

Inferred evidence of webbing in a possible Cretaceous avian track from northeastern British Columbia

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Abstract: Northeastern British Columbia is of global significance with regard to Mesozoic avian tracks, and new discoveries from the region can be anticipated. A possible short avian trackway has been identified on a surface known to contain a variety of tetrapod tracks and traces preserved in fine detail. The putative outer digits (digits II and IV) of the best-preserved track exhibit incurving, which in extant bird tracks can be regarded as a proxy for webbing. If the putative tiny tracks are indeed avian in origin, and if webbing in Mesozoic avian tracks also resulted in incurved outer digit impressions, then this ichnosite is among the oldest in the global record with evidence of fully webbed feet in avians. It would also be the youngest (most recent) of the known fossil avian tracksites in B.C., the first from the Late Cretaceous, and the first from the Dunvegan Formation.

Key words: Mesozoic, Cenomanian, Dunvegan Formation, avian palaeoichnology, webbing.

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Introduction

Cretaceous rocks from the Peace Region of northeastern B.C. are known to contain numerous tracks and traces of dinosaurs, turtles, crocodylians and avians. Dinosaur tracks were first identified in 1922 in the Peace River Canyon (McLearn 1923). In reviewing vertebrate track-bearing formations from the Mesozoic in Western Canada, McCrea *et al.* (2014) noted that this track record from the Cretaceous Period is one of the most complete and continuous at a global level, and that tracks and traces had been identified in all the terrestrial geological formations that had been investigated.

The world's first Mesozoic Era avian tracks (assigned the genus *Ignotornis*) were described from Colorado (Mehl 1931) and are 100–95 Ma (million years old). This was followed by a report of Early Cretaceous avian tracks from South Korea (Kim 1969). The third report came from the Peace River Canyon of 117 Ma tracks assigned to *Aquatilavipes swiboldae*. The tracks were thought to have been made by a small shorebird, and at the time they provided the oldest evidence in the world of avian tracks (Currie 1981).

The known North American fossil avifauna remained relatively sparse until further discoveries were made in northeastern B.C. and neighbouring Alberta, which are briefly reviewed here in chronological order of identification. As suggested by Lockley *et al.* (2021), avian track sizes can be conveniently grouped into categories of small, medium and large (< 5.0, 5.0–10.0 and >10.0 cm respectively).

A loose slab, first identified in 1994 on Mt. Roman (southeast of Tumbler Ridge), containing a 100 Ma avian trackway, was airlifted by helicopter to the Tumbler Ridge Museum in 2014. Under optimal lighting not only were fifty tridactyl tracks evident that could possibly be ascribed to *Aquatilavipes swiboldae*, but larger tracks with a faint hallux impression could be discerned. Combined with the discovery of similar tracks near Grande Cache in northwestern Alberta, this led to the naming of *Ignotornis canadensis* (Buckley *et al.* 2018).

Crane-like tracks were reported from near Grande Cache in northwestern Alberta (McCrea and Sarjeant 2001), followed by a similar discovery in 2005 of moderately large ~117 Ma tracks on the shore of Williston Lake near Hudson's Hope in northeastern B.C. The tracks were named *Limiavipes curriei* (McCrea *et al.* 2014).

Also in 2005, ~110 Ma plover-like tracks were identified on Mt. Babcock (southeast of Tumbler Ridge). The 72 avian tracks, found beside theropod tracks and a single ornithopod track, were named *Paxavipes babcockensis* by McCrea *et al.* (2015).

Although not yet formally described, fossil avian (or avian-like) tracks have subsequently been identified from further localities in the Tumbler Ridge area. One slab identified in 2014 was in Earliest Cretaceous sediments (~140–130 Ma), and thus contained some of the oldest known avian tracks in the world. It was airlifted out of a canyon by helicopter to the Tumbler Ridge Museum after theropod tracks had been noted on its surface. The two avian tracks, 6 cm in length, were only observed under optimal lighting conditions in the museum.

The second example is of the enigmatic track type known as *Magnoavipes*. While its name (translated as ‘big bird-foot’) suggests that such tracks were made by large birds, its avian affinity is not proven. No body fossils of birds of this size have been found from the Cretaceous Period, and the current consensus seems to favour a small to medium-sized non-avian theropod dinosaur, such as an ornithomimid, as the trackmaker (Lockley *et al.* 2021). The controversy can be avoided by simply noting that *Magnoavipes* is a large track made by a large bird-like dinosaur. One 95 Ma track from near Tumbler Ridge has been assigned to *Magnoavipes*, with a recorded length of 23.4 cm (McCrea *et al.* 2014). While this was the first *Magnoavipes* track to be recorded from B.C. and Canada, similar tracks (~117 Ma) have subsequently been identified at the Six Peaks tracksite near Hudson’s Hope (McCrea *et al.* 2017).

In combination, these findings form an important part of the global avian ichnofossil record. They illustrate the capacity of the region to harbour well-preserved avian tracks, and the potential for further discoveries. A possible newly identified avian trackway is detailed below, with the purpose of describing the site and considering possible implications, as well as the limitations to detailed interpretation.

Geological context

The possible short trackway was identified on the same surface as tracks and traces of giant crocodiles, ankylosaurs, ornithopods and turtles, reported by Plint *et al.* (2022). The loose slab containing the tracks lay in the ditch beside Highway 29 in the Sukunka valley between Tumbler Ridge and Chetwynd in northeastern B.C. Its origin was in cliff bands which had been created during highway construction, from a laterally persistent layer which contained numerous vertebrate tracks and traces. These non-marine sediments form part of the Dunvegan Formation from the middle Cenomanian Stage (97–95 Ma) of the Late Cretaceous Period. A palaeolatitude of 61°–66° can be in-

ferred, implying prolonged periods of winter darkness (Van Hinsbergen *et al.* 2015) during the temperate climatic conditions of the Late Cretaceous.

The Dunvegan Formation represents a substantial delta complex in the proximal foredeep of the Western Canada Foreland Basin, and the sediments from the region of the tracksite were inferred to have been located ~100 km from the western shoreline of the Western Interior Seaway, which joined the Polar Ocean to the Gulf of Mexico (Plint *et al.* 2022). The environment would have comprised shallow lakes, channels, crevasse splays and well-vegetated lowlands, with alternating phases of flooding and emergence. These cycles influenced whether vertebrates swam or were able to walk on the muddy or silty substrates.

The finest tracks and traces are preserved in hyporelief (*i.e.*, as natural casts), representing the (usually sandy) layer of sediment that filled in the track-bearing surface. Tracks and traces exhibiting high morphological detail would typically have been registered in cohesive mud that was neither too firm nor too wet. This would have allowed for preservation of features in high fidelity (*e.g.*, skin impressions and slide marks in dinosaur tracks and scale striations in crocodylian swim traces). Tracks could be seen *in situ* on the undersides of overhangs, forming part of the relatively level, main track-bearing layer. If they become inverted, loose blocks falling from the cliffs into the ditch beside the highway may thus show evidence of tracks in hyporelief.

Methods

After light brushing of the surrounding surface, track measurements included length, width, depth, putative pace length, and interdigital angles. Photographs were taken, including photogrammetric analysis (Matthews *et al.* 2016). 3-D models were generated with Agisoft MetaShape Professional (v. 1.0.4) using an Olympus TG-5 camera (focal length 4.5 mm; resolution 4000 x 3000; pixel size 1.56 x 1.56 µm). The final images were rendered using CloudCompare (v.2.10-beta).

Results

Three small raised areas were noted in hyporelief in a near-linear pattern (Figure 1) on the surface of a loose block that also contained numerous other tetrapod tracks. The proximal and distal ‘tracks’ were amorphous, but the middle feature closely resembled a tridactyl avian track (Figure 2). The proximal track exhibited the most relief, with a depth of just less than 1 cm.

In the middle track, each of the three putative digits tapered sharply anteriorly, and the outer digits exhibited

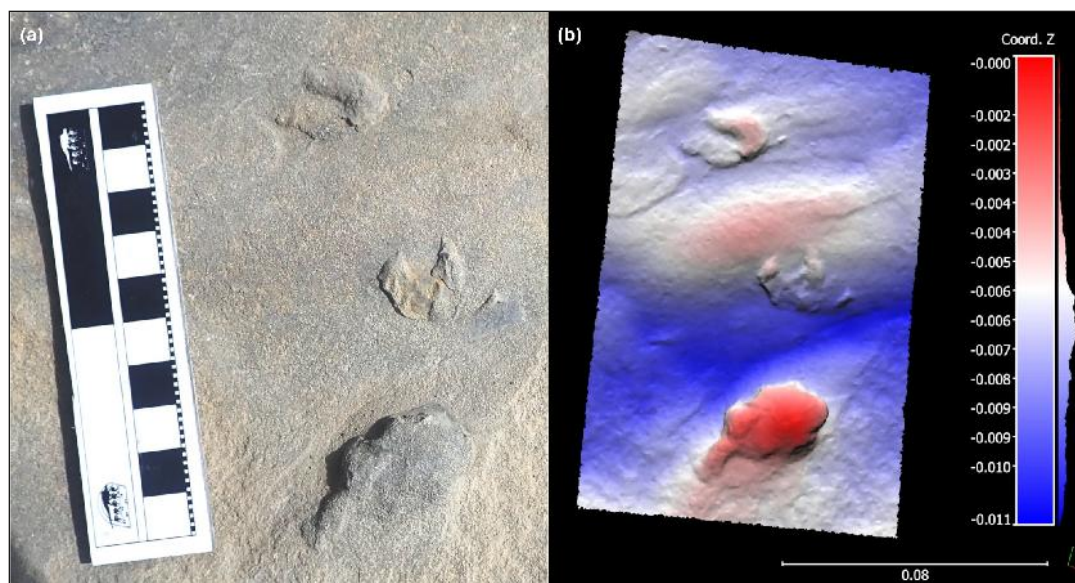


Figure 1. (a) The putative short avian trackway; scale bar is in cm and mm. (b) 3D photogrammetry image of the putative avian trackway, using 23 images. Photos were taken average 27.3 cm from the surface. The reprojection error is 0.306 pix. Vertical and horizontal scales are in metres.

incurving. There was no evidence of a digit I (hallux) impression. Track length of 2 cm, track width of 3 cm, and depth of ~ 0.3 cm were recorded. Antecedent divarication angles (Scott *et al.* 2012) were $\sim 80^\circ$ between digits II and III, $\sim 80^\circ$ between digits III and IV, and $\sim 160^\circ$ between digits II and IV.

The distance between the proximal and middle putative track features, and between the middle and distal features (*i.e.*, the putative pace length) was 5 cm. The proximal putative track arguably showed evidence of digits, in a pattern that was symmetrical with those of the middle track, but if so, they were vague in outline and rounded (*i.e.*, they exhibited poorly preserved morphology). Even less could be interpreted in the amorphous distal feature. The three features did not occur in a straight line, but displayed an angle of 150° .

Discussion

The problem in interpreting the purported avian trackway is made clear through heeding the sage advice of Sarjeant (1989, p. 369), which remains fundamental to palaeoichnology:

Quite evidently a trackway – a series of successive footprints of both, or of all four, feet – is the best possible basis for the definition of a footprint ichnospecies. A set of prints... is the next best basis.

A trackway with good preservation of detail and sufficient numbers of tracks would be ideal, but clearly in this case there is just one possible track that exhibits adequate morphological detail. Although it contains

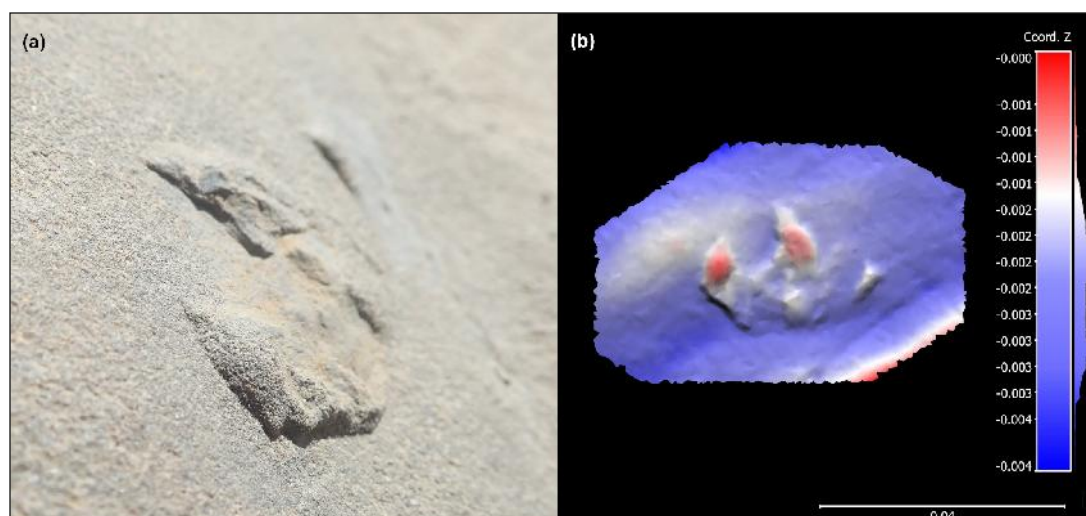


Figure 2. (a) Oblique view of the middle track. (b) Tight 3D photogrammetry image of the middle track, with the same metrics as in Figure 1 (b).

enough features to suggest an avian origin, an alternative explanation of a non-biogenic feature that happens to closely resemble an avian track cannot be totally excluded.

The regular spacing of the three raised areas likewise suggests a short trackway or trackway segment – the amorphous nature of the first and third features could be ascribed either to substrate variations or to the mechanics of alighting and taking off. The measured angle of 150° between the three putative tracks might imply a direction change in a narrow-straddle trackway, or may represent a wider-straddle trackway. Without a longer trackway, no further inferences can be made. However, this is speculative, and alternative explanations cannot be fully excluded. The fact that these possible avian tracks were identified on a surface with the proven capacity to preserve vertebrate tracks and traces in outstanding detail increases the likelihood of their being a genuine ichnological phenomenon, but this too does not constitute proof.

Nonetheless, if the assumption is accepted that the observed features are of probable avian origin, intriguing considerations emerge:

- At 97–95 Ma, it would be the youngest (most recent) of the known fossil avian tracks in B.C., the first from the Late Cretaceous, and the first from the Dunvegan Formation.
- The middle track is tiny; nowadays a sandpiper or tern might register a track with these dimensions.
- In extant species, incurving of the outer digits can be regarded as a proxy for the presence of full (palmate) webbing (Elbroch and Marks 2001).

If a similar phenomenon occurred in the Mesozoic, and incurving of digit II and IV impressions can be regarded as a proxy for palmate webbing in Mesozoic tracks, and if the described track indeed is of avian origin, then this might be the oldest reported evidence in North America of webbing in avians. The oldest reported ichnological evidence of webbed avian tracks comes from South Korea, dated to ~117 Ma (Kim *et al.* 2006) and China, dated to ~110 Ma (Lim *et al.* 2000). In the body fossil record, avian webbing has been reported from approximately the same time period (115–105 Ma) from China (You *et al.* 2006). Within North America, web impressions have been demonstrated in 80 Ma avian tracks from Alaska (Fiorillo *et al.* 2011). It should be noted that Mehl (1931) considered that *Ignotornis* might exhibit possible evidence of webbing, but Lockley *et al.* (2009) in reviewing this material found no such evidence. It has also been suggested that what appear to be web impressions in fossil avian tracks might in some cases be preservational features (Falkingham *et al.* 2009). Using incurving of digits II and IV as a proxy for webbing would side-step such debate.

The above-mentioned sites from which ancient evidence of webbing has been reported involve partial webbing, similar perhaps to that of the Semipalmated Plover (*Charadrius semipalmatus*) or Semipalmated Sandpiper (*Calidris pusilla*), in which the webbing does not extend the full length of the digits. Full (palmate) webbing is evident at ~85 Ma from South Korea, through tracks resembling those of ducks (Yang *et al.* 1996). It is conceivable that the putative northeastern B.C. track, at 97–95 Ma, therefore represents the oldest evidence in the global ichnology record for fully webbed feet in avians.

Among extant North American birds, the Least Tern (*Sternula antillarum*) might be capable of making tracks of this size and morphology. Indeed, a similar short Pleistocene (~130 ka) trackway of three tracks has been reported from the Cape south coast of South Africa (Helm *et al.* 2020), and ascribed to a small tern trackmaker (Figure 3).

Avian tracks are often small, fragile and shallowly impressed. Dedicated searching is required to find them in the fossil record, compared with the search for the tracks of larger tetrapods such as dinosaurs, which can often be identified at a walking pace. As demonstrated in two northeastern B.C. examples, examination of surfaces under optimal lighting conditions may lead to the identification of tracks that were not initially evident. A bright LED light shone from a controlled angle might help identify such tracks during fieldwork. The possibility that the putative track described here may represent the oldest ichnological evidence in the world for birds with fully webbed feet can act as a spur for further thorough searching on suitable surfaces in northeastern B.C.

Every discovery of this nature can be regarded as a miracle of preservation: track-containing sediments were



Figure 3. Pleistocene avian track from the South African coast; scale bar is in cm and mm.

buried for millions of years, then re-exposed through erosion or cliff collapse, and identified and interpreted in the brief window of time between re-exposure and destruction. Over time, many hundreds or thousands of fossil avian tracksites may have been exposed and may have disappeared in northeastern B.C. without ever being recognized. Finding such sites requires dedicated searching, rewarded by the potential of a glimpse of structure and diversity in deep ornithological time.

Conclusions

Northeastern B.C. is of global significance in Mesozoic avian ichnology. The evidence from the Sukunka valley site beside Highway 29 is tantalizing and suggestive, but not incontrovertible. It is possible that features described from the site represent not only the youngest avian tracks in B.C. and the oldest evidence of webbing in North America, but also the oldest ichnological evidence of full (pal-mate) webbing yet identified globally. Given these rather profound implications, a cautious approach is warranted, and a thorough search for similar phenomena is indicated in northeastern B.C.

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