A trace fossil made by a walking crayfish or crayfish-like arthropod from the Lower Jurassic Moenave Formation of southwestern Utah, USA

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New invertebrate trace fossils from the Lower Jurassic Moenave Formation at the St. George Dinosaur Discovery Site at Johnson Farm (SGDS) continue to expand the ichnofauna at the site. A previously unstudied arthropod locomotory trace, SGDS 1290, comprises two widely spaced, thick, gently undulating paramedial impressions flanked externally by small, tapered to elongate tracks with a staggered to alternating arrangement. The specimen is not a variant of any existing ichnospecies, but bears a striking resemblance to modern, experimentally generated crayfish walking traces, suggesting a crayfish or crayfish-like maker for the fossil. Because of its uniqueness, we place it in a new ichnospecies, *Siskemia eurypyge*. It is the first fossil crayfish or crayfish-like locomotion trace ever recorded.

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Abstract

New invertebrate trace fossils from the Lower Jurassic Moenave Formation at the St. George Dinosaur Discovery Site at Johnson Farm (SGDS) continue to expand the ichnofauna at the site. A previously unstudied arthropod locomotory trace, SGDS 1290, comprises two widely spaced, thick, gently undulating paramedial impressions flanked externally by small, tapered to elongate tracks with a staggered to alternating arrangement. The specimen is not a variant of any existing ichnospecies, but bears a striking resemblance to modern, experimentally generated crayfish walking traces, suggesting a crayfish or crayfish-like maker for the fossil. Because of its uniqueness, we place it in a new ichnospecies, *Siskemia eurypyge*. It is the first fossil crayfish or crayfish-like locomotion trace ever recorded.

Introduction

Paleoichnology, the study of ichnofossils (fossil tracks and traces), contributes a substantial body of paleobiological information to the understanding of extinct organisms. This is because ichnofossils are direct results of ancient animal behavior (Osgood, 1975) that could only otherwise be inferred from body fossils. Furthermore, the global commonness of ichnofossils compared to body fossils means that the ichnological record often can preserve evidence of the presence of organisms not otherwise or poorly represented in the body fossil record (Osgood, 1975), especially of invertebrates that lack hard parts and therefore fossilize only under exceptional conditions. Except for conchostracans (*sensu* Kozur & Weems, 2010) and ostracods, which have biomineralized carapaces, arthropods, when compared to their evolutionary diversity, are among the less commonly preserved body-fossil components of terrestrial (including freshwater) paleoecosystems except in various Konservat-Lagerstätten (fossiliferous sites of exceptional preservational quality) (e.g., Charbonnier et al., 2010; Luque et al., 2019; Selden & Nudds, 2012; Smith, 2012). Yet from the mid-Paleozoic through the Cenozoic, arthropods—especially insects and arachnids—were certainly the most populous and diverse metazoan components of most terrestrial ecosystems (Labandeira & Beall, 1990), and their paleoecological importance cannot be underestimated.

Arthropod ichnofossils can be more common and abundant than arthropod body fossils, and may indicate the presences of various arthropod taxa in terrestrial paleoecosystems for which body fossils may be entirely absent. Burrows (domichnia) made by arthropods comprise one such body of evidence. For example, several burrow ichnotaxa in eolian sandstones have been attributed to arthropods (Ekdale, Bromley & Loope, 2007). Some *Macanopsis*, *Psilonichnus*, and *Skolithos* burrows may have been made by spiders (Uchman, Vrenozi & Muceku, 2018); other *Psilonichnus* have been attributed to crabs (Curran, Savarese & Glumac, 2016). *Camborygma* burrows, attributed to crayfish (Hasiotis & Mitchell, 1993), are the primary body of evidence for crayfish in the fossil record. Perhaps more familiarly, walking tracks (repichnia) of arthropods have an extensive geological history, spanning from the Cambrian (and possibly latest Precambrian [Chen et al., 2018]) through the Holocene (e.g., Eiseman & Charney, 2010). They

54   constitute some of the earliest evidence of metazoan life venturing onto land (reviewed in Minter

55   et al., 2016a; Minter et al., 2016b) and are known from virtually every paleoenvironment, from

56   near shore and shallow marine environments (e.g., Collette, Hagadorn & Lacelle, 2010;

57   MacNaughton et al., 2002; Pirrie, Feldmann & Buatois, 2004; Shillito & Davies, 2018; Trewin &

58   McNamara, 1994) and, terrestrially, from proglacial systems (e.g., Anderson, 1981; Lima,

59   Minter & Netto, 2017; Lima et al., 2015; Uchman, Kazakauskas & Gaigalas, 2009; Walter,

60   1985) to desert ergs (e.g., Gilmore, 1927; Good & Ekdale, 2014; Sadler, 1993).

61   The St. George Dinosaur Discovery Site at Johnson Farm (SGDS) in St. George,

62   Washington County, Utah (Fig. 1) has been called a Konzentrat-Ichnolagerstätte (Hunt & Lucas,

63   2006a) because of its exceptional concentration of well-preserved ichnofossils from a broad

64   spectrum of terrestrial organisms. The site preserves a detailed "snapshot" of an earliest Jurassic

65   ecosystem from on- and offshore portions of a freshwater, lacustrine paleoenvironment. The

66   "Dinosaur Discovery" part of the name of the site indicates the concentration of dinosaur tracks

67   at this locality (Milner, Lockley & Johnson, 2006; Milner, Lockley & Kirkland, 2006; Milner et

68   al., 2009), but tracks of other vertebrates (Lockley, Kirkland & Milner, 2004; Milner, Lockley &

69   Johnson, 2006) and a moderately diverse invertebrate ichnofauna (Lucas et al., 2006a) are also

70   preserved. Burrows pertaining to *Helminthoidichnites*, *Palaeophycus*, and *Skolithos* are abundant

71   at the site, but locomotory trackways made by arthropods, referred to cf. *Bifurculapes*,

72   *Diplichnites*, and cf. *Kouphichnium*, are also present. Ichnospecies of *Bifurculapes* have been

73   variably attributed to insects, possibly beetles, and to crustaceans (Getty, 2016, 2018; Hitchcock,

74   1858, 1865); ichnospecies of *Diplichnites* have been attributed to myriapods (Briggs, Rolfe &

75   Brannan, 1979; Davis, Minter & Braddy, 2007; Pollard, Selden & Watts, 2008; Shillito &

76   Davies, 2018), notostracans (Lucas et al., 2006a; Minter et al., 2007), and other arthropods

77   (Melchor & Cardonatto, 2014; Minter et al., 2007); and ichnospecies of *Kouphichnium* have

78   been attributed to limulids (Caster, 1944; King, Stimson & Lucas, 2019; Lomax & Racay, 2012).

79   A previously unstudied SGDS specimen, SGDS 1290, is an arthropod locomotory trace

80   that differs markedly from any other SGDS specimen, indicating the presence of a heretofore

81   unrecognized component of the SGDS ichnofauna. SGDS 1290 is an arthropod locomotory trace

82   because it includes distinct footprints in a discernible cycle, but lacks any features of vertebrate

83   tracks, such as distinct toes (*sensu* Seilacher, 2007). The trace thus resembles numerous other

84   fossil traces attributed to arthropods, as well as those generated experimentally. The fossil was

85   discovered and collected March 11, 2010 by SGDS volunteer Jon Cross.

86

87 Geological Setting

88   Most of the fossils preserved at the SGDS, including the ichnofossil described below,

89   occur in the Whitmore Point Member of the Moenave Formation (Kirkland & Milner, 2006;

90   Kirkland et al., 2014), which conformably overlies the Dinosaur Canyon Member of the

91   Moenave Formation and disconformably underlies the Springdale Sandstone Member, which

92   itself has been assigned as both the lowest member of the Kayenta Formation (Lucas & Tanner,

93   2006) and the uppermost member of the Moenave Formation (Steiner, 2014a). The richest source

94 of the ichnofossils at the SGDS, again including the trace described below, occur within a fine-
95 grained sandstone near the base of the Whitmore Point Member initially called the "Main Track
96 Layer" (Kirkland & Milner, 2006; Milner, Lockley & Johnson, 2006; Milner, Lockley &
97 Kirkland, 2006) and, later and more formally, the Johnson Farm Sandstone Bed (unit 40 of
98 Kirkland et al., 2014) (Fig. 2). SGDS 1290 comes from the uppermost strata of this unit,
99 specifically one of several thinly bedded, apparently conformable, fine-grained-sandstone "Top
100 Surface Tracksite" horizons (*sensu* Kirkland et al., 2014; Milner, Lockley & Johnson, 2006;
101 Milner, Lockley & Kirkland, 2006). The Whitmore Point Member preserves sediments deposited
102 in and around the large, freshwater Lake Whitmore (formerly called Lake Dixie) (Kirkland &
103 Milner, 2006; Kirkland et al., 2014); at the SGDS itself, the Johnson Farm Sandstone Bed
104 preserves ichnofossils and sedimentary structures made in both subaerial and subaqueous
105 conditions, indicating a shoreline paleoenvironment (Milner, Lockley & Kirkland, 2006).
106 Ichnologically, invertebrate ichnofossils in this paleoenvironment pertain to the *Scoyenia*
107 ichnofacies (Buatois & Mángano, 2004; Lucas et al., 2006a), while the associated vertebrate
108 ichnofauna pertains to the *Eubrontes* ichnocoenosis of the *Grallator* ichnofacies (Hunt & Lucas,
109 2006b; Hunt & Lucas, 2006c).
110   Age determinations for the Whitmore Point Member have varied. The unit typically has
111 been placed entirely within the Hettangian (earliest Jurassic) largely on biostratigraphic grounds
112 (see discussions in Kirkland et al., 2014; Milner et al., 2012; Parrish et al., 2019; and Tanner &
113 Lucas, 2009), but was also determined to straddle the Triassic–Jurassic boundary (201.3 ± 0.2
114 Ma) on magnetostratigraphic grounds (Donohoo-Hurley, Geissman & Lucas, 2010), in which
115 system the Johnson Farm Sandstone Bed would be Rhaetian (latest Triassic) in age. However,
116 Steiner (2014b) recovered Hettangian paleomagnetic sequences from the Whitmore Point
117 Member, and Suarez et al. (2017) calibrated the magnetostratigraphic data of Donohoo-Hurley,
118 Geissman & Lucas (2010) with high-precision U–Pb dates to re-situate the Triassic–Jurassic
119 boundary stratigraphically farther down in the Dinosaur Canyon Member of the Moenave
120 Formation, also making the Whitmore Point Member entirely earliest Jurassic in age. The
121 Johnson Farm Sandstone Bed and its fossils therefore are Hettangian in age, approximately 200
122 million years old.
123

Materials & Methods

125   Ichnological terminology for arthropod locomotory traces used herein follows Minter,
126 Braddy & Davis (2007) and Genise (2017). Minter, Braddy & Davis (2007) defined "tracks" as
127 discrete marks made by locomotory appendages, "impressions" as continuous traces made by
128 another portion of the anatomy of a trace maker, and "imprints" as discontinuous such traces;
129 they also provided terms for trackway arrangement and measurements. Genise (2017) outlined
130 various descriptive terms for individual track morphologies. Measurements of SGDS 1290 (Fig.
131 3C, Table 1) were taken using digital calipers. The measurements were: track length and width,
132 internal and external widths between paramedial impressions, distances between tracks and
133 adjacent paramedial impressions, and widths of left and right paramedial impressions.

134   Measurements pertaining to the paramedial impressions were taken adjacent to individual
135   tracks/track sets.
136   The electronic version of this article in Portable Document Format (PDF) will represent a
137   published work according to the International Commission on Zoological Nomenclature (ICZN),
138   and hence the new names contained in the electronic version are effectively published under that
139   Code from the electronic edition alone. This published work and the nomenclatural acts it
140   contains have been registered in ZooBank, the online registration system for the ICZN. The
141   ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed
142   through any standard web browser by appending the LSID to the prefix http://zoobank.org/. The
143   LSID for this publication is: urn:lsid:zoobank.org:pub:D78963CE-11C8-4447-8E26-
144   BBCCF0E37143. The LSID for the herein described *Siskemia eurypyge* isp. nov. is:
145   urn:lsid:zoobank.org:act:769B0815-8991-4F0E-B32C-99C87A9D293B. The online version of
146   this work is archived and available from the following digital repositories: PeerJ, PubMed
147   Central and CLOCKSS.
148

Description of SGDS 1290

150   SGDS 1290, a natural cast (convex hyporelief), consists of two parallel, undulating,
151   paramedial ridges flanked externally by eight sets of small tracks that range in shape from ovoid
152   to tapered (teardrop-shaped) to elongate (Fig. 3A, B). Tracks within each set are closely
153   appressed; track sets are, however, spaced well apart from one another. The track sets are
154   oriented perpendicular to the trackway axis, though tapered and elongate individual tracks within
155   each set have long axes that parallel or are oblique to the trackway axis. Track sets average 4.5
156   mm long anteroposteriorly and 5.4 mm wide mediolaterally (Table 1). Left (L) and right (R) sets
157   of tracks are arranged in an alternating pattern. Based on Fairchild & Hasiotis (2011), the
158   tapering ends of the tapered tracks are presumed to be anterior reflectures, indicating the
159   direction of movement. Most tracks have long axes oriented parallel to the trackway axis; a few
160   (such as in sets L1, L4, and R2) are oblique to the axis. Track R1 is markedly elongate rather
161   than tapered, but also parallel to the trackway axis. Track sets L1, L3, and R4 consist of three
162   distinct but appressed tracks; sets L2, L4, and R2 consist of pairs of appressed tracks, and R1 and
163   R3 appear to consist of single tracks, although the possibility that each comprises multiple,
164   conjoined tracks cannot be ruled out.
165   The paramedial impressions typically are thick mediolaterally, though they vary and taper
166   briefly to nothingness in a few places (being more continuous than repeating, we consider them
167   "impressions" and not "imprints"). The impressions follow gently undulating (non-linear and
168   low amplitude) pathways. They span approximately 7.5 cm along the slab of rock. Overprints of
169   short segments of the paramedial impressions that are not accompanied by tracks are visible
170   behind the main trace segment on a slightly higher stratum. The impressions vary in width along
171   their lengths, ranging from 0–3.1 mm (mean = 2.0 mm) for the left impressions and 0–3.0 mm
172   (mean = 1.6 mm) for the right (Table 1). The width of the trace from left impression to right
173   impression averages 9.4 mm when measured from the lateral (external) edges and 5.6 mm when

174   measured between the medial (internal) edges (Table 1). The distances between the impressions
175   thus are greater than the distances between the impressions and their flanking tracks (mean = 1.6
176   mm); the ratio of the distance between a paramedial impression and its flanking track to the
177   distance between the medial edges of the paramedial impressions ranges from 0-0.78 (mean =
178   0.31; see Supplemental Material), so on average, the paramedial impressions are roughly three
179   times farther apart from each other than either is from its flanking tracks. The impressions taper
180   slightly in cross sectional view: they are wider at their bases and narrower at their rounded
181   apices.
182

Comparisons to Arthropod Repichnial Ichnotaxa

Arthropod repichnia lacking medial or paramedial impressions

185   Several arthropod locomotory (walking) ichnotaxa are readily distinguished from SGDS
186   1290 by (usually) lacking medial or paramedial impressions, but are worth comparing to SGDS
187   1290 to ascertain whether or not it might be a morphological variant of such ichnotaxa. These
188   ichnotaxa are *Acanthichnus* (Hitchcock, 1858), *Asaphoidichnus* (Miller, 1880), *Bifurculapes*
189   (Hitchcock, 1858), *Coenobichnus* (Walker, Holland & Gardiner, 2003), *Copeza* (Hitchcock,
190   1858), *Danstairia congesta* (Smith, 1909), *Diplichnites* (Dawson, 1873), *Eisenachichnus* (Kozur,
191   1981), *Foersterichnus* (Pirrie, Feldmann & Buatois, 2004), *Hamipes* (Hitchcock, 1858),
192   *Laterigradus* (de Carvalho et al., 2016), *Lithographus* (Hitchcock, 1858), *Hornburgichnium*
193   (Kozur, 1989), *Maculichna* (Anderson, 1975a), *Merostomichnites* (Packard, 1900),
194   *Mirandaichnium* (Aceñolaza, 1978), *Octopodichnus* (Gilmore, 1927), *Petalichnus* (Miller,
195   1880), *Pterichnus* (Hitchcock, 1865), *Tasmanadia* (Chapman, 1929), and *Umfolozia* (Savage,
196   1971). Most of these ichnotaxa further differ from SGDS 1290 in the shapes and configurations
197   of their tracks. The comparisons below specify track-making taxa only when one or more have
198   been proposed for the ichnotaxon.
199   *Acanthichnus* tracks (Fig. 4A), attributed to a chelicerate such as a solifugid, are
200   oppositely arranged, short, elongate impressions in two (or four, per Dalman & Lucas, 2015)
201   parallel rows; tracks either are parallel to or angle slightly away from the trackway axis (Dalman
202   & Lucas, 2015; Hitchcock, 1858). This morphology and organization are both unlike those of
203   SGDS 1290.
204   *Asaphoidichnus* tracks (Fig. 4B), attributed to trilobites, are elongate to crescentic,
205   possess 3–4 crescentic branches at one end, and are oriented oblique to the trackway axis (Miller,
206   1880). They are far more complex in structure than the tracks of SGDS 1290.
207   *Bifurculapes* (Fig. 4C), attributed to an insect, possibly a beetle (Getty, 2016), comprises
208   adjacent pairs (rarely triplets) of slightly staggered, elongate, straight to crescentic tracks that lie
209   parallel or slightly oblique to the trackway axis, unlike the tracks of SGDS 1290. Tracks in each
210   pair sometimes converge toward one end in *Bifurculapes*. This ichnotaxon typically does not
211   possess paramedial impressions, but a specimen described by Getty (2016: fig. 1) possess two
212   such traces, albeit faintly, that lie closer to the tracks than to the trackway axis, as in SGDS 1290.
213   These impressions are far less pronounced than their associated tracks, unlike those of SGDS

214   1290. Getty (2020) ascertained that *Bifurculapes* traces were made subaqueously and may have
215   been made by a terrestrial insect that would have left different tracks subaerially.
216   *Coenobichnus* tracks (Fig. 4D), attributed to a hermit crab, are thick, crescentic to
217   ellipsoidal, roughly parallel and closely appressed to the trackway axis, and asymmetrical, with
218   the left tracks larger than the right tracks (Walker, Holland & Gardiner, 2003), all of which
219   differentiate this ichnotaxon from SGDS 1290.
220   *Copeza* (possibly a variant and synonym of *Lithographus* [Lull, 1953; Rainforth, 2005];
221   Fig. 4E) consists of triplets of roughly oppositely arranged, linear, elongate tracks in which the
222   anteriormost lies roughly perpendicular to the trackway axis while the posteriormost pairs lie
223   parallel or oblique to the trackway axis (Lull, 1953). This rare ichnotaxon is thus unlike SGDS
224   1290.
225   *Danstairia congesta* (Fig. 4F) comprises circular to crescentic tracks in closely appressed
226   sets of up to six that are oriented oblique to the trackway axis; tracks often overlap to form V-
227   shaped structures (Walker, 1985), unlike in SGDS 1290.
228   *Diplichnites* (possibly including *Acripes* per Häntzschel [1975] and Hammersburg,
229   Hasiotis & Robison [2018]; also see below) tracks span a range of morphologies. *D. aenigma*
230   (Fig. 4G), ostensibly the ichnospecies lectotype except that no specimen was designated as such
231   (Stimson et al., 2018), typically comprises elongate, closely packed tracks in parallel rows on
232   either side of the trackway axis; the tracks lie perpendicular to the trackway axis (Dawson,
233   1873). *D. gouldi* Type A (Fig. 4H) comprises parallel rows of closely spaced, oppositely
234   arranged, simple, roughly circular to oblong to comma-shaped or irregular tracks with varying
235   orientations to the trackway axis; *D. gouldi* Type B comprises closely spaced, elongate
236   impressions oriented perpendicular, or nearly so, to the trackway axis, matching the general
237   description of *D. aenigma*; *D. gouldi* Type C is similar to Type B, but the tracks are oriented
238   oblique (~ 45 °) to the trackway axis (Trewin & McNamara, 1994). *D. cuithensis*, attributed to
239   large arthropleurid myriapods, is similar to both *D. aenigma* and *D. gouldi* Type B, but is very
240   large and has widely spaced rows of tracks (Briggs, Rolfe & Brannan, 1979). *D. binatus* tracks
241   often occur as closely appressed pairs of imprints (Webby, 1983). *D. triassicus* tracks are small
242   and circular to ovoid rather than elongate, and frequently paired on either side of the trackway
243   axis (e.g., Pollard, Selden & Watts, 2008); this ichnospecies has been alternately suggested to be
244   a synonym of *D. gouldi* (e.g., Lucas et al., 2006b) or to pertain to *Acripes* (e.g., Machalski &
245   Machalska, 1994; Pollard, 1985). *D. metzi* possesses a midline impression that is sometimes
246   interrupted by connections between tracks in the closely appressed rows (Fillmore et al., 2017).
247   The ichnogenus is in need of thorough review (Smith et al., 2003), but in all cases, the tracks are
248   of different morphologies and arrangements than those of SGDS 1290.
249   *Eisenachichnus* tracks (Fig. 4I) are elongate, paired, and oblique to the trackway axis
250   (rarely perpendicular), but the patterns of the pairs on either side of the trackway axis normally
251   are asymmetrical: on one side, the paired tracks lie end to end, while on the other, they are more
252   adjacent (Kozur, 1981). This morphology and arrangement are unlike those of SGDS 1290.

253   *Foersterichnus* (Fig. 4J), attributed to a crab, consists of widely spaced, paired rows of
254   elongate tracks in sets of 3–4; rows are parallel to oblique to the trackway axis, and tracks in
255   each set frequently overlap (Pirrie, Feldmann & Buatois, 2004). The wide spacing, clustering of
256   tracks, and orientations of the tracks are unlike those of SGDS 1290.
257   *Hamipes* tracks (Fig. 4K) consist of closely spaced, paired, elongate to crescentic
258   impressions oriented parallel to the trackway axis; the outer tracks are longer than their
259   accompanying inner tracks, and the tracks are staggered or alternately arranged (Getty, 2018;
260   Hitchcock, 1858). Track morphology readily differentiates *Hamipes* from SGDS 1290.
261   *Laterigradus* tracks (Fig. 4L), attributed to sideways-walking crabs, comprises
262   asymmetrical trackways consisting of sets of up to four tracks (de Carvalho et al., 2016).
263   Individual tracks vary widely in shape, ranging from elongate to tapered to comma-shaped to
264   roughly circular. Track sets fall within a narrow trackway width and exhibit different stride
265   lengths along the course of a trackway. While some individual track shapes resemble those of
266   SGDS 1290, the overall arrangement and layout of the tracks is distinct.
267   *Lithographus* (including *Permichnium sensu* Minter & Braddy, 2009) tracks (Fig. 4M),
268   which match those made by pterygote insects, especially extant cockroaches (Davis, Minter &
269   Braddy, 2007), comprise trios (or pairs, in the case of the *Permichnium* variant) of elongate to
270   comma-shaped, rather than circular or tapering, tracks that are arranged at different angles to one
271   another, some of which are oriented perpendicular to the trackway axis, and others of which are
272   oblique to the trackway axis (Guthörl, 1934; Hitchcock, 1858; Minter & Braddy, 2009). These
273   track morphologies and arrangements are distinct from those of SGDS 1290. *Hornburgichnium*
274   reportedly is similar to *Permichnium*, but has three tracks on either side of the midline instead of
275   two, and at least one of each set is oriented parallel to the trackway axis (Kozur, 1989); it may
276   also be a variant of *Lithographus* (Lucas et al., 2005a). Trackways of *Lithographus* can transition
277   into trackways that Hitchcock (1858) called *Hexapodichnus* (Davis, Minter & Braddy, 2007;
278   Minter, Braddy & Davis, 2007), so the latter may be considered a behavioral and/or substrate-
279   consistency variant of the former, and also unlike SGDS 1290.
280   *Maculichna* (including *Guandacolichnus* and *Paganzichnus* of Pazos [2000] per Buatois
281   & Mángano [2003]) tracks (Fig. 4N) comprise pairs (sometimes more) of small, circular to
282   slightly elongate tracks arranged in closely appressed, slightly staggered rows. Pairings are
283   oriented virtually parallel to the trackway axis (Anderson, 1975a); occasionally, short segments
284   of linear, singular medial or closely spaced, paired paramedial imprints are also preserved that
285   can be offset to one side of the trackway axis (Anderson, 1975a: fig. 8b, d, e). The pairing of
286   *Maculichna* tracks differs from that of SGDS 1290. Aceñolaza & Buatois (1991, 1993) and
287   Archer & Maples (1984) described *Maculichna* traces that exhibit the pairing of classic
288   *Maculichna* from South Africa, but in which tracks are more ellipsoidal to shaped like slightly
289   inflated isosceles triangles; the long axes of the triangles are oriented close to perpendicular to
290   the trackway axis. Pazos (2000) recognized this morphology as the separate ichnotaxon
291   *Paganzichnus*. This morphology is also unlike that of SGDS 1290.

292   The ichnospecies holotype of *Merostomichnites narragansettensis* (Fig. 4O) consists of
293   parallel rows of roughly oppositely arranged circular to elongate to comma-shaped tracks whose
294   long axes are perpendicular to the trackway axis (Packard, 1900). *Merostomichnites beecheri*
295   tracks are circular and connected across the trackway axis by curvilinear, shallow, M-shaped
296   imprints, creating a sort of segmented midline impression (Packard, 1900: fig. 4). These track
297   and trace morphologies do not match those of SGDS 1290.
298   *Mirandaichnium* (Fig. 4P) consists of two rows of elongate, linear tracks that terminate
299   laterally in small, circular impressions. Tracks are oriented perpendicular or oblique to the
300   trackway axis, oppositely situated, and often grouped into series of eight (Aceñolaza & Buatois,
301   1993; Buatois et al., 1998), unlike those of SGDS 1290.
302   *Octopodichnus* (Fig. 4Q) ichnospecies, attributed to arachnids, have different
303   morphologies. *O. didactylus* tracks are circular to crescentic to bifurcate or trifurcate oriented
304   parallel to the trackway axis in alternating, arcuate sets of four (Sadler, 1993). *O. minor* tracks
305   have a similar organization, but the tracks are more amorphous; *O. raymondi* tracks consist of
306   clusters of four circular to crescentic marks arranged in checkmark-like patterns (Sadler, 1993).
307   These track morphologies and distinctive arrangements are substantially unlike those of SGDS
308   1290.
309   *Petalichnus* (Fig. 4R), attributed to trilobites (Braddy & Almond, 1999), comprises sets
310   of 2–3 elongate to crescentic tracks oriented perpendicular to the trackway axis (Miller, 1880).
311   Anderson (1975b) and Braddy & Almond (1999) diagnosed *Petalichnus* tracks as sometimes
312   bifurcate and occurring in series of 9–12; they further noted that the ichnotaxon needs review.
313   Both track morphology and organization are unlike those of SGDS 1290.
314   *Pterichnus* tracks (Fig. 4S), attributed to isopods, frequently are segmented and are more
315   linear and elongate than any in SGDS 1290. Tracks (or series of segments) are oriented oblique
316   (Types 1 and 2 of Gaillard et al., 2005) or parallel (Types 3 and 4 of Gaillard et al., 2005) to the
317   trackway axis, and approximately symmetrically arranged in two parallel rows (Gaillard et al.,
318   2005; Hitchcock, 1865) that are somewhat closer together than are those of the morphologically
319   similar *Diplichnites*. Types 3 and 4 of Gaillard et al. (2005) morphologically grade into
320   *Diplopodichnus* (Uchman et al., 2011). Hammersburg, Hasiotis & Robison (2018) suggested that
321   *Pterichnus* comprises undertracks of *Lithographus* and is thus a junior synonym of that
322   ichnotaxon. In any case, *Pterichnus* tracks are readily distinguished from SGDS 1290.
323   *Tasmanadia* traces (Fig. 4T) consist of two rows of closely packed, elongate, linear tracks
324   oriented generally perpendicular to the trackway axis; occasionally, tracks overlap at one end,
325   creating narrow, V-shaped structures (Chapman, 1929; Glaessner, 1957). Morphologically, this
326   ichnotaxon resembles *Diplichnites gouldi* Type B and *Umfolozia* (but lacks the organization of
327   the latter), and differs from SGDS 1290 for the same reasons as those ichnotaxa.
328   *Umfolozia* (Fig. 4U), attributed to syncarid and peracarid crustaceans (Lima, Minter &
329   Netto, 2017; Savage, 1971), consists of parallel rows of irregularly shaped to crescentic tracks
330   oriented perpendicular or oblique to the trackway axis that follow a unique repeating pattern
331   (Anderson, 1981; Savage, 1971) unlike anything discernible in SGDS 1290. Aceñolaza &

332   Buatois (1993) noted morphological similarities between *Mirandaichnium*, *Tasmanadia*, and
333   *Umfolozia* and postulated similar track makers.
334   In summary, SGDS 1290 is not a variant of any of these ichnotaxa.
335

Arthropod repichnia possessing one medial impression
337   Several other arthropod locomotory (walking) ichnotaxa are also readily distinguished
338   from SGDS 1290 by possessing singular medial, rather than paired paramedial, impressions;
339   again, comparison is warranted to ascertain whether or not SGDS 1290 is a morphological
340   variant of such ichnotaxa. These ichnotaxa are *Kouphichnium* (Caster, 1938; Nopcsa, 1923),
341   "*Merostomichnites* isp." (Hanken & Stormer, 1975), *Oniscoidichnus* (Brady, 1947, 1949),
342   *Palmichnium* (Richter, 1954), *Paleohelcura* (Gilmore, 1926), *Protichnites* (Owen, 1852),
343   *Robledoichnus* (Kozur & Lemone, 1995), *Shalemichnus* (Kozur & Lemone, 1995), *Stiallia*
344   (Smith, 1909), and *Stiaria* (Smith, 1909). As with traces lacking any medial impressions, these
345   ichnotaxa further differ from SGDS 1290 in track morphology. As before, possible track makers
346   are specified only when available.
347   *Kouphichnium* traces (Fig. 4V) are attributed to limulids and occur in a variety of
348   configurations. Tracks in clear *Kouphichnium* walking traces that possess singular medial
349   impressions (e.g., many *K. lithographicum*, but not, for example, *K. minkinensis* [King, Stimson
350   & Lucas, 2019; q.v. Gaillard, 2011a; Shu et al., 2018]) typically occur in sets of up to five in
351   rows oriented oblique to the medial impression and trackway axis; individual tracks range from
352   circular and ellipsoidal to elongate, and can split into anywhere from 2–5 branches at their ends
353   (Caster, 1938, 1944; King, Stimson & Lucas, 2019; Shu et al., 2018). Well-preserved
354   *Kouphichnium* tracks are dissimilar to those of SGDS 1290.
355   Traces referred to as "*Merostomichnites*" (Fig. 4W) and attributed to the eurypterid
356   *Mixopterus* by Hanken & Stormer (1975) consist of three elongate and crescentic tracks in
357   oblique rows on either side of an intermittent medial impression; the tracks increase in size
358   laterally, and some split into two or more branches on one end. In any of these cases, however,
359   the tracks are substantially more complex than those of SGDS 1290.
360   *Oniscoidichnus* tracks (Fig. 4X) are elongate to crescentic, oriented perpendicular or
361   oblique to the trackway axis, closely packed and closely appressed to the single midline
362   impression (Brady, 1947; Davies, Sansom & Turner, 2006). In all these details, *Oniscoidichnus*
363   traces differ markedly from SGDS 1290.
364   Ichnospecies of *Palmichnium* (Fig. 4Y), also attributed to eurypterids, vary in
365   morphology. Generally, they comprise complex sets of tracks lying lateral to a medial
366   impression that can be either continuous or discontinuous. Tracks range in shape from elongate
367   to crescentic to ovoid to chevron shaped, and they generally parallel the trackway axis. The
368   tracks occur in oblique rows in sets of up to four; in some traces, the lateralmost tracks are
369   elongate and curved, while the more medial tracks are linear and oriented parallel to the
370   trackway axis (Braddy & Milner, 1998; Minter & Braddy, 2009; Poschmann & Braddy, 2010;
371   Richter, 1954). Tracks are both more numerous and differently shaped than those of SGDS 1290.

372   *Paleohelcura* (including *Mesichnium* per Braddy [1995] and *Triavestigia* per Kozur,
373   Löffler & Sittig [1994]; possibly a junior synonym of *Stiaria*; Fig. 4Z) traces, attributed to
374   scorpions (Brady, 1947; Davis, Minter & Braddy, 2007), comprise small, circular tracks in sets
375   of three in either rows, triangular arrangements, or checkmark-like patterns that lie external and
376   oblique to the medial impression (Gilmore, 1926; Lagnaoui et al., 2015; Sadler, 1993). This
377   distinctive layout is unlike that of SGDS 1290. Peixoto et al. (2020) attributed traces lacking a
378   medial impression and comprising closely appressed pairs or triplets of mostly elliptical tracks
379   from the Upper Jurassic or Lower Cretaceous of Brazil to a new ichnospecies of *Paleohelcura*
380   and attributed them to a pterygote insect track maker. Tracks in this ichnospecies are arranged in
381   rows oriented oblique to the trackway axis, and track sets in this ichnospecies lie close to the
382   midline. This morphology is also unlike that of SGDS 1290.
383   *Protichnites* traces (Fig. 4AA) comprise thick, often segmented medial impressions
384   (sometimes absent except on trackway turns) flanked by oppositely arranged, subcircular to
385   ellipsoidal to irregularly shaped tracks with varying orientations to the trackway axis (Burton-
386   Kelly & Erickson, 2010; Collette, Gass & Hagadorn, 2012; Hagadorn & Seilacher, 2009). They
387   differ substantially from the tracks of SGDS 1290.
388   *Robledoichnus* tracks (Fig. 4BB), attributed to flying insects, resemble tracks of
389   *Eisenachichnus* but possess a discontinuous, faint medial trace consisting entirely of periodic, V-
390   shaped marks flanked by asymmetrical pairs of tracks. On one side, the tracks are short, tapered,
391   and oriented oblique to the trackway axis; on the other side, the tracks are longer and crescentic,
392   oriented closer to perpendicular to the trackway axis (Kozur & Lemone, 1995). Lucas et al.
393   (2005b) considered *Robledoichnus* a probable junior synonym of *Paleohelcura* or *Stiaria*, and
394   the ichnotaxon differs from SGDS 1290 for similar reasons as those ichnotaxa, in addition to the
395   asymmetry.
396   *Shalemichnus* traces (Fig. 4CC), for which only half a trackway is known, consist of a
397   straight medial impression punctuated at intervals by V-shaped marks. This impression is
398   flanked by sets of three tapered tracks in straight rows oriented perpendicular to the trackway
399   axis; individual tracks have their long axes parallel to the trackway axis (Kozur & Lemone,
400   1995). Minter & Braddy (2009) considered *Shalemichnus* a junior synonym of *Stiaria*. The
401   tracks of *Shalemichnus* bear some similarity to those of SGDS 1290, but the paramedial
402   impressions of SGDS 1290 lack the V-shaped markings of the medial impression of
403   *Shalemichnus*.
404   *Stiallia* traces (Fig. 4DD) consist of paired rows of long, linear impressions parallel or
405   slightly oblique to the trackway axis and that frequently overlap. *Stiallia pilosa* lacks any medial
406   or paramedial impressions, but *Stiallia* (*Carrickia* of Smith [1909]) *berriana* possesses a medial
407   row of crescentic to chevron-shaped marks (Smith, 1909; Walker, 1985). Pollard (1995)
408   suggested that *Stiallia* could be an arthropod swimming, rather than a walking, trace, though it
409   also resembles traces made by bristletail insects walking in highly saturated mud (Getty et al.,
410   2013: fig. 6F, G). *Stiallia* tracks are markedly unlike those of SGDS 1290.

411   *Stiaria* tracks (including some ichnospecies of *Danstairia* of Smith [1909]; Fig. 4EE)),
412   attributed to scorpionids (Braddy, 2003; Lucas, Lerner & Voigt, 2013) and monuran insects
413   (Genise, 2017; Kopaska-Merkel & Buta, 2013), are oppositely situated groups of 2–4 generally
414   circular to tapered tracks in a linear to crescentic arrangement lying roughly perpendicular to the
415   trackway axis (Walker, 1985). In some specimens and ichnospecies of *Stiaria*, the singular
416   medial impression actually varies in position, meandering from medial to almost lateral to their
417   tracks (Fillmore, Lucas & Simpson, 2012: fig. 26d; Walker, 1985: fig. 5b, c). In some
418   Mississippian specimens from Pennsylvania, the medial impression is flanked by thin,
419   discontinuous, but closely appressed paramedial imprints (Fillmore, Lucas & Simpson, 2012: fig.
420   26d–g). Track arrangement alone differentiates *Stiaria* from SGDS 1290. Genise (2017) asserted
421   that *Stiaria* should be considered a junior synonym of *Siskemia* (the latter has page priority over
422   the former).
423   As with locomotory traces lacking medial impressions, SGDS 1290 is not a variant of
424   any of these ichnotaxa.
425
426   **Arthropod repichnia possessing three or more medial and paramedial impressions**
427   *Mitchellichnus* (Fig. 4FF), attributed to archaeognathan insects (Getty et al., 2013), is
428   distinguished from SGDS 1290 by possessing three medial impressions (Walker, 1985).
429   *Mitchellichnus* tracks are complex, comprising two distinct types and arrangements. An inner
430   set, lying close to the medial impressions, consists of apparently elongate tracks in sets of up to
431   six that lie parallel to slightly oblique to the trackway axis; an outer set consists of larger,
432   amorphous impressions (Walker, 1985). Tracks are thus more numerous in *Mitchellichnus* than
433   in SGDS 1290, and the tracks differ in arrangement and morphology. Like *Stiaria*, Genise (2017)
434   asserted that *Mitchellichnus* should be considered a junior synonym of *Siskemia*.
435   *Keircalia* (Fig. 4GG) is distinguished from SGDS 1290 by possessing four medial
436   impressions (Smith, 1909; Walker, 1985). *Keircalia* tracks are crescentic to irregularly shaped,
437   generally are oriented perpendicular to the trackway axis, and have no discernible arrangement
438   (Walker, 1985). Both track morphology and organization are unlike those of SGDS 1290.
439
440   **Arthropod repichnia possessing paired paramedial impressions**
441   A few ichnotaxa, as well as some experimentally produced tracks of extant arthropods,
442   resemble SGDS 1290 by possessing paired paramedial impressions in at least some specimens.
443   Such ichnotaxa are *Danstairia vagusa* (Smith, 1909), *Glaciichnium* (Walter, 1985),
444   *Warvichnium* (Walter, 1985), and *Siskemia* (Smith, 1909); similar extant traces include those
445   made by notostracans (Trusheim, 1931) and crayfish (Fairchild & Hasiotis, 2011).
446   *Danstairia vagusa* (Fig. 4HH) possesses intermittent, thin, linear imprints that do not
447   always parallel their accompanying trackways. Tracks are circular to triangular, generally have
448   their long axes perpendicular to the trackway axis, and lack any coherent layout (Walker, 1985),
449   unlike those of SGDS 1290. *D. vagusa* somewhat resembles *Keircalia* traces, but its tracks are
450   spaced more widely apart.

451   *Glaciichnium* traces (Fig. 4II), which resemble traces made by isopods (Gibbard &
452   Stuart, 1974; Lima, Minter & Netto, 2017; Uchman, Kazakauskas & Gaigalas, 2009; Uchman et
453   al., 2011), comprise 1–3 elongate, linear tracks ("bars" that are divided into segments [Uchman,
454   Kazakauskas & Gaigalas, 2009]) that lie oblique to the trackway axis and are staggered on either
455   side of that axis, unlike the tracks of SGDS 1290; their linear, serial but discontinuous
456   paramedial imprints are widely spaced, consistently abutting the medial ends of the tracks
457   (Walter, 1985), farther apart than those of SGDS 1290. Walter (1985) and Lima et al. (2015)
458   described the paramedial imprints in Brazilian specimens as comprising successive pairs of C-
459   shaped imprints rather than strictly linear structures, further unlike SGDS 1290. Some
460   *Glaciichnium* traces also possess a medial imprint as well (Uchman, Kazakauskas & Gaigalas,
461   2009; Walter, 1985).
462   *Warvichnium* traces (Fig. 4JJ) are complex, comprising pairs to multiple sets of linear,
463   discontinuous medial and paramedial imprints flanked by varying numbers of linear to crescentic
464   tracks in two or more sets: an inner set, close to the medial imprints, that are oriented slightly
465   oblique to the trackway axis, and an outer set oriented closer to perpendicular to the trackway
466   axis (Walter, 1985), quite unlike SGDS 1290. Getty (2020) noted similarities between
467   *Warvichnium* and subaqueous *Bifurculapes*.
468   Among described arthropod repichnia, SGDS 1290 architecturally most closely
469   resembles ichnospecies of *Siskemia* by possessing discreet, compact (not linear) tracks and track
470   sets flanking paired paramedial impressions. Three ichnospecies of *Siskemia* are presently
471   recognized (Walker, 1985):

- 472   *S. bipediculus* (Fig. 4KK) comprises small, circular tracks in closely appressed pairs
  473   (occasionally trios) in rows oriented perpendicular or slightly oblique to the trackway axis;
  474   the pairs are spaced apart at approximately regular intervals and evenly distant from the
  475   uniformly straight and narrow paramedial impressions (Walker, 1985). The paramedial
  476   impressions lie close to the midline axis, well away from their adjacent tracks (the average
  477   ratio of the distance between a paramedial impression and its flanking track to the distance
  478   between the medial edges of the paramedial impressions is 1.34; see Supplemental
  479   Material).

- 480   *S. elegans* (Fig. 4LL) has similarly shaped tracks in sets of up to four tracks; the sets
  481   similarly lie well away from the likewise straight, narrow, and closely appressed
  482   paramedial impressions (the average ratio of the distance between a paramedial
  483   impression and its flanking track to the distance between the medial edges of the
  484   paramedial impressions is 1.75; see Supplemental Material). *S. bipediculus* and *S. elegans*
  485   differ primarily in the orientations of their track rows to the trackway axis and the
  486   continuities and thicknesses of their paramedial impressions (Walker, 1985), though these
  487   could be behavioral and/or substrate-driven variants.

- 488   *Siskemia latavia* (Fig. 4MM; called "*lata-via*" by Smith [1909] and Walker [1985], but the
  489   ICZN does not permit hyphens in genus or species names) tracks comprise tapered or
  490   ovoid tracks arranged in roughly triangular sets of three. Most individual tracks have their

491   long axes oriented oblique to the trackway axis; track sets have varying orientations to the

492   trackway axis. Tracks in individual *S. latavia* sets usually are spaced well apart from each

493   other; rarely do two individual tracks in a set contact one another. *S. latavia* tracks lack the

494   regular spacing and arrangements of those of *S. elegans* and *S. bipediculus*, and occasional

495   individual tracks lie close to the paramedial impressions, farther medially than in either of

496   the other two *Siskemia* ichnospecies (the average ratio of the distance between a

497   paramedial impression and its flanking track to the distance between the medial edges of

498   the paramedial impressions is 0.80; see Supplemental Material). Each paramedial

499   impression of *S. latavia* is slightly wider than those of the other two *Siskemia* ichnospecies

500   (probably a function of the larger overall size of specimens attributed to this

501   ichnospecies), but retain the close appression to the trackway midline and the uniform

502   straightness.

503   The tracks of SGDS 1290 vary more in morphology than those of any known *Siskemia*

504   ichnospecies, but grossly share their layout. Tracks in all three *Siskemia* ichnospecies have a

505   staggered distribution, similar to, but less pronounced than, that of SGDS 1290. SGDS 1290

506   differs most markedly from any of the three *Siskemia* ichnospecies in the morphology and

507   positions of the paramedial impressions: in SGDS 1290, the impressions vary in thickness along

508   their lengths and undulate, in contrast to the thin, straight impressions of all three *Siskemia*

509   ichnospecies. Additionally, the impressions in SGDS 1290 lie farther apart than those of the

510   three *Siskemia* ichnospecies. In fact, all of the ichnospecies of *Siskemia* erected by Smith (1909),

511   as well as both specimens later attributed to this ichnogenus (e.g., Getty et al., 2013; McNamara,

512   2014; Pollard, Steel & Undersrud, 1982) and *Siskemia*-like traces made by extant,

513   archaeognathan insects (Getty et al., 2013), have such thin, linear, closely appressed paramedial

514   impressions (sometimes offset toward one side of the trackway). The only time when

515   archaeognathan traces approach the paramedial impression spacing of SGDS 1290 is when both

516   abdominal styli (laterally) and gonostyli (medially) of the trace makers register impressions and

517   imprints in wet mud, producing two sets of paramedial traces (Getty et al., 2013: fig. 6K, L), but

518   even then the linear, lateralmost paramedial impressions still do not resemble the thick,

519   undulating impressions of SGDS 1290. Simultaneously, in such wet mud, archaeognathan tracks

520   are elongate and oriented oblique to the trackway axis, unlike those in SGDS 1290. In total,

521   SGDS 1290 does not fit neatly into any known *Siskemia* ichnospecies and does not seem to be an

522   archaeognathan insect trace.

523   Among traces made by extant arthropods, SGDS 1290 bears similarities to traces made

524   by both notostracans and crayfish. Interpretive drawings of experimental traces made by

525   notostracans figured by Trusheim (1931) depict elongate, crescentic, or tapered tracks oriented

526   perpendicular to paramedial impressions; the tracks are arranged oppositely, unlike those of

527   SGDS 1290. Additionally, the thin, linear paramedial impressions figured by Trusheim (1931)

528   lie so far from the trackway axis that they often contact their accompanying tracks, a

529   phenomenon that only occurs in SGDS 1290 near L4 and R4, where the lateral margins of its

530   undulating paramedial impressions meander particularly far laterally. Tasch (1969) noted,

531 though, that the drawings presented by Trusheim (1931) were misleading compared to his own
532 experimentally generated notostracan traces. However, he described the morphologies of his
533 notostracan tracks only as "minute en echelon stripes" (Tasch, 1969: 327), which does not
534 adequately specify how they differed from those of Trusheim (1931); track details are impossible
535 to discern in his lone photographic figure (Tasch, 1969: pl. 1.2). Gand et al. (2008) also
536 conducted neoichnological experiments with notostracans, recovering locomotory traces that
537 were less orderly than those illustrated by Trusheim (1931) (Gand et al., 2008: figs. 16.1, 16.2,
538 17.1). Their extant notostracan tracks comprised multiple tracks with rather chaotic distributions
539 lateral to their paramedial impressions, unlike the regular distribution seen in SGDS 1290. Gand
540 et al. (2008) found their notostracan traces to fall within the "etho-morphotype" of *Acripes*, as
541 exemplified by their novel ichnospecies *A. multiformis* from the Permian of France. (Linck
542 [1943] and Pollard [1985] also referred *Acripes* [*Merostomichnites* of Linck, 1943] tracks to
543 notostracans, but not based on neoichnological experiments.) *A. multiformis* traces, unlike classic
544 *Acripes* (Matthew, 1910), possess paramedial imprints, albeit inconsistently. Hammersburg,
545 Hasiotis & Robison (2018), Häntzschel (1975), Miller (1996), and Pemberton, MacEachern &
546 Gingras (2007) all supported classic *Acripes* as a junior synonym of *Diplichnites*; the issue of
547 synonymy is beyond the scope of this paper, but we note at least that the tracks in fossils that
548 Gand et al. (2008) called *A. multiformis* differ from SGDS 1290 in the same ways that
549 *Diplichnites* tracks do (see above). Lastly, Knecht et al. (2009: figs. 5, 6) also illustrated traces
550 made by extant notostracans (Fig. 4NN), which are "tidier" than those of Gand et al. (2008) and
551 resemble those of classic *Acripes* and *Diplichnites*, albeit with discontinuous paramedial and
552 curvilinear lateral (external) imprints. The tracks in these traces comprise irregular, ellipsoidal
553 sets oriented oblique to the trackway axis, unlike those of SGDS 1290. In total, SGDS 1290 is
554 unlikely to be a notostracan trace.
555   Fairchild & Hasiotis (2011) conducted neoichnological experiments with crayfish to
556 examine their locomotory traces. These traces varied in morphology depending on substrate
557 conditions (sediment grain size and saturation) and slope; in general, when clearest, they consist
558 of sets of 1–4 circular, tapering, ellipsoidal, or elongate tracks, occasionally of different sizes,
559 that are oriented parallel to the trackway axis and that lie lateral to a pair of undulating, variably
560 thick paramedial impressions that lie closer to their flanking tracks than to each other (Figs. 3D,
561 4OO). Morphologically, the tracks and impressions match those of SGDS 1290, although the
562 tracks made by extant crayfish often are larger than those of SGDS 1290 when produced in dry
563 substrate (Fairchild & Hasiotis, 2011: fig. 9). Track sets in extant crayfish traces have complex
564 arrangements: when comprised of multiple traces, they frequently are in rows oriented
565 perpendicular to the trackway axis, but sometimes rows are oblique to the trackway axis. When
566 fewer tracks are preserved, sets can appear to lie in single, parallel rows on either side of the
567 paramedial impressions. Track positions can be opposite to staggered to alternating, also as in
568 SGDS 1290. In both track and paramedial impression morphology, as well as in overall trace
569 architecture, SGDS 1290 strongly resembles crayfish traces made in damp silt and clay
570 (Fairchild & Hasiotis, 2011: fig. 2e, f), dry and saturated, very fine-grained sand (Fig. 3D;

571 Fairchild & Hasiotis, 2011: fig. 4a, b, e, f), dry and damp, fine-grained sand (Fairchild &
572 Hasiotis, 2011: fig. 5a–d), and saturated medium sand (Fairchild & Hasiotis, 2011: fig. 6e, f).
573 SGDS 1290 is preserved in, and was presumably registered in, a fine-grained sandstone,
574 lithologically matching one set of experimental conditions in Fairchild & Hasiotis (2011).
575 However, SGDS 1290 is not as detailed as many of the experimentally generated crayfish traces
576 in comparable sediments. This could indicate one or more things: the fossil could be a slight
577 overtrack (*sensu* Bertling et al., 2006) rather than a direct natural cast; the trace maker may have
578 been partly buoyant; and/or trace-maker behavior and sediment consistency combined such that
579 the lighter limbs did not impress as deeply as the heavier tail.
580

Discussion

Trace maker

583   The stronger resemblance of SGDS 1290 to experimental crayfish locomotion traces than
584 to any known ichnotaxon, or other documented extant arthropod trace, implies a crayfish or
585 crayfish-like maker for the fossil. Whether SGDS 1290 had a crayfish-like or an actual crayfish
586 maker depends on whether the term "crayfish" is used to refer to members of a monophyletic
587 clade (Parastacidae + (Astacidae + (Cambaridae + Cricoidoscelosidae)); Karasawa, Schweitzer
588 & Feldmann, 2013) of freshwater (and brackish water if *Protastacus* is included, *sensu*
589 Karasawa, Schweitzer & Feldmann [2013]) lobsters, or, more broadly, to any freshwater, lobster-
590 like crustacean regardless of phylogenetic position, which presumes that more than one crayfish-
591 like lineage colonized terrestrial environments in the past. Here we use the term in the
592 monophyletic sense: true crayfish comprise Astacida (*sensu* Karasawa, Schweitzer & Feldmann,
593 2013; Schram & Dixon, 2004; Shen, Braband & Scholtz, 2015). Whether or not the maker of
594 SGDS 1290 was a true crayfish is unclear: the oldest undisputed crayfish body fossils are from
595 the Early Cretaceous (Garassino, 1997; Martin et al., 2008; Shen, 2003; Taylor, Schram & Shen,
596 1999), although unnamed, Late Jurassic specimens from western Colorado also have been called
597 crayfish (Hasiotis, Kirkland & Callison, 1998). Despite this, a Triassic or earlier origin for true
598 crayfish has been hypothesized frequently (Breinholt, Pérez-Losada & Crandall, 2009; Crandall
599 & Buhay, 2008; Porter, Pérez-Losada & Crandall, 2005; Schram, 2001; Schram & Dixon, 2004;
600 Wolfe et al., 2019) and possibly substantiated by fossil burrows referred to crayfish from the
601 Early Permian (Hembree & Swaninger, 2018) and Late Permian–Early Triassic (Baucon et al.,
602 2014; Hasiotis & Mitchell, 1993).

603   Several Late Triassic body-fossil specimens also have been reported as crayfish (Hasiotis,
604 1995; Hasiotis & Mitchell, 1993; Miller & Ash, 1988; Olsen & Huber, 1997; Santucci &
605 Kirkland, 2010), but the identities of these specimens as true astacidans has not been established.
606 Miller & Ash (1988) placed a Late Triassic specimen from Petrified Forest National Park,
607 Arizona in *Enoploclytia*, which is an erymid lobster, not an astacidan, genus. That generic
608 placement subsequently has been contested (Amati, Feldmann & Zonneveld, 2004; Schweitzer et
609 al., 2010; Urreta, 1989), so the specimen needs detailed restudy, but if it pertains to Erymidae
610 rather than Astacida, then it indicates that a lineage of erymid lobsters colonized terrestrial

611   environments, possibly before true (monophyletic) crayfish. Some older analyses (reviewed in
612   Rode & Babcock, 2003) postulated crayfish origins within Erymidae, but more recent
613   phylogenetic analyses (Devillez, Charbonnier & Barreil, 2019; Karasawa, Schweitzer &
614   Feldmann, 2013; Rode & Babcock, 2003; Schram & Dixon, 2004; Stern & Crandall, 2015) have
615   recovered (a frequently paraphyletic) Erymidae with members at varying distances from
616   Astacida. If those hypothesized phylogenetic relationships are correct, then no erymid can, in a
617   monophyletic sense, be considered a crayfish, even if it was a freshwater taxon. But regardless of
618   semantics or phylogenetic relationships, crayfish and erymid morphological similarities suggest
619   that their locomotory traces might be indistinguishable, making a definitive attribution of SGDS
620   1290 impossible.
621   A crayfish or crayfish-like trace maker for SGDS 1290 is tenable both chronologically
622   and ecologically. As mentioned above, multiple crayfish-like morphotypes have been found in
623   the Upper Triassic Chinle Formation of Arizona and Utah (Hasiotis, 1995; Miller & Ash, 1988;
624   Santucci & Kirkland, 2010). The Moenave Formation overlies the Chinle Formation in
625   southwestern Utah, so crayfish or crayfish-like decapods plausibly could have been present in
626   and around freshwater Lake Whitmore both geographically and stratigraphically. As-yet-
627   undescribed, crayfish or crayfish-like body fossils also have been recovered from lacustrine
628   sediments of the uppermost Triassic Chatham Group (Newark Supergroup) in North Carolina
629   (Olsen & Huber, 1997), attesting to how widespread such arthropods were in terrestrial
630   environments in North America even prior to the Jurassic.
631
632   **Ichnotaxonomy**
633   To date, no fossil arthropod locomotory ichnotaxon has been attributed definitively to a
634   crayfish or crayfish-like trace maker. Several such ichnotaxa have been attributed, for various
635   reasons, to crustaceans (e.g., Braddy, 2003; Gand et al., 2008; Lima, Minter & Netto, 2017;
636   Pirrie, Feldmann & Buatois, 2004; Savage, 1971; Walker, Holland & Gardiner, 2003);
637   additionally, some purported crustacean tracks have not been assigned to particular ichnotaxa
638   (e.g., Imaizumi, 1967; Karasawa, Okamura & Naruse, 1990; Matsuoka et al., 1993), including
639   mortichnial trackways leading to *Eryma*, *Eryon*, and *Mecochirus* lobster body fossils from the
640   marine, Upper Jurassic lithographic limestones of Germany (Glaessner, 1969: fig. 243A;
641   Seilacher, 2008: fig. 2; Viohl, 1998: fig. 6). None of these German taxa are crayfish, though
642   morphological similarities of *Eryma* and *Mecochirus* to crayfish might mean that they would
643   have produced indistinguishable locomotory ichnofossils during normal, forward locomotion.
644   None of their traces have been granted detailed description or ichnotaxonomic assignment.
645   Only three locomotory ichnotaxa have been attributed specifically to crayfish. First,
646   Heidtke (1990) erected *Pollichianum repichnum* for Early Permian ichnofossils from Germany
647   that he attributed to the "crawfish" (in the English abstract; "Krebses" in the German abstract)
648   *Uronectes fimbriatus*, also from the Early Permian of Germany. However, *Uronectes* has long
649   been recognized as a syncarid (Brooks, 1962; Calman, 1934; Perrier et al., 2006), not an
650   astacidan, or even a decapod, so the term appearing in the English abstract likely is a simple

651 translation error. Furthermore, however, *P. repichnum* is not differentiable from the resting trace
652 (cubichnion) *P. cubichnum* (O'Brien, Braddy & Radley, 2009) and therefore is a junior synonym
653 and is not a locomotory trace. In any case, *Pollichianum* is morphologically quite unlike both
654 SGDS 1290 and experimentally generated crayfish traces (Fairchild & Hasiotis, 2011). Second,
655 Bolliger & Gubler (1997) hypothesized that their novel, early Miocene ichnospecies *Hamipes*
656 *molassicus* was made by a buoyed (presumably swimming) crayfish. Getty (2018) referred these
657 specimens to *Conopsoides*; later, Getty & Burnett (2019) suggested that at least some of the
658 specimens may pertain to *Acanthichnus*, and they differ from SGDS 1290 for the same reasons
659 outlined above for *Acanthichnus*. Third, de Gibert et al. (2000) attributed Early Cretaceous,
660 Spanish specimens that they assigned to *Hamipes didactylus* to crayfish. Getty (2018) attributed
661 these tracks to *Bifurculapes* and maintained a crustacean track maker for *H. didactylus*, but was
662 not more specific. However, neither *Bifurculapes* nor *Hamipes* resemble experimentally
663 generated crayfish traces (Fairchild & Hasiotis, 2011), or any of the mortichnial decapod traces,
664 and thus are unlikely to have been made by a crayfish-like decapod, at least while walking.
665 Lastly, we also note that unnamed trackways attributed to crayfish from the Upper Triassic
666 Chinle Formation of Utah were mentioned, but not described, by Hasiotis (1991); Fairchild &
667 Hasiotis (2011) did not note whether or not these were similar to their experimentally generated
668 traces. Additionally, an unnamed "crayfish locomotion trace" was figured, but not described, by
669 Rainforth & Lockley (1996: fig. 1b); it does not resemble either SGDS 1290 or experimentally
670 generated crayfish traces (Fairchild & Hasiotis, 2011).
671   As detailed above, SGDS 1290 does not fit neatly into any existing ichnospecies of
672 *Siskemia*. Whether or not to place it in a novel ichnospecies, or even ichnogenus, is, therefore, an
673 open question. Bertling et al. (2006), Gaillard (2011b), and Minter, Braddy & Davis (2007)
674 provided solid criteria for the erection of new ichnotaxa, the latter particularly for arthropods.
675 One criterion is that a new ichnotaxon ideally should be represented by a substantial number of
676 specimens that demonstrate behavioral and substrate-based morphological variation; this
677 prevents erecting several ichnotaxa for minor, readily explained variations in trace morphology.
678 SGDS 1290, as a singular specimen, certainly does not meet that criterion, but Minter, Braddy &
679 Davis (2007) also allowed that truly unique morphologies exhibited by singular specimens can
680 support an ichnotaxon. In terms of uniqueness, another criterion is whether or not a new
681 morphotype falls onto a continuum, established or hypothetical, of morphologies within an
682 established ichnotaxon. SGDS 1290 is closest morphologically to ichnospecies of *Siskemia*, but
683 has several distinctions from any established ichnospecies therein, particularly the thick and
684 undulating paramedial impressions and the wider spacing between the paramedial impressions
685 and consequent closer appression of the paramedial impressions to the tracks: the average ratios
686 of the distance between a paramedial impression and its flanking track to the distance between
687 the medial edges of the paramedial impressions are 1.34 for *S. bipediculus*, 1.75 for *S. elegans*,
688 and 0.80 for *S. latavia* compared to 0.31 for SGDS 1290 (see Supplemental Material). No
689 published specimen of *Siskemia* demonstrates the features of SGDS 1290; nor do *Siskemia*-like
690 traces made by archaeognathan insects in experimental conditions (Getty et al., 2013). Thus,

691   SGDS 1290 does not appear to fall within the established *Siskemia* continuum. The greater
692   prominence (depth) of the paramedial impressions of SGDS 1290 than their associated tracks
693   suggests either a trace maker with heavier tail elements than the gonostyli of an archaeognathan
694   insect or an archaeognathan trace maker with unusually large styli adopting an unusual posture
695   (possibly partly buoyant), flexing its caudal region downward to create deep styli impressions
696   but not deep track impressions. We consider the latter unlikely; thus, SGDS 1290 does not
697   appear to fall within a hypothetical *Siskemia* continuum, either. However, SGDS 1290 falls
698   within the continuum of trace morphologies made by extant crayfish in experimental conditions
699   (Fairchild & Hasiotis, 2011). No philosophical basis has been established for the recognition of
700   novel ichnotaxa on the basis of comparison with traces made by extant organisms; only by
701   comparison with fossil ichnotaxa because extant traces cannot be the basis for an ichnotaxon
702   (Bertling et al., 2006; International Commission on Zoological Nomenclature, 1999).
703   SGDS 1290 clearly is morphologically distinctive. Lacking a sufficient number of
704   specimens with which to determine ranges of morphological variation, however, erecting a new
705   ichnogenus for it clearly is unwarranted. Yet we feel that its unique morphology warrants
706   ichnotaxonomic distinction. Given its distant similarity to *Siskemia* ichnospecies, we therefore
707   herein place it in a new ichnospecies of that ichnogenus.
708
709   **Systematic Ichnology**
710
711   **Ichnofamily** Protichnidae Uchman, Gaździcki & Błażejowski 2018
712
713   **Ichnogenus** *Siskemia* Smith 1909
714
715   **Type Ichnospecies** *Siskemia elegans* Smith 1909
716   **Diagnosis.** Trace consisting of parallel rows of grouped tracks on either side of two parallel,
717   paramedial impressions. Each group of tracks consists of up to four imprints arranged in series,
718   transversely or obliquely to the midline of the trackway (following Walker, 1985). Walker
719   (1985) further specified that *Siskemia* was diagnosed by paramedial impressions with maximum
720   widths of 0.5 mm, but following Bertling et al. (2006), size is not a suitable ichnotaxobase.
721
722   **Ichnospecies** *Siskemia eurypyge* isp. nov.
723   Figure 3A, B
724
725   **Diagnosis.** Two parallel, undulating, paramedial impressions flanked externally by closely
726   appressed sets of 1–3 small, ovoid to tapered to elongate tracks; tapered and elongate tracks have
727   long axes parallel or oblique to the trackway axis. Track sets are oriented perpendicular to the
728   trackway axis. Left and right tracks are arranged in a staggered to alternating pattern. Paramedial
729   impressions are mediolaterally thick, but discontinuous, tapering out of existence briefly in some
730   places. Impressions are gently undulating (low amplitude). The paramedial impressions lie far

731 from the trackway axis, generally closer to (and sometimes in contact with) the tracks than to the
732 midline axis or each other.
733 **Holotype.** Natural cast specimen SGDS 1290, St. George Dinosaur Discovery Site, St. George,
734 Utah, USA.
735 **Type locality.** "Bug Crossing Quarry," SGDS Loc. 87, St. George Dinosaur Discovery Site, St.
736 George, Washington County, Utah, USA (Fig. 1).
737 **Stratigraphy.** "Top Surface" of Johnson Farm Sandstone Bed (unit 40 of Kirkland et al., 2014),
738 Whitmore Point Member, Moenave Formation (Fig. 2). Hettangian, Lower Jurassic.
739 **Derivation of name.** From the Greek ευρυς (eurys), meaning "broad" or "wide," and πυγή
740 (pyge), meaning "rump." The ichnospecies name refers to the wider spacing between the
741 paramedial impressions, made by the rear end of the trace maker, than those of other *Siskemia*
742 ichnospecies.
743

Conclusions

745   SGDS 1290, from the Lower Jurassic (Hettangian) Whitmore Point Member of the
746 Moenave Formation, consists of two paramedial impressions that are flanked by staggered to
747 alternating sets of tapered or elongate tracks. The traces closely resemble those made by extant
748 crayfish (Fairchild & Hasiotis, 2011) and are similar in components to traces placed in the
749 ichnogenus *Siskemia* (Smith 1909; Walker, 1985). In previously recognized *Siskemia*
750 ichnospecies, the paramedial impressions are thin, relatively straight, and closely appressed to
751 the trackway axis. But in SGDS 1290, paramedial impressions have the opposite morphology
752 and arrangement: they are thick and lie closer to their tracks than the medial axis of the trackway.
753 SGDS 1290 paramedial impressions also undulate, which is not seen in any previously known
754 *Siskemia* ichnospecies. Thus, we erect a new ichnospecies, *Siskemia eurypyge*, to house SGDS
755 1290 and as-yet undiscovered traces with this morphology and arrangement.
756   Placing SGDS 1290 in *Siskemia* extends the known range of the ichnogenus into the
757 Early Mesozoic. All other reported occurrences of the ichnogenus are Paleozoic in age: Early
758 Silurian (McNamara, 2014; Trewin & McNamara, 1994), Late Silurian (Davies, Sansom &
759 Turner, 2006), Early Devonian (Pollard, Steel & Undersrud, 1982; Pollard & Walker, 1984;
760 Smith, 1909; Walker, 1985), and Pennsylvanian (Getty et al., 2013). However, age should not be
761 a factor in ichnotaxonomy (Bertling et al., 2006). At least some Paleozoic *Siskemia* traces likely
762 were made by archaeognathan insects (Getty et al., 2013), which are extant and for which body
763 fossils are known as early as the Devonian. Based on their similarity to traces made by extant
764 crayfish (Fairchild and Hasiotis, 2011), *S. eurypyge* likely was made by a crayfish or crayfish-
765 like crustacean, for which body fossils are known as early as the Late Triassic and which also are
766 extant. Thus, *Siskemia* ispp. traces would be expected to occur from Early Silurian to Recent, but
767 thus far have not been documented except for the occurrences noted above.
768   SGDS 1290 expands the ichnological record of crayfish and crayfish-like animals to
769 include repichnia in addition to domichnia. Fossil burrows (*Camborygma* ispp.), usually
770 attributed to crayfish, are well known at some sites and in some formations (e.g., Hasiotis, 1995;

771 Hasiotis & Bown, 1996; Hasiotis & Honey, 1995; Hasiotis & Mitchell, 1993; Hasiotis, Kirkland
772 & Callison, 1998; see Schram & Dixon [2004] concerning pre-Cretaceous examples), attesting to
773 the presences—and, in some places, abundances—of crayfish and/or crayfish-like taxa in
774 Mesozoic–Cenozoic freshwater paleoecosystems. Yet locomotion traces made by these
775 burrowers oddly have never before been documented as ichnofossils, possibly because they
776 infrequently venture far from their burrows in substrates suitable for registering locomotory
777 traces, as with modern crayfish (Martin, 2013). SGDS 1290 is the first documented locomotory
778 ichnofossil made by a freshwater crayfish or crayfish-like organism, as well as the first fossil
779 evidence of such a taxon in the Lower Jurassic Moenave Formation and indeed the Early Jurassic
780 of the southwestern US. The absence of *Camborygma* burrows in the Moenave Formation that
781 would have been made by the SGDS 1290 trace maker is puzzling, and may be a consequence of
782 a lack of recognition; alternatively, the producer of SGDS 1290 was not a burrower.
783

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1361   **FIGURE CAPTIONS**

1362

1363   **Figure 1: Location of the St. George Dinosaur Discovery Site at Johnson Farm.** (A) Map
1364   showing the location of the St. George Dinosaur Discovery Site in St. George, Utah. (B)
1365   The museum at the St. George Dinosaur Discovery Site. Photograph by Jerald D. Harris.
1366   **Figure 2: Stratigraphic section at and immediately around the St. George Dinosaur**
1367   **Discovery Site (SGDS) in St. George, Utah.** Arthropod locomotory trackway SGDS
1368   1290 comes from the "Top Surface Tracksite" layers of the Johnson Farm Sandstone Bed
1369   (red arrows).
1370   **Figure 3: Arthropod locomotory ichnofossil SGDS 1290.** (A) Photograph of specimen; scale
1371   in mm. (B) Schematic diagram of specimen. Arrow indicates direction of movement. L =
1372   left track; R = right track; Ov = overtracks. Numbers indicate position of tracks in
1373   sequence from posterior to anterior. Photograph by Andrew R.C. Milner. (C) Schematic
1374   diagram of specimen, showing examples of how measurements were taken. IEW =
1375   external width between paramedial impressions; IIW = internal width between
1376   paramedial impressions; IW = paramedial impression width; TL = track length; TTI =
1377   distance between track and adjacent paramedial impression; TW = track width. (D)
1378   Photograph of extant crayfish walking trace made in saturated, very fine sand for
1379   comparison to fossil in (A); scale in cm. Arrow indicates direction of travel; photograph
1380   rotated to have the same orientation as (A). Modified from Fairchild & Hasiotis (2011:
1381   fig. 4E); reproduced with permission from SEPM.
1382   **Figure 4: Schematic diagrams of locomotory (presumably walking) ichnofossils attributed**
1383   **to arthropods (A–MM) and extant walking traces made by arthropods (NN–OO)**
1384   **compared to SGDS 1290 (PP).** Diagrams not to scale. (A) *Acanthichnus cursorius*
1385   (traced from Hitchcock, 1858). (B) *Asaphoidichnus trifidus* (traced from Miller, 1880).
1386   (C) *Bifurculapes laqueatus* (traced from Getty, 2016). (D) *Coenobichnus currani* (traced
1387   from Walker, Holland & Gardiner, 2003). (E) *Copeza triremis* (traced from Hitchcock,
1388   1858). (F) *Danstairia congesta* (traced from Walker, 1985). (G) *Diplichnites aenigma*
1389   (traced from Dawson, 1873). (H) *Diplichnites gouldi* Type A (traced from Trewin and
1390   McNamara, 1994). (I) *Eisenachichnus inaequalis* (traced from Kozur, 1981). (J)
1391   *Foersterichnus rossensis* (traced from Pirrie, Feldmann & Buatois, 2004). (K) *Hamipes*
1392   *didactylus* (traced from Getty, 2018). (L) *Laterigradus lusitanicus* (traced from de
1393   Carvalho et al., 2016). (M) *Lithographus hieroglyphicus* (traced from Hitchcock, 1858).
1394   (N) *Maculichna varia* (traced from Anderson, 1975a). (O) *Merostomichnites*
1395   *narrangansettensis* (traced from Packard, 1900). (P) *Mirandaichnium famatinense* (traced
1396   from Aceñolaza, 1978). (Q) *Octopodichnus didactylus* (traced from Gilmore, 1927). (R)
1397   *Petalichnus multipartatus* (Miller, 1880). (S) *Pterichnus centipes* (traced from Hitchcock,
1398   1865). (T) *Tasmanadia twelvetreesi* (traced from Glaessner, 1957). (U) *Umfolozia*
1399   *sinuosa* (traced from Anderson, 1981). (V) *Kouphichnium lithographicum* (traced from
1400   Gaillard, 2011). (W) "*Merostomichnites* isp." (traced from Hanken & Stormer, 1975). (X)

1401   *Oniscoidichnus filiciformis* (traced from Brady, 1947). (Y) *Palmichnium antarcticum*
1402   (traced from Braddy & Milner, 1998). (Z) *Paleohelcura tridactyla* (traced from Gilmore,
1403   1926). (AA) *Protichnites septemnotatus* (traced from Owen, 1852). (BB) *Robledoichnus*
1404   *lucasi* (traced from Kozur & Lemone, 1995). (CC) *Shalemichnus sittigi*, half of trackway
1405   (traced from Kozur & Lemone, 1995). (DD) *Stiallia berriana* (traced from Smith, 1909).
1406   (EE) *Stiaria quadripedia* (traced from Walker, 1985). (FF) *Mitchellichnus ferrydenensis*
1407   (traced from Walker, 1985). (GG) *Keircalia multipedia* (traced from Walker, 1985).
1408   (HH) *Danstairia vagusa* (traced from Walker, 1985). (II) *Glaciichnium liebegastensis*
1409   (traced from Walter, 1985). (JJ) *Warvichnium ulbrichi* (traced from Walter, 1985). (KK)
1410   *Siskemia bipediculus* (traced from Walker, 1985). (LL) *Siskemia elegans* (traced from
1411   Walker, 1985). (MM) *Siskemia latavia* (traced from Walker, 1985). (NN) Extant
1412   notostracan traces (traced from Knecht et al., 2009). (OO) Extant crayfish trace in
1413   saturated, very fine sand (traced from Fairchild & Hasiotis, 2011). (PP) SGDS 1290.
1414

1415 **TABLE CAPTIONS**

1416

1417 **Table S1: Measurements (in mm) of arthropod locomotory ichnofossil SGDS 1290.**

1418 Measurements in parentheses are approximated based on faint portions of paramedial

1419 impressions. See Fig. 3C for a depiction of the measurements taken.

Figure 1

Location of the St. George Dinosaur Discovery Site at Johnson Farm.

(A) Map showing the location of the St. George Dinosaur Discovery Site in St. George, Utah.

(B) The museum at the St. George Dinosaur Discovery Site. Photograph by Jerald D. Harris.
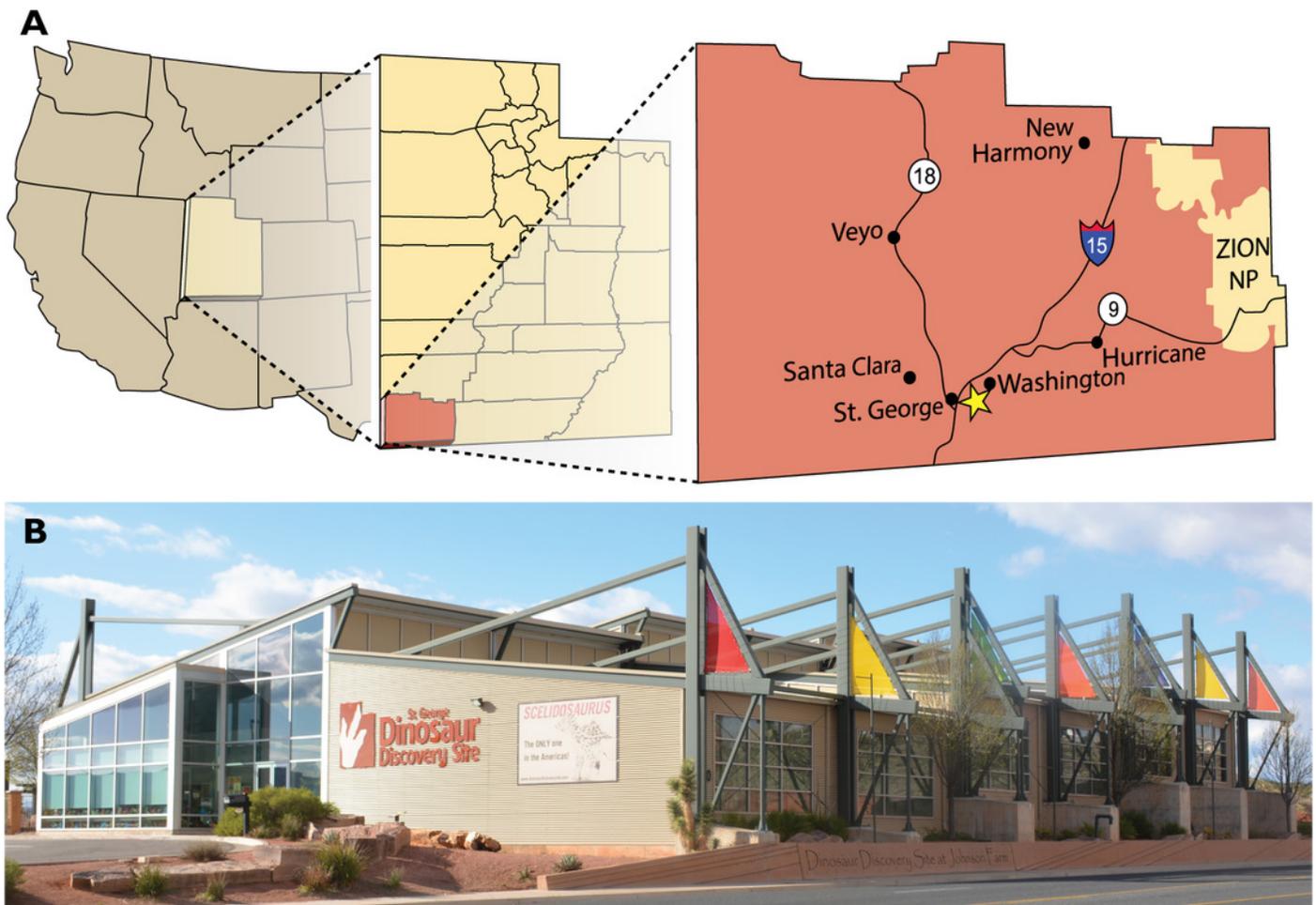
Figure 2

Stratigraphic section at and immediately around the St. George Dinosaur Discovery Site (SGDS) in St. George, Utah.

Arthropod locomotory trackway SGDS 1290 comes from the "Top Surface Tracksite" layers of the Johnson Farm Sandstone Bed (red arrows).

LEGEND

|			
conglomerate	nodular carbonate/ limestone	ripple cross-bedding	conchostracans
sandstone	shale/ mudstone	stromatolites	fish body fossils
sandy mudstone/ shale	coarse cross-bedded sandstone	plant fossils	fossil footprints
silty mudstone/ shale	cross-bedded sandstone	ostracods	dinosaur body fossils
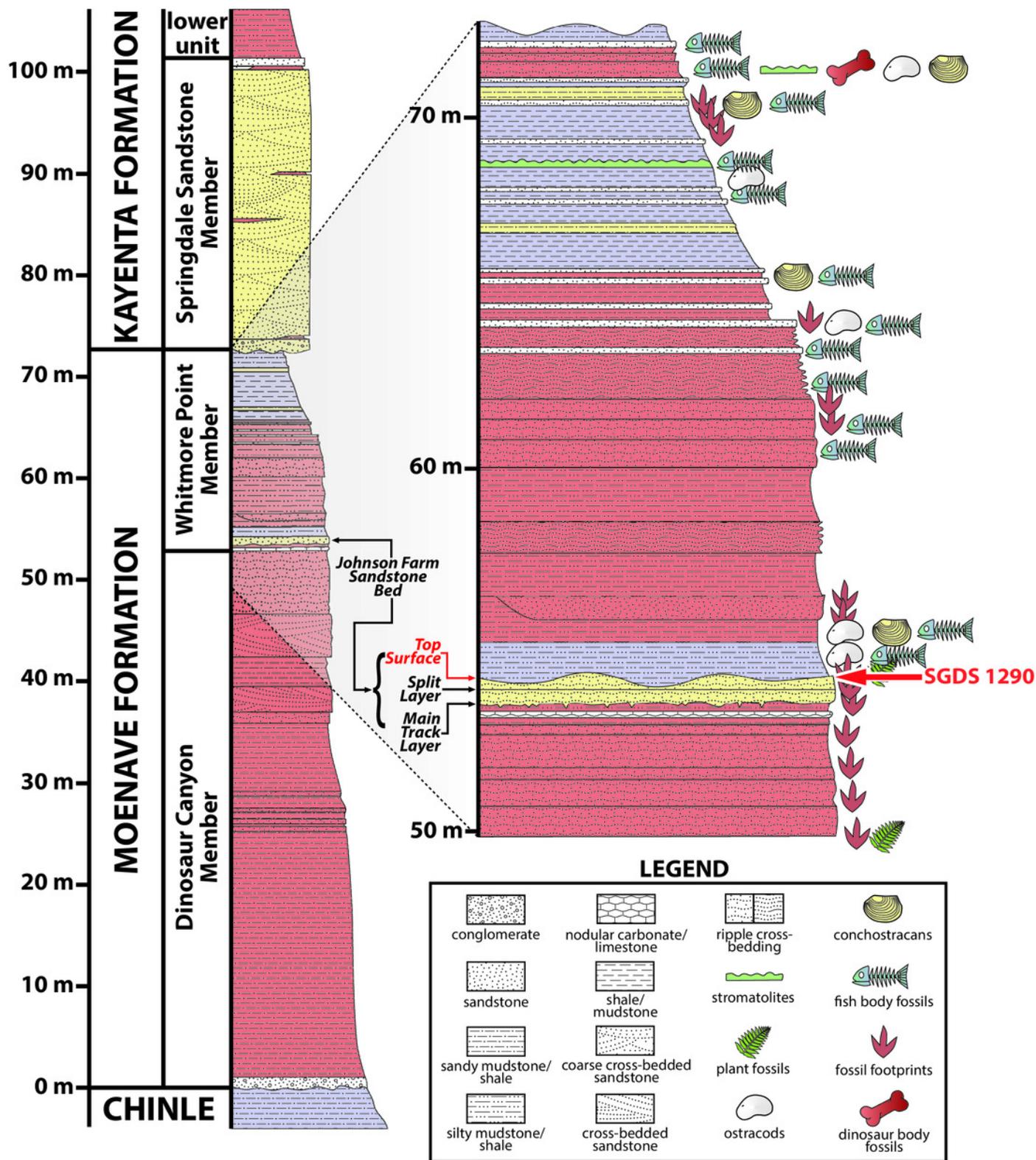
Figure 3

Arthropod locomotory ichnofossil SGDS 1290.

(A) Photograph of specimen; scale in mm. (B) Schematic diagram of specimen. Arrow indicates direction of movement. L = left track; R = right track; Ov = overtracks. Numbers indicate position of tracks in sequence from posterior to anterior. Photograph by Andrew R.C. Milner. (C) Schematic diagram of specimen, showing examples of how measurements were taken. IEW = external width between paramedial impressions; IIW = internal width between paramedial impressions; IW = paramedial impression width; TL = track length; TTI = distance between track and adjacent paramedial impression; TW = track width. (D) Photograph of extant crayfish walking trace made in saturated, very fine sand for comparison to fossil in (A); scale in cm. Arrow indicates direction of travel; photograph rotated to have the same orientation as (A). Modified from Fairchild & Hasiotis (2011: fig. 4E); reproduced with permission from SEPM.
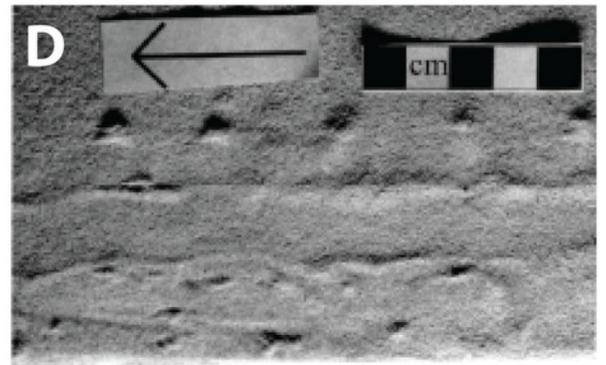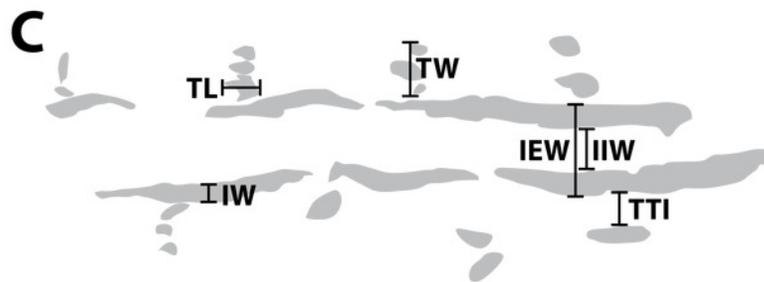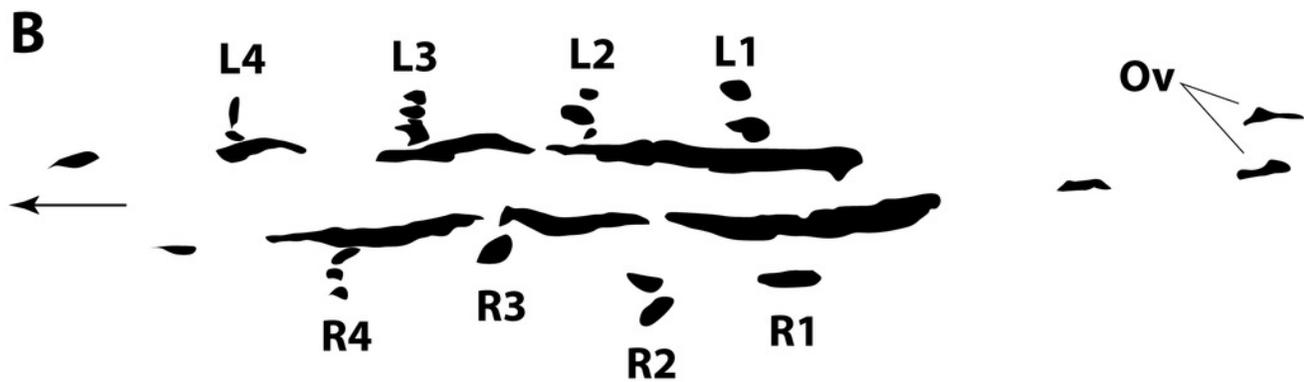
Figure 4

Schematic diagrams of locomotory (presumably walking) ichnofossils attributed to arthropods (A–MM) and extant walking traces made by arthropods (NN–OO) compared to SGDS 1290 (PP).

Diagrams not to scale. (A) *Acanthichnus cursorius* (traced from Hitchcock, 1858). (B) *Asaphoidichnus trifidus* (traced from Miller, 1880). (C) *Bifurculapes laqueatus* (traced from Getty, 2016). (D) *Coenobichnus currani* (traced from Walker, Holland & Gardiner, 2003). (E) *Copeza triremis* (traced from Hitchcock, 1858). (F) *Danstairia congesta* (traced from Walker, 1985). (G) *Diplichnites aenigma* (traced from Dawson, 1873). (H) *Diplichnites gouldi* Type A (traced from Trewin and McNamara, 1994). (I) *Eisenachichnus inaequalis* (traced from Kozur, 1981). (J) *Foersterichnus rossensis* (traced from Pirrie, Feldmann & Buatois, 2004). (K) *Hamipes didactylus* (traced from Getty, 2018). (L) *Laterigradus lusitanicus* (traced from de Carvalho et al., 2016). (M) *Lithographus hieroglyphicus* (traced from Hitchcock, 1858). (N) *Maculichna varia* (traced from Anderson, 1975a). (O) *Merostomichnites narrangansettensis* (traced from Packard, 1900). (P) *Mirandaichnium famatinense* (traced from Aceñolaza, 1978). (Q) *Octopodichnus didactylus* (traced from Gilmore, 1927). (R) *Petalichnus multipartatus* (Miller, 1880). (S) *Pterichnus centipes* (traced from Hitchcock, 1865). (T) *Tasmanadia twelvetreesi* (traced from Glaessner, 1957). (U) *Umfolozia sinuosa* (traced from Anderson, 1981). (V) *Kouphichnium lithographicum* (traced from Gaillard, 2011). (W) *"Merostomichnites* isp."* (traced from Hanken & Stormer, 1975). (X) *Oniscoidichnus filiciformis* (traced from Brady, 1947). (Y) *Palmichnium antarcticum* (traced from Braddy & Milner, 1998). (Z) *Paleohelcura tridactyla* (traced from Gilmore, 1926). (AA) *Protichnites septemnotatus* (traced from Owen, 1852). (BB) *Robledoichnus lucasi* (traced from Kozur & Lemone, 1995). (CC) *Shalemichnus sittigi*, half of trackway (traced from Kozur & Lemone, 1995). (DD) *Stiallia berriana* (traced from Smith, 1909). (EE) *Stiaria quadripedia* (traced from Walker, 1985). (FF)

Mitchellichnus ferrydenensis (traced from Walker, 1985). (GG) *Keircalia multipedia* (traced from Walker, 1985). (HH) *Danstairia vagusa* (traced from Walker, 1985). (II) *Glaciichnium liebegastensis* (traced from Walter, 1985). (JJ) *Warvichnium ulbrichi* (traced from Walter, 1985). (KK) *Siskemia bipediculus* (traced from Walker, 1985). (LL) *Siskemia elegans* (traced from Walker, 1985). (MM) *Siskemia latavia* (traced from Walker, 1985). (NN) Extant notostracan traces (traced from Knecht et al., 2009). (OO) Extant crayfish trace in saturated, very fine sand (traced from Fairchild & Hasiotis, 2011). (PP) SGDS 1290.
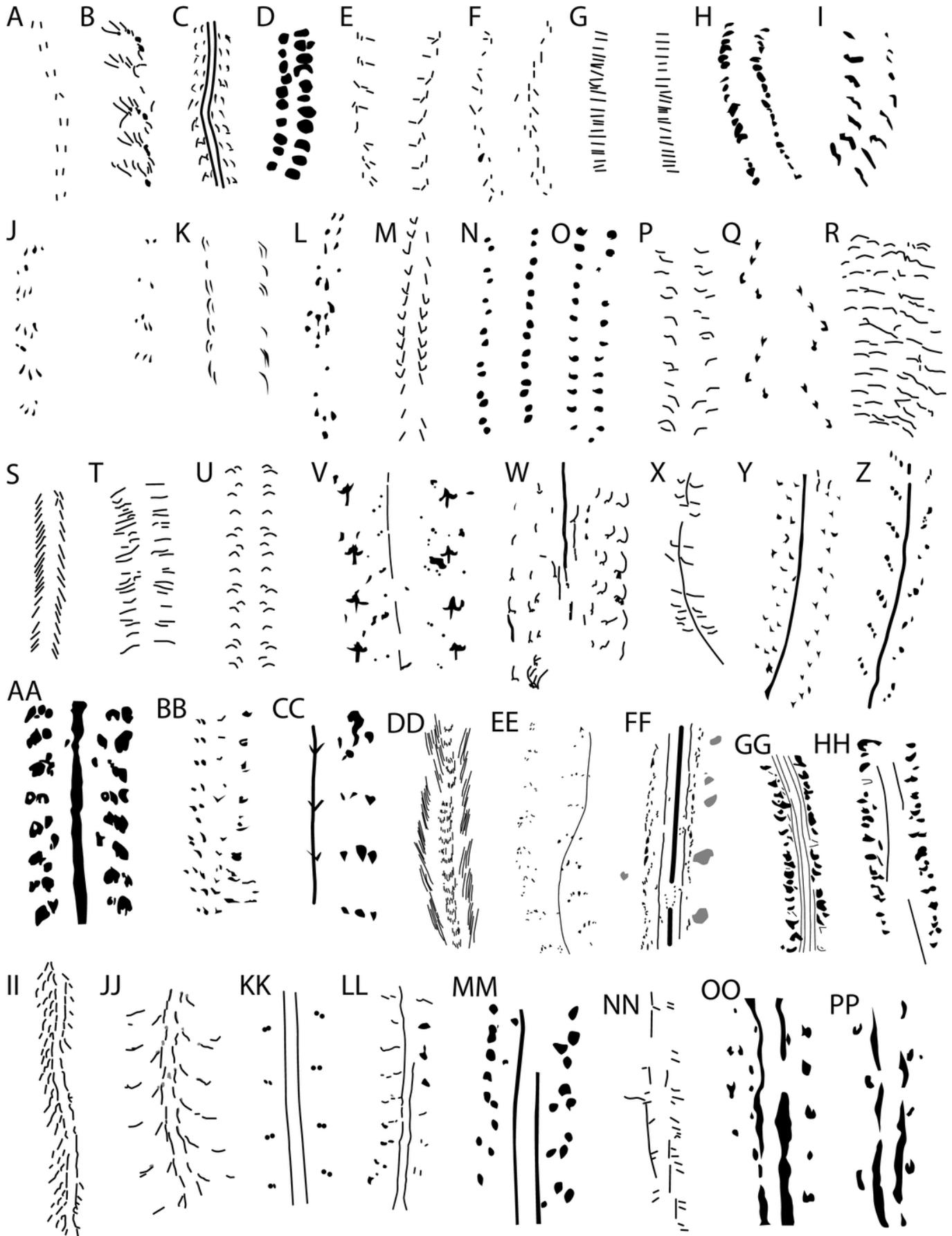
Table 1(on next page)

Measurements (in mm) of arthropod locomotory trace fossil SGDS 1290.

Measurements in parentheses are approximated based on faint portions of paramedial impressions.

1 **Table 1: Measurements (in mm) of arthropod locomotory trace fossil SGDS 1290.**
2 Measurements in parentheses are approximated based on faint portions of paramedial
3 impressions.
4

Track Position	Length	Width	Impression Internal Width	Impression External Width	Track to Impression Distance	Left Impression Width	Right Impression Width
L1	4.3	6.4	4.7	9.1	1.8	3.1	2.5
L2	4.2	5.7	5.9	9.5	1.5	2.6	2.2
L3	5.2	5.8	5.8	9.7	0.0	1.6	1.6
L4	3.2	5.6	(8.1)	(11.2)	0.0	1.9	0.0
R1	6.8	2.5	4.2	9.2	3.0	3.0	2.4
R2	4.6	5.3	5.4	8.8	4.2	2.7	0.0
R3	4.5	6.4	6.5	9.2	2.4	1.3	1.3
R4	3.0	5.8	6.9	10.6	0.0	0.0	3.0

5
6