LOWER JURASSIC INVERTEBRATE ICHNOFOSSILS FROM A CLASTIC LAKE MARGIN, JOHNSON FARM, SOUTHWESTERN UTAH

SPENCER G. LUCAS[1], ALLAN J LERNER[1], ANDREW R. C. MILNER[2] AND MARTIN G. LOCKLEY[3]

[1]New Mexico Museum of Natural History and Science, 1801 Mountain Road NW, Albuquerque, NM 87104;
[2]St. George Dinosaur Discovery Site at Johnson Farm, 2180 East Riverside Drive, St. George, UT 84790;
[3]Dinosaur Tracks Museum, University of Colorado at Denver, PO Box 173364, Denver, CO 80217

Abstract—The St. George Dinosaur Discovery Site at Johnson Farm (SGDS) in southwestern Utah is principally known for its theropod dinosaur tracks, which are in clastic lake-margin facies of the Lower Jurassic Whitmore Point Member of the Moenave Formation. A low diversity invertebrate ichnofossil assemblage associated with the dinosaur tracks includes cf. *Bifurculapes* ichnosp., *Diplichnites triassicus*, cf. *Kouphichnium* ichnosp., *Helminthoidichnites tenuis*, *Palaeophycus tubularis*, *Palaeophycus* ichnosp. and *Skolithos* ichnosp. This ichnofossil assemblage belongs to the *Scoyenia* ichnofacies and suggests that the lake margin paleoenvironment at the SGDS was one of relatively low energy and was periodically submerged/emergent. The SGDS invertebrate ichnofossil assemblage fits well with other Late Triassic-Early Jurassic lake-margin ichnofossil assemblages of the *Scoyenia* ichnofacies. The ichnofauna at the SGDS also suggests that taphonomic and sedimentological factors may have produced some of the differences between the lake margin ichnoassemblages evident in the Upper Triassic-Lower Jurassic record. Thus, arthropod walking traces may be rare at the SGDS (and some other sites) simply because of the relative coarseness of the sediment and the reworking of sediment surfaces by wave action or sheetflow.

INTRODUCTION

The St. George Dinosaur Discovery Site at Johnson Farm (SGDS) is located within the city limits of St. George, Utah (Fig. 1). This locality yields an extensive assemblage of tetrapod footprints, mostly of the ichnogenera *Grallator* and *Eubrontes*, which are the tracks of theropod dinosaurs (e.g., Kirkland et al., 2002; Milner et al., 2004; Milner and Lockley, 2006; Milner et al., this volume a). In addition to the tetrapod tracks, a low diversity invertebrate ichnofossil assemblage is present at the SGDS (Lucas et al., 2005; Milner and Lockley, 2006). The ichnofossils at the SGDS (Figs. 2-4) are from clastic lake-margin facies of the Lower Jurassic Whitmore Point Member of the Moenave Formation. They are primarily present in an approximately 1 m-thick interval of sandstone that includes the "Main Track Layer" (MTL) at Johnson Farm. Here we document the invertebrate ichnofossils from the SGDS and discuss their paleoecological and taphonomic significance. In this paper, SGDS = specimens in the collection of the St. George Dinosaur Discovery Site at Johnson Farm.

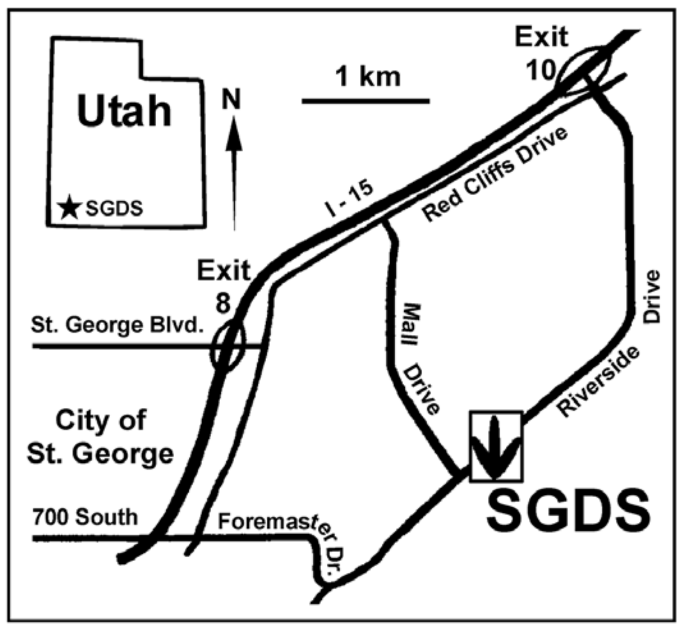

FIGURE 1. Index map showing location of the St. George Dinosaur Discovery Site at Johnson Farm (SGDS) in southwestern Utah. Courtesy of J. Kirkland.

SYSTEMATIC ICHNOLOGY

Ichnogenus *Bifurculapes* Hitchcock, 1858
cf. *Bifurculapes* ichnosp.
Figure 3B

Referred specimen: SGDS 197, single part and counterpart trackway preserved in concave epirelief and convex hyporelief from the SGDS "Split Layer."

Description: SGDS 197 consists of two double rows of simple, elongate, transverse imprints. The faint, inner rows of imprints are straight and oriented parallel to the trackway midline when preserved. The outer rows of imprints are more defined than the inner rows, are transverse, and show hook-like projections on their ends. The outer imprints vary from roughly 5 to 10 mm long and from 1 to 1.5 mm wide, whereas the inner imprints are from 5-12 mm long and up to 1 to 1.5 mm wide. Spacing between the outer imprints is about 20 mm. The hook-like projections on the outer rows face in alternate directions, with a pattern showing markings alternating from right to left. The track row is 200 mm long and has a course that is mostly straight to slightly undulating.

Remarks: Although the SGDS 197 specimen only preserves faintly impressed tracks, the paired rows displayed in a nearly mirror image trackway resemble *Bifurculapes laqueatus* (e.g., Hitchcock, 1858; Lull, 1953; Lockley et al., 2002). The SGDS example, however, is narrower in comparison to other reports and not as well preserved. This specimen was figured in Milner and Lockley (2006, fig. 6D). The ichnogenus *Lithographus* is similar, but has imprints in sets of three rather than two as in *Bifurculapes* and SGDS 197. Indeed, *Bifurculapes* probably is just a preservational variant of *Lithographus* and therefore synonymous (N. Minter, written commun., 2006).

Another possible arthropod trackway from the SGDS, specimen SGDS 308, consists of a single row of simple, elongate, transverse im-

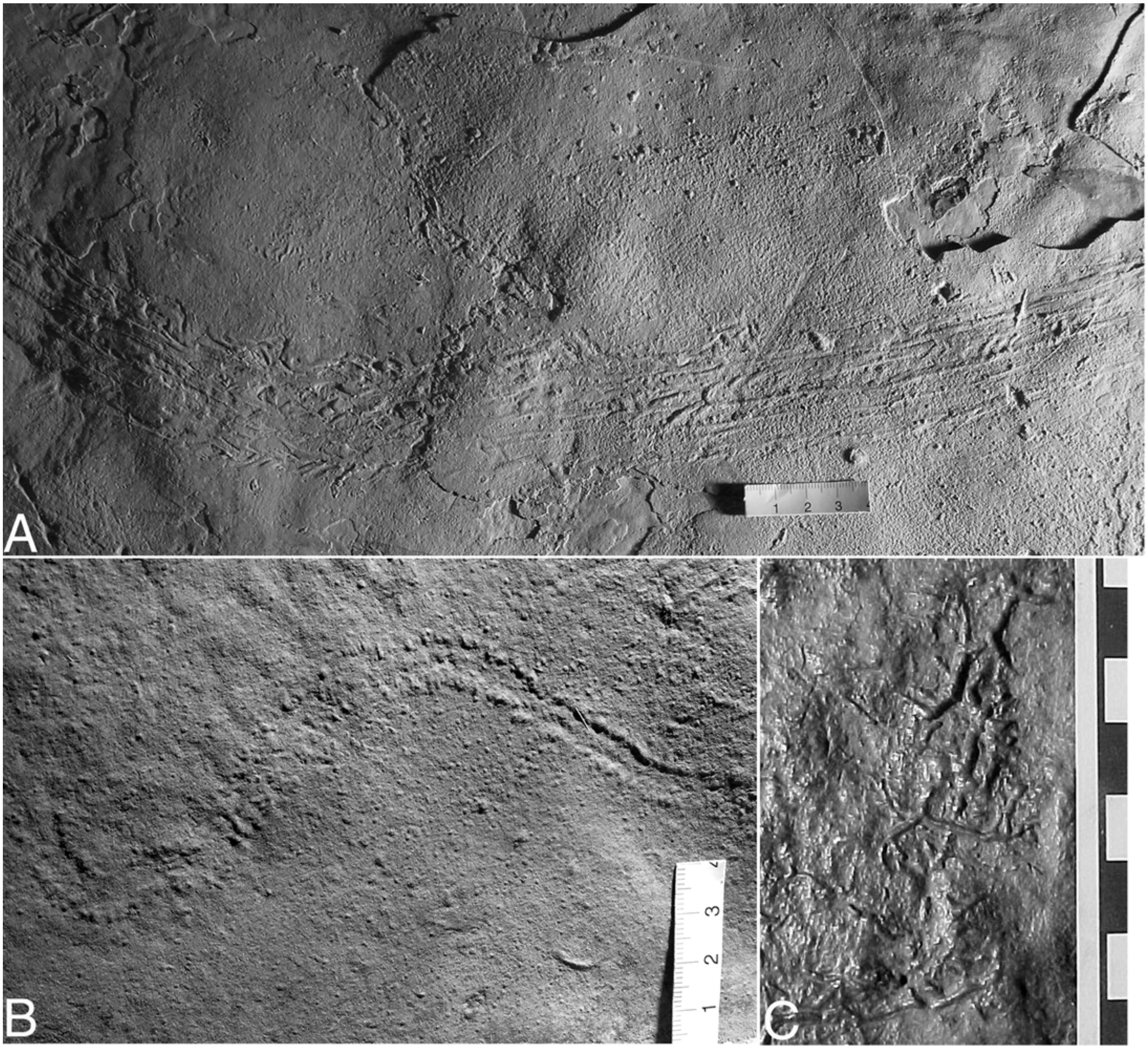

FIGURE 2. Selected invertebrate ichnofossils (walking traces and grazing trails) from Johnson Farm. **A**, SGDS 258, trackway of *Kouphichnium* ichnosp. in convex hyporelief. **B**, SGDS 197, trackway of *Diplichnites triassicus* in convex hyporelief. **C**, SGDS 375, grazing trails of *Helminthoidichnites tenuis* in convex hyporelief.

prints. Most of these transverse imprints show hook-like projections on their ends. The imprints vary from roughly 5 to 10 mm long and from 1 to 1.5 mm wide. Spacing between imprints is about 2 mm apart. The hook-like projections face in alternate directions, although a regular pattern is not seen. One end of the track row shows several adjacent, rounded imprints that are separated from the transverse imprints by distances of about 2 mm. The track row is 200 mm long and has a course that is mostly straight to slightly undulating. There is no indication of an associated second track row.

This specimen resembles two others that were recently reported by Voigt et al. (2005) from a terrestrial ichnofauna in the Pennsylvanian-Permian Maroon Formation of Colorado. The St. George specimen is not as well preserved and differs from the Maroon Formation material in having adjacent rounded imprints along part of its course. As noted by Voigt et al., the traces are unusual in that they lack bilateral symmetry. Outwardly, these traces resemble *Tasmanadia* but lack a second track row. While it is possible that this limited material represents a previously unknown and recurring ichnotaxon, it is more likely that it consists of undertracks in which only one of two track rows was recorded on the exposed bedding plane.

Bifurculapes has been attributed to insect track makers, especially beetles (Hitchcock, 1858; Lockley et al., 2002). Hitchcock (1858) also suggested crustaceans as possible track makers of *Bifurculapes*.

Ichnogenus *Diplichnites* Dawson, 1873

Diplichnites triassicus (Linck, 1943)

Figure 2B

Referred specimens: SGDS 38, single trackway in convex hyporelief (float specimen from the “Top Surface”); SGDS 197, single

FIGURE 3. Selected invertebrate ichnofossils (walking traces) from the Johnson Farm. **A**, SGDS 366, cf. *Kouphichnium* ichnosp. **B**, SGDS 197, cf. *Bifuculapes* ichnosp.

trackway part preserved in concave epirelief and counterpart in convex hyporelief (from the SGDS "Split Layer"); SGDS 463, single trackway found as a float specimen, probably from the "Top Surface" layer, preserved as a possible undertrack.

Description: A single part and counterpart specimen (SGDS 197: Fig. 2B) has a small trackway containing two rows of simple imprints that vary from perpendicular to oblique in their orientation to the trackway midline. The imprints are mostly elongate to crescentric in shape, although some are punctate. No imprint series is detected. Some of the imprints are arranged slightly en echelon. The external trackway width is about 10 mm, and the internal width is about 7 mm. The trackway course is straight to curved and is up to 200 mm long. No median furrow is seen.

Specimen SGDS 38 shows a single trackway circling and crossing over its own course. This specimen has an external trackway width of 7 mm and an internal width of 4-5 mm. If outstretched, the entire preserved trackway would measure ~150 mm long. Foot imprints are identical to those described above.

SGDS 463 is a cf. *Diplichnites* ichnosp. trackway that is not well preserved. This may be the largest *Diplichnites* specimen recorded from the SGDS, with an external width of 10-12 mm and a trackway length of ~150 mm. An internal trackway width was not measurable because of the specimen's poor preservation.

Remarks: These simple arthropod locomotion trails are similar in most aspects to other reports of *Diplichnites triassicus* (Linck, 1943; Bromley and Asgaard, 1979; Pollard, 1985; Goldring et al., 2005). The ichnotaxonomy of the species of *Diplichnites* is in dire need of revision. For example, Pollard (1985) attributed material with en echelon series to *D. triassicus*, but *D. gouldi* is also frequently used for such trackways. Here, we assign the specimens to *D. triassicus,* following the usage of Pollard (1985), but *D. gouldi* could also be applied to the Johnson Farm specimens.

Branchiopod crustaceans, most likely notostracans, are thought to have been the producers of these traces (Pollard, 1985).The counterpart of SGDS 197 was illustrated in Milner and Lockley (2006, fig. 6C).

Ichnogenus *Helminthoidichnites* Fitch, 1850
***Helminthoidichnites tenuis* Fitch, 1850**
Figure 2C

Referred specimens: SGDS 375, in convex hyporelief (float specimen); SGDS 741, 742, 743, and 747 preserve negative relief impressions collected *in situ* from the upper track bed at the Stewart-Walker Tracksite near the SGDS museum.

Description: All slab surfaces show numerous simple, horizontal

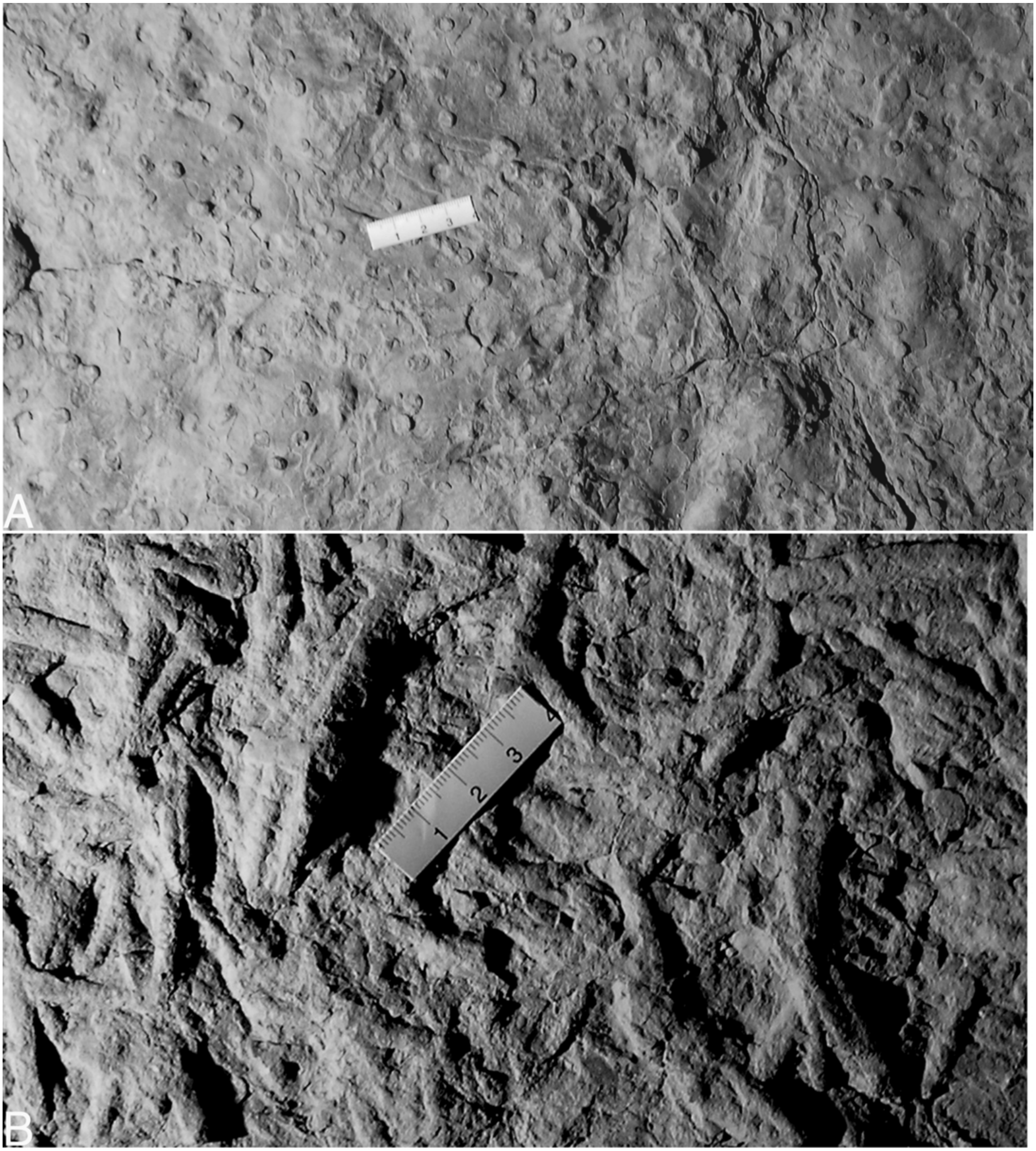

FIGURE 4. Selected invertebrate trace fossils (burrows) from Johnson Farm. **A**, SGDS 453, *Skolithos* ichnosp. in bedding plane view. **B**, SGDS 191, *Palaeophycus tubularis* in convex hyporelief.

trails that are preserved in convex hyporelief or in concave epirelief. Diameters are thin and average about 1.0 mm. The greatest trail length is 14 cm. Burrow fill is similar to the host slab. Trails courses are mostly straight to gently curved. Overlap is commonly seen between individual trails, but there is no self-overcrossing.

Remarks: Reports of *Helminthoidichnites* from nonmarine settings range from the Carboniferous to the Cretaceous and include one Jurassic record from deposits in China (Buatois et al., 1996). Nematomorphs or insect larvae are thought to have been the producer of these simple grazing trails in nonmarine settings (Buatois et al., 1997; Metz, 2000).

Ichnogenus *Kouphichnium* Nopsca, 1923

cf. *Kouphichnium* ichnosp.

Figures 2A, 3A

Referred specimens: SGDS 258, single trackway in convex hyporelief; SGDS 366, partial trackway in concave epirelief of cf. *Kouphichnium* ichnosp. (float, probably from "Top Surface" layers); SGDS 452, two partial trackways preserved on actual tracking surface and as undertracks in concave epirelief (a close to *in situ* specimen collected from the "Top Surface" layers on former Darcy Stewart property); SGDS 641, partial, single trackway preserved as undertracks in concave epirelief (float specimen from uncertain horizon).

Description: The best preserved single trackway (SGDS 258: Fig. 2A) consists largely of discontinuous drag marks that are oriented approximately parallel to the trackway axis. Discrete imprints are not well seen except on a narrow segment where the trackway course curves. This segment shows a track row with four elongate imprints that are oblique to the trackway midline. The imprints are straight to curved and measure up to 1 cm long. A medial telson drag mark is intermittently seen within the length of the trackway. The trackway course is straight to gently curving and is up to 70 cm long. The external trackway width is up to 40 mm.

Digitate "pusher" foot impressions are not preserved on this specimen, and for this reason definite assignment to *Kouphichnium* is not made. Indeed, SGDS 258 shows some similarities to *Dendroidichnites*, which consists of two rows of elongate imprints and chevron markings, and has the overall apperance of a feather-like structure (e.g., Demathieu et al., 1992; Santi, 2003). However, the similarity of SGDS 258 to *Kouphichnium* is greater than to *Dendroidichnites*, so we identify it as cf. *Kouphichnium*. Similarly, SGDS also show some similarities to *Keircalia* from the Devonian of Scotland, which is two parallel rows of very closely spaced imprints with four central grooves (Smith, 1909; Walker, 1985). However, in SGDS 258 the tracks are not so clear nor are the rows, so we maintain a tentative assignment to *Kouphichnium.*

Another larger slab shows two partial cf. *Kouphichnium*-like trackways (SGDS 452), one with clear foot falls in an arcing trackway (external trackway width ~11.5 cm; trackway length ~30 cm) (Milner and Lockley, 2006, fig. 6B). A second, poorly-preserved trackway on this same slab is straight, measuring 13 cm in length, with an external trackway width of ~50 mm.

Remarks: Although the SGDS 258 trackway and others can tentatively be assigned to cf. *Kouphichnium,* an ichnospecific assignment is not given due to the overall poor preservation and due to the confused ichnospecific taxonomy of *Kouphichnium*. As noted by Buatois et al. (1998), a taxonomic revision of *Kouphichnium* is much needed due to the probability that most of its ichnospecies are the result of undertrack fallout. *Kouphichnium* has previously been recorded in western North American Jurassic continental deposits (e.g., Hasiotis, 1996, 2004), and is particularly well known from the Upper Triassic of Utah, Arizona and New Mexico (Caster, 1944; Hunt et al., 1993). Limuloid xiphosurans (horseshoe crabs) are recognized as having been the producers of *Kouphichnium* (Häntzschel, 1975).

Another specimen from Johnson Farm (SGDS 366) displays two cf. *Kouphichnium* ichnosp. trackways that appear to overlap each other (Fig. 3A). The better trackway displays "pusher" foot marks that are in sets of three and sometimes four. This specimen also resembles trackways assigned to the ichnogenus *Harpepus* (Hitchcock, 1865; Lull, 1953; Lockley et al., 2002). *Harpepus* has been attributed to insects, especially coleopterans (Lockley et al., 2002).

Ichnogenus *Palaeophycus* Hall, 1847
***Palaeophycus tubularis* Hall, 1847**
Figure 4B

Referred specimens: SGDS 191, 843, 844, 845, and many *in situ* specimens from the "green conchostracan bed," all preserved in convex hyporelief; SGDS 847, collected in float from a light brown, coarse sandstone unit, preserved in convex hyporelief.

Description: Very large *in situ* surfaces (lateral extent approximately 60 m), heavily bioturbated, and covered with numerous irregularly cylindrical, thinly-lined burrows with straight to gently-curved horizontal courses. Surface walls are irregularly smooth and lack striations or annulations. Burrow diameters typically are about 7-9 mm. The burrow fill is the same as the surrounding rock. Branching is absent, although cross-cutting and interpenetration is seen between specimens. Preservation is in convex hyporelief.

Remarks: These simple burrows are assigned to *P. tubularis* based on their smooth, unornamented walls and on the presence of a thin wall lining (Pemberton and Frey, 1982). *Palaeophycus* represents passive sedimentation within open dwelling burrows (domichnia) constructed by a predaceous or suspension feeding animal (Pemberton and Frey, 1982), and a variety of other behaviors and animal types (q.v. Metz, 1998). *Palaeophycus* is a facies-crossing ichnotaxon that ranges in age from Proterozoic to Holocene in both nonmarine and marine rocks.

Ichnogenus *Skolithos* Haldeman, 1840
***Skolithos* ichnosp.**
Figure 4A

Referred specimens: Hundreds of individual specimens are preserved *in situ* on the "Slauf Burrow Bed and "Sally's Burrow Bed" at the SGDS. Several samples were also examined for this study: SGDS 453, 504, 505, 639, 679, and 854.

Description: These slab surfaces are covered with numerous endichnial, vertical, single entrance burrows that appear as circular holes or raised circular protuberances. Diameters range from 0.5 to 0.75 mm. Total lengths of shafts cannot be determined. Burrow fill is the same as the surrounding host rock, and linings are not present. Distances between shafts vary, and some are seen to touch.

Remarks: These specimens are assigned to *Skolithos* based on their simple morphology and vertical orientation. No ichnospecific assignment is attempted due to the lack of observable vertical cross sections. *Skolithos* is common in Mesozoic nonmarine assemblages from North America (e.g., MacNaughton and Pickerill, 1995; Gillette et al., 2003). Modern makers of simple vertical dwelling burrows (domichnia) in nonmarine settings include insects and spiders (Gierlowski-Kordesch, 1991). *Skolithos* is a facies-crossing ichnotaxon that ranges in age throughout the Phanerozoic (Alpert, 1974). SGDS 453 was illustrated in Milner and Lockley (2006, fig. 6F).

INORGANIC STRUCTURES

The SGDS museum Top Surface also contains load casts, a variety of tool marks and rill marks that superficially resemble biogenic structures. Zigzag lines on the sediment bear some similarity to insect grazing traces such as *Treptichnus* (Fig. 5A), but given their size, lack of continuity, lack of vertical burrow pits, and the polygonal shapes they circumscribe, two of us (SGL and AJL) believe they are more likely shrinkage cracks in the sediment. One of us (ARM) still interprets these as invertebrate grazing traces based on their association with certain sedimentary structures and other ichnites. This is beyond the scope of this paper and will be discussed elsewhere.

Mud lumps or load casts (Fig. 5B) bear some similarity to *Margaritichnus* (e.g., Bandel, 1967; Hakes, 1976), but they lack centralized shafts that connect the proximal and distal ends (cf. Pemberton et al., 1987; Mángano et al., 2000). Linear tool marks or chevron marks (Fig. 5C) bear some similarity to *Protovirgularia* (bivalve walking traces in Kim et al. [2000] and Lucas and Lerner [2004] and dragonfly larval trails in Metz [2002]). Milner and Lockley (2006, fig. 6E) illustrated specimen SGDS 38 as *Protovirgularia*, although recently, several well-preserved chevron marks have been located on the *in situ* tracksite at the SGDS and we reinterpret this specimen as chevron tool marks rather than *Protovirgularia*. Some soft-sediment deformation structures at the

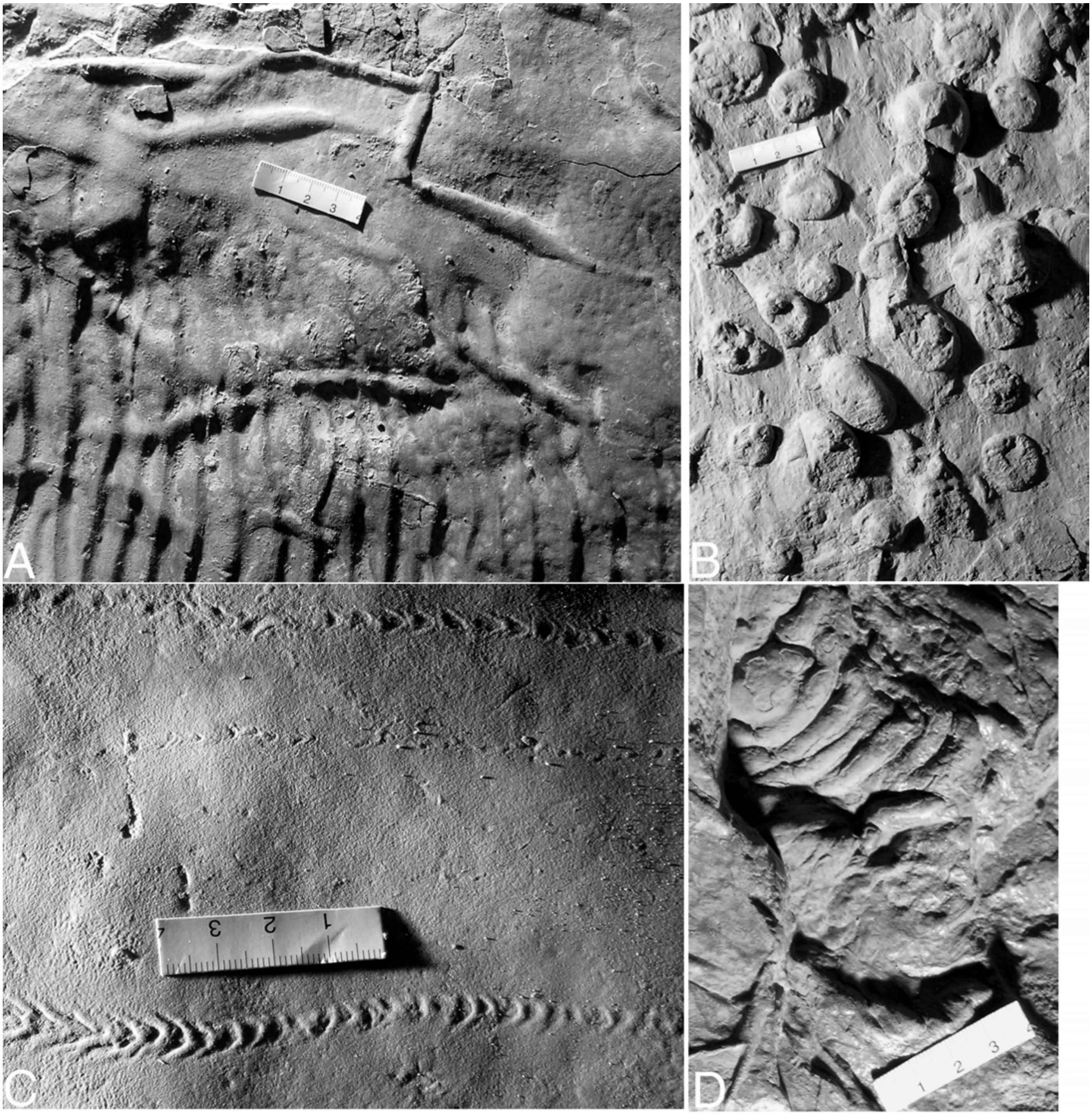

FIGURE 5. Selected inorganic structures that resemble trace fossils from Johnson Farm. **A**, SGDS 18, shrinkage cracks that resemble *Treptichnus*. **B**, SGDS 438, load casts that resemble *Margaritichnus*. **C**, SGDS 38, chevron marks that resemble *Protovirgularia*. **D**, SGDS 25, soft sediment deformation structures that resemble *Rhizocorallium*.

SGDS (Fig. 5D) mimic *Rhizocorallium*.

DISCUSSION

The SGDS site contains a moderately low diversity invertebrate ichnofauna that consists of horizontal and vertical burrows (*Palaeophycus*, *Skolithos*), grazing traces (*Helminthoidichnites*) and arthropod locomotion trails (*Kouphichnium*, *Diplichnites*, and cf. *Bifurculapes*). Among these invertebrate trace fossils, only *Skolithos* and smaller *Palaeophycus* are abundant, occurring in large numbers on multiple bedding planes. Larger *Palaeophycus* are also locally abundant in prolific concentrations, such as the specimen illustrated here (Fig. 4B). The other invertebrate ichnotaxa are rare, represented by only one or a few specimens. This relative abundance of invertebrate ichnotaxa appears to be a real phenomenon, not an artifact of collecting bias. This is because very large surfaces (up to about 18 x 50 m^2) have been excavated at and in the vicinity of the SGDS to reveal the dinosaur tracks for study and exhibition. Yet, these surfaces yield few invertebrate traces other than *Skolithos* and smaller *Palaeophycus*. The smaller *Palaeophycus* are extremely abundant on the submerged MTL surface associated with dinosaur swim tracks (Milner et al., this volume b).

We assign the SGDS invertebrate ichnofossil assemblage to the *Scoyenia* ichnofacies because it is characterized by horizontal, lined feeding burrows, unlined feeding burrows, vertical cylindrical to irregular shafts, and is associated with vertebrate footprints (e.g., Buatois and Mángano, 1995). The *Scoyenia* ichnofacies is usually considered characteristic of low energy, periodically-submerged or emerged environments. This supports sedimentological analysis of the lake-margin lithofacies at the SGDS that indicates just such a paleoenvironment (Milner and Lockley, 2006; Kirkland and Milner, this volume; Milner et al., this volume a, b).

Lake margin invertebrate ichnofossil assemblages of Late Triassic-Early Jurassic age have been described from New Mexico (Hester and Lucas, 2001; Gillette et al., 2003; Lucas and Lerner, this volume), the eastern United States (Metz, 1989, 1995, 1996, 2000; Gierlowski-Kordesch, 1991), Greenland (Bromley and Asgaard, 1979, 1991; Dam and Stemmerik, 1994), Germany (Schlirf et al., 2001) and Argentina (Melchor et al., 2001; Melchor, 2004). Other than Upper Triassic lacustrine delta deposits in Argentina, which are in realtively distal zones and have an invertebrate ichnofossil assemblage of the *Mermia* ichnofacies (Melchor, 2004), these lake margin facies yield low diversity ichnofossil assemblages of the *Scoyenia* ichnofacies. These are ichnofossil assemblages dominated by simple horizontal or vertical grazing traces and burrows (e.g., *Treptichnus*, *Cochlichnus*, *Planolites*, *Palaeophycus*, *Skolithos*, *Helminthoidichnites*, *Helminthopsis*, *Spongeliomorpha*) and meniscate backfilled burrows (e.g., *Scoyenia*, *Taenidium*), with some arthropod walking traces (mostly *Diplichnite*s) and conchostracan/bivalve resting traces (*Lockeia*). The SGDS invertebrate ichnofossil assemblage fits well with these other Upper Triassic-Lower Jurassic lake-margin ichnofossil assemblages of the *Scoyenia* ichnofacies (Lucas and Lerner, this volume).

However, these lake-margin ichnofossil assemblages fall into three categories that may, upon further study, be found to represent three distinct ichnocoenoses. Thus, most of the assemblages lack either arthropod walking trails or bivalve/conchostracan resting traces. Some assemblages have the arthropod walking traces, whereas others have the conchostracan/bivalve resting traces. These differences may reflect real differences between the paleocommunities of invertebrates that inhabited Late Triassic-Early Jurassic lake margins. For example, in the Upper Triassic Redonda Formation of eastern New Mexico, *Lockeia* is extremely abundant in the lake margin facies of what was a carbonate rich lake, whereas no such abundance of *Lockeia* is documented in other published Upper Triassic-Lower Jurassic lake margin ichnofacies that pertain to clastic lakes where water conditions apparently did not favor a community with large populations of conchostracans.

The SGDS trace fossils also suggest that taphonomic and sedimentological factors may have produced some of the differences between the lake margin ichnoassemblages evident in the Upper Triassic-Lower Jurassic record. Thus, arthropod walking traces may be rare at the SGDS (and some other sites) simply because of the relative coarseness of the sediment (which is a fine sandstone to siltstone, although mudstone, claystone and shale are present) and the reworking of sediment surfaces by wave action or sheetflow. Firmer substrates have already been demonstrated to cause a bias among vertebrate ichnites at the SGDS (Milner et al., 2005), and this will also affect light-weight invertebrate traces. Some of the arthropod walking traces from the SGDS (*Diplichnites*, cf. *Bifurculapes*, *Kouphichnium*) probably represent terrestrial trackways across an aerially exposed sandy-silty-muddy substrate. This possibility needs to be investigated further in all lake-margin ichnofossil assemblages because the nature of the substrate and relative energy of the environment may be biasing the record by preventing or eliminating preservation of the most delicate trace fossils seen in lake margin ichnofossil assemblages, namely the walking traces of arthropods.

ACKNOWLEDGMENTS

We thank: SGDS staff and volunteers; donations from Dr. Sheldon Johnson, Darcy and Colleen Stewart, John Timpson (Bodega Bay, LLC), Layton Ott, Paul Jensen, the Church of Jesus Christ of Latter Day Saints and the Washington County School District for the donation of specimens and allowing access to properties for research; partial funding for this research by the City of St. George and the DinosaurAh!Torium Foundation. We also thank the Utah Friends of Paleontology for volunteer assistance. Thanks to Jim Kirkland (Utah Geological Survey) and Jerry Harris (Dixie State College) for helpful discussion. Luis Buatois, Jerry Harris and Nick Minter offered helpful reviews of the manuscript.

REFERENCES

Alpert, S.P., 1974, Systematic review of the genus *Skolithos*: Journal of Paleontology, v. 48, p. 661-669.

Bandel, K., 1967, Trace fossils from two Upper Pennsylvanian sandstones in Kansas: The University of Kansas, Paleontological Contributions, v. 18, p. 1-13.

Bromley, R.G. and Asgaard, U., 1979, Triassic freshwater ichnocoenoses from Carlsberg Fjord, east Greenland: Palaeogeography, Palaeoclimatology, Palaeoecology, v.28, p. 39-80.

Bromley, R.G. and Asgaard, U., 1991, Ichnofacies: a mixture of taphofacies and biofacies: Lethaia, v. 24, p. 153-163.

Buatois, L.A. and Mángano, M.G., 1995, The paleoenvironmental and paleoecological significance of the lacustrine *Mermia* ichnofacies: an archetypical subaqueous nonmarine trace fossil assemblage: Ichnos, v. 4, p. 151-161.

Buatois, L.A., Wu, X. and Zhang, G., 1996, Trace fossils from Jurassic lacustrine turbidites of the Anyao Formation (central China) and their environmental and evolutionary significance: Ichnos, v. 4, p. 287-303.

Buatois, L.A., Jalfin, G. and Aceñolaza, F.G., 1997, 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., Genise, J. and Taylor, T., 1998, The ichnologic record of the continental invertebrate invasion: evolutionary trends in environmental expansion, ecospace utilization, and behavioral complexity: Palaios, v. 13, p. 217-240.

Caster, K.E., 1944, Limuloid trails from the Upper Triassic (Chinle) of the Petrified Forest National Monument, Arizona: American Journal of Science, v. 242, p. 74-84.

Dam, G. and Stemmerik, L., 1994, East Greenland lacustrine complexes, *in* Gierlowski-Kordesch, E. and Kelts, K., eds., Global geological record of lake basins, volume 1: Cambridge, Cambridge University Press, p. 19-27.

Dawson, J.W., 1873, Impressions and footprints of aquatic animals and imitative markings on Carboniferous rocks: American Journal of Science and Arts, v. 5, p. 16-24.

Demathieu, G., Gand, G. and Toutin-Morin, N., 1992, La palichnofaune des bassins Permien Provençaux: Geobios, v. 25, p. 19-54.

Fitch, A., 1850, A historical, topographical and agricultural survey of the County of Washington. Part 2-5: Transactions of the New York Agricultural Society, v. 9, p. 753-944.

Gierlowski-Kordesch, E., 1991, Ichnology of an ephemeral lacustrine/alluvial plain system: Jurassic East Berlin Formation, Hartford Basin, USA: Ichnos, v. 1, p. 221-232.

Gillette, L., Pemberton, S.G. and Sarjeant, W.A.S., 2003, A Late Triassic invertebrate ichnofauna from Ghost Ranch, New Mexico: Ichnos, v. 10, p. 141-151.

Goldring, R., Pollard, J. and Radley, J., 2005, Trace fossils and pseudofossils from the Wealden strata (non-marine Lower Cretaceous) of southern England: Cretaceous Research, v. 26, p. 665-685.

Hakes, W.G., 1976, Trace fossils and depositional environment of four clastic units, Upper Pennsylvanian megacyclothems, northeast Kansas: University of Kansas Paleontological Contributions, v. 63, p. 1-46.

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, Privately printed, 3 p.

Hall, J., 1847, Geology of New York, volume I: Albany, State of New York, 338 p.

Häntzschel, W., 1975, Trace fossils and problematica, *in* C. Teichert, ed., Treatise on invertebrate paleontology, part W, miscellanea, supplement I: Lawrence, Geological Society of America and University of Kansas Press, p. 1-26.

Hasiotis, S., 1996, Terrestrial and freshwater trace fossils, Upper Jurassic Morrison Formation, Colorado Plateau: Museum of Northern Arizona, Bulletin 60, p. 355-371.

Hasiotis, S., 2004, Reconnaissance of Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain Region, USA: paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses: Sedimentary Geology, v. 167, p. 177-268.

Hester, P.M. and Lucas, S.G., 2001, Lacustrine depositional environments of the Upper Triassic Redonda Formation, east-central New Mexico: New Mexico Geological Society, Guidebook 52, p. 153-168.

Hitchcock, E., 1858, Ichnology of New England. A report on the sandstone of the Connecticut Valley especially its fossil footmarks: Boston, W. White, 199 p. (Reprinted by Arno Press in the Natural Sciences in America series).

Hitchcock, E., 1865, Supplement to the ichnology of New England. Boston, Wright and Porter, 96 p.

Hunt, A.P., Lucas, S.G. and Lockley, M.G., 1993, Fossil limuloid trackways from the Petrified Forest National Park, Arizona, USA: New Mexico Museum of Natural History and Science, Bulletin 3, p. 205-207.

Kim. J.-Y., Kim, K.-S. and Pickerill, R.K., 2000, Trace fossil *Protovirgularia* McCoy, 1850 from the nonmarine Cretaceous Jinju Formation of the Sacheon area, Korea: Journal of the Korean Earth Science Society, v. 21, p. 695-702.

Kirkland, J.I., Lockley, M. and Milner, A.R., 2002, The St. George dinosaur tracksite: Utah Geological Survey Notes, v. 34, p. 4-5, 12.

Kirkland, J.I. and Milner, A.R.C., this volume, The Moenave Formation at the St. George Dinosaur Discovery Site at Johnson Farm: New Mexico Museum of Natural History and Science, Bulletin 37.

Linck, O., 1943, Die Buntsandstein-Kleinfahrten von Nagold (*Limulidichnulus nagoldensis* n.g. n.s., *Merostomichnites triassicus* n. sp.): Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Monatshefte, Abteilung B, v. 1943, 9-27.

Lockley, M., Peterson, J., and Manning, M., 2002, Cretaceous beetle tracks from the Fossil Trace Golf Course, Golden, Colorado: Friends of Dinosaur Ridge Annual Report for 2002, p. 25-28.

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 25, p. 285-289.

Lucas, S.G. and Lerner, A.J, this volume, Invertebrate ichnofossil assemblages of the Upper Triassic Redonda Formation at Mesa Redonda, east-central New Mexico: New Mexico Museum of Natural History and Science, Bulletin 37.

Lucas, S.G., Lerner, A.J. and Milner, A.R.C., 2005, Early Jurassic invertebrate ichnofauna of the St. George Dinosaur Discovery Site, Moenave Formation: The Triassic/Jurassic Terrestrial Transition, Abstracts Volume, p. 14-15.

Lull, R.S., 1953, Triassic life of the Connecticut Valley: State of Connecticut, State Geological and Natural History Survey, Bulletin 81, p. 1-336.

MacNaughton, R.B. and Pickerill, R.K., 1995, Invertebrate ichnology of the nonmarine Lepreau Formation (Triassic), southern New Brunswick, eastern Canada: Journal of Paleontology, v. 69, p. 160-171.

Mángano, M.G., Buatois, L.A., Maples, C.G. and West, R.W., 2000, A new ichnospecies of *Nereites* from Carboniferous tidal-flat facies of eastern Kansas, USA: implications for the *Nereites-Neonereites* debate: Journal of Paleontology, v. 74, p. 149-157.

Melchor, R.N., 2004, Trace fossil distribution in lacustrine deltas: examples from the Triassic rift lakes of the Ischigualasto-Villa Unión basin, Argentina, *in* McIlroy, D., ed., The application of ichnology to palaeoenvironmental and stratigraphic analysis: Geological Society of London Special Publication, v. 228, p. 335-354.

Melchor, R.N., Genise, J.F. and Verde, M., 2001, Invertebrate trace fossils from Triassic continental successions of San Juan Province, Argentina: Asociación Paleontológica Argentina, Publicación Especial, v. 7, p. 127-131.

Metz, R., 1989, *Scoyenia* ichnofacies from the Passaic Formation (Upper Triassic) near Milford, New Jersey: Northeastern Geology, v. 11, p. 212-217.

Metz, R., 1995, Ichnologic study of the Lockatong Formation (Late Triassic), Newark Basin, southwestern Pennsylvania: Ichnos, v. 4, p. 43-51.

Metz, R., 1996, Newark Basin ichnology: the Late Triassic Perkasie Member of the Passaic Formation, Sanatoga, Pennsylvania: Northeastern Geology and Environmental Sciences, v. 18, p. 118-129.

Metz, R., 1998, Silurian trace fossils from marginal marine deposits, Lizard Creek Member of the Shawangunk Formation, Delaware Water Gap, New Jersey: Northeastern Geology and Environmental Sciences, v. 20, p. 101-116.

Metz, R., 2000, Triassic trace fossils from lacustrine shoreline deposits of the Passaic Formation, Douglasville, Pennsylvania: Ichnos, v. 7, p. 253-266.

Metz, R., 2002, Nonmarine Cretaceous *Protovirgularia*: possible dragonfly larva tracemaker: Ichnos, v. 9, p. 75-76.

Milner, A.R., Lockley, M., Kirkland, J., Bybee, P. and Mickelson, D., 2004, St. George tracksite, southwestern Utah: remarkable Early Jurassic (Hettangian) record of dinosaurs walking, swimming, and sitting provides a detailed view of the paleoecosystem along the shores of Lake Dixie: Journal of Vertebrate Paleontology, v. 24, p. 94A.

Milner, A.R.C. and Lockley, M.G., 2006, History, geology and paleontology: St. George Dinosaur Discovery Site at Johnson Farm, Utah, *in* Reynolds, R.E., ed., Making tracks across the southwest, the 2006 Desert Symposium Field Guide and Abstracts from Proceedings. Californian State University, Desert Studies Consortium and LSA Associates, Inc., p. 35-48.

Milner, A.R.C., Kirkland, J.I., Lockley, M.G. and Harris, J.D., 2005, Relative abundance of theropod dinosaur tracks in the Early Jurassic (Hettangian) Moenave Formation at a St. George dinosaur tracksite in southwestern Utah: bias produced by substrate consistency: Geological Society of America Abstracts with Programs, v. 37, p. 5.

Milner, A.R.C., Lockley, M.G. and Johnson, S.B., this volume a, The story of the St. George Dinosaur Discovery Site at Johnson Farm: an important new Lower Jurassic dinosaur tracksite from the Moenave Formation of southwestern Utah: New Mexico Museum of Natural History and Science, Bulletin 37.

Milner, A.R.C., Lockley, M.G. and Kirkland, J.I., this volume b, A large collection of well preserved theropod dinosaur swim tracks from the Lower Jurassic Moenave Formation, St. George, Utah: New Mexico Museum of Natural History and Science, Bulletin 37.

Nopsca, F.B., 1923, Die Familien der Reptilien: Fortschritte de Geologie und Paläontologie, v. 2, p. 121-210.

Pemberton, S.G., and Frey, R., 1982, Trace fossil nomenclature and the *Planolites-Palaeophycus* dilemma: Journal of Paleontology, v. 56, p. 843-881.

Pemberton, S.G., Frey, R.W. and Bromley, R., 1987, The ichnotaxonomy of *Conostichnus*: Canadian Journal of Earth Science, v. 25, p. 866-892.

Pollard, J.E., 1985, *Isopodichnus*, related trace fossils and notostracans from Triassic fluvial sediments: Transactions of the Royal Society of Edinburgh, Earth Sciences, v. 76, p. 273-285.

Santi, G., 2003, Overview about the Lower Permian invertebrate ichnology of the Orobic basin (northern Italy): Atti Ticinensi di Scienze della Terra, v. 44, p. 111-116.

Schlirf, M., Uchman, A. and Kümmel, M., 2001, Upper Triassic (Keuper) non-marine trace fossils from the Hassberge area (Franconia, south-eastern Germany): Paläontologische Zeitschrift, v. 75, p. 71-96.

Voigt, S., Small, B. and Sanders, F., 2005, A diverse terrestrial ichnofauna from the Maroon Formation (Pennsylvanian-Permian), Colorado: Biostratigraphic and paleoecological significance: New Mexico Museum of Natural History and Science, Bulletin 30, p. 342-351.