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Probable deinonychosaur tracks from the Upper Cretaceous Wapiti Formation (upper Campanian) of Alberta, Canada

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Abstract

Late Cretaceous tracks attributable to deinonychosaurs in North America are rare, with only one occurrence of *Menglongipus* from Alaska and two possible, but indeterminate, occurrences reported from Mexico. Here we describe the first probable deinonychosaur tracks from Canada: a possible trackway and one isolated track on a single horizon from the Upper Cretaceous Wapiti Formation (upper Campanian) near Grande Prairie in Alberta. The presence of a relatively short digit IV differentiates these from argued dromaeosaurid tracks, suggesting the trackmaker was more likely a troodontid. Other noted characteristics of the Wapiti specimens include a rounded heel margin, the absence of a digit II proximal pad impression, and a broad, elliptical digit III. Monodactyl tracks occur in association with the didactyl tracks, mirroring similar discoveries from the Early Cretaceous Epoch of China, providing additional support for their interpretation as deinonychosaurian traces. Although we refrain from assigning the new Wapiti specimens to any ichnotaxon because of their relatively poor undertrack preservation, this discovery is an important addition to the deinonychosaur track record; it helps to fill a poorly represented geographic and temporal window in their known distribution, and demonstrates the presence of a greater North American deinonychosaur ichnodiversity than has previously been recognized.

1. Introduction

Members of Deinonychosauria, here treated as the monophyletic grouping of Dromaeosauridae and Troodontidae (*sensu* Norell *et al.* 2001), were functionally didactyl theropods with a characteristic sickle-shaped claw on their second pedal digit that was raised off the ground during normal locomotion (Ostrom, 1969). Although forming a conspicuous component of many Late Jurassic – Late Cretaceous terrestrial ecosystems in Laurasia and Gondwana (Makovicky & Norell, 2004; Norell & Makovicky, 2004; Weishampel *et al.* 2004; Turner *et al.* 2012), their tracks were undescribed until 1994. However, the rate at which new deinonychosaur tracks were discovered increased exponentially in the years that followed. While a recent review in 2016 demonstrated the occurrence of deinonychosaur tracks from at least 16 localities (Lockley *et al.* 2016*a*, table 11.1), a plethora of ongoing discoveries, especially from China, has since increased the global track record of these dinosaurs to at least 26 localities (Table 1). The morphology of these prints is variable but generally they are didactyl (representing digits III and IV), sometimes with a rudimentary impression of a third digit (digit II) depending on the degree of retraction of digit II or the substrate conditions (Xing *et al.* 2015*a*). Certain monodactyl prints, which may occur in association with didactyl tracks, have also been attributed to deinonychosaurs (Xing *et al.* 2018*a*, *b*). Digits III and IV may be conjoined by the presence of a heel pad or divided into distinct, typically parallel toe marks with no 'heel' impression (Xing *et al.* 2015*a*, fig. 5). Digital pads are often visibly defined in well-preserved specimens. As deinonychosaurs are predominantly known from the Cretaceous Period (Makovicky & Norell, 2004; Norell & Makovicky, 2004), almost all convincing tracks attributed to these dinosaurs are Cretaceous in age; the only exceptions are a possible Middle Jurassic occurrence from Argentina (Casamiquela, 1964; De Valais, 2011; Xing *et al.* 2018*a*), and latest Jurassic or earliest Cretaceous occurrences from China (Xing *et al.* 2009*a*, 2015*b*, 2020; Table 1).

In 2018, the Boreal Alberta Dinosaur Project investigated a Late Cretaceous multi-taxic dinosaur-dominated tracksite along the Redwillow River in NW Alberta, Canada that preserves a didactyl footprint in possible trackway association with three monodactyl traces, as well as an additional isolated didactyl print located nearby on the same track layer. The purpose of this

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Table 1. Summary of reported deinonychosaur track occurrences, modified and expanded from Lockley *et al.* (2016*a*, table 11.1) and Xing *et al.* (2019, table 4).

Location	Formation	Age	Ichnotaxa	Reference(s)
North America				
El Aguaje, Michoacán, Mexico	Aguililla Sandstone	Late Cretaceous: Maastrichtian? (JA Ortíz-Mendieta, Dissertation, Universidad Nacional Autónoma de México, 2001; Ramírez-Velasco *et al.* 2014)	Dubious didactyl tracks	JA Ortíz-Mendieta, Dissertation, Universidad Nacional Autónoma de México (2001), Rodríguez-de la Rosa *et al.* (2004)
Denali National Park, Alaska, USA	lower Cantwell	Late Cretaceous: late Campanian–early Maastrichtian (Ridgway *et al.* 1997; Tomsich *et al.* 2014)	*Menglongipus*	Fiorillo *et al.* (2014)
Arches National Park, Utah, USA	Cedar Mountain (Ruby Ranch Member)	Early Cretaceous: late Aptian–Albian (Kirkland & Madsen, 2007)	*Dromaeosauripus*	White & Lockley (2002), Lockley *et al.* (2004)
Mill Canyon Dinosaur Tracksite, Utah, USA	Cedar Mountain (Ruby Ranch Member)	Early Cretaceous: late Aptian–Albian (Kirkland & Madsen, 2007)	*Dromaeosauripus*	Cowan *et al.* (2010), Lockley *et al.* (2014*a*, *b*)
Las Águilas tracksite, Coahuila, Mexico	Cerro del Pueblo	Late Cretaceous: late Campanian (Ramírez-Velasco *et al.* 2014; Vogt *et al.* 2015)	Dubious and/or unfigured didactyl tracks	Meyer *et al.* (2008), Rivera-Sylva *et al.* (2017)
Dinosaur Ridge, Colorado, USA	South Platte (Plainview Sandstone)	Early Cretaceous: Albian (Lockley *et al.* 2016*b*)	*Dromaeosauripus*	Lockley *et al.* (2016*b*)
Tyrants Aisle tracksite, Alberta, Canada	Wapiti (Unit 4)	Late Cretaceous: late Campanian (Fanti & Catuneanu, 2009)	Indet. probable troodontid	This paper
South America				
Estancia Laguna Manantiales, Santa Cruz Province, Argentina	La Matilde	Middle–earliest Late Jurassic: Aalenian–Oxfordian (De Valais, 2011)	Indet. possible deinonychosaur (*Sarmientichnus*)	Casamiquela, (1964), De Valais (2011), Xing *et al.* (2018*a*)
Toro Toro, Potosí Department, Bolivia	Toro Toro	Late Cretaceous: late Campanian (Apesteguía *et al.* 2011)	Indet. probable deinonychosaur	Apesteguía *et al.* (2011)
Europe				
Obernkirchen (‘Chicken yard’) tracksite, Lower Saxony, Germany	Bückeberg (Obernkirchen Sandstone)	Early Cretaceous: Berriasian–early Valanginian (Hornung *et al.* 2012)	Indet. troodontid	Van der Lubbe *et al.* (2009), Richter & Böhme (2016)
Mylnarka Mount, Poland	Not reported	Late Cretaceous: latest Campanian (Gierliński, 2015)	*Velociraptorichnus*	Gierliński (2007, 2009, 2015), Gierliński *et al.* (2008)
Asia				
Bajiu tracksite, Zhaojue County, Sichuan Province, China	Feitianshan (uppermost)	Early Cretaceous: Berriasian–Barremian (Tamai *et al.* 2004)	cf. *Dromaeopodus*	Xing *et al.* (2016*c*)
Chu Island, South Korea	Haman	Early Cretaceous: Albian (Kang & Paik, 2013; Paik *et al.* 2017)	*Dromaeosauripus hamanensis*	Kim *et al.* (2008)
Emei County, Sichuan Province, China	Jiaguan	Early Cretaceous: Barremian–Albian (HX Chen, M.Sc. thesis, Chengdu University of Technology, 2009)	*Velociraptorichnus sichuanensis*	Zhen *et al.* (1994)
Shimiaogou tracksite, Gulin County, Sichuan Province, China	Jiaguan	Early Cretaceous: Barremian–Albian (HX Chen, M.Sc. thesis, Chengdu University of Technology, 2009)	cf. *Velociraptorichnus*	Xing *et al.* (2016*b*)
Leibei tracksite, Gulin County, Sichuan Province, China	Jiaguan	Early Cretaceous: Barremian–Albian (HX Chen, M.Sc. thesis, Chengdu University of Technology, 2009)	cf. *Dromaeopodus*	Xing *et al.* (2016*a*)
Chabu 15B, Inner Mongolia, China	Jingchuan	Early Cretaceous: early Aptian (Li, 2017)	*Dromaeosauripus*	Wang *et al.* (2017)
Bito Island, South Korea	Jinju	Early Cretaceous: late Aptian–early Albian (Kang & Paik, 2013)	*Dromaeosauripus jinjuensis*	Kim *et al.* (2012)
Baodaoshili site IV, Shaanxi Province, China	Luohe	Early Cretaceous: Barremian (Xing *et al.* 2018*a*)	*Sarmientichnus*	Xing *et al.* (2018*a*)

(*Continued*)

Table 1. (*Continued*)

Location	Formation	Age	Ichnotaxa	Reference(s)
Junan County, Shandong Province, China	Tianjialou	Early Cretaceous: Barremian–Albian (Liu *et al.* 2003; Li *et al.* 2008; Xing *et al.* 2017*b*)	*Dromaeopodus shandongensis*; *Velociraptorichnus*	Li *et al.* (2008, 2015)
Jishan, Linshu County, Shandong Province, China	Tianjialou	Early Cretaceous: Barremian–Albian (Liu *et al.* 2003; Li *et al.* 2008; Xing *et al.* 2017*b*)	Indet. dromaeosaurid	Xing *et al.* (2013*b*)
Houmotuan tracksite, Shandong Province, China	Tianjialou	Early Cretaceous: Barremian–Albian (Liu *et al.* 2003; Li *et al.* 2008; Xing *et al.* 2017*b*)	cf. *Menglongipus*	Xing *et al.* (2018*b*)
Chicheng County, Hebei Province, China	Tuchengzi	Late Jurassic–Early Cretaceous: Kimmeridgian–Valanginian (Swisher *et al.* 2002; Zhang *et al.* 2009; Xing *et al.* 2009*a*; Xu *et al.* 2014; Xing *et al.* 2015*b*)	*Menglongipus sinensis*	Xing *et al.* (2009*a*)
Shicaogou tracksite, Yanqing County, Beijing, China	Tuchengzi (Third member)	Close to the Jurassic–Cretaceous boundary (Xing *et al.* 2015*b*)	*Velociraptorichnus*?	Xing *et al.* (2015*b*)
Madigou site, Chengde area, Hebei Province, China	Tuchengzi (Third member)	Close to the Jurassic–Cretaceous boundary (Xing *et al.* 2015*b*, 2020)	*Velociraptorichnus*	Xing *et al.* (2020)
Mujiaowu tracksite, Xide County, Sichuan Province, China	Xiaoba (First member)	Early Cretaceous: Barremian–Albian? (Tamai *et al.* 2004; Xing *et al.* 2015*a*, 2019)	*Velociraptorichnus zhangi*; *Velociraptorichnus*	Xing *et al.* (2015*a*)
Apuruha tracksite, Xide County, Sichuan Province, China	Xiaoba (First member)	Early Cretaceous: Barremian–Albian? (Tamai *et al.* 2004; Xing *et al.* 2015*a*, 2019)	cf. *Velociraptorichnus*	Xing *et al.* (2019)
Yanguoxia tracksite, Liujiaxia Dinosaur National Geopark, Yongjing County, Gansu Province, China	Yanguoxia	Early Cretaceous: Barremian–Aptian (Fujita *et al.* 2012), but see Du *et al.* 2018 for alternative age assignments	*Dromaeosauripus yongjingensis*	Xing *et al.* (2013*a*)
Yangmeikeng tracksite, Nanxiong County, Guangdong Province, China	Zhutian	Late Cretaceous: Maastrichtian (Xing *et al.* 2009*b*)	Uncertain large didactyl tracks	Xing *et al.* (2017*a*)

study is to document and identify these footprints, which contribute data to a poorly represented temporal and geographic interval in the deinonychosaurian track record.

2. Geological setting and age

The tracks described here occur at the Tyrants Aisle locality – a *c.* 1400 m^2, dinosaur-dominated tracksite – situated along the Redwillow River in NW Alberta, *c.* 65 km WSW of the city of Grande Prairie (Fig. 1). The site exposes rocks from lower Unit 4 of the Wapiti Formation, which is upper Campanian in age (Fanti & Catuneanu, 2009) and temporally equivalent to the Drumheller Member of the lower Horseshoe Canyon Formation in southern Alberta (Eberth & Braman, 2012; Eberth & Bell, 2014; Eberth & Kamo, 2019). More specifically, a bentonite layer exposed *c.* 16 km upstream and also within the lower part of Unit 4 yielded an Ar/Ar date of 72.58 ± 0.09 Ma (Bell *et al.* 2014). This bentonite layer is roughly coeval or slightly lower in section than Tyrants Aisle, but provides an approximate age for the locality. Unit 4 is a coal-rich deposit composed of overbank, crevasse splay, levee and channel-fill sediments (Fanti & Catuneanu, 2009) that were deposited at a palaeolatitude of *c.* 63° N (van Hinsbergen *et al.* 2015). In addition to the didactyl and monodactyl traces described here, other tracks at the Tyrants Aisle locality include those of hadrosaurids, and both large (track length > 40 cm) and small tridactyl theropods. These tracks will be described elsewhere within a broader synthesis of the palaeoecology of the site, although we provide comparative descriptions and discussion of some of these (such as the small tridactyl theropod tracks) that are pertinent for the interpretation of the didactyl tracks.

3. Methods

3.a. Photogrammetry

Tracks were photographed using a Nikon D810 SLR camera with 14–24 mm lens, set to 24 mm for all images. These images were imported into VisualSFM version 0.5.26 (http://www.cs.washington.edu/homes/ccwu/vsfm) to create sparse point cloud reconstructions of each track, before dense point cloud reconstructions were created using CMVS/PMVS (Furukawa & Ponce, 2010; Furukawa *et al.* 2010). Meshes were then cropped in MeshLab (version 2016.12; Cignoni *et al.* 2008) and Screened Poisson surface reconstructions of each were produced (Kazhdan & Hoppe, 2013). Digital elevation models of the Poisson meshes were created in CloudCompare version 2.9.1 (http://www.cloudcompare.org/), and final colour changes made in Paraview (version 5.5.2; Ahrens *et al.* 2005). In accordance with current protocol (Matthews *et al.* 2016; Falkingham *et al.* 2018), these digital elevation models were used to better support the track descriptions/interpretations and are

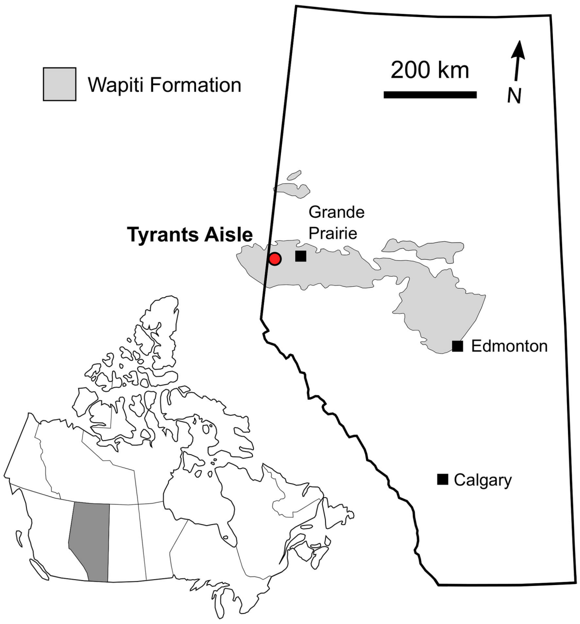

Fig. 1. (Colour online) Location of deinonychosaur tracks described here from the Tyrants Aisle locality in north-western Alberta. Scale as indicated. Grey shading represents the extent of the Wapiti Formation (after Fanti & Miyashita, 2009).

available for download in polygon file format (online Supplementary Figs S1–S7, available at http://journals.cambridge.org/geo).

3.b. Measurements

Track orientation and possible stride and pace lengths were measured on-site using a compass and tape measure, respectively. Track length, width and digit divarication were measured digitally in Inkscape version 0.92.3 (https://inkscape.org/) using screen captures of the digital elevation models to more accurately identify track contours.

3.c. Preservation assessment

Quality of track preservation was assessed using the grading system of Belvedere & Farlow (2016) and Marchetti *et al.* (2019), which allows preservation quality to be quantified and more clearly interpreted and expressed. Each system grades track quality from 0 through to 3, where 0 represents the poorest quality and 3 the highest (for specific grading criteria, see Belvedere & Farlow, 2016, table 6.1; Marchetti *et al.* 2019, table 1). These preservation quality designations influenced the track interpretations and trackmaker identifications expressed here.

4. Track descriptions

The possible trackway consists of an unusual series of four consecutive markings on the same bedding plane (Fig. 2a–h; online Supplementary Figs S1–S3). Each of the individual traces (here Di.Tw1.1.27D, Di.Tw1.2.27D, Di.Tw1.3.28D and Di.Tw1.4.29D) are eroded due to modern fluvial activity, although visible claw marks are still present on at least two of the four footprints. The first track in the sequence, Di.Tw1.1.27D (Fig. 2a–c, h, k; online Supplementary Fig. S1), is the only example from this sequence that is unequivocally didactyl (track length, 12.0 cm; track width, 6.9 cm; length/width ratio, 1.74). Two digit impressions are present, united by a shallowly impressed and rounded metatarsophalangeal area that is best visible when the track surface is wet (Fig. 2b). The left digit is shorter and shallower than the right digit and, following the interpretation that this track was produced by a deinonychosaur (see Section 5.d on ichnotaxonomic affinities), this suggests that the former is digit IV and the latter is digit III (i.e. the track was made by a left foot). Divarication between digits III and IV is 32°. The central portion of digit III is the most deeply impressed part of the track (Fig. 2c). Digit III is elliptical in overall shape and terminates in a small, sharp claw mark that is slightly medially in-turned. Digit IV is roughly two-thirds the length of digit III (length of digit IV/III measured from the heel base, 0.68) and terminates in a broad, subcircular impression that lacks any indication of a claw mark. No proximal pad of digit II is present. Overall, the general shape of the entire print remains visible (including distinguishable digit impressions), but because interphalangeal digital pad outlines, skin impressions and a claw mark on digit IV are absent, and the 'heel' area is particularly faint, a sub-optimal preservation grade of 1 is assigned to Di.Tw1.1.27D.

The second track in the sequence is a small ovoid depression, Di.Tw1.2.27D (length, 6.5 cm; width, 3.7 cm), located 0.36 m to the SW of Di.Tw1.1.27D (Fig. 2h, k; online Supplementary Fig. S1). This depression is widest towards the posterior end and tapers distally to a blunt termination, although any recognizable digit morphology, such as pad impressions or claw marks, is absent. Accordingly, a poorest preservation grade of 0*p* is assigned, where '*p*' indicates partial preservation (after Marchetti *et al.* 2019). The third trace, Di.Tw1.3.28D, is located 1.15 m west of Di.Tw1.1.27D and displays one clear digit impression and possible evidence of a second (Fig. 2d–e, h, k; online Supplementary Fig. S2). The largest digit, presumably digit III, consists of a teardrop-shaped impression (length, 8.0 cm; width, 3.0 cm), tapering distally, lacking any obvious digital pads, and terminating in a prominent, narrow claw mark. A possible short, narrow trace (length, 2.1 cm) near the base and to the left of digit III may represent evidence of an adjacent digit, although it is uncertain if this mark is actually part of the track, as it shows only a slight depth difference to the surrounding substrate from the digital elevation model (Fig. 2e). Based on the single digit III impression that is recognizable, which possesses a prominent claw mark, the preservation grade of Di.Tw1.3.28D is 0.5*p*.

The final trace within this sequence, Di.Tw1.4.29D (Fig. 2f–h, k; online Supplementary Fig. S3), consists of a tear-drop shaped (tapering proximally) monodactyl impression with rounded margins (length, 9.0 cm; width, 3.2 cm). A possible sharp claw mark is present at the distal end, although this could also be exaggerated by a fracture in the rock. A distance of 0.83 m separates Di.Tw1.3.28D and Di.Tw1.4.29D (Fig. 2h), the latter of which is oriented in a slightly different direction (axis offset from that of Di.Tw1.3.28D by *c.* 14°). A poorest preservation grade of 0*p* is assigned to Di.Tw1.4.29D, given that no clear digit morphology is present.

In addition to the possible trackway, at least one other isolated didactyl trace was identified. The additional track, Di.I.34E (track length, 13.0 cm; track width, 7.7 cm; length/width ratio, 1.69), is located on the same bedding plane *c.* 6.5 m to the SW of Di.Tw1.1.27D (Fig. 2i–k; online Supplementary Fig. S4). Both prints are oriented in the same direction (bearing of 252–254°). However, Di.I.34E is laterally offset from the possible trackway by *c.* 2.5 m and is therefore unlikely to have been produced by the same individual. Assuming that the trackmaker was a deinonychosaur (see Section 5.d on ichnotaxonomic affinities), Di.I.34E is a left foot based on the relative size difference between the two digit impressions. The proximal portion of digit III is narrower than at its mid-length, with a rounded proximal margin that is deeper than the impression of the 'heel' area (Fig. 2i–j). Distally, digit III tapers to a sharp point. Digit IV

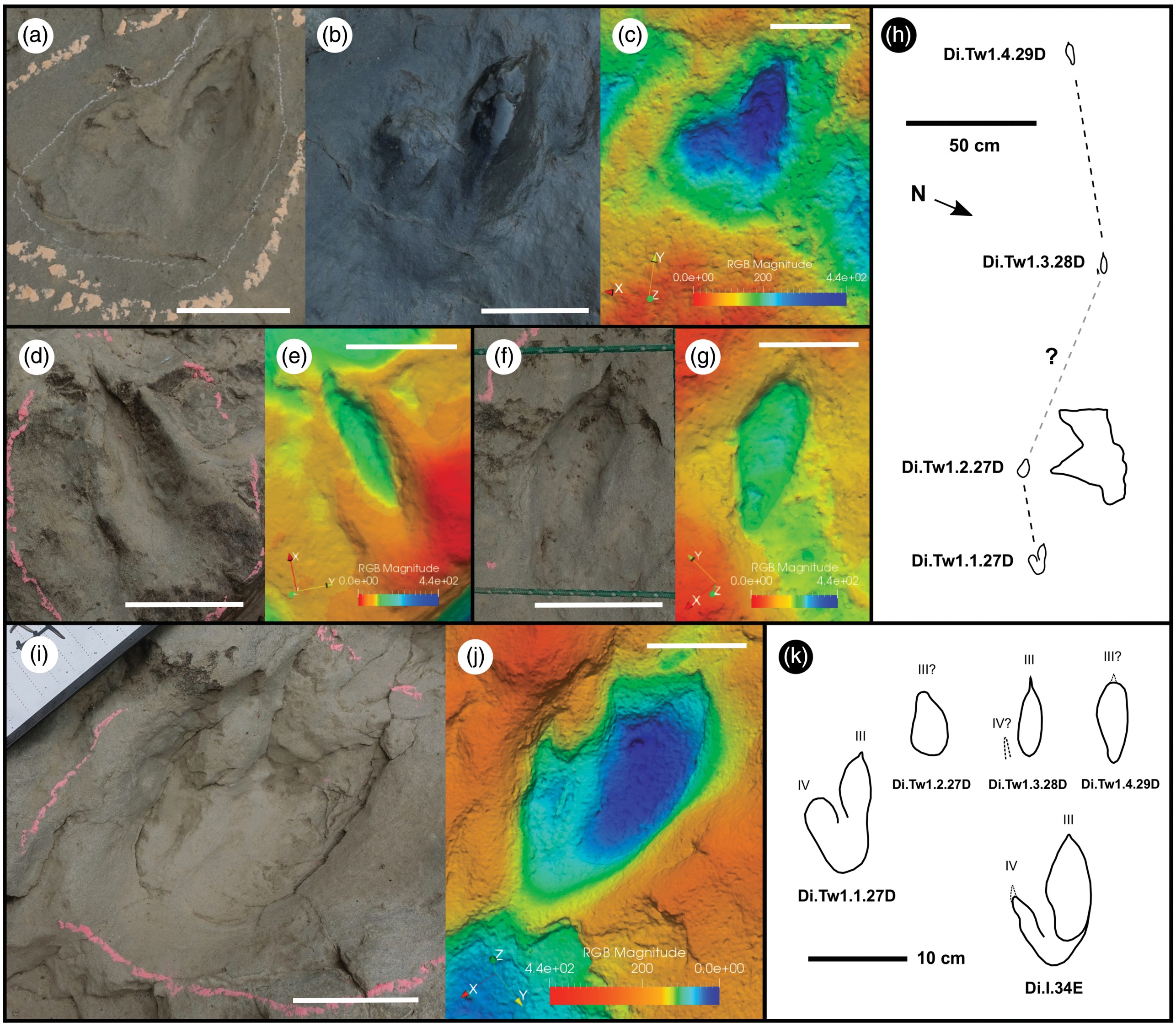

Fig. 2. Photographs, digital elevation models and interpretive line drawings of probable deinonychosaur tracks. Di.Tw1.1.27D photographs of (a) dry surface, (b) wet surface and (c) digital elevation model; Di.Tw1.3.28D (d) photograph and (e) digital elevation model; Di.Tw1.4.29D (f) photograph and (g) digital elevation model; (h) map of traces Di.Tw1.1.27D, Di.Tw1.2.27D, Di.Tw1.3.28D, Di.Tw1.4.29D and the tridactyl theropod undertrack Th.Tw3.1.27D, with inferred trackway associations as dashed lines (black – likely association; grey – tentative association); and Di.I.34E (i) photograph and (j) digital elevation model; (k) interpretive line drawings of specimens, scale as indicated. Scale bars for (a–g) and (i–j): 5 cm. Relative depth is indicated in the digital elevation models using colours, where cool colours represent topographic lows and warm colours are topographic highs. Three-dimensional meshes used to create the digital elevation models are available as online Supplementary Figures S1–S4.

is arcuate and, in comparison to digit III, much shorter (length of digit IV/III, 0.68–0.6, depending on whether a possible claw mark on digit IV is included), narrower (width of III, 4.5 cm; width of IV, 1.8 cm) and more shallowly impressed (Fig. 2j). Divarication of digits III–IV is 35–38°, dependent on the termination point of digit IV that is used. Interphalanageal pads (aside from the proximal-most part of digit III) are not visible on digits III or IV and there is no indication of digit II. As in Di.Tw1.1.27D, a raised ridge of sediment separates the impression of digit III from IV. The heel is rounded and deeply impressed into the substrate. A fair preservation grade of 1.5 is assigned to Di.I.34E, as the overall track shape is clearly discernible, claw marks are present and at least one interphalangeal pad outline (i.e. at the base of digit III) is visible. When comparing the morphology of Di.Tw1.1.27D and Di.I.34E, they differ in the shape of digit IV; digit IV is rounded in the former, but more narrow and arcuate in the latter. Similarly, the hypex between digits III and IV is located more anteriorly in Di.Tw1.1.27D. Both tracks nevertheless have a broad, robust digit III that terminates in a claw mark, a relatively short digit IV compared to digit III and rounded heel margins, and they are similar in overall track size (Table 2).

5. Discussion

5.a. Track preservation

Preservation level directly influences the accuracy, reliability and amount of anatomical data that can be obtained from tracks (Belvedere & Farlow, 2016; Marchetti *et al.* 2019). There is considerable preservation variation at the Tyrants Aisle locality, with tracks ranging from clearly impressed with well-defined track margins and interphalangeal pads, through to highly eroded depressions representing former footprints, with no recognizable foot morphology

Table 2. Track and trackway measurements for prints described here. L – left foot; R – right foot; III – digit III; IV – digit IV. Preservation grade based on Belvedere & Farlow (2016) and Marchetti *et al.* (2019).

Track	Left/ right	Length (cm)	Width (cm)	Length: width ratio	Divarication of digit III, IV	IV length/ III length	Axis bearing	Pace length (m)	Stride length (m)	Preservation grade
Di.Tw1.1.27D	L	12.0	6.9	1.74	32°	0.68	252°	–	–	1
Di.Tw1.2.27D	R?	6.5 (digit III only)	3.7 (digit III only)	–	–	–	260°	0.36 from Di.Tw1.1.27D	–	0*p*
Di.Tw1.3.28D	L?	8.0 (digit III only)	3.0 (digit III only)	–	–	–	268°	–	0.85 from Di.Tw1.2.27D (possible stride?)	0.5*p*
Di.Tw1.4.29D	R?	9.0 (digit III only)	3.2 (digit III only)	–	–	–	254°	0.83 from Di.Tw1.3.28D (pace or stride?)	0.83 from Di.Tw1.3.28D (pace or stride?)	0*p*
Di.I.34E	L	13.0	7.7	1.69	35–38°	0.6–0.68	254°	–	–	1.5

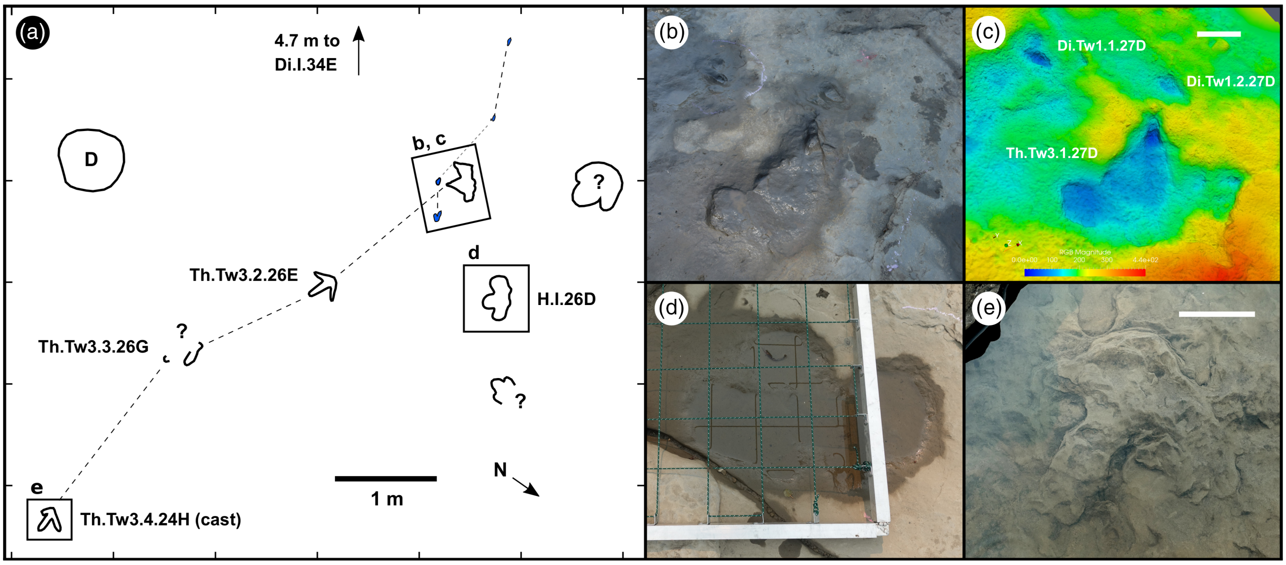

Fig. 3. (Colour online) Tracks surrounding the possible didactyl trackway (in blue). (a) Outline map redrawn from field sketches. D – depression, question marks (?) – uncertain traces, probable trackway associations – black, long-dashed lines; less certain trackway associations – grey, short-dashed lines. Scale as indicated. (b) Photograph and (c) digital elevation model of theropod undertrack Th.Tw3.1.27D alongside didactyl traces Di.Tw1.1.27D and Di.Tw1.2.27D. Scale bar: 10 cm. (d) Photograph of hadrosaurid undertrack H.I.26D, which is naturally filled with water. Each grid square internal division represents 10 cm^2. (e) Photograph of theropod track Th.Tw3.4.24H, preserved as an *in situ* natural cast. Image contrast, saturation and brightness have been adjusted for improved underwater visibility. Scale bar: 10 cm.

remaining. This variation is almost certainly related to the uneven topography of the site and its position within an active riverbed, as the track-bearing layers are generally within the flow of the Redwillow River for much of the year. The most relevant portion of the tracksite for this work (i.e. the immediate area surrounding the described traces) demonstrates only a moderate level of track preservation (Fig. 3). For instance, a larger tridactyl theropod trackway partly overlaps the described didactyl sequence, and shows considerable intratrackway morphological variation (Fig. 3a–c, e). The first track from this sequence, Th.Tw3.1.27D, occurs less than half a metre from Di.Tw1.1.27D and Di.Tw1.2.27D (Fig. 3a–c). Th.Tw3.1.27D is preserved as a natural mould with well-defined track margins, but the track is shallow, no interphalangeal pad margins are discernible, and the overall shape of the print is highly irregular. The heel margin is almost straight, which makes the track very short relative to its width, and digit II is rounded, whereas digits III and IV are more pointed (Fig. 3b–c). In comparison, the fourth track from this sequence, Th.Tw3.4.24H, is preserved as an *in situ* natural cast (positive epirelief) that has been flattened by erosion, but the heel is more typically V-shaped (Fig. 3e), rather than straight as in Th.Tw3.1.27D. Although the natural cast preservation of Th.Tw3.4.24H differs from the preceding tracks in this sequence, which are preserved as natural moulds (Fig. 3a–c), a collective trackway association is inferred based on similar orientation, alignment and track spacing and a lack of evidence for additional mid-sized theropod trackmakers within this immediate vicinity (Fig. 3a). No interphalangeal pads are visible in Th.Tw3.4.24H. An isolated hadrosaurid track just over 1 m from Di.Tw1.1.27D (Fig. 3a, d) reveals the overall shape of the foot and short, rounded digits, but the print is considerably eroded and possesses short track walls, with no defined interphalangeal pad outlines. Considering the shallow preservation of the tracks within this area, the general lack of visible interphalangeal pads, absence of skin impressions and sometimes irregular foot morphologies, it is likely that these tracks (and the described didactyl tracks) represent eroded, shallow undertracks rather than 'true' tracks (*sensu* Milán & Bromley, 2006). Accordingly, the morphology of the described didactyl traces is treated cautiously, as undertracks often provide a poorer representation of the pedal anatomy of the trackmaker than true tracks (e.g. Milàn & Bromley, 2008, fig. 5).

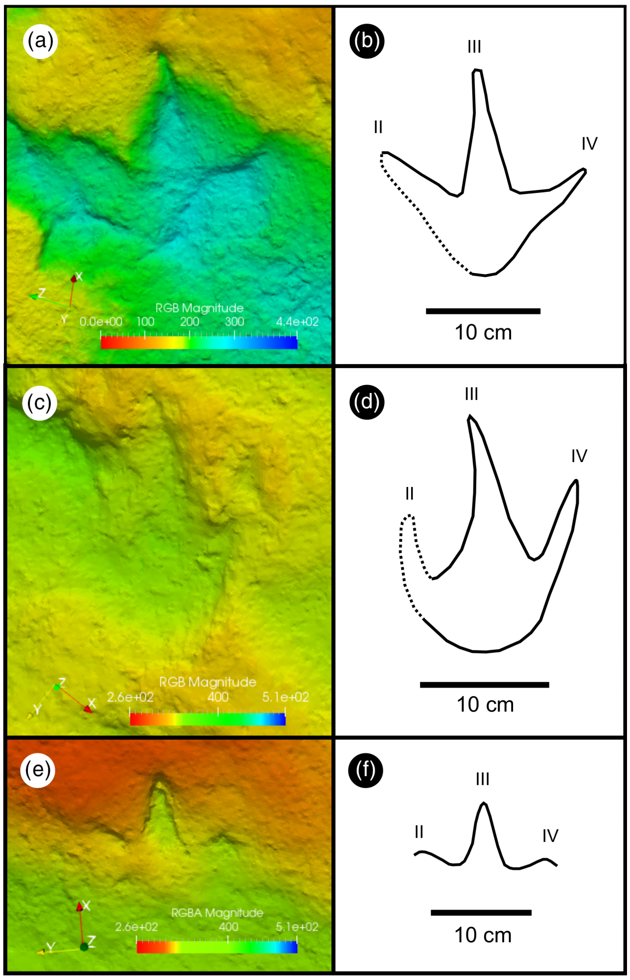

Fig. 4. (Colour online) Small, tridactyl theropod tracks from the same track layer as the described didactyl traces, shown here to demonstrate their morphological differences. Th.Tw5.3.72-A (a) digital elevation model and (b) line drawing; Th.Tw2.2.9C (c) digital elevation model and (d) line drawing; and Th.Tw4.4.70-A (e) digital elevation model and (f) line drawing. Dashed black lines indicate poorly visible track margins. All scales as indicated. Three-dimensional meshes used to create the digital elevation models are available as online Supplementary Figures S5–S7.

5.b. Comparisons with associated tridactyl theropod tracks

It is important to compare the morphology and preservation of the described didactyl traces with similarly sized tridactyl theropod tracks on the same layer, as it is possible that differences in digit counts may simply reflect preservational, substrate or kinematic-driven differences rather than anatomical difference. The clearest and most size-equivalent tridactyl theropod tracks on the same layer at Tyrants Aisle measure *c.* 18 cm in length and 13–18 cm in width (Fig. 4; online Supplementary Figs S5–S7). As for the described didactyl traces, these tracks are also heavily eroded; however, some evidence of all three digit impressions is consistently retained. In contrast, Di.Tw1.1.27D and Di.I.34E show no evidence of a third digit impression (Fig. 2). In particular, Di.I.34E is deeply impressed, making it unlikely that a third weight-bearing toe (if present) would fail to register on the substrate, as can sometimes occur in extant 'pseudodidactyl' bird tracks (Milán, 2006, fig. 12C; Richter & Böhme, 2016, fig. 17.7). Where this phenomenon of pseudodidactyly was observed in extant birds, the substrate was firm and damp, and tracks were only shallowly impressed.

Digit III morphology in the small tridactyl theropod tracks at Tyrants Aisle also differs from that of Di.Tw1.1.27D and Di.I.34E. In the small tridactyl tracks, digit III is narrow, and the base of its free length is consistently the widest portion of that digit, which then tapers continuously towards the tip (Fig. 4). In contrast, digit III in both Di.Tw1.1.27D and Di.I.34E is more elliptical and the widest point occurs near the midpoint of its free length (Fig. 2). As previously discussed, Di.Tw1.1.27D and Di.I.34E likely represent shallow undertracks, so the possibility that this distinct digit III morphology is a preservation artefact cannot be ruled out. Nevertheless, given that some of the morphologically distinct tridactyl theropod tracks also appear to represent eroded undertracks, we suggest that digit III shape remains a reliable distinction between the two track types. We therefore do not consider a tridactyl trackmaker for Di.Tw1.1.27D and Di.I.34E to be the most likely scenario, and instead interpret that they were formed by a functionally didactyl trackmaker.

5.c. Monodactyly and trackway interpretations

The didactyl track Di.Tw1.1.27D occurs in possible trackway association with three monodactyl impressions: Di.Tw1.2.27D, Di.Tw1.3.28D and Di.Tw1.4.29D (Fig. 2h). A similar phenomenon occurs within four parallel trackways from the Lower Cretaceous Houmotuan tracksite of Shandong Province, China, where recognizably didactyl tracks become monodactyl impressions within the same trackways (Xing *et al.* 2018*b*, fig. 5). The didactyl tracks within these sequences were used to infer a deinonychosaur maker for the trackways, as no non-avian or avian dinosaur is currently known to possess a monodactyl pes (Xing *et al.* 2018*b*). However, the recent description of *Vespersaurus* from the early Late Cretaceous Epoch of Brazil indicates that at least some theropods may have been functionally monodactyl (Langer *et al.* 2019). It was speculated by Xing *et al.* (2018*b*) that the monodactyl impressions at the Houmotuan tracksite may have been produced if both digits III and IV were held together closely enough to produce a single depression on the substrate. However, the widths of the monodactyl traces at Tyrants Aisle are no greater than the width of digit III on its own in the two didactyl traces (Table 2; Fig. 2). We instead hypothesize that the monodactyl impressions at Tyrants Aisle (Di.Tw1.2.27D, Di.Tw1.3.28D and Di.Tw1.4.29D) represent more highly eroded, deeper undertracks than the didactyl traces, as only the most deeply impressed portion of the foot remains (i.e. the impression of digit III). This is supported by the fact that digit III is the most deeply impressed area of both Di.Tw1.1.27D and Di.I.34E (Fig. 2c, j). Digit III would therefore presumably deform the sediment at a greater depth than any other portion of the foot, and should also be the last part of the track to disappear from ongoing modern fluvial erosion. Experimental work with modern emu tracks has demonstrated a similar phenomenon, as the impression of digit III is all that remains beyond a certain depth, creating an apparently monodactyl track (Milán & Bromley, 2006, fig. 1H, I).

Monodactyl tracks could also potentially represent a swimming sequence, where the trackmaker was either fully or partially buoyant and did not consistently touch its entire foot onto the substrate. In general, the criteria used to identify swim traces are absent from the Tyrants Aisle specimens, which include the presence of raised sediment mounds at the posterior end of the track, digit reflectures resulting from directional changes within a single foot placement, kick-off scours and long claw drag marks that (in theropods) typically consist of parallel sets of one to three sinuous scratches (McAllister 1989; Milner & Lockley, 2016). Furthermore, in both Di.Tw1.1.27D and Di.I.34E, the entire foot appears to have contacted the sediment due to the presence of a heel impression and a normal weight-bearing stance is implied. We therefore conclude that a more deeply impressed digit III, in conjunction with greater erosion, is the most likely scenario for the formation of our monodactyl traces.

Close proximity and similar size, shape and general alignment provide the main basis for grouping Di.Tw1.1.27D, Di.Tw1.2.27D, Di.Tw1.3.28D and Di.Tw1.4.29D as traces potentially made by the same trackmaker, although the overall placement and spacing of each trace relative to each another is abnormal. As Di.Tw1.1.27D is interpreted as a left foot, the next right footfall would be expected to occur in front of and to the right of this track. However, the monodactyl impression Di.Tw1.2.27D instead occurs in front of and to the left of Di.Tw1.1.27D (Fig. 2h). This creates a problem if the trackmaker is then inferred to have produced Di.Tw1.3.28D as its third footfall. Di.Tw1.3.28D is considerably further away (0.85 m from Di.Tw1.2.27D), and once again on the wrong side of the trackway midline if Di.Tw1.2.27D was indeed created by a right foot (Fig. 2h). Changes in relative foot position (i.e. a pace angulation exceeding 180°) have been observed in modern ratites and the trackways of some non-avian theropods, which likely relates to the hindlimbs being positioned closely together and/or discontinuous locomotion, where the trackmaker briefly stopped in midstride (Breithaupt *et al.* 2006, 2019). In addition to the apparent crossover gait observed for the described Wapiti Formation tracks, a similar phenomenon is observable within the didactyl and monodactyl trackway T23 from the Houmotuan site (Xing *et al.* 2018*b*, fig. 5). However, given the suboptimal undertrack preservation of Di.Tw1.1.27D, Di.Tw1.2.27D, Di.Tw1.3.28D and Di.Tw1.4.29D, and the abnormal spacing between each footfall (Fig. 2h; Table 2), it is likely that the apparent crossover gait observed here is partly explained by an absence of additional tracks (e.g. between Di.Tw1.2.27D and Di.Tw1.3.28D). It is also possible that the four traces correspond to at least two different individuals moving in close proximity, as was the case at the Houmotuan tracksite (Xing *et al.* 2018*b*, fig. 5). Ultimately, the abnormal track positioning, poor preservation and probable absence of additional footprints precludes a confident interpretation of the Wapiti Formation sequence described here, and we therefore acknowledge that the collective trackway association of each trace is tentative rather than conclusive.

5.d. Ichnotaxonomic affinities

Small, didactyl tracks within dinosaur-bearing strata are most often referred to members of Deinonychosauria, as these dinosaurs are suitably sized, possess a functionally didactyl pes and have a body fossil record that spans Laurasia and Gondwana (Makovicky & Norell, 2004; Turner *et al.* 2012). As Di.Tw1.1.27D and Di.I.34E are hypothesized to pertain to functionally didactyl trackmakers, and the presence of deinonychosaurs within Unit 4 of the Wapiti Formation has been confirmed by body fossils (Fanti *et al.* 2015), we mirror the rationale of Xing *et al.* (2018*a*) and suggest that a deinonychosaur was probably responsible for producing the didactyl and monodactyl tracks described here. The aforementioned *Vespersaurus* – which may have been functionally monodactyl – belongs to the subfamily Noasaurinae, whose members are currently identified only from Gondwanan continents (Langer *et al.* 2019; Brougham *et al.* 2020) and are therefore unlikely to be responsible for producing the monodactyl traces described here.

Tracks that have been attributed to deinonychosaurs are assigned to five ichnogenera: *Velociraptorichnus*, *Dromaeopodus*, *Dromaeosauripus*, *Menglongipus* and *Sarmientichnus* (Lockley et al. 2016*a*; Xing *et al.* 2018*a*). The Middle Jurassic type material of *Sarmientichnus* (Casamiquela, 1964; De Valais, 2011) possibly pre-dates the first definitive deinonychosaurs identified from skeletal remains, and it therefore remains an open question whether the maker of these Middle Jurassic traces was a true deinonychosaur. *Velociraptorichnus*, *Dromaeopodus* and *Dromaeosauripus* have generally been treated as probable dromaeosaurid ichnotaxa in prior literature based on their usually subequal lengths of digits III and IV, following osteological observations that these two digits are typically of similar length (Lockley *et al.* 2016*a*). Troodontid pedal skeletons, by comparison, tend to possess a relatively shorter digit IV (van der Lubbe *et al.* 2009, 2011; Lockley *et al.* 2016*a*). This distinction in digit IV length was the main criterion used to identify *Menglongipus* as a possible, albeit dubious, troodontid ichnotaxon (Lockley *et al.* 2016*a*). Similarly, a large collection of more than 86 unnamed didactyl tracks from at least 17 distinct trackways at the Obernkirchen track locality in Germany have been treated as the only conclusive examples of troodontid tracks based on a repeatedly shorter digit IV that is roughly 0.8 times the length of digit III (van der Lubbe *et al.* 2009, 2011; Lockley et al. 2016*a*; Richter & Böhme, 2016). However, we note that the *Velociraptorichnus sichuanensis* holotype CFEC-B-1 possesses a digit IV/III length ratio of 0.84 (measured from the heel base; Lockley *et al.* 2016*a*, fig. 11.4A), very similar to that of the Obernkirchen tracks, and therefore agree that a troodontid maker for *V. sichuanensis* cannot be ruled out (Lockley *et al.* 2016*a*).

The Obernkirchen didactyl tracks differ most notably from those from the Wapiti Formation described here in the shape of digit III: those from Tyrants Aisle are elliptical and broad, whereas the German tracks possess narrow digit III impressions (Fig. 5f). In addition, digit IV is relatively shorter in the Wapiti specimens (IV/III length ratio of 0.8 for the German tracks; 0.68–0.6 for Di.Tw1.1.27D and Di.I.34E) and the German specimens are also larger in overall size (track lengths from the Obernkirchen locality are typically > 20 cm, with a range of 13–23.3 cm; Lockley *et al.* 2016*a*). As a result, these tracks likely pertained to distinct trackmakers.

The Wapiti Formation tracks differ from Chinese *Velociraptorichnus sichuanensis* prints in lacking a proximal pad impression of digit II and having a notably shorter digit IV (IV/III length ratio for the *V. sichuanensis* holotype, 0.84). Nevertheless, similarities include overall track size, where *V. sichuanensis* holotype and paratype tracks vary over the range 11–11.5 cm in length and 6–6.5 cm in width (Zhen *et al.* 1994; see Table 2 for Wapiti track measurements), as well as relatively broad digit III impressions and a rounded heel. Additional tracks referred to *Velociraptorichnus* from China also

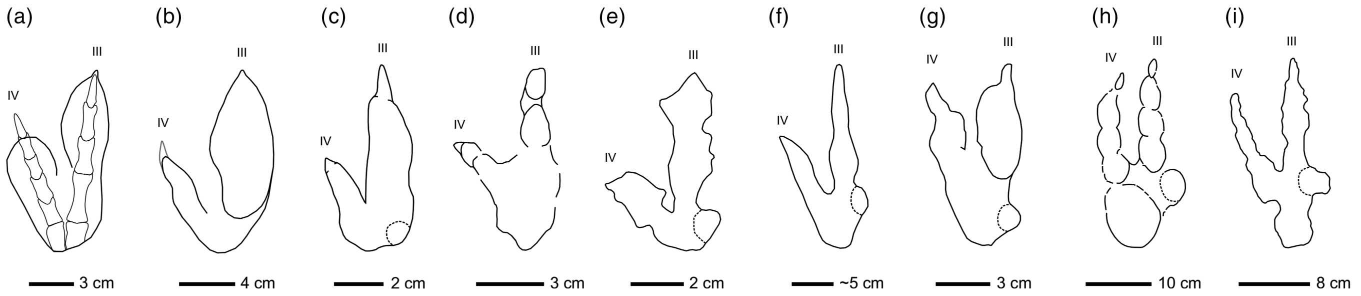

Fig. 5. (Colour online) Comparison of tracks described here with other select deinonychosaur tracks: (a) Di.Tw1.1.27D, with superimposed pedal skeleton of a troodontid (*Talos sampsoni*; adapted from Zanno *et al.* 2011); (b) Di.I.34E, with possible digit IV claw mark in grey; (c) cf. *Menglongipus* track HMT-T22-R6 from the Houmotuan tracksite in Shandong Province, China (reversed and redrawn from Xing *et al.* 2018*b*, fig. 5); (d) *Menglongipus* track DMNH 21365 from Riley Creek, Denali National Park, Alaska, USA (after Fiorillo *et al.* 2014, fig. 7, excluding a possible trace of the proximal end of digit II); (e) track T.A.1 of the *Menglongipus sinensis* holotype trackway from Hebei Province, China (after Xing *et al.* 2009*a*); (f) troodontid track A2 from the Obernkirchen track locality in Germany (after Lockley *et al.* 2016*a*, fig. 11.13); (g) *Velociraptorichnus* track from Shandong Province, China (after Li *et al.* 2008, fig. 2); (h) representative print from the *Dromaeopodus shangdongensis* holotype trackway CU 214.111, from Shandong Province, China (after Li *et al.* 2008, fig. 2); and (i) *Dromaeosauripus* track from the Mill Canyon Dinosaur Tracksite, Utah, USA (adapted from Lockley *et al.* 2014*b*, fig. 6). Dashed lines denote the approximate location of a digit II proximal pad impression (when present). Scales as indicated.

display a number of similarities. One well-preserved specimen from Shandong Province (Fig. 5g; Li *et al.* 2008, fig. 2a, b) has a comparably rounded heel and an elliptical, broad digit III impression that is particularly reminiscent of that seen in Di.Tw1.1.27D and the monodactyl trace Di.Tw1.3.28D. However, this Chinese track differs from the Wapiti specimens in the relative length of digits III and IV, which are subequal, and by possessing a proximal pad impression of digit II. Another example from Sichuan Province (MJW-T2-R1; Xing *et al.* 2015*a*, fig. 3) possesses a relatively short digit IV comparable to that of Di.Tw1.1.27D and Di.I.34E, although its preceding track MJW-T2-L1 and others on the same bedding plane instead show subequal digit lengths, suggesting that the shortness of digit IV in MJW-T2-R1 may be a preservation artefact. These particular tracks, assigned to the ichnospecies *Velociraptorichnus zhangi*, also lack the broad digit impressions of the Wapiti specimens and represent a tridactyl deinonychosaur morphotype where digit II is fully impressed, either due to particular substrate conditions or a suitable amount of claw retraction (Xing *et al.* 2015*a*). The Wapiti tracks lack any such trace of digit II. We ultimately reject the referral of Di.Tw1.1.27D and Di.I.34E to *Velociraptorichnus* based on greater relative shortness of digit IV compared with III and the absence of a digit II proximal pad impression.

Dromaeopodus shandongensis was named by Li *et al.* (2008) on the basis of well-preserved trackways of Early Cretaceous age in Shandong Province, China. These tracks display a proximal pad impression of digit II, subequal digit III and IV lengths, and are larger than the Wapiti specimens (length, 24–28.5 cm; Li *et al.* 2008, table 1). Additionally, digits III and IV of *D. shandongensis* are relatively narrow and both curve medially (Fig. 5h), while those of Di.Tw1.1.27D and Di.I.34E are either straight or, in the case of digit IV from Di.I.34E, curve laterally. A well-rounded heel impression that unites the proximal portions of digits III and IV is the only notable similarity between the two track morphotypes; we therefore reject assignment of the Wapiti tracks to *D. shandongensis*.

Three ichnospecies of *Dromaeosauripus* are known from the Early Cretaceous Epoch. These are *Dromaeosauripus hamanensis* and *Dromaeosauripus jinjuensis* from South Korea (Kim *et al.* 2008, 2012), and *Dromaeosauripus yongjingensis* from China (Xing *et al.* 2013*a*). Additional tracks referred to *Dromaeosauripus* are known from both Utah and Colorado (Lockley *et al.* 2014*a*, *b*, 2016*b*). All occurrences of *Dromaeosauripus* are characterized by narrow digit impressions that are subequal in length, which differ from the broader, unequal-length digits seen in Di.Tw1.1.27D and Di.I.34E. *Dromaeosauripus* tracks may also show a proximal pad impression of digit II, the presence of which is variable within a single trackway (Lockley *et al.* 2012; Xing *et al.* 2013*a*). In *Dromaeosauripus jinjuensis*, the proximal pad of digit II is missing, while digits III and IV are represented by completely separate and parallel impressions, with no evidence of the heel pad (Kim *et al.* 2012). The separated toes and absence of a heel impression seen in *Dromaeosauripus jinjuensis*, as well as certain examples of both *Dromaeosauripus hamanensis* and *Dromaeosauripus yongjingensis* (Kim *et al.* 2008; Xing *et al.* 2013*a*), is distinct from the rounded heel pad that unites digits III and IV in the Wapiti Formation tracks. In addition, both the Chinese and North American tracks assigned to *Dromaeosauripus* were produced by slender-toed trackmakers (Fig. 5i), while the didactyl tracks from the Wapiti Formation possess a more robust, broader digit morphology. Finally, digit IV in the Wapiti tracks is also notably shorter than in any of the three *Dromaeosauripus* ichnospecies. Collectively, these differences indicate that the Wapiti specimens cannot be referred to *Dromaeosauripus*.

The most comparable deinonychosaurian ichnotaxon to those from Tyrants Aisle, especially in the relative shortness of digit IV, is *Menglongipus sinensis* (Fig. 5e), an ichnospecies that was erected based on a trackway of four poorly preserved didactyl moulds (T.A.1–4; Xing *et al.* 2009*a*) from the latest Jurassic or earliest Cretaceous period of Hebei Province, China. Average digit IV/III length of these prints is 0.62 (measured from heel to digit tip; Xing *et al.* 2009*a*), consistent with ratios obtained for Di.Tw1.1.27D and Di.I.34E (Table 2). However, the overall size of each complete *M. sinensis* print is only 5.8–6.7 cm in length, suggestive of a smaller-bodied trackmaker. Additionally, three of the four *M. sinensis* holotype tracks show a proximal pad impression of digit II (Xing *et al.* 2009*a*), a feature that is missing – albeit possibly due to erosion – from the Wapiti Formation tracks. Further occurrences of *Menglongipus* have since been reported from other localities both within and outside China. From the lower Cantwell Formation of Riley Creek, within Denali National Park in Alaska (upper Campanian – lower Maastrichtian), an isolated didactyl track, DMNH 21365, was referred to *Menglongipus* based on the relative shortness of digit IV in comparison to digit III (Fiorillo *et al.* 2014; Fig. 5d). This track is the most temporally and geographically comparable specimen to those from Tyrants Aisle and, as for the Tyrants Aisle specimens, the shortness of digit

IV in DMNH 21365 suggests that it probably pertains to a troodontid rather than a dromaeosaurid (see the following section on referral to Troodontidae). However, DMNH 21365 differs from the Wapiti Formation tracks in possessing relatively narrower and less-rounded digits, especially that of digit III. The previously discussed collection of four parallel trackways containing didactyl and monodactyl tracks at the Houmotuan tracksite from the Dasheng Group of Shandong Province in China have also been tentatively referred to cf. *Menglongipus* (Xing *et al.* 2018*b*; Fig. 5c). These Houmotuan tracks display a striking similarity to the Wapiti specimens in both the relative shortness of digit IV compared to digit III (IV/III length ratio for T22-R6 is 0.56; Xing *et al.* 2018*b*, fig. 5; Fig. 5c) and also the broad, robust morphology of digit III in certain track examples (e.g. T22-L6; Xing *et al.* 2018*b*, fig. 5). Furthermore, the presence of teardrop-shaped monodactyl impressions (Xing *et al.* 2018*b*, fig. 5) in association with these didactyl tracks matches the co-occurrence of didactyl and similarly shaped monodactyl impressions observed at Tyrants Aisle. These cf. *Menglongipus* tracks from Shandong are therefore the most morphologically comparable tracks to our described specimens. However, we conservatively refrain from referring the Wapiti Formation tracks to *Menglongipus* due to the suboptimal preservation of the Wapiti tracks themselves, and the poor quality of the holotype trackway used to erect *Menglongipus sinensis* (Xing *et al.* 2009*a*), which is therefore a potentially dubious ichnotaxon (Lockley *et al.* 2016*a*).

5.e. Referral to Troodontidae

Within Deinonychosauria, the relative digit proportions of the didactyl tracks at Tyrants Aisle are most consistent with that of a troodontid. Troodontids generally possess a digit IV that is up to 20% shorter than digit III and less anteriorly projected, whereas these two digits tend to be of subequal length in dromaeosaurids (van der Lubbe *et al.* 2011; Lockley *et al.* 2016*a*). Among North American troodontids, complete pedes are known for *Stenonychosaurus inequalis* from the upper Campanian Dinosaur Park Formation of southern Alberta, Canada, (CMN 8537; Sternberg, 1932) and *Talos sampsoni* from the upper Campanian Kaiparowits Formation of Utah, USA (UMNH VP 19479; Zanno *et al.* 2011), both of which have a digit IV/III length ratio of 0.8. Superimposing the foot skeleton of *T. sampsoni* onto Di.Tw1.1.27D results in an imperfect fit (Fig. 5a), as the relative digit IV length in the latter (and also Di.I.34E) is shorter than that of *T. sampsoni*. Nevertheless, a member of Troodontidae remains the most plausible trackmaker for these prints given the smaller discrepancy in relative digit IV length when compared to a typical dromaeosaurid. Within North America, isolated troodontid teeth commonly occur at many Campanian–Maastrichtian microvertebrate sites, although skeletal material is relatively rare and our understanding of their taxonomic diversity remains contentious (Evans *et al.* 2017; van der Reest & Currie, 2017). From the Wapiti Formation specifically, troodontids are so far represented only by an isolated metatarsal, TMP 89.55.1008, and teeth referred to *Troodon* (Ryan & Russell, 2001; Fanti & Miyashita, 2009; Fanti *et al.* 2015). *Troodon* teeth, along with those of indeterminate dromaeosaurids, were recovered within Unit 4 at the Wapiti River *Pachyrhinosaurus* bonebed (Fanti *et al.* 2015), confirming the presence of both deinonychosaur families within the same stratigraphic unit as the tracks described here. Additional *Troodon* teeth are known from close to the Unit 3–Unit 4 boundary, within the Pipestone Creek *Pachyrhinosaurus* bonebed (Currie *et al.* 2008), as well as at the Kleskun Hill microsites within Unit 3, where they are the most abundant small theropod tooth type (Fanti & Miyashita, 2009). The dromaeosaurids *Boreonykus certekorum* and teeth referred to *Saurornitholestes* sp. (including '*Paronychodon*'-type teeth; see Currie & Evans 2020) and *Richardoestesia* are also known from Unit 3 (Currie *et al.* 2008; Fanti & Miyashita, 2009; Bell & Currie, 2015). The discovery of probable troodontid footprints within the Wapiti Formation, although novel, is therefore not an unexpected find and further adds to a growing non-avian dinosaur ichnodiversity, which also includes hadrosaurids, tyrannosaurids, possible oviraptorosaurs, indeterminate tridactyl theropods and scarce ankylosaur and/or ceratopsian tracks (Fanti *et al.* 2013; McCrea *et al.* 2014).

5.f. Importance within the fossil record of Deinonychosauria

While skeletal material and/or teeth from deinonychosaurs have been found on all seven continents (Makovicky & Norell, 2004; Norell & Makovicky, 2004; Weishampel *et al.* 2004; Turner *et al.* 2012), their track record is currently limited to North America, South America, Europe and Asia (Fig. 6). In particular, the majority of track occurrences are from the Early Cretaceous Epoch of China (Table 1).

Deinonychosaur tracks from North America were first identified from Aptian–Albian strata in eastern Utah, within the Ruby Ranch Member of the Cedar Mountain Formation at Arches National Park (White & Lockley, 2002; Lockley *et al.* 2004) and at the nearby Mill Canyon Dinosaur Tracksite (Cowan *et al.* 2010). The Mill Canyon tracks are referred to the ichnogenus *Dromaeosauripus* on the basis of their slender-toed morphology and the presence of a slight impression of the proximal portion of digit II (Fig. 5i; Lockley *et al.* 2014*a*, *b*). *Dromaeosauripus* tracks have also been identified from the Albian Plainview Sandstone of Dinosaur Ridge in Colorado (Lockley *et al.* 2016*a*, *b*), and a single track referred to *Menglongipus* is known from the Late Cretaceous Epoch of Alaska within Denali National Park (Fiorillo *et al.* 2014). Other reports of North American deinonychosaur tracks are more dubious. Alleged Late Cretaceous dromaeosaurid tracks from El Aguaje in Michoacán, Mexico have been reported (JA Ortíz-Mendieta, Dissertation, Universidad Nacional Autónoma de México, 2001), although these require re-evaluation as they may represent a superficially didactyl variation of a tridactyl track morphotype (Rodríguez-de la Rosa *et al.* 2004). Similarly, an alleged large dromaeosaurid trackway from near the Las Águilas tracksite in Coahuilia, Mexico (Meyer *et al.* 2008) is regarded as a poorly preserved ornithopod sequence by some workers (Bravo-Cuevas & Rodríguez-de la Rosa, 2014). Additional deinonychosaur tracks from Las Águilas have since been reported (Rivera-Sylva *et al.* 2017), but have not been figured or described. North American deinonychosaur ichnodiversity is therefore restricted to only two definitive morphotypes, comprising three occurrences of *Dromaeosauripus* from the Early Cretaceous Epoch of Utah and Colorado, and one occurrence of *Menglongipus* from the Late Cretaceous Epoch of Alaska. We add to this record probable troodontid prints described here from the Late Cretaceous Epoch of Canada, which establishes the presence of at least three distinct deinonychosaur track morphotypes from North America. These findings demonstrate that there is considerable scope for further increasing the deinonychosaur ichnodiversity from North America, as has occurred in Asia, through ongoing exploration of dinosaur track-bearing strata in the coming years.

Conflict of interest. None.

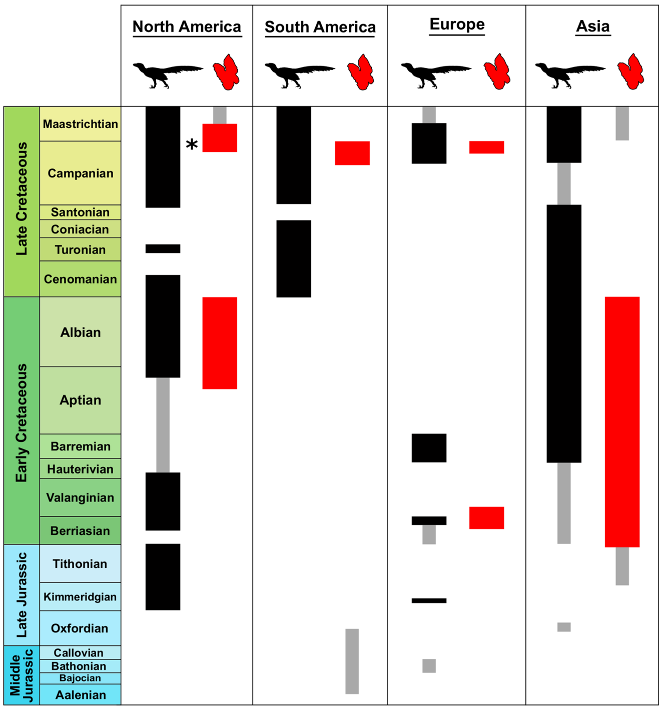

Fig. 6. (Colour online) Temporal comparison of deinonychosaur tracks and body fossils for continents where deinonychosaur tracks have been reported. Body fossils are coloured with black bars and tracks with red bars. Thinner grey bars indicate a possible occurrence, either due to inconclusive taxonomy or poorly resolved dating of host strata. An asterisk (*) denotes the temporal position of the presently described tracks. Dromaeosaurid silhouette copyright of Emily Willoughby, available under Creative Commons licence (CC BY-SA 3.0). Track silhouette adapted from Lockley *et al.* (2016*a*, fig. 11.4.A).

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