Possible eucynodont (Synapsida: Cynodontia) tracks from a lacustrine facies in the Lower Jurassic Moenave Formation of southwestern Utah (#87860)

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Abstract

Nine fossil tetrapod footprints from lake-shore deposits in the Lower Jurassic Moenave Formation at the St. George Dinosaur Discovery Site (SGDS) in southwestern Utah cannot be assigned to the prevalent dinosaurian (*Anomoepus*, *Eubrontes*, *Gigandipus*, *Grallator*, *Kayentapus*) or crocodyliform (*Batrachopus*) ichnotaxa at the site. The tridactyl and tetradactyl footprints are incomplete, consisting of digit- and digit-tip-only imprints. Eight of the nine are likely pes prints; the remaining specimen is a possible manus print. The pes prints have digit imprint morphologies and similar anterior projections and divarication angles to those of *Brasilichnium*, an ichnotaxon found primarily in eolian paleoenvironments attributed to eucynodont synapsids. Although their incompleteness prevents clear referral to *Brasilichnium*, the SGDS tracks nevertheless suggest a eucynodont track maker and thus represent a rare, Early Mesozoic occurrence of such tracks outside of an eolian paleoenvironment.

Introduction

Fossil tetrapod tracks attributed to pre-Cenozoic synapsids have been found throughout the southwestern United States in strata ranging from Lower Permian (e.g., McKeever & Haubold, 1996; q.v., Marchetti et al., 2019) through Upper Cretaceous (Lockley & Foster, 2003). The vast majority of these tracks, particularly from the Early Permian and Late Triassic–Early Jurassic, occur in eolian facies (the *Chelichnus* ichnofacies of Hunt & Lucas [2006a]; Hunt & Lucas [2006b]). In Utah specifically, such synapsid tracks are common in the eolian, Upper Triassic–Lower Jurassic Nugget Sandstone and correlative (per Sprinkel, Kowallis & Jensen, 2011) Wingate Sandstone and Navajo Sandstone (Lockley, 2011; Lockley & Hunt, 1995; Lockley et al., 2004, 2011; Tweet & Santucci, 2015; Engelmann & Chure, 2017); they have also been reported from the roughly correlative Aztec Sandstone of California and Nevada (Reynolds, 2006; Rowland & Mercadante, 2014). In contemporaneous, non-eolian strata in the southwestern United States, non-synapsid tetrapod tracks otherwise predominate, while synapsid tracks are rare (e.g., Hunt & Lucas, 2006a; Hunt & Lucas, 2006b; Klein & Lucas, 2021; Lockley & Gierliński, 2006, 2014; Lockley, Kirkland & Milner, 2004). Ichnologically, Early Mesozoic synapsids thus appear to have preferentially inhabited eolian environments. However, synapsid body fossils are known from Upper Triassic and Lower Jurassic, non-eolian strata in the same region (e.g., Kligman et al., 2020; Jenkins, Crompton, & Downs, 1983; Sues & Jenkins, 2006), indicating that the eolian track record is not a complete story, and that synapsid tracks should occur in other environments as well.

The St. George Dinosaur Discovery Site (SGDS) in southwest Utah (Fig. 1) preserves an abundant and moderately diverse ichnofauna in lacustrine and marginal lacustrine environments (the *Grallator* ichnofacies of Hunt & Lucas [2006a], Hunt & Lucas [2006b]) of the Whitmore Point Member of the Moenave Formation, including invertebrate, fish, and sauropsida tracks and trails (Milner et al., 2011). Possible synapsid tracks at the site have been briefly mentioned (Milner, Lockley, & Johnson, 2006; Milner et al., 2011), but until now have not been studied in detail. Their tentative synapsid attribution stemmed from a combination of their small size; a similarity to some tracks referred to the ichnotaxon *Brasilichnium*, which has long been attributed to synapsids; and a general inability to refer them to any of the sauropsid ichnotaxa at the site, in the region, and from the earliest Jurassic.

Geological Setting

Most of the fossils at the SGDS are from the lowermost Jurassic (Suarez et al., 2017) Whitmore Point Member of the Moenave Formation. This unit overlies the Dinosaur Canyon Member, which contains the Triassic–Jurassic boundary, and is overlain by the Springdale Sandstone Member at the base of the Kayenta Formation (Kirkland & Milner, 2006; Kirkland et al., 2014; Fig. 2). The Whitmore Point Member consists of multiple fossiliferous horizons, the most prominent and fossiliferous of which is the Johnson Farm Sandstone Bed (Kirkland et al., 2014). The Johnson Farm Sandstone Bed is itself divided into a lower Johnson Farm Main Track Layer, a lower–middle Johnson Farm Split Track Layer, and several thinly bedded, apparently conformable, fine-grained-sandstone Top Surface horizons (Fig. 2), all of which preserve abundant vertebrate tracks, invertebrate traces, sedimentary structures, and rare body-fossil remains (Milner, Lockley & Johnson, 2006; Milner et al., 2011). The fossils and sedimentary structures reveal the paleoenvironment of the Johnson Farm Sandstone Bed as having been deposited along the shore of Lake Whitmore (formerly Lake Dixie), a large freshwater lake Kirkland et al., 2014; Milner, Lockley & Johnson, 2006; Tanner & Lucas, 2009). The tracks described herein all come from the Top Surface horizons and are *in situ*, except SGDS 190, which is *ex situ*.

Materials and Methods

Measurements of the tracks (Fig. 3) described here were taken using digital calipers on the specimens or replicas of the specimens. The divarication angles between digit imprints were measured using photographs taken orthogonal to the planes in which the specimens lay, using a protractor between straight lines drawn through the long axes of the imprints. For curved digit imprints, the long axes used in divarication measurements were straight lines drawn through the proximal, not distal, ends of the imprints. Stereophotos were taken with a Nikon D5200 digital camera outfitted with an AF-S Nikkor 18-140 mm VR lens under artificial lighting.

Descriptions

Herein we follow Minter, Braddy & Davis (2007) by using the term “imprint” when discussing a discrete, non-continuous trace, such as a digit or sole imprint, and the term “impression” when discussing a more continuous trace. Although this descriptive system was developed for use with arthropod, rather than vertebrate, traces, the system is useful for describing vertebrate traces as well; its adoption here is simply for the sake of clarity.

As far as is currently known, all Early Mesozoic synapsids (dicynodonts, non-mammaliaform eucynodonts [*sensu* Hopson & Kitching, 2001], and mammaliaforms [*sensu* Rowe, 1988]; q.v. Sereno [2006]) had pentadactyl manus and pedes. None of the tracks described herein, however, possess five digit imprints, making determining which imprints correspond to which digits impossible. Herein we number the digit imprints using the system common to other tetrapods in which digit lengths increase from digits I–IV and decrease again in digit V (i.e., ectaxony). We acknowledge, however, that these relative digit proportions may not apply to any or all Early Mesozoic synapsids (see below), and that proportions of digit imprints made by at least some of these taxa are complicated by their apparent possession of digital arcades (Kümmell & Frey, 2012).

All the tracks described herein are natural molds (concave/negative epirelief).

SGDS 190 (Fig. 4)

SGDS 190 is a single, *ex situ*, ectaxonic right track that comprises four moderately deep digit imprints only, here interpreted as digits II–V using the aforementioned reasoning (Table 1). The imprints lack discernible digital pad and claw traces. Digit imprints II and III are more diamond-shaped, but still rounded distally. Imprints IV and V do not taper either proximally or distally; instead they have rounded proximal and distal ends that are approximately the same widths as the midpoints of the imprints. The imprints of digits II and III are parallel and straight; the proximal end of the imprint of digit IV parallels those of II and III, but distally the imprint curves laterally to parallel the short and straight imprint of digit V. The curvature of digit IV could be due to some slipping in wet sediment when the track maker pushed off. SGDS 190 lacks a clear sole mark, but the outermost margins of the outermost digit imprints angle inward toward the bases of the other digit imprints in such a way as to suggest the sole region was short anteroposteriorly.

SGDS 18-T3 (Figs. 5–8)

SGDS 18-T3 is a short *in situ* trackway of five apparent pes prints (SGDS 18-T3-1, -2, -3, -4, & -6) and one possible manus print (SGDS 18-T3-5) (Fig. 5). Tracks T3-1, -2, and -6 have a slight outward rotation from the trackway axis.

SGDS 18-T3-1 (Fig. 6A), an apparent mesaxonic right pes print, has three subparallel digit imprints, herein interpreted as digits III–V, The imprints are straight, narrow, and roughly oblong, tapering distally; digit IV, the longest and centrally placed imprint, tapers proximally as well. The distal tapers of the imprints suggest short claws. The proximal ends of the imprints all lie approximately at the same level. As with SGDS 190, the digit imprints lack discernible digital pads.

SGDS 18-T3-2 (Fig. 6B), an apparent mesaxonic left pes print, has four imprints, herein interpreted as digits II–V. Unlike those of 18-T3-1, the imprints divaricate markedly (Table 1). The imprint of digit V is short and curved outward; the other imprints are straight. The imprint of digit II is faint and short. The both proximally and distally tapering imprint of digit III is the deepest and most pronounced trace; it is also the longest and most distally extended, unlike the apparent pattern in 18-T3-1. The imprints of digits IV and V have rounded proximal and distal ends. As with 18-T3-1, all imprints lack discernible digital pads. Both 18-T3-1 and 18-T3-2 possess longer digit imprints than the rest of the tracks in the trackway, but otherwise are similar in relative digit lengths and by tapering on the distal ends.

SGDS 18-T3-3, 18-T3-4, and 18-T3-5 (Fig. 7) are unusual, comprising primary tracks connected to secondary sets of imprints by clear, linear, but shallow, drag impressions (Figs. 5, 7), each spanning roughly 30 mm between their primary and secondary tracks. The primary track of SGDS 18-T3-3, a paraxonic to ectaxonic right pes print, comprises four short, relatively narrow digit-tip imprints (II–V) that, as in SGDS 190, increase in length from digit II to IV and decrease again in digit V, but unlike in SGDS 190, the imprint of digit II is the shortest (Table 1). Digit imprints II and III are subparallel, but angle inward whereas digit imprints IV and V angle outward, giving the track a paraxonic sense. The imprint of digit IV tapers distally into what may be a short claw trace, but the remaining digit imprints are rounded distally. The secondary track of SGDS 18-T3-3 (labeled 18-T3-3-2 in Table 1) comprises imprints only of digits III and IV; unlike their primary-track counterparts, these imprints taper distally. Their angulations mirror those of their primary-track counterparts.

The primary track of left pes SGDS 18-T3-4 resembles 18-T3-3 except that its imprints are shorter and all rounded distally, though that of digit IV is still the longest of the set. The secondary track of 18-T3-4 (labeled 18-T3-4-2 in Table 1) comprises imprints of all four digits, but they are shorter and shallower than those of 18-T3-3. Unlike in 18-T3-3, the secondary imprints of 18-T3-4 appear rounded distally. Tracks 18-T3-3 and 18-T3-4 lie close to their trackway midline.

The primary track of SGDS 18-T3-5 lies lateral and slightly anterior to 18-T3-4, a position that suggests it might be a manus print. However, its morphology differs markedly from those of 18-T3-3 and 18-T3-4. The primary track comprises three faint, narrow, and shallow digit-tip imprints, likely those of digits III–V. Unlike those of 18-T3-3 and 18-T3-4, each roughly triangular imprint tapers sharply to a point distally, suggesting they may be claw traces. Rather than lying in an approximate, shallowly arcuate row, as do the imprints of 18-T3-3 and 18-3-4, the imprints of 18-T3-5 lie at markedly different levels with respect to each other, with the imprint of digit IV lying far anterior to the imprints of digits III and V. Their configuration is reminiscent of a *Grallator* theropod dinosaur track, but the close association of 18-T3-5 with 18-T3-4, plus the drag impressions and secondary print shared with 18-T3-3 and 18-T3-4, strongly suggest it was made by the same track maker as the other SGDS 18-T3 tracks. The imprints of digit III and V curve slightly distally in opposing directions. The secondary track of 18-T3-5 (labeled 18-T3-5-2 in Table 1) is virtually identical to the primary track, but fainter.

SGDS 18-T3-6 (Fig. 8) is a single apparently right pes print that somewhat resembles SGDS 190 and 18-T3-1; it is virtually the same size as SGDS 190. It comprises three distally tapering digit imprints, presumably of digits III–V. The imprints of digit III and V are straight;

that of digit IV curves slightly outward at its tip. Swollen, rounded areas immediately proximal to the tapered claw imprints could be digital pad imprints.

SGDS 18-T6-2 (Fig. 9)

SGDS 18-T6-2 is an *in situ,* apparent ectaxonic right track with four digit imprints (presumably II–V), although the imprint of digit V is faint. The imprints of digits II, III, and V taper distally, but that of digit IV is rounded. The tapering distal end of the digit II imprint is proximally attached to an inflated, ovoid proximal end that may be the imprint of a digital pad, but the imprints of digits III, IV, and V lack such a feature. The imprints of digits II and III both curve outward toward their distal ends.

SGDS 18-T7 (Fig. 10)

SGDS 18-T7 is a single, *in situ*, tetradactyl, apparent paraxonic to ectaxonic right pes print that is similar to SGDS 190, 18-T3-3, and 18-T3-4 in overall morphology. As in SGDS 18-T3-3 and T3-4, the subequal imprints of digits II and III are subparallel to each other and angle inward; the shorter imprints of digits IV and V are subparallel to each other and angle outward, giving the track a paraxonic sense. Digit imprints IV and V appear to curve outward slightly at their distal ends. All four imprints taper toward their distal ends, but not as sharply as in 18-T6-2. No obvious digital pad imprints are discernible.

Comparisons

The mostly tetradactyl SGDS tracks described herein are markedly unlike the dominantly tridactyl, mesaxonic ornithischian (*Anomoepus*) and theropod (*Eubrontes*, *Gigandipus*, *Grallator*, *Kayentapus*) dinosaur tracks, all made primarily by bipedal track makers, known from Late Triassic–Early Jurassic of North America and that are abundant at the SGDS and in its geographic and stratigraphic vicinity. *Anomoepus* can include manus prints, demonstrating facultative quadrupedality by their track makers, but manus tracks are pentadactyl and entaxonic (Olsen & Rainforth, 2003), and therefore unlike the SGDS tracks described herein. Additionally, *Anomoepus* manus prints unassociated with pes prints are unknown and unexpected given that the weight-bearing hind limbs of presumed *Anomoepus* track makers (facultatively quadrupedal basal ornithischian dinosaurs) would be expected to register much deeper and more pronounced tracks than the manus. Late Triassic–Early Jurassic sauropodomorph ichnotaxa (*Eosauropus*, *Evazoum*, *Kalosauropus*, *Otozoum*, *Pseudotetrasauropus*), while being tetradactyl to pentadactyl, are all far larger than the SGDS tracks described herein; they also have markedly different digit and sole imprint morphologies and proportions (Lallensack et al., 2017; Mukaddam et al., 2020; Rainforth, 2003), and thus can be readily excluded as possible referrals for the SGDS tracks.

The number of Mesozoic, non-dinosaurian tetrapod ichnotaxa to which the SGDS tracks described herein could be compared is substantial. We limit our comparisons ~~below~~ to ichnotaxa known from Upper Triassic–Early Jurassic strata of the western United States because those are temporally and geographically the closest to the SGDS tracks and therefore the most likely to be possibly congeneric. We exclude various Triassic ichnotaxa (e.g., chirotheriid tracks) that are understood to not extend into the Jurassic (Klein & Lucas, 2021).

Batrachopus Hitchcock, 1845 (Fig. 11A)

Batrachopus is particularly important to compare to the SGDS tracks described herein because *Batrachopus* is one of the most common tetrapod ichnotaxa at the SGDS. The ichnotaxon is attributed to early crocodyliforms, such as *Protosuchus* (Olsen & Padian, 1986). *Batrachopus* tracks are found in Lower Jurassic strata of France (Moreau et al., 2019), the northeastern (Hitchcock, 1845; Olsen & Padian, 1986) and southwestern (Lockley, Kirkland & Milner, 2004; Lockley et al., 2018) United States, and possibly southern Africa (Lockley, Kirkland, & Milner, 2004; Lockley et al., 2018) and Colombia (Mojica & Macia, 1987), as well as Middle?–Upper Jurassic strata of Morocco (Masrour et al., 2020) and Lower Cretaceous strata of South Korea (Kim et al., 2020). *Batrachopus* manus tracks are pentadactyl (though often tridactyl or tetradactyl, as well) with varying digit orientations: usually the digit imprints are spread such that digit II points anteriorly, digit IV points laterally, and digit V points posteriorly (Olsen & Padian, 1986), but numerous referred specimens have more variable digit orientations, including having digit imprints with low divarication angles. Digit imprints are typically short but wide, and may or may not terminate in narrower claw imprints. *Batrachopus* pes tracks are ectaxonic and tetradactyl (digits I–IV), with digit III being the longest. Digit V, if present, consists of an oval imprint behind that of digit III. Digit imprints are longer than those of the manus, but also relatively wide. *Batrachopus* trackways demonstrate that the manus and pes prints rotate markedly outward. Numerous *Batrachopus* tracks at SGDS fit this general description and differ markedly from the tracks described in this paper. However, we note that the sheer diversity of track morphologies that have been attributed to *Batrachopus* renders comparisons to this ichnotaxon somewhat problematic, and strongly suggests that it requires detailed and updated review and revision.

The relative narrowness and separation of digit imprints, as well as the low divarication angles between digit imprints, of all of the SGDS tracks described herein, except for 18-T3-2, preclude them from being classic *Batrachopus* manus prints. Additionally, the isolated SGDS tracks (190, T6-2, 18-T7) are unlikely to be manus prints because inferred *Batrachopus* track makers (protosuchian crocodyliforms) would likely have left more pronounced pes than manus prints, making the absence of associated pes prints with these SGDS tracks bizarre. Also except for 18-T3-2, the anterior projections of the digit imprints of the tetradactyl SGDS tracks (190, T3-3, T3-4, 18-T7) are proportionately more subequal than those of *Batrachopus* pes tracks, in which the innermost imprint (digit I) is much shorter than the other digit imprints (Lockley et al., 2018; Moreau et al., 2019; Olsen & Padian, 1986). The tridactyl SGDS tracks (T3-1, T3-6, T6-2) are more equivocal in this regard, although T3-1 and T3-6 are part of the T3 trackway, and thus associated with tetradactyl tracks T3-3 and T3-4, so they can be inferred to have had similar overall digit imprint proportions had they been tetradactyl. The absence of distinct claw imprints in the relatively deeply impressed SGDS 190, plus its inferred short sole imprint, also further distinguish that specimen from *Batrachopus* pes tracks. Overall, a case for attributing the SGDS tracks to *Batrachopus* is not well supported.

Ameghinichnus Casamiquela, 1961 (Fig. 11B)

Ameghinichnus tracks are usually attributed to mouse-sized mammaliaforms and have been found in Upper Triassic–Middle Jurassic strata of Argentina (Casamiquela, 1961; de Valais, 2009), South Africa (Olsen & Galton, 1984), Poland (Gierliński, Pieńkowski & Niedźwiedzki, 2004), and the western (Lockley et al., 2004) and possibly eastern (Olsen, 1988; Olsen & Rainforth, 2001) United States. Classic *Ameghinichnus* tracks, as described by de Valais (2009), comprise quadrupedal trackways with pentadactyl manus and pes tracks that are wider than long. Digit imprints II–V are subequal in length; all digit imprints lack claw imprints (except in possible specimens from the Newark Supergroup [Olsen & Rainforth, 2001, fig. 59A]) and are rounded and swollen distally, making them wider than more proximal parts of their imprints. Symmetrical manus tracks have subequal divarication angles between digit imprints; pes tracks have markedly greater divarication angles between digits I–II and IV–V than between II–III and III–IV. Thus, in both the manus and pes tracks, the digit imprints splay markedly, and are not subparallel. In *A. patagonicus*, smaller manus tracks lie medial to the pes tracks and are rotated inward, toward the midline, while the somewhat larger pes prints are rotated outward, away from the midline. Both manus and pes tracks are wider than they are long. Most *Ameghinichnus* tracks have distinct sole imprints.

The SGDS tracks described herein are all tridactyl or tetradactyl and lack sole imprints, unlike *Ameghinichnus*. Some of the SGDS tracks described herein possess distally tapering digit imprints, also unlike *Ameghinichnus*; those that lack claw imprints and are rounded distally lack distal swellings (though the digit IV imprint of SGDS 190 comes close), also unlike classic *Ameghinichnus*. The SGDS tracks generally lack the consistent splay (divarication angles) exhibited by *Ameghinichnus* tracks, sometimes possessing subparallel digit imprints. Tracks in trackway SGDS 18-T3 do not display the degrees of rotation that tracks in *Ameghinichnus* trackways do, and the possible manus track in this trackway lies lateral to the pes track, opposite the configuration in *Ameghinichnus*. Thus, the SGDS tracks do not fit within the *Ameghinichnus* paradigm.

Navahopus Baird, 1980 (Fig. 11C)

Navahopus is an uncommon ichnotaxon thus far reported exclusively from Lower Jurassic strata of the southwestern United States (Baird, 1980; Hunt & Lucas, 2006c; Milàn, Loope & Bromley, 2008; Reynolds, 2006). The *Navahopus* track maker is unclear: the tracks have been attributed to sauropodomorph dinosaurs (Baird, 1980; Milàn, Loope & Bromley, 2008) and large therapsid synapsids (Lockley & Hunt, 1995; Shibata, Matsukawa & Lockley, 2006). *Navahopus* manus tracks are tridactyl, with two short, anteriorly oriented digit imprints and a large, laterally oriented, “falciform” claw imprint (Baird, 1980; Milàn, Loope & Bromley, 2008; q.v., Hunt & Lucas, 2006c). The manus imprints are mediolaterally elongate but anteroposteriorly short. *Navahopus* pes tracks are functionally tetradactyl with all digits rotated slightly laterally; all digit imprints taper distally, terminating in claw marks. They possess pronounced, posteriorly convex, though irregularly shaped sole imprints.

In addition to its much greater size, *Navahopus* morphology is distinctly different from those of the SGDS tracks. None of the SGDS tracks resemble *Navahopus* manus tracks, possessing more digits and lacking the "falciform" pollex claw imprint. The SGDS tracks lack the distinct sole imprint of *Navahopus* pes prints, but are similar in generally possessing subparallel digit imprints. However, the digit imprints of *Navahopus* are quite thin and distally tapering, while the SGDS track digit imprints are mostly wider, even if they taper distally. The SGDS tracks thus cannot be readily referred to *Navahopus.*

Pentasauropus Ellenberger, 1970 (Fig. 11D)

Pentasauropus manus and pes tracks are, as their name implies, pentadactyl, and similar in size and morphology (D'Orazi Porchetti & Nicosia, 2007). The originally described specimens from Upper Triassic strata of Lesotho (Ellenberger, 1970, 1972), as well as specimens from Lower Triassic strata of Argentina (Citton et al., 2018) and Upper Triassic strata of western North America (Gaston et al., 2003; Lockley & Hunt, 1995) and Argentina (Marsicano & Barredo, 2004), consist almost exclusively of small, generally ovoid digit-tip imprints arranged roughly equally spaced in an anteriorly convex, arcuate pattern; the digit-tip imprints are generally, but not universally, wider than long. Other Late Triassic specimens from Argentina, as well as subsequently discovered specimens from the Middle Triassic of Argentina (Lagnaoui et al., 2019), also include large, mediolaterally wide, oval-, kidney-, or D-shaped palm/sole imprints that are loosely connected or entirely unconnected to the digit imprints. *Pentasauropus* trackways are wide gauge and have low pace angulation values. Although initially referred by Ellenberger (1970) to amphibians and sauropodomorph dinosaurs, and by Haubold (1984) to a sauropod or therapsid, *Pentasauropus* has more typically been attributed to dicynodont therapsids (D'Orazi Porchetti & Nicosia, 2007; Kammerer, 2018; Olsen & Galton, 1984), an interpretation supported by their restriction to Triassic strata.

Although size is a poor ichnotaxobase, known *Pentasauropus* tracks dwarf the SGDS specimens. While some of the SGDS tracks described herein similarly consist of digit-tip-only imprints, the imprints are all longer than wide and not generally distributed in the neat arc seen in *Pentasauropus*; the other SGDS tracks described herein consist of more elongate and narrow digit imprints, thus also differing from *Pentasauropus*. Tracks in the SGDS 18-T3 trackway have higher pace angulation values than do *Pentasauropus* trackways. The SGDS tracks do not pertain to *Pentasauropus*.

Therapsipus Hunt, Santucci, Lockley & Olson, 1993 (Fig. 11E)

Therapsipus tracks, thus far described only from the Middle Triassic of Arizona, were made by a large, wide-bodied quadruped (Hunt et al., 1993). Tracks are tetradactyl to pentadactyl and consist of short, wide, typically blunt digit imprints connected to anteroposteriorly short but mediolaterally wide palm/sole imprints; this connection, plus the morphologies of the digits and palm/sole imprints and a greater degree of heteropody between the manus and pes, differentiate this ichnotaxon from *Pentasauropus*. Nevertheless, like *Pentasauropus*, *Therapsipus* tracks have been attributed to dicynodont therapsids and are restricted to Triassic strata.

The SGDS tracks described herein differ markedly from *Therapsipus* for much the same reasons as they differ from *Pentasauropus*: their digit imprint morphologies, absence of palm/sole imprints, and much smaller size all prevent referral to *Therapsipus*.

Dicynodontipus **Rühle von Lilienstern, 1944 (Fig. 11F, G)**

Dicynodontipus has been reported from “Middle” Permian–Upper Triassic strata of Brazil (Francischini et al., 2018), Italy (Conti et al., 1977), South Africa (de Klerk, 2002), Argentina (Citton et al., 2021; Marsicano et al., 2004; Melchor & de Valais, 2006), Australia (Retallack, 1996), and Germany (Rühle von Lilienstern, 1944; de Valais et al., 2020). *Dicynodontipus* trackways are unknown after the Triassic, although some of the questionable, Early Jurassic ichnotaxa from Lesotho named by Ellenberger have some similarities (Melchor & de Valais, 2006). Despite their name and original attribution to dicynodont therapsids (e.g., Conti et al., 1977; Retallack, 1996; Rühle von Lilienstern, 1944), *Dicynodontipus* tracks likely were made by cynodont therapsids (e.g., da Silva et al., 2008; Haubold, 1971, 1984; Marsicano et al., 2004). If correct, and if all tracks referred to this ichnogenus truly belong in it, then the temporal extent of this ichnogenus suggests that cynodont manus and pedes were evolutionarily rather conservative from the Permian through the Triassic.

Both manus and pes tracks are pentadactyl, plantigrade, mesaxonic to slightly ectaxonic, wider than long, and have short, subequal digit imprint lengths (da Silva et al., 2008); some referred specimens are tetradactyl or tridactyl (da Silva et al., 2008). Digit imprints are all oriented anteriorly (Melchor & de Valais, 2006). The tracks resemble those of *Therapsipus* but have longer, more tapering digit imprints and longer, more posteriorly extensive, convex, and rounded sole imprints (da Silva et al., 2008; Rühle von Lilienstern, 1944). *Dicynodontipus* trackways also have higher pace angulations than do those of *Pentasauropus* or *Therapsipus* (Melchor & de Valais, 2006).

The SGDS tracks described herein are not pentadactyl or plantigrade, unlike *Dicynodontipus* tracks. Some tracks referred to *Dicynodontipus* have long, tapering digit imprints (e.g., Marsicano et al., 2004: fig. 5); others (originally placed in the ichnotaxon *Gallegosichnus* by Casamiquela [1964]) have shorter, distally rounded digit imprints (e.g., Melchor & de Valais, 2006: fig. 5A; Fig. 11F); and still others (originally placed in the ichnotaxon *Calibarichnus* by Casamiquela [1964]) have shorter, distally tapering digit imprints (e.g., Melchor & de Valais, 2006: fig. 5B; Fig. 11G). Both of the latter morphologies more closely resemble those of many of the SGDS tracks described herein. Additionally, the digit imprints of the SGDS tracks are similar to those of *Dicynodontipus* in divarication angles and the relative degrees of anterior projection (Marsicano et al., 2004; Melchor & de Valais, 2006).

However, the consistent lack of pentadactyly, mesaxony, and sole imprints prevents us from readily referring the SGDS tracks to *Dicynodontipus*.

Cynodontipus Ellenberger, 1976

Ellenberger (1976) described a single, incomplete fossil—ostensibly a track that includes hair imprints—from the Middle Triassic of France as *Cynodontipus* and attributed it to a (presumably non-mammaliaform) cynodont therapsid. Additional specimens were reported from the Middle and Late Triassic of Morocco and eastern North America (Olsen, Et-Touhami & Whiteside, 2012). Subsequent work, however, demonstrated that the type specimen is not a singular track at all, though interpretations of it vary. Olsen, Et-Touhami & Whiteside (2012) and Sues & Olsen (2015) interpreted specimens as procolophonid burrows; Klein & Lucas (2021) regarded the French specimen as a partial chirotheriid track with microbially induced sedimentary structures and the ichnotaxon as a *nomen dubium*. In either case, it is incomparable to any of the SGDS specimens, but it is mentioned here because it otherwise is one of only a few Mesozoic ichnotaxa to have been (albeit incorrectly) attributed to a non-mammaliaform cynodont.

Brasilichnium Leonardi, 1981 (Fig. 11G)

Brasilichnium and *Brasilichnium*-like tracks have been reported from primarily eolian deposits of Early Triassic–Late Cretaceous age almost globally (see Leonardi & de Souza Carvalho [2020] for a review of occurrences). The variety of morphologies that have been attributed to this ichnotaxon suggest that, like *Batrachopus*, it may have become something of an ichnotaxonomic "wastebasket" (Leonardi & de Souza Carvalho, 2020). *Brasilichnium* and *Brasilichnium*-like tracks generally have been attributed to a derived synapsid (derived, non-mammaliaform eucynodont or basal mammaliaform—see discussion in D'Orazi Porchetti, Bertini & Langer [2016]); within that interpretation, the general brevity of the digit imprints in such tracks suggests that their track makers had digital arcades (*sensu* Kümmell & Frey, 2012), supporting a therapsid attribution. However, because most *Brasilichnium* and *Brasilichnium*-like tracks were registered on dune faces in eolian sediments, many, if not most, have been affected by extramorphological phenomena, such as sediment collapse and deformation features, as well as asymmetrical push-up rims (e.g., Engelmann & Chure, 2017; Leonardi, de Souza Carvalho & Fernandes, 2007; q.v. Loope, 2006), that create rather variable track morphologies and complicate interpretations of the manus and pes morphologies of the track makers.

The type ichnospecies, *B. elusivum,* as revised by Fernandes & de Souza Carvalho (2008; q.v., Buck et al., 2016; D'Orazi Porchetti, Bertini & Langer, 2018), comprises quadrupedal trackways that lack tail traces. Detailed pes prints and less common manus prints typically are wider mediolaterally than long anteroposteriorly. Both the smaller manus prints, when preserved, and the larger pes prints are ectaxonic and tetradactyl (digits II–V; digit I is always absent), but many referred specimens exhibit fewer digit imprints, or even no discreet digit imprints. When preserved on both the manus and pes, digit imprints are short and teardrop-shaped (typically rounded proximally and tapered distally), but imprints can also be rounded distally. Either digit imprints III and IV (for *B. elusivum*; Buck et al., 2016) or II and III (for *B. anaiti*; D'Orazi Porchetti, Bertini & Langer, 2018) are longest. Sole marks are rounded and usually wider than long. Manus prints tend to be located anterior to the pes prints.

The general brevity of the SGDS track digit imprints, the divarication angles, and the nearly co-equal anterior projections of the digit imprints of the tetradactyl SGDS tracks (190, 18-T3-3, 18-T3-4, 18-T7) all resemble those of *Brasilichnium* manus and pes tracks. Even the possible SGDS manus track (18-T3-5) proportionally bears some resemblance to a *Brasilichnium* manus track that lacks a digit II imprint, but its position largely lateral to its associated pes print, rather than anterior to it, is unlike *Brasilichnium*. Although it is not a diagnostic feature of the ichnogenus, some *Brasilichnium* tracks exhibit apparent paraxony, with imprints of digits II and III angled inward and digits IV and V angled outward (e.g., D'Orazi Porchetti, Bertini & Langer, 2016, fig. 2), as in SGDS 18-T3-3, 18-T3-4, and 18-T7. Further comparisons between the SGDS specimens and *Brasilichnium sensu stricto* are limited, however, because the SGDS specimens lack sole marks, and have variably tapering or rounded distal digit imprints. Furthermore, many *Brasilichnium* tracks in trackways are rotated slightly inward (e.g., D'Orazi Porchetti, Bertini & Langer, 2018, fig. 2), but tracks in the SGDS 18-T3 trackway appear rotated slightly outward, as are some trackways referred to *Brasilichnium* from elsewhere in the American Southwest (Lockley, 2011; Rowland & Mercadante, 2014). These distinctions could arise from anything from track-making-species idiosyncrasies to differing locomotory strategies, sediments, and paleoenvironments between those of typical *Brasilichnium* tracks (loose, coarser sands on dune slopes) and those of the SGDS tracks (fine-grained, likely wet sand on a flat lake shore). Nevertheless, of the ichnotaxa compared in this section, the SGDS tracks most closely resemble *Brasilichnium*.

Discussion

The enigmatic SGDS tracks described herein cannot be conclusively assigned, or even referred, to any established ichnotaxon or ichnotaxa. However, they are too few in number, and too incompletely preserved, to warrant establishing a new ichnotaxon for them. Based on digit-imprint morphology and overall preserved track morphology, they are better attributed to a synapsid track maker than a crocodyliform or dinosaurian one. Morphologically overall, they share more in common with *Brasilichnium* than with any other ichnotaxon, though in some respects they also resemble some tracks referred to *Dicynodontipus*; both of these ichnotaxa have been attributed to cynodont track makers. *Brasilichnium* and *Brasilichnium*-like tracks, however, are known primarily from coarser, eolian sandstone deposits, whereas the SGDS tracks were made in wet, lake-shore, fine-grained sand, as were many tracks referred to *Dicynodontipus* (da Silva et al., 2008; Melchor & de Valais, 2006). If the SGDS tracks were made by similar track makers as were *Brasilichnium* tracks, then the morphological differences between them may reflect substrate, environmental, and/or behavioral differences. Nevertheless, the SGDS tracks constitute rare instances of Early Mesozoic—specifically, post-Triassic—synapsid tracks outside of an eolian paleoenvironment (i.e., in the *Eubrontes* ichnocoenose of the *Grallator* ichnofacies, rather than in the *Brasilichnium* ichnocoenose of the *Chelichnus* ichnofacies [Hunt & Lucas, 2006a; Hunt & Lucas, 2006b]). They raise the question of what *Brasilichnium* track-maker tracks made outside of eolian settings might look like. If both *Brasilichnium* and *Dicynodontipus* were made by cynodonts, further comparisons of tracks referred to each ichnotaxon would test whether they were made by track makers with similar manual and pedal morphologies, and their differing track morphologies stem largely from environmental factors, or they were made by taxa with distinct manual and pedal morphologies.

Synapsid—specifically non-mammaliaform eucynodont or mammaliaform—track makers for the SGDS tracks described herein are plausible for two reasons:

1. Tracks (specifically *Brasilichnium*) attributed to such animals have been reported from Lower Jurassic strata elsewhere in the American Southwest (Engelmann & Chure, 2017; Hamblin & Foster, 2000; Lockley, 2011; Reynolds, 2006; Rowland & Mercadante, 2014); and

2. Derived, non-mammaliaform eucynodont (specifically tritylodontid) and basal mammaliaform skeletal materials are known from both Upper Triassic and Lower Jurassic strata in the American Southwest, albeit not yet from the Moenave Formation, or from Utah. Derived, non-mammaliaform eucynodonts (Kligman et al., 2020) and basal mammaliaforms (Lucas & Luo, 1993) are known from the Upper Triassic Tecovas Formation (Dockum Group) of west Texas and the Chinle Formation of northern Arizona. Similarly, and more abundantly, derived, non-mammaliaform eucynodonts (Hoffman & Rowe, 2018; Kermack, 1982; Lewis, 1986; Sues, 1985, 1986; Sues, Clark, & Jenkins, 1994; Sues & Jenkins, 2006) and basal mammaliaforms (Crompton & Luo, 1993; Jenkins, Crompton, & Downs, 1983; Sues, Clark, & Jenkins, 1994) are known from the Lower Jurassic Kayenta Formation of northern Arizona.

The Chinle and Kayenta formations stratigraphically bracket the Moenave Formation (Fig. 2), so the presence of similar taxa in southwestern Utah during Moenave Formation time can be assumed. However, known skeletal material of the aforementioned early Mesozoic basal mammaliaforms does not, as yet, include manual or pedal material, so how the manus and pedes of these taxa might align with the SGDS tracks cannot be determined. Skeletal material of the Kayenta Formation tritylodontid *Kayentatherium* includes manual (Hoffman & Rowe, 2018; Sues & Jenkins, 2006) and pedal (Lewis, 1986) material; an indeterminate (per Sues, Clark, & Jenkins, 1994), partial tritylodontid skeleton from the overlying Navajo Sandstone also preserves manual material (Winkler et al., 1991). Relative digital proportions in these non-mammaliaform eucynodonts have not been described, however. All are pentadactyl, so understanding their digital proportions and locomotory postures relates directly to whether or not they could be predicted to have normally made pentadactyl or tetradactyl tracks and what the nominal, expected relative lengths and projections of their digit imprints would be, even incorporating digital arcades (*sensu* Kümmell & Frey, 2012).

Ichnological evidence of a derived, non-mammaliaform eucynodont or basal mammaliaform (or, conceivably, both) in the Whitmore Point Member of the Moenave Formation of southwestern Utah increases the known ichnofaunal, and consequent faunal, diversity of the unit and the region. At the SGDS specifically, tetrapod ichnofossils are, as present, otherwise limited to those of crocodyliforms (*Batrachopus*), dinosaurs (*Anomoepus*, *Characichnos*, *Eubrontes*, *Gigandipus*, *Grallator*, *Kayentapus*), and possibly sphenodontians (*Exocampe*) (Milner et al., 2011). Additionally, a diverse invertebrate ichnofauna is also present (Lucas et al., 2006; Rose, Harris & Milner, 2021), as are *Undichna* fish swim trails (Milner et al., 2011). The Whitmore Point Member thus ichnologically preserves a detailed "snapshot" of an earliest Jurassic terrestrial ecosystem that now likely includes either or both non-mammaliaform or mammaliaform eucynodont therapsids.

Future excavations of the Top Surface and other track-bearing horizons at the SGDS potentially may uncover more tracks that may clarify the nature of the enigmatic SGDS track maker(s) and the ichnotaxon/ichnotaxa to which the tracks described herein pertain. Additionally, further work exploring the effects of substrate differences and/or slope angles on synapsid track formation is needed. This could constitute digital modeling and/or experimentation with extant mammals that possess manual and pedal morphologies similar to those of derived, non-mammaliaform eucynodonts and basal mammaliaforms. Controlled experimentation to determine the relationship between substrate characteristics and track formation has become more common for invertebrate ichnological track work (e.g., Azain, 2006; Davis, Minter, & Braddy, 2007; Fairchild & Hasiotis, 2011; Schmerge, Riese & Hasiotis, 2013), but for vertebrates, similar work, while invaluable, often has been observational in natural, rather than controlled, conditions (e.g., Farlow & Elsey, 2010; Farlow et al., 2017; Genise et al., 2009; but see Buck et al. [2016], Leonardi [1982], Marchetti et al. [2019], Milàn [2006], and Turner & Gatesy [2021] for experimental examples). This undoubtedly is due to difficulties in handling and controlling the locomotory behaviors of (especially larger) vertebrates. Nevertheless, small mammals might be manageable for such experimental work (e.g., Buck et al., 2016).

Conclusions

Several enigmatic, partial fossil tracks from the Lower Jurassic Whitmore Point Member of the Moenave Formation at the SGDS are most likely attributable to a eucynodont (derived, non-mammaliaform or basal mammaliaform) track maker. The tracks described herein include a single possible manus track along with several pes tracks. The possible manus is tridactyl with only the digits imprints preserved that taper distally. The pes prints are tetradactyl with only digits imprints preserved. Some taper proximally and/or distally, but others are rounded on both ends. These tracks are most similar among known and contemporaneous ichnotaxa to *Brasilichnium*, which is widely understood to pertain to a derived, non-mammaliaform or basal mammaliaform track maker. However, morphological differences between the SGDS tracks and those of *Brasilichnium* may be functions of substrate differences: the former were made in probably wet, fine-grained, lake-shore sands, whereas the latter are known only from coarser, eolian sands. The discovery of further, more complete specimens and/or experimental work to better establish a relationship between substrate and track morphology are needed to clarify the nature of the SGDS tracks.

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Figure 1

Map showing the location of the St. George Dinosaur Discovery Site in Washington County, St. George, Utah.

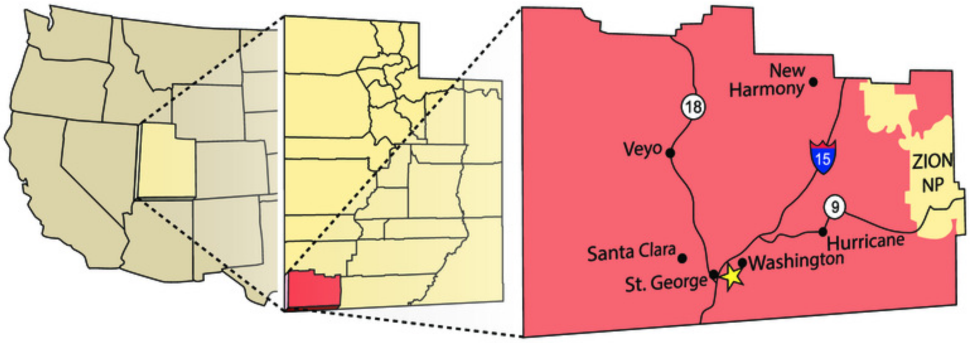

New Harmony
18
Veyo
15
ZION NP
9
Hurricane
Santa Clara
Washington
St. George

Figure 2

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

Possible synapsid tracks SGDS 18 and 190 come from the Top Surface Tracksite horizon of the Johnson Farm Sandstone Bed (red arrows).

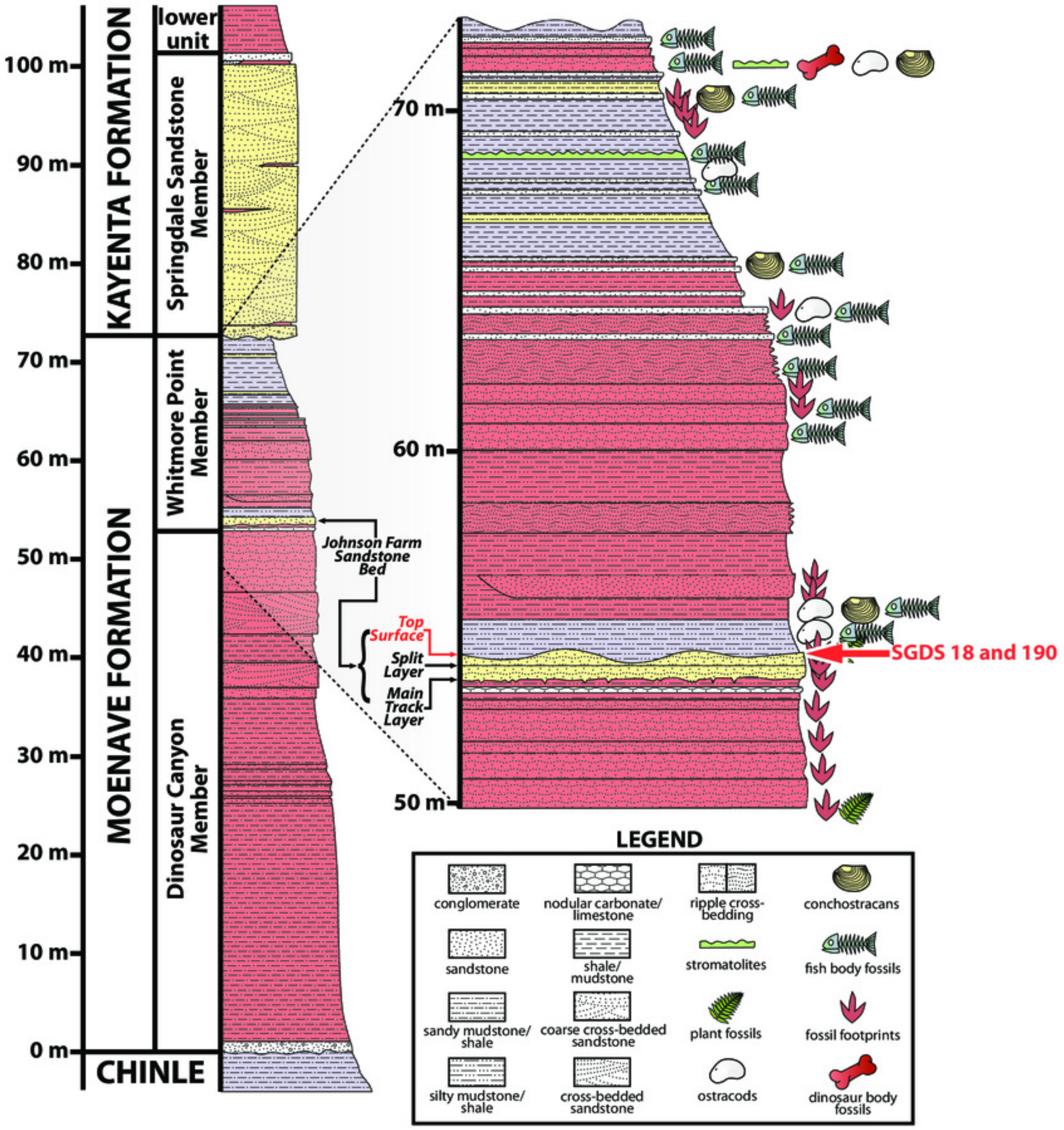

KAYENTA FORMATION
MOENAVE FORMATION
CHINLE
lower unit
Springdale Sandstone Member
Whitmore Point Member
Dinosaur Canyon Member
100 m
90 m
80 m
70 m
60 m
50 m
40 m
30 m
20 m
10 m
0 m
Johnson Farm Sandstone Bed
Top Surface
Split Layer
Main Track Layer
70 m
60 m
50 m
SGDS 18 and 190
LEGEND
conglomerate
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

Schematic depicting how measurements of possible eucynodont tracks SGDS 18 and 190 were taken.

Diagrams use a tracing of SGDS 18-T7 as a model. (A) Track measurements: dl = digit length; tl = track length; tw = track width. (B) Measurements of divarication angles between individual digit traces (II–V).

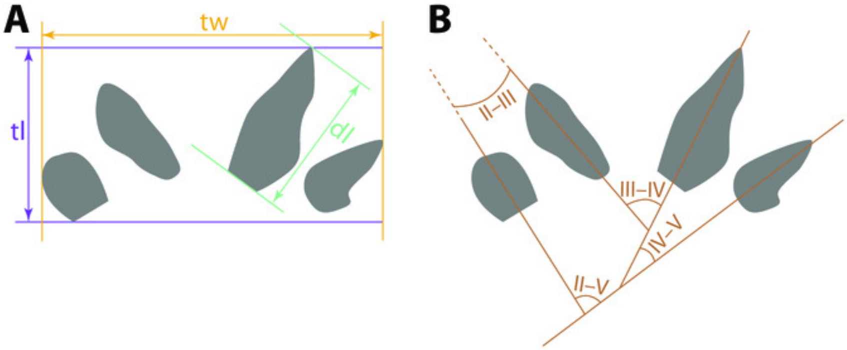

A
tw
tl
dl
B
II–III
III–IV
IV–V
II–V

Figure 4

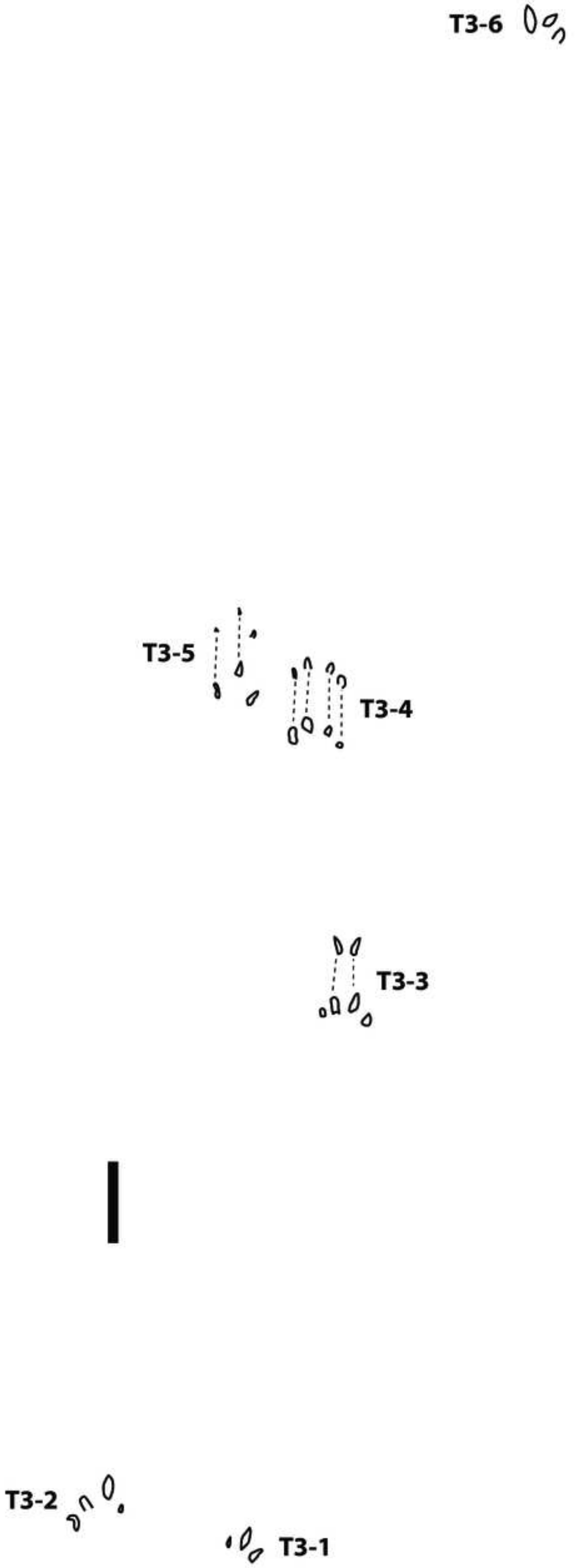
Stereophotograph pair of possible eucynodont track SGDS 190 from the Lower Jurassic Moenave Formation of St. George, Utah.

Scale bar = 1 cm.

Figure 5

Schematic depicting relative positions of possible eucynodont tracks 1–6 in trackway SGDS trackway 18-T3.

Scale bar = 5 cm. See Figs. 6–8 for individual track details.



T3-6
T3-5
T3-4
T3-3
T3-2
T3-1

Figure 6

Stereophotograph pairs of possible eucynodont tracks SGDS 18-T3-1 and 18-T3-2 from the Lower Jurassic Moenave Formation of St. George, Utah.

(A) SGDS 18-T3-1. (B) SGDS 18-T3-2. Scale bars = 1 cm.

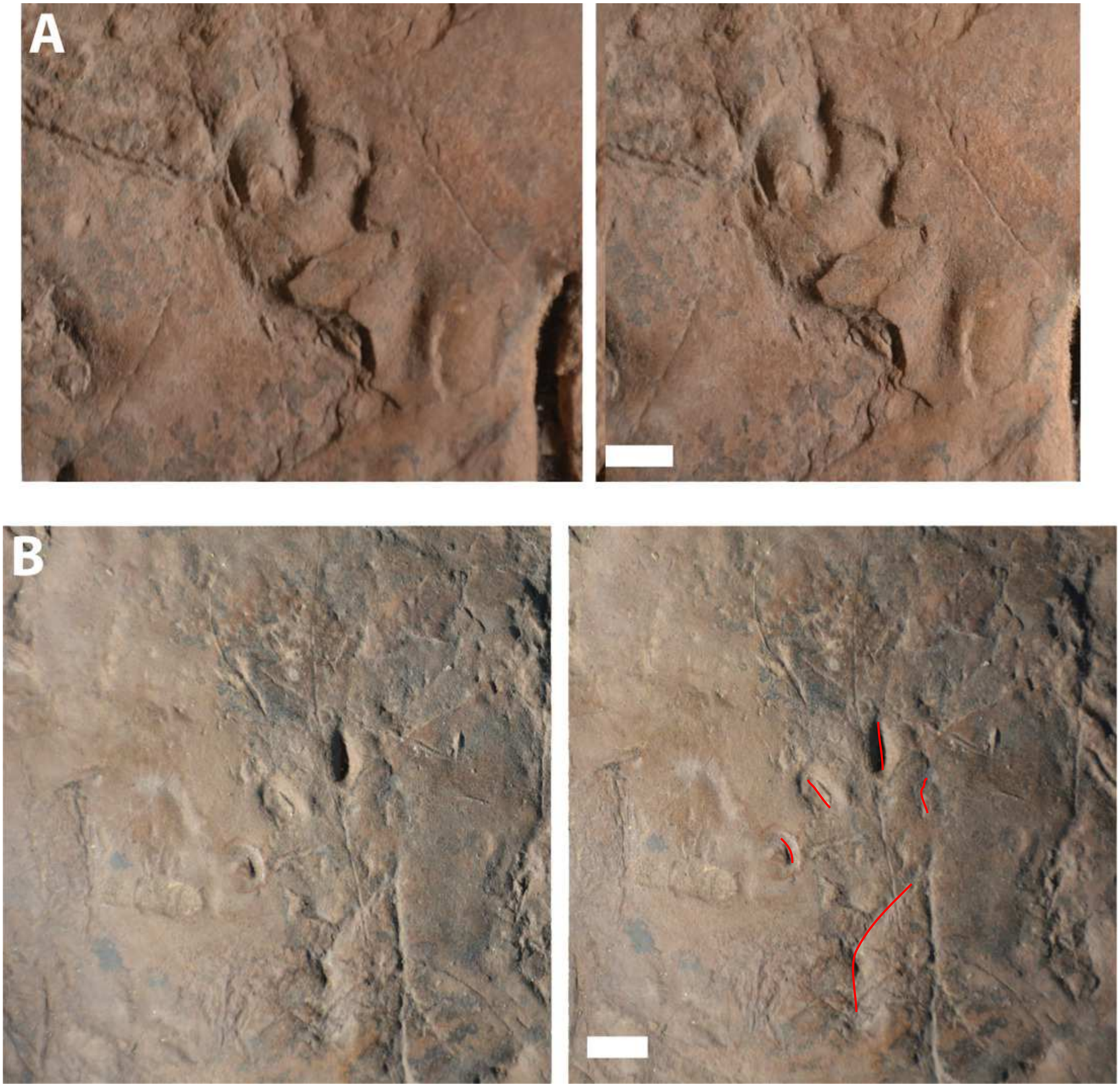


Figure 7

Stereophotograph pairs of possible eucynodont tracks SGDS 18-T3-3, -4, and -5 from the Lower Jurassic Moenave Formation of St. George, Utah.

Scale bar = 1 cm.


T3-5
T3-4
T3-3

Figure 8

Stereophotograph pair of possible eucynodont track SGDS 18-T3-6 from the Lower Jurassic Moenave Formation of St. George, Utah.

Scale bar = 1 cm.

Figure 9

Stereophotograph pair of possible eucynodont track SGDS 18-T6-2 from the Lower Jurassic Moenave Formation of St. George, Utah.

Scale bar = 1 cm.

Figure 10

Stereophotograph pair of possible eucynodont track SGDS 18-T7 from the Lower Jurassic Moenave Formation of St. George, Utah.

Scale bar = 1 cm.

Figure 11

Schematic morphological comparisons between manus and pes prints of (A) *Batrachopus* and (B–H) Mesozoic synapsid ichnotaxa (not to scale).

(A) Composite *Batrachopus* from the Lower Jurassic Moenave Formation, Arizona (traced from Olsen & Padian, 1986). (B) *Ameghinichnus* from the Middle Jurassic La Matilde Formation, Santa Cruz, Argentina (traced from de Valais, 2009). (C) *Navahopus* from the Lower Jurassic Navajo Sandstone, Arizona, USA (traced from Baird, 1980). (D) *Pentasauropus* from the Middle Triassic Cerro de las Cabras Formation, Mendoza, Argentina (traced from Lagnaoui et al., 2019). (E) *Therapsipus* from the Middle Triassic Holbrook Member of the Moenkopi Formation, Arizona, USA (traced from Hunt et al., 1993). (F) *Dicynodontipus* (“*Gallegosichnus*” type) from the Upper Triassic Vera Formation, La Rioja, Argentina (traced from Melchor & de Valais, 2006). (G) *Dicynodontipus* (“*Calibarichnus*” type) from the Upper Triassic Vera Formation, La Rioja, Argentina (traced from Melchor & de Valais, 2006). (H) *Brasilichnium* from the Lower Cretaceous Botucatu Formation, São Paulo, Brazil (traced from Fernandes & de Souza Carvalho, 2008).

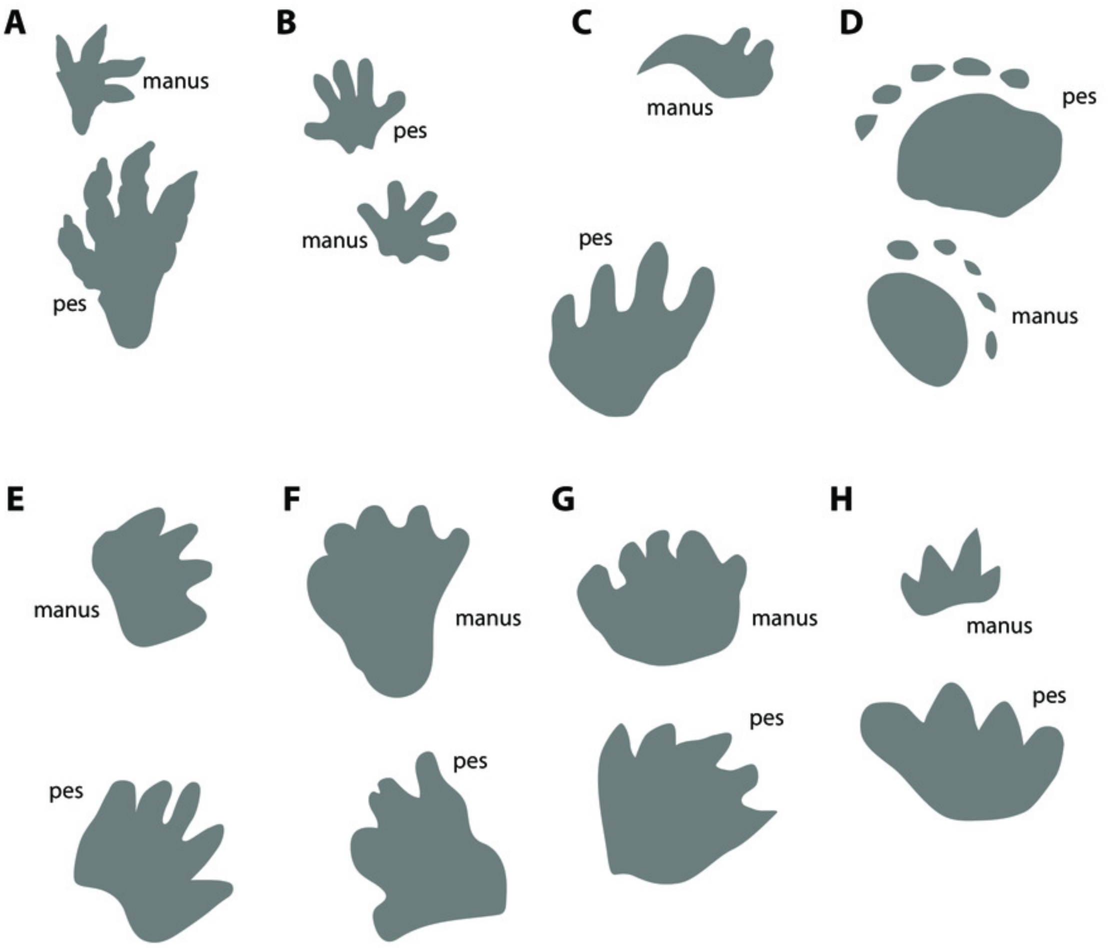

A
manus
pes
B
pes
manus
C
manus
pes
D
pes
manus
E
manus
pes
F
manus
pes
G
manus
pes
H
manus
pes

Table 1(on next page)

Measurements for possible eucynodont tracks from the Lower Jurassic Moenave Formation of St. George, Utah.

∠ = divarication angle; * = angle anterior, rather than posterior, to track; ? = one digit impression too vague to accurately determine axis; n/a = not applicable.

Track	**Total Length (mm)**	**Total Width (mm)**	**Digit II length (mm)**	**Digit III length (mm)**	**Digit IV length (mm)**	**Digit V length (mm)**	**∠ II–III (°)**	**∠ III–IV (°)**	**∠ IV–V (°)**	**∠ Outer-most Digits (°)**
190	13.0	15.1	8.6	9.7	10.5	5.8	4.0	27.0	29.0	59.0
18-T3-1	18.7	19.9	n/a	5.1	15.5	9.6	n/a	20.0	12.0	32.0
18-T3-2	12.8	33.9	7.7	11.7	8.2	6.5	?	36.5	24.0	?
18-T3-3	16.0	26.5	5.6	7.8	11.0	7.2	11.0	14.0	37.0	61.0
18-T3-3-2	11.8	15.6	n/a	8.0	9.0	n/a	n/a	32.0	n/a	n/a
18-T3-4	14.5	27.0	2.4	5.7	8.4	9.5	4.0	18.0	21.0	43.0
18-T3-4-2	12.0	27.5	n/a	6.0	6.9	6.0	7.0	11.0	9.0	28.0
18-T3-5	23.1	23.0	n/a	9.0	7.3	7.9	n/a	32.0	22.0	53.0
18-T3-5-2	18.7	16.9	n/a	7.2	9.3	6.3	n/a	13.0	17.0	29.0
18-T3-6	12.8	24.6	n/a	12.3	10.4	6.7	n/a	53.0	31.0*	24.0
18-T6-2	18.6	25.1	6.0	11.5	10.3	12.4	18.0*	29.0	26.0	37.5
18-T7	10.0	21.7	7.5	8.5	7.8	6.0	8.0	67.0	24.0	98.0