

A busy time at the beach: multiple examples of gregarious dinosaur behaviour inferred from a set of trackways from the Late Cretaceous of Alberta, Canada

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Abstract

A diverse collection of dinosaur tracks and trackways preserved on a single bedding plane record activities of many animals over a very short time, possibly just a few days or less. The assemblage is exposed on a detached slab of siltstone from the Campanian–Maastrichtian St. Mary River Formation in southwestern Alberta, Canada. Members of four different groups of dinosaurs are identified as the makers of either isolated tracks, or trackways of varying lengths, and include inferred hatchling tyrannosaurids, medium and large ornithomimids, small and medium-sized ornithopods, and a small hadrosaurid. All but one of the seven trackways attributed to hatchling tyrannosaurids occur as codirectional, equally spaced pairs, but one pair walked in the opposite direction, albeit parallel, to the other two. The pair of ornithomimid trackways also appears to represent two animals walking at the same speed, in the same direction, and turning together. The trackway attributed to a medium-sized biped, possibly *Parksosaurus warreni*, is the first evidence for the presence of these dinosaurs in the environment recorded by the St. Mary River Formation.

Key words: Dinosaurs, trackways, Late Cretaceous, Alberta, St. Mary River Formation

Résumé

Une collection diversifiée d'empreintes et de pistes d'empreintes de dinosaures préservée dans un unique plan de litage témoigne de l'activité de nombreux animaux sur une courte période de temps, possiblement quelques jours ou moins. L'assemblage est exposé dans une plaque détachée de siltstone de la Formation campanienne–maastrichtienne de St. Mary River, dans le sud-ouest de l'Alberta (Canada). Des membres de quatre groupes de dinosaures différents sont identifiés comme ayant produit soit des empreintes isolées ou des pistes d'empreintes de longueurs variées, et ils comprennent des bébés tyrannosauridés inférés, de moyens et grands ornithomimidés, des ornithopodes de petite et moyenne taille et un petit hadrosauridé. Toutes les sept pistes d'empreintes attribuées à des bébés tyrannosauridés sauf une se présentent en paires de pistes de même direction montrant le même espacement, mais une des paires va dans la direction opposée, bien que parallèle, à celle des deux autres. La paire de pistes d'empreintes d'ornithomimidé semble aussi représenter deux animaux marchant à la même vitesse, dans la même direction et tournant ensemble. La piste d'empreintes attribuée à un bipède de taille moyenne, possiblement *Parksosaurus warreni*, constitue le premier indice de la présence de ces dinosaures dans le milieu préservé par la Formation de St. Mary River. [Traduit par la Rédaction]

Mots-clés : dinosaures, pistes d'empreintes, Crétacé tardif, Alberta, Formation de St. Mary River

Introduction

The province of Alberta has one of the best body fossil records of Late Cretaceous dinosaurs in the world. Its trace fossil record, in the form of footprints and trackways left by dinosaurs, is not nearly as good, but there are a few records of tracks and trackways at scattered locations across the province that range in age from Early to Late Cretaceous (Currie 1989; McCrea et al. 2014b). The St. Mary River Formation, recording an interval from the latest Campanian to the latest Maastrichtian, and exposed in the southwest of the

province, is a notable exception. Although the body fossil record of dinosaurs from the St. Mary River Formation is very limited — just nine genera are known from partial skeletons or isolated bones (Brown et al. 2015) — it has a very good dinosaur trackway record (Langston 1960; Lockley 1991; Lockley et al. 2003). The ichnofaunal record of this formation has been known and studied for many years. The earliest report was of a single, three-dimensional cast of a hadrosaur foot that showed the form of the fleshy pads that underlay the digits (Langston 1960). The dinosaur tracks are most frequently

Fig. 1. Maps showing the location of the polytypic dinosaur trackway block. (A) Regional map showing the location of the province of Alberta in western Canada, with the trackway site being in the grey box in the extreme southwest. Produced using the mapping software provided with the scientific visualization package PV-WAVE (Perforce Software). (B) Expanded view of the grey box showing the location of the trackway slab (white arrow), and the local extent of the fossil-trackway-rich, Late Cretaceous St. Mary River Formation. Adapted from the Geological Map of Alberta (Hamilton et al. 1999).

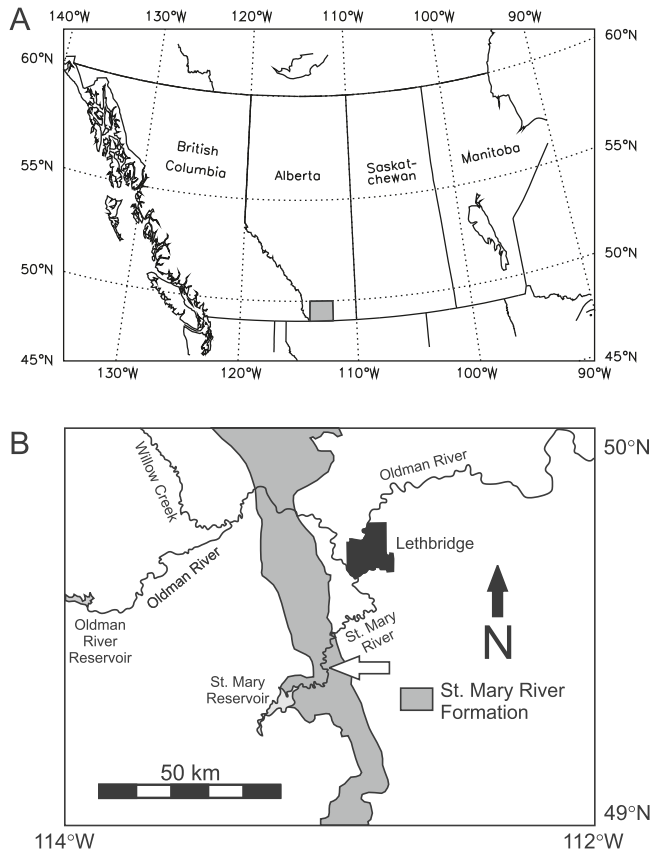
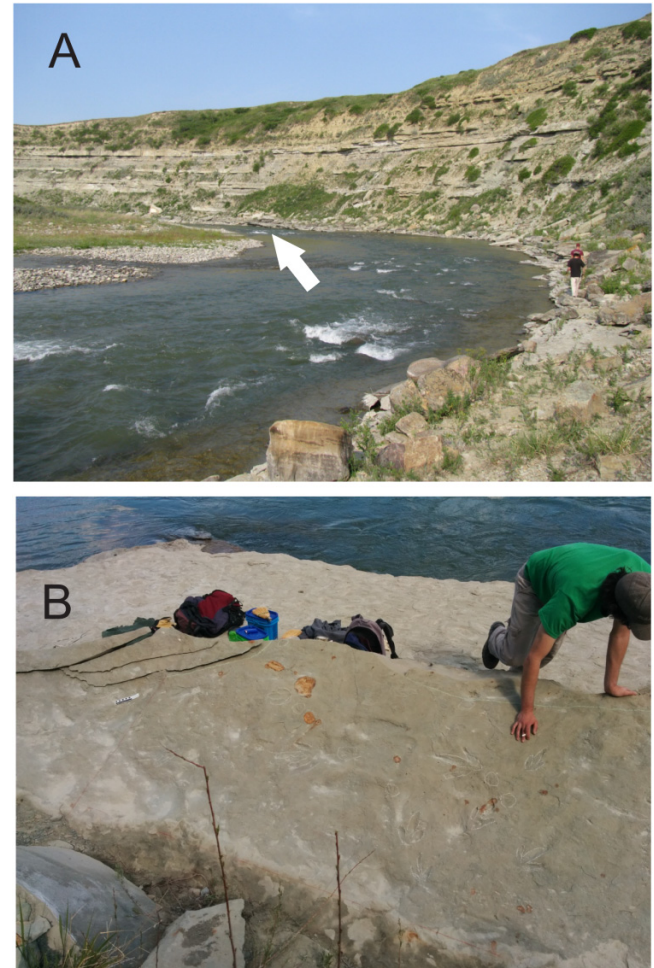


Fig. 2. Views of the fossil location. (A) Steep exposures of the St. Mary River Formation. The white arrow shows the approximate location of the trackway hosting block, which fell from an undetermined point on the cliff face. (B) Detailed view of the trackway surface with some of the larger, three-toed dinosaur tracks highlighted with chalk outlines. Many more tracks were found when examining a cast made from a latex peel of the track-bearing surface. [Colour online.]



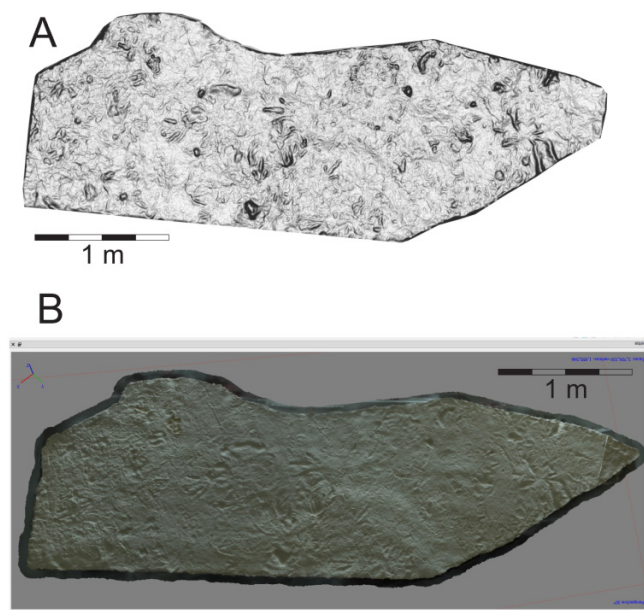
found in light grey sandstones that record floodplain sediments deposited in lakes and marshes close to fluvial channels (Currie et al. 1991). Detailed summaries of the sedimentology of the St. Mary River Formation can be found in Currie et al. (1991) and Nadon (1993). The present paper reports the discovery of an assemblage of dinosaur trackways, produced by multiple individuals of different dinosaur groups and preserved on a single large slab from the St. Mary River Formation, that record a brief, but very busy interval along a riverbank in the Late Cretaceous.

Materials and methods

The trackway assemblage comes from the banks of the St. Mary River in southwestern Alberta (Fig. 1) and was discovered in 2015 during a general fossil survey (Borkovic and Sanchez 2016) along rivers in the southern half of the province that was initiated after major flooding occurred

across the region in 2013 (Pomeroy et al. 2015). As is typical for the trackways of the St. Mary River Formation, the tracks are exposed on the surface of a single large slab of siltstone that fell from a steep cliff and came to rest close to the shoreline of the St. Mary River (Fig. 2). The exact stratigraphic horizon that produced the slab is unknown. The slab must have fallen several decades ago, and the track bearing surface is strongly eroded, resulting in many of the tracks having very low relief. The St. Mary River tracks were emplaced in distal splay and marsh-lacustrine silts and muds after flooding events (Currie et al. 1991). Sediments are conducive to recording and preserving tracks only for a short spell, based on their water content, and evaporation of the water will eventually make the sediments too stiff to deform and record tracks. This trackway assemblage may record the activities of animals over just a few days or less.

Fig. 3. Shaded relief maps of the track-bearing surface derived from laser and photogrammetry methods. (A) Laser scan map. Unfortunately, the image is dominated by the many small contours of the rough, heavily eroded surface, with only a few of the largest and deepest track impressions visible and morphologically distinct. We were unable to extract much useful data from this image. (B) Photogrammetry map. More details of a wider size range of tracks were resolved. Although not visible in this large-scale image, small tracks and track details are shown in subsequent figures. Note that (A) lacks the small, triangular patch which was captured with photogrammetry. [Colour online.]



The track-bearing slab is approximately 4 m long, 50 cm thick, and 1.2 m at its widest. The size, mass, and location of the slab precluded its collection. Instead, two latex (Chemionix Mould-all 1000) peels, reinforced with an open-weave, cotton fabric (“cheesecloth”), were made in the field, one covering almost the entire surface and the other being a smaller triangular patch that recorded some faint tracks that were missed at the outset. In the preparation laboratory of the Royal Tyrrell Museum of Palaeontology (RTMP) these peels were used as moulds to cast replicas (Aqua-Resin laminating/casting resin), and form a more permanent record of this important trackway assemblage. The RTMP catalogue numbers for the peel and the cast are TMP2015.022.0012 and TMP2016.022.0003, respectively.

The tracks were mapped from the casts using a grid system, and employing low-angle lighting to highlight low-relief tracks. The resultant mapsheets were scanned electronically and imported into the drawing program **Corel DRAW** (2018). The traces recorded on the sheets were then individually digitized and assembled into a single Corel DRAW image. Measurements of the tracks and trackways were made using the linear and angular measuring tools in Corel DRAW

Two electronic/digital methods were also tried in an attempt to extract more details from the slab. First, a high-resolution, digital elevation model was produced using an industrial laser scanner (Faro Focus3D X 330 Laser Scanner). The resulting scan data was processed using FARO Scene for initial registering and processing, CloudCompare to improve the display, and ArcGIS Desktop with Spatial Analyst for model shading and generating PDFs. Second, photogrammetry was used to produce a 3D model, with Agisoft Metashape Professional used to process the images for the model. Once the images were aligned into tie points, the “Gradual Selection” feature was used to control the reconstruction uncertainty, the projection accuracy, and the reprojection error. The camera alignment was optimized after each of these steps. The “detect markers” feature was used to automatically detect the coded targets in the photographs, which were used to create scale bars, input measurements, and scale the model. A dense point cloud was generated, from which a mesh was produced, and then a texture was applied.

For estimating the hip heights of the various trackmakers, and to compare the results of using different estimation methods, two hip height estimation formulae for small theropods from **Thulborn (1990)** were used to make the estimates—a simple linear expression where hip height is equal to $4.5 \times FL$, and a nonlinear expression where hip height is given by $3.06 \times FL^{1.14}$, where FL is foot length as measured from the proximal margin of a track to the tip of the central toe. In cases where the proximal margin of a track was not preserved, its position was taken as the rear intersection point of a pair of central lines drawn through the medial and lateral digits. The estimated hip heights are used to compute relative speeds of trackmakers by dividing stride length by the hip height.

Institutional abbreviations: **ROM**, Royal Ontario Museum, Toronto, Ontario, Canada; **TMP**, (Royal) Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada.

Results

Figure 3 shows the results of the electronic-digital mapping methods applied to the track-hosting slab. Both maps are presented as shaded relief maps. Unfortunately, it turned out to be very difficult to see track details on the model produced by the laser scan (**Fig. 3A**), with only the deepest tracks being conspicuous. The image was overwhelmed by the many rough, erosion-enhanced irregularities of the sedimentary layers, which obscured the details of the very shallowly impressed (or heavily eroded) tracks. This was especially true for the smallest tracks, which were on the order of 5–8 cm long. **Figure 3B** shows the trackbearing surface as revealed by photogrammetry. The digital model much better, and although not visible at this large scale, the small, shallowly impressed tracks could be seen under low-angle lighting on an individual basis. Three sources of information were combined to define, illustrate, and study the tracks: (i) the manually produced map was used to identify trackways, (ii) photographs of the latex peels were used to see details of smaller, fainter tracks and to confirm observations from the map, and

Fig. 4. Basic map of the track-bearing surface. Given the rock fall origin of the slab, its original geographic orientation is unknowable. The two outline contours bounding the tracks conform to the two latex peels made in the field. See Methods for more details.

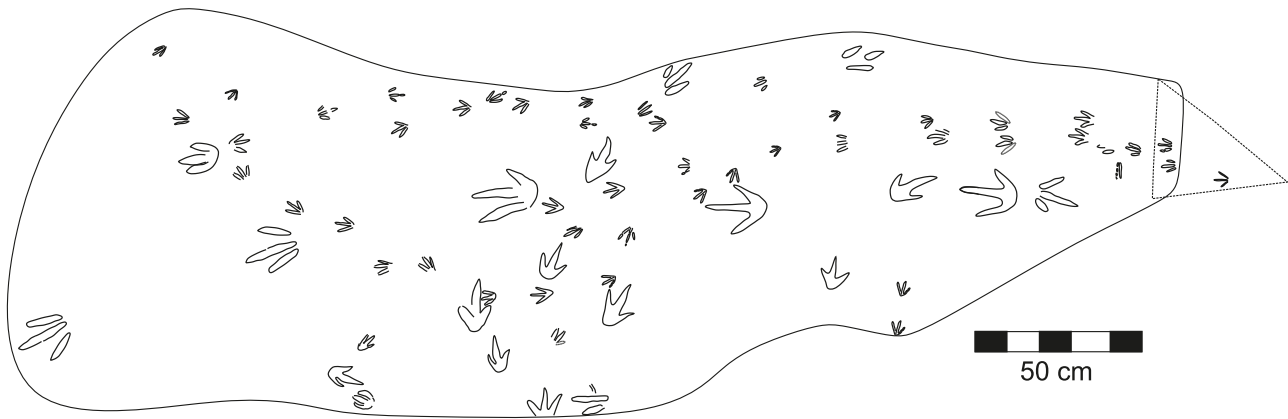
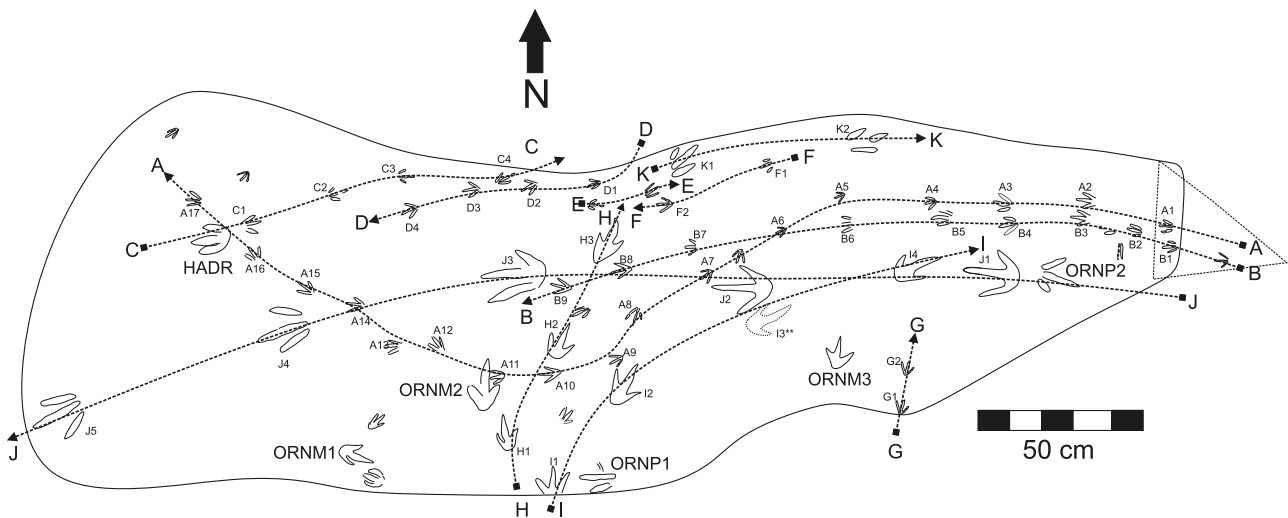


Fig. 5. Identifications and interpretations of the dinosaur track-bearing surface. The best-preserved trackways are highlighted with dashed lines and identified with single, block capitals. Isolated tracks are identified and labelled with abbreviated names. Trackway makers: A–G, hatchling tyrannosaurids; H and I, medium-sized ornithomimids; J and K, medium-sized basal ornithopods. The black squares and arrow heads mark the beginnings and endings, respectively, of trackways. I3** is a reconstruction of a track that is not visible on the slab, having presumably been lost to erosion, and its position was arbitrarily set at the midpoint between I2 and I4. Isolated tracks: HADR, young hadrosaur; ORNM1–3, ornithomimids; ORNP1–2, small-bodied ornithopods. See Results section for details. The choice of a north for the map was arbitrary as the original orientation of the fallen slab is unknown.



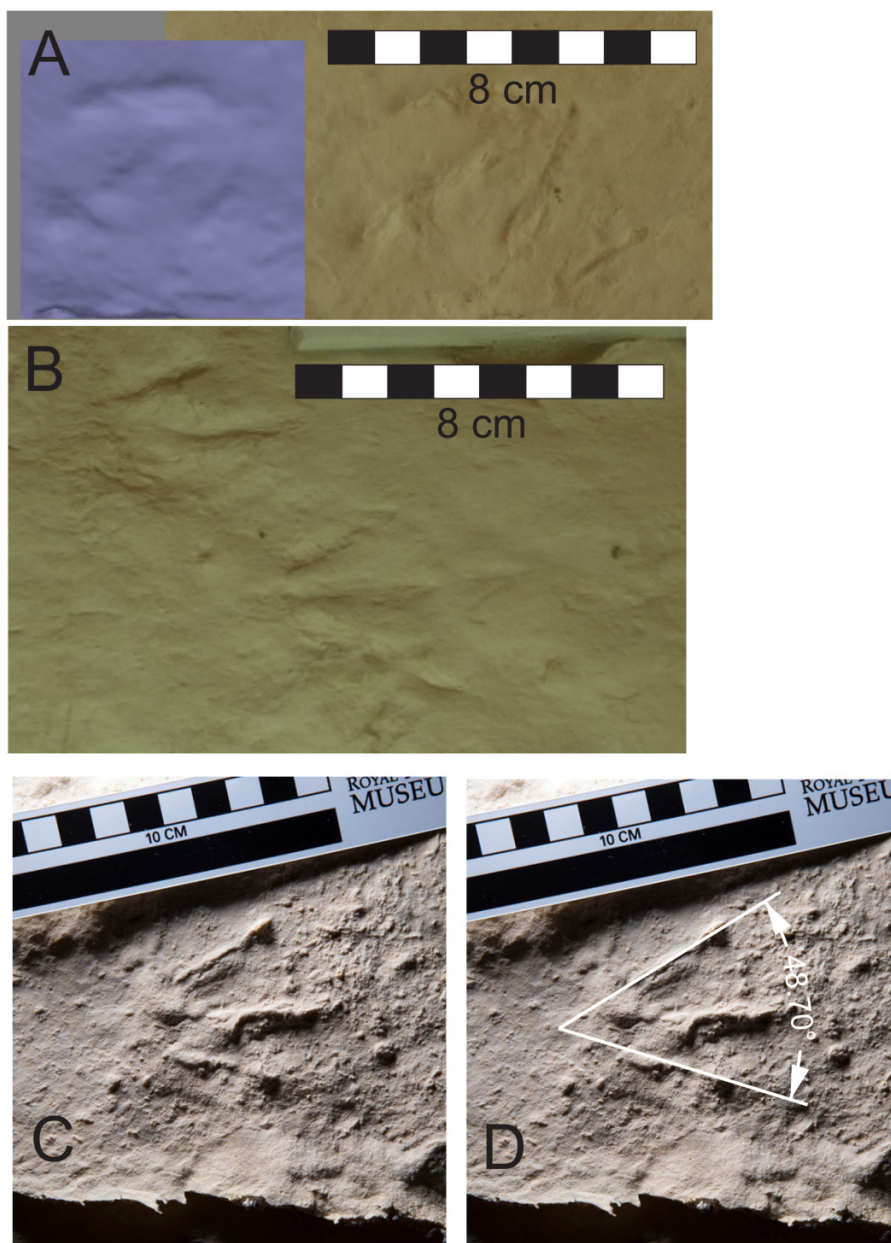
(iii) shaded relief images from the photogrammetry model were used to visualize the very faint, shallow tracks.

Figure 4 presents the assembled tracings of the best-preserved dinosaur tracks as a map. There were also various narrow (5 mm wide), slightly curved, low-rimmed trails preserved on the slab that were interpreted as gastropod grazing trails. One of these is visible in Fig. 10C. At first glance, the assemblage would appear to be just a random assortment of 69 tracks left by many individuals of different types of dinosaur, but Fig. 5 clarifies the situation. Four different types of dinosaur are identified as the trackmakers, and the tracks can be seen to constitute 11 distinctive

trackways, of varying lengths, along with several isolated tracks that could not be associated into trackways. The four trackmaker types proposed are: small tyrannosaurids, small- and medium-sized ornithomimids, small-bodied ornithopods, and a small hadrosaur. As detailed below these trackmakers were identified using the distinctive features of various tracks, the limited body fossil record of the St. Mary River Formation, and the much better body fossil record of the time equivalent, and geographically adjacent, Horseshoe Canyon Formation.

Unfortunately, most of the tracks are very faint and difficult to see, and even more difficult to capture as clear images.

Fig. 6. Details of some of the best-preserved small tyrannosaurid tracks. The tracks are interpreted to have been very lightly impressed and then subjected to extensive erosion. (A) Track C4 as a shaded image from the photogrammetry model (left) and as a photograph of the cast of the surface made from the latex peel. (B) Tracks from two parallel trackways — B5 (top) and A4 (bottom), photographed from the cast. (C) Track D1 recorded with the latex peel and photographed with low-angle lighting. (D) Track D1 used to illustrate how the total digit divarication was measured using the angular measure tool of Corel DRAW on the tyrannosaur tracks. See Fig. 5 for track identification codings. [Colour online.]

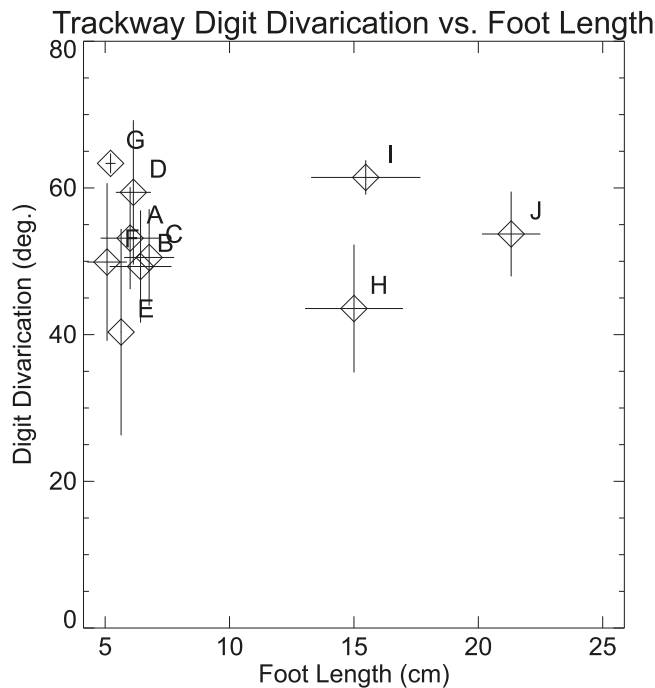


This problem is most likely a combination of initially shallow impressions made by small, light-bodied animals, and the effects of subsequent erosion. Using the numerical quality ranking scale of Belvedere and Farlow (2016), they are in the range of 1–2, with most being 1. Ungual marks are frequently preserved, but there are traces of subdigital pads. There is not much in the way of small-scale, morphological details that are consistent from track to track. Given this lack of detail, and lacking well defined digit margins, it was felt

that making outline drawings of tracks would be a very subjective exercise and not contribute much to the analysis. Instead, images of the best representatives of the four different types of tracks are presented, and quantitative measures of gross morphological features are used to distinguish the different types.

Trackways labelled A through G in Fig. 5 are interpreted as those left by juvenile, possibly hatchling, tyrannosaurids. Figure 6 presents detailed views of some of the better

Fig. 7. Average digit divarications (angle between innermost and outermost digits) for the trackways of Fig. 5, plotted against the corresponding average foot lengths (FL). The thin lines extending vertically and horizontally indicate ± 1 standard deviation (SD) about the mean divarications and FLs. See Table 1 for summary data for each trackway.



preserved tracks in this category in three different ways. Isolated remains of the tyrannosaur *Albertosaurus* are known from the St. Mary River Formation (Brown et al. 2015). These potential tyrannosaurid tracks are composed of three slender digits of equal length that taper distally, have sharp tips, and have an average length of 5.89 cm (standard deviation (SD) = 0.620 cm) as measured along digit III. The mean total digit divarication (as measured between digits II and IV) for trackways A through G is 52.3° (SD = 7.46°) (Fig. 7; Table 1) lies within the 50° – 60° range observed for large theropods (Thulborn 1990, p. 147). Also consistent with a theropod identification are the pace angulation measures for trackways A–D (the only ones for which this value could be determined), as shown in Table 1. This angular measure is typically between 160° and 180° for large theropods, and between 160° and 170° for theropods with a small adult body size (Thulborn 1990). The observed range of pace angulations for trackways A–D, 166° – 173° , fits within the total range associated with small and large theropods. Figure 4 of McCrea et al. (2014a) shows a short trackway from northeastern British Columbia, of Campanian–Maastrichtian age, that is attributed to a tyrannosaurid. The pace angulation as measured from this figure is 173° , and is thus consistent with the pace angulations measured in the present study, further supporting a tyrannosaurid identification. There is the remote possibility that trackways A through G could have been left by juvenile ornithomimids. However, ornithomimid tracks have a

distinctly longer digit III, and the digit traces are frequently connected posteriorly (Sternberg 1926). These features are not seen in trackways A through G.

Trackways interpreted as those of ornithomimids were first identified by Sternberg (1926) from the Horseshoe Canyon Formation, at a site southwest of the hamlet of Rumsey, Alberta (approximately 40 km north of the RTMP). These tracks, known as *Ornithomimipus*, are characterized by a central digit III that is much longer than digits II and IV, with the latter two digits being sub-in equal length and set at a high mutual digit divarication angle of about 78° , and by lacking any impression of the proximal segment of digit II. Trackways H and I of Fig. 5 are also interpreted as having been made by ornithomimids, but in a form that more fully recorded the shape of the foot, possibly a result of contact with a wetter, softer substrate. Figures 8 and 9 show details of three of the *Ornithomimipus* tracks. The long digit III and the modest shape and directional asymmetry of the flanking second and fourth digit impressions are reminiscent of *Ornithomimipus*, but their lower total digit divarication when compared to the type, 48.7° and 61.4° for trackways H and I, respectively (Fig. 5; Table 1), may reflect slightly different conditions at the time of track formation.

Body fossil evidence for small bodied ornithopods is lacking for the St. Mary River Formation, but body fossils of the small (~3 m total length) neornithiscian *Parksosaurus warreni* are known from the Horseshoe Canyon Formation (Parks 1926; Brown et al. 2015), and it is reasonable to infer that *Parksosaurus*, or something similar, also inhabited the environment recorded in the St. Mary River Formation. Trackway J of Fig. 5, representing the longest trackway of the assemblage as it spans the full length of the slab, was likely made by a medium-sized ornithopod. It consists of five variably preserved tracks: two tracks with complete perimeters that unite the proximal margin of the track and the digits (J1 and J2), one track showing partially connected digit impressions (J3), and two tracks showing the distal three-quarters of digits II, III, and IV (J4 and J5). Figure 10 shows details of the best preserved track of the J series – J3. The very short trackway K is represented by two tracks comprising unconnected impressions of digits II, III, and IV, similar to those of trackway J, but smaller. Again, there is a remote possibility that these could be ornithomimid tracks, but the toes lack the noticeably long digit III of *Ornithomimipus*, and are much larger than, and different from, the tracks from trackways H and J, and the single ORNM1–3 of Fig. 5, all of which that are considered to be *Ornithomimipus*. A cast of *P. warreni* (ROM 804) is held in the collections of the RTMP (TMP1980.51.3), and digits II, III, and IV of the right foot of the cast almost perfectly match the size, shape, and uniform pedal digit widths recorded by trackway J, as shown in Fig. 11. In particular, note the correspondingly long digit IV in the track and the skeletal model.

There is limited body fossil evidence for the presence of the hadrosaur *Edmontosaurus* sp. in the St. Mary River Formation (Langston 1976). One modest-sized track preserved on the slab, approximately 12 cm long (labelled “HADR” in Fig. 5) preserved on the slab could have been left by a young hadrosaur. This possible hadrosaur footprint is presented in more detail in Fig. 12. The detailed shaded relief

Table 1. Measurements of trackways identified in Fig. 5. Reported data are the means for each trackways, with standard deviations in parentheses.

Trackway	Track count	Foot length (cm)	Stride length (cm)	Pace angulation (degrees)	Total digit divarication (degrees)
Juvenile tyrannosaurid					
A	17	6.00 (1.19)	47.3 (9.43)	166 (26.4)	53.2 (6.96)
B	9	6.42 (1.24)	57.6 (20.9)	173 (9.32)	49.3 (7.65)
C	4	6.77 (1.00)	59.9 (1.40)	169 (11.3)	50.5 (6.85)
D	4	6.13 (0.705)	43.4 (0.400)	171 (4.24)	59.4 (9.84)
E	2	5.64 (0)	38.0*	–	40.4 (14.1)
F	2	5.08 (0.798)	65.0*	–	49.9 (10.7)
G	2	5.21 (0.200)	38.0*	–	63.4 (1.34)
Ornithomimid					
H	3	14.6 (2.56)	80.1 (0)**	180 (0)**	48.7 (5.00)
I	4	15.5 (2.20)	97.0 (12.7)	160 (12.0)	61.4 (2.34)
Small ornithopod					
J	5	21.3 (1.17)	167 (4.38)	171 (5.13)	53.7 (5.78)
K	2	15.7 (0.100)	108 (0)*	–	35.9 (7.64)

*Only two tracks, so stride length approximated with twice pace length, and no pace angulation.

**Only three tracks, so single measures of stride length and pace angulation.

map is able to show the digits (Fig. 12A), but in contrast, low-angle lighting photographs were not effective (Fig. 12B). The trackways of large hadrosaurs are well documented from the St. Mary River Formation (Currie et al. 1991). The present possible hadrosaur track shows three, thick, subparallel digits, and looks similar to the Early Cretaceous *Amblydactylus* (Currie 1983), only much smaller. The hadrosaurian ichnite described by Langston (1960) shows three thick digits and a prominent proximal margin of track pad. The ichnite of Langston was redescribed by Lockley et al. (2004) as the holotype of the newly erected ichnospecies *Hadrosauropodus langstoni* and is Late Cretaceous in age. The present track is just 17% as long as that holotype specimen and its digits are not as strongly divergent. Nor are the distal lobes of the toes as expanded as in the holotype. There may be a faint trace of a two-lobed proximal margin of track pad in the present specimen. Perhaps a proximal margin of track pad would only become more prominent at large body size. Given these differences, this track cannot be assigned to *Hadrosauropus*, but can be identified as having been made by a hadrosaur.

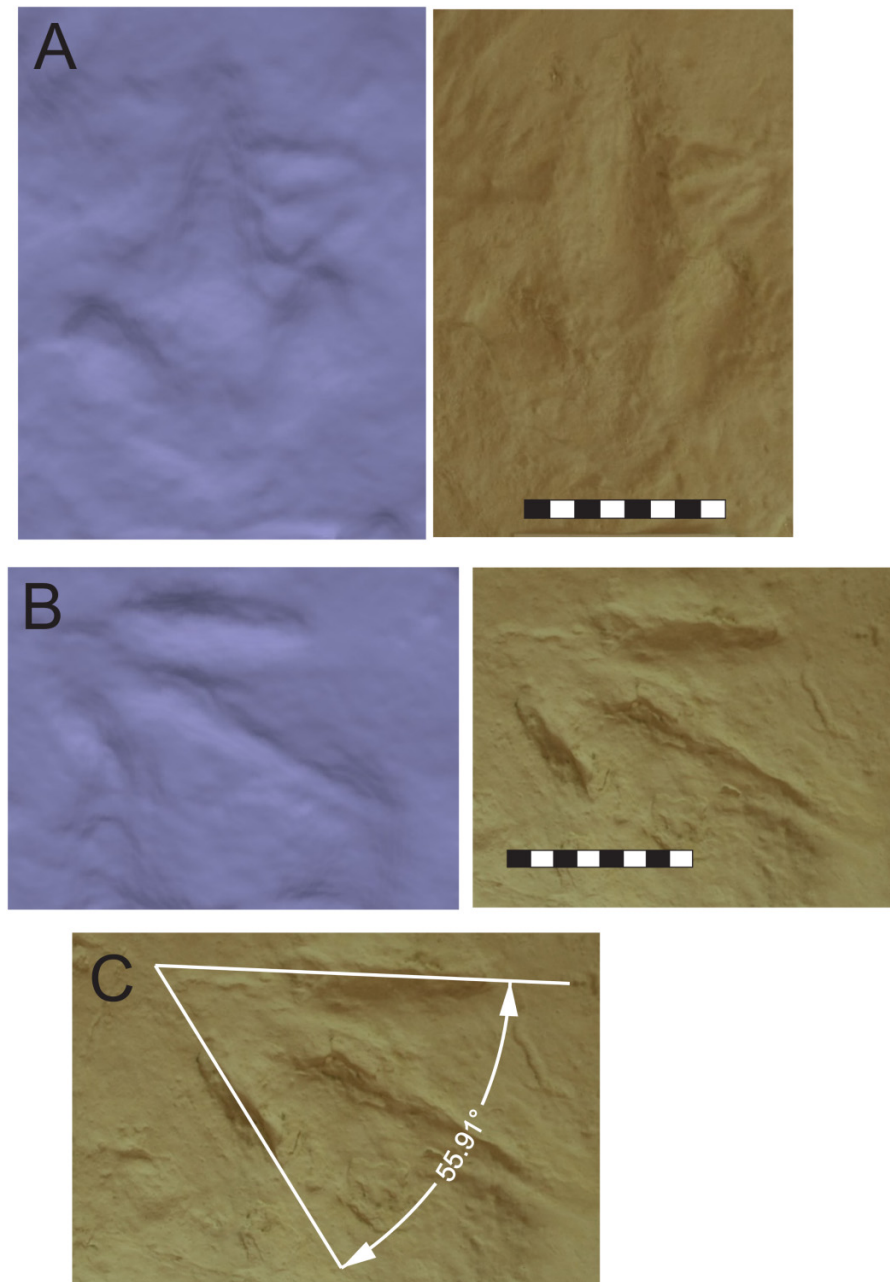
Discussion

The Horseshoe Canyon Formation is time-equivalent to the St. Mary River Formation, and in marked contrast to the latter, hosts 24 dinosaur genera known from body fossils (Brown et al. 2015), but very little in the way of dinosaur tracks. The dinosaurs of the Horseshoe Canyon Formation are represented by fossils of varying degrees of completeness, but include high quality fossils in the forms of complete skulls (e.g., *Arrhinoceratops brachyops*, Dodson et al. 2004) and partial skeletons (e.g., *Pachyrhinosaurus canadensis*, Dodson et al. 2004). The meagre number, and poor quality, of the body fossils from

the St. Mary River Formation is associated with the greater proportion of palaeosols in this formation. The implication is that dinosaur carcasses were left exposed on the surface and subject to subaerial decay and scavenging, instead of being buried in fluvial sediments as they were in the Horseshoe Canyon Formation (Currie et al. 1991).

The tracks of trackways J and K differ from those of *Ornithomimipus* in that the digit impressions are never connected at their bases. Instead, they are reminiscent of the Early Jurassic ichnogenus *Anomoepus*, which is attributed to small ornithiscians (Thulborn 1990, Fig. 6.26). The total digit divarication of tracks like *Anomoepus* ranges from 40° to 80°, but is commonly about 60° (Thulborn 1990, p. 184). The average total digit divarication for trackway J is 53.7° (SD = 5.78°), which lends more support to the interpretation that it was made by a small ornithopod. The pace angulation for small ornithopods is in the range of 150°–170° (Thulborn 1990). The average pace angulation of trackway J is 171° (SD = 5.13°), and falls only just outside the range for small ornithopods. It is possible that the tracks of trackway J could have been made by a pachycephalosaurid with three toes in contact with the substrate, as there is evidence in the form of skull domes for the presence of the pachycephalosaurid *Sphaerotherolus edmontonensis* in the neighbouring Horseshoe Canyon Formation (Eberth et al. 2013; Woodruff et al. 2021). However, if *Sphaerotherolus* had the same body size as the better-preserved *Stegoceras validum* (Lambe 1902), then its FL would only be about 11 cm, approximately half the size of the average FL of 21.3 cm for trackway J. This FL estimate for *S. validum* is based on measurements from two mounted, composite, replica skeletons (TMP 1985.00.02 and TMP 1985.03.15) on display at the RTMP. It is considered unlikely that something like *Sphaerotherolus* could have been the maker of trackway J.

Fig. 8. Details of two of best preserved *Ornithomimipus* tracks. (A) Track ORNM1 as a shaded image from the photogrammetry model and as a photograph taken with low-angle lighting of the cast of the trackway. (B) Track ORNM2 as a shaded relief image and photograph. (C) Track ORNM2 used to illustrate how the total digit divarication was measured using the angular measure tool of Corel DRAW on the *Ornithomimipus* tracks. See Fig. 5 for track identification codings. [Colour online.]



Indeterminate ornithomimid fossil material is known from the St. Mary River Formation, but three species — *Dromiceiomimus brevitertius*, *Ornithomimus edmontonicus*, and *Struthiomimus altus* — are known from the Horseshoe Canyon Formation (Brown et al. 2015). The pace angulation values for trackways left by small theropods ranges from 160° to 170° , but can reach 180° (Thulborn 1990). Trackway H shows a pace angulation of 180° , but that of trackway I is much lower at 160° . This discrepancy is explained by the observation that

trackmaker H was walking in a straight line, while trackmaker I was in the process of turning to the right. In addition to the two, short trackway sets, there are three isolated occurrences of ornithomimid-like tracks labelled “ORN1–3” in Fig. 5. Presumably, these were also originally included in trackways, but the extensive erosion of the slab has removed the evidence. Trackways H and I have approximately parallel trajectories that arc up and to the right, and tracks “ORN2” and “ORN3” have a similar orientation to the first tracks in

Fig. 9. *Ornithomimipus* track H1. The view is reversed left-right as the low-angle lighting photograph was taken from the latex peel. See Fig. 5 for track identification coding. [Colour online.]



trackways H and I. Lockley et al. (2011) report on at least 15 tracks assigned to the ichnogenus *Ornithomimipus* from the Upper Cretaceous “Mesaverde” Group in western Colorado that record animals walking in the same direction and virtually parallel to one other. Based on the average FLs of trackways H and I, respectively, 14.6 and 15.5 cm, the predicted hip heights of these trackmakers are estimated to be in the range of 65–70 cm (Fig. 13; Table 2). As a check on the hip heights estimated from the formulae, a mounted ornithomimid skeleton (TMP 1989.7.3) on display in a standing pose at the RTMP was examined. This mount has a FL of 24.5 cm (length of digit III of 21.5 cm plus the distance to the postero-distal end of metatarsal III). The measured hip height of the mount is 118 cm from the sole of the foot to the centre of the acetabulum. The ratio of hip height to FL for this mount is 4.82, a value similar to the factor of 4.9 in the linear hip height formula for large theropods proposed by Thulborn (1990, p. 251). It should be noted that TMP 1989.7.3 is based on ROM 37207 with additions from other unidentified ROM ornithomimid specimens. The FL of TMP 1989.7.3 is about 63% greater than the average values for trackways H and I, and the hip height is approximately 76% greater than the estimated hip heights for their trackmakers.

The meagre body fossil record for small theropods from the St. Mary River Formation includes remains of *Troodon*, unidentified dromaeosaurids, and the tooth-based genus *Richardoestesia* (a probable troodontid). Troodontids and dromaeosaurids are known to have produced didactyl tracks formed by digits III and IV, as the innermost toe (digit II)

Fig. 10. Three views of the best preserved track interpreted to have been left by a small-bodied ornithopod. This is track J3 from trackway J of Fig. 5. (A) Shaded relief model from photogrammetry. (B) Photograph of the cast of the track. (C) Photograph of the latex peel. This latex replica is reversed top-to-bottom from the original. Note the gastropod trail on the lower right. [Colour online.]

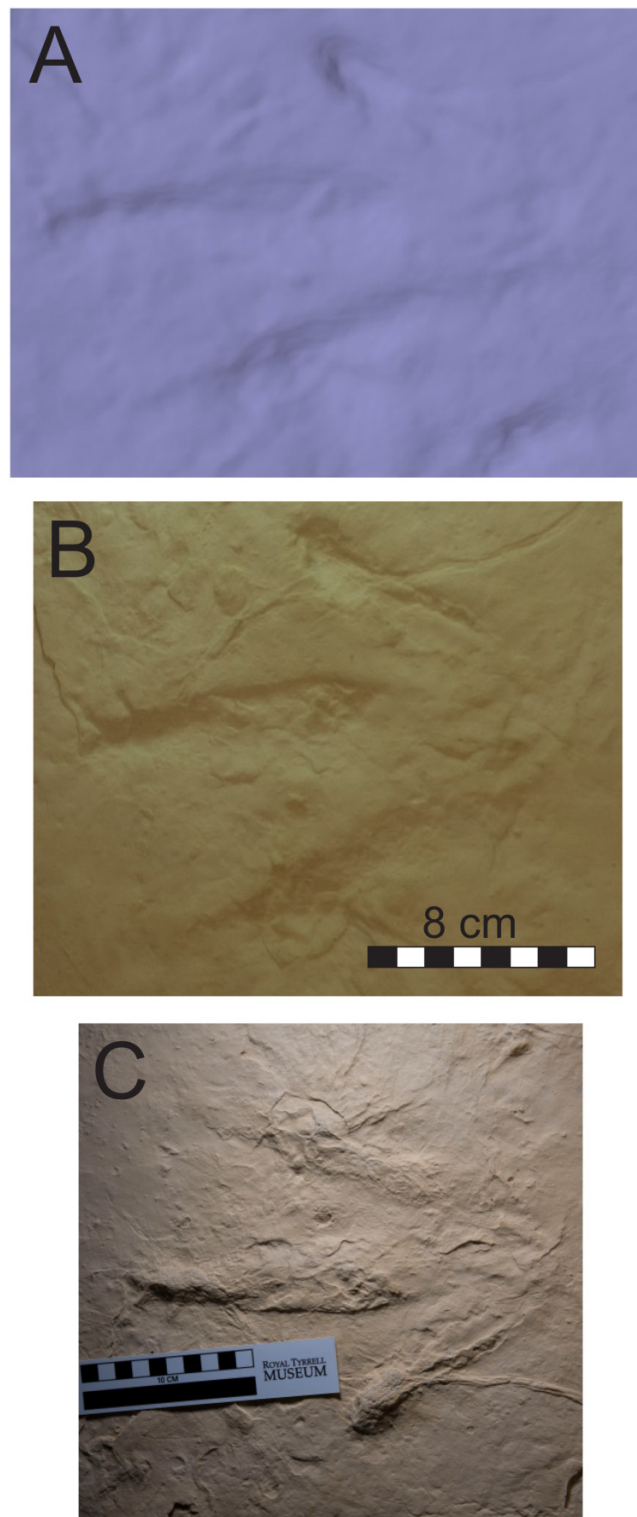
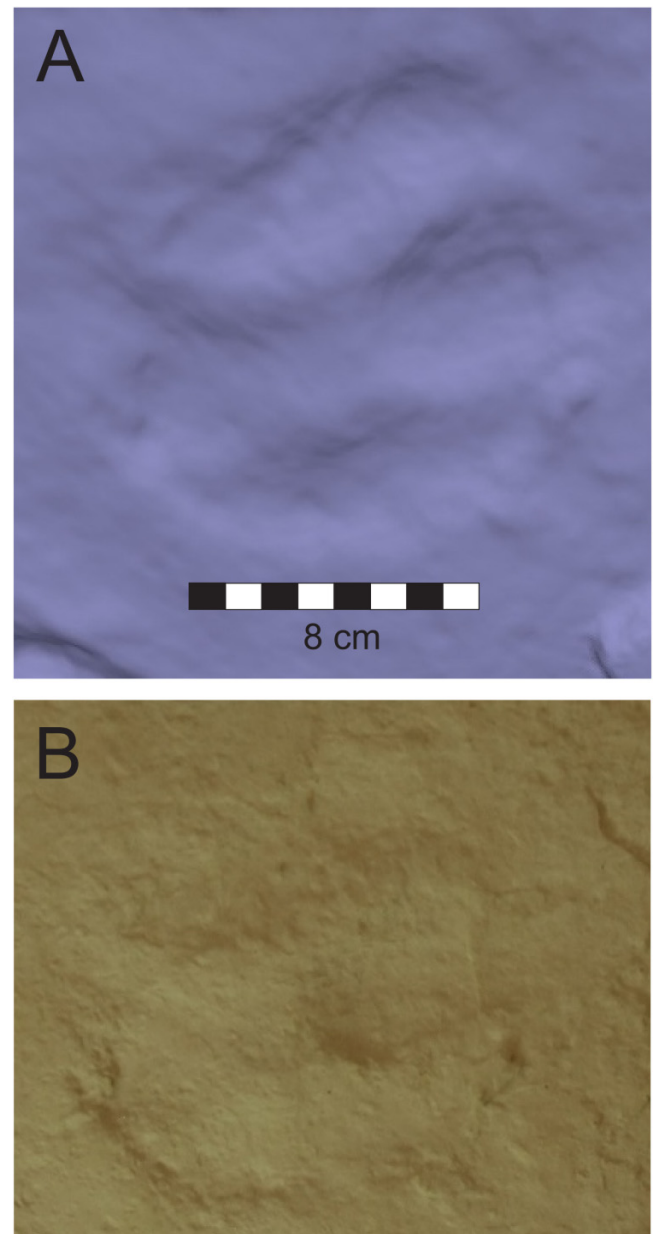


Fig. 11. Track J3 of Fig. 5 with the cast of the right foot of *Parksosaurus warreni* (TMP1980.51.3) to show the close correspondence in size and shape between the two. [Colour online.]



supported a sickle-clawed ungual that was held clear of the ground (Lockley et al. 2016). The tridactyl footprints recorded in trackways A–G are unlike those expected to have been produced by troodontids or dromaeosaurids. There is the possibility that a small theropod such as *Albertonykus borealis* (Longrich and Currie 2009), known from the Horseshoe Canyon Formation, could have been a St. Mary River Formation trackmaker. This alvarezsaurid is closely related to the Mongolian *Mononykus olecranus* (Xu et al. 2011; Agnolin et al. 2012). Unfortunately, there is no complete foot available for *Albertonykus*, but there is a complete foot known for *Mononykus*. The lengths of digits II, III, and IV of the latter are 4.15, 5.09, and 4.61 cm, respectively (Altangerel et al. 1994, table 4), making them just a bit shorter than the digits measured for the smallest St. Mary tracks. However, the three pedal digits of *Mononykus* show marked variation in the thicknesses of the digits, with the widths increasing from digit II to digit IV (Altangerel et al. 1994, fig. 18). In contrast, the small St. Mary River tracks show digits of uniform slenderness (Fig. 6C — track D1), making it unlikely that something like *Albertonykus*/*Mononykus* could be the trackmaker. Juvenile ornithomimids trackmakers can also be excluded as digit III of ornithomimid tracks is much longer than the lateral and medial digits, and their digit divarication is much greater at 78° (Thulborn 1990, p. 163). Of course, this dismissal of

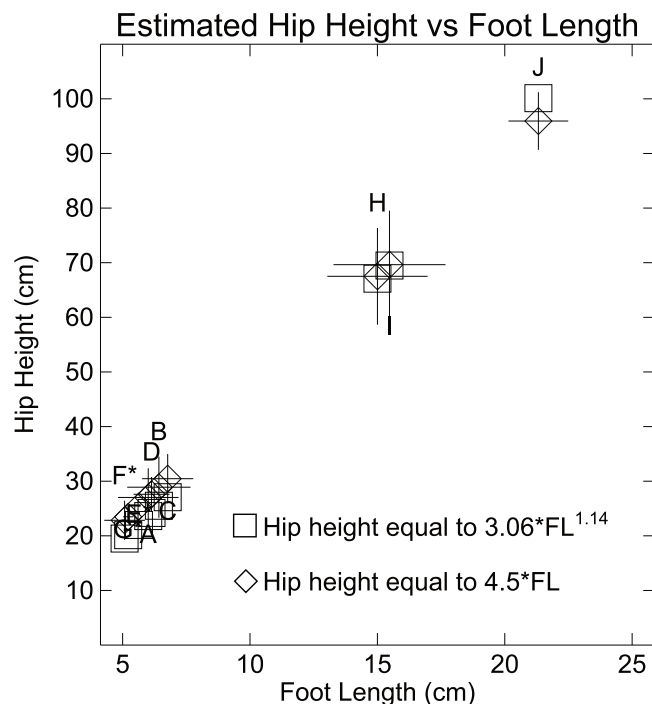
Fig. 12. Possible small hadrosaur track. (A) Shade relief map derived from the photogrammetry model. (B) Photograph of the same from the cast that demonstrates the difficulty of illustrating many of the tracks from this surface. [Colour online.]



juvenile ornithomimids as possible trackmakers assumes that they possessed digit proportions similar to those of adults. The possibility that these small tracks could have been left by birds can also be dismissed. The average divarication between digits II and IV of birds is rarely less than 100° (Currie 1981), while the average divarication for trackways A–G is not more than 65° (Fig. 7).

In his review of Canadian tyrannosaurids, Russell (1970) presented a reconstruction of a hypothetical tyrannosaurid hatchling, and this is produced here (Fig. 14). The stated

Fig. 13. Predicted average hips heights plotted against average FLs for the trackmakers of Fig. 5. Heights are estimated using FL via the two different formulae of *Thulborn (1989)*, linear and exponential, for small theropods. The thin lines extending vertically and horizontally indicate ± 1 SD about the mean hip heights and FLs. Asterisks indicate trackways with just two tracks. See Table 2 for the estimated hip height values.



length of the hatchling femur was 100 mm, the physical length of the femur image on the printed page was 2.6 cm, and these two numbers were used to calculate a scale factor for the figure. Based on this scale factor of 3.85 mm/cm, the length of digit III of the left foot (measured as the combined lengths of the four pedal phalanges) in fig. 3 of *Russell (1970)* was found to be 6.54 cm, a value just 11% more than the observed average FL of 5.89 cm (SD = 0.620 cm) for trackways A through G in Fig. 5 (Table 1). The hip height of the illustrated hatchling was also measured from Russell's fig. 3. This was taken as the length of a straight line down from the acetabulum and perpendicular to a horizontal line tangent to the undersides of the left and right feet, and was found to have a value of 31.2 cm. Using the average FL from each of trackways A through J, the estimated hip heights associated with each trackway are plotted in Fig. 13. Those associated with trackways A through G range from a minimum of 19.5 cm (trackway F, nonlinear formula) to a maximum of 30.5 cm (trackway B, linear formula). The predicted hip heights for the hypothetical hatchling of *Russell (1970)* are 29.4 cm (linear formula) and 26.0 cm (nonlinear formula), and lie towards the high end of the distribution seen in Fig. 6 for trackways A–G. The stance of the hypothetical tyrannosaurid hatchling is very digitigrade (almost unguligrade), and the restored hip height of 31.2 cm could easily be reduced by at least 2 cm

by positioning the full length of digit III on the substrate. This reduction would bring the hip height of the hypothetical juvenile closer to the hip heights predicted from the two formulae.

Except for trackway G, which goes its own way, trackways A through I can be grouped into directional pairs with approximately constant separation between member of each the pair, which suggests that animals were walking together, side-by-side. Lacking the original orientation for the displaced track-hosting slab, we will arbitrarily assume that the direction towards the top of Fig. 5 is north for descriptive purposes. Among the presumed hatchling tyrannosaurids, trackways A and B head west together with an approximately constant separation between them for the first half of trackway A. At its halfway point, the latter turns northwest, but simultaneously we lose the trail of B due to erosion. However, the last footprint, B9, is also directed west-northwest, and it is tempting to assume that the maker of B stayed parallel with A. Along the northern edge of the slab, trackways D and F head west-southwest, in parallel, and are separated by about the same distance as the first half of the A–B trackway pair. Also along the northern edge, trackways C and E would appear to head east-northeast in parallel, and be approximately as far apart as the A–B pair, but unfortunately the preserved parts of these trackways are not side-by-side. The trackways interpreted to have been made by ornithomimids, H and I, are also roughly parallel. Both trackways are directed northwards where they start at the southern edge of the slab, but with subsequent steps they turn to the northeast. Unfortunately, we lose trackway H after the third track. It is the theropod trackways that suggest possible social behaviour via pairing and common directions of travel, while the single ornithopod trackway, J, is solitary. This apparent pattern may be merely an artifact of small sample size, but is in contrast to the many cases in which social behaviour has been inferred from multiple, parallel, simultaneously formed trackways attributed to other ornithopods, e.g., hadrosaurs (*Currie 1983*) and iguanodontids (*Diedrich 2004*).

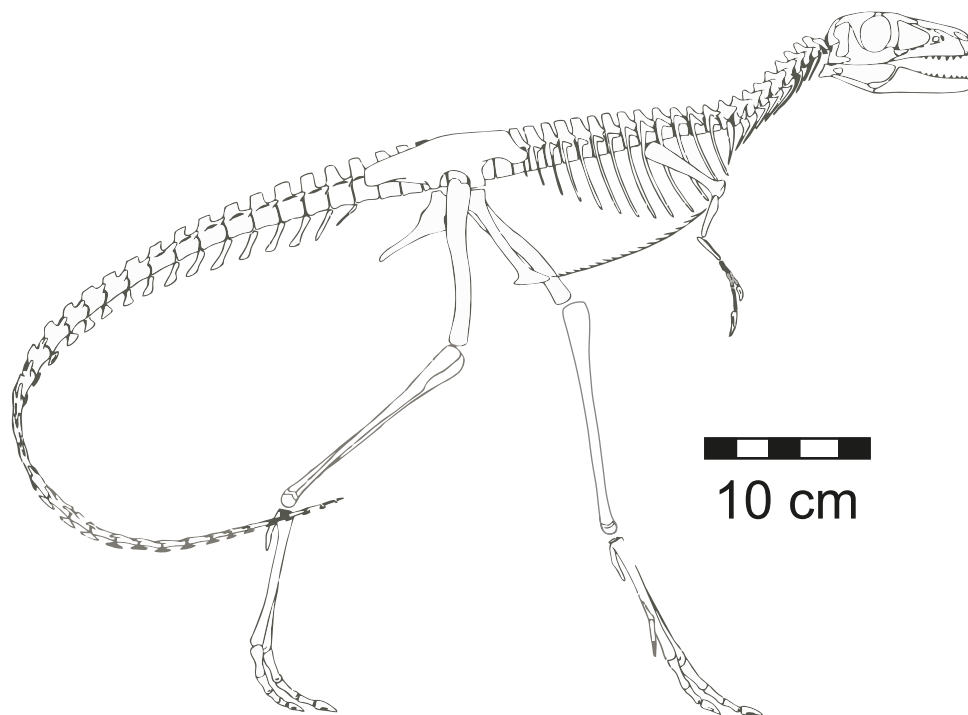
Despite the apparent evidence for discrete pairs of animals walking side by side, when their relative speeds of locomotion are computed, by dividing the observed stride lengths divided by the predicted hip heights, the walking speeds inferred for the trackways, presumed to represent simultaneously formed pairs are not identical (Fig. 15; Table 2). The best examples of a pair of animals walking simultaneously, and at similar speeds, is provided by trackways H and I, the ones interpreted to have been made by medium-sized ornithomimids (Fig. 5). They are estimated to have been similar in hip height (Fig. 13), and their stride length to hip height ratios are similar, lying well within ± 1 SD of each other (Fig. 15). This observation holds true for both hip height estimation methods, linear and nonlinear. However, it is not absolutely essential that animals walking together maintain the exact same speed of travel. Only at high speeds would a collection of animals need to precisely match speeds and maintain near-parallel trajectories (*Cotton et al. 1998*). The trackway samples recorded on the slab represent just a brief snapshot of activity, and cannot be truly representative of the animals' velocities over longer periods. On a positive note,

Table 2. Estimated hip heights (HH) and relative stride speeds (SL/hh) for trackways identified on Fig. 5.

Trackway	HH (linear) (cm)	hh (nonlinear) (cm)	SL/hh (linear)	SL/hh (nonlinear)
Juvenile tyrannosaurid				
A	27.0	23.6	1.75	2.00
B	28.9	25.5	1.99	2.26
C	30.5	27.1	1.97	2.21
D	27.6	24.2	1.57	1.79
E	25.4	22.0	0.749	0.864
F	22.8	19.5	1.42	1.67
G	23.8	20.1	0.809	0.944
Ornithomimid				
H	65.6	64.9	1.28	1.29
I	69.6	69.4	1.39	1.40
Small ornithopod				
J	95.9	1.00	1.74	1.670
K	70.4	70.4	1.67	1.67

Note: Linear refers to the estimation formula $HH = 4.5 \times FL$, and nonlinear refers to the estimation formula $HH = 3.06 \times FL^{1.14}$, where FL is the average foot length for a trackway.

Fig. 14. Hypothetical *Gorgosaurus libratus* hatchling from Russell (1970). The FL and hip height of this reconstructed hatchling are 6.54 cm and 31.2 cm, respectively, and similar to the values observed with trackways A–G in Fig. 5. The almost unguligrade stance of this reconstruction exaggerates the hip height by about 2 cm. See “Discussion” for more details. Image copyright Canadian Museum of Nature and used with permission.



the plotted relative speeds of the small tyrannosaurids, trackways A–G, do form a cluster (Fig. 15), suggesting some sort of common group speed that individuals were attempting to stay close to.

Figures 16 and 17 present rose diagram plots of the heading directions of the trackways, with compass North again taken as the up direction on Fig. 5. Rather than measuring the

orientations of the long-axes of the individual tracks, the direction data taken was taken at regular intervals along the lines that highlight the individual trackways. These data are the compass headings (degrees measured clockwise from North) of a series of vectors tangent to the trackway line. The wider spread of directions for trackway A results from its more meandering nature when compared to the other

Fig. 15. Relative speeds (stride length divided by hip height) for the trackways of Fig. 5 plotted against FLs. The thresholds that define walking, trotting and running are based on the criteria of Thulborn (1990). As is typical of dinosaur trackways, the animals all appear to be walking. Calculations were done using estimates of hip height based on foot length, which in turn used the two different formulae of Thulborn (1989) for small theropods. (A) Linear formula. (B) Exponential formula. The thin lines extending horizontally and vertically indicate ± 1 combined SD (stride length and FL) about the mean values. The starred trackways do not include a documented proper stride (just two tracks), so stride length was estimated as twice the observed pace length.

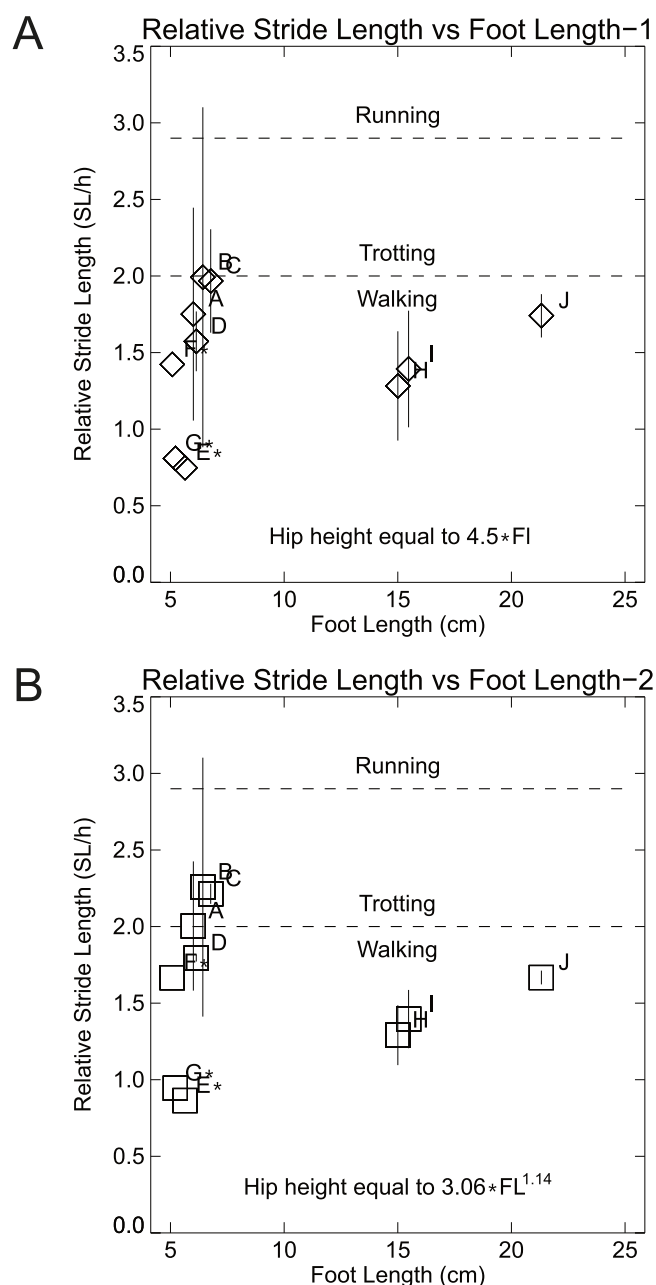
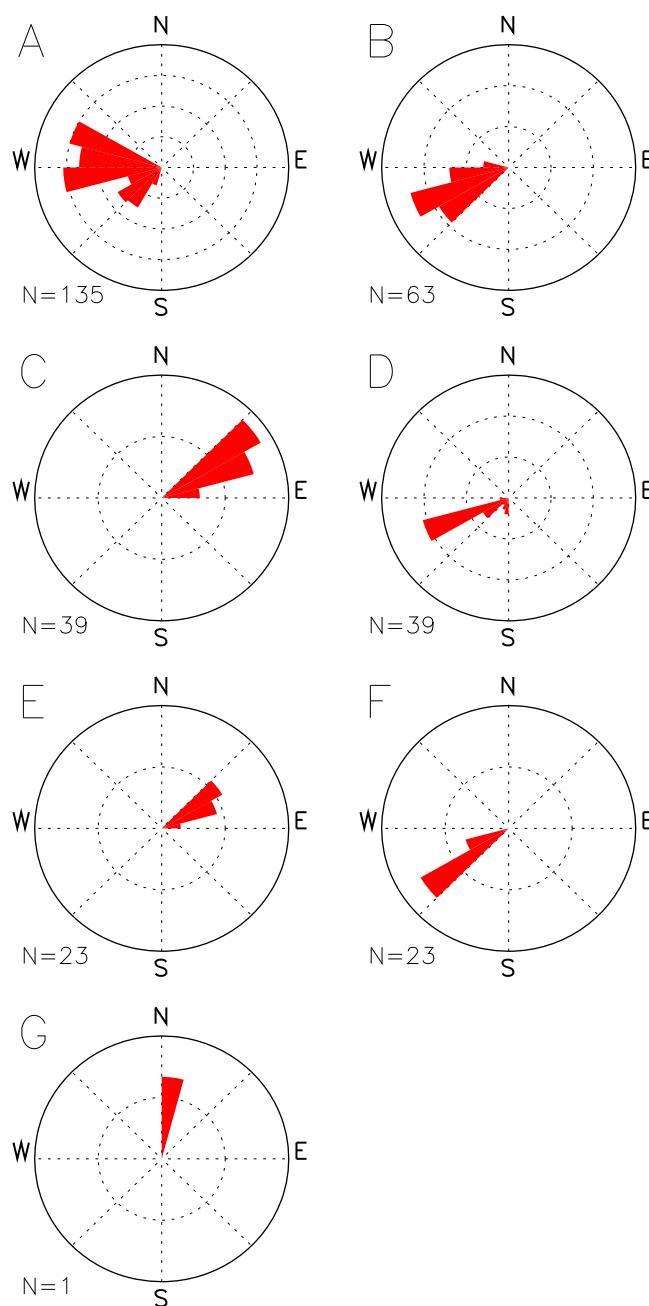
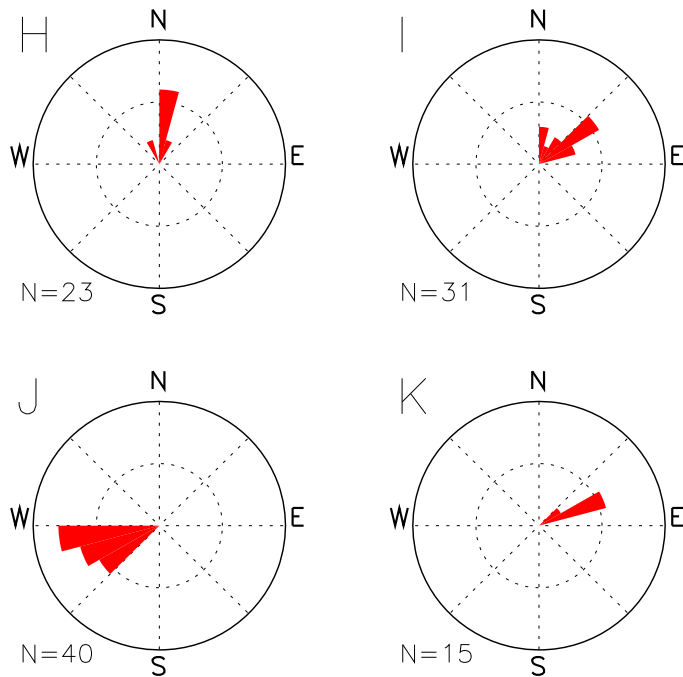


Fig. 16. Rose diagrams showing the heading directions of the smallest trackways of Fig. 5 which are interpreted to have been made by small tyrannosaurids. The plots are identified as per the labelled trackways in Fig. 5. The direction data to produce these plots comes from the orientations of tangent vectors at regularly spaced intervals along each trackway line. Orientation is measured as degrees clockwise from North. Number of vectors plotted ("N") shown in lower left of each plot. [Colour online.]



trackways. All the trackways are approximately parallel, other than H and G, but do not always go in the same direction. This likely reflects some sort physical boundary in the neighbourhood that constrained the animals to walk

Fig. 17. Rose diagrams showing the heading directions of the larger tracks which are presumed to have been made by larger, nontyrannosaurid taxa. Details as per Fig. 16. [Colour online.]



bi-directionally. Given the fluvial nature of the depositional environment (Currie et al. 1991), the direction of traffic may have been controlled by a combination of the river itself and the marginal vegetation. It will also be noted that the trackways lie parallel to the long edges of the slab. The planes of weakness of the parent rock of the slab will have controlled how the rock broke, both initially at the cliff face and when the slab hit the ground. The orientation of these future fracture planes may have been determined by how the sands, silts, and muds were originally deposited, and reflect their orientation with respect to the river channel.

Conclusions

Body fossils of dinosaurs are extremely rare in the St. Mary River Formation, but trackways are abundant at particular horizons. The fortuitous presence of the geographically adjacent and time-equivalent Horseshoe Canyon Formation, along with the much better dinosaur body fossil record of the former, makes it possible to identify four different trackmakers, of varying body sizes, on the discovery slab. The two most notable features of this trackway assemblage are: multiple, paired tracks left by hatchling tyrannosaurids (most likely *Albertosaurus sarcophagus*), and the indications of the presence of a medium-sized neornithiscian (most likely *P. warreni*). Although the discovery slab was heavily eroded, there is every expectation of future discoveries of more pristine trackways from the formation that will have the potential to reveal more details.

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Data availability

The raw data used to construct Tables 1 and 2 is available upon request from the corresponding author.

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Benjamin Borkovica and Joseph Sanchez contributed equally to this work.

Author contributions

DMH, BB, and JS performed the fieldwork. ALK produced the photogrammetry model. DMH wrote the text with input from BB, JS, and ALK. All authors contributed to the delineation of individual trackways. DMH collected the quantitative data, performed the calculations, and produced the figures.

Competing interests

The authors declare there are no competing interests.

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References

- Agnolin, F.L., Powell, J.E., Novas, F.E., and Kundrát, M. 2012. New alvarezsaurid (Dinosauria, Theropoda) from uppermost Cretaceous of north-western Patagonia with associated eggs. *Cretaceous Research*, 35: 33–56. doi:10.1016/j.cretres.2011.11.014.
- Altangerel, P., Chiappe, L.M., Rinchen, B., Clark, J.M., and Norell, M.A. 1994. Skeletal morphology of *Mononykus olecranus* (Theropoda,

- Avialae) from the late Cretaceous of Mongolia. *American Museum Novitates*, (3105): 1–29.
- Belvedere, M., and Farlow, J.O. 2016. A numerical scale for quantifying the quality of preservation of vertebrate tracks. *In* *Dinosaur tracks: the next steps*. Edited by P.L. Falkingham, D. Marty and A. Richter. Indiana University Press, Bloomington, IN. pp. 92–99.
- Borkovic, B., and Sanchez, J. 2016. Southern Alberta Flood Mitigation Project—Palaeontology. Royal Tyrrell Museum of Palaeontology, Drumheller.
- Brown, C.M., Ryan, M.J., and Evans, D.C. 2015. A census of Canadian dinosaurs: more than a century of discovery. *In* *All animals are interesting: A Festschrift in honour of Anthony P. Russell*. Edited by Bininda-Emonds. BIS Verlag, Oldenburg, Germany. pp. 151–209.
- Corel Draw. 2018. Corel Corporation, Ottawa, ON.
- Cotton, W.D., Cotton, J.E., and Hunt, A.P. 1998. Evidence for social behavior in ornithomimid dinosaurs from the Dakota Group of northeastern New Mexico, U.S.A. *Ichnos*, 6(3): 141–149. doi:10.1080/10420949809386445.
- Currie, P.J. 1981. Bird footprints from the Gething Formation (Aptian, Lower Cretaceous) of northeastern British Columbia, Canada. *Journal of Vertebrate Paleontology*, 1: 257–264. doi:10.1080/02724634.1981.10011900.
- Currie, P.J. 1983. Hadrosaur trackways from the Lower Cretaceous of Canada. *Acta Palaeontologica Polonica*, 28(1-2): 63–73.
- Currie, P.J. 1989. Dinosaur footprints of western Canada. *In* *Dinosaur tracks and traces*. Edited by D.D. Gillette and M.G. Lockley. Cambridge University Press, Cambridge. pp. 293–300.
- Currie, P.J., Nadon, G.C., and Lockley, M.G. 1991. Dinosaur footprints with skin impressions from the Cretaceous of Alberta and Colorado. *Canadian Journal of Earth Sciences*, 28(1): 102–115. doi:10.1139/e91-009.
- Diedrich, C. 2004. New important iguanodontid and theropod trackways of the tracksite Obernkirchen in the Berriasian of NW Germany and megatracksite concept of central Europe. *Ichnos*, 11: 215–228. doi:10.1080/10420940490444924.
- Dodson, P., Forster, C.A., and Sampson, S.D. 2004. Ceratopsidae. *In* *The Dinosauria*. 2nd ed. Edited by D.B. Weishampel, P. Dodson and H. Osmlska. University of California Press, Berkeley, CA. pp. 494–513.
- Eberth, D.A., Evans, D.C., Brinkman, D., Therrien, F., Tanke, D.H., and Russell, L.S. 2013. Dinosaur biostratigraphy of the Edmonton Group (Upper Cretaceous), Alberta, Canada: evidence for climate influence. *Canadian Journal of Earth Sciences*, 50: 701–726. doi:10.1139/cjes-2012-0185.
- Hamilton, W.N., Price, M.C., and Langenberg, C.W. (compilers), 1999. Geological Map of Alberta. Alberta Geological Survey, Alberta Energy and Utilities Board, Map No. 236, scale 1:1,000,000.
- Lambe, L.M. 1902. On vertebrata of the mid-Cretaceous of the Northwest Territory. 2. New genera and species from the Belly River Series (mid-Cretaceous). *Contributions to Canadian Palaeontology*, 3: 25–81.
- Langston, W.J. 1960. A hadrosaurian ichnite. *Natural History Papers*, National Museum of Canada, 4: 1–9.
- Langston, W.J. 1976. A Late Cretaceous vertebrate fauna from the St. Mary River Formation in western Canada. Edited by C.S. Churcher. Athlons, Royal Ontario Museum Toronto, ON. pp. 114–133.
- Lockley, M. 1991. *Tracking dinosaurs*. Cambridge University Press, Cambridge.
- Lockley, M.G., Nadon, G., and Currie, P.J. 2004. A diverse dinosaur-bird footprint assemblage from the Lance Formation, Upper Cretaceous, eastern Wyoming: implications for ichnotaxonomy. *Ichnos*, 11(3–4): 229–249. doi:10.1080/10420940490428625.
- Lockley, M.G., Cart, K., Martin, J., and Milner, A.R.C. 2011. New theropod tracksites from the Upper Cretaceous Mesaverde Group, western Colorado: implications for ornithomimid track morphology. *New Mexico Museum of Natural History and Science Bulletin* 53: 321–239.
- Lockley, M.G., Xing, L., Matthews, N.A., and Briethaupt, B.H. 2016. Didactyl raptor tracks from the Cretaceous, Plainview Sandstone at Dinosaur Ridge. *Cretaceous Research*, 61: 161–168. doi:10.1016/j.cretres.2016.01.007.
- Longrich, N.R., and Currie, P.J. 2009. *Albertonykus borealis*, a new alvarezsaur (Dinosauria: Theropoda) from the Early Maastrichtian of Alberta, Canada: implications for the systematics and ecology of the Alvarezsauridae. *Cretaceous Research*, 30(1): 239–252. doi:10.1016/j.cretres.2008.07.005.
- McCrea, R.T., Buckley, L.G., Farlow, J.O., Lockley, M.G., Currie, P.J., Matthews, N.A., and Pemberton, S.G. 2014a. A "Terror of Tyrannosaurs": the first trackways of tyrannosaurids and evidence of gregariousness and pathology in Tyrannosauridae. *PLoS ONE*, 9(7): 1–13. doi:10.1371/journal.pone.0103613.
- McCrea, R.T., Buckley, L.G., Plint, A.G., Currie, P.J., Haggart, J.W., Helm, C.W., and Pemberton, S.G. 2014b. A review of vertebrate track-bearing formations from the Mesozoic and earliest Cenozoic of western Canada with a description of a new theropod ichnospecies and reassignment of an avian ichnogenus. *New Mexico Museum of Natural History and Science Bulletin*, 62: 5–93.
- Nadon, G.C. 1993. The association of anastomosed fluvial deposits and dinosaur tracks, eggs, and nests: implications of floodplain environments and a possible survival strategy for ornithomids. *Palaio*, 8: 31–44. doi:10.2307/3515220.
- Parks, W.A. 1926. *Thescelosaurus warreni*, a new species of orthopodous dinosaur from the Edmonton Formation of Alberta. *University of Toronto Studies (Geological Series)*, 21: 1–42.
- Pomeroy, J.W., Stewart, R.E., and Whitfield, P.H. 2015. The 2013 flood event in the South Saskatchewan and Elk River basins: causes, assessment, and damages' *Canadian Water Resources Journal*, 41: 105–117. doi:10.1080/07011784.2015.1089190.
- Russell, D.A. 1970. Tyrannosaurs from the Late Cretaceous of western Canada. *National Museum of Natural Sciences Ottawa*, Publications in Palaeontology, 1: 1–34.
- Sternberg, C.M. 1926. Dinosaur tracks from the Edmonton Formation of Alberta, *Museums Bulletins, Geological Series*, 44: 85–87.
- Thulborn, T. 1989. The gaits of dinosaurs. *In* *Dinosaur Tracks And Traces*. Edited by D.D. Gillette and M.G. Lockley. Cambridge University Press, Cambridge. pp. 39–50.
- Thulborn, T. 1990. *Dinosaur tracks*. Chapman and Hall, London.
- Woodruff, D.C., Goodwin, M.B., Lyson, T.R., and Evans, D.C. 2021. . *Zoological Journal of the Linnean Society*, 193 563–601. doi:10.1093/zoolinnean/zlaa179.
- Xu, X., Sullivan, C., Pittman, M., Choiniere, J. N., Hone, D. W. E. Upchurch, P., et al. 2011. A monodactyl nonavian dinosaur and the complex evolution of the alvarezsaurid hand. *Proceedings of the National Academy of Sciences*, 108(6): 2338–2342. doi:10.1073/pnas.1011052108.