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New dinosaur track occurrences from the Upper Jurassic Salt Wash Member (Morrison Formation) of southeastern Utah: Implications for thyreophoran trackmaker distribution and diversity



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ABSTRACT

Recent construction at the Moab Giants dinosaur museum property ~10 miles (~16 km) north of Moab, in Grand County, Utah in 2014–2015 revealed a number of moderately well preserved dinosaur tracks from the Upper Jurassic, Salt Wash Member of the Morrison Formation. The best specimens were preserved as natural casts on the underside of massive sandstone beds, many containing dense assemblages of invertebrate traces. Here we describe several tridactyl theropod tracks, an ornithischian manus attributable to ichnogenus *Stegopodus* and an ornithischian pes track attributed to ichnogenus *Deltapodus*. Variably preserved *Deltapodus* have now been reported from the Tidwell, Salt Wash and Brushy Basin members of the Morrison Formation from Garfield, Grand and San Juan counties respectively, suggesting a wide distribution in space and time. The Salt Wash specimen is considered to be the most representative of *Deltapodus* morphologies reported from large samples in other regions, notably in Spain, Portugal western China and North Africa. Differences between *Stegopodus* and *Deltapodus* are reviewed. *Deltapodus* is reported from Europe and Asia as well as North America, in the Middle Jurassic through Late Cretaceous, and is often represented by abundant trackways. *Stegopodus* is presently reported from the Jurassic where it occurs in the Late Jurassic of North America as isolated tracks, and, with some debate, as trackways and isolated tracks from Europe. A middle Jurassic occurrence from Morocco is also reported.

1. Introduction

Several previous studies have provided overviews of the track assemblages known from the Morrison Formation (Foster, 2003; Foster and Lockley, 2006; Lockley et al., 2015). These revealed that, at latest count, there were at least 64 known tracksites yielding a diversity of dinosaur and other tetrapod tracks. Here we report an additional significant tracksite (number 65, named the Moab Giants site) in the Salt Wash Member of the Morrison Formation near Moab Utah, which has yielded two significant theropod tracks and two tracks of thyreophorans, all preserved as natural casts (convex hyporeliefs). Most significantly, one of the thyreophoran tracks is a diagnostic example of *Deltapodus*, which was previously known only from three isolated reports with sub-optimal preservation (Fig. 1). The first was a cast reported from the Tidwell Member (Lockley et al., 2008), below the Salt

* Corresponding author. *E-mail address:* martin.lockley@ucdenver.edu (M. Lockley). Wash Member in Garfield County, Utah, the second was a cast reported from and Brushy Basin Member above the Saltwash Member, in San Juan County (Milan and Chiappe, 2009) and the third, an impression from near the Moab Giants site, is a small, isolated track (only 15 cm long) originally described as a "small *Deltapodus* print of possible ankylosaurian affinity" (Gierlinski et al., 2010). Given the increased number of reports of well-preserved *Deltapodus* in trackways (notably Cobos et al., 2010; Mateus and Milàn, 2010; Mateus et al., 2011; Xing et al., 2013), interpreted as stegosaurian, the interpretation of this small, isolated impression of *Deltapodus* as ankylosaurian is open to question.

We consider the *Deltapodus* occurrence from the Salt Wash Member at the Moab Giants site of particular importance. The material consists of a well-preserved pes, without associated manus trace that is strikingly similar to the *Deltapodus* pes tracks described by Lockley et al. (2008) and Cobos et al. (2010) from the Late Jurassic of Spain, by Mateus et al. (2011), from the Upper Jurassic of Portugal, by Belvedere and Mietto (2009) from the Upper Jurassic of Morocco, and by Xing et al.

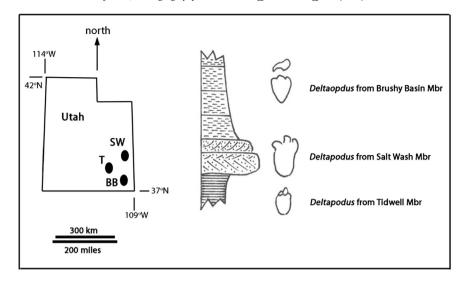


Fig. 1. Location of three known *Deltapodus* tracksites in the Morrison Formation of southeastern Utah. In ascending stratigraphic order they are associated with the Tidwell (T) Member (Lockley et al., 2008), the Salt Wash (SW) Member (this study) and the Brushy Basin (BB) Member. Simplified section shown schematically. A fourth track labelled as *Deltapodus* is mentioned in the text.

(2013) from the Early Cretaceous of China. The lack of manus trace in the Moab Giants specimen is probably due to post-exhumation damage to the track-bearing block (Fig. 2).

2. Description of material and methods

The tracks found in the Late Jurassic Salt Wash Member of the Morrison Formation from Moab Giants property are variable in quality, and represent several morphotypes. Most recognizable tracks are preserved as natural casts (convex hyporeliefs). Because they were discovered as a result of excavation of many large slabs their precise stratigraphic occurrence is not known. The most diagnostic track is the specimen designated here as *Deltapodus* (Fig. 2). Arguably this is the most significant track discovery at the present site. The track is preserved as a natural cast with three short, rounded blunt toes and an elongate subrectangular heel. Total track length is ~45.0 cm and maximum width, across the anterior end, is ~31.0 cm. The toes are subcircular to transversely oval with the largest digit trace (? digit I) revealing a transverse diameter of about 10.0 cm and an anterior-posterior diameter of about 8.0 cm. The middle digit (II) is also about 10.0 cm wide and 7.0 cm long, whereas the third digit (III) is smaller with both width and length ~7.0 cm. In order to protect the track, it was collected and moved into the Moab Giants museum as specimen MGL1, where a mold was made. Replicas were distributed to the Museum of Western Colorado as MWC 8477, and to the University of Colorado Museum as UCM 194.3. The latter repository also holds full sized tracings (T1699 and T 1700) of the tracks illustrated in Fig. 3, and the tracing (T1718) of the *Deltapodus* track (Fig. 4B₂).

In order to obtain an accurate 3D image of this track cast a series of overlapping photographs were taken with a 20.1 megapixel Nikon Coolpix L32 digital camera. Seventeen photographs were taken at an average height of 56 cm above the subject. An analytical set of photographs - including a line of photographs in landscape orientation and

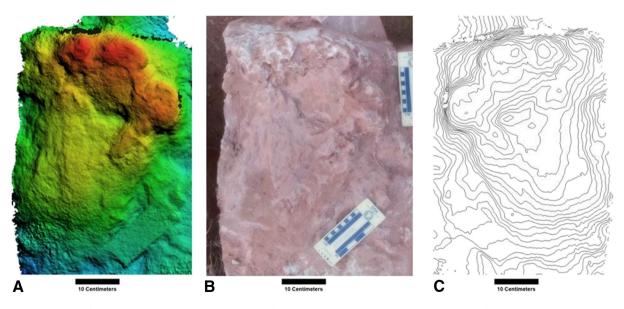


Fig. 2. Photogrammetric image of a distinctive *Deltapodus* pes track (MWC 8477) from the Salt Wash member of the Morrison Formation, from the Moab Giants site near Moab, Utah. A: Color depth map derived from Digital Elevation Model, color indicates change in depth of 15 cm. B: Orthophoto mosaic of a portion of the track block. C: Five centimeter topographic contour map. Topographic map has been reversed to show correct orientation. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

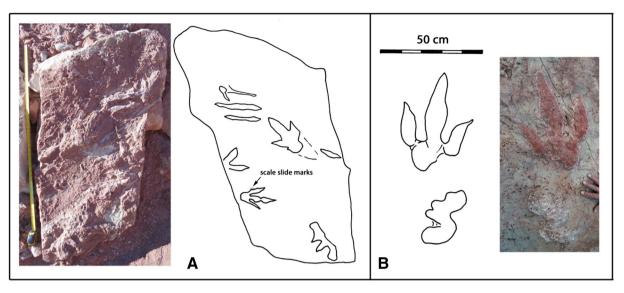


Fig. 3. Photographs and corresponding tracings of track casts recovered from the Late Jurassic Salt Wash Member of the Morrison Formation at Moab Giants. A: shows small theropod tracks, associated scratch marks and a probable ornithischian trace: yellow tape = 1 m, based on Tracing T1699. B: shows a large theropod track cast and probable ornithischian manus cast, based on tracing T 1700. Theropod track cast has been highlighted with light red paint as it is part of an exhibit. Both line drawings have been reversed from negative, cast aspect to show right and left in correct positive, impression orientation. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

lines in portrait oriented with the camera turned at 90 and 270° – were taken with approximate overlap of 66%. The combination of landscape and portrait oriented photographs provide coverage of the subject, as well as, additional information for the optimal handling of camera and lens distortion removal. The photographs were processed using Agisoft PhotoScan Professional Version 1.2.5. A strategy of alignment, error removal and optimization was followed to ensure the most accurate results were achieved (Matthews et al., 2016). The ground sample distance (or pixel size) was 0.135 mm/pixel, with total project error determined to be approximately 1 mm. A digital elevation model, digital orthophoto mosaic and topographic contours were generated within Agisoft PhotoScan (Fig. 2).

A second slab (Fig. 3A) reveals two relatively small and deep theropod track casts representing registration of tracks on a soft muddy substrate with many small desiccation features. The smaller track is a digitigrade footprint 18 cm long with small, scale slide marks on the track wall. The larger track is a plantigrade footprint about 23 cm long with an elongated heel trace. The slab also reveals elongate scratch marks, including three that are parallel and roughly aligned with the three digits traces of the larger theropod track. Another track feature appears to be a right, four-toed (tetradactyl) ornithischian manus, or it could represent an overlapping configuration of tridactyl tracks. In the former interpretation the digit traces decrease in size from one side (presumed digit I on the inside) to the other (presumed digit IV on the outside). Thus the posterior of the track appears transverse to the digit orientations, and very slightly concave.

A third large slab of Salt Wash sandstone also reveals tracks preserved as natural casts on a surface with desiccation cracks and invertebrate traces which is situated inside the main entrance courtyard as part of the outdoor exhibit. The largest and most complete cast is a theropod track almost 50 cm long. All three digits are well defined (Fig. 3B) with sharp digit trace terminations, and a well-defined heel. Tracks of this general size and type from the Morrison Formation have been named *Megalosauripus* and *Hispanosauropus* (Foster, 2015) and attributed to theropods like *Allosaurus*. This track cast occurs close to another track feature interpreted as an ornithischian manus (Fig. 3B) which appears to be four- or five-toed (tetradactyl or pentadactyl). This track has a large inner digit trace (presumably right digit I) with much smaller medial and lateral digit traces. The posterior of the track is strongly concave. Thus, it shares a number of features with the *Stegopodus* manus specimen CU-MWC 195.1 (Lockley and Hunt, 1998) found close to *Stegopodus* pedal type specimen (sensu Gierlinski and Sabath, 2008).

3. Discussion

As noted above, the sample of Late Jurassic thyreopohoran tracks is small, especially in North America. Both Stegopodus and Deltapodus are interpreted as thyreophoran tracks by all authors, and as stegosaurian tracks by most authors. A single report of a large (30 cm wide), wellpreserved thyreophoran manus (cf., Tetrapodosaurus) from the Morrison Formation has been attributed to a large ankylosaur (Hups et al., 2008a, 2008b). The differences between Stegopodus and Deltapodus are somewhat ambiguous. Lockley and Hunt (1998) originally named Stegopodus czerkasi from the basal Salt Wash member from near Moab airport, a location near the Moab Giants site discussed here. The original description was based on a distinctive ectaxonic, tetradactyl, manus cast with possible small digit V trace (Fig. $4A_3$) with an associated pes cast that may or may not have been registered by the same animal responsible for the manus track. Gierlinski and Sabath (2008) subsequently emended the diagnosis of Stegopodus to include a revised description of the pes, indicating that it was transverse (wider than long) and tridactyl with blunt digits and a short heel trace. This reconstruction was consistent with the conjectural trackway reconstruction of Thulborn (1990, fig. 6.39b).

In contrast to *Stegopodus*, which is known from manus tracks with well-defined digit traces (Lockley and Hunt, 1998) and a wide pes with relatively short heel traces (Gierlinski and Sabath, 2008), type *Deltapodus* from the Middle Jurassic of England (Whyte and Romano, 2001) was named on the basis of a bluntly tridactyl pes with a very elongate heel and poorly defined (preserved) crescentic manus. Thus type *Stegopodus* and type *Deltapodus* are ostensibly different in both manus and pes morphology. However, these differences are in part due to sub-optimal preservation. In reference to North American material so far attributed to *Stegopodus* and *Deltapodus*, all come from the Morrison Formation. *Stegopodus* as defined by Lockley and Hunt (1998), on the basis of the manus is known only from the type locality cited above, near Moab. However, as defined by Gierlinski and Sabath (2008) on the basis of the pes from the Cleveland-Lloyd Dinosaur Quarry, near Price Utah, *Stegopodus* has a wider distribution, including an isolated

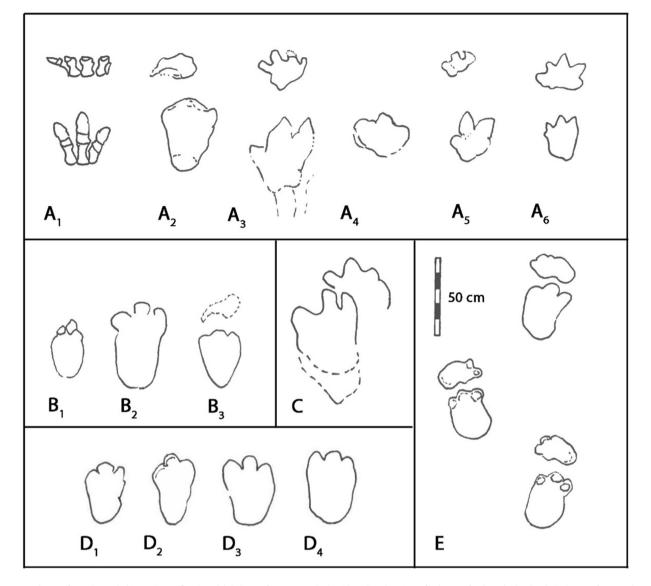


Fig. 4. $A_1 - A_6$ redrawn after Milan and Chiappe (2009, fig. 3). Pedal skeleton of *Stegosaurus* (A₁), with outline drawings of holotype of *Deltapodus brodericki* (A₂), type of *Stegopodus czerkasi* (A₃), pes track from Morrison Formation (after Bakker, 1996) [compare with other tracks from Cleveland-Lloyd Dinosaur Quarry near Price, Gierlinski and Sabath (2008)], (A₄), Late Jurassic manus pes set from Poland (A₅) and manus and pes tracks from Cretaceous of, Australia (A₆). B₁–B₃ respectively, *Deltapodus* from Tidwell, Salt Wash (based on T1718) and Brushy Basin Members of the Morrison Formation of southeastern Utah. Compare with Fig. 1. C. *Stegopodus* from the Morrison Formation near Morrison Colorado (after Mossbrucker et al., 2008). D₁–D₄, four examples of isolated *Deltapodus* tracks from the Upper Jurassic of Spain (after Lockley et al., 2008). E: *Deltapodus curriei* from the Lower Cretaceous of China. All tracks drawn to the same scale (E). See text and cited references for details.

pes specimen purportedly from the Morrison Formation at Como Bluff, Wyoming (Bakker, 1996). Note, however, that Lockley and Hunt (1998) noted that this specimen's actual provenance was the Cleveland-Lloyd Dinosaur Quarry. Moreover, Bakker did not use the term Stegopodus, which had not been named in 1996. He only inferred a stegosaurian trackmaker, implying that it might also have been a biped. There is also a Polish occurrence (Gierlinski and Sabath, 2002, 2008) which these authors use as evidence that the Stegopodus trackmaker may have been bipedal, as implied by Bakker (1996). Stegopodus has also been reported from the type section of the Morrison Formation at Dinosaur Ridge near Morrison Colorado (Mossbrucker et al., 2008: Fig. 4C herein), but here the specimen is a manus-pes set indicating quadrupedal progression. Additionally, the five trackways from the Tereñes Formation of Asturias in Spain, originally supposed of ornithopod origin by Piñuela et al. (2002), were referred to Stegopodus by Gierlinski and Sabath (2008). A track labelled cf. Stegopodus was also reported from Bathonian beds (Isli Formation by Charriere et al., 2009) near Tabanast in Morocco (Gierlinski et al., 2009). This African specimen represented by an illustrated replica (JuraPark J388, in Gierlinski et al., 2009, fig. 5) is potentially important as the only known trackway attributed to *Stegopodus*. This specimen also indicates a bipedal trackmaker.

A track with skin impressions from the Tidwell Member of the Morrison Formation in Garfield County near Bullfrog, Utah, previously interpreted by Lockley and Hunt (1995) as a small "sauropod pes track" was reinterpreted as "similar to the Asturian *Deltapodus* morphotype" by Lockley et al. (2008, p. 60: Fig. 4B₁ herein). The digit traces on the Garfield specimen (CU 194.1) are more irregular and pointed than the rounded digit traces seen in the San Juan County specimen, also a cast, described by Milan and Chiappe (2009, fig. 3), and the Grand County (Moab Giants) specimen (MGL1) described here (Fig. 4B₂). The reinterpretation by Lockley et al. (2008) was made on the basis of comparison of the Garfield County specimen with a relatively large sample of track casts from the Upper Jurassic Lastres Formation of Asturias, Spain (Lockley et al., 2008, fig. 11), some of which, which, like the track from Garfield County, show similar skin impression traces with a pattern of small polygons, which are clearly not sauropodan skin traces. A replica of this track (CU 194.1) is on display at Moab Giants under the label *Deltapodus*. Recent finds in the Upper Jurassic Lourinhã Formation of Portugal reveal *Deltapodus* pes tracks with similar skin trace patterns (Mateus et al., 2011, fig. 3).

Subsequently Milan and Chiappe (2009) identified the aforementioned San Juan County manus pes set as Deltaopdus brodericki, with the pes cast preserved as Los Angeles County Museum (LACM) specimen 7708/154065 (Fig. 4B₃). The poorly preserved manus cast (also Fig. $4B_3$) was not collected. In the pes track the toe traces are very short and wide without well-defined posterior margins, and the heel trace is long. Based on the comparison of the Garfield County specimen with Spanish Deltapodus, (Lockley et al., 2008) the San Juan County specimen (Milan and Chiappe, 2009) was not the first report of Deltapodus from the Morrison Formation, although it was clearly the first report referred to the ichnospecies D. brodericki, as acknowledged by Lockley et al. (2008, table 1). This species level identification was evidently made on the basis of similarity with the type from England (Whyte and Romano, 2001) which is not well-preserved, although admittedly morphologically similar to the D. brodericki type. Since 2009, Milàn et al. (2015), fig. 6) reported a poorly preserved pes cast labelled "possible thyreophoran track cf. Deltapodus" from the basal part of the Burro Canyon Formation in southeastern Utah. However, although the track bearing units are immediately overlying the Morrison Formation they are much younger, and according to Milàn et al. (2015) represent the Early Cretaceous (Barremian).

The *Deltapodus* pes track from Moab Giants illustrated and described here (Fig. 2) is arguably the best example currently known from the Morrison Formation. It is also most similar, both in size and morphology to tracks from the relatively large Late Jurassic (Oxfordian-Kimmeridgian) sample from Asturias, (Lockley et al., 2008) and the slightly younger Tithonian-Berriasian sample from Teruel Spain (Cobos et al., 2010). Comparisons with *Deltapodus* described from Early Cretaceous assemblages from Xinjiang Province, China (Xing et al., 2013) are particularly striking because these tracks show very prominent rounded pes toe traces in which the posterior margin is well-defined, thereby suggesting unguals that were morphologically separate from the fleshy part of the foot responsible for registering the large elongate and undifferentiated heel trace.

It is important to note that some of the differences between Stegopodus and Deltapodus, especially with regard to the length of the pes heel trace and the clarity of manus digit traces may be due to differential preservation. This problem was well-highlighted by Li et al. (2012) who showed that Shenmuichnus, representing a quadrupedal ornithischian, probably a thyreophoran, from the Triassic-Lower Jurassic transition in China, is quite like both Stegopodus and Moyenosauripus. Ichnogenus Shemuichnus shows well preserved manus digit traces and a tridactyl pes without heel traces when preserved as shallow tracks, but appears much more like Deltapodus, with long pes heel traces and indistinct crescentic manus, when preserved as deep tracks. The implications of these observations raise the question of whether differences between Stegopodus and Deltapodus reflect differences in trackmaker foot morphology, implying greater thyreophoran diversity, or variable preservation, which may indicate less diversity in trackmaker foot morphology.

Milan and Chiappe (2009) and Gierlinski and Sabath (2008) reviewed the distribution of purported stegosaur tracks around the time that Lockley et al. (2008) described several examples of *Deltapodus* from Spain. The pooled data summarized by Lockley et al. (2015) for the Morrison Formation clearly shows that saurischians (sauropods and theropods) make up more than 70% (~71.4%) of the reported trackways, with ornithischian tracks making up only about 11.5%. Of this latter proportion only 4 trackways of thyreophorans had been reliably reported, representing only 1.2% of the total of 311 recorded trackways through 2015. Given the scarcity of tracks that can be confidently assigned to Thyreophora, the finds add important data points to the overall census: i.e., increasing the sample to 6 reports representing 1.9% of the total of 313 trackways (Table 1).

The occurrence of stegosaur tracks from three members of the Morrison Formation in Utah reflects the stratigraphic distribution of the genus *Stegosaurus* from the lower Salt Wash Member up into the upper Brushy Basin Member (Turner and Peterson, 1999). Although southeastern Utah also contains members such as the Bluff and Westwater Canyon, these are to varying degrees lateral equivalents of the Tidwell and Salt Wash in most of the Colorado Plateau area of Utah farther north so that in the Moab area the only members are the Tidwell, Salt Wash, and Brushy Basin. Thus, the distribution of *Deltapodus* and *Stegopodus* both extends the confirmed record of stegosaurs into the Tidwell Member and mirrors that record in the overlying members.

Although *Stegosaurus* appears to be the most stratigraphically wideranging dinosaur genus in the Morrison Formation (Turner and Peterson, 1999), and although it is numerically (Mean Number of Individuals) among the five most abundant dinosaurs preserved in the formation (Foster, 2003; along with *Allosaurus* and the sauropods, *Camarasaurus*, *Apatosaurus*, and *Diplodocus*), it is surprising that stegosaur tracks are apparently so rarely preserved. Rare tracks of purported ankylosaurs in the Morrison reflect the relative scarcity of skeletal remains of these animals, but the same is not the case for stegosaurs. Relatively common skeletal remains but rare tracks suggest a possible dichotomy between paleoenvironmental preference and preservational modes for stegosaurs in the Morrison Formation. Such a pattern has had equivocal support based strictly on skeletal material (Dodson et al., 1980; Foster, 2003).

Since 2008–2009 when Deltapodus and Deltapodus-like tracks were first reported from the Morrison Formation in Utah, the global distribution of this ichnogenus has become better known. The most significant Upper Jurassic assemblages are found in Spain and Portugal, where a distinction can be made between occurrences in the Lastres and Lourinhã formations of pre-Tithonian age and the Jurassic-Cretaceous (Tithonian-Berriasian) assemblages described by Cobos et al. (2010). The Spanish tracks are represented by trackways and individual tracks of the type found in the samples from Portugal and Utah. Current evidence suggests that Deltapodus tracks from England and Morocco are older (Middle Jurassic) while Deltapodus from China is younger (Early Cretaceous). An isolated track from the Upper Cretaceous of India Mohabey (1986) was labelled as Deltapodus-like by Mateus et al. (2011), who note that this is potentially a very young occurrence, and would post-date the known age of any possible stegosaurian trackmakers.

Table 1

Summary of the number of identifiable trackways of main track types (top row) reported from 65 Morrison Formation localities (middle row) with corresponding % of total trackway count. Lower row shows frequency of occurrence of track types across all sites (with corresponding % occurrence). Modified after Foster and Lockley (2006, table 1) with updates. Percentages less than 1% omitted. Thyreoph., ptero., croc., ?lac., and misc. refer to thyreophoran, pterosaurian, crocodylian, ?lacertiform, and miscellaneous tracks respectively. Modified after Lockley et al. (2015).

Category	Theropod	Sauropod	Ornithopod	Thyreoph.	Ptero.	Croc.	Turtle	?lac.	Misc.	Total
Number trackways (%)	138 (44.4%)	84 (27.0%)	32 (10.3%)	6 (1.9%)	3 (1.0%)	4 (1.2%)	2	1	43 (13.8%)	313
Number sites (%)	34 (56.3%)	25 (39.1%)	8 (12.5%)	4 (6.2%)	3 (4.7%)	4 (6.2%)	2	1	5	65

In comparison with *Deltapodus*, ichnogenus *Stegopodus* is more problematic. A Middle Jurassic occurrence reported by Gierlinski et al. (2009) suggest a bipedal trackmaker. This interpretation is consistent with the interpretations of Gierlinski and Sabath (2008) for certain "bipedal" trackways from the Upper Jurassic (Kimmeridgian) of Asturias. However, this interpretation has recently been rejected by Piňuela et al. (2016) who attribute the trackways to ornithopods, as they did previously (Piñuela et al., 2002).

In summary, therefore, the interpretation that Deltapodus tracks represent quadrupedal stegosaurs, with elongate pes, is quite widely accepted, based on a significant sample of Middle Jurassic through Early Cretaceous trackways from around the world, broadly similar to the stratigraphic range of stegosaurian body fossils. This sample is made more coherent by the occurrence of similar skin traces patterns associated with Deltapodus from Spain, Portugal and the USA. However, the claim of bipedal stegosaurs is controversial and based on isolated pes casts from the Upper Jurassic of Utah, a single trackway from the Middle Jurassic of Morocco and controversial Upper Jurassic trackways from Spain that others have interpreted as ornithopodan. Moreover there is one manus pes set with the Stegopodus label (Mossbrucker et al., 2008), which indicates guadrupedal progression. The use of the label Stegopodus to differentiate this ichnogenus from Deltapodus is problematic, and there are no known skin traces that might provide diagnostic clues. Nevertheless, based on present definitions, the original description of Stegopodus based on pentadactyl manus (Lockley and Hunt, 1998) and possible associated, short wide (transverse) pes, reanalyzed by Gierlinski and Sabath (2008)) leaves the question of differences between Stegopodus and Deltapodus open for further study.

4. Conclusions

The fourth report of *Deltapodus* from the Morrison Formation, based on a pes cast from the new Moab Giants locality, Utah is also the most diagnostic report from the Upper Jurassic of southeastern Utah and from all of North America. It is also very similar to *Deltapodus* tracks reported from the Upper Jurassic of Spain, Portugal and the Lower Cretaceous of China. This report from the Moab Giants site is associated with a thyreophoran, *Stegopodus*-like manus from the same locality.

Together these two tracks make the fifth and sixth reports of thyreophoran tracks from the Morrison Formation. Given that an estimated 313 trackways are known from 65 tracksite in the Morrison Formation the number of convincing thyreophoran track reports is still very small (about 2%). *Deltapodus* is reported from Europe, Asia, North Africa and North America, from the Middle Jurassic through Early Cretaceous, where it is often represented by abundant trackways. However, *Stegopodus* despite ostensibly widespread geographic occurrence in North America, Europe and North Africa is limited to the Jurassic and mostly represented by isolated specimens. Claims that the *Stegopdus* trackmaker was often bipedal, i.e., a facultative biped, are intriguing and potentially provide evidence to differentiate it from the *Deltapodus* trackmaker(s). However, to date the bipedal stegosaur hypothesis remains controversial, with several workers.

The ichnotaxonomic differences between *Stegopodus* and *Deltapodus* are still somewhat ambiguous because in both cases the type material is based on small samples of sub-optimal material, rather than well-defined trackways. It is suggested that these ichnotaxonomic differences may be in part attributable to variable preservation.

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