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AN ASSEMBLAGE OF SMALL ORNITHOPOD TRACKWAYS FROM THE CRETACEOUS DAKOTA GROUP OF WESTERN COLORADO

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Abstract—An assemblage of more than 40 ornithopod tracks comprising at least 12 trackway segments has been discovered in the Little Park recreation area just south of Grand Junction. The longest trackway (T1) which represents the smallest individual, with a mean hind footprint length (FL) of ~14.4 cm, is smaller than any previously reported from the Cretaceous of the western USA. This trackway also unequivocally indicates quadrupedal progression, whereas other trackways of larger individuals (FL ~ 20.0-25.0 cm) mostly indicate bipedal progression. All are assigned to ichnogenus *Caririchnium*. Existing geologic maps show the site in an area covered by recent (Holocene-Pleistocene) colluvium. However, we can demonstrate that the site represents outcroppings of Cretaceous bedrock in the Burro Canyon-Dakota Formation (Aptian-Cenomanian) succession. The track assemblage most closely resembles those that are widely known from the Dakota Formation and includes fossil microbial mat structures. This report adds to the previous list of at least 128 tetrapod tracksites from the Dakota Group, and enhances the record in the Grand Valley region of western Colorado.

INTRODUCTION

Recent studies of dinosaur-dominated tracksites in the Cretaceous of western Colorado have focused on sites in the Delta region of western Colorado (Lockley et al., 2014a,b, 2015, 2016, 2018a,b; Noe et al., 2014). These studies focus almost exclusively on sites in the Dakota Sandstone Formation or "Dakota Group" alternatively referred to as the Naturita Formation (Young, 1960; Carpenter, 2014). Here we report on a recently discovered assemblage of ornithopod tracks preserved from Dakota Sandstone, in the Little Park area near Grand Junction in Western Colorado (Fig. 1). As discussed below, ornithopod tracks assigned to ichnogenus *Caririchnium* and representing both bipedal and quadrupedal progression are common in the Dakota Group, and other Cretaceous deposits. The site here designated as the Little Park Dinosaur Trackite (LPDT) was discovered by EE in 2017 and is in a much frequented recreation area. The aim of the study is to describe the tracks and to reconstruct their preservation and the paleoenvironment using lithological parameters.

GEOLOGICAL SETTING OF THE TRACKSITE

According to the Geologic Map of the Grand Junction area (Scott et al., 2002) the tracksite is situated in an area where extensive colluvial, Holocene to Pleistocene deposits cover Cretaceous Burro Canyon (Aptian and Albian) and Dakota Formation (?Albian-Cenomaninan) outcrops. However, *contra* Scott et al. (2002) the colluvial cover is not as extensive as originally inferred by these authors and the Cretaceous deposits are moderately well exposed. Following Young (1960), Carpenter (2014) calls the Dakota Formation, the Naturita Formation. This assignment is also based on arguments pertaining to the priority and duplication of names allowed by the North American Commission on Stratigraphic Nomenclature (NASC).

A section through the main track-bearing unit was measured (Fig. 2). The lower part of the measured section consists of ~2.5 meters of massively bedded conglomerate composed of limestone and sandstone pebbles up to 5 cm in diameter, and containing large lenses of sandstone. The conglomerates are overlain by moderately well-sorted, fine- to medium-grained thick bedded sandstone with small stringers of granules and small pebbles. This unit continues up through a partially covered section to the main track-bearing bed.

The track-bearing surface (Figs. 2-3) represents the top of a resistant tan colored sandstone bed about 15 cm thick that dips gently to the northeast at ~10°. Most of the surface reveals a tattered texture pointing towards an ancient microbial mat cover. In places the mat appears to have been disturbed by trackmaking activity (Fig. 4). Some of the track outlines are made more visible by a thin (~1.0 mm-thick), smooth, brown 'veneer' or 'rind' of iron-strained sediment that adheres to the track floors, but not to the entire surface of the bedding plane between tracks. Locally, the digit traces are filled by the friable white sandstone that overlies the track-bearing surface. The veneer is locally covered by a white caliche crust of recent origin. A few large roots ~3.0 cm in diameter follow, fill and help widen joints and fractures in the track-bearing surface (Fig. 2-3). The impermeability of the algal veneer on the track-bearing surface may have facilitated the recent precipitation of caliche on the surface and may also have led to the extreme friability of the overlying sandstone, possibly through the dissolution of cement.

Overlying the main track-bearing bed is a partially covered sequence of sandstones approximately 1.8 meters thick. The lower 40 cm is highly friable, crumbling in the hand. The upper 80 cm of the sandstone sequence contains three surfaces with large symmetric wave ripples with crest-crest-distance of ~7.0 cm and crest orientations striking between 20° and 35°. The uppermost surface which is extensively exposed but deeply weathered reveals a single presumed ornithopod track preserved in pedestal or convex epirelief. This unusual form of preservation may be the result of compaction caused by the trackmaker in a sedimentary layer now mostly eroded away. This occurrence is of limited importance in comparison with the main track-bearing surface which contains abundant tracks some of which comprise trackways yielding valuable morphological information

MATERIAL AND METHODS

The track-bearing layer that is the focus of this study represents the bedding surface described above. It has an area of 15 x ~2.0 m = 30 m^2 (Fig. 3). The elongate exposure has its long axis along a trail, frequented by pedestrians and mountain bikers. Given this traffic it is fortuitous that the surface appears

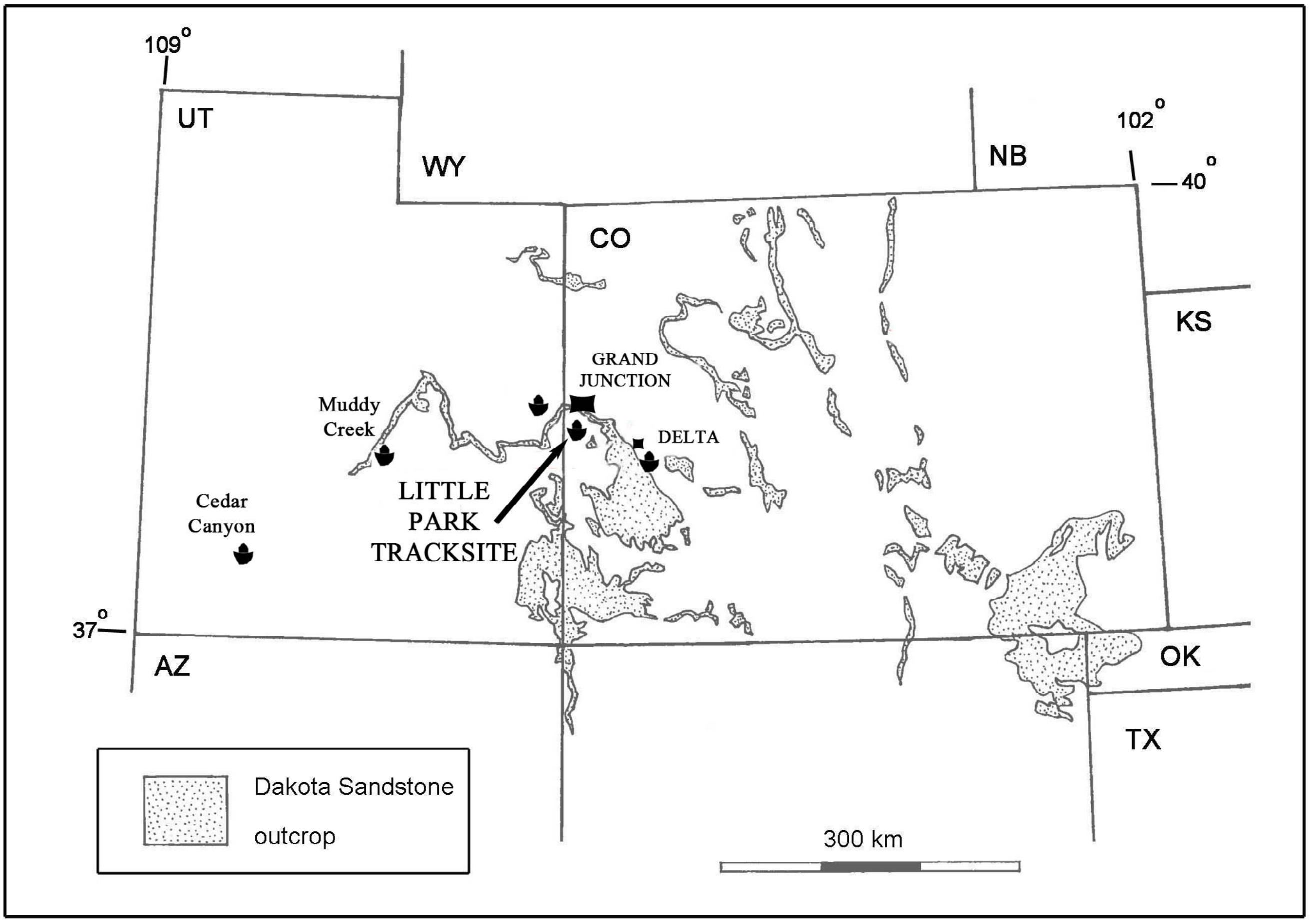

FIGURE 1. Locality map

relatively resistant to erosion and has become a naturally-exposed, gently-inclined ledge separating partially covered slopes representing less resistant lithologies (friable sandstone) above and below (Fig. 2). The aforementioned microbially induced veneer or rind, likely contributed to the resistance of the track-bearing layer, making it a distinctive paleosurface. Due to being a gently inclined sandstone unit sitting on mudstone there has been some separation or 'creep' of the surface manifest by the widening of the main joints which run NNE-SSW (Fig 3). However, most tracks are not cut by joints and it is possible to obtain accurate measurements, as noted below.

Photogrammetric documentation of the track surface was conducted in two episodes. The entire surface (2.75 x 14 meters) was photographed in June 2017 (E.E.) using a Nikon D80 Digital Single Lens Reflex (DSLR) camera equipped with a zoom lens fixed at 18mm. After the surface was cleaned of a thin layer of dirt and small stones, overlapping stereoscopic imagery was taken. Four sets of images (297 images total) were taken from both a nadir and high-oblique perspectives. The focus and aperture were fixed for each set, and additional imagery was taken in both landscape and portrait camera orientations to support a high-quality camera calibration (Matthews, 2008; Matthews and Breithaupt, 2011). The images were taken with the camera mounted on a tripod and in a hand-held mode at an average height 1.1 meters above the surface. This resulted in one image pixel representing 0.37 millimeters on the ground (or ground sample distance, GSD). In June of 2020, prior to permitted replication of a small portion of the track surface, an area of approximately 0.5 x 1 meter was photographed (E.E.). Two sets of stereoscopic images (44 images total) were taken from a nadir perspective at an average height of 0.57 meters above the surface resulting in a GSD of 0.12 millimeters per pixel. Photogrammetric process was conducted in AgiSoft Metashape Professional 64-bit version 1.6.2. Images from all episodes and heights were processed together (6 sets totaling 341) following the robust error reduction workflow described in Matthews, et al. (2016). Calibrated scale bars were utilized to provide real world units to the photogrammetric products. The resulting was a measurement confidence of 0.5 and 0.25 millimeters, respectively. Digital surface model, digital orthorectified image mosaic, and topographic contours maps were generated with respect to a leveled plain in order to optimize visualization of track depth and morphology. These products were used to aid in analysis of the track surface, only the contour map is presented here in (Fig. 3).

As many of the tracks lack significant relief and much of the surface shows a tattered texture, individual tracks are not readily apparent in the digital surface model. However, the 3D image of the track-bearing surface (Fig. 3) provides useful base map for mapping in the trackways. In this study, after outlining tracks in chalk, a map was made using traditional tracing methods: i.e., tracing a full-scale map on clear transparent plastic sheeting. This tracing was then remapped onto graph paper at a scale of 2 cm to 1.0 m.

Due to lack of clearly defined tracks towards the southern end of the exposure, the total mapped areas was only ~ 9.0 x 2.0 m (= 18 m^2): Fig. 3. Several trackways were identified and cataloged as T1, T2 etc., (Figs. 3-4). Two of the best preserved

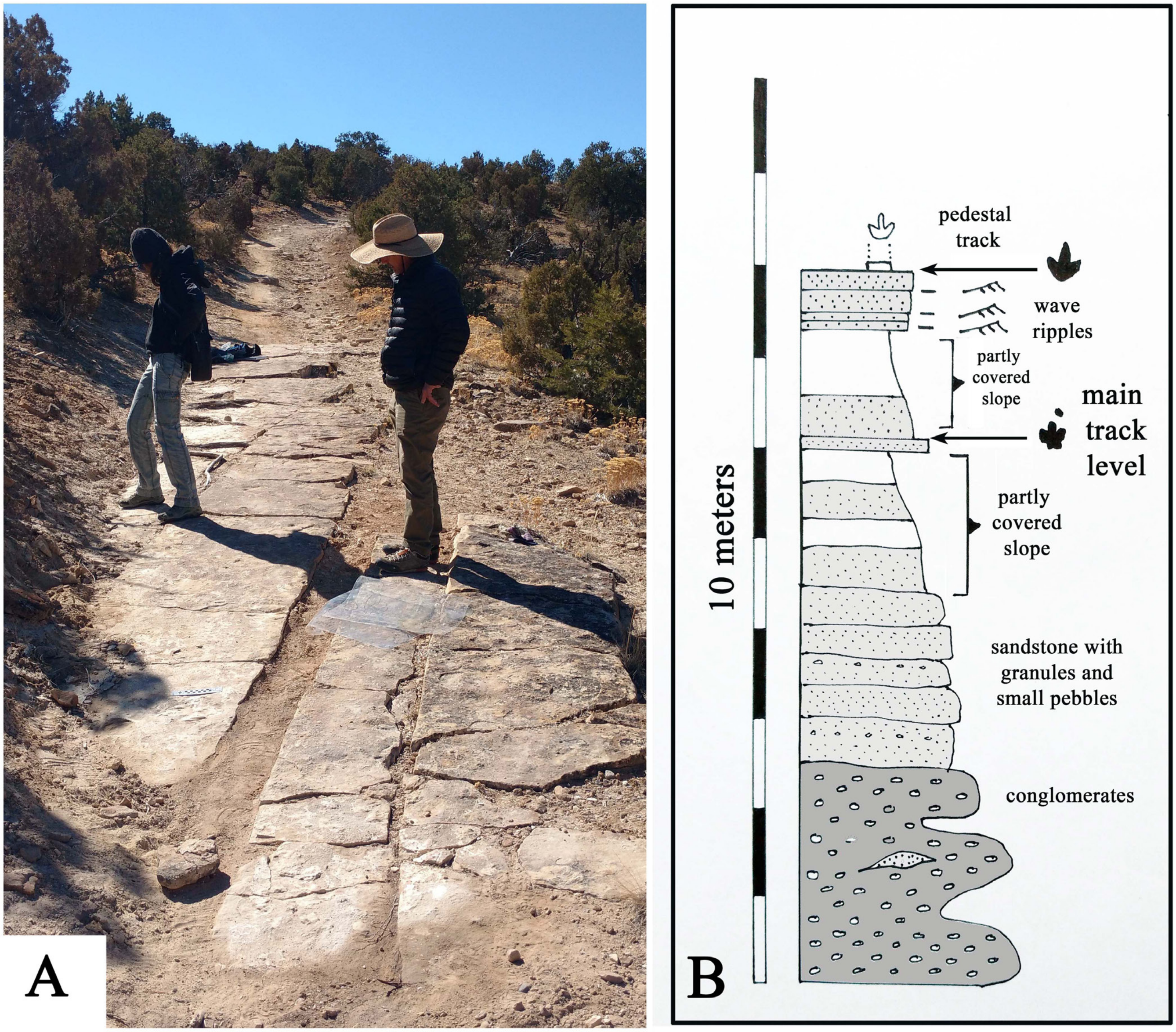

FIGURE 2**A**, View of main track-bearing surface looking south. **B**, stratigraphic section through the main track-bearing section.

manus pes sets in the longest trackway were selected for additional photogrammetric treatment prior to being molded with latex rubber. After removal of the latex, the mold was again subjected to photogrammetic treatment for comparison with the corresponding portion of the original surface. The photogrammetric images not used in this paper are on file with the Bureau of Land Management (Grand Junction Office and National Operations Center). The mold was used to make plaster replica cataloged as Museum of Western Colorado (MWC) specimen number MWC 9432 (Figs. 3 and 5). Measurements of standard morphometric parameters were obtained including length (L), width (W), L/W ratio, for both pes and manus; step, stride and pace angulation for pes (measured from mid point of pes); outer trackway width (OTW); and pes rotation measured as angle between digit III axis and trackway midline (Table 1).

DESCRIPTION OF TRACKS AND TRACKWAYS

Only four unambiguous trackway segments (T1-T3 and T8) were recognized in addition to several isolated tracks (T4-T7 and T9-T12) with clear outlines. All appear to be attributable to ornithopods and have yielded useful comparative measurements (Table 1). These identifiable tracks are in addition to poorly preserved tracks from which outlines and orientations could not be inferred. All of the tracks are relatively shallow and in some cases partially filled by thin veneers (probably microbial mat induced) and recently deposited caliche. The important features of the main trackways are described as follows.

Trackway T1

Trackway T1 is the most complete at the LPDT (Fig. 5A). It consists of a series of 13 manus-pes sets of which the first four (lmp1-rmp2), the sixth (rmp3), eleventh and twelfth (lmp6 + rmp6) are complete. Of the remaining six manus pes sets two (lmp5 + rmp5) are missing entirely and the other four are incomplete. The trackway orientation is slightly east of north (~340°). The trackway represents the smallest individual in the assemblage with a mean pes length and width of (14.43 and 13.93 cm respectively: L/W 1.03). The step and stride average 35.67 and 68.0 respectively, with a mean pace angulation of 162°. This high angulation value correlates with a low pes outer trackway width (OTW), only ~3.0 cm wider than the pes tracks, and a correspondingly narrow manus trackway width (within the

TABLE 1. Morphometric parameters obtained from trackways T1-T3 and T8 and isolated tracks T4-T7 and T9-T12 from the LPDT. Pace A = pace angulation. OTW = outer trackway width

TRACK ID	length	width	L/W	step	stride	pace A	rotation	OTW
T1 lp1	16.0	14.0	1.14				18º in	
T1 lm1	2.8	4.2	0.67				52º out	
T1 rp1	13.5	14.5	0.93	38.5	71.0	160º	45º in	18.0
T1 rm1	3.5	5.2	0.67				52º out	16.0
T1 lp2	14.0	13.0	1.08	33.5	68.0	164º	14º in	17.0
T1 lm2	3.0	3.9	0.77				98º out	12.5
T1 rp2	14.0	14.5	0.97	35.0			50º in	
T1 rm2	2.5	4.0	0.63				38º out	
T1 lp3	-	-			65.0			
T1 lm3	3.2	4.9	0.65					
T1 rp3	14.0	14.5	0.97					
T1 rm3	3.5	5.0	0.70					
T1 lp4	-	-						
T1 lm4	3.0	4.6	0.65					
T1 rp4	-	-						
T1 rm4	3.0	4.4	0.68					
T1 lp6	14.5	14.0	1.03					
T1 lm6	3.0	4.2	0.71					
T1 rp6	15.0	13.0	1.15					
T1 rm6	3.0	4.0	0.75					
T1 p means	**14.43**	**13.93**	**1.04**	**35.67**	**68.0**	**162º**	**31.75º**	**17.50**
T1 m means	**3.05**	**4.56**	**0.67**				**62º**	**14.25**
T2 rp1	21.5	19.0	1.13				10º	
T2 rm1								
T2 lp1	20.5	20.0	1.03	47.0	92.0		23º	
T2 lm1								
T2 rp2	24.0	20.5	1.17	48.0		145º	21º	32.0
T2 rm2								
T2 means	**22.0**	**19.83**	**1.11**	**47.5**	**68.0**	**145º**	**18º**	**32.0**
T3 lp1	21.5	19.0	1.13				0º	
T3 lm1	-	-	-					
T3 rp1	20.0	20.0	1.00	45.0	87.0	145º	15º	32.0
T3 rm1	5.5	7.5	0.73					
T3 lp1	20.0	20.0	1.00	46.0			3º	
T3 lm1								
T3 rp3	20.0	19.5	1.03					
T3 lp4	19.5	17.5	1.11	40.0				
T3 means	**20.2**	**19.2**	**1.05**	**43.67**	**87.0**		**6º**	
T4 isolated	25.5	21.0	1.21					
T5 isolated	21.0	17.2	1.22					
T6 isolated	23.0	21.0	1.10					
T7 isolated	23.0	20.0	1.15					
T8 trackway	20.0	19.0	1.05	47.5				
T9 isolated	20.0	20.5	0.98					
T10 isolated	20.0	20.0	1.00					
T 11 isolated	20.0	20.0	1.00					
T 12 isolated	21.0	21.0	1.00					

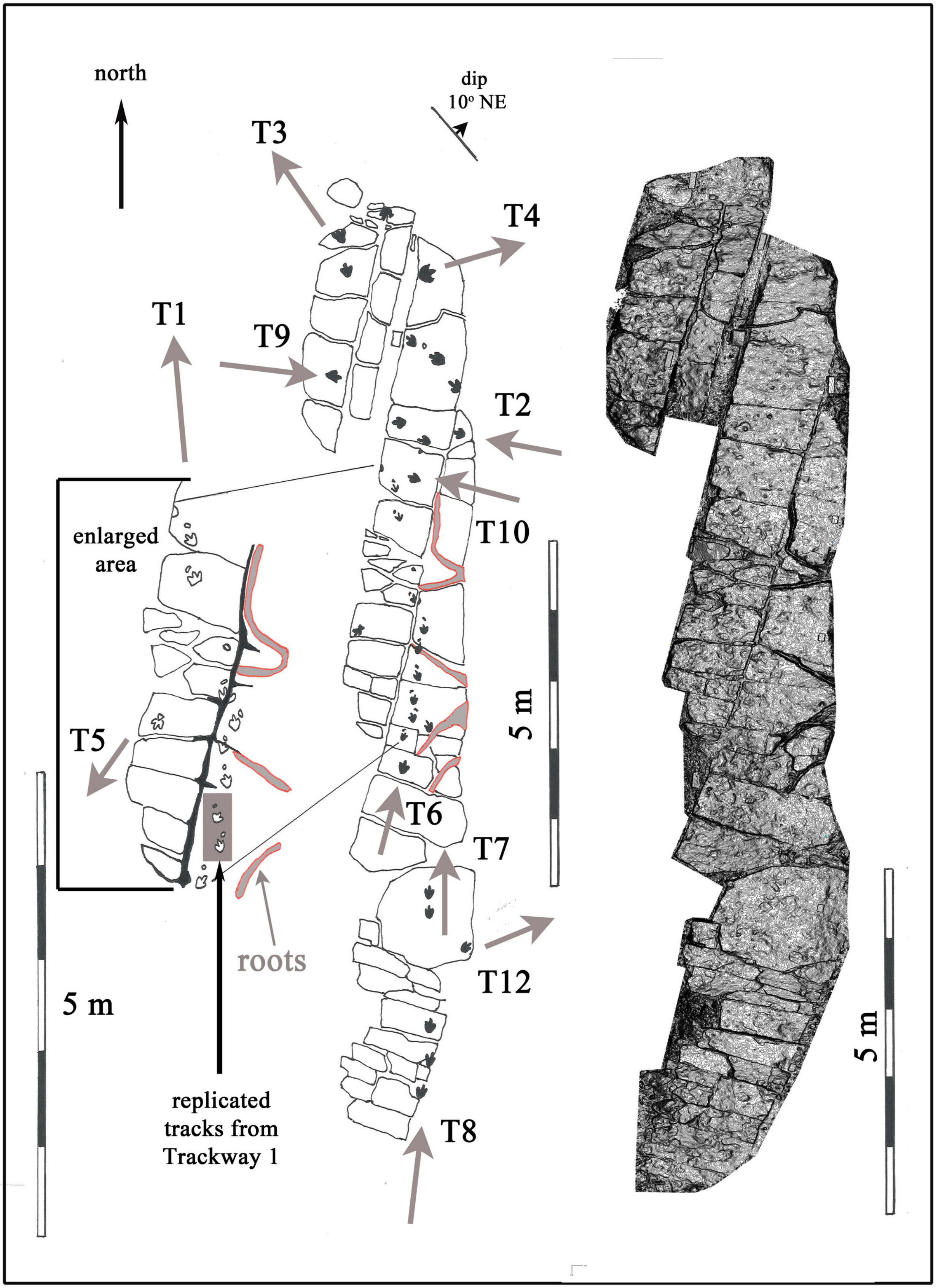

FIGURE 3. Map of the Little Park tracksite based on photogrammetric image (right) and full size plastic overlay (center): see text for details. All tracks and trackways are indicated by arrows T1-T12. Trackway T1, shown enlarged (left), is the only one indicating consistently quadrupedal progressions. Two consecutive manus-pes sets (rp1, rm1 and lp2, lm2) from T1 were molded and replicated as MWC 9432. Compare with Figures 4 and 5. See text for details.

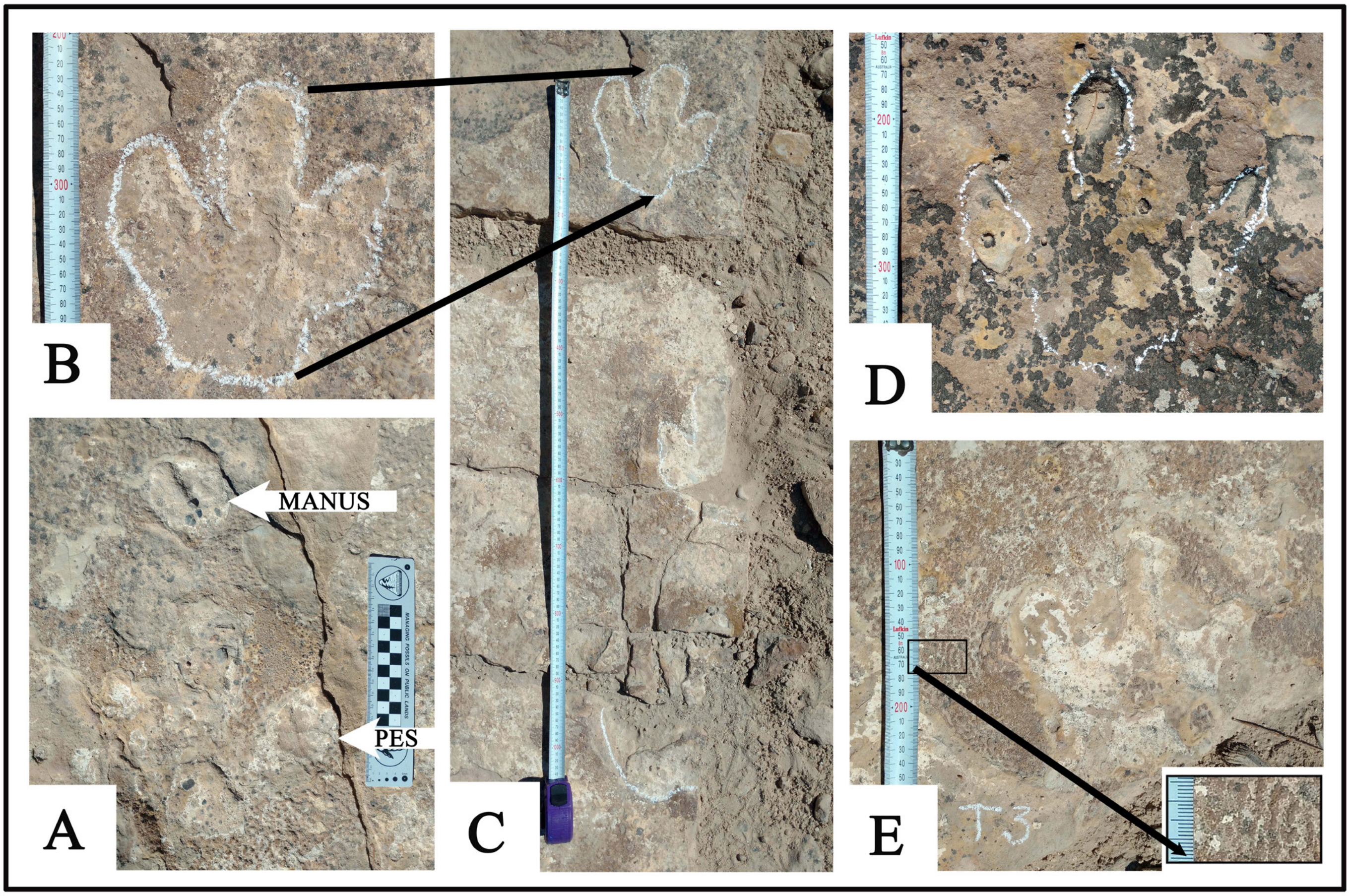

FIGURE 4**A**, manus pes set from trackway T1, compare with Fig. 5A. **B** and **C**, right pes track (B) from trackway T8 and source trackway (C). **D**, track T 9: **E**, left pes track from trackways T3: compare with Fig. 5C. Track shows pustulose mat texture. Individual pustules fuse to concentric ridges around left margin of track: see inset for details.

pes OTW). The manus tracks are oval in most cases and wider than long (4.56 and 3.05 cm respectively).

The pes tracks show high inward rotation (mean 31.75°) typical of ornithopods. In this trackway the proximal part of the sequence show a strong asymmetry with the left rotation averaging only 16° while the right averages 47.5°. The manus trackways are outwardly rotated an average of 60°: i.e., in the opposite direction to the pes, with the long axis rotated antero-laterally outward.

Trackway T2

Trackway T2 (Fig. 5B) consists of only three pes tracks (rp1, lp1 and rp2) with mean lengths widths and L/W of 22.0 cm, 19.83 cm, and 1.11 respectively. The step, stride and pace angulation are 47.5 cm. 92.0 cm and 145° respectively. Thus, the trackmaker was larger than the maker of T1 and the trackway is wider (OTW = 32.0 cm) with lower pace angulation. Inward pes rotation averages 18°.

Trackway T3

Trackway T3 (Fig. 4E and 5C) consists of five pes tracks (lp1, rp1, lp2 separated by a gap from rp3 and lp4) with mean lengths widths and L/W of 20.2 cm, 19.2 cm and 1.05 respectively. The step, stride and pace angulation are 45.5 cm. 87.0 cm, and 145° respectively. Thus, the trackmaker like the maker of T2 was larger than the maker of T1. The T3 trackway is also wider (OTW = 32.0 cm) with lower pace angulation. Inward pes rotation averages 6°. A single manus track appears to be associated with rp1.

Trackway T8

Trackway T8 is the only trackway other than T1-T3 that shows a recognizable sequence, in this case lp1-rp1-lp1. However, only track lp2 is complete yielding L,W and L/W values of 20.0, 19.0 cm and 1.05. The two consecutive step values are 45.0 cm and 50.0 cm.

Tracks T4-T6, T7 and T9-T12.

Tracks T4-T6, T7 and T9-T12 all have quite different orientations from the trackway segments T1-T3 and T8, and therefore can be inferred to represent different individuals. Track T4 (L, W, L/W : 25.5 cm, 21.0 cm L/W 1.21) is the largest, in the assemblage. Track T5 (L, W and L/W: 21.0cm 17.2 cm, 1.22) shows a distinctive quadripartite morphology with a triangular heel (Figs. 5C and 5E). Track 6 (L, W, L/W: 23.0 cm, 21.0 cm 1.10) and Track 7 (L,W, L/W 23.0, 20.0 1.15) are closest in size and proportion to tracks in trackways T2, T3 and T8, and isolated tracks T9-T12. Track T7 has another track 37 cm behind it, but it is not possible to determine if it belongs to the same trackway as T7: the preservation is too poor to obtain reliable measurements. Isolated Tracks T9-T12 are all very similar in size (Table 1).

DISCUSSION

Given the previous uncertainty surrounding the stratigraphic position of the track-bearing layer, implied by the aforementioned mapping of the Little Park area by Scott et al., (2002) it is important to attempt to determine which stratigraphic unit the tracks originate from: the Burro Canyon, (which correlates with the more extensively-distributed Cedar

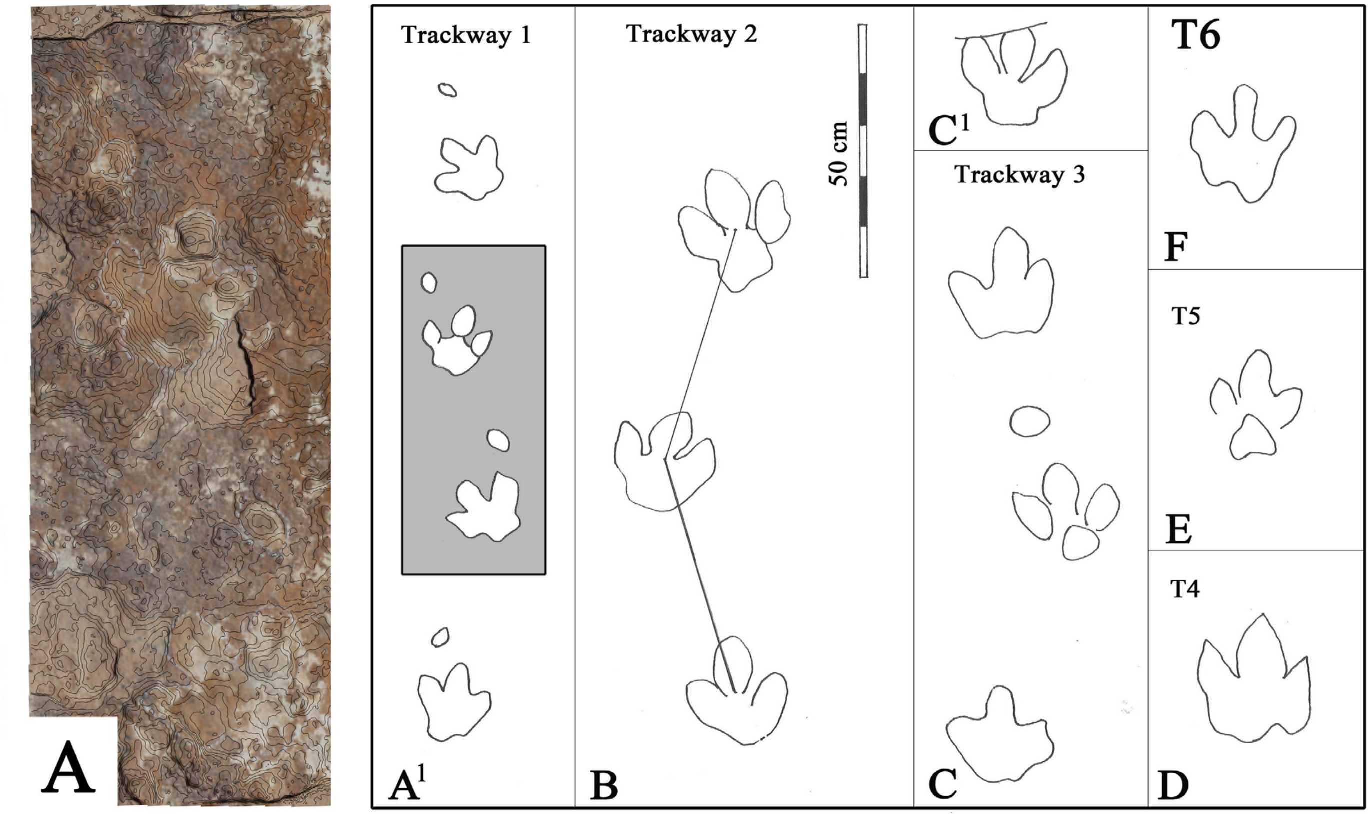

FIGURE 5. Photo and outline drawings of ornithopod trackways from the Little Park site. **A**, 3D photogrammetric image of two manus pes sets from trackway T1 that correspond to mold and replica MWC 9432. Note superimposed contours. A[1] Trackway T1 showing four manus pes sets and portion replicated as MWC 9432. **B-C**, Trackways T2-T3 respectively represent larger ornithopods compare with Figs. 3-4A. T2 (B) shows no recognizable manus, T3 (C) shows one manus associated with first right pes, and C[1] represents left pes 4: compare with Fig. 4E. **D-F**, represent isolated tracks designated as T4-T6 respectively. All drawn to same scale.

Mountain Formation of Utah) or the overlying Dakota / Naturita Formation. The tracks potentially assist in this determination, as ornithopod dominated track assemblages are common in the Dakota Group of the western slope (Lockley et al., 2014a,b; Lockley, 2018) but hitherto unknown in the Burro Canyon Formation. The lithostratigraphic evidence and corresponding paleoenvironmental indicators are also useful in indicating that the tracks belong to the Dakota Group. The presence of larger scale wave ripples and microbial mat structures indicate a marginal marine environment consistent with Dakota / Naturita Formation facies rather than the Burro Canyon Formation.

The presence of the fossil microbial mat points towards an episodic or periodic syndepositional exposure of the ancient surface. Two main generations of microbial mats can be distinguished (but more must be assumed). Several tracks include mat chips in the depressions of the dinosaur track (Fig. 6A). Interestingly, the chips appear to have been rotated so that the underside is facing upwards. The registration of the foot evidently caused the mat fragments to get briefly attached to the foot sole from where they dropped down again while the foot was lifted up. Moreover, the chips in Fig. 6A show a deformation on the left sides, perhaps a result of the dinosaur's foot motion while moving forward. Figure 6B is a modern example of three microbial mat chips deposited top-down and one top-up on the sedimentary surface. Some of the surface appears tattered (Fig. 6, D and E).

The presence of the fossil microbial mat together with microbial mat chips distributed at random on the surface sometimes forming individual heaps, this tattered appearance indicates a seasonal climate with mats decaying in seasons not conducive to their development. Once a mat is decaying, microbial mat fragments form that are being somewhat dislocated by wind or gentle currents (Noffke et al., 2019). Some mat chips that have been deposited top down at random on the surface show signs of regrowth. The tattered surface and accompanied mat chips and overflips resemble that of lower supratidal settings at Dinosaur Ridge (Dakota Sandstone), Noffke et al., 2019. At that location, microbially induced sedimentary structures (MISS) record similar paleoenvironmental conditions.

As reviewed by Lockley (2018), 54 named and 2 additional unnamed Dakota Group / Naturita tracksites have been identified on the "western slope" (total of 56 sites west of the present continental divide) in addition to 72 on the "eastern slope" (Lockley et al., 2006). The LPDT increases the western slope total to 57 sites, and the total of all Dakota sites to at least 129. Most of these sites are concentrated in the Delta area southwest of Grand Junction (Lockley et al., 2014a,b, 2015, 2016, 2018a,b; Noe et al., 2014) and it is only comparatively recently that sites have been documented to the west, for example in Utah near Westwater, Muddy Creek (Lockley et al, 2018) and Cedar Canyon (Lockley et al., 2018b), the only three significant Dakota Group sites west of the LPDT (Fig. 1) . All previous reports of Dakota Group sites near Grand Junction, i.e., in the Grand Valley (sensu Lockley et al., 2018c) have dealt with isolated tracks, mostly not found in situ. Thus, the LPDT is the first from the Grand Valley region to document a large number of in situ tracks, including several recognizable trackways, that add valuable information to larger database.

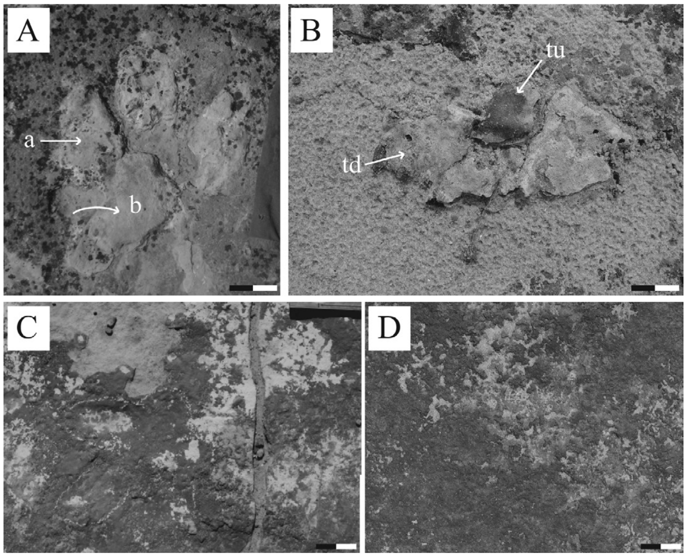

FIGURE 6. Fossil microbial mats and mat fragments in the outcrop and modern examples. A: Microbial mat chips in the depressions of right pes track in trackway T2. The arrow "a" points towards one chip. The chip indicated by arrow "b" was rotated to the right after being turned over. Scale 5 cm; B: Modern microbial mat chips on the lower supratidal flats of Portsmouth Island, Virginia, USA. "td" = top-down oriented microbial mat chips. The light color represents the sediment beneath the mat layer atop the chip; "tu" = top-up oriented mat chip. The dark color represents the actual mat layer atop the sediment. Scale: 2 cm. C: Fossil microbial mat in outcrop (dark). The microbial mat appears tattered and many cm and smaller sized mat chips are distributed at random on its surface. Scale: 5 cm; D: Similar microbial mat (dark) on the lower supratidal flats, Portsmouth Island, Virginia, USA. Photo take in fall 2004, when degradation of the microbial mat gives rise to its tattered appearance. Scale: 10 cm.

The present database for the western slope region (Lockley, 2018) indicates that ornithopod tracks (ichnogenus *Caririchnium*) are the second most common track types (16 of 54 sites), with ankylosaur tracks (*Tetrapodosaurus*) being the most abundant (21 of 54 sites). Thus, given that we identify the tracks as *Caririchnium*, the LPDT is typical of many Dakota / Naturita Formation sites, as well as Lower to 'mid' Cretaceous sites in other regions (Lockley et al., 2014c; Diaz-Martinez et al., 2015). In comparison, tetrapod tracksites are very rare in the Burro Canyon Formation and have been reported from only one site in Utah (Milàn et al. 2015), and none in Colorado. In fact, even when including the small number of known Cedar Mountain tracksites described in detail (Lockley et al, 2014d,e, 2015) they contain quite different ichnofaunas, most notably including sauropod tracks which are not known from the Dakota Group (*contra* Noffke et al., 2019), due to the sauropod hiatus at this time (Lucas and Hunt 1989; Mannion and Upchurch 2011, and references therein).

According to Matsukawa et al. (1999), a large sample of ornithopod tracks from the Dakota Group of eastern Colorado (N =283) range in foot length from 16.5 – 55.0 cm, and fall into three size classes: 16.5-21.7 cm, 21.7-29.3 cm and 29.3- 55.0 cm. Thus, the tracks in Trackway T1 from the LPDT are only 87% as long as the smallest reported in that study, or from any other any other subsequently reported Dakota Group site. A footprint length (FL) of 14.4 cm gives and estimated hip height (h) of 69.0 cm based on the h = 4.8 FL ratio proposed by Thulborn (1990) for small ornithopods. This was not a large animal.

Norman (1985) suggested "as a general guide, iguanodonts are medium sized herbivores, primarily bipedal though tending toward quadrupedality in larger forms" (Norman 1989, p. 58). It is generally known that "phylogenetically," most primitive ornithopods were bipedal, but without trackway evidence it is uncertain as to whether larger more derived forms were obligatory bipeds, facultative bipeds or obligatory quadrupeds: see Maidment and Barrett (2014) for arguments based on osteology. During the ontogeny of *Iguanodon* the fore limbs became longer (60% of hindlimb length versus 70% for adults: Norman 2004) giving rise to the inference that "it appears that *Iguanodon* became more quadrupedal as it got older and heavier. https://en.wikipedia.org/wiki/Iguanodon#cite_note-DBN04-28. This shift in locomotor posture that could be inferred to be broadly consistent with the phylogenetic tendency of small, primitive members of various dinosaur clades to be bipedal, whereas larger more derived members tend to be quadrupedal (Lockley 2007). For example, Hubner (2016) and Richter and Boehme (2016) reported that trackways of five small ornithischians (ornithopods) from the basal Cretaceous of Germany, plus three isolated tracks represent small bipeds: mean length and width of 13.1 cm and 10.9 cm respectively (mean L/W = 1.20) which is only 91% as long and 78% as long as wide as trackway T1. However, at this site the larger ornithopod tracks indicate quadrupedal progression (Richter and Bohme 2016). A similar situation is reported at the La Cerradicas site in Spain (Castenera et al., 2013).

However, the trackway evidence from the Dakota Group may suggest the opposite trend. First, trackway T1 from the LPDT challenges Norman's inference about ontogenetic differences in gait between bipedality among juveniles giving way to quadrupedality in larger forms. Second, dealing with the Dakota Group more generally Matsukawa et al (1999, p. 47) reached the conclusion that "the ratio of bipeds to quadrupeds gradually increases from juvenile to adult stages" and gave the proportions of bipeds/ quadrupeds as increasing from 6/23 to 35/ 26 to 26/11 in the three aforementioned increasing size groups (i.e., the % of quadrupeds decreased with trackmaker size from 21% to 57% to 70%, in what appears to be a clear trend). Recently discovered trackways of small ornithopods (*Caririchnium*) from broadly coeval Early to 'mid' Cretaceous deposits in Korea, (Lockley and Kim unpublished data) are even smaller than those from the LPDT, and also indicate quadrupedal progression. This indicates the need to reevaluate the relationship between size gait in the growing sample of ornithopod trackways from the Dakota Formation and the Cretaceous rock record more generally.

According to Matsukawa et al. (1999) the smaller tracks in the eastern slope Dakota Group sample (footprint length 16.5-21.7 cm) may represent a statistically distinct size cohort (N) with different growth rates from the larger tracks (21.7-55.0 cm) representing later cohorts (N +1, N +2 etc.). It is outside the scope of this study to consider the implications of ornithopod (*Caririchnium*) ontogeny based on a single trackway representing a trackmaker smaller than any other previously reported. However, a few observations are of interest. In comparison with Trackways T2 and T3 which represent larger trackmakers, the T1 trackway is narrower (pace angulation 162^{o} compared with 145^{o}). It is also noticeable that pes tracks rp1 and rp2 are more strongly inwardly rotated than the corresponding left footprints. It is possible that this above average inward rotation of right footprints in the proximal part of the trackway indicates an inclination to turn towards the left as suggested by the veering of the distal portion of the trackway (lp6, lm6 and rp6, rm6) to the left. Unfortunately, the pes tracks in the intermediate series (lp3-rp5) are either missing or too poorly preserved to provide useful rotation measurements.

CONCLUSIONS

The Little Park Dinosaur Tracksite (LPDT) is the most significant Dakota Group Dinosaur Tracksite known in the Grand Valley Region of western Colorado and adds to a significant inventory of tracksites in the greater western slope region. It occurs in an accessible recreation area that was previously mapped as mostly covered by colluvium (Scott et al., 2002). However, our studies reveal significant outcrops of the Dakota Group including the LPDT which includes a bedding plane outcrop of ~ 30m^2, with microbial mat structures that suggest a supratidal paleoenvironment. The surface reveals ~ 40 recognizable dinosaur tracks that all appear to be attributable to the ornithopod ichnogenus *Caririchnium*. The longest trackway represents a small individual progressing quadrupedally, and based on track site it represents the smallest ornithopod trackmaker known from the Dakota Group. In contrast, whereas the other tracks and trackway segments appear to represent larger individuals that progressed bipedally. Despite suggestions that small ornithopods were more likely to progress bipedally than large individuals, data from the Dakota Group appears to suggest the opposite trend.

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