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Didactyl raptor tracks from the Cretaceous, Plainview Sandstone at Dinosaur Ridge

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ABSTRACT

Two natural casts of two-toed (didactyl) tracks from the Cretaceous (Albian) Plainview Sandstone (Plainview Member) of the South Platte Formation (Dakota Group) at Dinosaur Ridge, Colorado are attributed to deinonychosaurian theropod dinosaurs and placed in the ichnogenus *Dromaeosauripus*. This is both the first report of tracks from this unit in the Dinosaur Ridge area and the first report of deinonychosaurian tracks from Colorado. It is also only the third report of this track type from North America. The rarity of tracks from the Albian-aged, Plainview Sandstone (Dakota Group Sequence 2) contrasts with their abundance in the upper (Cenomanian) part of the overlying South Platte Formation (Dakota Group Sequence 3), which has yielded more than 120 sites mostly in Colorado, giving rise to the "Dinosaur Freeway" concept. As no deinonychosaurid tracks are known from the sequence 3 part of the South Platte Formation, despite the large vertebrate and invertebrate ichnological database available, it is evident that the sparse vertebrate ichnofauna from the Plainview Member (Sequence 2) is inherently different. This striking difference in both track abundance and track type reflects differences in both age and depositional environment. Based on the Albian age, and track type, the Plainview tracks invite comparison with the ichnofaunas of the Cedar Mountain Formation and not with those well-known from the upper part of the South Platte Formation known as the Dinosaur Freeway.

1. Introduction

Recent studies of didactyl tracks attributed specifically to the deinonychosaurian (dromaeosaurid and troodontid) clade of theropod dinosaurs, have shown that such track occurrences have, until now, mostly been reported from east Asia. Until recently there have been very few North American deinonychosaurian track occurrences reported. Thus, the purpose of this paper is to describe a new discovery at Dinosaur Ridge, Colorado, an important locality, already well-known for an abundance of quite different track types. Moreover, the significance of the tracks is emphasized by their occurrence in stratigraphic unit, the Plainview Sandstone, which had not previously yielded any tetrapod tracks from this area.

As reviewed in detail by Lockley et al. (2016a), the first report of this track type was of small didactyl tracks, named *Velociraptorichnus sichuanensis*, from the Cretaceous of Sichuan Province, China (Zhen et al., 1994). A second ichnogenus, *Dromaeopodus*, based on much larger tracks from the Cretaceous of Shandong Province, China was named by Li et al. (2008) from a locality also yielding *Velociraptorichnus*, and a third ichnogenus, *Dromaeosauripus*, based on medium-sized tracks, was named on the basis of a trackway reported from Korea (Kim et al., 2008; Lockley et al., 2012). At least six additional examples of *Dromaeosauripus* (or *Dromaeosauripus*-like) and *Velociraptorichnus*-like tracks were reported from Asia between 2009 and the present: four from China (Xing et al., 2009, 2013a,b, 2015a,b, 2016a,b) and two from Korea (Kim et al., 2012). This record includes three additional deinonychosaurian track occurrences from the Cretaceous of Sichuan, one of which has traces of the distal portion of the claw-bearing digit II and is thus a rare example of a tridactyl morphotype of a *Velociraptorichnus*-like track (Xing et al., 2015a). Other isolated examples include a track from Yanqing, Beijing area, China (Xing et al., 2015b).

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In contrast to the abundance of deinonychosaurian track occurrences in Asia, comprising at least 11 localities (Table 1), occurrences in other regions such as North America and Europe have been rare. The first report, based on isolated, and ambiguously-preserved footprints from the Cedar Mountain Formation of Utah (Lockley et al., 2004) was later supported by the discovery of two well preserved trackways from the same formation (Cowan et al., 2010) named *Dromaeosauripus* (Lockley et al., 2014b,c), which constituted the first unequivocal evidence of dromaeosaurid trackways from North America. Likewise reports of deinonychosaurian trackways from Europe have also proved elusive. The best-preserved occurrence is from the Lower Cretaceous of Germany (Lubbe et al., 2009; Lockley et al., 2016a), the other, from the Upper Cretaceous of Poland (Gierlinski, 2007), involves material that is not well preserved, and has been partially lost due to site damage since it original discovery.

In summary, 11 of these 16 occurrences (~69%) are from China and Korea, all apparently from the Lower Cretaceous (Table 1). In comparison, the two previous North American reports as well as one of the European occurrences are also Early Cretaceous in age, with only the Polish occurrence being Late Cretaceous. Here we report a third North American occurrence, also Early Cretaceous in age, originating from Dinosaur Ridge, a well-known locality near Denver, Colorado.

Abbreviations: CU: University of Colorado Denver, Dinosaur Tracks Museum. UCM: University of Colorado Museum of Natural History, Boulder.

2. Geological setting

The Cretaceous sedimentary geology of Dinosaur Ridge is well-known and has been quite intensively studied since the late 1960s and early 1970s (Figs. 1 and 2). Most of these studies have divided the Dakota Group, also known as the Dakota Sandstone or South Platte Formation into a lower sandy unit, the Plainview Member (sensu Weimer and Land, 1972; Chamberlain, 1976a), a middle shaley unit, the Skull Creek Shale, and an upper unit, the Muddy Formation or “J” Formation (sensu Eicher, 1960; MacKenzie, 1963, 1965). Much of the early work, conducted in the heyday of paleoecological and paleoenvironmental facies analysis focused on interpretation of the depositional environments and invertebrate trace fossil assemblages in the upper part, (MacKenzie, 1968, 1971, 1972; Weimer and Land, 1972; Weimer et al., 1972; Chamberlain, 1976a,b,c, 1985). Subsequent studies shifted the focus to the footprints of dinosaurs and other tetrapods (Lockley, 1985, 1987, 2003; Lockley et al., 1992, 2010, 2014a; Lockley and Hunt, 1995) and helped to explain the extensive track-bearing units of the South Platte Formation in their sequence stratigraphic context: i.e., as the result of aggradation associated with transgressive system tracts deposited during the onset of sea level associated with the T6 transgression, or Sequence 3, of early Cenomanian age (sensu Kauffmann, 1977; Weimer, 1989; Lockley et al., 1992). However, the Plainview Member and the tracks described here predate the Skull Creek Shale interval which represents the T5 transgression of Albian age.

Two of the aforementioned studies (MacKenzie, 1972; Weimer and Land, 1972) presented measured sections for the roadcut sections along Alameda Parkway where it cuts the so-called Dakota Hogback. Today these outcrops are within the larger area formally named as Dinosaur Ridge, which also encloses one of the properties within the Morrison-Golden Fossil Area National Natural Landmark. Although these two studies used different stratigraphic numbering schemes, one from the bottom up (Weimer and Land, 1972) and the other from the top down (MacKenzie, 1972), see Fig. 2, it is relatively easy to identify individual bedded units in the field, and identify the trace fossil assemblages. In fact we can identify the level from which the tracks originate as unit # 9 (Weimer and Land, 1972, Plate 4e).

Previously the Plainview Sandstone, at Dinosaur Ridge and throughout most of the region, had yielded only a few invertebrate

Table 1
Summary data on 16 reported deinonychosaurian tracksites from the Cretaceous of Asia, North America, and Europe, with ichnotaxonomic designations, details of sample size, track size, quality of preservation, and sources of information. L = length; W = width. Note that two distinct morphotypes are known from the Junan County site in Shandong province. Modified after Lockley et al. (2016a).

Site	Ichnotaxon	# Tracks/trackways	L and W (cm)	Preservation	Reference(s)
Emei County, Sichuan, China	*Velociraptorichnus sichuanensis*	4/3	L ~10	Good, deep casts	Zhen et al. (1994)
Junan County, Shandong, China	*Dromaeopodus shandongensis* *Velociraptorichnus*	14/7	L 28.0 L 10	Excellent molds in type; others variable	Li et al. (2008)
Linshu County, Shandong, China	Dromaeosaurid track indet.	5/1	L ~19.0 W ~10.5	Fair, deep molds	Xing et al. (2013b)
Chicheng, Hebei, China	*Menglongipus sinensis*	4/1–2	L = 6.3 W = 4.3	Poor molds	Xing et al. (2009)
Gansu, China	*Dromaeosauripus yongjingensis*	71/7	L 14.8 W 6.4	Fair to good molds	Xing et al. (2013a)
Chu Island, Korea	*Dromaeosauripus hamanensis*	4/1	Mean L = 15.5	Fair, shallow molds	Kim et al. (2008) and Lockley et al. (2012)
Bito Island, Korea	*Dromaeosauripus jinjuensis*	12/1	Mean L = 9.3	Deep incomplete molds	Kim et al. (2012)
Arches National Park, Utah	Unnamed, probable deinonychosaurian	2/2	L ~28–?~35	Fair, very deep molds	Lockley et al. (2004)
Mill Canyon site, Utah	*Dromaeosauripus* isp.	4/1	L 21/	Good, shallow molds	Cowan et al. (2010)
Obernkirchen, Germany	Unnamed, probable troodontid	–/86	L = 13–23.3	Good molds	van der Lubbe et al. (2009, 2012)
Młynarka Mount, Poland	*Velociraptorichnus* isp.	3/1	L 17.0	Poor molds	Gierlinski (2007, 2008, 2009)
Mujiaowu, Sichuan, China	*Velociraptorichnus zhangi*	2/0		Good molds	Xing et al. (2015a)
	Velociraptorichnus isp.	3/1	L ~10.4 W 9.4 L 11.3	Good molds	
Yanqing, Beijing, China	? *Velociraptorichnus*	1/1	L 10.8 W 5.3	Good mold	Xing et al. (2015b)
Bajiu, Sichuan, China	cf. *Dromaeopodus*	2/2	L 17.4–24.8 W 5.9–14.5	Good mold	Xing et al. (2016b)
Shimiaogou, Sichuan, China	*Velociraptorichnus* isp.	5/1	L ~7.1 cm	Fair molds	Xing et al. (2016a)
Dinosaur Ridge, Colorado	*Dromaeosauripus* isp.	2/2	L ~16.0–17.0	Natural casts	This paper

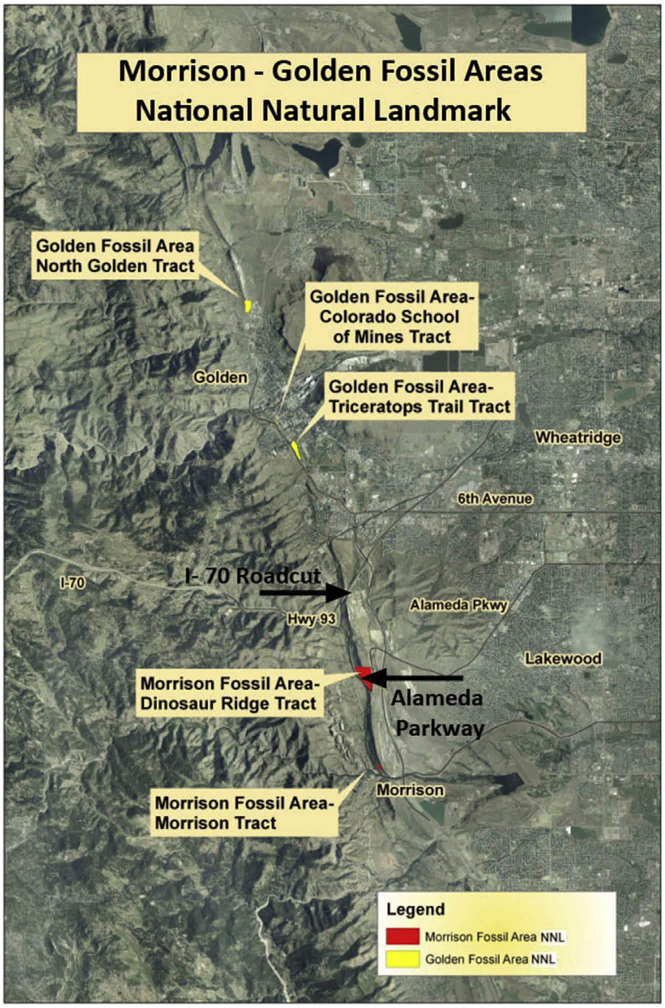

Fig. 1. Dromaeosaurid tracks occur in Dinosaur Ridge Tract of Morrison Fossil Area. Locality map modified after Lockley et al. (2015).

traces assigned to *Skolithus*, *Planolites* and *Trichichnus* (Chamberlain, 1976a) whereas the overlying units, especially the Muddy Sandstone, a much greater diversity of invertebrate traces, including at least 14 named ichnogenera. In addition, this unit has yielded at least six distinct vertebrate morphotypes including the ichnogenera *Magnoavipes*, *Caririchnium*, *Hatcherichnus* and *Ostenichnus* (Lockley et al., 2016b), nearby occurrences of the bird track *Ignotornis*, and unnamed turtle and pterosaur tracks. The abundance of tracks at this level has given rise to the concept of the Dinosaur Freeway, associated with aggradation during the initial phase of T6 transgression associated with Sequence 3 (Weimer, 1989). The dromaeosaur tracks described here come from the aforementioned T5 transgression phase of Sequence 2.

Here we describe the Plainview tracks as a first occurrence of *Dromaeosauripus* isp. from the entire Dakota Group. According to Chamberlain (1976a) they originate from the sequence containing, in ascending order, beds 9–13 of Weimer and Land (1972), or the equivalent beds 13–15 (in descending order) of MacKenzie (1972) which Chamberlain (1976a, p. 244–246) described as consisting of “light-gray, fine-grained sandstone with some shale partings” with trace fossils in the upper part which represent “two suspension feeders and a crawling or deposit feeding trace developed in a relatively slow transgressive facies” (Fig. 2). The detailed section provided by Weimer and Land (1972, pl. 1) shows the Plainview “member” as representing a change in facies from the fluvial floodplain deposits of the underlying Lytle Formation. Specifically they identified “swamp or marsh(?), splays (?)” in the lower units (9 and 10) of the Plainview and “tidal flat deposits” in the upper units (11–13).

3. Materials and methods

Due to the fragile nature of the tracks, preserved on the undersurface of an overhang it was deemed judicious to use non-invasive techniques to document the tracks. This objective was achieved by taking a series of overlapping photographs for 3-D photogrammetric analysis (Breithaupt et al., 2004; Matthews et al., 2006, 2016). The methods used were as follows: Image capture was conducted by MGL using a Canon PowerShot A1400. Overlapping photos were taken hand held, from a Nadir, upward facing orientation. Camera to subject distance was approximately 80 cm resulting in a ground resolution of 0.176 mm/pix. To accommodate lighting and access issues imposed by the overhang the camera was set to automatic and adjusted to the widest lens angle. While an overlap between photos of approximately 66% is optimal, overlap ranged from 60% to 80% due to the physicality of the surface. To accommodate camera calibration, crossing lines of photos taken at 90° and 270° to the main strips were also taken (see Matthews, 2008; Matthews and Breithaupt, 2011; Matthews et al., 2016).

Photogrammetric processing was conducted by NAM in Agisoft PhotoScan Professional Version 1.2 (www.agisoft.com). Photographs were imported into the software and a mathematical procedure known as aerotriangulation was conducted. This process derived initial camera calibration and triangulated an approximate geometric location for each camera by projecting vectors from conjugate groups of pixels algorithmically identified in the overlap of adjacent images. A camera calibration is necessary for the quantification and mathematical removal of distortions due to imperfections in the lens and misalignment of the lens to the sensor, common in all cameras. After initial alignment was complete a strategy of error detection, bad point removal, and optimization (aerotriangulation) was utilized and repeated until a reprojection error of 0.161 pix was reached. A sparse point cloud populated with thousands of x,y,z data points was generated during the alignment and optimization phase.

Real world units (meters) were assigned via scale bar and measuring tape. In order to reduce the observational bias due to orientation, or dip, of the surface and to facilitate the derivation of the most meaningful surface calculations, a plane was “fit” to the sparse point cloud. This best fit plane was used as a datum, or reference plane, for the purpose of generating the color depth maps and the topographic contours, and served to set up a user defined coordinate system within PhotoScan.

A dense surface model, consisting of millions of x,y,z coordinates, r,g,b color values derived from the original imagery, and surface normal values, was generated within PhotoScan. A triangular mesh was then created from the dense point cloud, the connectivity of the mesh and the image texture assigned to it was intelligently derived from the aligned images and are an inherent part of the photogrammetric process. Digital orthophotomosaics and digital elevation models (DEM) were also generated and exported as a 3D .ply file.

CloudCompare v. 2.6.2 (www.cloudcompare.org) an open source 3D point cloud and mesh processing software was used for analysis and visualization of the digital surface models and to generate color depth maps and topographic contours. Topographic contours were generated from the 3D point data by converting the points to a raster grid and interpolating topographic contours from the grid. Density of grid and contour interval was based on the

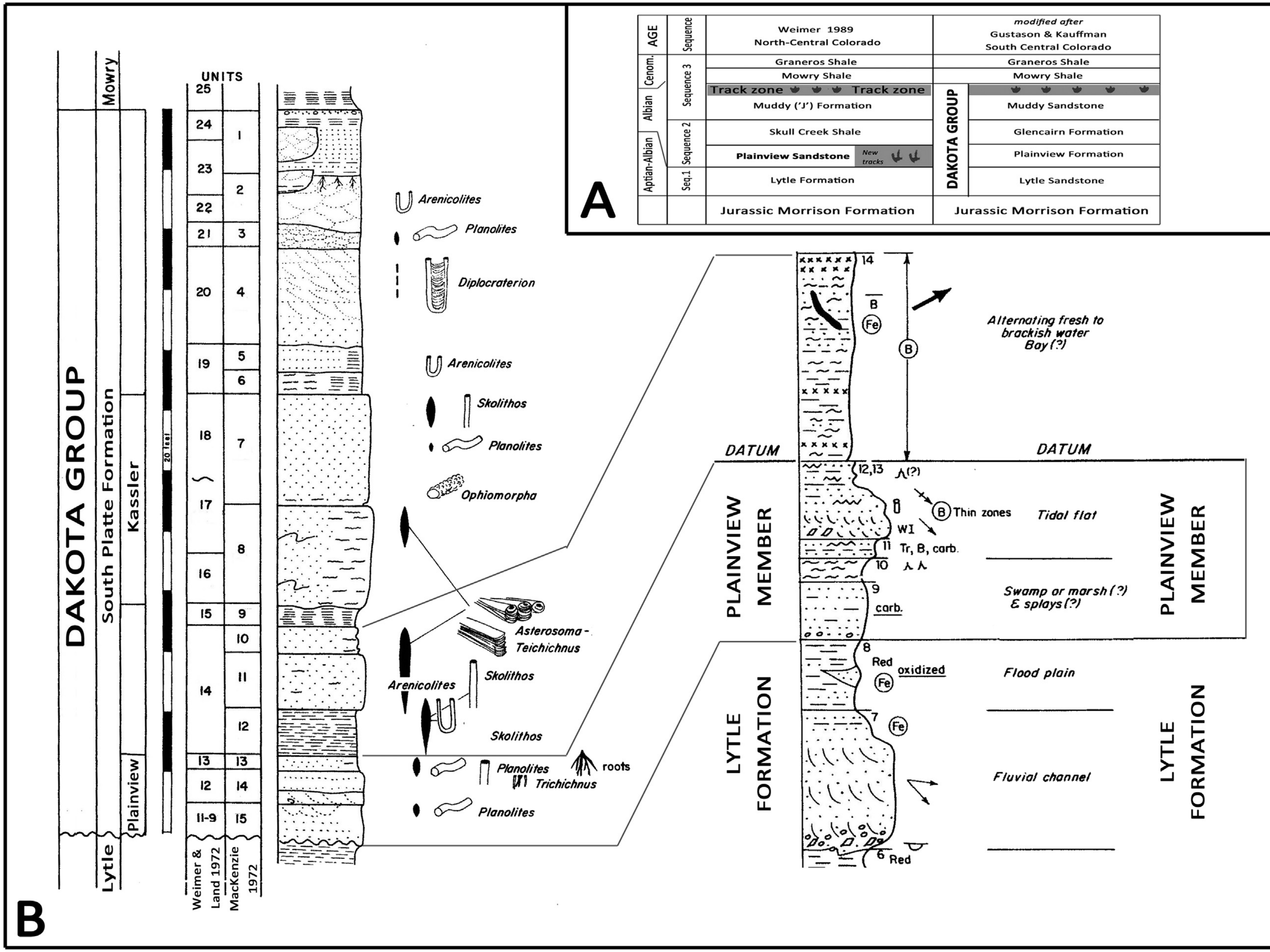

Fig. 2. Stratigraphy of Dakota Group at Dinosaur Ridge showing various formations and members referred to in text. A. Shows sequence stratigraphic framework and indicates that new tracks described here occur in the Albian, Plainview Member representing Sequence 2, whereas most tracks occur in the basal Cenomanian track zone known as the dinosaur Freeway. B. Shows details stratigraphy of Plainview Member: modified after Weimer and Land (1972) and other sources.

density of the point data in the digital terrain model. The resulting 3D models and orthoimage products constitute a digital recordation of the surface at the time of this investigation.

A tracing of the two tracks was obtained using clear acetate film, which was used as the basis of outline drawings of the tracks and then archived as UCM tracing T 1682. In order to obtain permanent replicas we used a soft foam product known as *Easy Tread*, obtainable in the form of slabs or bricks which can be pressed gently against a surface with relief in order to obtain impressions. These impressions were then cast in Plaster of Paris to obtain replicas of the original track cast, designated as specimen UCM 200.57 and UCM 200.58. After plaster is poured separating it from the cast causes the Easy Tread mold to disintegrate, leaving only the "hard copy" replica.

4. Description of tracks

Two tracks occur as natural casts on the underside of a sandstone bed that is heavily bioturbated with invertebrate traces (Fig. 3). Both tracks have similar orientations towards the west, and may belong to the same trackway, although this is unlikely. The best-preserved track is located to the west and is represented in the UCM collections by replica UCM 200.57 and full-size tracing T 1682. This track is a natural cast of a right footprint 17.2 cm long, 6.8 cm wide (L/W ratio = 2.53) and 1.4 cm in maximum depth. The digit III trace has the longest anterior projection (17.2 cm from heel to toe tip, or 10.0 cm excluding heel area) with slight convex-out curvature and pronounced tapering of the distal end. The digit IV trace is 14 cm long (from heel to toe tip, or 11.2 cm excluding heel area) also with slight convex-out curvature and pronounced tapering of the distal end: (thus, digit III/digit IV length ratio is 1.23). The posteriorly-convex, proximal ends of both digit traces form the widest points (about 2.0 cm), and are well-rounded into pads. The divarication between digits II and IV is only about 10°. The cast of the digit II trace is a rounded protruberance about 1.7 cm long and 1.3 cm wide, situated just posterior-medially to the posterior margin of the proximal pad on digit III (Figs. 3–5).

Fig. 3. Photograph of track-bearing surface, with black arrows indicating tracks UCM 200.57 (above), in a more westerly location, and UCM 200.58 (below) in a more easterly location.

The more easterly situated of the two natural casts also represents a right footprint (UCM 200.58). It is similar in size to the west-situated track (about 16.0 cm long and 9.5 cm wide: L/W = 1.68) with similar ratio of digits III IV heel to toe-tip length (16.0/14.0 cm = 1.14) but wider III–IV digit divarication of 20°. The trace of digit II (length and width of 2.8 and 2.2 cm, respectively) is slightly larger than in the west-situated track, and situated medial to the proximal pad of digit III which is well defined. As noted below, based on morphology, we attribute these tracks to *Dromaeosauripus* isp., representing the ichnogenus originally described by Kim et al. (2008) from Korea, which is currently the only confidently identified deinonychosaurian ichnotaxon in North America.

The relationship between the two track casts is equivocal. As both represent right footprints ~63.0 cm apart, they would only represent part of the some trackway if we infer a stride of ~63.0 cm and a step of 63/2 cm (about 31.5 cm) and a missing left footprint, presumably due to preservational factors. Alternatively assuming longer steps and strides typical of known dromaeosaurid tracks, it would be possible to infer that the two tracks represent different trackways. In the case of the western-most track, the distance between the anterior of the west-situated track and the edge of the outcrop (about 30 cm), is less than the distance one might predict between the toe of one track and the heel of the next: i.e., the next track would have to have been registered beyond the present outcrop surface. The distance between the anterior margin of the east-situated track and the edge of the outcrop is about 95 cm. This then is the minimum distance necessary between the toe of this track and the heel of the next, if the next track was not to register on the surface. This inference requires us to add another 16.0 cm for the length of the next track, implying a minimum step of 1.11 m. Alternatively, we could infer at least one missing track.

5. Comparative ichnology

To date all reported deinonychosaur tracks have been assigned to only four ichnogenera. In order of discovery these are *Velociraptorichnus* (Zhen et al., 1994) known from seven Chinese localities, and with less certainty from one Polish locality, *Dromaeopodus*, known from one Chinese locality (Li et al., 2008), *Dromaeosauripus* (Kim et al., 2008) known from two Korean and two north American localities, including Dinosaur Ridge and the least-known ichnogenus *Menglongpus* (Xing et al., 2009) known from only one Chinese locality.

Based on size and morphology the differences between these ichnogenera are as follows. Type *Velociraptorichnus*, as well as most other examples, is a very small (footprint length, FL, less than about 11–12 cm), in all cases except the Polish report. The ichnogenus generally has poorly defined digital pad traces and relatively straight digits. Likewise *Menglongpus*, which is poorly preserved is also small (FL 6.3 cm), with relatively straight digit traces. By contrast *Dromaeopodus* is large (FL 28.0 cm) with robust, curved (outwardly convex) traces of digits III and IV, and very well defined pads. *Dromaeosauripus*, including the Dinosaur Ridge specimen is intermediate in size (9.3–21.0 cm) with curved digital traces and relatively well defined pads on digits III and IV. The Dinosaur Ridge specimen belongs to a sample too small to warrant detailed

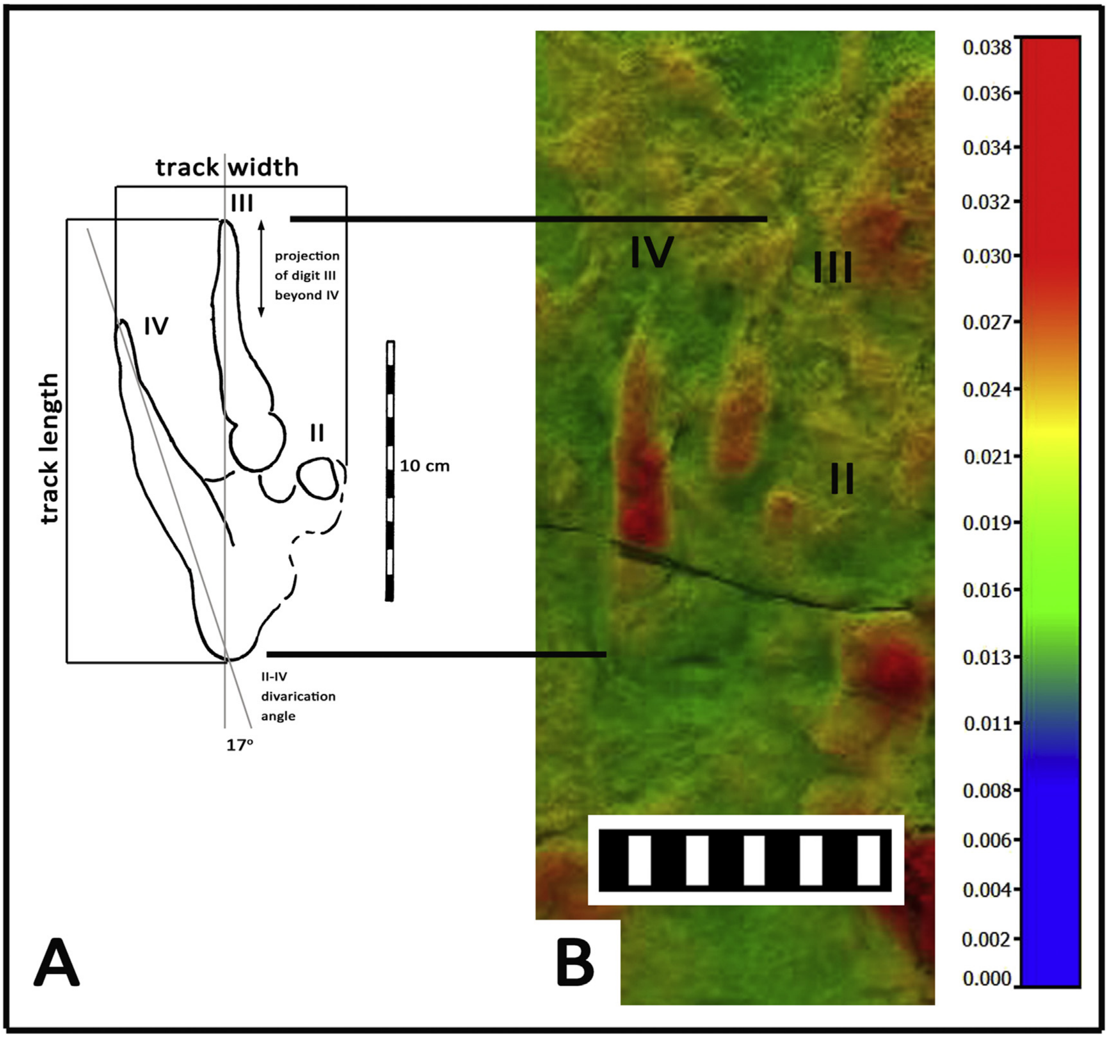

Fig. 4. A. Outline of UCM 200.57, showing length width and relative length of digits III and IV. Photogrammetric orthophoto images of *Dromaeosauripus* from Dinosaur Ridge Color depth map of trackway with relative depth legend in meters. Contour interval 1 mm.

systematic analysis or erection of a new ichnotaxon. For this reason we refer to it simply as *Dromaeosauripus* isp.

6. Discussion

The number of reports of deinonychosaur tracks grew from one in 1994, to 11 in 2014 and has now reached at least 16 (Table 1). It is notable that ~94% (15/16) occur in the Early Cretaceous. In the case of the Plainview occurrence of *Dromaeosauripus* from Dinosaur Ridge, the tracks occur in the basal, Albian part of the Dakota Group, which had previously yielded no tetrapod tracks, except at the Cañon City locality, described by Kurtz et al. (2001), 140 km south of Dinosaur Ridge. At this locality the track assemblage is also different from that found in the upper, Cenomanian age, part of the Dakota Group. The Dinosaur Ridge occurrence is not only significant as the first theropod (deinonychosaurian) track report from this unit, but it provides a striking contrast with the ichnological assemblage known from the overlying, mostly Lower Cenomanian units of the Dakota Group (Muddy or "J" Sandstones), which have yielded literally thousands of trackways of avian and non-avian theropods, ornithopods, ankylosaurs, pterosaurs, crocodylians and turtles from hundreds of localities along the so-called "Dinosaur Freeway" (Lockley et al., 1992, 2010, 2014a) without a single report of a deinonychosaurian track.

One simple explanation is that the dromaeosaur tracks were abundant in the Albian, but not in the Cenomanian, at least in North America. Two lines of evidence are consistent with this interpretation. First, tracks from the Cañon City locality, which are also of Albian age, are different from those that occur so abundantly in the younger Cenomanian aged track-bearing beds of the Muddy or "J" sandstones. Second the occurrence of dromaeosaur tracks (and skeletal remains) in a pre-Cenomanian member of the Cedar Mountain Formation of Eastern Utah (Lockley et al., 2014b,c), which lies stratigraphically below the Dakota Group, is consistent with the footprint occurrences in the older Dakota Group units on Dinosaur Ridge.

Alternatively it could be argued that the Plainview Member of the Dakota Group represents a different paleoenvironment from the Muddy Formation. In as much as the Plainview has sometimes been lumped in with the fluvial Lytle Formation (MacKenzie, 1972, fig. 1) this argument might be suggestive of a different depositional setting from the upper part of the Dakota Group (Muddy or "J" sandstones) representing more organic, wet, plant-rich, locally-coal-bearing coastal plain facies. However, in the case of the Plainview at Dinosaur Ridge, a coastal plain setting has also been

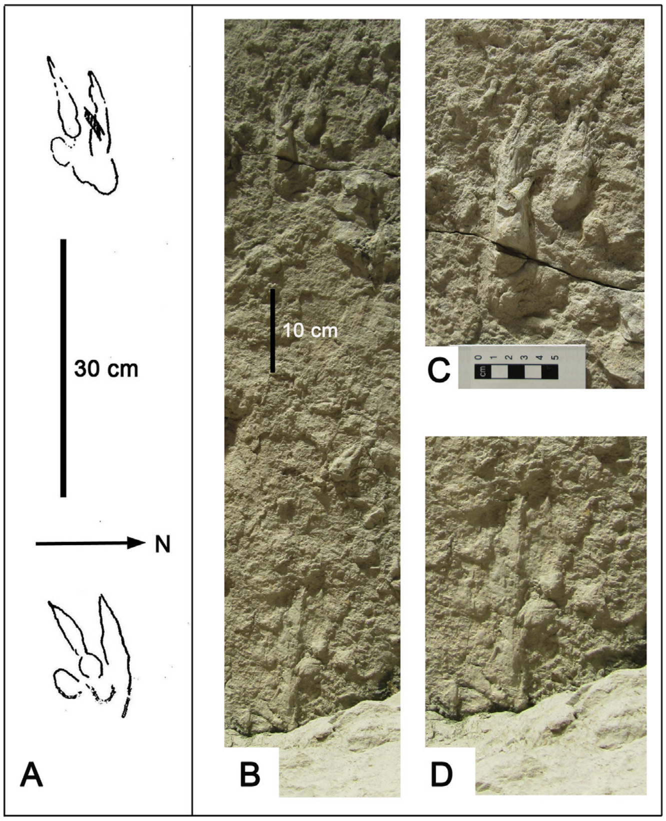

Fig. 5. Detail of tracks. A: Line drawing of tracks outline, reversed to show positive view of natural impression; same scale as B. B: View of natural casts, same scale as A. C: Detail of track on western sector of surface, represented in UCM collections as UCM 200. 57. D: Detail of track on eastern sector of surface represented in UCM collections as UCM 200. 58.

inferred, thus implying little pronounced difference in habitat between the *Dromaeosauripus*-bearing level, and the track-rich assemblages in the upper part of the Dakota Group, characterized as the Dinosaur Freeway. In fact, at both levels the tracks are preserved in aggrading deposits associated with early transgressive systems tracts (T5 and T6). Nevertheless, the majority of dromaeosaurid track occurrences are associated with fluvio-lacustrine, red bed inland depositional settings as typically found in China and Korea where the majority of sites occur.

It is not possible to choose unequivocally between the former interpretation based on age, or the latter based on paleoenvironment. Both factors may have influenced the distribution of dromaeosaurid trackmakers. Nevertheless the growing global sample is large enough to provide a small data set (Table 1) which allows questions of spatial, temporal and paleoenvironmental distribution to be explored. Traditional ichnocartography and ichnophotogrammetric methods together allow for the most thorough documentation of tracksites, such as this; and allows for enhanced visualizations of the surface to be created and high resolution (sub millimeter) ichnology data to be captured and utilized for current and future studies.

7. Conclusions

1) At least 16 well-documented occurrences of didactyl deinonychosaurian tracks have been reported globally since 1994, most since 2008. Of these 11 occur in China and Korea, two in Europe and three in North America.
2) With one exception, all occurrences have been dated as Early Cretaceous.
3) The tracks described here, from the well-known Dinosaur Ridge locality, in Colorado, are attributed to the ichnogenus *Dromaeosauripus*, and represent the first report from the track-rich Dakota Group. This group has been divided into a lower unit known as the Plainview Sandstone, and an upper unit known as the Muddy Sandstone. These represent deposition associated with the Albian-aged T5, or Sequence 2, transgressive cycle, and the Cenomanian aged, T6 or Sequence 3 transgression, respectively.
4) The difference between the ichnofaunas in these two sequences is striking. The T5 Plainview Sandstone has yielded only two sparse tetrapod track occurrences including the *Dromaeosauripus* assemblage described here, whereas the T6 Muddy Sandstone has yielded very abundant ichnofaunas, documented from more than 120 localities, none of which contain *Dromaeosauripus.*
5) The striking difference between the older *Dromaeosauripus* assemblage from the Plainview sandstone and the younger ichnofaunas abundantly distributed throughout Colorado, may be attributed to age, facies or a combination of both factors.
6) Globally most deinonychosaurian track occurrences are associated with fluvial, or fluvi-lacustrine facies, rather than coastal plain systems of the type represented in the Dakota Group of Colorado.

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