60 mm; shaft width, about 2 mm; maximum observed length, 9.5 cm.

Remarks. In *Treptichnus bifurcus* Miller, 1889, branching is predominantly zigzag, but topotypes include a broad range of forms, including systems branching nearly in a straight line or branched consistently to one side to form an arc. Burrow diameter bulges toward the center or is nearly constant in this ichnogenus, and the burrow segments presumably curved upward to reach the sediment-water interface.

Treptichnus apsorum resembles *T. bifurcus* in most respects. However, well-preserved specimens of *T. apsorum* have distinctive longitudinal striation, in some cases on each of several laminae on the floor of the burrow. Also, *T. apsorum* has a relatively great size range compared to *T. bifurcus*, whose segments in its type area

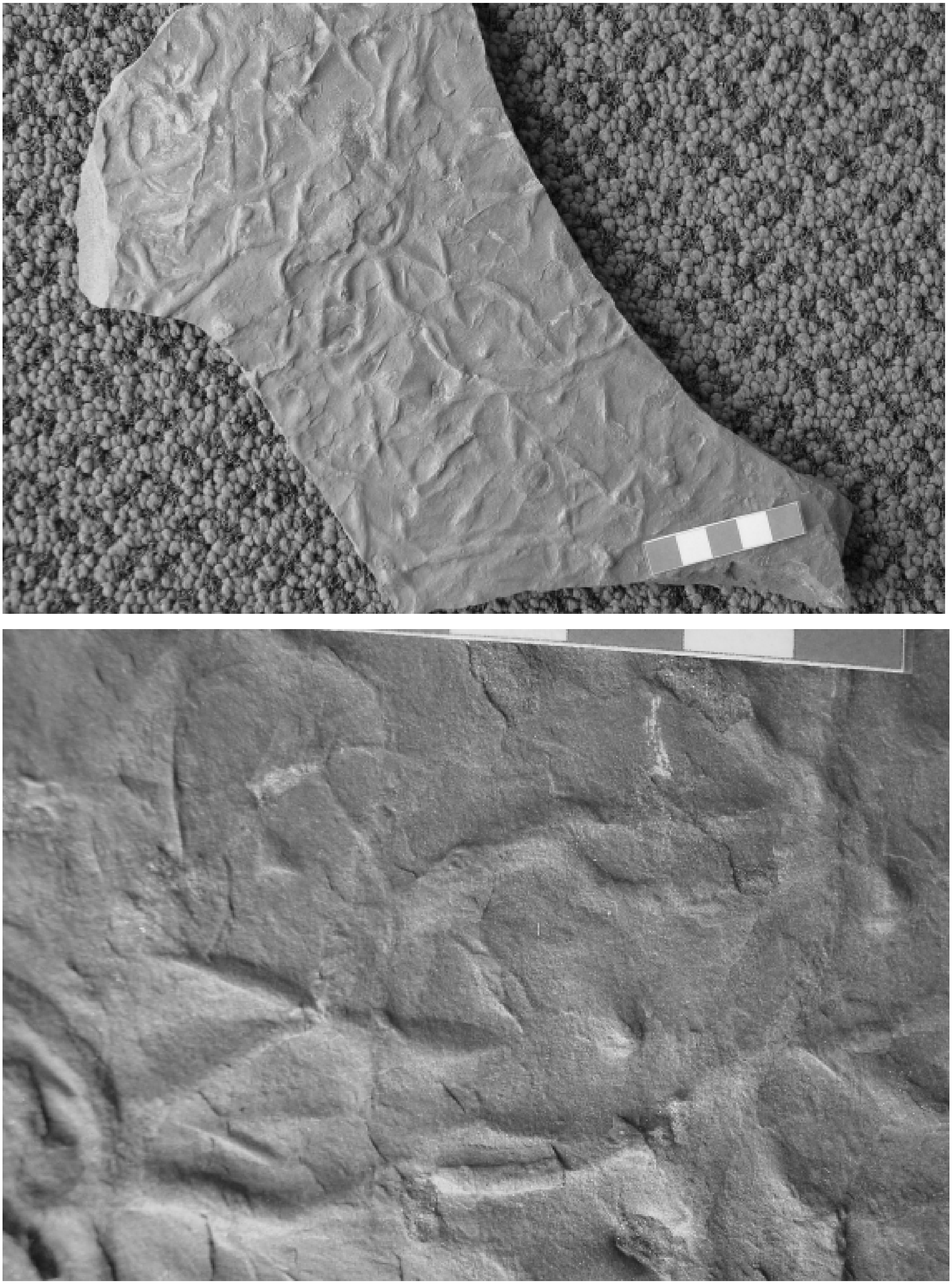

FIGURE 9. A (top). *Treptichnus apsorum* with relatively straight, smooth pattern (reminiscent of *Planolites*) at depth within the substrate. Note the angularity of the burrows' course. Lower surface. B (bottom): Closer view.

TABLE 2. Species attributed to *Treptichnus* Miller, 1889 by various authors.

Mostly Carboniferous freshwater or marginal-marine forms: *Treptichnus sensu stricto*
Treptichnus bifurcus Miller, 1889 = *T. bifurcus* (type species)
Plangtichnus erraticus Miller, 1889 = *T. bifurcus*
Spirodesmos interruptus Andre, 1920, *sensu* Archer & Maples, 1984 = *T. bifurcus*
Treptichnus pollardi Buatois & Mángano, 1993a = *T. pollardi*
Treptichnus apsorum n.isp.
Post-Cambrian marine forms: cf. *Belorhaphe* Fuchs, 1895
"Feather-stitch trail", Wilson, 1948
Treptichnus aequalternus Schlirf, 2000
Treptichnus meandrinus, Uchman et al., 1998
Treptichnus pedum, sensu Han & Pickerill, 1995
Belorhaphe protopalaeodictyum Bandel, 1973
Cambrian marine forms (*pedum* group): unnamed ichnogenus
Treptichnus coronatum MacNaughton & Narbonne, 1999
Treptichnus lublinensis Pacześna, 1996
Phycodes pedum Seilacher, 1955
Treptichnus rectangularis Orlowski & Żylińska, 1996
Treptichnus triplex Palij, 1976

range from 2.0 to 8.4 mm long (Maples and Archer, 1987).

Range in Alabama. Lower Pennsylvanian Pottsville Formation, Steven C. Minkin Paleozoic Footprint Site near Union Chapel, Walker County, Alabama.

Holotype. UCM 2026.

***Treptichnus bifurcus* Miller, 1889**
Figs. 10, 11

* 1889 *Treptichnus bifurcus* Miller, p. 581, fig. 1095 [Lower Pennsylvanian, Indiana].
* 1889 *Plangtichnus erraticus* Miller, p. 580, fig. 1093 [Lower Pennsylvanian, Indiana].
1977 *Treptichnus bifurcus*, Forney et al., p. 32 [Lower Pennsylvanian, Indiana].
1977 *Plangtichnus erraticus*, Forney et al., p. 30 [Lower Pennsylvanian, Indiana].
1984 *Plangtichnus erraticus*, Archer and Maples, p. 452, figs. 5C, E, G, 6A-D [Lower Pennsylvanian, Indiana].
1984 *Treptichnus bifurcus*, Archer and Maples, p. 455, figs. 5B, D, F, I [Lower Pennsylvanian, Indiana].
1984 *Spirodesmos interruptus* Andrée, Archer and Maples, p. 455, fig. 5B [Lower Pennsylvanian, Indiana].
? 1985 ?*Thalassinoides* Ehrenberg, Miller and Knox, p. 89, pl. 1A [Pennsylvanian, Tennessee].
1990 *Treptichnus*, Rindsberg, p. VI-95, fig. VI-39e [Lower Pennsylvanian, Alabama].
1991 *Treptichnus bifurcus*, Rindsberg, p. 141, pl. 2, fig. 6 [Upper Mississippian, Alabama].
partim 1993a *Treptichnus bifurcus*, Buatois and Mángano, p. 221, figs. 2A-D [Lower Pennsylvanian, Indiana].
? 1995 *Plangtichnus erraticus*, Archer et al., p. 2034, figs. 7a-c [Carboniferous, Nova Scotia].
? 1995 *Plangtichnus* sp., Greb and Archer, p. 99, fig. 9B [Middle Pennsylvanian, Kentucky].
1997 *Treptichnus bifurcus*, Buatois et al., figs. 5B, 7D [Upper Pennsylvanian, Kansas].
non 1997 *Treptichnus bifurcus*, Jensen, p. 91, fig. 62A [Lower Cambrian, Sweden].
1998 Insect trackways, Archer, fig. [1] [Lower Pennsylvanian, Indiana].
1998a *Treptichnus bifurcus*, Buatois et al., figs. 21, 24 [Upper Pennsylvanian, Kansas].
1998b *Treptichnus bifurcus*, Buatois et al.,

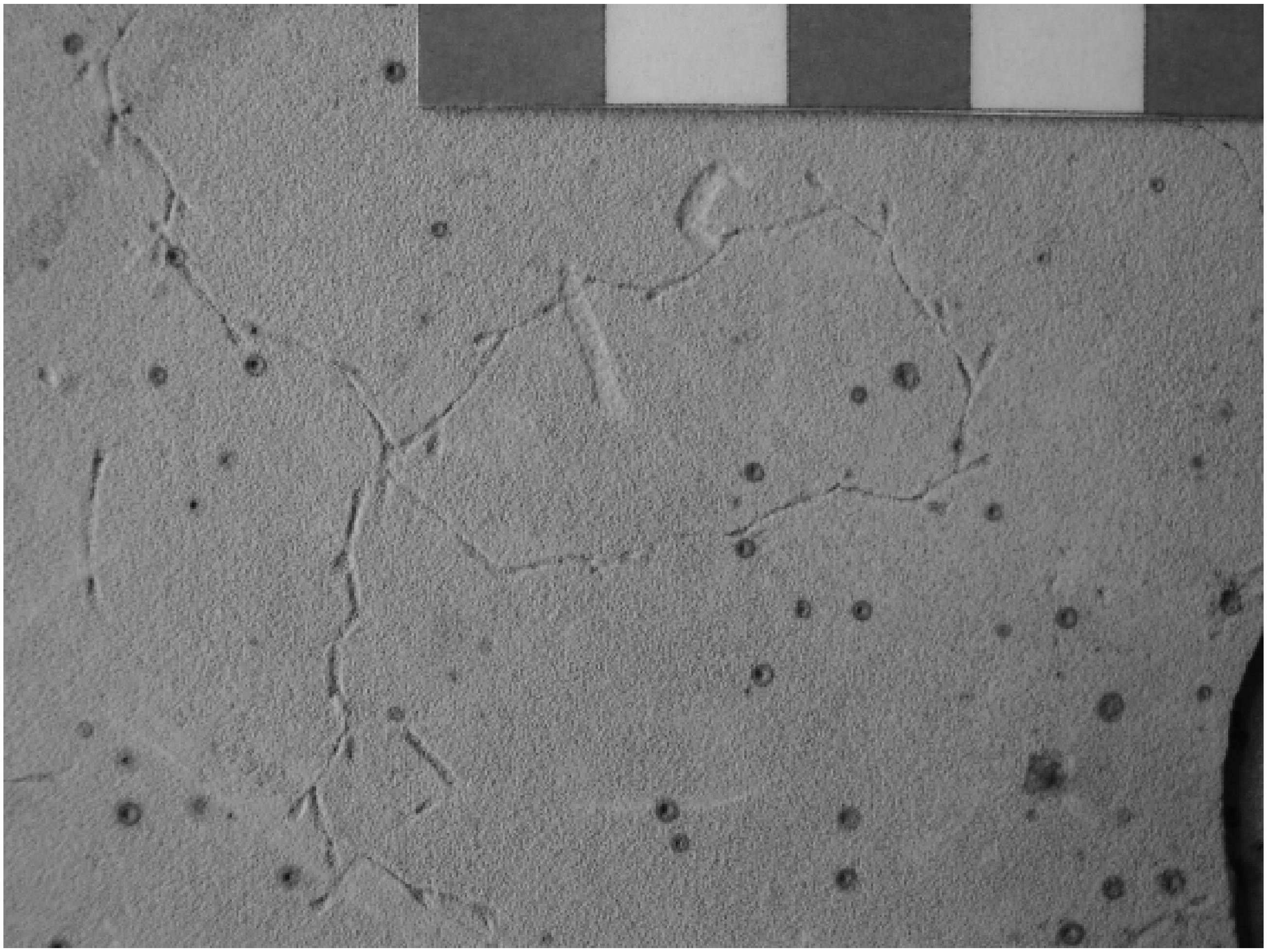

FIGURE 10. Holotype of *Treptichnus bifurcus* from the Lower Pennsylvanian Hindostan whetstone beds (Mansfield Formation) of Orange County, Indiana. Field Museum of Natural History, UC 54099, upper surface.

p. 158, fig. 4.6 [Upper Pennsylvanian, Kansas].

? 1998a Irregular networks, Buatois et al., fig. 21 [Pennsylvanian, Kansas].

non 1998 *Treptichnus bifurcus*, Uchman et al., p. 273-274 [Eocene, Poland] [cf. *Belorhaphe*].

non 2000 *Treptichnus bifurcus*, Schlirf, p. 157-158, figs. 12A, B, pl. 2, figs. 7, 8, 10 [Upper Jurassic, France] [cf. *Belorhaphe*].

2004 *Treptichnus* isp., Uchman et al., p. 140, figs. 5C, 6F, 9B [Oligocene, Switzerland].

Original diagnoses. *Treptichnus bifurcus:* “A zigzag, half-cylindrical, continuous trail, quite evenly depressed, and forked at each angle; the bifurcation takes place in the direction in which the animal moved, but generally is less sunken than the trail, and sometimes shows simply a dot disconnected with the angle” (Miller, 1889, p. 581).

Plangtichnus erraticus: “A simple, irregularly zigzag, half-cylindrical, broken trail, running in any and every direction; depressed in spots deeper than the general trail” (Miller, 1889, p. 580).

Emended diagnosis. Subhorizontal burrow consisting of a series of U-shaped segments joined angularly at or near their ends; burrow commonly but not invariably zigzag; surface of burrow smooth.

Remarks. *Plangtichnus erraticus* is a preservational aspect of *Treptichnus bifurcus* (Maples and Archer, 1987; Buatois and Mángano, 1993a). *Treptichnus pollardi* Buatois and Mángano, 1995 differs from *T. bifurcus* in having shafts extending upward from segment junctions rather than as part of the segments themselves.

Range in Alabama. *T. bifurcus?:* Upper Mississippian lower Parkwood Formation, Irondale, Jefferson County, Alabama (Rindsberg, 1991); Lower Pennsylvanian Pottsville Formation (Mary Lee coal zone), Walker County, Alabama (Rindsberg, 1990).

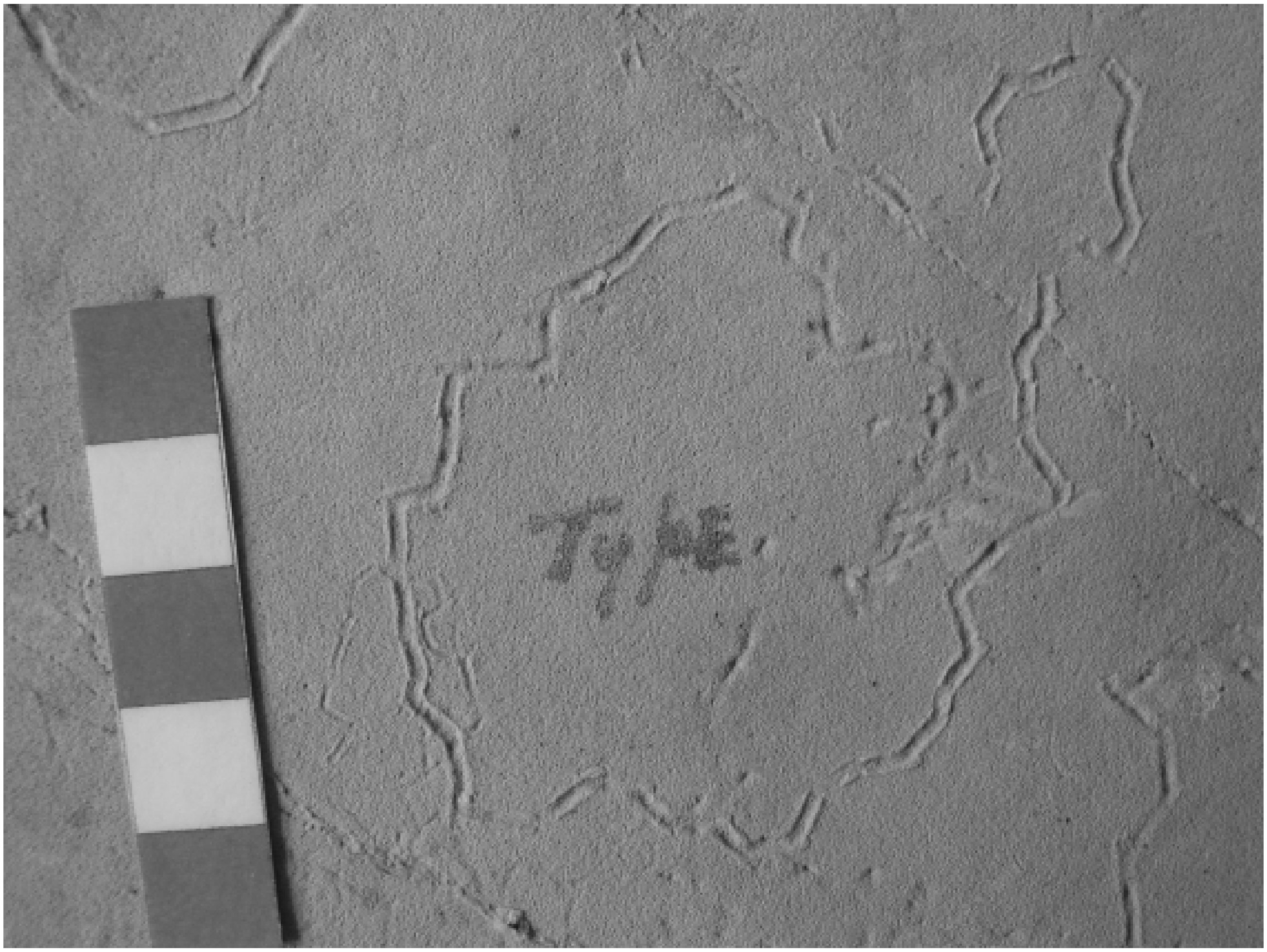

FIGURE 11. Holotype of *Plangtichnus erraticus* from the Lower Pennsylvanian Hindostan whetstone beds (Mansfield Formation) of Orange County, Indiana. Field Museum of Natural History, UC 36077, upper surface.

Ichnogenus *Haplotichnus* Miller, 1889

* 1889 *Haplotichnus* Miller, p. 578, fig. 1086 [Lower Pennsylvanian, Indiana].
1984 *Haplotichnus*, Archer and Maples, p. 450, fig. 4F [Lower Pennsylvanian, Indiana].
? 1985 *Gordia* Emmons, Miller and Knox, p. 84, pl. 2E [Pennsylvanian, Tennessee].
1987 *Haplotichnus*, Maples and Archer, p. 890 [Lower Pennsylvanian, Indiana].
1994 *Haplotichnus*, Rindsberg, p. 59 [Upper Mississippian, Alabama].
partim 1998b *Gordia*, Buatois et al., p. 155 [*G. indianaensis* only].

Original diagnosis. "Simple, small, half-cylindrical trails running in any direction" (Miller, 1889, p. 578).

Diagnosis. Simple trail, straight to curved, commonly in a self-penetrating "scribbled" pattern; path turned smoothly or sharply.

Type Species. *Haplotichnus indianensis* Miller, 1889 by original designation.

Remarks. *Haplotichnus* differs from the superficially similar *Gordia* in two ways. First, *Gordia* is apparently a burrow, whereas *Haplotichnus* is a trail or at most a very shallow burrow. Second, as pointed out by Maples and Archer (1987) and Buatois et al. (1997), *Haplotichnus* has relatively angular turns as compared to *Gordia*. The sharp turns are significant because short-bodied animals such as arthropods can change direction more easily than long-bodied worms (Rindsberg and Martin, 2003). Thus, *Gordia* may be the work of polychaetes, oligochaetes, and other vermiform animals; *Haplotichnus* is evidently the work of insects and other arthropods, as recognized by Miller (1889).

Haplotichnus indianensis Miller, 1889
Fig. 12

1889 *Haplotichnus indianensis* Miller, p. 578, fig. 1086 [Lower Pennsylvanian, Indiana].
1977 *Haplotichnus indianensis*, Forney et al., p. 28-29 [Lower Pennsylvanian,

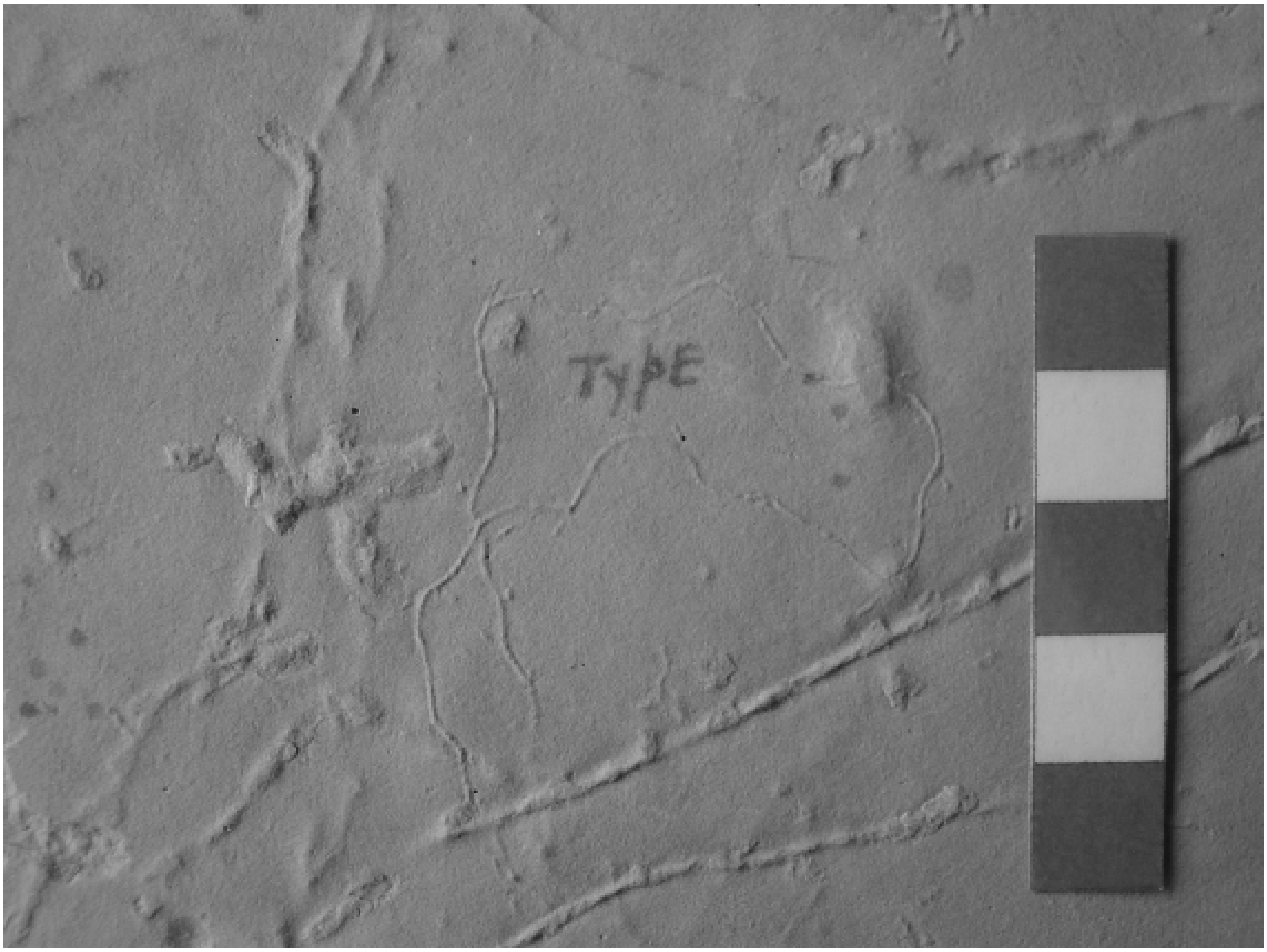

FIGURE 12. Holotype of *Haplotichnus indianensis* from the Lower Pennsylvanian Hindostan whetstone beds (Mansfield Formation) of Orange County, Indiana. Field Museum of Natural History, UC 36076, upper surface. Straight *Treptichnus bifurcus* is also present.

Indiana].
1984 *Haplotichnus indianensis,* Archer and Maples, p. 450, fig. 4F [Lower Pennsylvanian, Indiana].
1987 *Haplotichnus indianensis,* Maples and Archer, p. 890-891, fig. 2.1 [Lower Pennsylvanian, Indiana].
? 1993b *Haplotichnus indianensis,* Buatois and Mángano, p. 242, fig. 3E [Upper Carboniferous, Catamarca, Argentina].
? 1995 *Haplotichnus*? sp., Archer et al., p. 2031-2034, fig. 6e [Lower Pennsylvanian, Nova Scotia].
1997 Irregular networks, Buatois et al., fig. 8D [Upper Pennsylvanian, Kansas].
1997 *Gordia indianaensis*, Buatois et al., fig. 8B [*nom. null.*] [Upper Pennsylvanian, Kansas].
1998a *Gordia indianaensis*, Buatois et al., fig. 17 [*nom. null.*] [Upper Pennsylvanian, Kansas].
1998b *Gordia indianaensis*, Buatois et al., p. 155, fig. 4.2 [*nom. null.*] [Upper Pennsylvanian, Kansas].

Original diagnosis: "A simple half-cylindrical trail, needle-like in size, running in straight or crooked lines, or crossing itself" (Miller, 1889, p. 578).

Haplotichnus ornatus **n.isp.**
Fig. 13

1990 *Haplotichnus,* Rindsberg, fig. VI-41I [Lower Pennsylvanian, Alabama].
1994 *Haplotichnus* isp., Rindsberg, p. 59, pls. 18D, E [Upper Mississippian, Alabama].

Etymology. Latin *ornatus*, ornate.

Diagnosis. *Haplotichnus* consisting of a steep-sided groove flanked by pads of sediment.

Description. Trail irregularly meandering, tending to concentrate on particular areas of sediment. Trails may penetrate themselves and even retrace older segments, but do not truly branch. Trails may dive into the sub-

FIGURE 13. Holotype of *Haplotichnus ornatus*. Upper Mississippian Hartselle Sandstone, Fielder Ridge, Colbert County, Alabama (Rindsberg, 1994, pl. 18E). GSA 1052-245.

strate for short segments. Pads nearly normal to the axis, distinct only in siltstone to fine-grained sandstone.

Remarks. These trails are very similar to *H. indianensis* Miller, 1889 in morphologic details and overall course, differing in sculpture. *H. indianensis* is smooth (C.G. Maples, oral communication, 1989; Buatois et al., 1998b). The sculpture of *Oniscoidichnus filiciformis* (Brady, 1947) is similar to that of *H. ornatus*, and is supposed to be the work of isopods similar to recent *Oniscus*.

Haplotichnus ornatus is not known at the Steven C. Minkin Site, but is one of the commonest trace fossils of the freshwater ichnocoenose at other Lower Pennsylvanian sites in Walker County, Alabama (Rindsberg, 1990). The makers are probably arthropods. It also occurs in the Upper Mississippian Hartselle Sandstone, where it is associated with shallow-marine traces such as *Asteriacites* as well as plant debris (Rindsberg, 1994).

Holotype. Geological Survey of Alabama Paleontological Collection, GSA 1052-245. Upper Mississippian Hartselle Sandstone, Fielder Ridge, Colbert County, Alabama (Rindsberg, 1994, pl. 18E).

CONCLUSIONS

Two common, longitudinally striate trace fossils found at the Union Chapel Mine are assigned to new ichnospecies: *Treptichnus apsorum* and *Arenicolites longistriatus*. *Treptichnus apsorum* consists of two or more connected U-shaped burrows that commonly combine to approximate a zigzag form. *Arenicolites longistriatus* consists of a single U-shaped burrow. On the basis of co-occurrence, similar size range, similar U-shaped burrow building blocks, and similar sculpture (longitudinal striae in well-preserved specimens), we argue that both ichnospecies were made by the same organisms. Comparison to modern traces with known makers indicates that *T. apsorum* and *A. longistriatus* were made by arthropods with behavior similar to modern dipteran larvae.

Both *T. apsorum* and *A. longistriatus* co-occur with *Undichna* (a fish swimming trace) and with invertebrate trackways (not undertracks) that were made on wet muddy surfaces but with no signs of desiccation. Hence, the makers of *T. apsorum* and *A. longistriatus* were certainly active on sediment surfaces underneath shallow water, and possibly also briefly exposed to the air at low tide. *T. apsorum* varies greatly in size, but not on any one slab, suggesting that tracemaker populations consisted of same-aged cohorts. Slabs with bimodal size ranges may indicate superposition of traces made at different times. The great overall size range suggests that deposition of the *Cincosaurus* beds encompassed at least one season: time for insect larvae to grow to maturity.

Haplotichnus indianensis may have been made by small insect larvae; in contrast, *Haplotichnus ornatus* from other Alabama Carboniferous units was more likely made by marine arthropods. Ichnogenus *Treptichnus* is confined to *T. bifurcus* (the type ichnospecies), *T. apsorum,* and *T. pollardi*. Ichnofamily Arenicolitidae is revised.

For additional photographs of invertebrate trackways and other traces from the Union Chapel Mine, see Buta et al. (2005).

ACKNOWLEDGMENTS

We thank with pleasure those who shared their knowledge of *Treptichnus* and *Arenicolites* with us. The list only begins with Alfred Uchman (Jagiellonian University), Sören Jensen (Universitad de Extremadura), Jordi M. de Gibert (Universitat de Barcelona), and Luis A. Buatois and M. Gabriela Mángano (University of Saskatchewan). We also thank the many collectors who selflessly donated specimens to preserve them for the public. W. Edward Osborne (Geological Survey of Alabama) reviewed the manuscript.

REFERENCES

Aldrich, T. H., Sr., 1930, Description of tracks; in Aldrich, T.H., Sr. and Jones, W.B., Footprints from the Coal Measures of Alabama: Alabama Museum of Natural History, Museum Paper, 9, p. 13-64, 17 pls.

Andrée, K., 1920, Über einige fossile Problematika, I. Ein Problematikum aus dem Paläozoikum von Battenberg an der Eder und das dasselbe beherbergende Gestein: Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, 1920(1), p. 55-88, 1 pl.

Archer, A. W., 1998, Implications of Carboniferous cyclic rhythmites. Geotimes, v. 43(5), p. 23-26.

Archer, A. W., Calder, J. H., Gibling, M. R., Naylor, R. D., Reid, D. R. and Wightman, W. G., 1995, Invertebrate trace fossils and agglutinated foraminifera as indicators of marine influence within the classic Carboniferous section at Joggins, Nova Scotia, Canada: Canadian Journal of Earth Sciences, v. 32(12), p. 2027-2039.

Archer, A. W. and Maples, C. G., 1984, Trace-fossil distribution across a marine-to-nonmarine gradient in the Pennsylvanian of southwest Indiana: Journal of Paleontology, v. 48(2), p. 448-466.

Atkinson, T. P., 2005, Arthropod body fossils from the Union Chapel Mine; in Buta, R. J., Rindsberg, A. K. and Kopaska-Merkel, D. C., eds., Pennsylvanian footprints in the Black Warrior basin of Alabama: Alabama Paleontological Society, Monograph, no. 1, p. 169-176.

Balistieri, P., Netto, R. G. and Lavina, E. L. C., 2002, Ichnofauna from the Upper Carboniferous-Lower Permian rhythmites from Mafra, Santa Catarina State, Brazil: ichnotaxonomy: Revista Brasileira de Paleontologia, v. 4, p. 13-26.

Bandel, K., 1973, Trace fossils from the Upper Devonian Nehden siltstone of Wuppertal-Barmen (Nordrhein-Westfalen, Germany): Palaeontographica, ser. A, v. 174, p. 157-176, pls. 37-39.

Bentz, A., 1929, Fossile Röhrenbauten im Unterneokom des Isterbergs bei Bentheim. Prussia, Preussische Geologische Landesanstalt und Bergakademie, Jahrbuch, v. 49(2 [for 1928]): p. 1173-1183, pl. 74.

Billings, E., 1872, On some fossils from the primordial rocks of Newfoundland: Canadian Naturalist, n.ser., v. 6, 465-479.

Binney, E. W., 1852, On some trails and holes found in rocks of the carboniferous strata, with remarks on the *Microconchus carbonarius:* Manchester Literary and Philosophical Society, Memoirs and Proceedings, (2) 10(6), p. 181-201, pls. 1-2.

Brady, L. F., 1947, Invertebrate tracks from the Coconino sandstone of northern Arizona: Journal of Paleontology, v. 21, p. 466-472, pls. 66-69.

Brasier, M., Cowie, J. and Taylor, M., 1994, Decision on the Precambrian-Cambrian boundary stratotype: Episodes, v. 17(1-2):, p. 3-8.

Buatois, L. A. and Mángano, M. G., 1993a, The ichnotaxonomic status of *Plangtichnus* and *Treptichnus:* Ichnos, v. 2(3), p. 217-224.

Buatois, L. A. and Mángano, M. G., 1993b, Trace fossils from a Carboniferous turbiditic lake: implications for the recognition of additional non-marine ichnofacies: Ichnos, v. 2(3), p. 237-258.

Buatois, L. A., Mángano, M. G. and Maples, C. G., 1997, The paradox of non-marine ichnofaunas in tidal rhythmites: integrating sedimentologic and ichnologic data from the Late Cretaceous of eastern Kansas, USA: Palaios, v. 12(5), p. 467-481.

Buatois, L. A., Mángano, M. G., Maples, C. G. and Lanier, W. P., 1998a, Allostratigraphic and sedimentologic applications of trace fossils to the study of incised estuarine valleys: an example from the Virgilian Tonganoxie Sandstone Member of eastern Kansas: Kansas Geological Survey, Current Research in Earth Sciences, no. 241(1), p. 1-27.

Buatois, L. A., Mángano, M. G., Maples, C. G. and Lanier, W. P., 1998b, Ichnology of an Upper Carboniferous fluvio-estuarine paleovalley: the Tonganoxie Sandstone, Buildex Quarry, eastern Kansas, USA: Journal of Paleontology, v. 72(1), p. 152-180.

Buta, R. J., Kopaska-Merkel, D. C., Rindsberg, A. K., and Martin, A. J., 2005, Atlas of Union Chapel Mine invertebrate trackways and other traces; in Buta, R. J., Rindsberg, A. K. and Kopaska-Merkel, D. C., eds., Pennsylvanian Footprints in the Black Warrior Basin of Alabama: Alabama Paleontological Society Monograph no. 1, p. 277-337.

Chamberlain, C. K., 1971, Morphology and ethology of trace fossils from the Ouachita Mountains, southeastern Oklahoma: Journal of Paleontology, v. 45(2), p. 212-246, pls. 29-32.

Chamberlain, C. K., 1977, Ordovician and Devonian trace fossils from Nevada: Nevada Bureau of Mines and Geology, Bulletin 90, 24 pp.

Droser, M. L., Jensen, S. and Gehling, J. G., 2002, Trace fossils and substrates of the terminal Proterozoic-Cambrian transition: implications for the record of early bilaterians and sediment mixing: Proceedings of the National Academy of Sciences of the United States of America, v. 99(20), p. 12572-12576.

Enders, H .E., 1908, Observations on the formation and enlargement of the tubes of the marine annelid, (*Chaetopterus variopedatus*): Proceedings of the Indiana Academy of Science, v. 1907, p. 128-135, 2 pls.

Evenhuis, N. L., 2004, Catalogue of the fossil flies of the world (Insecta: Diptera). URL http://hbsbishopmuseu.org/fossilcat, accessed March 9, 2005. Originally published 1994, Leiden, Backhuys Publishers.

Fliche, P., 1906, Flore fossile du Trias en Lorraine et en Franche-Comté Société des Sciences de Nancy: Bulletin des Séances, (3) 6 (1905), p. 1-66, pls. 1-5.

Forney, G. G., Jenkins, D. T. and Nitecki, M. H., 1977, Type fossil Miscellanea (worms, problematica, conoidal shells, trace fossils) in Field Museum: Fieldiana, Geology, v. 37(1), p. 1-41.

Fuchs, T., 1895, Studien über Fucoiden und Hieroglyphen: Akademie der Wissenschaften zu Wien, mathematisch-naturwissenschaftliche Classe, Denkschriften, v. 62, p. 369-448, 1 pl.

Fnrsich, F. T., 1974, On *Diplocraterion* Torell 1870 and the significance of morphological features in vertical, spreiten-bearing, U-shaped trace fossils: Journal of Paleontology, v. 48(5),

p. 952-962.
Goldring, R., 1962, The trace fossils of the Baggy Beds (Upper Devonian) of north Devon, England: Paläontologische Zeitschrift, v. 36, p. 232-251, pls. 22-23.
Greb, S. F. and Archer, A. W., 1995, Rhythmic sedimentation in a mixed tide and wave deposit, Hazel Patch sandstone (Pennsylvanian), Eastern Kentucky Coal Field: Journal of Sedimentary Research, v. B65(1), p. 96-106.
Häntzschel, W., 1975, Trace fossils and problematica; in Teichert, C., ed., Treatise on invertebrate paleontology, part W. Miscellanea, supplement 1, *W*269 pp. Boulder, Colorado, Geological Society of America and Lawrence, Kansas, University of Kansas Press.
Hall, J., 1847, Palaeontology of New-York, v. 1. Containing descriptions of the organic remains of the lower division of the New-York System, (equivalent in part to the Lower Silurian rocks of Europe). Natural History of New York. Albany, C. van Benthuysen, xxiii + 338, 87 + 1 pls.
Hall, J., 1852, Palaeontology of New York, v. 2. Containing descriptions of the lower Middle Devonian of the New York System (equivalent in part to the Middle Silurian rocks of Europe). Natural History of New York. Albany, C. van Benthuysen, viii + 363 p., '85' [101] pls.
Han, Y. and Pickerill, R. K., 1995, Palichnology of the Lower Devonian Wapske Formation, Perth-Andover-Mount Carleton region, northwestern New Brunswick, eastern Canada: Atlantic Geology, v. 30(for 1994), p. 217-245.
Haubold, H., Allen, A., Atkinson, T. P., Buta, R. J., Minkin, S. and Relihan, B., 2005, Interpretation of the tetrapod footprints from the Early Pennsylvanian of Alabama; in Buta, R. J., Rindsberg, A. K. and Kopaska-Merkel, D. C., eds., Pennsylvanian footprints in the Black Warrior Basin of Alabama: Alabama Paleontological Society, Monograph no. 1, p. 75-111.
Hundt, R., 1941, Das mitteldeutsche Phycodesmeer. Gustav Fischer, Jena, 136 pp.
Jensen, S., 1997, Trace fossils from the Lower Cambrian Mickwitzia sandstone, south-central Sweden: Fossils and Strata, v. 42, 111 pp.
Kvale, E. P., Archer, A. W. and Johnson, H. R., 1989, Daily, monthly and yearly tidal cycles within laminated siltstones of the Mansfield Formation (Pennsylvanian) of Indiana: Geology, v. 17(4), p. 365-368.
Lessertisseur, J., 1956, Traces fossiles d'activité animale et leur significance paléobiologique: Mémoires de la Société Géologique de France, n.ser., v. 74, p. 1-150.
Lucas, S. G., Lerner, A. J., Bruner, M. and Shipman, P., 2004, Middle Pennsylvanian ichnofauna from eastern Oklahoma, USA: Ichnos, v. 11(1-2), p. 45-55.
MacGinitie, G.E. and MacGinitie, N., 1968, Natural history of marine animals (2nd edition). New York, McGraw-Hill, 523 pp.
MacNaughton, R. B. and Narbonne, G. M., 1999, Evolutionary and environmental controls on Neoproterozoic-Early Cambrian ichnofossils, NW Canada: Palaios, v. 14(2), p. 97-115.
Mägdefrau, K., 1932, Über einige Bohrgänge aus dem unteren Muschelkalk von Jena: Paläontologische Zeitschrift, v. 14, p. 150-160, pl. 5.
Maples, C. G. and Archer, A. W., 1987, Redescription of Early Pennsylvanian trace-fossil holotypes from the nonmarine Hindostan whetstone beds of Indiana: Journal of Paleontology, v. 61(5), p. 890-897.
Martin, A. J. and Pyenson, N. D., 2005, Behavioral significance of vertebrate trace fossils from the Union Chapel Mine; in Buta, R. J., Rindsberg, A. K. and Kopaska-Merkel, D. C., eds., Pennsylvanian footprints in the Black Warrior Basin of Alabama: Alabama Paleontological Society, Monograph no. 1, p. 59-73.
Metz, R., 2000, Triassic trace fossils from lacustrine shoreline deposits of the Passaic Formation, Douglassville, Pennsylvania: Ichnos, v. 7(4), p. 253-266.
Miller, M. F. and Knox, L., W. 1985, Biogenic structures and depositional environments of a Lower Pennsylvanian coal-bearing sequence, northern Cumberland Plateau, Tennessee, U.S.A; in Curran, H. A., ed., Biogenic structures: their use in interpreting depositional environments. Society of Economic Paleontologists and Mineralogists, Special Publication, v. 35, p. 67-97.
Miller, S. A., 1879, Description of twelve new fossil species, and remarks upon others: Journal of the Cincinnati Society of Natural History, v. 2(2), p. 104-118, pls. 9-10.
Miller, S. A., 1889, North American geology and paleontology for the use of amateurs, students and scientists: Cincinnati, Ohio, Western Methodist Book Concern, 664 pp.
Miller, S. A. and Dyer, C. B., 1878, Contributions to paleontology [no. 1]: Journal of the Cincinnati Society of Natural History, v. 1, p. 24-39, pls. 1-2.
Orlowski, S. and Zylinska, A., 1996, Non-arthropod burrows from the Middle and Late Cambrian of the Holy Cross Mountains, Poland. Acta Palaeontologica Polonica, v. 41(4), p. 385-409.
Osgood, R. G., 1970, Trace fossils of the Cincinnati area. Palaeontographica Americana, v. 6(41), p. 277-444, pls. 57-83.
Paczesna, J., 1996, The Vendian and Cambrian ichnocoenoses from the Polish part of the East-European Platform: Prace Panstwoego Instityutu. Geologicznego, v. 152, p. 1-77.
Palij, V. M., 1976, Ostatki besskieletnoiy fauny i sledy zhiznedelatelnosti iz otlozheniy vierhnoho dokembria i nizhneho kembria Podolii; in Paleontologia i stratigrafia verkhneho dokembria i nizneho paleozoia yugo-zapada Vostochno-Evropeiskoi platformy. Naukova Dumka, Kiev, p. 63-77.
Pashin, J. C., 2005, Pottsville stratigraphy and the Union Chapel lagerstätte; in Buta, R. J., Rindsberg, A. K. and Kopaska-Merkel, D. C., eds., Pennsylvanian footprints in the Black Warrior basin of Alabama: Alabama Paleontological Society, Monograph no. 1, p. 39-58.
Pemberton, S. G. and Frey, R. W. 1982. Trace fossil nomenclature and the *Planolites-Palaeophycus* dilemma: Journal of Paleontology, v. 56(4), p. 843-881, 5 pls.
Pollard, J. E., 1981, A comparison between the Triassic trace fossils of Cheshire and south Germany: Palaeontology, v. 24(3), p. 555-588, pls. 86-90.
Pollard, J. E., 1999, *Arenicolites carbonarius* in the Manchester region: ichnofabrics of a deltaic opportunist. In Pollard, J. and Taylor, A., eds. Fifth International Ichnofabric Workshop IIW5, Manchester University, 12th-14th July 1999, Abstract volume, unpaginated.
Richter, R., 1924, Flachseebeobachtungen zur Paläontologie und Geologie, VII. Arenicola von Heute und "*Arenicoloides*," eine Rhizocorallide des Buntsandsteins, als Vertreter verschiedener Lebensweise: Senckenbergiana, v. 6, p. 119-140.
Richter, R., 1926, Flachseebeobachtungen zur Paläontologie und Geologie XII. Bau, Begriff und paläogeographische Bedeutung von *Corophioides luniformis* (BLANCKENHORN, 1917): Senckenbergiana, 8: 200-219, pl. 3.
Rindsberg, A. K., 1990, Freshwater to marine trace fossils of the Mary Lee coal zone and overlying strata (Westphalian A, Pottsville Formation of northern Alabama); in Gastaldo, R. A., Demko, T. M. & Liu, Y., eds., Carboniferous coastal environments and paleocommunities of the Mary Lee coal zone, Marion and Walker Counties, Alabama: Geological Society of America, Southeastern Section, Field Trip 6, Alabama Geological Survey, Guidebook Series, 3-6: VI-82 to VI-95.
Rindsberg, A. K., 1991, Ichnology of the Carboniferous Parkwood Formation in the Cahaba synclinorium near Birmingham, Alabama; In Thomas, W.A. and Osborne, W.E., eds. Missis-

sippian-Pennsylvanian tectonic history of the Cahaba synclinorium: Alabama Geological Society, Annual Field Trip, Guidebook, v. 28, p. 133-147, 2 pls.
Rindsberg, A. K., 1994, Ichnology of the Upper Mississippian Hartselle Sandstone of Alabama, with notes on other Carboniferous formations: Geological Survey of Alabama, Bulletin 158, 107 pp., 22 pls.
Rindsberg, A. K., 2005, Gas-escape structures and their paleoenvironmental significance at the Steven C. Minkin Paleozoic Footprint Site (Early Pennsylvanian, Alabama); in Buta, R. J., Rindsberg, A. K. and Kopaska-Merkel, D. C., eds., Pennsylvanian footprints in the Black Warrior Basin of Alabama: Alabama Paleontological Society, Monograph no. 1, p. 177-183.
Rindsberg, A. K. and Kopaska-Merkel, D. C., 2003, *Treptichnus* and related trace fossils from the Union Chapel Mine (Langsettian, Alabama, USA): Workshop on Permo-Carboniferous Ichnology, Tuscaloosa, Alabama, p. 27-28.
Rindsberg, A. K. and Martin, A. J., 2003, *Arthrophycus* in the Silurian of Alabama (USA) and the problem of compound trace fossils: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 192, p. 187-219.
Rindsberg, A. K., Martin, A. J. and Pyenson, N. D., 2001, Ichnofossil-Lagerstätte in Alabama: a world-class Carboniferous (Westphalian A) tracksite. Program and Abstracts; NAPC 2001, North American paleontological convention 2001, Paleontology in the new millennium. University of California, Museum of Paleontology. Berkeley, California: PaleoBios, v. 21(2, Suppl.), p. 109.
Rindsberg, A. K., Uchman, A. and Kopaska-Merkel, D. C., 2004, *Treptichnus* made by insect larvae in the Pennsylvanian of Alabama (USA): First International Congress on Ichnology, April 19-23, 2004, Trelew, Patagonia Argentina, Museo Paleontológico Egidio Feruglio, p. 70.
Salter, J. W., 1856, On fossil remains in the Cambrian rocks of the Longmynd and north Wales: Quarterly Journal of the Geological Society of London, v. 12, p. 246-252, pl. 4.
Salter, J. W., 1857, On annelide-burrows and surface-markings from the Cambrian rocks of the Longmynd, No. 2: Quarterly Journal of the Geological Society of London, v. 13, p. 199-206, pl. 5.
Schlirf, M., 2000, Upper Jurassic trace fossils from the Boulonnais (northern France): Geologica and Palaeontologica, v. 34, p. 145-213.
Seilacher, A., 1953, Studien zur Palichnologie. I. Über die Methoden der Palichnologie: Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, v. 96(3), p. 421-452, pl. 14.
Seilacher, A., 1955, Spuren und Fazies im Unterkambrium; in Schindewolf, O. H. and Seilacher, A, Beiträge zur Kenntnis des Kambriums in der Salt Range (Pakistan): Akademie der Wissenschaften und der Literatur zu Mainz, mathematisch-naturwissenschaftliche Klasse, Abhandlungen, v. 10, p. 373-399.
Seilacher, A. and Hemleben, C., 1966, Beiträge zur Sedimentation und Fossil-führung des Hunrückschiefers, Teil 14, Spurenfauna und Bildungstiefe des Hunrückschiefers: Notizblatt des Hessisches Landesmat für Bodenforschung, v. 94, p. 40-53, pls. 2-4.
Seilacher, A. and Meischner, D., 1965, Fazies-Analyse im Paläozoikum des Oslo-Gebeites: Geologische Rundschau, v. 54 (for 1964), p. 596-619.
Serres, M. de, 1840, Description de quelques mollusques fossiles nouveaux des terrains infra-jurassiques et de craie compacte inférieure du Midi de la France: Annales des Sciences Naturelles, Zoologie, (2) v. 14, p. 5-25, pls. 1, 2.
Tessier, B., Archer, A. W., Lanier, W. P. and Feldman, H. R., 1995, Comparison of ancient tidal rhythmites (Carboniferous of Kansas and Indiana, USA) with modern analogues (the Bay of Mont-Saint-Michel, France); in Fleming, B. W. and Bartholomä, A., eds., Tidal signatures in modern and ancient sediments: International Association of Sedimentologists, Special Publication, v. 24, p. 259-271.
Uchman, A., 2005, *Treptichnus*-like traces produced by insect larvae (Diptera: Chironomidae, Tipulidae); in Buta, R. J., Rindsberg, A. K. and Kopaska-Merkel, D. C., eds., Pennsylvanian footprints in the Black Warrior Basin of Alabama: Alabama Paleontological Society, Monograph no. 1, p. 143-146.
Uchman, A., Bromley, R. G. and Leszczynski, S., 1998, Ichnogenus *Treptichnus* in Eocene flysch, Carpathians, Poland: taxonomy and preservation: Ichnos, v. 5(4), p. 269-275.
Uchman, A., Pika-Biolzi, M. and Hochuli, P. A., 2004, Oligocene trace fossils from temporary fluvial plain ponds: an example from the Freshwater Molasse of Switzerland: Eclogae Geologicae Helvetiae, v. 97, p. 133-148.
Vialov, O. S., 1961, Materialy k klassifikatsii iskopaemykh sledov i sledov zhiznedeyatelnosti organizmov: Paleontologicheskiy Sbornik, v. 1(5), p. 125-129.
Wetzel, A. and Uchman, A., 1997, Ichnology of deep-sea fan overbank deposits of the Ganei Slates (Eocene, Switzerland) — a classical flysch trace fossils locality studied first by Oswald Heer: Ichnos, v. 5(2), p. 139-162.
Wilson, A. E., 1948, Miscellaneous classes of fossils, Ottawa Formation, Ottawa-St. Lawrence Valley. Geological Survey of Canada, Department of Mines and Resources, Bulletin, 11, 116 pp., 28 pls.

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