LOWER PENNSYLVANIAN INVERTEBRATE ICHNOFOSSILS FROM THE UNION CHAPEL MINE, ALABAMA: A PRELIMINARY ASSESSMENT

SPENCER G. LUCAS and ALLAN J LERNER

New Mexico Museum of Natural History and Science, 1801 Mountain Road NW, Albuquerque, New Mexico 87104, USA

ABSTRACT: A preliminary assessment of the invertebrate ichnofossil assemblage from the Union Chapel Mine (Lower Pennsylvanian, Pottsville Formation, Alabama) indicates that the assemblage is dominated by *Kouphichnium* isp., *Arborichnus repetita*, and *Treptichnus bifurcus*. *Selenichnites, Cochlichnus, Protovirgularia, Palaeophycus,* and *Diplichnites gouldi* are rare elements of the assemblage. The Union Chapel Mine invertebrate ichnofossil assemblage is characteristic of an estuarine tidal flat ichnofauna in being dominated by arthropod trackways, grazing traces, and subsurface feeding traces.

INTRODUCTION

Aldrich and Jones (1930) first documented the presence of extensive assemblages of tetrapod footprints found in coal mines developed in Lower Pennsylvanian strata of the Warrior basin coal field of Alabama. Until recently, this remained essentially all that was known of these footprint assemblages. However, the discovery of tetrapod footprints at the Union Chapel Mine in Walker County, Alabama (Fig. 1), by Ashley Allen in the 1990s, initiated new interest in the Pennsylvanian tetrapod footprint record in Alabama that was culminated by a recent symposium on the footprints held by the University of Alabama, and by the publication of this volume. These tetrapod footprints are part of an extensive trace fossil assemblage that includes numerous invertebrate ichnofossils (see http://bama.ua.edu/~rbuta/monograph/ database/database.html, as well as Rindsberg, 1990; Buta et al., 2005). Our purpose here is to provide a preliminary assessment of the invertebrate ichnofossils from the Union Chapel Mine pending more detailed studies. In this article, UCM = Union Chapel Mine collection, stored at various sites (mostly private collections) in Alabama.

GEOLOGICAL CONTEXT

The Union Chapel Mine is near Jasper, Alabama, and the track-bearing strata at the Union Chapel Mine are in the Mary Lee coal zone (Fig. 1). The track-bearing interval at the Union Chapel Mine is in sandstone-shale couplets interpreted as tidal rhythmites (Pashin, 2003). Invertebrate ichnotaxa in these strata include abundant xiphosuran trails and resting traces (*Kouphichnium*, etc.) and insect feeding traces (*Treptichnus*), as well as less common walking and feeding traces (Rindsberg and Kopaska-Merkel, 2003) that are discussed here. Elsewhere in this volume, Rindsberg and Kopaska-Merkel (2005) document the specimens of *Treptichnus* from the Union Chapel Mine (also see Uchman, 2005). Fish swimming traces (*Undichna*) are

also present, as are the tracks of small amphibians (*Batrachichnus*), small captorinomorph reptiles (*Notalacerta* and *Cincosaurus*) and larger tetrapods (*Attenosaurus, Alabamasauripus, Dimetropus*; Haubold et al., 2005; Martin, 2003; Hunt et al., 2004). Indeed, tracks assigned to *Cincosaurus* so dominate the footprint assemblage that local collectors refer to the trace-fossil-bearing strata at the Union Chapel Mine as the "*Cincosaurus* beds."

SYSTEMATIC ICHNOLOGY

Cochlichnus Hitchcock, 1858 Cochlichnus isp. Fig. 2A

Description: These specimens are smooth, thin, unbranched, unlined, unornamented, horizontal burrows. Preservation is in positive hyporelief. The assigned burrows display regular courses that resemble sine waves. Some of these small burrows are in close proximity and overcross. The burrow diameters are approximately 1 mm, and the average burrow length is between 30 and 50 mm.

Discussion: The specimens are contained on a single block (UCM 1650) that has an extensively worked surface of relatively small and large horizontal burrows (Fig. 2A). The smaller burrows are tentatively assigned to *Cochlichnus*, and are found in association with larger burrows tentatively assigned to *Palaeophycus*. Both ichnotaxa are seen to overcross. Some of the smaller burrows on this slab display a less regularly sinusoidal course than is seen in *Cochlichnus*, and they more closely resemble *Helminthopsis*.

Insect larvae and nematodes are thought to have been the producers of *Cochlichnus* in this type of nonmarine assemblage (Buatois et al., 1997a; Metz, 1998). *Cochlichnus* ranges in age from Precambrian to Holocene and has a wide facies range, including fluviatile (*Mermia* ichnofacies) and marginal marine (*Cruziana* ichnofacies) settings (e.g., Häntzschel, 1975; Fillion and

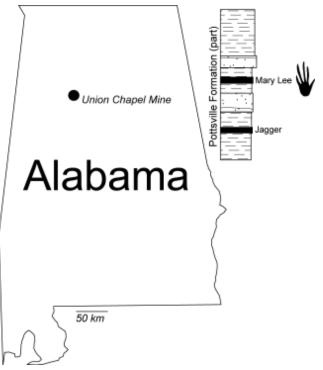


FIGURE 1. Index map of Alabama and simplified stratigraphic section of part of the Pottsville Formation (after Metzger, 1965), showing geographic location and stratigraphic position in Mary Lee coal zone of Union Chapel Mine ichnofossil assemblage.

Pickerill, 1990; Buatois and Mángano, 1993).

Palaeophycus Hall, 1847 Palaeophycus isp. Fig. 2A

Description: These specimens consist of horizontal burrows that are generally smooth and subcylindrical. Preservation is in positive hyporelief. They display variable courses that are alternately straight to loosely winding. There is frequent touching and overcrossing between burrows. The burrow widths are generally constant and are approximately 5 mm in diameter. The average burrow lengths approach 50 mm.

Discussion: These larger burrows, which are found on UCM 1650 in association with *Cochlichnus* and *Helminthopsis*-like trails are assigned to *Palaeophycus* largely because the burrow fill is identical to the surrounding matrix (cf. Lucas and Lerner, 2004). *Palaeophycus* is a facies-crossing ichnospecies that ranges in age from Proterozoic to Holocene, and is generally thought to have been produced by worms or wormlike organisms (Lucas and Lerner, 2004).

Ichnogenus Protovirgularia M[°]Coy, 1850 Protovirgularia isp. Fig. 2B

Description: The illustrated specimen is a horizontal, unbranched trace with a narrow central furrow and regularly-spaced, lateral, chevron-shaped elevations. Width is up to 20 mm.

Discussion: We assign this specimen to *Protovirgularia* based on Han and Pickerill's (1994) emended diagnosis of the ichnogenus (also see Lucas and Lerner, 2004). *Protovirgularia* is the locomotion trace of a cleft-foot bivalve. It has been recorded from a variety of facies, including tidal flats, that range in age from Ordovician to Holocene. It is rare in the UCM collection.

Ichnogenus Diplichnites Dawson, 1873 Diplichnites gouldi Gevers in Gevers et al., 1971 Fig. 2D

Description: UCM 154 is a single slab that contains three trackways composed of simple, biserial track rows. The trackway courses are straight to curving. There is one section in which two of the trails overcross. Trackway length extends to 100 mm, and the width is about 10 mm. The imprints are small and mostly ellipsoidal in shape. A few imprints appear as short, elongated scratches that are perpendicular to the trackway axis. All three trackways are of similar imprint morphology and dimensions, suggesting that they were made by a single animal.

Discussion: These trails are assigned to *Diplichnites gouldi*, based on their having simple track rows and closely spaced imprints (Buatois et al., 1998). These specimens appear similar to other reports of this ichnotaxon (e.g., Buatois et al., 1997b, 1998; Lucas et al., 2004). Specimens of *Diplichnites gouldi* are commonly thought to have been produced by myriapods, which are infrequently preserved as body fossils.

Ichnogenus Kouphichnium Nopsca, 1923 Kouphichnium isp. Fig. 2E

Description: The Union Chapel ichnofauna includes numerous epirelief and hyporelief trackways that are assigned to this well-known ichnogenus. Specimens commonly show two rows of symmetrically arranged heteropodous imprints bordering medial drag marks. Imprint shapes generally consist of elongate scratches, small bifid scratches and ellipsoidal marks but show considerable variation. Characteristic digitate "pusher" tracks, oriented parallel to the central axis, are commonly seen. External drag marks are rare. Trackway courses meander and frequently intersect. External trackway widths average 30 to 40 mm.

Discussion: The Union Chapel Mine invertebrate ichnofauna is notable for having an abundance of wellpreserved *Kouphichnium* trackways. These trackways provide a large sample of the preservational variation and undertrack fallout that has often been noted for *Kouphichnium*, and which has complicated its ichnotaxonomy. Buatois et al. (1998) stated that a taxonomic review of *Kouphichnium* ichnospecies is needed, and we wholeheartedly concur. The UCM ichnofauna has great potential for utility in this regard, and should be a pivotal sample in resolving the ichnospecies-level taxonomy of *Kouphichnium*.

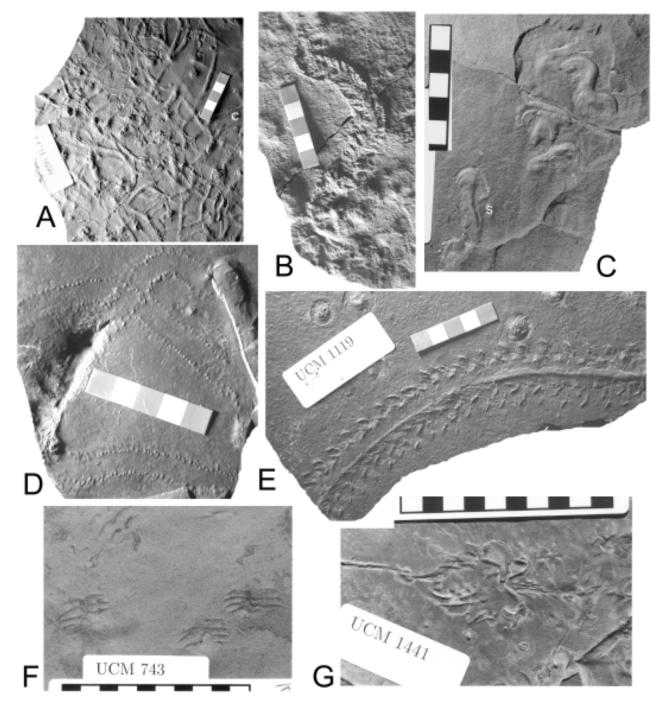


FIGURE 2. Representative invertebrate ichnofossils from the Union Chapel Mine. All scale bars are in cm. A, UCM 1650, *Cochlichnus* isp. and *Paleophycus* isp. A good example of *Cochlichnus* is to the immediate left of the "c." B, UCM uncatalogued, *Protovirgularia* isp. C, UCM 107, *Selenichnites* isp. Note the shallow angle imprint to the left of the "s." D, UCM 154, *Diplichnites gouldi*. E, UCM 1119, *Kouphichnium* isp. F, UCM 743, *Arborichnus repetita*. G, UCM 1441, xiphosuran resting trace.

Selenichnites Romano and Whyte, 1987 Selenichnites isp. Fig. 2C

Description: UCM 107 is preserved as a part and an incomplete counterpart. The part contains a series of repeated crescentric impressions that are preserved in convex hyporelief. The entire group of crescentric impressions is aligned in a similar direction. An interval of 30 mm typically separates these impressions, although several intervening impressions are seen to overlap. The crescents range from 15 to 20 mm wide, and are highest anteriorly. The lateral lobes of the crescents range from 10 to 15 mm long and are arranged anterolaterally to the median line (where best seen). A single well-preserved impression appears to have been less steeply dug than the others (Fig. 2C, marked with a "s"). It shows an anterior crescent with a centralized posterior ridge that is 20 mm long. A faint, shallow furrow is medially present along the ridge, which separates it into pairs. Several closely spaced, convex, lateral scratch marks are preserved along one side of the ridge. The other side of the ridge is mostly smooth, gently curved, and preserves few scratch marks. The anterior of the crescent preserves a clear outline of a thin prosoma in ventral aspect. Similar outlines are faintly preserved on several of the other crescents. However, none of the other crescents show a centralized posterior ridge.

Discussion: These traces are assigned to Selenichnites based on the distinctive crescent shaped morphology that readily conforms to the ichnogeneric diagnosis. There are five recorded ichnospecies of Selenichnites, as well as two known occurrences of Selenichnites isp. (Draganits et. al., 2001). UCM 107 is most similar in shape to S. langridgei, although the absence of a characteristic medial trefoil shape precludes ichnospecific assignment. The Union Chapel specimens are smaller than the average width given for S. langridgei, although they are within the range reported by Trewin and McNamara (1995). Xiphosurans are generally thought to have produced Kouphichnium, as well as some Selenichnites. The width of the Union Chapel Selenichnites is noticeably smaller than Kouphichnium from the same ichnofauna. Thus, if a xiphosuran did produce the UCM Selenichnites, a juvenile individual probably made it. Other possible trace makers include eurypterids, trilobites, or crustaceans. Selenichnites that shows repeated digging behavior is thought to be a feeding trace, a behavior akin to that of modern Limulus (Trewin and McNamara, 1995).

Ichnogenus Arborichnus Romano and Meléndez, 1985

Arborichnus repetita Romano and Meléndez, 1985 Fig. 2F

Description: Numerous UCM specimens, preserved in both epirelief and hyporelief, are confidently assigned to this ichnospecies. These distinctive traces closely resemble the original diagnosis, being sets of short, symmetrical scratch marks and characteristic alignment, and with repeat distance between sets being approximately equal to the length of the set.

Discussion: *Arborichnus* was not formally described until Romano and Meléndez (1985), although it had been known for a considerable time (see Caster, 1938, fig. 1, plate 9, figs. 3, 4). Other than Romano and Meléndez's type descriptions from the Carboniferous of Spain, there are few recent reports of this ichnotaxon in the literature. The large number of UCM *A. repetita* specimens, which number in the hundreds, provides an extensive sample with which to broaden our understanding of xiphosuran behavior and further clarify the taxonomy of this ichnogenus.

Unassigned xiphosuran traces Fig. 2G

Description: A variety of specimens (e.g., UCM 487, 1051, 1053, 1058, 1060, 1061, 1437, 1441, 1568, 1752, 1755, 1762) record the linear and serial repetition of telson drags, opistosomal and genal spine imprints. Prosomal marks are occasionally present. Walking appendage imprints are absent or minimally present in the majority of specimens. Preservation is in both epirelief and hyporelief.

Discussion: The UCM specimens record behavior that is also documented by Kouphichnium rossendalensis Hardy, 1970, later transferred to Selenichnites by Romano and Whyte (1987). However, there are significant differences between the UCM specimens and these ichnotaxa. Hardy interpreted S. rossendalensis as having been formed when swimming xiphosurans briefly touched down on the sediment surface, dragged their telson and appendages, and retracted them before implanting lunate casts. The lunate casts of S. rossendalensis are deepest anteriorly and shallow posteriorly, and thought to represent burrowing for concealment or resting. The UCM traces show similar behavior in that swimming xiphosurans serially touched down on the substrate, which in this case recorded aspects of their posterior ventral surfaces. However, distinctively cresentric marks are absent from the UCM specimens, which precludes their assignment to Selenichnites.

The UCM specimens were most likely made with the xiphosuran's anterior inclined away from the bedding plane, as evidenced by the presence of genal spine and telson marks, and the relative absence of prosomal impressions. However, Hardy (1970) stated that in a few examples of *S. rossendalensis* the convex end (anterior) forms a cloven hoof mark. Similar anterior morphology is seen in several UCM specimens (Fig. 2G), which suggests that they may be undertracks of *S. rossendalensis* or extra-morphological variations due to substrate conditions. The UCM specimens also differ significantly from *Limulicubichnus* Miller, 1982, erected for limulid resting traces, in which the imprint of the prosoma is prominent.

The morphologic characteristics of these traces, which record general body and prosomal outlines, genal spines impressions, and telson marks, provide strong evidence of their having been produced by xiphosurans. Whatever the eventual outcome of their ichnotaxic assignment, it is highly probable that a closer examination of their size and shape, when compared to Upper Carboniferous xiphosurans known from body fossils, will reveal the identity of the xiphosuran producer.

DISCUSSION

The paleoenvironment of the *Cincosaurus* beds at the Union Chapel Mine has been described as an estuarine tidal flat in a coastal lowland region near the Early Pennsylvanian paleoequator (Minkin, 2005; Pashin, 2005). The trace-fossil-bearing interval at the mine is about 4 meters thick, and the trace fossils generally occur at the tops of graded couplets of siltstone-shale or sandstone-shale interpreted as tidal rhythmites (Pashin, 2005). The footprints and other traces were apparently made on the tidal flats at times of low tides.

The invertebrate ichnofossil assemblage at the Union Chapel mine is dominated by xiphosuran locomotion and resting traces, which comprise more than 90% of the assemblage. The next most common invertebrate ichnotaxon is Treptichnus bifurcus, and all other invertebrate ichnotaxa are rare, being known from one or a few specimens. In general, the Union Chapel Mine invertebrate ichnofossil assemblage is of low diversity, dominated by epifaunal trails and lacks any significant infaunal traces. It thus is a characteristic estuarine tidal flat ichnofossil assemblage in being dominated by arthropod trackways (Kouphichnium, Diplichnites), grazing traces (*Palaeophycus*, *Cochlichnus*) and subsurface feeding traces (*Treptichnus*), and is accompanied by fish traces (Undichna) and abundant tetrapod footprints (cf. Buatois et al., 1998; Mángano and Buatois, 2003, 2004; Lucas et al., 2004).

Editors' note: For additional photographs of invertebrate traces from the Union Chapel Mine, see Buta et al. (2005).

ACKNOWLEDGMENTS

We are grateful for the generosity and assistance of Prescott Atkinson, Ron Buta, Adrian Hunt, and Steve Minkin, which made this paper possible. Comments on the manuscript by L. A. Buatois and M. G. Mángano improved its content and presentation.

REFERENCES

- Aldrich, T. H., Sr. and Jones, W. B., 1930, Footprints from the coal measures of Alabama: Geological Survey of Alabama, Museum Paper 9, 64 p.
- Buatois, L. A. and Mángano, M. G., 1993, The ichnotaxonomic status of *Plangtichnus* and *Treptichnus*: Ichnos, v. 2, p. 217-224.
- Buatois, L. A., Jalfin, G. and Aceñolaza, F. G., 1997a, Permian non-marine invertebrate trace fossils from southern Patagonia, Argentina: Ichnologic signatures of substrate consolidation and colonization sequences: Journal of Paleontology, v. 71, p. 324-336.
- Buatois, L. A., Mángano, M. G., Maples, C. G. and Lanier, W. P., 1997b, The paradox of non-marine ichnofaunas in tidal rhythmites: Integrating sedimentologic and ichnologic data

from the Late Carboniferous of eastern Kansas, USA: Palaios, v. 12, p. 467-481.

- Buatois, L. A., Mángano, M. G., Maples, C. G. and Lanier, W. P., 1998, Ichnology of an Upper Carboniferous fluvio-estuarine paleovalley: The Tonganoxie Sandstone, Buildex Quarry, eastern Kansas, USA: Journal of Paleontology, v. 72, 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.
- Caster, K. E., 1938, A restudy of the tracks of *Paramphibius*: Journal of Paleontology, v. 12, p. 3-60.
- Dawson, J. W., 1873, Impressions and footprints of aquatic animals and imitative markings on Carboniferous rocks: American Journal of Science and Arts, v. 105, p. 16-24.
- Draganits, E., Braddy, S., and Briggs, D.E.G., 2001. A Gondwanan coastal arthropod ichnofauna from the Muth Formation (Lower Devonian, northern India): Paleoenvironment and tracemaker behavior: Palaios, v. 16, p. 126-147.
- Fillion, D. and Pickerill, R. K., 1990, Ichnology of the Lower Ordovician Bell Island and Wabana Groups of eastern Newfoundland: Palaeontographica Canadiana, v. 7, p. 1-119.
- Gevers, T. W., Frakes, L. A., Edwards, L. N. and Marzolf, J. E., 1971, Trace fossils from the Lower Beacon sediments (Devonian), Darwin Mountains, southern Victoria Land, Antarctica: Journal of Paleontology, v. 45, p. 81-94.
- Hall, J., 1847, Paleontology of New York, v. 1: Albany, C. van Benthuysen, 338 p.
- Han, Y. and Pickerill, R. K., 1994, Taxonomic reassessment of *Protovirgularia* M^CCoy, 1850 with new examples from the Paleozoic of New Brunswick, eastern Canada: Ichnos, v. 3, p. 203-212.
- Häntzschel, W., 1975. Trace fossils and problematica; in Teichert, C., ed., Treatise on Invertebrate Paleontology, Part W, Miscellanea, Supplement I: Boulder and Lawrence, Geological Society of America and University of Kansas Press, p. 1-269.
- Hardy, P. G., 1970, New xiphosurid trails from the Upper Carboniferous of northern England: Palaeontology, v. 13, p. 188-190.
- Haubold, H., Allen, A., Atkinson, T. P., Buta, R. J., Lacefield, J. A., Minkin, S. C. and Relihan, B. A., 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.
- Hitchcock, E., 1858, Ichnology of New England: A report on the sandstone of the Connecticut Valley, especially its footprints: Boston, W. White, 220 p.
- Hunt, A. P., Lucas, S. G. and Lockley, M. G., 2004, Large pelycosaur footprints from the Lower Pennsylvanian of Alabama, USA: Ichnos, v. 11, p. 39-44.
- Lucas, S. G., and Lerner, A. J., 2004. Extensive ichnofossil assemblage at the base of the Permian Abo Formation, Carrizo Arroyo, New Mexico: New Mexico Museum of Natural History and Science, Bulletin no. 25, p. 285-289.
- Lucas, S. G., Lerner, A. J, Bruner, M. and Shipman, P., 2004, Middle Pennsylvanian Ichnofauna from Eastern Oklahoma, USA: Ichnos, v.11, p.1-11.
- Mángano, M. G. and Buatois, L. A., 2003, Comparative ichnologic analysis of Pennsylvanian tidal flats of the North American midcontinents; in Martin, A. J., ed., Workshop on Permo-Carboniferous Ichnology, Program and Abstracts: Tuscaloosa. Alabama Museum of Natural History, p. 18-19.
- Mángano, M. G. and Buatois, L. A., 2004, Reconstructing early Phanerozoic intertidal ecosystems: Ichnology of the Cambrian Campanario Formation in northwest Argentina; in Webby, B.

D., Mángano, M. G. and Buatois, L. A., eds., Trace fossils in evolutionary palaeoecology: Fossils and Strata, v. 51, p. 17-38.

- Martin, A. J., 2003, Undichna: A trace fossil bridging the gap between fish and tetrapods; in Martin, A. J., ed., Workshop on Permo-Carboniferous Ichnology, Program and Abstracts: Tuscaloosa, Alabama Museum of Natural History, p. 19-21.
- M Coy, F., 1850, On some genera and species of Silurian Radiata in the collection of the University of Cambridge: Annals and Magazine of Natural History, ser. 2, v. 6, p. 270-290.
- Metz, R., 1998, Nematode trails from the Late Triassic of Pennsylvania: Ichnos, v. 5, p. 303-308.
- Metzger, W. J., 1965, Pennsylvanian stratigraphy of the Warrior basin, Alabama: Geological Survey of Alabama, Circular 30, 80 p.
- Miller, M. F., 1982, *Limulicubichnus*: A new ichnogenus of limulid resting traces: Journal of Paleontology, v. 56, p. 429-433.
- Minkin, S. C., 2005, Paleoenvironment of the *Cincosaurus* beds, Walker County, 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. 31-38.
- Nopsca, F. B., 1923, Die Familien der Reptilien: Fortschritte in der Geologie und Paläontologie, v. 2, p. 1-210.
- Pashin, J., 2003, Stratigraphy of the Union Chapel Mine in its regional context; in Martin, A. J., ed., Workshop on Permo-Carboniferous Ichnology, Program and Abstracts: Tuscaloosa. Alabama Museum of Natural History, p. 25-26.
- 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.
- 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. and Liu, Y., eds., Carboniferous coastal environments and paleocommunities of the Mary Lee Coal zone, Marion and Walker counties, Alabama. A guidebook for field trip VI, Southeastern Section, Geological Society of America. Tuscaloosa, Geological Survey of Alabama, p. 82-95.
- Rindsberg, A. K. and Kopaska-Merkel, D. C., 2003, *Treptichnus* and related trace fossils from the Union Chapel Mine (Langsettian, Alabama, USA); in Martin, A. J., ed., Workshop on Permo-Carboniferous Ichnology, Program and Abstracts: Tuscaloosa. University of Alabama, p. 27-28.
- Rindsberg, A. K. and Kopaska-Merkel, D. C., 2005, *Treptichnus* and *Arenicolites* from the Steven C. Minkin Paleozoic Footprint Site (Langsettian, Alabama, USA); 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. 121-141.
- Romano, M. and Mélendez, B., 1985, An arthropod (merostome) ichnocoenosis from the Carboniferous of northwest Spain: Ninth International Geological Congress, Urbana, Illinois, v. 5, p. 317-325.
- Romano, M. and Whyte, M. A., 1987, A limulid trace fossil from the Scarborough Formation (Jurassic) of Yorkshire; its occurrence, taxonomy and interpretation: Proceedings of the Yorkshire Geological Society, v. 46, p. 85-95.
- Trewin, N. H., and McNamara, K. J., 1995, Arthropods invade the land: Trace fossils and palaeoenvironments of the Tumblagooda Sandstone (?Late Silurian) of Kalbarri, Western Australia: Transactions of the Royal Society of Edinburgh, Earth Sciences, v. 85, p. 77-210.

Uchman, A., 2005, Treptichnus-like traces made 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.

AUTHORS' E-MAIL ADDRESSES

Spencer G. Lucas: slucas@nmmnh.state.nm.us Allan J Lerner: hanallaine@aol.com