Journal of Paleontology, 86(6), 2012, p. 996–1001
Copyright © 2012, The Paleontological Society
0022-3360/12/0086-996$03.00

A POSSIBLE TRACEMAKER FOR *ARTHROPHYCUS ALLEGHANIENSIS*

VICTORIA E. McCOY,[1] PAUL K. STROTHER,[2] AND DEREK E. G. BRIGGS[1,3]

[1]Department of Geology and Geophysics, Yale University, P.O. Box 208109, New Haven, CT 06520-8109, USA, <victoria.mccoy@yale.edu>; [2]Weston Observatory of Boston College, Department of Earth and Environmental Science, 381 Concord Rd, Weston, MA 02493, USA, <strother@bc.edu>; and [3]Yale Peabody Museum of Natural History, Yale University, New Haven, CT 06520-8118, USA, <derek.briggs@yale.edu>

ABSTRACT—*Arthrophycus alleghaniensis* is a well-known trace fossil common in the lower Silurian of the Appalachian Basin, eastern U.S.A. Despite the distinctive morphology of this trace, with few exceptions, hypotheses about the nature of the tracemaker have not extended beyond that of a long-bodied, segmented organism. A single organic compression of a long-bodied arthropod discovered in shale interbedded with sandstones containing *A. alleghaniensis* in the Silurian (Llandovery) Tuscarora Formation at Mann Narrows, Pennsylvania is described. The specimen preserves evidence of two trunk tagmata: an anterior tagma with tergites extending into broad, rectangular pleurae, and a posterior tagma bearing long, curved spines. Head and appendages are not preserved. The new arthropod, *Pleuralata spinosa* n. gen. n. sp., matches the size and general morphology required for an *A. alleghaniensis* tracemaker. Precise systematic affinities of this new arthropod could not be determined. This discovery supports the conclusion that the tracemakers of various *Arthrophycus* ichnospecies are likely poorly preserved, and presently unknown, members of the Ecdysozoa.

INTRODUCTION

ORGANISMS ARE rarely preserved with the traces they make. There are a few exceptions, most notably the famous mortichnia (Seilacher, 2007) from the Jurassic Solnhofen Limestone, including the *Mesolimulus* Størmer, 1952 "death marches." Other examples include the Cambrian euthycarcinoid arthropod *Mictomerus* Collette and Hagadorn, 2010 (Collette et al., 2010), the Jurassic isopod *Archaeoniscus* Milne-Edwards, 1843 (Gaillard et al., 2005) at the end of their trackways, the Eocene decapod *Callianassa* Leach, 1814 (Stilwell et al., 1997) and the Pleistocene spatangoid echinoid *Echinocardium* Gray, 1825 (Bromley and Asgaard, 1975) at the end of their burrows. In exceptional cases, size and/or morphological details of the trace itself may lead to the identification of a specific tracemaker, as in trackways attributed to *Arthropleura* Meyer, 1853 (Briggs et al., 1979, 1984) or eurypterids (Hanken and Størmer, 1975; Briggs and Rolfe, 1983).

The makers of the various Paleozoic burrow systems assigned to *Arthrophycus* Hall, 1852 remain the subject of discussion. *Arthrophycus* often covers entire bedding planes either as distinct, worm-like annulated trails (*A. harlanii* form) or as bunched overlapping trails (*A. alleghaniensis* form). The organisms that made *Arthrophycus* were active deposit feeders (Brandt et al., 2012; Miller et al., 2009; Rindsberg and Martin, 2003). Disarticulated eurypterid cuticles (Johnson, 1985) and rare lingulids are the only animal fossils previously found in association with *Arthrophycus* in the Tuscarora Formation. These carbonized body fossils occur in interbedded olive green mudstones that also contain unambiguously non-marine cryptospore assemblages (Strother and Traverse, 1979). Neither lingulids nor eurypterids appear related to the *A. alleghaniensis* (Harlan, 1831) tracemaker. The wide stratigraphic and geographic range of *Arthrophycus* suggests that there may be multiple tracemakers. Thus it is unlikely that the new arthropod described here was responsible for all the ichnospecies of *Arthrophycus*.

Arthrophycus is described as an elongate feeding burrow. It ranges in age from the Cambrian (Mángano et al., 2005) to the Carboniferous (Brandt et al., 2010) with greatest frequency in the Ordovician and Silurian (e.g., Häntzschel, 1975; Seilacher, 2000). Reports of post-Paleozoic examples of *Arthrophycus* are typically based on short, isolated sections with very poor resolution of the diagnostic features, and cannot be assigned to the ichnogenus with confidence (Mángano et al., 2005). *Arthrophycus* from the Appalachian region of the United States (e.g., Yeakel, 1962) is most commonly recorded and discussed in the literature but the trace fossil has an essentially worldwide distribution, e.g., Spain (Pickerill et al., 1984), Argentina (Mángano et al., 2005), the Kandi Basin in West Africa (Alidou et al., 1991), Libya (Turner and Benton, 1983), Australia (Davies et al., 2011), and Antarctica (Cooper et al., 1983). *Arthrophycus* mostly occurs in sandstone, interpreted as nearshore, tidally influenced environments similar to those of the Tuscarora Formation where frequent mudstone interbeds were presumably mined for nutrients by the tracemaker.

The nature of the *Arthrophycus* tracemaker has historically been a matter of debate with two main hypotheses: the tracemaker is an arthropod, possibly a trilobite (e.g., Rindsberg and Martin, 2003), or that it is a worm-like animal (Seilacher, 2000). Most current hypotheses (e.g., Seilacher, 2000) suggest that the tracemaker is long-bodied and segmented. In one locality, *Arthrophycus* includes sharp turns, suggesting a short-bodied maker (Rindsberg and Martin, 2003). However, the majority of *Arthrophycus* burrows, including all those known from the Tuscarora section at Mann Narrows, show a smooth, gradual curvature which is more indicative of a long-bodied maker (Seilacher, 2000). A recent analysis of modern and fossil traces, which compared the methods of locomotion of arthropods and worms, strongly supports the arthropod hypothesis (Brandt et al., 2012).

The Tuscarora Formation in central Pennsylvania (Fig. 1) yields abundant examples of *Arthrophycus*. A new enigmatic arthropod from the Tuscarora Formation is closely associated with *Arthrophycus alleghaniensis* in the field. The specimen was found in mudstone beds a few decimeters thick, interbedded with similarly thin sandstones. All the sandstone interbeds within a meter above or below the mudstone layer that yielded the specimen contain *Arthrophycus*. This arthropod is a possible candidate for the tracemaker of *A. alleghaniensis* in the lower Silurian of the Appalachian region.

THE DEPOSITIONAL ENVIRONMENT OF THE TUSCARORA FORMATION

The interbedded sandstones and shales comprising the lower Silurian (Aeronian) Tuscarora Formation (Castle, 1998) in central Pennsylvania were deposited in a series of fluvial and

https://doi.org/10.1666/11-133R1.1 Published online by Cambridge University Press

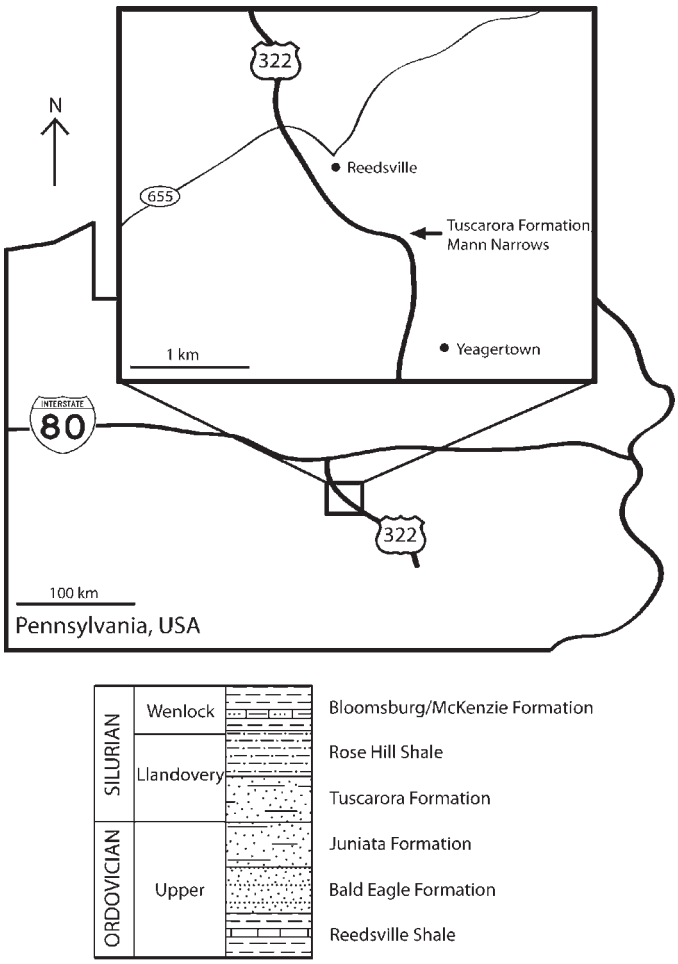


FIGURE 1—Location map and stratigraphic column for the location of *Pleuralata spinosa*.

near-shore (paralic) settings, which are sandwiched between the fluvial red beds of the Juniata Formation, and the Fe-rich marine sandstones and shales of the Rose Hill Formation (Fig. 1) (Berry and Boucot, 1970). The sandstones are interpreted as marine coast and shelf deposits, based on laterally continuous, non-channeled beds, wavy upper surfaces, and wave-generated, symmetrical ripples (Cotter, 1983). This is also supported by the presence of *Skolithos* Haldemann, 1840 and *Monocraterion* Torell, 1870 (Cotter, 1983). In contrast, abundant cryptospores and organic fragments of land plant origin occur in the bluish gray to olive green shales (Strother and Traverse, 1979; Johnson, 1985; Beck and Strother, 2008) indicating a non-marine origin. Regionally, the shales of the Tuscarora Formation and its lithostratigraphic equivalents in Virginia (Pratt et al., 1978; Tomescu et al., 2006) and New York (Miller and Eames, 1982) are important sources of early land plant remains (Gensel et al., 1990; Beck and Strother, 2008). Thus, the muds that are interbedded with the Tuscarora sands contain organic remains derived from freshwater rivers and streams. Combining the clear biological signal with sedimentological evidence, a paralic to estuarine setting characterized by low salinity due to freshwater influx is clearly indicated. These estuarine settings were sufficiently extensive to generate sand bars (Cotter, 1983), while the freshwater flux excluded normal marine invertebrates. This depositional setting is consistent with the sporadic occurrence of disarticulated eurypterids (mostly isolated tergites) and lingulids, which occur in the Tuscarora shales at Mann Narrows and throughout the central and southern Appalachians. Extensive bioturbation, evidenced by the abundance of *Arthrophycus* and other deposit-feeding traces in the Tuscarora, reflects high levels of nutrients delivered by this freshwater, terrestrial influx.

SYSTEMATIC PALEONTOLOGY

Phylum ARTHROPODA
Genus PLEURALATA new genus

Type species.—*Pleuralata spinosa* new species by monotypy.

Diagnosis.—As for species.

Etymology.—From Latin *pleura*, pleura; *lata*, wide, referring to the prominent pleurae.

Discussion.—As for species.

PLEURALATA SPINOSA new species
Figure 2

Diagnosis.—Axial and pleural regions each about one third of the body width; anterior trunk tagma comprising most of the length; each tergite overlapping the next most-posterior by almost half the length; posterior tagma short and broad with ten pairs of lateral spines of which the two terminal pairs are longest and curve slightly inwards.

Description.—The specimen is represented by part and counterpart, flattened parallel to bedding. The outline is defined by a carbonaceous film which is much denser in the axial region. The cuticle was presumably not biomineralized. The maximum preserved length is 51 mm but the head and additional anterior portions of the body, if any, are missing. Two trunk tagmata are represented but the appendages are not preserved. The preserved length of the anterior tagma is 45 mm, tapering distally from 20.4 mm to 10.6 mm in width. The trunk is trilobate. The anterior tagma preserves evidence of thirteen tergites, but this is a minimum number. The axial region, in particular, preserves evidence of overlap between the tergites. The gut is evident as a dark band sporadically expressed along the axis. The axis is flanked by pleurae which are subrectangular in outline. A linear structure runs near parallel to the outer edge of each pleura which may represent a feature on the external surface.

The posterior tagma is 6.2 mm long and 12.1 mm wide. Ten pairs of elongate spines project from the margin; they are directed laterally at the anterior of the tagma and more posteriorly toward the rear. The first eight spines are about 4 mm long, the last two up to 7 mm. The length of the two longest spines is preserved completely only on the right and additional spines may have been present. There is some evidence of divisions in the axial region of this posterior tagma but their relationship to the spines is not clear.

Etymology.—From the Latin *spinosa*, spiny, referring to the spine-like processes of the posterior tagma.

Holotype.—Yale Peabody Museum (YPM) 227997, part and counterpart, is the only known specimen (Fig. 2) and is designated the holotype.

Occurrence.—Tuscarora Formation, 165 m above the base, where it outcrops along Route 322 at Mann Narrows (Jacks Mountain), Pennsylvania; GPS datum WGS 84, N 40°39.103′, W 77°34.992′. Collecting at the locality in summer 2011 failed to yield additional material of the arthropod.

Remarks.—The synapomorphies of most arthropod groups involve features of the appendages or head; without such data it is difficult to determine where the affinities of *P. spinosa* lie.

Trilobites have a heavily calcified exoskeleton, which is lacking in *P. spinosa*, and they are fully marine. *Pleuralata spinosa* does not preserve features (primarily characters of the

https://doi.org/10.1666/11-133R1.1 Published online by Cambridge University Press

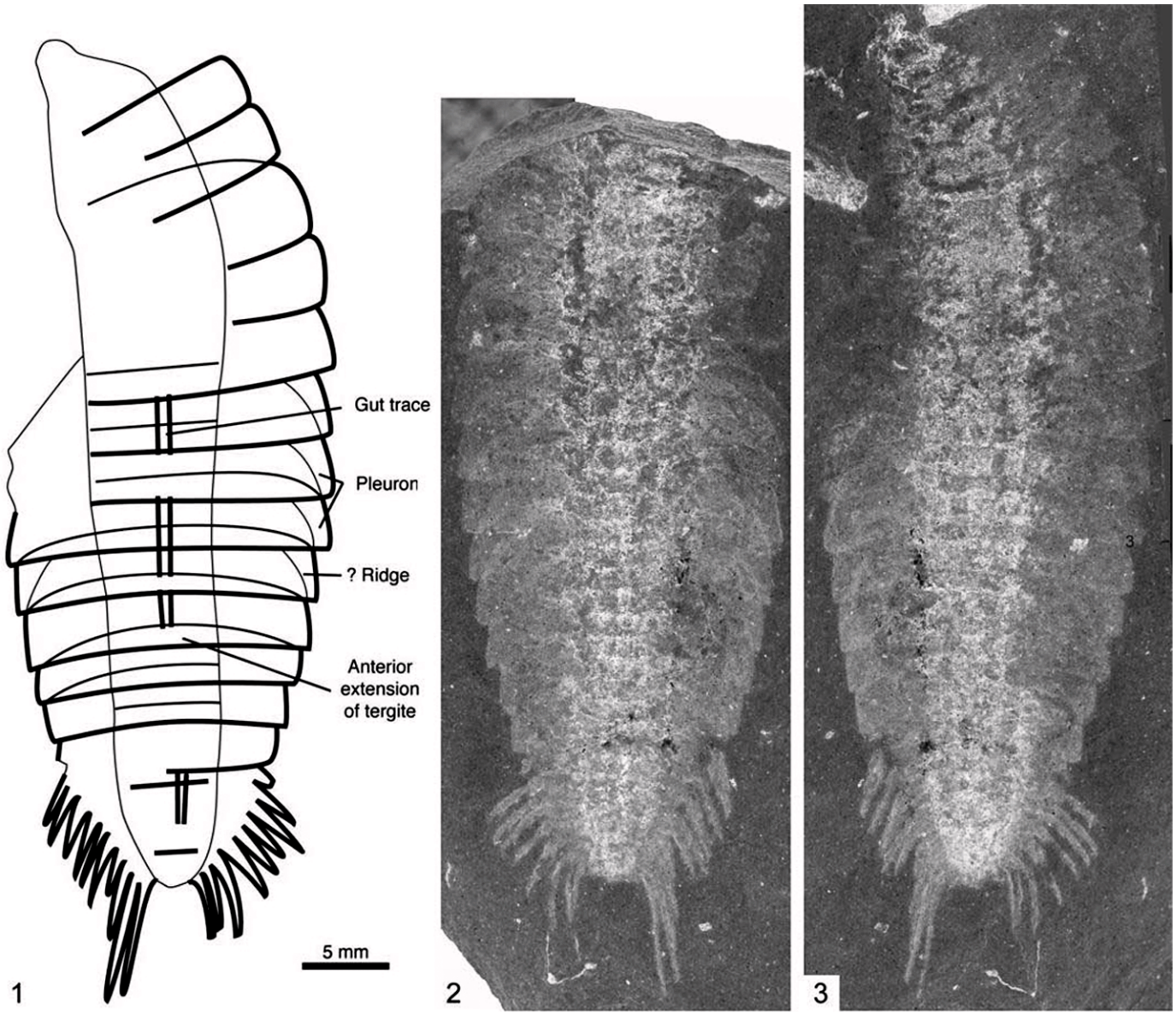


FIGURE 2—*Pleuralata spinosa*, n. gen. n. sp. (YPM 227997): *1*, line drawing incorporating information from part and counterpart; *2, 3*, part and counterpart photographs, respectively, taken in alcohol under polarized light, red channel only, grayscale, and inverted with the infrared filter in Photoshop.

appendages) diagnostic of chelicerates (Selden and Dunlop, 1998). Crustaceans have a wide range of morphologies, but the diagnostic characters are in the head and appendages (Wills, 1998), neither of which are preserved in *P. spinosa*. The general morphology of *P. spinosa* does not suggest an affinity with any of these three major arthropod groups. The long thin posterior tagma of the euthycarcinoids (Ortega-Hernández et al., 2010) also differs from the relatively short, wide posterior tagma of *P. spinosa*.

Pleuralata spinosa is unlikely to be a myriapod because all known myriapods lack a differentiated posterior tagma. It does share some similarities with arthropleurids including the long body, segments with significant overlap, and wide pleurae with a keel or terrace line. *Pleuralata spinosa* falls within the known size range of arthropleurids, from 38 to 2200 mm (Kraus, 2005). Two features of the dorsal exoskeleton are considered diagnostic of arthropleurids: diplosegments and paranotal tergal lobes (essentially pleurae) separated from the axis with a suture (Hannibal, 1997; Shear, 1997). There is no evidence that *P. spinosa* had diplosegments but without evidence of limbs this cannot be completely ruled out. Similarly, there is no evidence of a suture between the pleurae and the axis, although this area is poorly preserved (Fig. 2.2, 2.3). The Order Arthropleurida is characterized by large tubercules (Hahn et al., 1986; Hannibal, 1997) and an axis approximately one half the width of the body (e.g., Hahn et al., 1986) which contrast with the small size, smooth cuticle, and narrower axis (less than one third the width of the body) in *P. spinosa*. Whereas the posterior end is not well known among arthropleurids (Kraus, 2005), there is no posterior tagma like that in *P. spinosa* in juvenile *Arthropleura* from the late Carboniferous of Montceau-les-Mines (Briggs and Almond, 1994).

Pleuralata spinosa is more similar to members of the order Eoarthropleurida, which are smaller than arthropleurids (Shear and Selden, 1995; Shear, 1997) and, in some cases, have a smooth cuticle (Størmer, 1976). The posterior end of Eoarthropleurida,

https://doi.org/10.1666/11-133R1.1 Published online by Cambridge University Press

although incompletely known (Størmer, 1976, text-figs. 12–14), differs from that of *P. spinosa*. Members of the order Microdecemplicida reach only a few millimeters in length (Shear, 1997; Wilson and Shear, 2000) and the anal cone (Wilson and Shear, 2000, fig. 16) differs from the posterior morphology of *P. spinosa*. Arthropleurida, Eoarthropleurida and Microdecemplicida are all considered to be terrestrial forms. Even early Silurian stem forms are unlikely to have generated subaqueous burrows.

Pleuralata spinosa shows some similarity to the problematic *Oxyuropoda ligioides* Carpenter and Swain, 1908, from the Devonian of Ireland. *Oxyuropoda ligioides* has been allied tentatively with the isopods (Carpenter and Swain, 1908; Rolfe, 1969) or euthycarcinoids (Schram, 1971). Both *P. spinosa* and *O. ligioides* have differentiated anterior and posterior trunk tagma. The pleurae of *O. ligioides* are similar in shape and in proportion of the body width to those of *P. spinosa* (Carpenter and Swain, 1908). The tergites in the anterior trunk tagma of *O. ligioides* appear to be divided transversely and are much longer than the divisions in the posterior trunk tagma (Carpenter and Swain, 1908, fig. 1; Rolfe, 1969, fig. 394, 1c). The posterior tagma of *O. ligioides* is similar to that of *P. spinosa*; it is short and broad, and each division likewise possesses a pair of lateral spines (Carpenter and Swain, 1908). However, the trunk of *O. ligioides* consists of only six tergites, compared to more than twice as many in *P. spinosa*, and it terminates in a small telson bearing a pair of elongate rami.

PALEOBIOLOGY OF THE *ARTHROPHYCUS ALLEGHANIENSIS* TRACEMAKER

Pleuralata spinosa is a promising candidate for the tracemaker of *A. alleghaniensis*, however, this single specimen preserves too little detail to test this hypothesis. Thus, we propose two questions: 1) can an arthropod be the tracemaker of *A. alleghaniensis*? and 2) if so, what features of the tracemaker might be predicted as preserved in the specimen of *P. spinosa*?

Morphology of the trace Arthrophycus alleghaniensis.—*Arthrophycus alleghaniensis* was described originally as gently arched and recurved, cylindrical, with transverse wrinkles and a longitudinally depressed midline (Fig. 3) (Harlan, 1831; Hall, 1852). These transverse wrinkles, often called "ridges" or "annulations," are only present on the bottom of the burrow, presumably corresponding to the ventral surface of the tracemaker, although some authors infer their presence on all sides of the trace (Seilacher, 2007). More recently, the description of *A. alleghaniensis* was revised to include a squarish rather than cylindrical cross section, with retrusive backfill (Seilacher, 2007). The burrows occur mostly horizontally, in bundled or palmate associations (Brandt et al., 2010), and are typically 5 to 15 mm wide (Seilacher, 2000).

Can an arthropod be the tracemaker of Arthrophycus alleghaniensis*?*—Arthropods are known to generate bilobed traces with distinct scratches or annulations meeting at or near the midline, both in fossil, e.g., *Cruziana* and *Rusophycus* (Fortey and Seilacher, 1997), and in extant isopod trackways (Davis et al., 2007; Brandt et al., 2012). Moreover, *A. alleghaniensis* has been reported to form a morphological continuum with associated *Cruziana* d'Orbigny, 1842 and *Rusophycus* Hall, 1852 (Hall, 1852; Selley, 1970; Häntzschel, 1975; Baldwin, 1977; Turner and Benton, 1983), both of which are interpreted as arthropod traces (e.g., Fortey and Seilacher, 1997). This indicates that all of these traces were produced by slightly different arthropod behaviors (Rindsberg and Martin, 2003). All of these traces exhibit regular transverse ridges and a median furrow. *Arthophycus brongniartii,* which has the same basic morphological features as *A. alleghaniensis* including the regular transverse ridges and median furrow, has also been reported in continuity with a trace resembling *Nereites* MacLeay, 1839 at the same site where it also forms a morphological continuum with *Cruziana* and *Rusophycus* (Rindsberg and Martin, 2003). True *Nereites* is a worm trace (Màngano et al., 2000) but arthropods have been shown to produce a similar trace (Martin and Rindsberg, 2007). This, in combination with the morphological continuum with *Cruziana* and *Rusophycus* and marks that seem to correspond to trilobite genal spines (Rindsberg and Martin, 2003), suggest that *A. brongniartii* was produced by an arthropod—in this case a trinucleid trilobite. This overall similarity between trilobite generated traces and *Arthrophycus* strongly suggests that some form of arthropod could have produced *A. alleghaniensis*.



FIGURE 3—Specimen of *Arthrophycus alleghaniensis* from the Tuscarora Formation, on the bottom of a sandstone bed, found in float near the location of *Pleuralata spinosa* (YPM 576475).

A number of features of *Arthrophycus* burrows have suggested a worm, rather than an arthropod, as a possible tracemaker: the annulations are too broad to be arthropod limb scratches (Seilacher, 2007), and some specimens of *A. linearis* show fine transverse wrinkles (which have never been reported in *A. alleghaniensis*) indicating that the cuticle of the maker was soft and flexible (Seilacher, 2000, 2007). Seilacher in particular (2007, p. 117) considered that the maker may have been a long, segmented, soft-bodied worm-like organism with "parapodial protuberances." However, a more recent study showed that all known fossil and modern worm traces are smooth and unornamented, and no known worm locomotion could produce

https://doi.org/10.1666/11-133R1.1 Published online by Cambridge University Press

an ornamented trace such as *A. alleghaniensis* (Brandt et al., 2012).

Thus, *A. alleghaniensis* is more likely to have been produced by an arthropod.

What features of the tracemaker can be predicted?—First, the tracemaker would have spent at least part of its time in the area in which *A. alleghaniensis* was produced and might be preserved in association with the traces. Body fossils rarely occur with *A. alleghaniensis*. They include brachiopods (Chadwick, 1908; Grahn, 1992), molluscs (Turner and Benton, 1983; Grahn, 1992), graptolites (Turner and Benton, 1983), a trilobite (Chadwick, 1908), eurypterids (Johnson, 1985), and *Pleuralata spinosa*. Of these, only the trilobites, eurypterids, and *P. spinosa,* as mobile organisms, could represent the *A. alleghaniensis* tracemaker.

Second, the prevalence of smooth, gradual curves in *A. alleghaniensis* suggests that the tracemaker was long-bodied (Seilacher, 2000). *Pleurolata spinosa* is the only long-bodied body fossil that occurs in proximity to the trace.

Third, the *A. alleghaniensis* tracemaker must have burrowed actively (Miller et al., 2009) and thus was likely flexible in three dimensions. The extensive overlap between the trunk tergites of *P. spinosa* echoes that in *Eoarthropleura*, which Størmer (1976) argued would have resulted in considerable mobility both horizontally and vertically, and is consistent with that of an active burrower.

Fourth, the body width of the tracemaker would match the trace width of *A. alleghaniensis*. The limbs of *P. spinosa* are not preserved, but assuming they did not extend beyond the pleurae, they would have generated a trail no more than 20 mm wide. *Arthrophycus alleghaniensis* is typically between 10 and 20 mm wide, and the trails at the *P. spinosa* site are between 7 and 17 mm wide, consistent with the dimensions of the body fossil.

Fifth, the tracemaker would lack any protrusions which would leave extraneous marks in the sediment. The specimens of *A. alleghaniensis* preserve no marks that might have been made by the spines on the posterior tagma of *P. spinosa*. However, it is possible that these spines were kept free of the sediment, perhaps by *P. spinosa* burrowing in a head-down J-position (Seilacher 2007, plate 42). With the possible exception of the posterior spines, the preserved portions of *P. spinosa* present a good match for the predicted features of the tracemaker of *A. alleghaniensis*.

CONCLUSIONS

Pleuralata spinosa is the only body fossil associated with *A. alleghaniensis* with a morphology consistent with that of the trace fossil, making it the best candidate thus far for the tracemaker. More concrete evidence of the locomotion and potential trackways of *P. spinosa*, and a clearer understanding of its affinities, await the discovery of more complete specimens. In their discussion of the probable tracemaker of the Carboniferous *Arthrophycus parallelus*, Brandt et al. (2012, p. 4) concluded that *Arthrophycus* tracemakers should be sought "on an ichnospecies-by-ichnospecies and a fauna-by-fauna basis." The discovery of *Pleuralata spinosa* in stratigraphic proximity with *A. alleghaniensis* represents a contribution to such an inventory of probable *Arthrophycus* tracemakers.

The interbedded mudstones and sandstones of the Tuscarora Formation yield two distinct modes of preservation within the same depositional setting—organic compressions of body fossils and microscopic plant remains in the mudstones and trace fossils (primarily preserved in positive semi-relief at the base of sandstone beds) in the sandstones. Careful examination of such heterolithic sequences could lead to the discovery of associated tracemakers elsewhere in the rock column.

ACKNOWLEDGMENTS

We thank J. Collette and R. MacNaughton for reviews; C. T. Baldwin, D. Brandt, S. Darroch, G. Edgecombe, T. Hegna, E. Locatelli, M. McNamara, and J. Wolfe for discussion; J. Haug and C. Haug for help with photography; and Z. Jiang for help with the SEM analysis. S. Butts facilitated access to specimens in the collections of the Yale Peabody Museum of Natural History. V.E.M. is supported by a National Science Foundation Graduate Research Fellowship.

REFERENCES

Alidou, S., J. Lang, J. Bonvalot, E. Roman, and A. Seilacher. 1991. Marine influences in the so-called continental sediments of the Paleozoic–Mesozoic Kandi Basin (Northern Benin–West Africa). Journal of African Earth Sciences (and the Middle East), 12:55–65.

Baldwin, C. T. 1977. The stratigraphy and facies associations of trace fossils in some Cambrian and Ordovician rocks of northwestern Spain, p. 9–40. *In* T. P. Crimes and J. C. Harper (eds.), Trace Fossils 2. Volume 9. Seel House Press, Sydney.

Beck, J. H. and P. K. Strother. 2008. Miospores and cryptospores from the Silurian section at Allenport, Pennsylvania, U.S.A. Journal of Paleontology, 82:857–883.

Berry, W. B. N. and A. J. Boucot. 1970. Correlation of the North American Silurian rocks. Geological Society of America, Special Papers, 102, 289 p.

Brandt, D., M. Seitz, V. McCoy, J. Csonka, J. Barringer, E. Holmqist, S. Kraig, R. Morgan, J. Myers, and L. Paquette. 2010. A new ichnospecies of *Arthrophycus* from the Late Carboniferous (Pennsylvanian) of Michigan, U.S.A. Ichnos: An International Journal for Plant and Animal Traces, 17: 12–19.

Brandt, D., J. Csonka, M. Holycross, V. McCoy, and D. M. Seitz. 2012. In search of the *Arthrophycus parallelus* tracemaker. PALAIOS, 27:116–121.

Briggs, D. E. G. and J. E. Almond. 1994. The arthropleurids from the Stephanian (Late Carboniferous) of Montceau-les-Mines (Massif Central-France), p. 127–135. *In* C. Poplin and D. Heyler (eds.), Quand le Massif Central était sous l'équateur: un écosystème Carbonifère à Montceau-les-Mines. Mémoires de la Section des Sciences 12, Éditions du Comité des Travaux Historiques et Scientifiques, Paris.

Briggs, D. E. G., W. D. I. Rolfe, and J. Brannan. 1979. A giant myriapod trail from the Namurian of Arran, Scotland. Palaeontology, 22:273–291.

Briggs, D. E. G. and W. D. I. Rolfe. 1983. A giant arthropod trackway from the Lower Mississippian of Pennsylvania. Journal of Paleontology, 57:377–390.

Briggs, D. E. G., A. G. Plint, and R. K. Pickerill. 1984. *Arthropleura* trails from the Westphalian of eastern Canada. Palaeontology, 27:843–855.

Bromley, R. G. and U. Asgaard. 1975. Sediment structures produced by a spatangoid echinoid: a problem of preservation. Bulletin of the Geological Society of Denmark, 24:261–281.

Carpenter, G. H. and I. Swain. 1908. A new Devonian isopod from Kiltorcan, County Kilkenny. Proceedings of the Royal Irish Academy. Section B: Biological, Geological, and Chemical Science, 27:61–67.

Castle, J. W. 1998. Regional sedimentology and stratal surfaces of a lower Silurian clastic wedge in the Appalachian foreland basin. Journal of Sedimentary Research, 68:1201–1211.

Chadwick, G. H. 1908. Revision of "The New York Series." Science, 28:346–348.

Collette, J. H. and J. W. Hagadorn. 2010. Three-dimensionally preserved arthropods from Cambrian Lagerstätten of Quebec and Wisconsin. Journal of Paleontology, 84:646–667.

Collette, J. H., J. W. Hagadorn, and M. A. Lacelle. 2010. Dead in their tracks—Cambrian arthropods and their traces from intertidal sandstones of Quebec and Wisconsin. PALAIOS, 25:475–486.

Cooper, R. A., J. B. Jago, A. J. Rowell, and P. Braddock. 1983. Age and correlation of the Cambrian–Ordovician Bowers Supergroup, northern Victoria Land, p.128–131. *In* R. L. Oliver (ed.), Antarctic Earth Science. Cambridge University Press.

Cotter, E. 1983. Shelf, paralic, and fluvial environments and eustatic sea-level fluctuations in the origin of the Tuscarora Formation (lower Silurian) of central Pennsylvania. Journal of Sedimentary Research, 53:25–49.

Davies, N. S., I. J. Sansom, R. S. Nicoll, and A. Ritchie. 2011. Ichnofacies of the Stairway Sandstone fish-fossil beds (Middle Ordovician, Northern Territory, Australia). Alcheringa: An Australasian Journal of Paleontology, 35:553–569.

Davis, R. B., N. J. Minter, and S. J. Braddy. 2007. The neoichnology of terrestrial arthropods. Palaeogeography, Palaeoclimatology, Palaeoecology, 255:284–307.

d'Orbigny, A. 1842. Voyage dans l'Amérique Méridionale. Paris, 188 p.

https://doi.org/10.1666/11-133R1.1 Published online by Cambridge University Press

FORTEY, R. A. AND A. SEILACHER. 1997. The trace fossil *Cruziana semiplicata* and the trilobite that made it. Lethaia, 30:105–112.

GAILLARD, C., P. HANTZPERGUE, J. VANNIER, A. L. MARGERARD, AND J. M. MAZIN. 2005. Isopod trackways from the Crayssac Lagerstätte, Upper Jurassic, France. Palaeontology, 48:947–962.

GENSEL, P. G., N. G. JOHNSON, AND P. K. STROTHER. 1990. Early land plant debris (Hooker's "Waifs and Strays"?). PALAIOS, 5:520–547.

GRAHN, Y. 1992. Revision of Silurian and Devonian strata of Brazil. Palynology, 16:35–61.

GRAY, J. E. 1825. An attempt to divide the Echinida or sea eggs, into natural families. Annals of Philosophy, Series 2, 10:423–431.

HAHN, G., R. HAHN, AND C. BRAUCKMANN. 1986. Zur kenntnis von *Arthropleura* (Myriapoda; Ober-Karbon). Geologica et Palaeontologica, 20:125–137.

HALDEMAN, S. S. 1840. Supplement to number one of "A monograph of the Limniades, or freshwater univalve shells of North America," containing descriptions of apparently new animals in different classes, and the names and characters of the subgenera in Paludina and Anculosa. Philadelphia, 3 p.

HALL, J. 1852. Palaeontology of New York. C. Van Benthusyen, Albany, 358 p.

HANKEN, N. M. AND L. STØRMER. 1975. The trail of a large Silurian eurypterid. Fossils and Strata, 4:255–270.

HANNIBAL, J. T. 1997. Myriapods and arthropleurids, p. 172–183. *In* C. W. Shabica and A. Hay (eds.), Richardson's guide to the fossil fauna of Mazon Creek. Northeastern Illinois University Press, Chicago.

HANTZSCHEL, W. 1975. Trace fossils and problematica, 2nd edition. Treatise on Invertebrate Paleontology, Part W, Miscellanea Supplement 1. Geological Society of America and University of Kansas, Lawrence, Kansas, 269 p.

HARLAN, R. 1831. Description of an extinct species of fossil vegetable, of the family Fucoides. Journal of the Academy of Natural Sciences of Philadelphia, 6:289–295.

JOHNSON, N. G. 1985. Early Silurian palynomorphs from the Tuscarora Formation in central Pennsylvania and their paleobotanical and geological significance. Review of Palaeobotany and Palynology, 45:307–359.

KRAUS, O. 2005. On the structure and biology of *Arthropleura* species (Atelocerata, Diplopoda; Upper Carboniferous/Lower Permian). Verhandlungen des Naturwissenschaftlichen Vereins zu Hamburg, 41:5–23.

LEACH, W. E. 1814. Crustaceaology. *In* D. Brewster (ed.), Ediburgh Encyclopaedia 7. Edinburgh.

MACLEAY, W. S. 1839. Note on the Annelida. *In* R. I. Murchison (ed.), The Silurian System part 2. London.

MÀNGANO, M. G., L. A. BUATOIS, C. G. MAPLES, AND R. R. WEST. 2000. A new ichnospecies of *Nereites* from Carboniferous tidal-flat facies of eastern Kansas, U.S.A.: implications for the *Nereites-Neonereites* debate. Journal of Paleontology, 74:149–157.

MÀNGANO, M. G., N. B. CARMONA, L. A. BUATOIS, AND F. M. GUINEA. 2005. A new ichnospecies of *Arthrophycus* from the upper Cambrian–lower Tremadocian of northwest Argentina: implications for the arthrophycid lineage and potential in ichnostratigraphy. Ichnos: An International Journal for Plant and Animal Traces, 12:179–190.

MARTIN, A. K. AND A. K. RINDSBERG. 2007. Arthropod tracemakers of *Nereites*? Neoichnological observations of juvenile limulids and their paleoichnological applications, p. 478–491. *In* W. Miller (ed.), Trace Fossils: Concepts, Problems, Prospects. Elsevier, Amsterdam.

MEYER, H. VON. 1853. Mitteilung an Prof. Bronn. Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde, 1853:161–165.

MILLER, M. A. AND L. E. EAMES. 1982. Palynomorphs from the Silurian Medina Group (lower Llandovery) of the Niagara Gorge, Lewiston, New York, U.S.A. Palynology, 6:221–254.

MILLER, W., F. WEBB JR., AND L. A. RAYMOND. 2009. Clustering and morphologic variation in *Arthrophycus alleghaniensis* (lower Silurian of Virginia, U.S.A.) as evidence of behavioral paleoecology. Neues Jahrbuch für Geologie und Paläontologie–Abhandlungen, 251:109–117.

MILNE-EDWARDS, H. 1843. Note sur deux Crustacés fossiles de l'ordre des isopodes. Annales des Sciences Naturelles (Zoologie), 20:326–329.

ORTEGA-HERNÀNDEZ, J., D. A. LEGG, J. TREMEWAN, AND S. J. BRADDY. 2010. Euthycarcinoids. Geology Today, 26:195–198.

PICKERILL, R. K., M. ROMANO, AND B. MELÉNDEN. 1984. Arenig trace fossils from the Salamanca area, western Spain. Geological Journal, 19:249–269.

PRATT, L. M., T. L. PHILLIPS, AND J. M. DENNISON. 1978. Evidence of non-vascular land plants from the early Silurian (Llandoverian) of Virginia, U.S.A. Review of Palaeobotany and Palynology, 25:121–149.

RINDSBERG, A. K. AND A. J. MARTIN. 2003. *Arthrophycus* in the Silurian of Alabama (U.S.A.) and the problem of compound trace fossils. Palaeogeography, Palaeoclimatology, Palaeoecology, 192:187–219.

ROLFE, W. D. I. 1969. Arthropoda incertae sedis, p. 620–625. *In* R. C. Moore (ed.), Treatise on Invertebrate Paleontology, Part R, Arthropoda 4(2). Geological Society of America and University of Kansas, Lawrence, Kansas.

SCHRAM, F. R. 1971. A strange arthropod from the Mazon Creek of Illinois and the Trans Permo–Triassic Merostomoidea (Trilobitoidea). Fieldiana Geology, 20:85–102.

SEILACHER, A. 2000. Ordovician and Silurian arthrophycoid ichnostratigraphy, p. 237–258. *In* M. A. Sola and D. Worsley (eds.), Geological Exploration in Murzuq Basin. Elsevier, Amsterdam.

SEILACHER, A. 2007. Trace Fossil Analysis. Springer, New York, 226 p.

SELDEN, P. A. AND J. A. DUNLOP. 1998. Fossil taxa and relationships of chelicerates, p. 303–332. *In* G. D. Edgecombe (ed.), Arthropod Fossils and Phylogeny. Columbia University Press, New York.

SELLEY, R. 1970. Ichnology of Palaeozoic sandstones in the southern desert of Jordan: A study of trace fossils in their sedimentological context, p. 477–488. *In* T. P. Crimes and J. C. Harper (eds.), Trace Fossils. Liverpool Geological Society, Liverpool.

SHEAR, W. A. 1997. The fossil record and evolution of the Myriapoda, p. 211–219. *In* R. A. Fortey and R. H. Thomas (eds.), Arthropod Relationships. Systematics Association Special Volume 55. Chapman & Hall, London.

SHEAR, W. A. AND P. A. SELDEN. 1995. *Eoarthropleura* (Arthropoda, Arthropleurida) from the Silurian of Britain and the Devonian of North America. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 196:347–375.

STILWELL, J. D., R. H. LEVY, R. M. FELDMAN, AND D. M. HARWOOD. 1997. On the rare occurrence of Eocene callianassid decapods (Arthropoda) preserved in their burrows, Mount Discovery, East Antarctica. Journal of Paleontology, 71:284–287.

STØRMER, L. 1952. Phylogeny and taxonomy of fossil horseshoe crabs. Journal of Paleontology, 26:630–640.

STØRMER, L. 1976. Arthropods from the Lower Devonian (lower Emsian) of Alken an der Mosel, Germany. Part 5: Myriapoda and additional forms, with general remarks on fauna and problems regarding invasion of land by arthropods. Senckenbergiana Lethaea, 57:87–183.

STROTHER, P. K. AND A. TRAVERSE. 1979. Plant Microfossils from Llandoverian and Wenlockian Rocks of Pennsylvania. Palynology, 3:1–21.

TOMESCU, A. M. F., G. W. ROTHWELL, AND R. HONEGGER. 2006. Cyanobacterial macrophytes in an early Silurian (Llandovery) continental biota: Passage Creek, lower Massanutten Sandstone, Virginia, U.S.A. Lethaia, 39:329–338.

TORELL, O. 1870. Petrificata Suecana Formationis Cambricae. Lunds Universitet Arsskrift, 6:1–14.

TURNER, B. R. AND M. J. BENTON. 1983. Paleozoic trace fossils from the Kufra Basin, Libya. Journal of Paleontology, 57:447–460.

WILLS, M. A. 1998. Crustacean disparity through the Phanerozoic: comparing morphological and stratigraphic data. Biological Journal of the Linnean Society, 65:455–500.

WILSON, H. M. AND W. A. SHEAR. 2000. Microdecemplicida, a new order of minute arthropleurideans (Arthropoda: Myriapoda) from the Devonian of New York State, U.S.A. Transactions of the Royal Society of Edinburgh, Earth Sciences, 90:351–375.

YEAKEL, L. S. 1962. Tuscarora, Juniata, and Bald Eagle paleocurrents and paleogeography in the central Appalachians. Geological Society of America Bulletin, 73:1515–1539.

ACCEPTED 8 JUNE 2012

https://doi.org/10.1666/11-133R1.1 Published online by Cambridge University Press