Selected Studies on Terrestrial Vertebrate Palaeoichnology of Western Canada

by

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ABSTRACT

The past quarter century has seen a marked increase in the recognition of fossil vertebrate tracksites in western Canada, primarily in Alberta and British Columbia. Notable new finds include the first record of sauropods in Canada, evidence of herding behavior in tyrannosaurs and ankylosaurs, multiple avian track sites nearly spanning the entire Cretaceous Period, and recognition and description of pathologies from footprints. First discoveries of track specimens from several formations in western Canada include the Mountain Park Member of the Gates Formation in Alberta, and the Boulder Creek, Goodrich, Kaskapau, Cardium and Marshybank formations in northeastern British Columbia. Significant finds continue to be made in the Wapiti Formation in western Alberta near Grande Cache and in northeastern British Columbia.

Tracks are virtually unknown from pre-Cretaceous rocks in western Canada, with the only possible exception being the last stage of the Jurassic (Tithonian). The majority of the oldest tracksites are found in and around the Rocky Mountains of British Columbia, whereas the younger tracksites are found in the Foothills and Plains of both British Columbia and Alberta. The record of fossil vertebrate tracks in western Canada is important for filling the temporal gaps in known occurrences of terrestrial vertebrates left by a sparse skeletal record. Fossil tracks and trackways can also be used to interpret the behavior, biomechanics and ecology of extinct animals in ways not possible to realize solely from the study of skeletal remains.

ACKNOWLEDGEMENTS

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Charles Helm (M.D.) deserves special mention for his enthusiasm (shared by his family) and commitment to finding new fossil track sites in difficult terrain.

I also would like to gratefully acknowledge the time and attention of thesis committee members Dr. Tom Chacko, Dr. Murray Gingras, Dr. Alison Murray, and Dr. J.P. Zonneveld and external examiner Dr. Dave Eberth.

Lisa G. Buckley is my wife, and has also been my primary colleague/conspirator. Together we have built a museum, established a Global Geopark and have written many scientific papers. I will dare to say that the best is still to come.

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01 INTRODUCTION

The following chapters (02-08) were derived from peer-reviewed articles that, at the time of this writing, have either been published (02-07) or are in press (08). One of the main objectives of this research was to accomplish a comprehensive survey of vertebrate ichnology of western Canada which would be the foundation for future research. Currie (1989) was the first paper to make such a summary and Chapter 02 herein (based on McCrea et al., 2014a) greatly expanded on this subject and is well-suited to appear first in the order of the chapters based on peer reviewed articles that comprise the bulk of this thesis. The candidate considers the contents of Chapter 02 as critical to filling the previous gap in knowledge regarding the stratigraphic and geographic distribution of the record of vertebrate ichnology of western Canada. Without the foundation of research provided by Currie (1989) and McCrea et al., (2014) it would be impossible to place specific track occurrences (or local ichnofaunas) within a local or regional context which greatly weakens any attempt at comparisons to other ichnofaunas which occur in North America or other continents. It was previously impossible to make comparisons with temporal trends such as ichnofaunal occurrences over time, not to mention ichnofaunal turnover that have been observed and summarized on a global scale (Lucas, 2007). As a result of the articles by Currie (1989) and McCrea et al., (2014) Western Canada is now recognized as possessing one of the most complete vertebrate ichnology records for the Cretaceous in the world (Lockley and Lucas, 2014).

However, the treatment of track-bearing formations of western Canada by McCrea et al., (2014a) is not presented in a balanced fashion for the following reasons. First, not all formations are equal in how their vertebrate ichnological occurrences are expressed. Some formations, due to combination of an overall abundance of track-bearing layers and ideal exposure (e.g. Mist Mountain, Gething and Gates formations), provide a wealth of large-scale *in situ* track surfaces that make excellent subjects for study. Other formations (e.g. Dunvegan, St. Mary's River and Wapiti formations) have fewer large-scale in situ track surfaces that have been found, and instead have smaller track surface areas or a number of *ex situ* track blocks possessing one to several prints. Some formations (Boulder Creek, Dinosaur Park, Paskapoo, Porcupine Hills) have had only a few tracks discovered to date. Formations such as the Gorman Creek and perhaps one or two other formations within the Minnes Group are just becoming known for their relatively numerous, large-scale track surfaces due to recently directed research efforts.

The next several chapters (03-06) describe ichnological sites and specimens from single formations and these are presented in ascending stratigraphic order as follows: Minnes Group, Boulder Creek Formation, Judith River Group, Wapiti Formation, Paskapoo Formation and Porcupine Hills Formation. Chapter 07 is a comprehensive review of the literature of real and purported ichnopathologies which includes descriptions of a number of newly reported ichnopathologies from western Canada, as well as international occurrences. Chapter 07 is a synthesis rather than a description of specimens or sites within a single formation, so its placement is at the end of the order of the peer-reviewed papers that comprise the bulk of this thesis.

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McCrea, R.T., Buckley, L.G., Plint, A.G., Currie, P.J., Haggart, J.W., Helm, C.W., and Pemberton, S.G. 2014a. 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, pp. 5-

93. *In* Lockley, M.G., and Lucas, S.G. (eds.). Fossil footprints of western North America. *New Mexico Museum of Natural History and Sciences Bulletin*, 62.

2.0 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

This chapter was formatted from a paper of the same title published in the New Mexico Museum of Natural Sciences, Bulletin 62, pp. 269-277 in 2014. This paper was a result of a collaborative effort and in order of priority these are: Richard T. McCrea, Lisa G. Buckley, A. Guy Plint, Philip J. Currie, James W. Haggart, Charles W. Helm, and S. George Pemberton. This project was conceived by the candidate who wrote the majority of the paper (>85%).

Institutional Abbreviations: FGM - Fraser-Fort George Museum; NMC – National Museum of Canada (now CMN – Canadian Museum of Nature); PRPRC - Peace Region Palaeontology Research Center; PMA – Provincial Museum of Alberta (now RAB – Royal Alberta Museum); RBCM - Royal British Columbia Museum; ROM - Royal Ontario Museum; RTMP - Royal Tyrrell Museum of Palaeontology; UALVP University of Alberta Laboratory for Vertebrate Palaeontology

INTRODUCTION

It has been almost a quarter of a century since the last report on the status of vertebrate ichnology in western Canada (Currie, 1989), and an update is certainly in order. There has been an increase in the number of institutions conducting research on western Canadian vertebrate tracks, including the University of Saskatchewan, University of Alberta (Department of Biological Sciences and the Department of Earth and Atmospheric Sciences) as well as two new centers of research: the Peace Region Palaeontology Research Centre (PRPRC) based in northeastern British Columbia (established in 2003) and the soon to be built ‘Philip J. Currie Museum’ near Grande Prairie, Alberta. This paper will outline the geographic and temporal distribution of Mesozoic and Early Cenozoic vertebrate track localities in western Canada, including new reports of track specimens from previously unreported formations, notable track discoveries in western Canada since the most recent survey of Currie (1989), and new interpretations of both the diversity and behavior of terrestrial vertebrates of western Canada, based on recent track discoveries. This paper also includes the description of a new theropod ichnotaxon from the Late Cretaceous of British Columbia, and a re-diagnosis of an existing avian ichnotaxon.

Significant collections of western Canadian vertebrate tracks include the Canadian Museum of Nature (CMN - formerly National Museum of Canada NMC) and the Royal Ontario Museum (ROM) where many tracks and replicas from the Gething Formation of the Peace River Canyon are housed. The Provincial Museum of Alberta (PMA), now the Royal Alberta Museum (RAM), housed a large collection of Gething Formation tracks which were moved to the Royal Tyrrell Museum of Palaeontology (RTMP) after it was constructed. The RTMP also houses fossil tracks, partial trackways and many moulds and casts from both British Columbia and Alberta from formations of Early to Late Cretaceous age.

The PRPRC has been a major centre of vertebrate ichnology research and collection for nearly a decade with a comprehensive and expanding collection of original tracks and trackways, as well as replica moulds and casts from almost every formation that bears tracks in western Canada. The Fraser-Fort George Museum (FGM) in Prince George, British Columbia has a modest number of original tracks and some replica moulds and casts from the earliest to mid-Cretaceous of British Columbia. The Royal British Columbia Museum (RBCM) also possesses original tracks and some replicas, primarily from the Gething Formation of the Peace River Canyon in northeastern British Columbia, and recent additions include newly discovered tracks from the Bowser Basin in north-central British Columbia.

Significant parts of the new ichnological work (e.g. Rylaarsdam et al., 2006) have been conducted within a new high-resolution regional allostratigraphic framework, developed primarily at the University of Western Ontario (e.g. Plint et al., 1988; Plint, 1990, 2000; Varban and Plint, 2005; Kreitner and Plint, 2006; Roca et al., 2008; Hay and Plint, 2009; Hu and Plint, 2009). The allostratigraphic framework is based on the correlation of many thousands of wireline well logs, allowing genetic depositional sequences to be recognized. Depositional sequences can then be correlated to isolated, tectonized strata observed at outcrop in the Rocky Mountain Foothills. Because track-bearing strata are non-marine, it is commonly difficult to accurately assign such strata to standard geological stages or sub-stages which are based on marine biostratigraphy. The new allostratigraphy now allows isolated, track-bearing outcrop sections to be correlated with coeval marine strata for which molluscan biostratigraphy is generally available, and hence much better age determinations can be made.

Vertebrate tracksites are found in a variety of natural exposures such as river and creek bank exposures, and natural slopes of hills and mountains. Human-produced exposures are certainly responsible for uncovering the highest number of tracksites, as well as track surfaces with the largest surface areas. Tracksites have been uncovered in coal mines during tunneling (Currie, 1989), or after the removal of coal seams from steeply-dipping surfaces, and even during road construction within coal mines (McCrea, 2000a). Construction and maintenance of hydroelectric dams have also exposed new tracks and tracksites (Currie and Sarjeant, 1979). Gas wells, seismic surveys, pipeline and wind turbine construction projects and other ground disturbance activities also have the potential to expose fossil tracks.

The following is a review of known track occurrences in the Mesozoic terrestrial formations cropping out in western Canada (Fig. 2.1). The reports include previously unpublished field reports and summaries of works published after the last review article by Currie (1989).

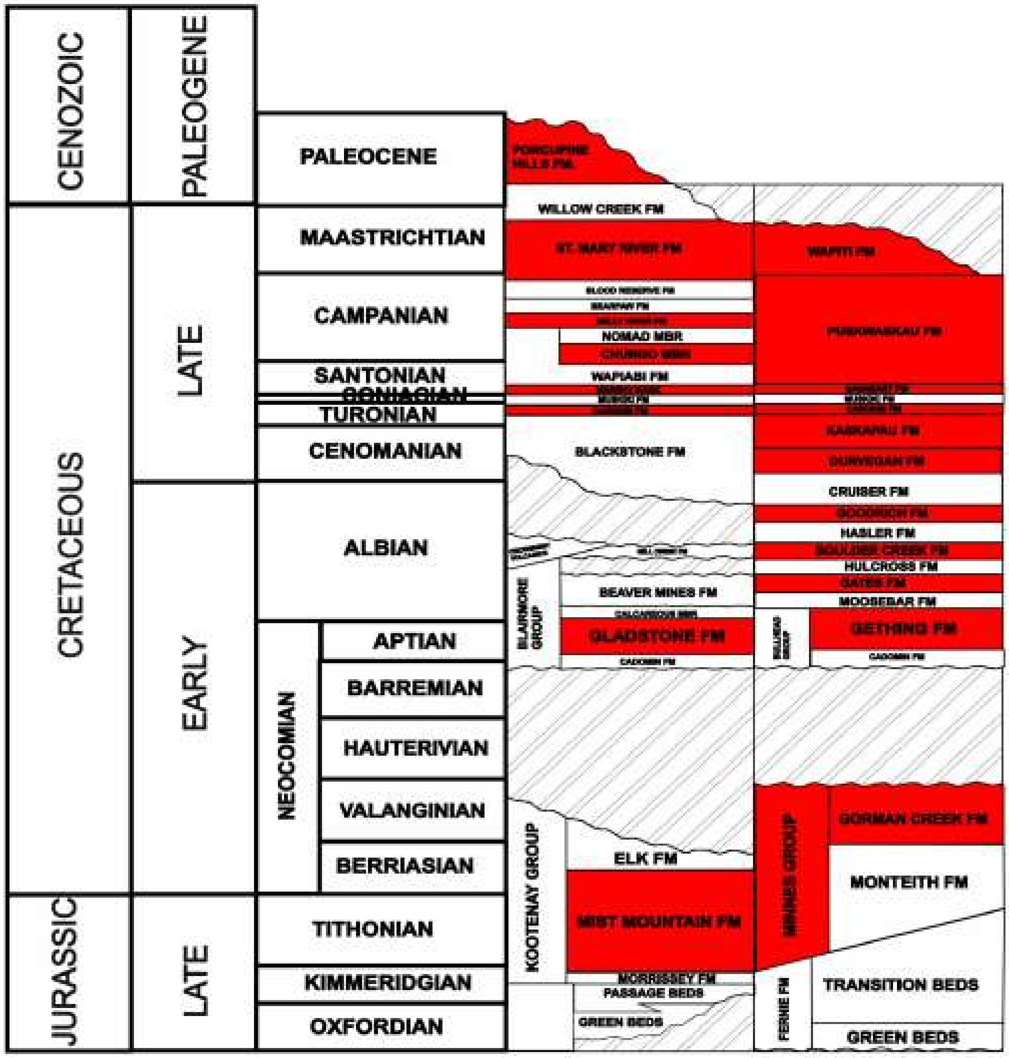

Fig. 2.1: Comparative stratigraphy of track-bearing formations in the Western Canada Foreland Basin (modified from Leckie and Smith, 1992). Shaded units are formations where vertebrate traces have been reported. Track-bearing formations further westward in British Columbia, and formations outside of British Columbia and Alberta have been omitted in this figure, but are covered in the paper.

BOWSER LAKE GROUP (LATEST JURASSIC – EARLIEST CRETACEOUS)

A number of track-bearing slabs were recovered during a series of expeditions in the Bowser Basin, near the Nass and Skeena rivers, in the summer of 2004 led by researchers from the Geological Survey of Canada (Evenchick et al., 2005; Hanke and McCrea, 2006). The specimens recovered represent the first reported occurrence of vertebrate tracks from the Bowser Basin. Based on marine macrofossils Evenchick et al. (2001; 2005) estimate the age of the track-bearing sediments to be the latest Jurassic to the earliest Cretaceous. The terrestrial sediments are interpreted to include those of deltaic, fluvial, and lacustrine environments (Evenchick et al., 2003).

Seven track-bearing slabs from the Bowser Basin were catalogued at the Royal British Columbia Museum and are described as follows:

RBCM EH2004.003.0010 - Slab with a trackway consisting of four very small (just over 7.0 cm length) natural mould tridactyl tracks (prints 1-4: RBCM E.H2004.003.0011-0014 respectively) preserved on a fine-grained, organic rich substrate. This trackway displays an uneven pace of the track-making animal (Pace of prints 1-2: 17 cm, prints 2-3: 18 cm, and prints 3-4: 14.5 cm). The prints display a positive rotation toward the midline of the trackway.

RBCM EH2004.003.0015 - Slab with two small (17 cm long) tridactyl prints (RBCM EH2004.003.0016 and 0017) partially encrusted with $CaCO_3$ (post-depositional). These tracks appear as natural casts, but the invertebrate burrows and deformation of the sediment in the metatarsal pad region of RBCM EH2004.003.0016 suggest that this is the original natural mould surface and that these tracks simply have adhering infill material. These prints are quite similar to small theropod (*Irenichnites* ichnosp.) track specimens described from the Gething Formation in the Peace River Canyon of northeastern British Columbia (Sternberg, 1932).

RBCM EH2004.004.0003 – Natural cast of a partially preserved medium-sized (21 cm long) tridactyl print. This print possesses distinct digital pad impressions and sharp claw impressions at the tips of two preserved digit impressions. Based on the divarication of the digits and the direction of curve of digit III this can be identified as a left print of a theropod.

RBCM EH2004.004.0004 – Partial medium-sized (20 cm long) natural mould of a tridactyl print (theropod), preserved on a fine-grained organic surface (Fig. 2.2).

Fig. 2.2: RBCM EH.2004.004.004, an isolated partial natural mould tridactyl print (theropod) from the Bowser Lake Group, northwestern British Columbia. Scale = 10.0 cm.

RBCM EH2004.004.0005 – Small natural cast of very small (8.0 cm footprint length) tridactyl print (right) with digit III and IV well-defined (Divarication: digits II-III 21°, digits III-IV 36 °; total divarication 57 °. This specimen is very similar in morphology to the RBCM EH2004.003.0010 specimens and was likely produced by a small theropod track-maker.

RBCM EH2004.004.0025 – Small (FL 19 cm) partially preserved natural cast of a tridactyl theropod track (left).

RBCM EH2005.017.0121 - Slab with two small (FL ~17 cm) natural mould tridactyl (theropod) tracks on a fine-grained rippled sandstone (Fig. 2.3).

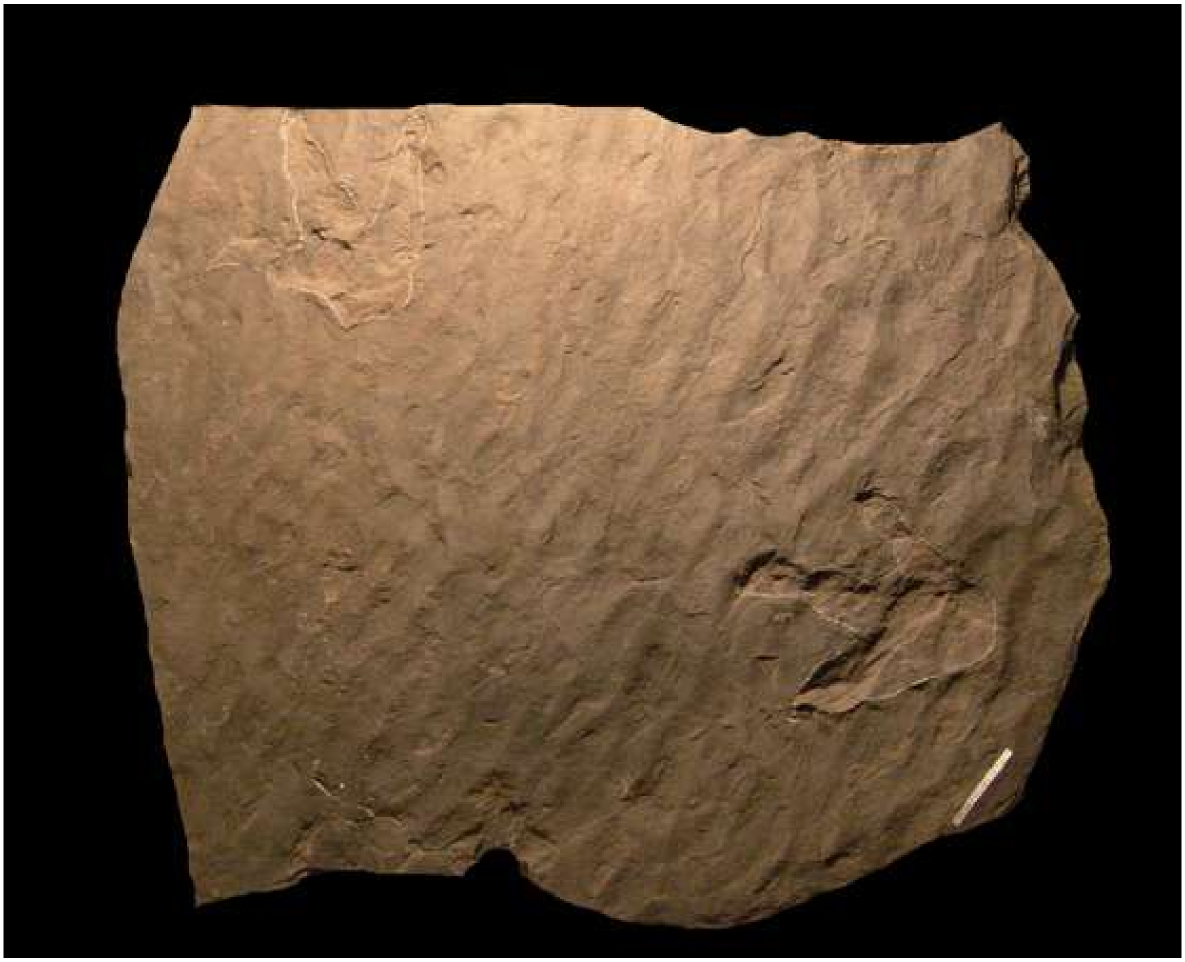

Fig. 2.3: RBCM EH.2005.017.0121, two small, natural mould tridactyl (theropod) tracks from the Bowser Lake Group, northwestern British Columbia.

In examining this small but important collection of tridactyl dinosaur tracks, there were found to be similarities in morphology to other Late Jurassic and Early

Cretaceous (Tithonian - Valanginian) tracks from western Canada. The Bowser Basin tridactyl tracks are particularly reminiscent of the very small to small tridactyl tracks found in the Mist Mountain and Gorman Creek formations of eastern British Columbia.

The strata of the Bowser Basin region contain the most westerly known dinosaur tracks in British Columbia (~56°N, 128°W), but the Ross River tracksite in the Yukon Territory (~132° 30’ N, 122° 5’W) is even further northwest. The potential for further fossil track finds in the Bowser Basin is high.

KOOTENAY GROUP

Mist Mountain Formation (Upper Jurassic - Lower Cretaceous: Berriasian – Valanginian)

Vertebrate tracks from the Mist Mountain Formation of southeastern British Columbia were first reported by Currie (1989a) and are among the oldest currently known in western Canada. The sediments of the Mist Mountain Formation were thought to have been deposited in the latest Jurassic (Tithonian) through the earliest Cretaceous (Berriasian) (Gibson and Poulton, 1994). However, Stott (1998) placed the Mist Mountain Formation in the Early Cretaceous (Berriasian - Valanginian). The Mist Mountain Formation tracksites are nearly equivalent to the Purbeck Group and Wealden Formation in England and contemporaneous track areas in northwestern Germany (i.e. Berriasian Bückeberg Formation) (Diedrich, 2004; Lockley et al., 2004, Hornung, et al., 2012) and other European localities. Dinosaur tracks are exposed from a number of large open pit mines in the Elk Valley Coal District in southeastern British Columbia. Currie (1989) reported tracks from underground mining in this area as well, but no reports of underground tracks have been reported since the last review.

The Mist Mountain strata have yielded a very impressive diversity of terrestrial vertebrate tracks from a number of localities, primarily within several open pit coal mines. The majority of track specimens are from isolated blocks from talus piles below active coal mine pits. The ichnodiversity ranges from some of the largest theropod tracks known (~1 m length) to very small reptile tracks (Fig. 2.4).

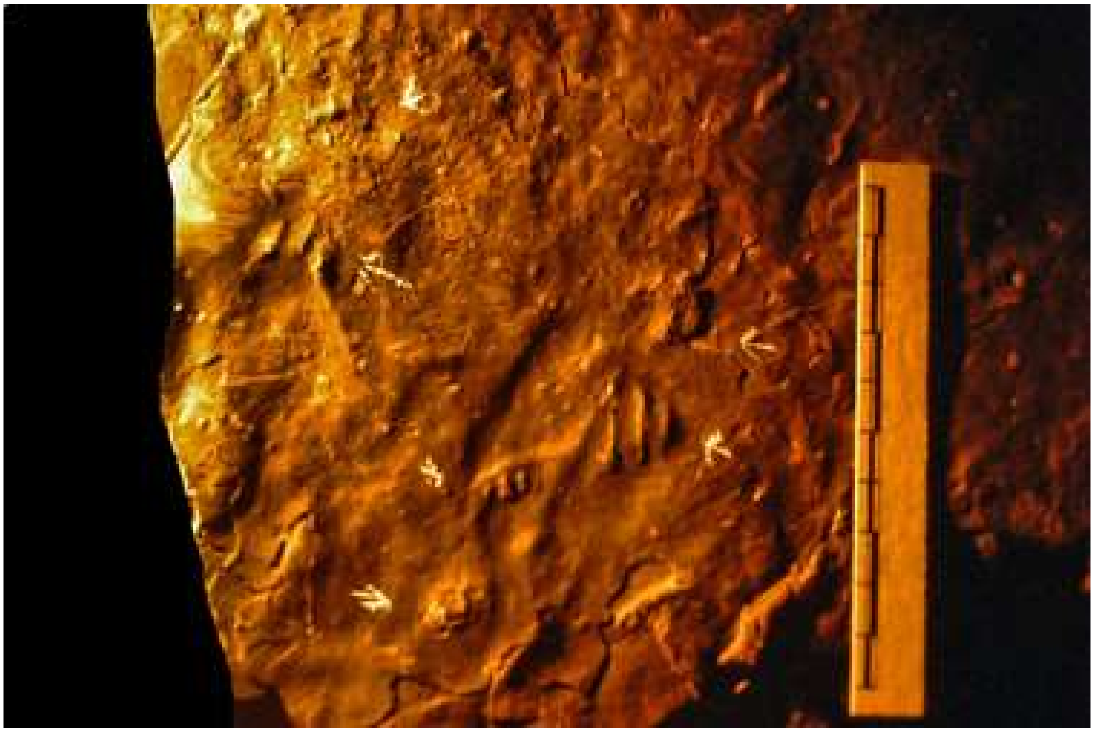

Fig. 2.4: Very small natural cast reptile traces from the Mist Mountain Formation of southeast British Columbia. Scale = 10 cm.

The Mist Mountain Formation ichnofauna also includes large ornithopod tracks (cf. *Iguanodontipus* ichnosp., Sarjeant et al., 1998) (Fig. 2.5). Only isolated pes or manus/pes specimens have been found so far.

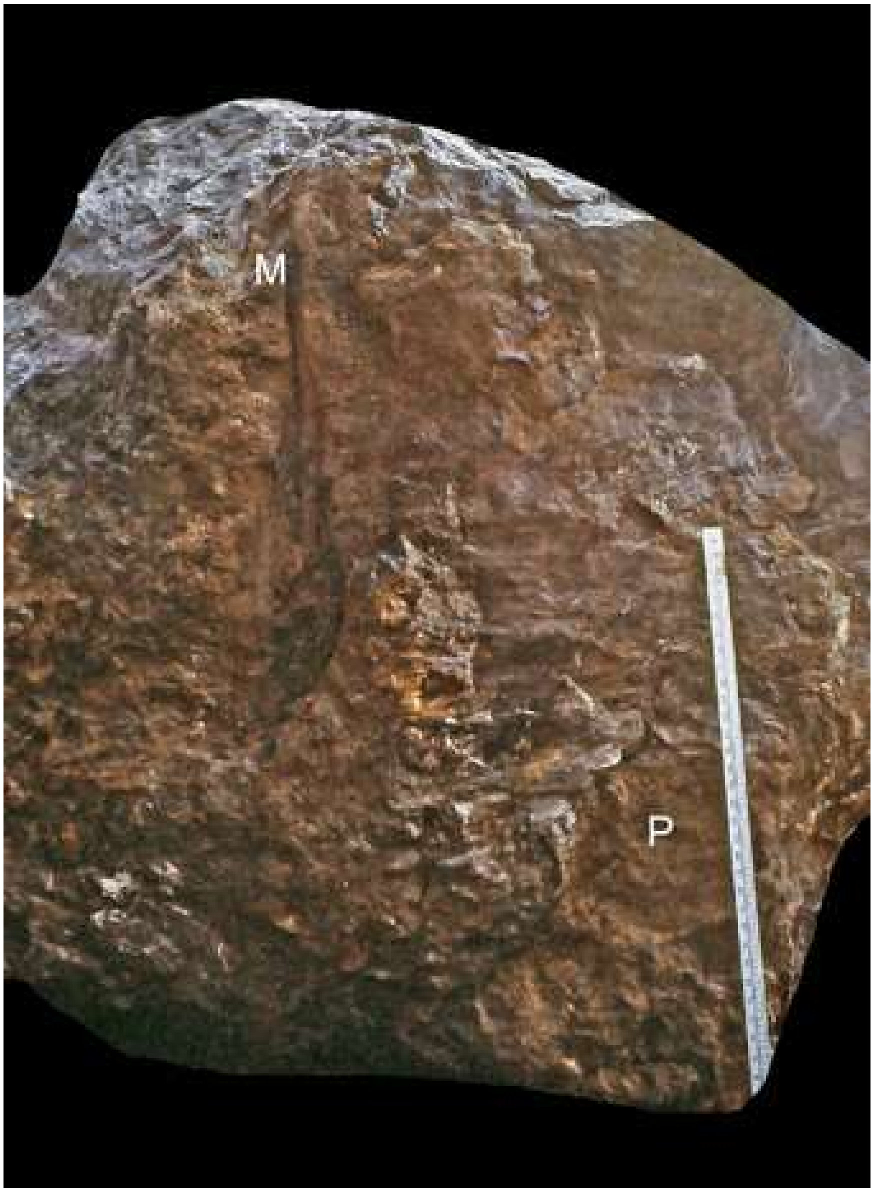

Fig. 2.5: Basal ornithopod natural cast manus (M) and pes (P)

from the Mist Mountain Formation of southeastern British Columbia.

Scale = 1 m.

There are an abundance of tracks of non-dinosaurian reptiles and trackways of quadrupedal reptiles, possible chelonian and crocodylomorph affinities, including walking (Fig. 2.6) and swimming traces (Fig. 2.7). The research on these well-preserved and somewhat enigmatic prints is ongoing.

Fig. 2.6: A large track slab containing small reptile trackways from the Mist Mountain Formation of southeastern British Columbia. Scale = 10 cm.

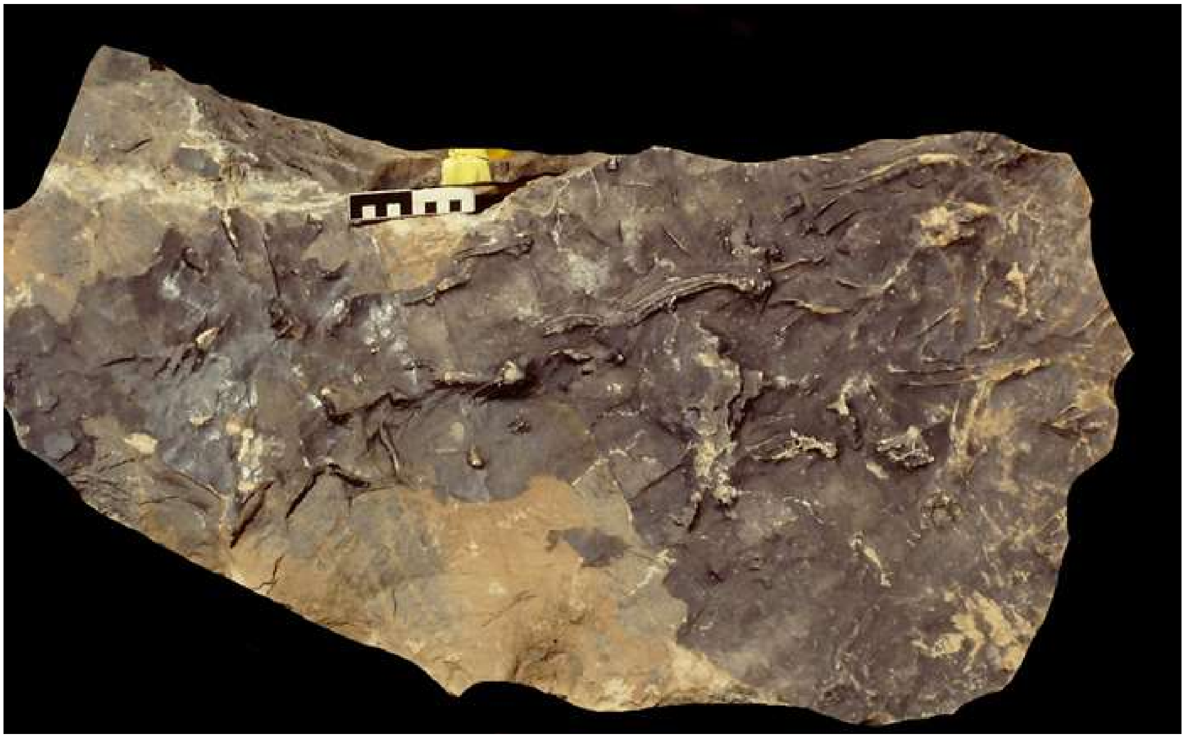

Fig. 2.7: Reptile swimming traces from the Mist Mountain Formation of southeastern British Columbia. Scale = 10 cm.

Some small natural cast reptilian trackways show manus impressions with a single elongate digit which may be attributable to pterosaurs (McCrea et al., 2005; McCrea and Buckley, 2005) (Fig. 2.8). The vertebrate ichnofauna also includes the oldest records of avian tracks in western Canada and one of the oldest in the world (McCrea et al., 2001). A latex mould of a similar, single larger avian-like track was made from an original found at the Lower Turn Pit in Fording River Operations. The mould is deposited along with a replica cast at the PRPRC. This single print (Fig. 2.9) is very similar in size and morphology to *Aquatilavipes curriei* described by McCrea and Sarjeant (2001) and redescribed here (below).

Fig. 2.8: Small reptilian natural cast tracks from the Mist Mountain Formation of southeastern British Columbia. The arrowed print with the long digit trace may be one of two pterosaur manus tracks on this surface.

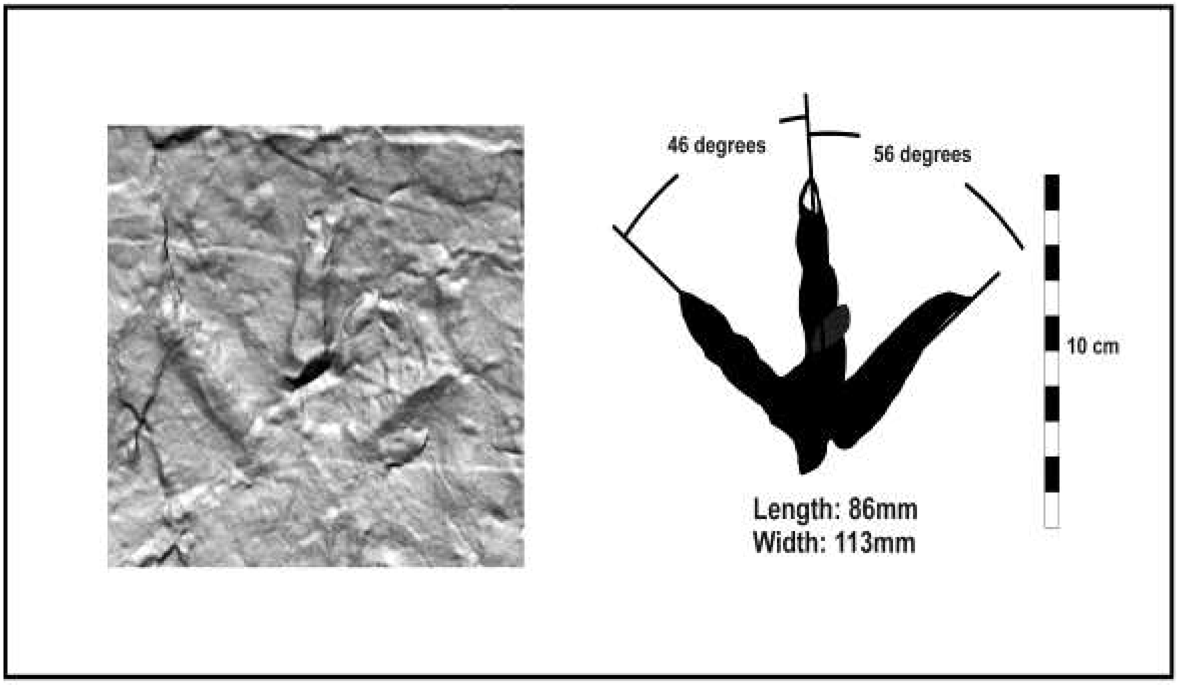

Fig. 2.9: Surface laser scan image (left) and drawing (right) of a possible avian print from the Mist Mountain Formation of southeastern British Columbia.

Two avian-like, natural cast trackways on an isolated slab were photographed by RTM, (Fig. 2.10) in an active coal mining area, Eagle Stage IV pit in the Fording River Operations near Elkford, British Columbia. The individual tracks (particularly those in Trackway A) appear to possess high divarication. Trackway A appears to have a low stride and pace and low pace angulation with the prints strongly rotated in the direction of the midline of the trackway.

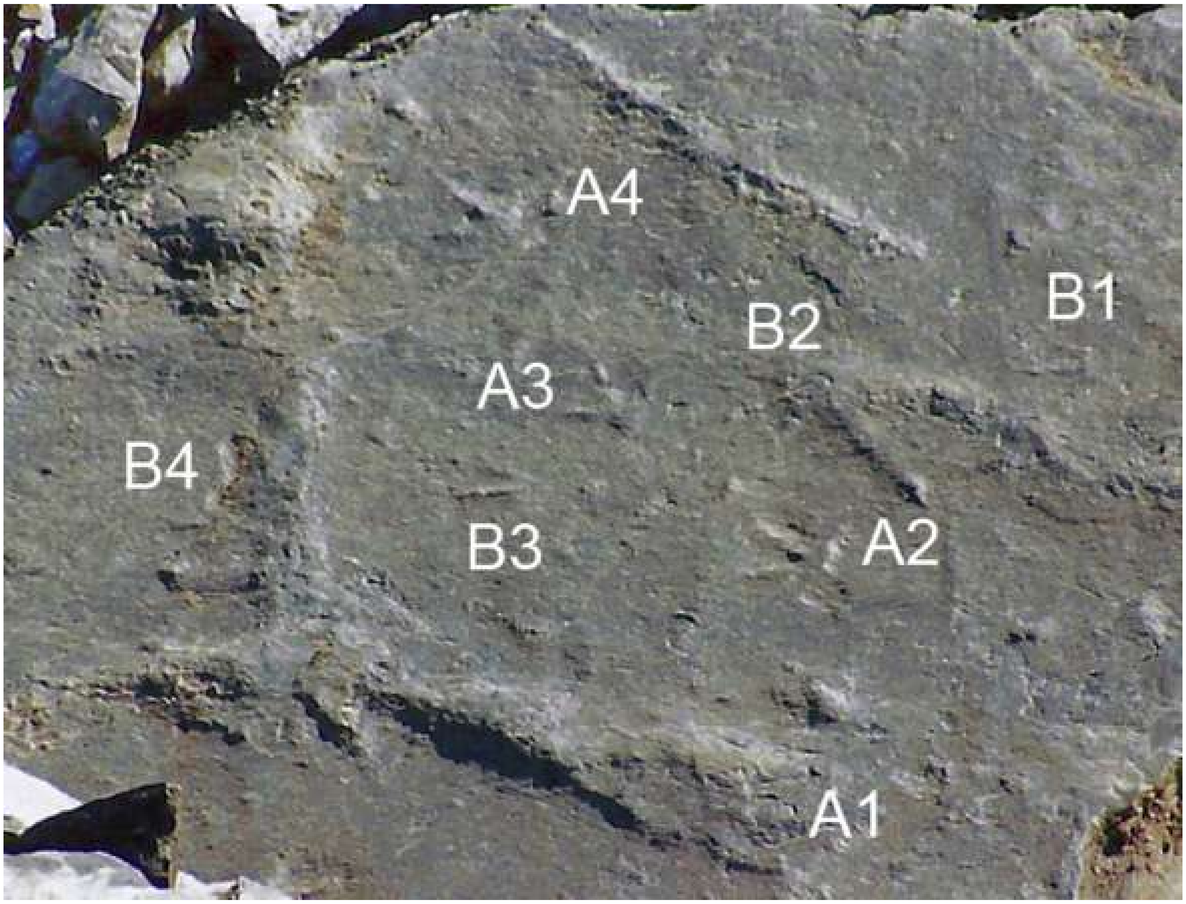

Fig. 2.10: Two possible avian trackways (left) from Eagle Stage IV Pit from the Mist Mountain Formation of southeastern British Columbia.

Lockley and Rainforth (2002) made a detailed summary of the global stratigraphic occurrence of avian tracks, and though the previously reported (McCrea et al., 2001) Mist Mountain Formation material was not mentioned. These possible avian track occurrences are, along with *Archaeornithipus meijdei* (Fuentes Vidarte,1996) from Spain and *Pullornipes aureus* from China (Lockley et al., 2006) among the oldest avian prints known.

There is at least one manus/pes set (Fig. 2.11) that might represent a very rare ichnological record of Mesozoic amphibians (Lockley and Hunt, 1995). These tracks do not appear similar to the frog tracks reported from the Upper Cretaceous of Price, Utah (Robinson, 1991; Lockley and Hunt, 1995), but there is a greater similarity to modern salamander tracks (fig. d in Peabody, 1959). Without a complete trackway it is difficult to rule out a turtle as the track-maker.

Fig. 2.11: Small reptilian, or possibly amphibian, natural mould manus and pes from the Mist Mountain Formation of southeastern British Columbia. Scale = 10.0 cm.

Other recent footprint finds in the Mist Mountain Formation include a variety of small, medium and large (Fig. 2.12) theropod prints and a single very large theropod footprint showing distinct digital pad and claw impressions that was measured at one meter in length. This print was outlined (by a coal mine employee) with a red-coloured industrial-grade wax marker which could not be removed without damaging the specimen. The wax marker outline shows the basic tridactyl nature of the print, but cuts off several centimeters of all the digits and the "heel" area as well.

Fig. 2.12: Isolated natural cast print of a large theropod pes (cf. *Megalosauripus* ichnosp.) from the Mist Mountain Formation of southeastern British Columbia. Scale = 10.0 cm.

Some of the large theropod tracks from this formation may have been produced by megalosaurid track-makers, although identifying and naming the tracks of megalosaurids has had its share of pitfalls (Lockley et al., 1996). We cautiously refer some of the large, robust theropod tracks to *Megalosauripus* (*sensu* Lockley et al., 1998).

Lockley et al. (2009) described a new ichnotaxon (*Neoanomoepus perigrinatus*) attributable to small, quadrupedal ornithischians from tracks found in sites in Thailand, Zimbabwe, and from British Columbia. The holotype (FGM 002.01.20a and CU 199.22) and paratype (FGM 002.01.20b and CU199.23) specimens are moulds and casts produced from the as-yet unrecovered original natural cast slab (Fig. 2.13) from the Fording River Operations coal mine in the Elk Valley Coal District of southeastern British Columbia. These specimens exhibit four pedal digits and five manual digits (Lockley et al., 2009).

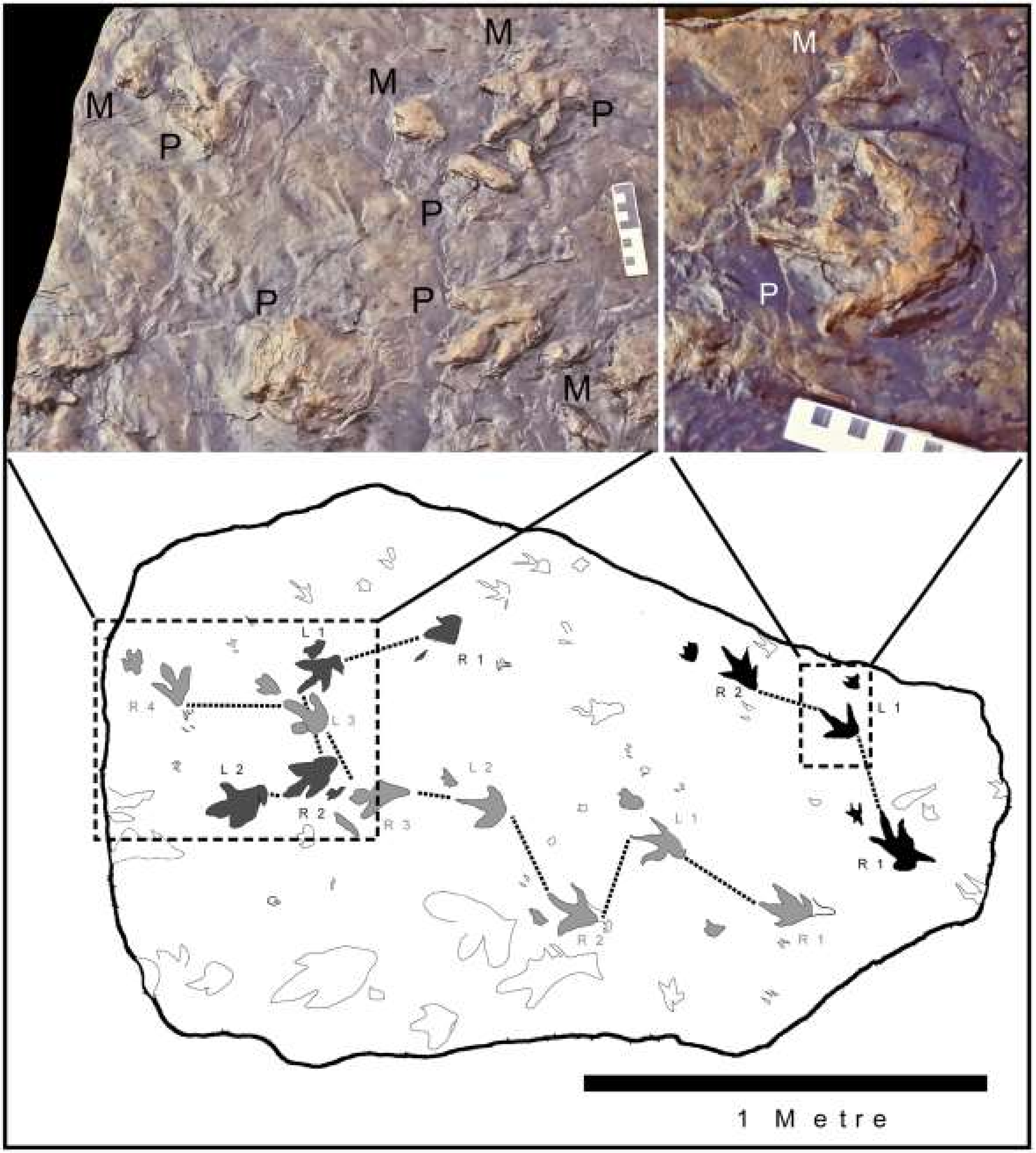

Fig. 2.13: Original natural cast slab with holotype and paratype of *Neoanomoepus perigrinatus* (Lockley et al. 2009) from the Mist Mountain Formation of southeastern British Columbia (Scale = 10cm). Top left: Section of the original slab with *N. perigrinatus* manus-pes sets (Scale = 10cm). Top Right: Close up of the second manus-pes set of the holotype of *N. perigrinatus*. Bottom: Trackway map of the original natural cast slab with three *N. perigrinatus* trackways.

Currie (1989) identified a natural cast trackway (RTMP 1985.105.0001) from the Mist Mountain Formation as belonging to *Anomoepus.* Currie (1989) observed that the tracks were tridactyl, but more recent observations revealed that print #1 of this trackway has four, forward facing digits (Fig. 2.14). We agree that this specimen was made by an ornithopod. Specimen RTMP 1985.105.0001 lacks obvious manual impressions and could be an example of bipedal progression of a small ornithopod.

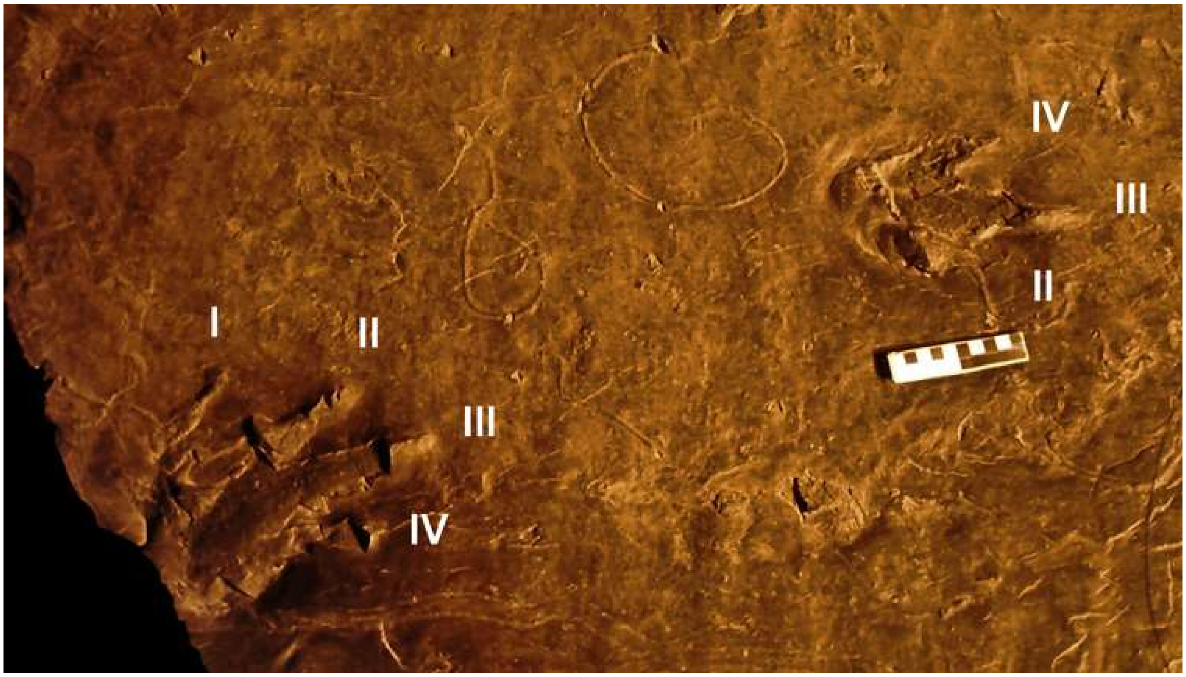

Fig. 2.14: Specimen (TMP 85.105.1) of a natural cast ornithopod trackway from the Royal Tyrrell Museum of Palaeontology collections figured in Currie. Scale = 10 cm.

One of the most significant vertebrate ichnology finds from the Mist Mountain Formation was the discovery of sauropod prints, the first record of this dinosaur group in Canada and the northernmost in North America (McCrea et al., 2005a). These initial specimens were isolated blocks of natural moulds and casts of pes prints, or indistinct, single manus/pes sets. A near-pristine natural cast of a left pes print (Fig. 2.15) was collected in 2000 (McCrea et al., 2005a) and eventually deposited in the Fraser-Fort George Museum located in Prince George, British Columbia (FGM 2001.13.1). A master cast replica of FGM 2001.13.1 is deposited at the Peace Region Palaeontology Research Centre (PRPRC 2000.01.001MC). Since the identification of sauropod tracks at the ichnogeneric level requires a trackway (Lockley and Hunt et al., 1994) the individual ichnites were only sufficient to prove the presence of sauropods in western Canada during the Mesozoic.

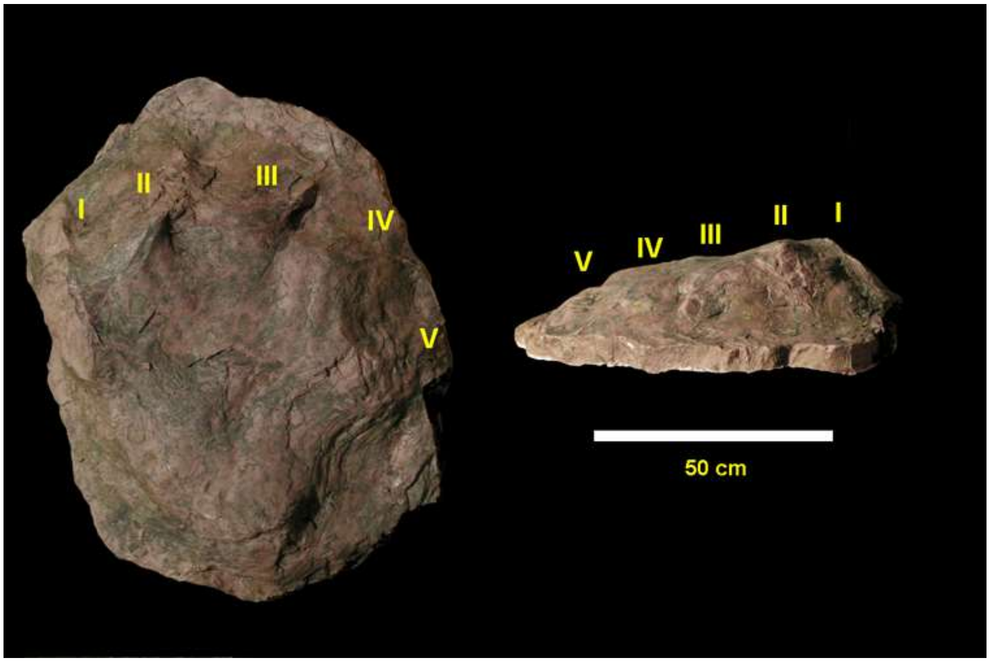

Fig. 2.15: PRPRC 2000.01.001MC, a natural cast left pes print of a sauropod collected from southeastern British Columbia. Left: plantar view of natural cast of left pes sauropod print. Right: View of the distal portion of the natural cast of PRPRC 2000.01.001MC to show depth of print and digits.

A field geologist at the Fording River operations (Mr. Barry Musil) showed RTM a collection of several large, roundly eroded cobbles that he collected from within a main coal seam at Eagle Stage IV pit that occurred together in what appeared to be a pile. The cobbles are uniform in size and are all of the same quartzite composition (Fig. 2.16). This form of quartzite is atypical for the Mist Mountain Formation and it is likely allochthonous. These cobbles bear a strong resemblance to the local quartzite found from the early Paleozoic deposits of southeastern British Columbia. The occurrence of cobbles was limited to a small collection from one locality to date and so does not seem to indicate an overall high energy environment within the very low energy depositional environment that produces thick coal seams. Several other possibilities should be considered to explain the presence of these stones in such an unusual context. Some of these possibilities could be non-biogenic. However, one interpretation that bears investigation is the possibility that these stones could be regurgitated gastroliths from a large vertebrate. Sauropod gastroliths have been previously reported by others (Jacobs, 1993; Gillette, 1994; Sanders et al., 2001). In the Mist Mountain Formation sauropod footprints and trackways are in close proximity geographically and stratigraphically (a sauropod pes print was discovered in the same Eagle Stage IV pit) to where the pile of cobbles was found. Skepticism is required, as for all palaeontological interpretation because there are cases where the interpretation of gastroliths has been called into question (Lucas, 2000; Whittle and Onorato, 2000; Wings, 2007; 2009; Wings and Sander, 2007).

Fig. 2.16: Quartzite pebbles (possibly gastroliths) collected from within a coal seam from the Mist Mountain Formation (Berriasian-Valanginian) of southeastern British Columbia. Scale = 10 cm.

Almost all of the above track finds were found as loose blocks in the talus pits at Fording River Operations and Greenhills mine near Elkford, British Columbia, which to date have generated no reports of *in situ* tracks on footwall surfaces. The Line Creek Mine near Sparwood is currently the only coal mine from the Elk Valley Coal District where large, *in situ* tracksites have been reported (McCrea and Buckley, 2005a). The first evidence of an *in situ* tracksite from the Line Creek Mine was the discovery of a number of trackways produced by bipedal, tridactyl animals (probably theropods), as well as an unmistakable trackway of a sauropod. This site was lost in the early 1990s before it could be formally studied, and only a few photographs taken by Line Creek Mine employee (Mr. John Kinnear) remain (Fig. 2.17). The existence of these photographs was reported by McCrea and Currie (1998) from a poster on coal mine footwall stability. The origin of these photographs was a mystery until RTM brought this poster to the Fording River Operations where an employee (Kim Barrowman) recognized the footwall and was able to identify its location within the Line Creek Mine. A few years later the photographer (Mr. John Kinnear) shared his only copies of these photographs and negatives with RTM and duplicate copies (of photographs and negatives) of this important record were able to be made. It was with these recovered photographs that the sauropod trackway could be studied and identified as *Brontopodus* ichnosp.

Fig. 2.17: First image of a sauropod trackway from Canada, taken in the 1990's. This unstable footwall collapsed not long after the photograph was taken. Trackway is proceeding from upper right to lower left in this image.

A second *in situ* tracksite from southeastern B.C. was reported to some of the authors (RTM and LGB) in 2004. When this site (Horseshoe Ridge Pit) was visited in the November of that year it was evident that there were several lengthy theropod trackways of medium to large size (>50 cm) on this 160 m^2 vertical surface. The individual footprints displayed exceptional preservation (Fig. 2.18) of phalangeal pad impressions (McCrea and Buckley, 2005a). No sauropod tracks were evident at this site.

Fig. 2.18: *In situ* track surface in the Line Creek Mine within the Elk Valley Coal District of southeastern British Columbia, showing a long trackway of a large theropod (left) The individual prints preserve digital pad impressions. For scale the large theropod tracks are estimated to be at least 50cm in length. Smaller theropod tracks may be seen in the top right portion of the image.

Several years later a new tracksite was reported from the Line Creek Mine near Sparwood, British Columbia which contained *in situ* trackways on a steep wall exposed during road construction in 2008. The ichnofauna consists of three lengthy sauropod trackways (*Brontopodus* ichnosp.) traveling in roughly the same direction (Fig. 2.19). Each sauropod trackway is associated with a trackway of a large theropod with more faintly impressed prints. No tracks within the large theropod trackways appeared to be missing (over-printed by the sauropod prints), or distorted, even though they were often in close proximity to the sauropod prints. Based on these observations it appears that the sauropods traveled this surface before the large theropods did. At least two small theropod trackways were present as well, proceeding in the same direction as the rest. Unimodal and bimodal tracksites can be indications of geographical features such as shorelines and may not be evidence of gregarious or predator-prey behavior, although Lockley (1986) made a compelling point that physical constraints (i.e. palaeogeographic controls) that act on an individual can also act on a group travelling together.

Fig. 2.19: *In situ* track surface from the Mist Mountain Formation within a coal mine in southeastern British Columbia, preserving long sauropod trackways, one of which was moulded in 2008 (PRPRC 2008.08.001M).

A latex mould (PRPRC 2008.08.001M) measuring ten meters by three meters was recovered from this new Line Creek site. This mould encompassed six manus/pes sets of one of the sauropod trackways along with a number of large theropod prints in one trackway. This mould required over 170 litres of latex and was visible from seven kilometers away.

Near the site of the sauropod trackways the tracks of a small theropod were discovered near the base of a steeply dipping anticline limb. Excavation revealed a trackway of six prints (Fig. 2.20). As this area was destined for road construction the original trackway was removed and is deposited at the PRPRC (PRPRC 2008.08.003) where it awaits formal description. A single block with an original natural mould of a large theropod track was discovered on the side of a switchback road leading to the sauropod tracksite. The slab was trimmed with a rocksaw to a manageable size and is now deposited at the PRPRC (PRPRC 2008.08.002).

Fig. 2.20: Natural mould trackway of a small theropod (PRPRC 2008.08.003) collected from a coal mine from the Mist Mountain Formation in southeastern British Columbia.

The apparent absence of sauropod bones or tracks from Canada was viewed as a mystery (Currie, 1989; Spalding, 1999; Lockley, 1992), especially since sauropods were known to occur in the U.S. Several reasons cited for the absence of sauropods in Canada ranged from palaeogeographic barriers to palaeoenvironmental preferences (Currie, 1989; Lockley, 1992). Sauropod track occurrences are found predominantly in carbonate platform deposits which characterize the *Brontopodus* ichnofacies (Lockley et al., 1994; Hunt and Lucas, 2007). These carbonate platforms are deposited within a certain range of the paleoaequatorial zone (30^{o}S and 30^{o}N latitudes) with only a minor record of occurrence in other types of deposits in other latitudes (Lockley et al., 1994).

However, Farlow (1992) suggests that the absence of sauropod tracks in an area may not mean they were absent from the region, and that the absence could simply be one of timing between the visit of a sauropod herd and the deposition of a bedding surface. We recognize another compelling reason for the perceived absence of sauropods in Canada, which was simply that no one had looked for their tracks!

In eastern Canada the youngest terrestrial deposits of the Mesozoic are Early Jurassic in age, and while discoveries of prosauropods (basal sauropodomorphs) have been made in the McCoy Brook Formation (Fedak, 2007) the tracks and bones of the Sauropodomorpha have not yet been found. In western Canada the oldest Mesozoic terrestrial strata containing vertebrate remains are from the earliest Cretaceous, a time of relatively low diversity for sauropods (Hunt et al., 1994). However, Lockley et al. (1994) note that sauropod tracksites were globally abundant in the Early Cretaceous.

These Canadian sauropod tracks are found north of 49°N present latitude, however palaeogeographic maps (Smith et al., 1994), indicate these tracksites were just north of 50°N when the Mist Mountain Formation sediments were being deposited. The Mist Mountain Formation is composed of sediments divisible into two units. The lower unit, with extensive coal seams was deposited in an interdeltaic, coastal plain environment (Vessey and Bustin, 2000). The upper unit with minor coal seams was deposited in a distal alluvial-fluvial flood plain environment (Vessey and Bustin, 2000). The western Canadian sauropod track record represents a substantial departure from the typical *Brontopodus* ichnofacies and palaeolatitude occurrence for sauropods.

It is possible that the large differences in vertebrate ichnofaunal composition between the Mist Mountain and Gorman Creek (described below) formations could indicate a significant temporal difference, and perhaps the Mist Mountain Formation is substantially older than Stott (1998) has indicated. We suggest that it is possible that the differences observed between these two vertebrate ichnofaunas could be attributable to palaeoenvironmental differences (coastal plain and distal alluvial-fluvial flood plains for the Mist Mountain Formation, and lake shore deposits for the Gorman Creek Formation). The Mist Mountain Formation will continue to be very productive for vertebrate footprint discoveries as long as coal mining is active in this area.

MINNES GROUP

Unidentified Minnes Group (Lower Cretaceous: Berriasian – Valanginian)

Sediments of the Minnes Group of northeastern British Columbia are roughly equivalent in age to those of the Kootenay Group (Stott, 1998). Aside from tracksites known from the Gorman Creek Formation, few tracks have been found in the Minnes Group (Currie, 1989a). In the fall of 2004 a large track slab was uncovered by a logging company (Canfor) during road construction on the side of a mountain south west of Chetwynd. A geological map (Stott, 1982: fig. 3a) indicates that Minnes Group strata are the only possible source for the track slab, but while precise locality data exists for the specimen it has proven difficult to determine from which formation (Bickford, Monach, Beattie Peaks, or Monteith formations) it originated due to the forest and ground cover. The Canfor track slab (dimensions - 4.7 m x 2.5 m x 0.4 m; mass - 9500kg) was donated by the District of Chetwynd to the PRPRC collections early in 2012 (PRPRC 2012.01.001). This specimen shows two partial, natural cast trackways of a large theropod and a large ornithopod, respectively (Fig. 2.21).

Fig. 2.21: Natural cast trackways of a large theropod; and a large ornithopod (PRPRC 2012.01.001, left, scale = 1.0 m) collected from an isolated block from the Minnes Group of northeastern British Columbia.

Preliminary studies of the three footprints of the theropod trackway show they are approximately 65 cm long and that the animal's pace was 1.3 meters with a 2.35 meter stride. These footprint specimens are very large with robust digit impressions (though still showing phalangeal pad impressions), differing in general form from the *Irenesauripus mclearni* and *I. acutus* tracks of Sternberg, (1932). These prints may be referred to cf. *Megalosauripus* (*sensu* Lockley et al., 1998).

The large ornithopod trackway also has three footprints, which are wider than long with three digit impressions with rounded, hoof-like terminations. No manual impressions are evident with this trackway, but it is possible that they were overprinted by the much larger pedal impressions. The ornithopod tracks are 45 cm long with a 95 cm pace and a 186 cm stride and could be referred to *Iguanodontipus* ichnosp. (Sarjeant et al.,1998).

The features of the tracks in both trackways suggest the ground on which the animals were walking was soft and wet, and that they were compelled to walk slowly. This is also suggested by the width of the trackways. The trackway width for large theropods is typically narrow, and there is a straight line of footprints with the individual tracks being oriented nearly parallel to the midline of trackway (i.e. high pace-angulation). The footprints of the PRPRC 2012.01.001 trackways are not in a straight line (low pace-angulation); they are staggered and the individual tracks are not parallel to the midline (McCrea and Pigeon this volume). The prints of the theropod trackway are rotated inward more than is typically seen when compared with most other tracksites.

A replica of this track slab (reproduced as a natural mould surface) is on display with complete interpretive signage in an outdoor park (Cedar Park) in the town of Chetwynd, northeastern British Columbia. A more complete description of this track slab is currently in preparation (McCrea and Pigeon, this volume).

Additional discoveries of tracks in Minnes Group strata have been made in the Tumbler Ridge area in the summer of 2010 by a group of Australian visitors who went hiking into the area while visiting a local ranch. The ranch owner (Tim Millward) reported these finds to the PRPRC. The locality was visited by CWH and documentation of the site was started. A short natural mould trackway with a number of small tridactyl prints and one or two medium tridactyl prints (Fig. 2.22) were found on the eroded surface near a vertical anticline fold forming the bank of a creek (Tim's Creek, an informal geographical name after the rancher who reported the site). The small print trackway is cautiously identified as theropod in origin; however, the pace angulation, stride and pace length values appear low for a typical theropod trackway. It is possible that, even though no manual prints have been recognized to date, this trackway could be that of a small quadrupedal ornithopod with tracks similar to *Neoanomoepus* ichnosp. described by Lockley et al. (2009) from the Mist Mountain Formation in southeastern British Columbia. This track surface also possesses a partial trackway of a large quadrupedal ornithopod (two pedal prints and one manual print).

Fig. 2.22: Isolated track block containing natural mould tracks of small theropods from Tim's Creek (informal designation) from the Minnes Group (Berriasian-Valanginian) of northeastern British Columbia.

Other tridactyl tracks have been found in this area on *in situ* surfaces as well as on isolated blocks in the river valley. On a high alpine summit now dubbed "Theropod Peak" local geologist Kevin Sharman discovered a single, large theropod track at this site while out mountain climbing. The prospect of new tracksite discoveries within the Minnes Group seems very promising based on what has been found in the Peace Region of British Columbia.

Gorman Creek Formation (Lower Cretaceous: Berriasian – Valanginian)

A large-scale vertebrate tracksite on a near vertical wall was reported from the banks of the Narraway River of British Columbia (Currie, 1989a; Sampson and Currie, 1996). The discoverer of the tracksite was geologist D.F. Stott who identified the track-bearing strata as belonging to the Gorman Creek Formation (1998).

The track surface was observed from a distance by PJC in 1981. The most dominant feature on the site was a long trackway of an obviously large theropod (Figure 2.23). Even from afar, it was easy to see that the track-maker had come to a stop, turned and continued in a direction nearly perpendicular to its original course (Figure 2.23a). The Narraway River large theropod track-maker follows a normal left-right footprint sequence preceding the turn (Figure 2.23b). Then the animal came to a stop on its right foot, with its left foot next coming to rest beside the right. At the moment of the turn the right foot took a very short step in the direction of the turn and by the time the left foot registered ahead, the turn was complete. From direct investigations of the vertebrate track fauna from the Kakwa Provincial Park locality (see below) it is probable that the footprint length of the large theropod tracks from the Narraway River were approximately 55cm.

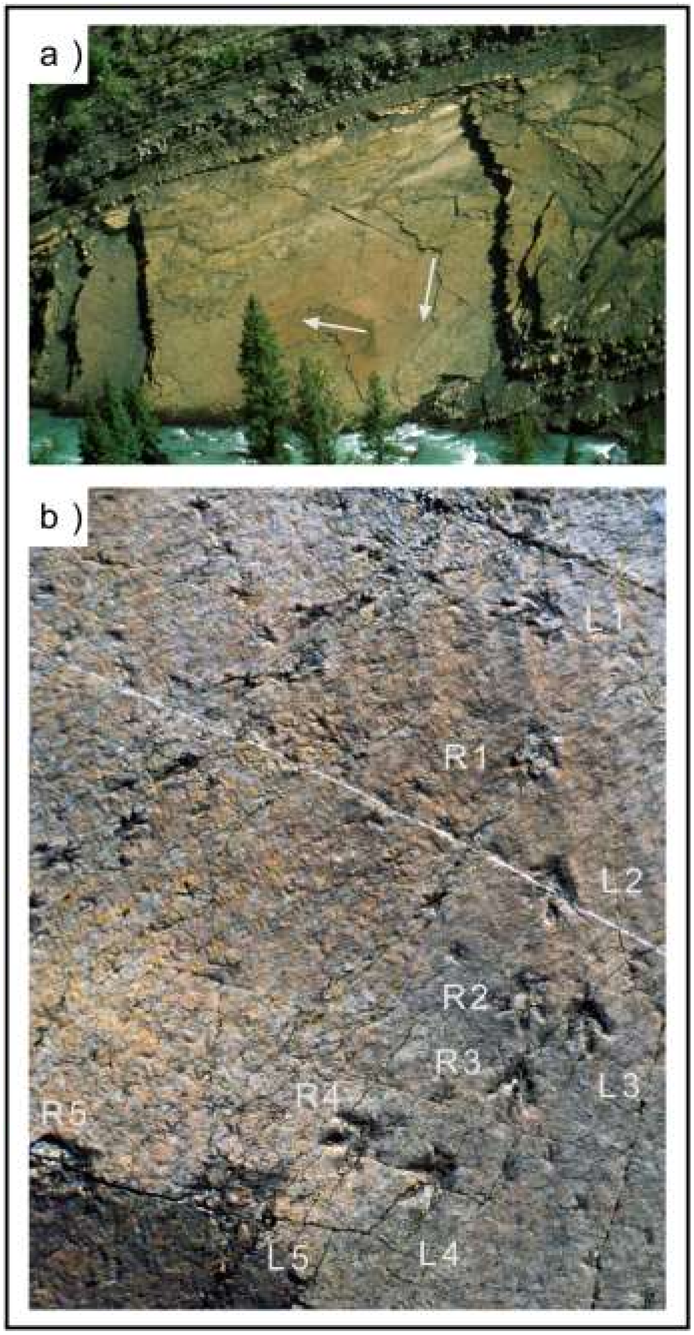

Fig. 2.23: a) 35mm slide image (PN81.30.022) of the vertical track surface on an anticline limb above the Narraway River; b) 35mm slide image (PN81.30.012) of a large theropod trackway displaying direction-change from the Narraway River site (Both images provided Courtesy of the Royal Tyrrell Museum of Palaeontology and Alberta Community Development).

The Narraway River tracksite is one of a handful of trackways showing direction change, and one of only two known to date for a large theropod changing direction the other being from Lark's Quarry, Australia (Thulborn, 2013; Thulborn and Wade, 1979; 1984).

There were several smaller trackways with tridactyl footprints, presumably of smaller theropods, but no detailed study of this site was possible due to the vertical nature of the track face and because the tracksite was on an unstable anticline limb (buckling of the track-layer can be seen from the photographs taken in 1981). It is not known if any smaller vertebrate ichnotaxa were present. The main Narraway River site was destroyed by a massive slope failure between 1981 and 1991 (Psihoyos and Knoebber, 1994; Sampson and Currie, 1996); however, there were other track-bearing layers below the main layer that are evident from previous photographs. The presence of footprints and trackways below the main track surface was confirmed by the first author (RTM) during a helicopter reconnaissance of the site in August, 2005. During this visit *Tetrapodosaurus*-like tracks and trackways were noticed and photographed on small sections of track surfaces. Efforts are currently underway to use digitally scanned 35mm slide images of this site taken in 1981 by PJC to recapture track and trackway information through processing with 3-D photogrammetry software. Initial results with this process are encouraging.

A new Gorman Creek Formation tracksite in Kakwa Provincial Park was reported to B.C. Parks by a group of hunters in 2004 (Fig. 2.24). The results of a preliminary survey by McCrea and Buckley (2005b) place the track-bearing strata within the Gorman Creek Formation. The track surface is encountered stratigraphically less than 500 meters above the lower Monteith Formation, although there are many structural folds present which may have affected this measurement. The Gorman Creek Formation in this area is typically overlain by the Cadomin Formation conglomerates (Stott, 1998); however, this association was not observed in the immediate vicinity. Based on the stratigraphic distance between the conformable contact with the underlying Monteith Formation (Stott, 1998) we estimate that the main track-bearing surface occurs near the middle of the Gorman Creek Formation, which can be up to 1100 meters thick (Stott, 1998).

Fig. 2.24: Vertical (~59° dip) *in situ* track surface from the Gorman Creek Formation in Kakwa Provincial Park in northeastern British Columbia. For scale, the largest tridactyl tracks visible are 55 cm in length.

The Gorman Creek Formation is almost contemporaneous with the dinosaur track-bearing sites in the Broome Sandstone of northwestern Australia (Thulborn et al., 1994, McCrea et al., 2011; Lockley et al., 2012). These two geographically distant regions (past and present) do share some common ichnofaunal components. These include the presence of thyreophoran tracks (cf. *Tetrapodosaurus* ichnosp.), as well as small- to large-sized theropod prints. The Broome Sandstone also possesses large ornithopod tracks as well as sauropod tracks (cf. *Brontopodus* ichnosp.), neither of which have been documented from the Gorman Creek Formation sites.

The first scientific reports from Kakwa Provincial Park (McCrea and Buckley, 2005b: 2006; 2007; 2008; McCrea, 2011) found the ichnofauna to be composed of the tracks and trackways of large quadrupedal dinosaurs referable to cf. *Tetrapodosaurus* ichnosp (Fig. 2.25). There were also trackways of large (55 cm FL) theropod dinosaurs (cf. *Megalosauripus*, *sensu* Lockley et al., 1998) (Fig. 2.26); and medium-sized theropod dinosaurs (cf. *Irenesauripus acutus* and *cf. Columbosauripus ungulatus* – Fig. 2.27), small theropod dinosaurs (~17 cm FL) currently being described (Fig. 2.28), small quadrupedal ornithopods (cf. *Neoanomoepus perigrinatus*) (Fig. 2.29), and some as-yet unidentified non-dinosaurian reptile tracks (possibly crocodylian or allied group). The majority of these cf. *Tetrapodosaurus* ichnosp. tracks and trackways are among the largest reported of this ichnogenus from any formation worldwide (Figs. 2.30 – 2.31), although one natural cast print (PRPRC 2000.02.001) from the Dunvegan Formation (Upper Cretaceous: Cenomanian) approaches the proportions seen in the cf. *Tetrapodosaurus* ichnosp. tracks from the Gorman Creek Formation. Seven manus/pes sets within a very long trackway (well over 30 manus/pes sets) were measured, and while this and other data recovered from this site will be published fully in the future, a short summary is included here. The average length of the cf. *Tetrapodosaurus* ichnosp. pes prints is 62.7 cm, and the average width of the pes prints is 45.1 cm. The average pace is 108.9 cm and average stride is 187.0 cm. The seven corresponding manual prints are proportionally large with an average length of 28.5 cm and an average width of 42.9 cm. Sternberg's measurements of the holotype of *Tetrapodosaurus borealis* (Sternberg, 1932) are almost half that of the Gorman Creek ankylosaurs. Such a difference in size could warrant the description of a new ichnospecies within *Tetrapodosaurus*. Latex moulds of portions of some Gorman Creek Formation ankylosaur trackways were collected by the PRPRC, but in our opinion these replicas are not sufficient to designate as a holotype. Furthermore, we do not feel it is prudent to solely designate a field specimen as a holotype. Further field work is planned in the future, with a top priority being the collection of more replica moulds.

Fig. 2.25: *In situ* track surface from the Gorman Creek Formation in Kakwa Provincial Park in northeastern British Columbia, showing a trackway of a large representative of *Tetrapodosaurus* ichnosp., as well the tracks of several small- and medium-sized theropods.

Fig. 2.26: Large and medium (cf. *Megalosauripus* ichnosp.) theropod prints on the *in situ* track surface from the Gorman Creek Formation in Kakwa Provincial Park, northeastern British Columbia. Scale = 10 cm.

Fig. 2.27: Medium-sized theropod prints (cf. *Columbosauripus* ichnosp.) on the *in situ* track surface of Kakwa Provincial Park from the Gorman Creek Formation in Kakwa Provincial Park, northeastern British Columbia. Scale = 10 cm.

Fig. 2.28: Very small- ,small-, and medium-sized theropod prints on the *in situ* track surface of Kakwa Provincial Park from the Gorman Creek Formation in Kakwa Provincial Park, northeastern British Columbia.

Fig. 2.29: Cf. *Neoanomoepus* ichnosp. from the talus debris in Kakwa Provincial Park from the Gorman Creek Formation in Kakwa Provincial Park, northeastern British Columbia. Scale = 10 cm.

Fig. 2.30: Large natural cast manus of *Tetrapodosaurus* ichnosp. (PRPRC 2005.17.002) from Kakwa Provincial Park from the Gorman Creek Formation (in Kakwa Provincial Park, northeastern British Columbia. Scale = 10 cm.

Fig. 2.31: Large natural mould, *in situ* pes of *Tetrapodosaurus* ichnosp.from Kakwa Provincial Park from the Gorman Creek Formation in Kakwa Provincial Park, northeastern British Columbia. Scale = 10 cm.

Manus-pes sets and partial trackways of small size have been found that may also be referred to *Tetrapodosaurus* ichnosp. These diminutive tracks have four short and thick pes digits and a proportionally large pentadactyl manus (with distinctive crescentic posterior margin) compared to the small quadrupedal ornithopods (*Neoanomoepus* ichnosp.) from the Mist Mountain and Gorman Creek Formations. These specimens are the smallest ankylosaur tracks that have been found globally to date (Fig. 2.32).

Fig. 2.32: Track block containing small, natural cast manus-pes set (PRPRC 2005.17.036) attributable to *Tetrapodosaurus* ichnosp. from Kakwa Provincial Park from the Gorman Creek Formation northeastern British Columbia. Scale = 10 cm.

Full-scale research on this site began in the summer of 2006 on the main footwall, but new specimens were studied from the talus debris as well (McCrea and Buckley, 2006). The characteristics of the small quadrupedal ornithopod footprints are distinctly *Anomoepus* – like (tetradactyl pes with long, narrow digits; pentadactyl manus that is proportionally small) and similar to specimens found recently in the slightly older Mist Mountain Formation (Tithonian/Berriasian) (Lockley et al., 2009). Near the end of the 2006 field season a short *in situ* natural mould trackway of cf. *Neoanomoepus perigrinatus* was discovered. This trackway has several manus-pes sets as well as a series of long and narrow, but intermittent impressions that are slightly sinuous in aspect. These impressions are interpreted as being left by the track-maker's tail rather than toe drag marks as they were not found to originate, terminate or cross any manual or pedal traces in this trackway sequence. It was not possible to make a replica mould, but several photographs (Fig. 2.33) and a tracing of this trackway were collected.

Fig. 2.33: *In situ* natural mould trackway cf. *Neoanomoepus perigrinatus*, containing several manus-pes sets and a series of long, sinuous impressions that are interpreted as intermittent tail drags from the Gorman Creek Formation in Kakwa Provincial Park, northeastern British Columbia. Scale = 10 cm.

The Gorman Creek Formation vertebrate ichnofauna is an important transition between the underlying Mist Mountain Formation and the overlying Gething Formation. The ichnofaunas of the Mist Mountain and Gething formations share few similarities, but the Gorman Creek Formation ichnofauna has footprint types in common with both (McCrea and Buckley, 2007; 2008; McCrea, 2011). These include the tracks and trackways of small quadrupedal ornithischians, identical or similar to *Neoanomoepus perigrinatus* from the Mist Mountain Formation, but which have no equivalent in the Gething Formation, and the tracks and trackways of ankylosaurs, which do not occur in the Mist Mountain Formation but which were first described from the Gething Formation (Sternberg, 1932). To date the Gorman Creek Formation vertebrate ichnofauna has not been found to contain sauropod prints, which are found in the older Mist Mountain Formation, nor does it contain the prints of large ornithopods, either *Iguanodontipus* ichnosp. from the older Mist Mountain Formation, or *Amblydactylus* ichnosp. known from the younger Gething Formation.

A number of original specimens (natural moulds and natural casts) as well as several latex replica peels were collected during the 2005 and 2006 expeditions. The list of thirty-one collected specimens can be found in two unpublished reports for B.C. Parks (McCrea and Buckley 2005b; 2006). Additional minor tracksites have been found within the boundaries of Kakwa Provincial Park in British Columbia, and an expedition from the Royal Tyrrell Museum of Palaeontology recently reported finding vertebrate tracks in the Gorman Creek Formation in western Alberta (Tanke and Neuman, 2007).

GETHING (LOWER CRETACEOUS: APTIAN – ALBIAN)

Some of the first dinosaur tracks found in Canada were from the Peace River Canyon of northeastern British Columbia by F.H. McLearn (1923; 1931) and Sternberg (1931). These tracksites were formally studied by C. M. Sternberg in 1930 and his impressive results were published two years later (Sternberg, 1932). Sternberg described several new Cretaceous ichnotaxa including those of a large ornithopod (*Amblydactylus*), small, medium and large theropods (*Irenichnites*, *Gypsichnites*, *Irenesauripus*, respectively), and one ichnotaxon (*Tetrapodosaurus*) attributable to ankylosaurs (Carpenter, 1984; McCrea et al., 2001). The Peace

River Canyon tracksites and other tracksites to the west were granted Provincial Heritage Resource status in 1930; at that time this was the highest protective designation for tracksites in Canada (McCrea and Buckley, 2012).

After Sternberg's research the Peace River tracks were ignored for over three decades until the mid-1960s, when construction began on the W.A.C. Bennett Dam, just upriver from the known tracksites. Several tracks and trackways were discovered during the clearing of the foundation of the dam, later identified as the base of the Gaylard Member (Gibson, 1992) and thus the base of the Gething Formation. A brief expedition by the ROM in 1965 documented some of the tracks and trackways and even made some latex moulds and recovered a few original specimens (Figure 2.34a and b). No results were published from this expedition.

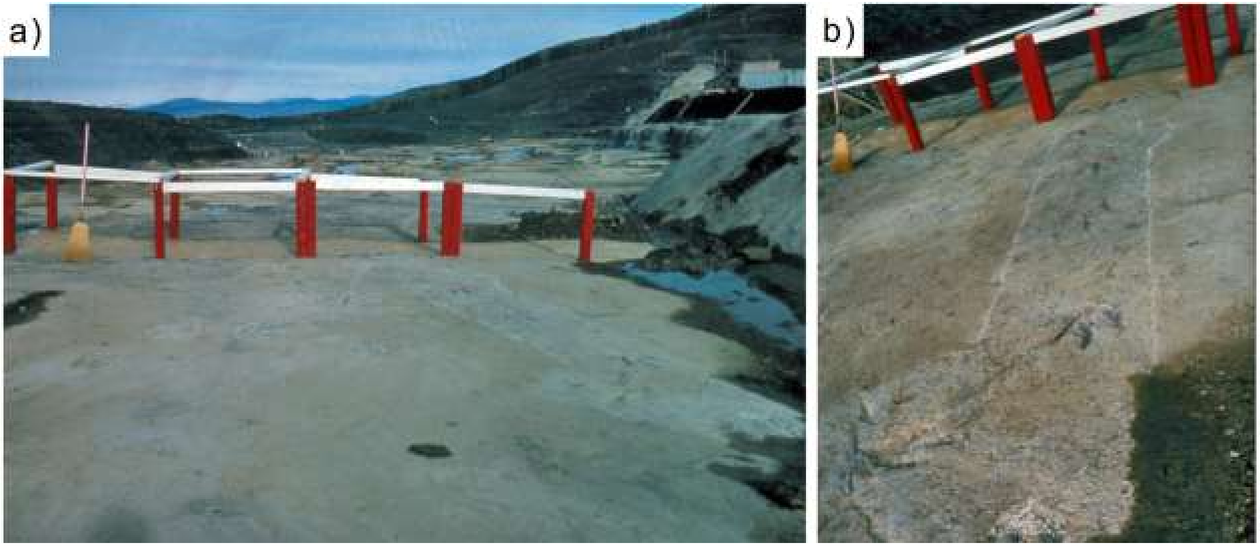

Fig. 2.34: 35mm slide images by Gordon Edmund (Royal Ontario Museum) from 1965 during the construction of the W.A.C. Bennett Dam on the Peace River a few kilometers upriver from Hudson's Hope, British Columbia; a) Image (PN78.33.009) of a large theropod trackway (*Irenesauripus mclearni*) ready for documentation and/or latex moulding; b) Image (PN78.33.010) showing context of exposed tracks at the cleared base for the construction of a large earthworks dam. (Both images provided Courtesy of the Royal Tyrrell Museum of Palaeontology and Alberta Community Development)

It was not until 1975, when construction began on the Peace Canyon Dam downstream from the W.A.C. Bennett Dam and to the east of the known tracksites, that a major research effort was mounted to document the vertebrate ichnofauna of the Peace River Canyon (Currie, 1980; Sarjeant, 1981; Mossman and Sarjeant, 1983). The research effort, led by PJC was based out of the PMA (now RAB), and lasted for four summers (1976-1979). More than 1,700 footprints were documented, 90 prints were recovered and more than 1,000 prints were mapped and measured (Currie, 1983, 1995; Currie and Sarjeant, 1979; Kool, 1981). Once the Peace Canyon Dam became operational in the fall of 1979 the majority of the tracksites were flooded (the resulting reservoir is now called "Dinosaur Lake"). One of the more significant results of PJC's Peace River Canyon expeditions was the discovery and description of small shorebird footprints (*Aquatilavipes swiboldae*). At that time this was the oldest record of bird tracks known (Currie, 1981) and was also the third avian ichnotaxon ever to be named. The two previously named avian ichnotaxa were *Ignotornis mcconnelli* (Mehl, 1931) from Colorado and *Koreanaornis hamanensis* (Kim, 1969) from South Korea. The latter ichnotaxon may be about the same age as *Aquatilavipes swiboldae*, but was not cited in Currie (1981). It is disheartening to consider that the provincial heritage designation granted to the Peace River Canyon tracksites in 1930 was revoked or ignored to clear the way for the development of these two hydroelectric projects (McCrea and Buckley, 2012).

In 1980, a chance discovery was made by Richard Kool of the RBCM, during a visit to the Dawson Creek Station Museum—of a small slab of grey siltstone from the Peace River Canyon, into which had been shallowly impressed what were thought to be a fore and a hind foot. It had been collected in 1963 by R.D. Duquette. The five digits of the manus were widely splayed and of similar length; in contrast, digit I of the pes was markedly opposed and digits II and III were slender, exhibiting what was thought to be syndactyly, a condition known only to occur in certain primitive marsupials (such as the living Australian brush-tailed possum). Placed by Sarjeant and Thulborn (1986) into a new ichnotaxon, *Duquettichnus kooli*, this discovery apparently represented not only the earliest mammal footprint from North America, but also the earliest marsupial footprint discovered anywhere in the world.

However, RTM examined the original holotype specimen (BCPM 1222) at the RBCM in 2006, and found that the purported pes impression was an unmistakable invertebrate burrow which penetrated this block through to the opposite side. The supposed pes was interpreted by Sarjeant and Thulborn (1986) to display syndactyly which was a key feature in the identification of this ichnotaxon as of marsupial affinity. With the pes now identified as an invertebrate burrow, only the manus remains to support the description of *Duquettichnus kooli*. In light of the current reinterpretation, and the fact that there are no other specimens to support this ichnotaxon, the status of *Duquettichnus kooli* is in doubt and should be considered a *nomen dubium*.

Gething Formation tracks continue to be found in northeastern British Columbia. During the excavation of a giant ichthyosaur at Pink Mountain (Nicholls and Manabe, 2004) footprint specimens of *Amblydactylus* ichnosp were discovered in nearby Gething Formation exposures. Some of these track specimens were removed to the RTMP while others went to the FGM (Fig. 2.35).

Fig. 2.35: Natural cast large tridactyl pes of *Ambydactylus* ichnosp. collected during the excavation of a large ichthyosaur at Pink Mountain in northeastern British Columbia from the Gething Formation. This specimen is stored at the Fort George Museum, Prince George, British Columbia.

Other fossil footprint finds have recently been made in the vicinity of the Peace River near Hudson’s Hope by locals and by palaeontologists, thus demonstrating that not all of the Gething Formation tracks were flooded. A small cluster of *in situ* sites and a variety of footprint-bearing talus blocks were discovered near Elisabeth Creek to the west of the W.A.C. Bennett Dam, including an *in situ* site with several *Amblydactylus gethingi* prints and partial trackways, one of which contains a clear, deep manual impression.

The second *in situ* site at Elisabeth Creek also has a long natural mould *Amblydactylus gethingi* trackway with manual impressions. Several isolated blocks were found to preserve an impressive variety of vertebrate tracks, including small reptilian traces (possibly turtle prints) (Figs. 2.36a and b; 2.37a and b), large avian prints (cf. *Aquatilavipes curriei* – however see Systematic section below) (Fig. 2.38), and a portion of a large theropod trackway (*Irenesauripus mclearni*) (Fig. 2.39).

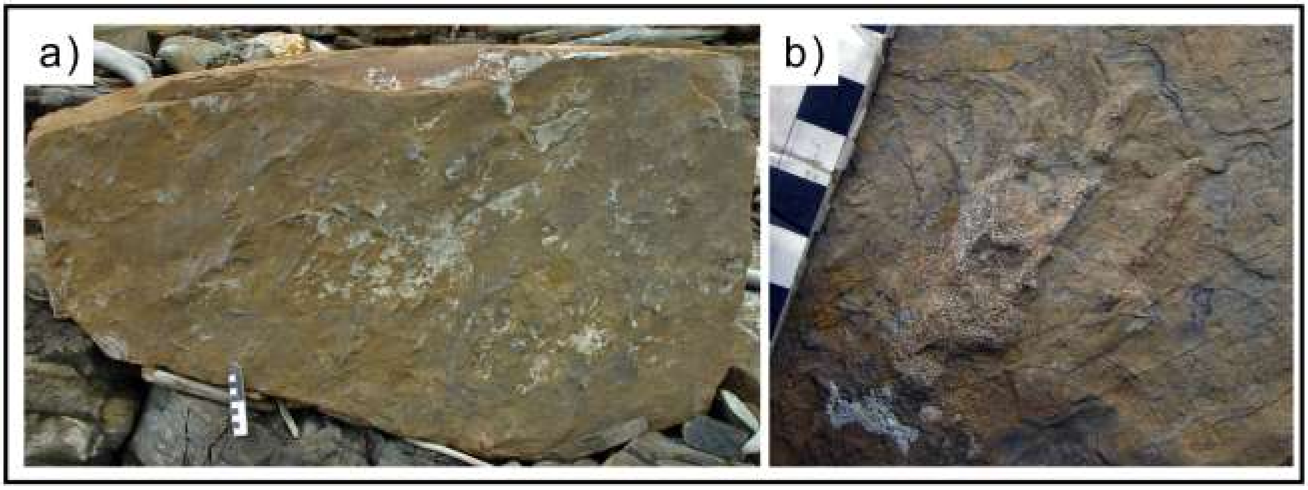

Fig. 2.36: a) large track block (PRPRC 2005.07.005, left) from the Gething Formation of northeastern British Columbia; b) closeup of a natural cast print of a small reptile. Scale for a & b = 10 cm.

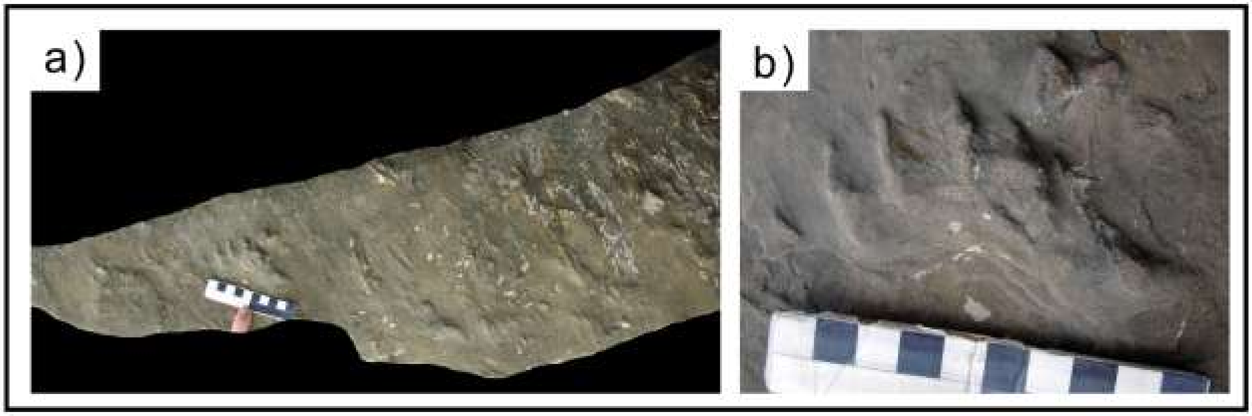

Fig. 2.37: a) large track block (PRPRC 2005.07.003) from the Gething Formation of northeastern British Columbia with several natural cast prints of small reptiles; b) closeup of a natural cast print (likely a turtle pes impression). Scale for a & b = 10 cm.

Fig. 2.38: Track block (PRPRC 2005.07.002) containing two natural cast tracks of cf. *Aquatilavipes curriei* (redescribed as *Limiavipes curriei* herien) from the Gething Formation of northeastern British Columbia. Scale = 10 cm.

Fig. 2.39: *In situ* natural mould print of a large theropod pes print (*Irenesauripus mclearni*) from the Gething Formation of northeastern British Columbia. Scale = 10 cm.

A number of small, *in situ* tracksites occur along the banks of Gething Creek possessing large *Amblydactylus* tracks (Fig. 2.40) and trackways, including some with distinct manus/pes sets (Fig. 2.41). This site is well known to the general public and the track surface has been subject to repeated acts of vandalism (Buckley and McCrea, 2012) (Fig. 2.42).

Fig. 2.40: *In situ* natural mould pes of *Ambydactylus* ichnosp. from the Gething Formation Gething Creek, northeastern British Columbia. Scale = 10 cm.

Fig. 2.41: *In situ* natural mould manus-pes set of *Ambydactylus* ichnosp. from the Gething Formation, Gething Creek, northeastern British Columbia. Scale = 10 cm.

Fig. 2.42: One example of vandalism in white spray paint on the *in situ* track surface along Gething Creek, northeastern British Columbia. Message reads “EVOLUTION = LIE”. Sometimes defacement occurs directly on the tracks.

A large scale tracksite was discovered by a local in the vicinity of Carbon Creek and is distinct from the site reported by Currie (1989) being just under three kilometers to the south. Unlike most of the other Gething Formation sites, this site is not exposed on the bank of a creek or river but rather at the top of a large, flat hill. While only a few hundred square meters of track surface were exposed during a visit by CWH and later by RTM it was easy to see that more than a thousand square meters could be uncovered with minimal effort. The track fauna observed consisted of large theropod tracks (*Irenesauripus mclearni*) (Fig. 2.43), medium-sized theropod tracks (*Columbosauripus ungulatus*), and the distinctive tracks of *Tetrapodosaurus borealis* and many others that were partially covered by sediment and modern plant material.

Fig. 2.43: Newly discovered *in situ* track surface, showing two distinct prints of *Irenesauripus mclearni*, from the Gething Formation, northeastern British Columbia.

There are currently three coal lease tenure claims in the Carbon Creek area and it remains to be seen if this site can be preserved for its heritage and research value. In this vein it is encouraging to report that very recently; additional *in situ* dinosaur tracksites have been reported in the Carbon Creek area by coal geologists. Photographs provided by these geologists and mine employees show large tridactyl theropod tracks and those of *Tetrapodosaurus* ichnosp. A major effort to document these sites is anticipated to begin summer 2013.

Construction activities around the hydroelectric dams near Hudson's Hope during the summer of 2011 led to the discovery of vertebrate tracks on large talus blocks. The finds were reported to the authors and photographed in October 2011. The tracks occur as both natural moulds and natural casts which are preserved in organic-rich, sometimes rippled fine sandstone. To date the ichnofauna of the reported find includes *Amblydactylus* ichnosp., *T. borealis*, and *I. mclearni*. No small traces have been reported from this site, but only a brief survey has been completed to date. While in an active construction site, the blocks have been set aside for eventual deposition in the collections of the Peace Region Palaeontology Research Centre.

It is very gratifying to see the interest industry has in reporting such finds over the last decade, and taking a responsible and active role in supporting their research and preservation. It can only be hoped that the Provincial Government of British Columbia will finally address this province's woeful shortcomings with fossil resource protection and no longer be the only province in Canada with significant palaeontological resources and no legislation or coherent plan to manage those resources.

GLADSTONE FORMATION (LOWER CRETACEOUS: APTIAN – ALBIAN)

Three *in situ* natural cast avian prints (RTMP 1990.030.0001) were discovered in a roadside outcrop near Grande Cache, Alberta (Lockley et al., 1992; McCrea and Sarjeant, 2001). They were originally thought to be from the Gates

Formation (Lockley, et al., 1992), but it was found that no Gates Formation outcrop was exposed nearby. McCrea and Currie (1998) speculated that these tracks might be from the Cadomin Formation (as the characteristic conglomerates were found within a few meters of the track horizon). However, a closer examination of the exposure revealed that the footprints were in fact from the base of the Gladstone Formation (Alberta equivalent of the Gething Formation) overlying the top of the Cadomin Formation (McCrea and Sarjeant, 2001). These avian tracks (Fig. 2.44) have been referred to *Aquatilavipes swiboldae* (Lockley et al., 1992; McCrea and Currie, 1998; McCrea and Sarjeant, 2001), and are essentially from the same formation (Gething Formation in British Columbia) from which the *A. swiboldae* holotype slabs were recovered (Currie, 1981).

Fig. 2.44: RTMP 1990.030.0001, three natural cast avian prints (cf. *Aquatilavipes swiiboldae*) from the Gladstone Formation, near Grande Cache in northwestern Alberta. Scale = 5 cm.

ROSS RIVER BLOCK, YUKON TERRITORY (CRETACEOUS: APTIAN – CENOMANIAN)

A substantial *in situ* dinosaur track area was discovered near Ross River in 1999 (Gangloff et al., 2000, Gangloff and May, 2004) which prompted Long et al., (2000) to question the previous Eocene age designation of the associated beds of the Ross River Block. The vertebrate ichnofauna reported by Gangloff and May (2004) includes the ichnogenera *Amblydactylus*, *Columbosauripus*, *Gypsichnites*, *Irenesauripus*, *Ornithomimipus*, and *Tetrapodosaurus*. Based on similarities with the vertebrate ichnofaunal assemblages of western Canada (Gething, Gates and Dunvegan formations) and more recent palynological work (Long et al., 2000), the Ross River Block has been estimated to be middle Albian - early Cenomanian in age. This track area (132^{o} 30’ N, 122^{o} 5’ W) is the most northwesterly occurrence of dinosaur tracks in Canada. However, a number of dinosaur tracksites in Alaska further extend the northerwesterly range of vertebrate ichnites in North America (Gangloff, 1998; Gangloff and May, 1998; Fiorillo, 2004).

GATES FORMATION (LOWER CRETACEOUS: ALBIAN)

Grande Cache Member

Dinosaur tracks in the No. 9 Mine and South Pit Lake area in the Smoky River Coal Mine near Grande Cache were first noticed by a party of Alberta Geological Survey (AGS) and Smoky River Coal geologists in July of 1988 and reported to the RTMP by the AGS (Langenberg and Mateeva, 2009). Additional tracks in the South Pit area were reported in 1989 and subsequently studied by palaeontologists of the RTMP and University of Saskatchewan (McCrea, 2003a; McCrea and Currie, 1998).

Some of the tracksites were composed of many track-bearing blocks in talus piles, while others were large *in situ* track surfaces on massive vertical footwalls directly accessible only through the use of ropes and harness (Fig. 2.45 – 2.46). The track ichnofauna is diverse, with footprints of small, medium and large theropods, ankylosaurs, birds, turtles and/or crocodylians (McCrea, 2003a; McCrea and Currie, 1998; McCrea et al., 2001; McCrea and Sarjeant, 2001). By far the most dominant footprint type is that attributed to ankylosaurs (*Tetrapodosaurus borealis*) (Fig. 2.47a and b). Ankylosaur prints are often the only track type found at most of the 20 known tracksites (McCrea, 2000a). However, at the largest tracksite (W3 Main) the footprints of large wading birds (*Aquatilavipes curriei*) (Fig. 2.48a and b) dominate the ichnofauna on two of the three mapped bedding planes (McCrea and Sarjeant, 2001). Within the mapped 500m^2 grid area prints of *A. curriei* account for 81% of all footprints on B-layer, 50% of the footprints on C-layer and 60% of footprints totaled from all three bedding planes (McCrea, 2000a, Table 10). In the Systematic Ichnology section herein we reassign *A. curriei* to a new ichnogenus because it does not fit Currie's (1981) description of *Aquatilavipes*.

Fig. 2.45: W3 Main track site in the then Smokey River Coal Mine, exposing large track-bearing surfaces of the Gates Formation near Grande Cache, Alberta.

Fig. 2.46: Close up of a small portion of the W3 Main track site showing a high diversity ichnofauna. For scale, the large theropod tracks are ~50 cm length.

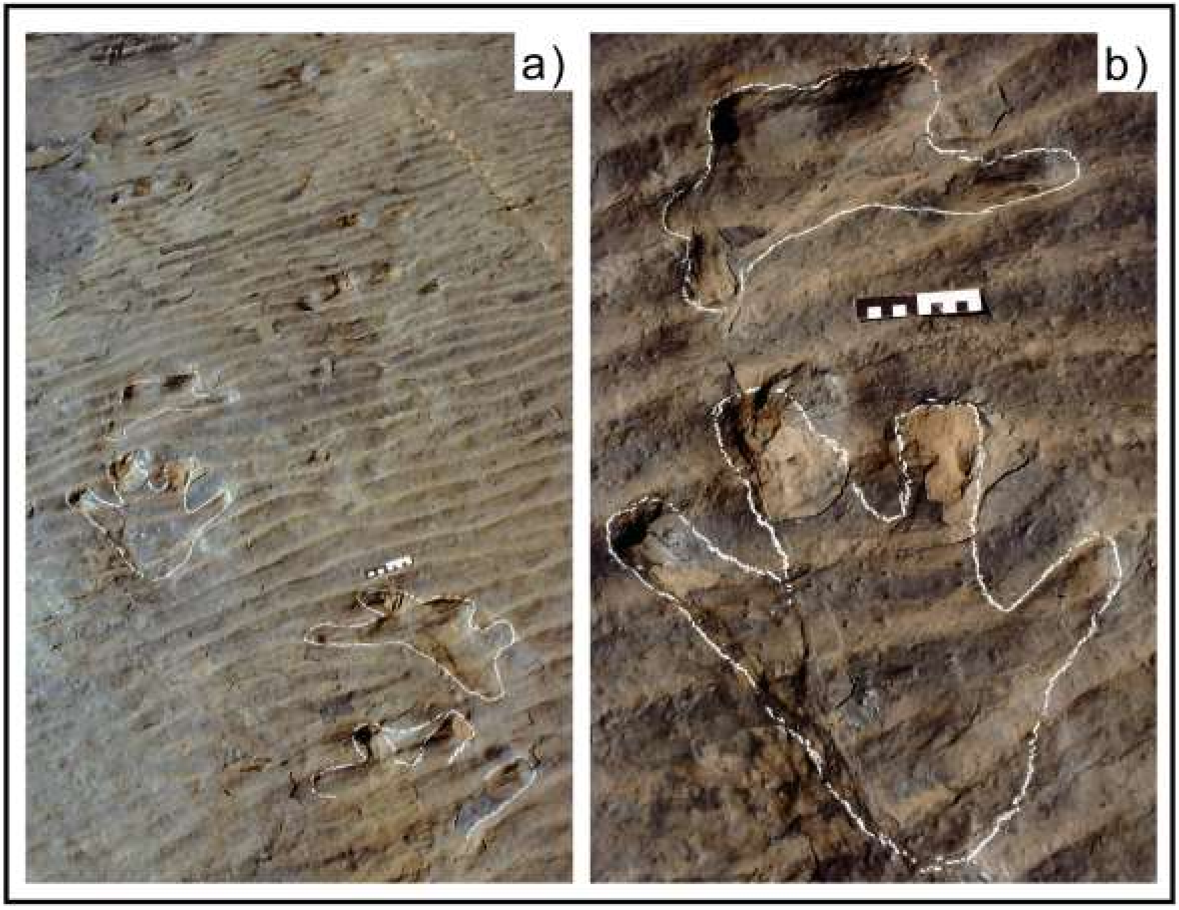

Fig. 2.47: a) *In situ* trackway of *Tetrapodosaurus borealis* from the Gates Formation W3 Extension Pit near Grande Cache, Alberta; b) A shallowly impressed yet well preserved manus –pes set. Scale = 10 cm.

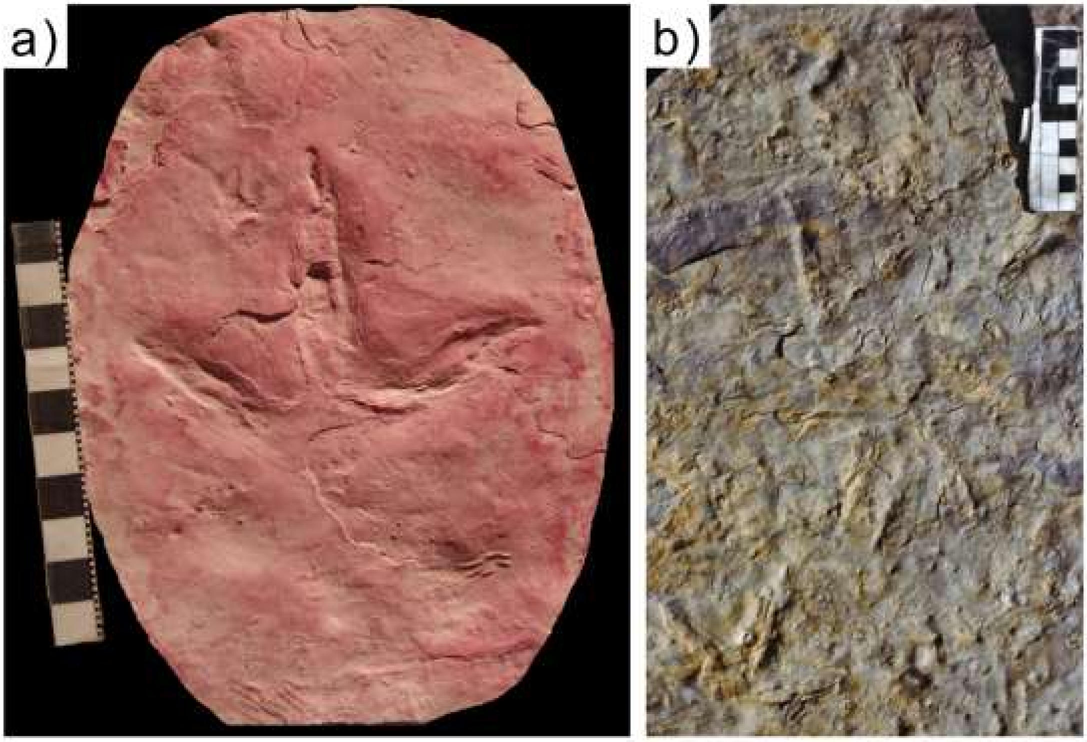

Fig. 2.48: *Aquatilavipes curriei* (redescribed as *Limiavipes curriei* herien) holotype cast from the Gates Formation near Grande Cache, Alberta. b) In situ paratype (later moulded then cast). Scales in cm.

It is a fact that the W3 Main track surface is both high and vertically oriented and that neither *A. curriei* tracks nor many small to medium tridactyl dinosaur tracks (theropod) are visible from the ground. Due to the shallow nature of many of the thousands of footprint impressions at this site, even large theropod and ankylosaur tracks are not always visible from the ground. When viewing vertical tracksites similar to the W3 Main site (Fig. 2.45 – 2.46**)** only 20-30% of the tracks present may be visible, even under ideal viewing conditions.

It is possible that such large, steep track-bearing surfaces might be documented with the use of high-resolution photogrammetry, or surface laser-scanning, these techniques being capable of resolving detail invisible to the human eye. The current resolution of the best available photogrammetric and surface laser-scanning images is close to 2 mm (Belvedere and Falkingham, 2012; Petti et al., 2008) which is certainly enough to pick up fine details of small avian tracks. It will be interesting to see if this resolution can be achieved on vertical track faces in the field.

Even if high-resolution photogrammetry, laser-scanning, or other remote-sensing techniques work on large-scale vertical sites they would (when rendered) create unmanageably large file sizes, particularly for laser-scanning if used at the highest resolution setting over the whole surface (less so for digital images which may be used in batches to make smaller, more manageable files). What this means is that if it is at all possible, the researchers should access the track surface directly to be sure where all the tracks on a surface are. When this on-site scouting has been accomplished, the researchers may then plan their photographic sweeps (for photogrammetric purposes), or surface scans, being sure to focus effort on areas with high concentrations of tracks (particularly small tracks). If there are areas with no tracks on certain parts of the surface these can be documented (photographed or scanned) in less detail, thereby saving precious time and hard drive space.

The Grande Cache sites contain the most compelling evidence to date of gregarious behavior in adult ankylosaurs. The W2 tracksite contains two groups of parallel trackways (McCrea, 2000a, fig. 4a; 2001, 2003a; McCrea et al., 2001) with several animals in each group.

One of the more interesting discoveries was of a large theropod trackway (*Irenesauripus mclearni*) with associated forelimb impressions (Fig. 2.49). The impressions consist of long, narrow scrapes, in two sets of three that appear to have been made by three clawed digits of both hands of the track-producing animal while it was in motion (McCrea, et al., 2002). Sadly this tracksite was buried and possibly destroyed by a large-scale slope failure within a year of its discovery (Fig. 2.50a and b); however, a latex replica was made at the time of discovery and a plaster cast (TMP 2001.35.01) of a four meter section of this trackway is preserved at the RTMP.

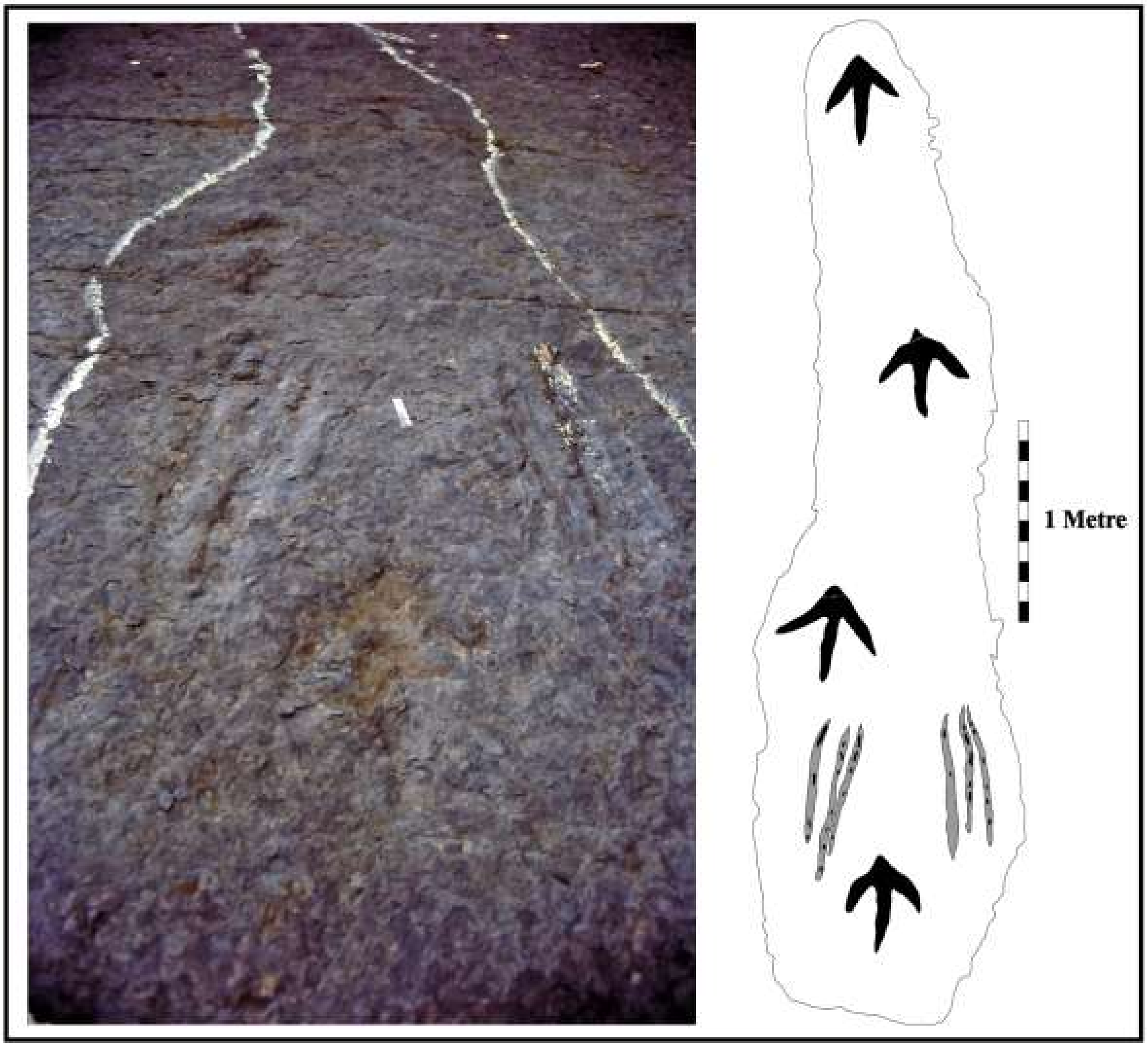

Fig. 2.49: Left **-** *In situ* trackway of *Irenisauripus mclearni* from the Barrett Wall track site near Grande Cache, Alberta (10 cm scale in photo). The trackway is associated with two sets of forelimb traces, each with three distinct claw drag impressions. Right – Map of the Barrett Wall trackway taken from the master cast (TMP 2001.35.01).

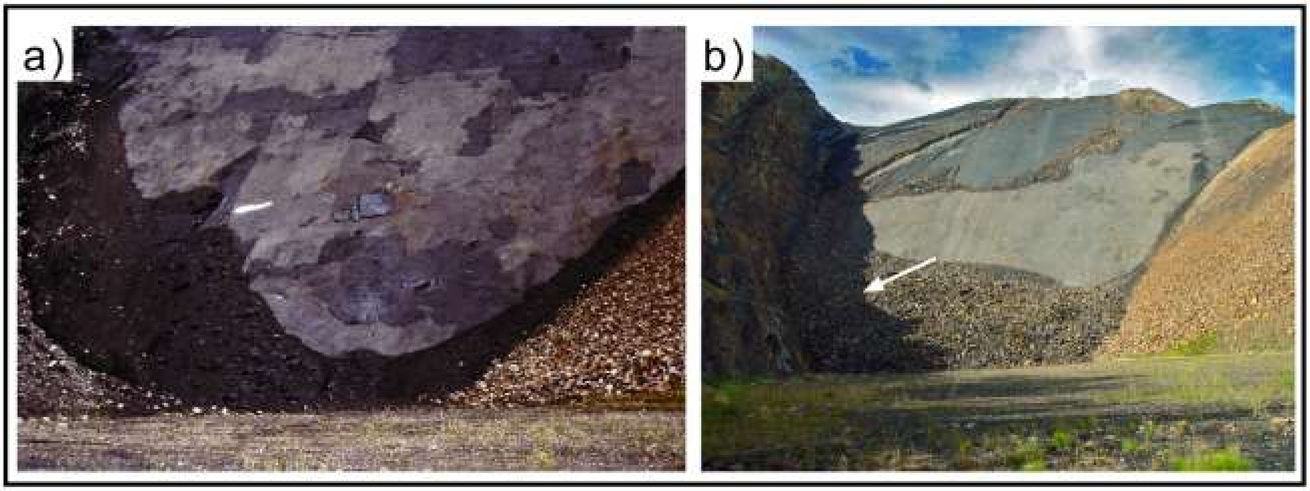

Fig. 2.50: a) The Barrett Wall site in the Gates Formation (Albian) displaying the *in situ* trackway of *Irenisauripus mclearni* (McCrea et al., 2002) being moulded shortly after its discovery in 2001. For scale the mould is approximately four metres in length. b) The footwall in the summer of 2002 after being buried by a massive slope failure. The white arrow indicates the approximate position of the trackway.

The majority of track sites in the Gates Formation near Grande Cache are mono-ichnospecific (contain *Tetrapodosaurus borealis* tracks and trackways exclusively). Some tracksites contain other vertebrate ichnotaxa (i.e. the W2 Site), but are *T. borealis*-dominated. Only a few sites are not dominated by *T. borealis* prints. These observations have led to some speculation regarding the distribution of track types from site to site. McCrea (2000a; 2000b; 2001; 2003) observed that on track surfaces composed of fine-grained sediments with substantial organic content, the ichnofauna consists almost exclusively of *T. borealis* prints and trackways. Track surfaces composed of coarser-grained sediments with low organic content have a higher diversity of vertebrate ichnofauna. The division between high and low vertebrate ichnofaunal diversity translates almost perfectly into quadruped vs. biped dominant palaeoenvironments. The bipedal vertebrates (avian and non-avian dinosaurs) did not normally frequent the low energy depositional environments. The quadrupedal vertebrates (ankylosaurs) appear to have been able to inhabit any terrestrial palaeoenvironment where tracks are found.

McCrea and Sarjeant (2001) named a new ichnospecies (*Tricorynopus brinkmani*) based on supposed mammal footprints found on a small isolated slab containing several natural mould prints of avian affinity (TMP 1999.089.0020). Sarjeant (2000) stated that the assignment of these “prints” to *Tricorynopus* (Sarjeant and Langston, 1994) was highly speculative. McCrea et al. (2004) were critical of these and other specimens of purported Mesozoic mammal tracks from western Canada and felt that none of them were *bona fide* mammal tracks. McCrea et al., (2004) suggested instead that *Tricorynopus brinkmani* prints might be partially impressed or preserved avian prints, or possibly a product of two or more overlapping avian prints. *Tricorynopus brinkmani* should be considered a *nomen dubium*.

The Gates Formation boasts an impressive diversity of avian prints, only one of which has been formally described (McCrea, 2000a; 2003a; McCrea and Sarjeant, 2001). The first avian prints were found on the W3 Main footwall in the Grande Cache Member of the Gates Formation. They are tracks and trackways of a large, long-legged bird, probably a wading type and were described by McCrea and Sarjeant, (2001) as a new ichnospecies of *Aquatilavipes* (*A. curriei*) (Fig. 2.48a and b) within Avipedidae. However, the assignment of these large, avian tracks to Avipedidae and *Aquatilavipes* was not well-founded. The emended diagnosis of Avipedidae and the ichnogeneric redescription of *Aquatilavipes* by McCrea and Sarjeant (2001) were over-stretched to include the Grande Cache tracks as the characteristics of this track type do not fit Currie's (1981) description of *Aquatilavipes*. This broad definition of the ichnogenus hides true ichnotaxonomic diversity, thereby creating similar problems to those that have plagued *Avipeda* (Lockley and Harris, 2010). *Avipeda* is based on very broad characters, relegating it to the functional status of a garbage ichnotaxon since a large number of currently separate ichnotaxa could technically fit into this ichnogenus.

Since the time of description of *A. curriei* several new ichnotaxa of avian tracks have been named, including additional ichnospecies of *Aquatilavipes*, *A. izumiensis* (Azuma et al., 2002) and *A. sinensis* (Zhen et al., 1995). Lockley and Hunt (2010) and Huh et al. (2012) suggest that *A. sinensis* should be reassigned to *Koreanornis*, which would leave three ichnospecies within *Aquatilavipes*. However, we agree with Lockley and Harris (2010) that *A. curriei* requires reassignment to a new ichnofamily and ichnogenus (see SYSTEMATIC ICHNOLOGY below). Recently data collected by some of the authors (RTM and LGB) on small tridactyl tracks and trackways from the Lotus Fortress track site from the mid-Cretaceous Jianguan Formation show a striking similarity to *Aquatilavipes curriei*. The Lotus Fortress tracks were originally described by Xing et al,. (2007) as a theropod ichnotaxon *Wupus agilis*, however, this ichnotaxon is more likely to be of avian affinity.

Talus blocks with a number of smaller tridactyl prints of avian affinity (Fig. 2.51) were noticed by RTMP palaeontologist Donald Brinkman in 1998. The bedding plane from which they originated was eventually found on the shoulder of the W3 Main tracksite (Fig. 2.52) and this track wall was subsequently dubbed the 'W3 Bird' site. The productive layer for tracks in the W3 Bird site is thick, fine-grained sandstone which weathers to a distinct buff color. This coloration makes it difficult to observe and measure these small, faint tracks, but fortunately 3-D surface laser-scanning is able to bring these delicate tracks into view (Fig. 2.53).

Fig. 2.51: A natural mould block from the W3 Bird track site near Grande Cache, Alberta. Scores of avian tracks are visible on this specimen which is stored at the RTMP. Scale = 10 cm.

Fig. 2.52: Photograph of *in situ* avian tracks from the W3 Bird track site near Grande Cache, Alberta. Scale in cm.

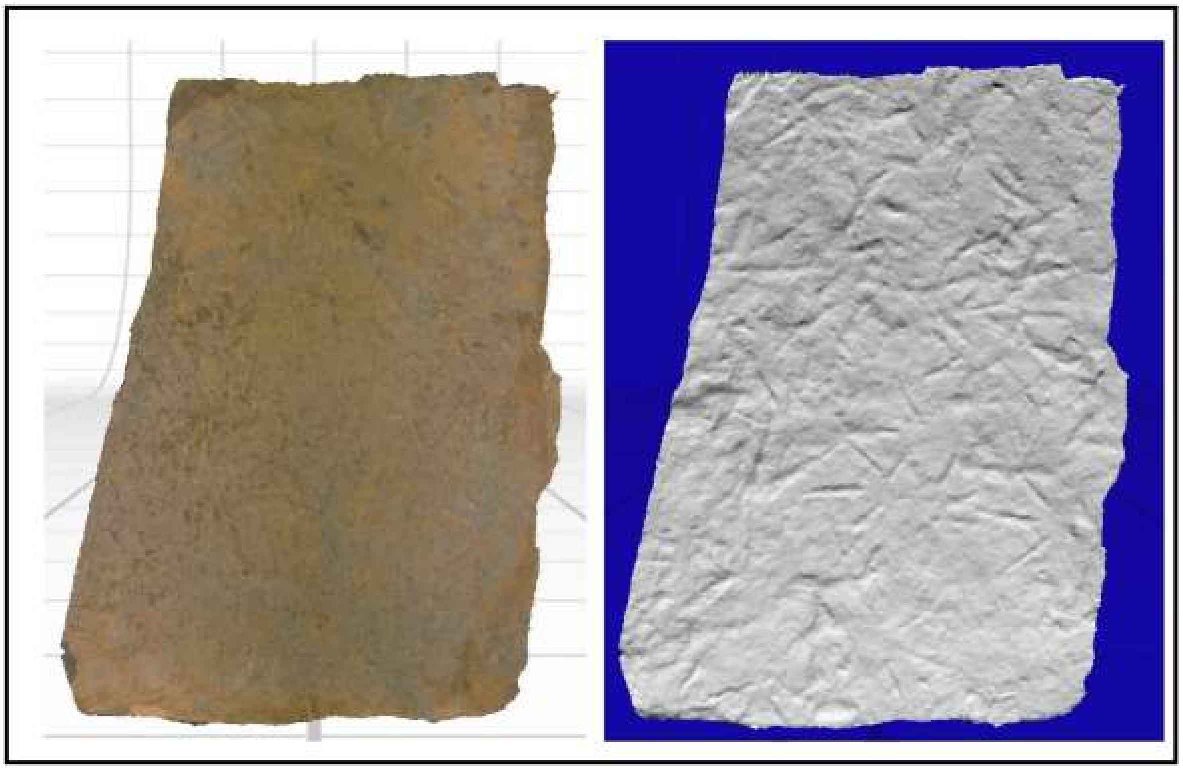

Fig. 2.53: Surface laser scan images (left: in natural colour; right: with colour removed to show topographic details) of a currently undescribed bird ichnotaxon from the W3 Bird locality from the Gates Formation (Albian) near Grande Cache, Alberta.

Few *in situ* avian tracks have been observed at the W3 Bird site, but the track layer is easily revealed by splitting the rocks that have fallen from this track face. Track density in this layer is greater than 100 tracks/m^2 and this layer occurs over a several thousand m^2 surface, making this site one of the highest density avian tracksites in the world. However, the density is not as high as some of the avian tracksite occurrences reported from South Korea, such as those found at Haman, Jindong, Goseong and Gajin, (Lockley et al., 1992; Lim et al., 1994; Kim et al., 2012; Lockley et al., 2012).

The W3 Bird tracks include *A. curriei* prints and short trackway segments, but there are potentially four to five other avian ichnotaxa that are currently under investigation. Avian tracks also occur on the W3 Extension tracksite and include tracks and trackways of *A. curriei* as well as another novel ichnotaxon of very small (3.5 cm FL) avian prints.

A large area with numerous dinosaur tracksites within the Gates Formation of the former Smoky River Coal Mine were granted Provincial Heritage Resource status by the government of Alberta (Spivak et al., 2006), a fitting tribute to one of the world's top tracksites.

Mountain Park Member

In the central Alberta Foothills, alluvial strata assigned to the Mountain Park Member of the Gates Formation underlie marine strata of the upper part of the Viking Formation. Lateral facies relationships established by Roca (2007) and subsequent geochronological studies of zircons from bentonite (S. Kamo pers comm, 2011) suggest that the upper part of the Mountain Park Member is time-equivalent to the marine Joli Fou Formation (early late Albian). On Ram River, a section near the top of the Mountain Park Member yielded tetradactyl track casts probably attributable to an ankylosaur (*Tetrapodosaurus* ichnosp.) (Fig. 2.54).

Fig. 2.54: Isolated tetradactyl cast, viewed from above. Mountain Park Member of the Gates Formation exposed on the Ram River, ~ 30 km downriver from Ram Falls, Alberta. Footprint is preserved in sideritized sandstone embedded in rubbly, pedogenically-modified green siltstone. Scale bar = 20 cm.

Northeastern British Columbia

Within the last two decades, Gates Formation tracks and trackways have been reported from northeastern British Columbia at industrial sites (open pit coal mines, gas wells) and from natural mountain exposures. The sites reported to date have not yet approached the number, or surface area of those from northwestern Alberta, but the potential for such finds is high.

The first reported discovery was an avian trackway, on a slab from atop Roman Mountain (Fig. 2.55). The first report and photographs of the Roman Mountain bird trackway was in one of the first locally-written books on Tumbler Ridge and surrounding areas (Helm, 2000; 2001, plate 14). These prints are similar in appearance to *Aquatilavipes swiboldae*, but the slab has not been recovered or researched. This avian track specimen is within Peace River Coal's Trend mine coal lease area. With active mining and blasting nearby the area has restricted access, but there are plans to collect this interesting slab in the future.

Fig. 2.55: Bird tracks (cf. *Aquatilavipes* ichnosp.) from the Gates Formation near the peak of Roman Mountain, northeastern, British Columbia. Scale = 10 cm.

Around the turn of the millennium a slab with natural mould theropod tracks (cf. *Irenichnites* ichnosp.) was discovered within the former Bullmoose coal mine just north of Tumbler Ridge (Helm, 2001, Plate 12). This specimen was removed to the Britannia Mine Museum (~40km north of Vancouver, BC) a few years prior to the establishment of the PRPRC.

Tracks and partial trackways of *Irenesauripus mclearni*, and *Tetrapodosaurus borealis* have also been found on an excavated footwall slope adjacent to a natural gas well site south of Tumbler Ridge. *T. borealis* dinoturbated footwall surfaces were reported to the PRPRC by local geologist Kevin Sharman at the Phase I Pit of Peace River Coal (formerly NEMI) Trend Mine (Fig. 2.56).

Fig. 2.56: Gates Formation (Albian) exposure of multiple ankylosaur tracks in the NEMI Mine near Tumbler Ridge, British Columbia.

Additional, although of poor quality, track discoveries have been made of isolated blocks within the Quintette coal mine near Tumbler Ridge. The Quintette mine is getting ready for coal production after a decade long hiatus. The prospects for coal and other industry operations uncovering tracks is always high in this region.

Even though vertebrate tracks remain elusive in the Quintette mine, large-scale, *in situ* surfaces of rippled, medium-fine grained sandstone, revealing multiple specimens of *Asteriacites* ichnosp. (Fig. 2.57), an invertebrate trace attributable to asteroids and ophiuroids, have been observed (Helm, 2008). These beds originate from the lower part of the formation (Kevin Sharman, pers. comm. 2013), and are on different bedding planes than those where vertebrate traces are found. The *Asteriacites* ichnosp. occurrences indicate the presence of a marine influence in the Gates Formation.

Fig. 2.57: *Asteriacites* ichnosp. traces from the Gates Formation within the Quintette coal mine. Scale = 10 cm.

Stratigraphic investigation of Mount Belcourt also revealed numerous horizons of dinoturbation in the Gates Formation, mainly in crevasse-splay deposits. No bedding plane exposures were available and no ichnospecific identifications could be made. Tracks have also been reported from recent and ongoing, mandated BC Hydro palaeontological surveys of the Peace River just downstream of the Peace Canyon Dam near the type section of the Gates Formation.

A large friable track surface was exposed during road construction at Falling Creek to the south west of Chetwynd, British Columbia by Western Coal in the fall of 2011. This site was promptly reported to the PRPRC in the fall of that year and Western Coal employees brought PRPRC palaeontologists to the site in October, 2011 (Fig. 2.58). This site has several faint, but lengthy trackways of *Tetrapodosaurus borealis* and also a very unusual trackway (possibly trackways) of *Irenesauripus* ichnosp. (Fig. 2.59). Either the *Irenesauripus* track-maker was walking with an extremely (and unprecedented) short pace and stride, or there were two track-makers, one following behind the other and both sharing a common trackway midline. The track surface at the Falling Creek locality is very friable and will likely not survive the harsh climate of the Peace Region for much longer.

Fig. 2.58: The Falling Creek track site from northeastern British Columbia showing ankylosaur and theropod trackways.

Fig. 2.59: Unusual theropod trackway (or trackways) from the Falling Creek track-site. Camera lens cap for scale.

The Gates Formation of British Columbia is the richest in Canada in terms of number of tracksites and numbers of tracks. To date the Gething Formation has a slightly greater diversity of ichnotaxa, although it is likely that the Mist Mountain Formation ichnofaunal diversity could exceed the combined Gates and Gething ichnodiversity. There are more than a half dozen coal mines in Alberta and British Columbia that are currently exploiting the economic coal seams of the Gates Formation. Each year brings new reports of track finds and a greater need to educate industry in identifying such resources. To this end the PRPRC unveiled a main gallery exhibit to the public in May, 2010 (Fig. 2.60) which is an interpretation of what is known to date from the Gates Formation vertebrate tracksites (including a reconstruction of the *Irenesauripus mclearni* trackway with claw strike impressions – Fig. 2.49). The PRPRC exhibit serves to educate and delight the residents and visitors to the museum, but it also serves a very important function in bringing awareness about these important palaeontological resources to a variety of industries that are heavily active in Alberta and British Columbia.

Fig. 2.60: The main exhibit of the PRPRC's Dinosaur Discovery Gallery.

BOULDER CREEK FORMATION (LOWER CRETACEOUS: MIDDLE – UPPER ALBIAN)

The first vertebrate tracks recovered from the Boulder Creek Formation are on a single small slab (PRPRC 2005.15.001, Fig. 2.61) with numerous natural cast avian footprints and a few small theropod prints (Buckley and McCrea, 2007; 2009; 2011) (Fig. 2.62). The avian prints present on PRPRC 2005.15.001 have characteristics in common with *Barrosopus slobodai* from the Anacleto Formation of Argentina (Coria et al., 2002). A full description of this specimen will be soon be submitted for publication.

Fig. 2.61: A natural cast slab (PRPRC 2005.15.001) with small theropod (cf. *Irenichnites* ichnosp.) and avian tracks from the Boulder Creek Formation, Boulder Gardens locality, south of Tumbler Ridge. Inset is a closeup of one of the small avian prints.

Fig. 2.62: A close view of a portion of a replica cast of PRPRC 2005.15.001 showing a small theropod print and several avian prints. Scale = 10 cm.

The Boulder Creek Formation, confined to the Foothills of B.C., spans the upper part of the Middle Albian to the lower part of the Upper Albian. The formation comprises a lower Cadotte Member that was deposited in a marine shoreface environment and hence contains no vertebrate traces. The overlying Walton Creek Member (equivalent to the Paddy Member of the Peace River Formation in Alberta) was deposited in coastal plain, lake and lagoonal environments, and contains numerous examples of dinoturbation but relatively few tracks exposed in plan view. A natural cast of a tridactyl track was noted *in situ* at the base of a crevasse-splay sandstone on Mount Spieker (Fig. 2.63). In the Quintette Mine access road and in the Shikano Mine Cut, two sections through the Walton Creek member reveal numerous dinoturbation structures plus a few plan views of indeterminate ?ankylosaur tracks; other examples of dinoturbation and undertracks are present in sections on Whatley Creek and Commotion Creek (Fig. 2.64 – 2.65).

Fig. 2.63: A tridactyl track preserved as a cast on the base of a crevasse splay sandstone overlying weakly pedogenically modified grey sideritic mudstone. Lower part of Walton Creek Member of Boulder Creek Formation, Mount Spieker, B.C. Scale bar = 20 cm.

Fig. 2.64: Tetradactyl track (pes) exposed on the base of a crevasse-splay sandstone in lower part of Walton Creek Member of Boulder Creek Formation exposed in the 'Shikano Cut' – an abandoned portion of the Quintette coal mine adjacent to the Murray River, Tumbler Ridge area, B.C. Visible portion of tape measure approx. 20 cm long.

Fig. 2.65: Trackway preserved as natural casts on the base of a crevasse-splay sandstone overlying grey, floodplain mudstone. Middle portion of Walton Creek Member of Boulder Creek Formation exposed in access road of (abandoned) Quintette Coal Mine, south of Tumbler Ridge, B.C. Stratigraphic top to right of photo. White arrows indicate tracks.

GOODRICH FORMATION (LOWER CRETACEOUS: LATE ALBIAN)

The Goodrich Formation is a sandstone-rich element of the predominantly marine Upper Albian succession and is present only in northeastern British Columbia. The Goodrich is under- and overlain by marine, mudstone-dominated strata of the Hasler and Cruiser formations respectively. The Goodrich represents the eastward progradation of deltaic and coastal plain systems into the shallow muddy ‘Mowry Sea’. Few bedding plane exposures are available and dinosaur track information comes from deformation (‘dinoturbation’) seen in vertical section. At Mount Belcourt, the Goodrich Formation is >190m thick and consists almost entirely of coastal plain deposits, including lenticular sandstone channel-fills, flood plain mudstones, paleosols, lake, crevasse splay and levee deposits.

Indeterminate ‘punch-down’ undertracks are present at numerous horizons, mainly in thinly-bedded sandstones representative of crevasse-splay and levee environments, although a few deformation structures were noted in sandstone channel-fills. Further to the north, on Dokie Ridge, the Goodrich succession is dominated by marine shoreface sandstone; interstratified but poorly-exposed coastal plain strata contain a few horizons of dinoturbation.

PASAYTEN(?) GROUP (LOWER CRETACEOUS: LATE ALBIAN)

In the fall of 2004, PRPRC staff were invited by the Lytton First Nations to investigate possible dinosaur tracks just outside the town of Lytton, British

Columbia (IR#2b) which were discovered on October 6, 2004 by archaeologist Mike Roussou. *In situ* tracks occur on a steeply dipping (68°) slope that forms the bank of the Fraser River in that area. The track surface is a few hundred square meters in area, but the surface is very fine-grained and friable with substantial organic content. Many natural moulds of tracks were faintly visible, although few but the largest showed any morphological detail (Fig. 2.66). Large theropod tracks (cf. *Irenesauripus* ichnosp.) and trackways of quadrupeds (cf. *Tetrapodosaurus* ichnosp.) were present. A second site with *in situ* natural cast prints and trackways was located a few meters away and stratigraphically above the other site. The natural casts were indistinct, but are probably a morphotype of *Tetrapodosaurus* ichnosp.

Fig. 2.66: A portion of a near-vertical track surface with theropod and ankylosaur tracks and trackways exposed on the bank of the Fraser River, southwestern British Columbia.

The track-bearing strata form one of a number of narrow, fault-bounded blocks along the Fraser River that is possibly correlated with the Pasayten Group exposed farther south in British Columbia, and which is of a general mid-Cretaceous (Albian – Cenomanian) age. This site is one of the most westerly occurrences of dinosaur tracks in Canada recognized to date (~50°N, 121° 35'W) and the strata may represent coastal exposures along the mid-Cretaceous coastline of British Columbia. The presence of tracks in Pasayten Group rocks along the Fraser River suggests that other trackways may be found in similar rocks in more southerly areas of British Columbia, such as Manning Park.

DUNVEGAN FORMATION (UPPER CRETACEOUS: LOWER – MIDDLE CENOMANIAN)

The Dunvegan Formation of western Alberta and northeastern British Columbia embraces a range of deltaic environments, of which the updip, delta plain deposits preserve an abundance of dinosaur tracks. Unfortunately, extensive bedding surfaces are rare, and tracks are typically found in small isolated blocks with single footprints, or partial trackways (Storer, 1975; Currie, 1989a; Scott, 2000). The dominant footprint type of the Dunvegan vertebrate ichnofauna was produced by ankylosaurs (*Tetrapodosaurus* ichnosp.) (McCrea et al., 1998; 2001).

Other components of the Dunvegan Formation ichnofauna are the prints of large ornithopods, small-medium theropod, birds, turtles and crocodylians (Currie, 1989a; Storer, 1975; McCrea, 2003b, McCrea et al., 2001; Scott, 2000; Scott et al., 2001). In a regional study, Plint (2000) examined the principal exposures of the Dunvegan Formation in Alberta and B.C.; measured stratigraphic sections in this paper record many horizons of dinosaur tracks scattered throughout the basin.

Currie (1989) reported on a slab (UALVP 25271) containing eight footprints that had been discovered by Dr. C.R. Stelck of the University of Alberta in 1951 (Fig. 2.67). Currie (1989) considered that these unusual prints may have been produced by hesperornithiform or ichthyornithiform birds. However, RTM viewed this specimen in the spring of 2000 and made a latex mould and then a plaster cast of it for study. Compared to other similar tracks from the same area and to similar tracks from other localities (Foster et al., 1998; Wright and Lockley, 2001), it was concluded that an avian affinity was unlikely and that these prints were more likely produced by one or more turtles.

Fig. 2.67: Photograph of UALVP 25271, a natural cast track slab with several turtle tracks. Scale = 10 cm.

The Dunvegan Formation to date lacks large scale track surfaces, but the comparatively few ankylosaur track specimens found show a reasonably complete growth series from small juvenile specimens (15.0 cm long, 12.0 cm wide, PRPRC 2004.16.001) (Fig. 2.68, far left), to very large adult specimens (50.0cm long and 49.5cm wide, PRPRC 2000.02.001) and several transitional sizes between (Fig. 2.68). A large natural cast pes print referable to *T. borealis* (PRPRC 2000.02.001) was recovered by the first author (RTM) in 2000 from the Kistkatinaw River and is deposited at the PRPRC (Fig. 2.68, far right).

Fig. 2.68: A set of natural cast pes prints from the Dunvegan Formation of northeastern British Columbia demonstrating a growth series for *Tetrapodosaurus borealis*.

Additionally, ankylosaur skin impressions are not uncommon and have been found at several localities both in Alberta and British Columbia (Fig. 2.69). This is notable as skin impressions of Cretaceous dinosaur footprints were limited to only two prints just over two decades ago (Currie, 1989a; Currie et al., 1991).

Fig. 2.69: Skin impressions associated with a *Tetrapodosaurus* ichnosp. print. Scale = 10 cm.

Many reports of vertebrate tracks from the Dunvegan Formation from northeast British Columbia are either from small *in situ* exposures along rivers and creeks, isolated track slabs that are out of context, or are isolated natural casts that have weathered from their original depositional layer. These sites are difficult to access or can only be accessed on foot. For example the only access to *T.*

borealis prints from a river not far from Dawson Creek, British Columbia is over a farmer's field. Despite the difficulty in access, discoveries are still made.

Large sandstone blocks are collected by farmers and ranchers from time to time for decorative purposes. One such is in Lone Prairie, where a slab which contained several large crocodylian tracks was collected to become a sign to the gate of a family farm (Fig. 2.70a and b). Also from a nearby creek were found additional crocodylian prints (Fig. 2.71) although these were originally reported (Scott, 2000; Lockley and Rainforth, 2002) as possible pterosaur pes prints (*Pteraichnus* ichnosp.). However, pterosaur pes prints can easily be confused for those of crocodylians and vice-versa (Padian and Olsen, 1984; Lockley et al., 1995; Padian, 2003) and these specimens are more likely crocodylian tracks (Scott et al., 2001), one or both of which are almost certainly swimming traces (see Lockley et al., this volume for discussion of criteria for separating crocodylian, pterosaur and turtle swim tracks). The same creek yielded prints and short trackways of one or more turtles (Fig. 2.72).

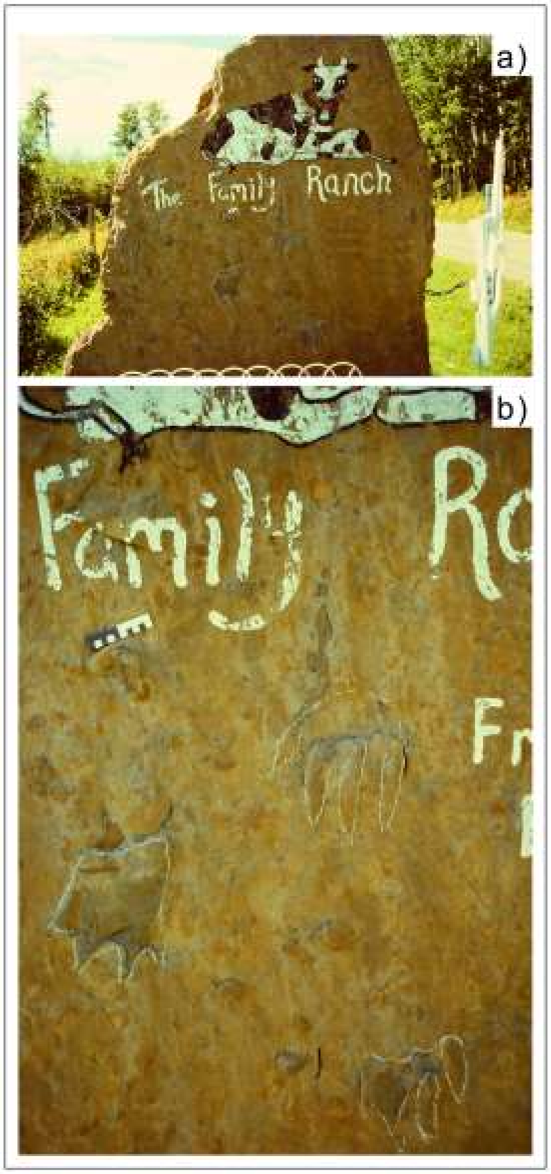

Fig. 2.70: a) A large sandstone block with natural casts of crocodylian prints and trackways being used as a decorative sign at the entrance of a local ranch in northeastern British Columbia. b) close up of track slab. Photographs have been modified to protect the privacy of the ranch owner who was previoulsy unaware of the presence of the tracks, but kindly allowed RTM to photograph and trace them. Scale = 10 cm for both figures.

Fig. 2.71: Two natural mould tracks attributable to crocodylians. The extensive posterior drag marks associated with the print on the lower left may be interpreted as a swim trace. Scale = 10 cm.

Fig. 2.72: Natural casts of turtle tracks from the Peace Region of northeastern British Columbia.

Scale = 10 cm.

A number of ankylosaur natural cast and some natural mould prints were discovered along both banks of a nearby river. An unusual small partial natural cast trackway was found with three main digit impressions (II-IV) and what looked like long, backward-facing hallux impressions with metatarsal drag marks. The divarication of these tracks was very high (well over 100 degrees) prompting comparison with avian ichnotaxa. However, one track was observed to have a faint, but unmistakable hallux and the previous hallux impressions were re-interpreted as metatarsal drag marks (Fig. 2.73). These observations support a theropod track-maker interpretation.

Fig. 2.73: Natural casts of two bird-like theropod prints from the Peace Region of northeastern British Columbia. Arrows indicate position of prints on slab and numbers indicate digits. MT = metatarsal impression. Scale is in cm.

An *in situ* track-bearing surface was discovered by RTM in 2001 along the banks of the Wolverine River. Only two theropod tracks were exposed initially (Fig. 2.74), but volunteers from the Wolverine Nordic and Mountain Society of Tumbler Ridge, B.C carefully excavated the site revealing several more tracks and trackways. The surface contains several natural mould trackways of small to medium theropod tracks (cf. *Irenichnites* and cf. *Columbosauripus*, respectively), and ankylosaur tracks with skin impressions. Some of the ankylosaur tracks are low relief and difficult to see, but the skin impressions are a reliable indicator of their presence. A good trail was built in 2002 down to this site by volunteers of the local Wolverine Nordic and Mountain Society of Tumbler Ridge, B.C., and it is now a popular tourist site for guided tours.

Fig. 2.74: *In situ* natural mould theropod prints which were discovered along the north bank of the Wolverine River a few kilometres north of Tumbler Ridge, British Columbia. Scale = 10 cm.

This public access has, however, come at some cost, with a vandalism incident that took place in the fall of 2004 was discovered during a visit to this site by RTM, LGB, CWH and guests (Fig. 2.75). The two theropod prints that had led to the discovery of this site had been chiseled and pried out of the *in situ* surface, a process that destroyed two cf. *Irenichnites* tracks near the edge of the river bank. This vandalism disrupted two of only a handful of theropod trackways at this site. The RCMP was alerted to this theft as the site was protected via a provincial non-staking reserve by the museum. The vandalism and theft were reported to the local and regional media and eventually the stolen tracks were recovered by the authorities and returned to the PRPRC (Fig. 2.76 – 2.77). It appears that the thieves had perpetrated their crime under cover of the night, making off with the track slab with the idea of turning it into a coffee table. The track slab will now require long-term management to ensure that the stresses of its removal do not cause further deterioration.

Fig. 2.75: CWH pointing to where the Wolverine River theropod tracks were the night of the discovery of the vandalism and theft at this site in the spring of 2004.

Fig. 2.76: CWH and Royal Canadian Mounted Police constable with recovered theropod track specimen from the Wolverine River site.

Fig. 2.77: Picture with oblique lighting of the recovered track slab complete with chisel impact and scrape marks.

Hikers led by CWH exploring Cool Kids Creek (informal designation) south of Tumbler Ridge discovered a short natural cast trackway (PRPRC 2005.04.002) of cf. *Tetrapodosaurus* ichnosp. in 2004 (Fig. 2.78). A segment of a natural mould trackway (cf. *Tetrapodosaurus* ichnosp., PRPRC 2005.21.001) was also discovered in Everlasting Creek (informal designation) near the Wolverine River by the Walkley and Zimmer families from Tumbler Ridge. Both specimens were recovered to the PRPRC with helicopter time donated by Talisman Energy (Fig. 2.79).

Fig. 2.78: A large natural cast block of a trackway of a quadrupedal dinosaur (thyreophoran, likely referable to Tetrapodosaurus ichnosp.) with relatively small manus and pes prints from “Cool Kids Creek”, northeastern British Columbia. Scale = 10 cm.

Fig. 2.79: The Cool Kids Creek ankylosaur track block (PRPRC 2005.04.002) arriving by helicopter at the museum in the summer of 2005.

Early in the investigation of the Everlasting Creek and the Wolverine tracksites both of these sites were visited by a Creation “scientist” investigating the possibility of the presence of human tracks at the behest of some of the local residents. The conclusions of this brief investigation were published with a negative result on the presence of human prints (Silvestru, 2004).

Additional track finds were made and reported in the next few years in the Peace Region of British Columbia, including a large track slab (Fig. 2.80) revealed by a bank collapse. This track slab (reported by Mr. Pete Shaw) contained natural mould trackways of large quadrupeds (ankylosaurs), small theropod tracks, and a trackway of an unusual small ornithischian (Fig. 2.81). The newly exposed track surface was fine-grained with a high organic content and showing signs of friability. This large and heavy track slab was in a precarious position, located below an unstable bank on the edge of a fast-flowing river. A recovery of the original slab by crane was considered, but the combination of this difficult location, the lack of resources and the likelihood of the slab falling to pieces under the stress during a lift precluded further pursuit of this option. A latex mould was made, which RTM and LGB knew would hasten the destruction of the original. As predicted a large amount of the track surface was pulled up when the latex peel (PRPRC 2004.10.001M) was recovered. The remaining track surface was monitored over several weeks and within a few months no tracks remained. Fortunately, the latex mould produced an excellent cast (PRPRC 2004.10.001MC) providing a permanent record of this ephemeral specimen.

Fig. 2.80: A large slab fallen from a river bank with natural moulds of thyreophoran (ankylosaur) tracks and trackways on a very friable surface. Specimen is from the Dunvegan Formation of northeastern British Columbia. Scale = 10 cm.

Fig. 2.81: An unusual an small tridactyl pes print from the slab from Fig. 2.80. This is one of several specimens with at least two trackways. Scale = 10 cm.

A larger tracksite with *in situ* ankylosaur trackways was found (by Mr. Pete Shaw) on a bank not far away (Fig. 2.82) and even contained skin impressions**.** In both of the above sites the ankylosaur tracks bore some resemblance to Sternberg's (1932) *Tetrapodosaurus* ichnosp. The manus/pes proportions were consistent with *Tetrapodosaurus* ichnosp.; there are five manual digit impressions, but there are only three pedal digit impressions instead of the four that usually characterize *Tetrapodosaurus*. These tracks are deeply impressed, but show no substrate-influenced distortion. The pedal and manual digit impressions are clear and well-defined. It is unlikely that the missing pedal digit is an artifact of preservation, instead it indicates the true morphology of the track-makers' pedal digits and will be described in more detail in a future publication.

Fig. 2.82: *In situ* thyreophoran (ankylsoaur) manus and pes from the Dunvegan Formation of northeastern British Columbia. Scale = 10 cm.

Many isolated track blocks containing individual natural cast prints have been recovered from many other localities including the banks of rivers and creeks as well as several road cuts. Among these finds were splendid natural cast manus (Fig. 2.83 – 2.84) and pes prints which are exceptionally well preserved. One natural cast specimen is among the smallest pes prints attributed to ankylosaurs (PRPRC 2004.16.001) (Fig. 2.68, far left). Some prints are found in cross-section in river or creek banks (Fig. 2.85) and it is sometimes possible to identify the track type and even remove the specimens.

Fig. 2.83: A natural cast of a thyreophoran manus (left) from the Dunvegan Formation of northeastern British Columbia. Scale = 10 cm.

Fig. 2.84: Mr. Pete Shaw making an impression in recent river bank sediments with a natural cast ankylosaur manus.

Fig. 2.85: Thyreophoran prints (manus on the right) exposed in section in the Dunvegan Formation of northeastern British Columbia. Scale = 10 cm.

Another industry-related track find by Tumbler Ridge resident Mr. Rob McIntyre in 2008, is of several track-bearing slabs discovered in the ditches near a newly constructed gaswell site. The track slabs (PRPRC 2008.10.001 – 009) contain natural mould and natural cast tracks and trackways of *Tetrapodosaurus* ichnosp. (Fig. 2.86a and b). The PRPRC contacted British Gas Canada who swiftly made arrangements to transport all of the track-bearing slabs to the PRPRC in the fall of 2008. Dinosaur tracks have also been found recently along the highway to Chetwynd (Hwy 29) just a few kilometers north of Tumbler Ridge. One track may be referable to *Magnoavipes* ichnosp. (Fig. 2.87). *Magnoavipes* was originally described by Lee (1997) as an avian ichnotaxon based on the high total digit divarication, however Lockley et al., (2001) convincingly argued that the *Magnoavipes* track-maker was likely a type of theropod dinosaur.

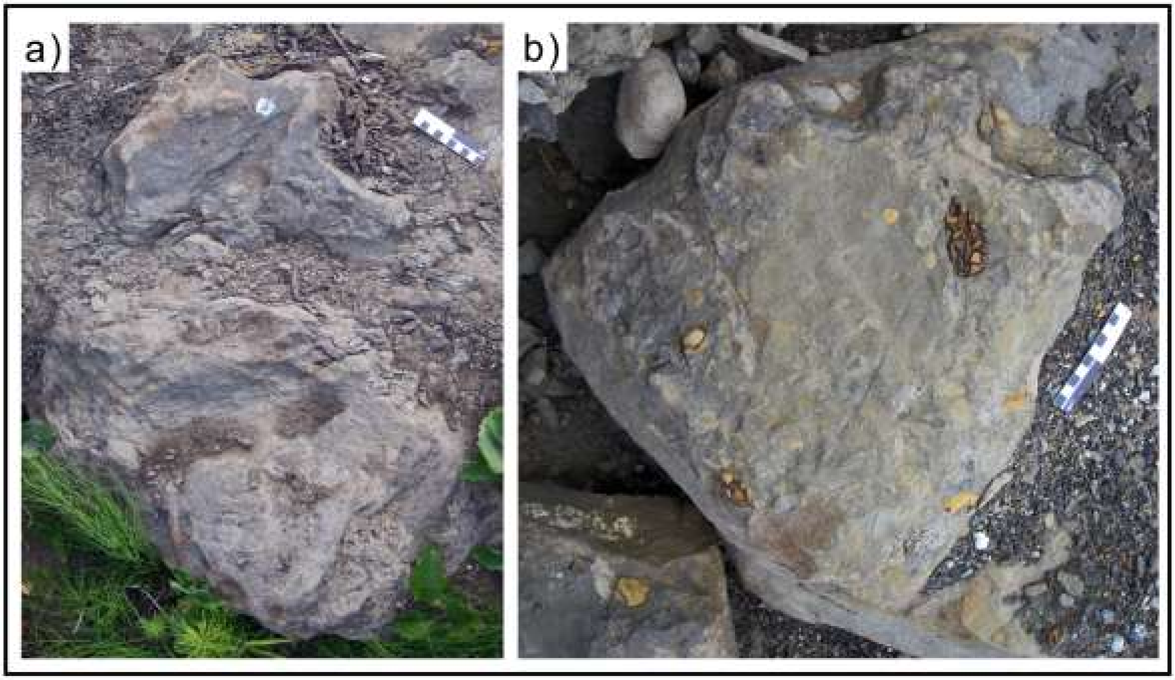

Fig. 2.86: A natural cast of a *Tetrapodosaurus* ichnosp. manus/pes set (left) and pes (right) from a BG Canada gaswell site in the Dunvegan Formation of northeastern British Columbia. Scales = 10 cm.

Fig. 2.87: A wide divarication natural cast theropod track (cf. *Magnoavipes* ichnosp.) from a ditch near Tumbler Ridge, Dunvegan Formation. Scale = 10 cm.

The Dunvegan Formation is one of the most extensively-exposed track-bearing formations in the Peace Region of Alberta and British Columbia and new discoveries will continue to be made. The Dunvegan Formation extends into the southern part of the Yukon Territory, although no track finds have yet been reported. It is very likely that any prospecting of the Dunvegan Formation outcrops in the Yukon Territory will have positive results.

KASKAPAU FORMATION (LATE CRETACEOUS: LATE CENOMANIAN - MIDDLE TURONIAN)

The Kaskapau Formation ranges in age from late Cenomanian to middle Turonian and is primarily of marine aspect. Indeed, some of the highest sea-levels of the Cretaceous are recorded at the Cenomanian-Turonian boundary (corresponding to Ocean Anoxic Event-2) and it is therefore no surprise that terrestrial deposits are rare.

Late Cenomanian

Global sea-level rise during the late Cenomanian drowned the middle Cenomanian Dunvegan delta complex and drove the shoreline to the north and west. The late Cenomanian seaway appears to have formed a very shallow embayment in northwestern Alberta and northeastern British Columbia. This embayment was fringed by low-energy deltaic shorelines that provided good habitat for dinosaurs. Well-preserved dinosaur tracks are known from Flatbed Creek, which exposes rocks of the lower Kaskapau, assigned to the A-X and Doe Creek units of Kreitner and Plint (2006). The same strata are exposed in Babcock Creek.

The first reported discovery of vertebrate tracks from the late Cenomanian Kaskapau Formation was made in 2000, when two boys (Daniel Helm, age 8 and Mark Turner, age 11) from Tumbler Ridge, discovered a lengthy trackway of a quadrupedal dinosaur (Fig. 2.88) in the nearby Flatbed Creek (McCrea, 2003b; Helm, 2004). The trackway was identified as *Tetrapodosaurus borealis* by McCrea

(2003b). The average pace of the pes prints was 78.0cm and the average stride was just over 132.0cm.

Fig. 2.88: An *in situ*, natural mould T. borealis trackway from the Kaskapau Formation in Flatbed Creek near Tumbler Ridge, British Columbia. Discoverers Mark Turner and Daniel Helm are at the top of the photograph. The prints have been enhanced with talcum powder for photographic purposes.

The discovery in 2000 prompted initial exploration of the immediate area, and in 2001 another *in situ* surface was discovered in Flatbed Creek by another local, (Al Durand). The new site, dubbed the Cabin Pool Site contains numerous natural mould tracks of ankylosaurs (*Tetrapodosaurus* ichnosp.), and two well preserved pes prints of medium-sized theropods (Fig. 2.89 a - c) (McCrea, 2003b). The site is open to public access and is a popular tourist destination in the region. This site has been subject to some vandalism including a few failed attempts at creating replicas of the theropod prints via direct casting with plaster.

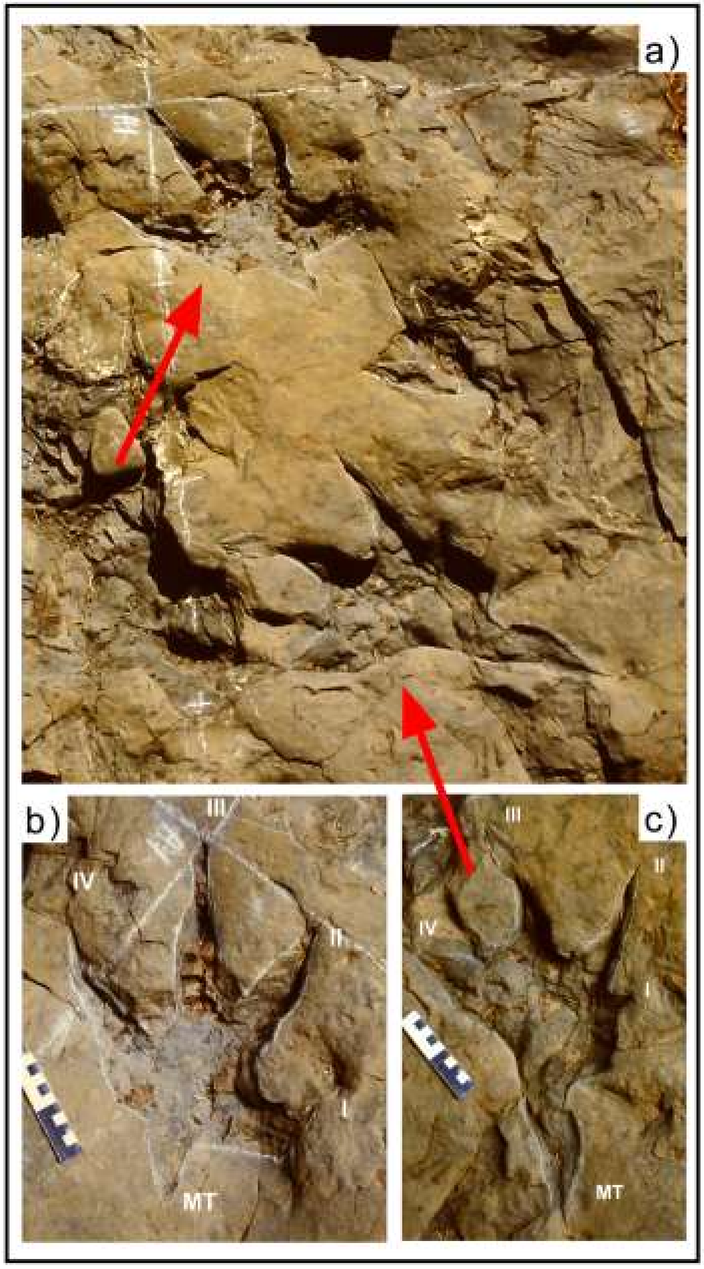

Fig. 2.89: a) *In situ* natural moulds of two theropod prints from the Cabin Pool locality (Kaskapau Formation) on Flatbed Creek near Tumbler Ridge, British Columbia; b & c) Both theropod tracks are left prints, complete with hallux and metatarsal impressions. The digit impressions are constricted due to sediment collapse shortly after the track-makers removed their feet from the substrate. Scale = 10 cm.

Vertebrate tracks were reported from another nearby creek, south of Tumbler Ridge in 2007. An *in situ* tracksite was discovered by DGC Veritas employees working on a seismic project in the Tumbler Ridge area; this locality (Veritas Site) contains several footprints and a two trackways of *Tetrapodosaurus borealis* prints (Fig. 2.90). This site was later found to contain bone and is part of the Doe Creek Member of the Kaskapau Formation of late Cenomanian in age. Another site was found the same year by a child, Carina Helm (Carina's Site) just upstream from the Veritas site. This site also contains ankylosaur prints. A natural cast of a theropod print has also been reported from another creek in the vicinity (Fig. 2.91).

Fig. 2.90: *In situ* natural mould of *Tetrapodosaurus borealis* trackway from the Veritas site (Kaskapau Formation) near Tumbler Ridge, British Columbia. Scale (top left) = 10 cm.

Fig. 2.91: Isolated natural cast of a small theropod print from the Kaskapau Formation of northeastern British Columbia.

Early - Middle Turonian

Early Turonian terrestrial deposits are unknown in Canada. The only known middle Turonian terrestrial sediments form thin wedges atop two successions of marine shoreface sandstones (the Tuskoola and Wartenbe Sandstones (unit III and IV of Varban & Plint, 2008) that prograded from the western margin of the basin. Marine transgression above the Wartenbe Sandstone resulted in the vertical aggradation of back-barrier, coastal plain environments that included marshes blanketing beach-ridges, freshwater lakes, brackish lagoons and tidal inlets. These sediments are exposed in the canyon of Quality Creek, near the town of Tumbler Ridge, and yield the only known record of Turonian vertebrate prints in the world to date (McCrea, 2003b; McCrea and Buckley, 2004, Rylaarsdam et al., 2006). A footprint prospecting trip in Quality Creek by CWH and RTM in 2002 led to the discovery of 50 track specimens as well as British Columbia's first dinosaur bone accumulation (McCrea, 2003b, McCrea and Buckley, 2004).

Several isolated natural cast prints of ornithopods, as well as a natural cast trackway of an ornithopod (PRPRC 2003.02.001M and MC) (fig. 17 in Rylaarsdam et al., 2006) were discovered by Brian Pate, Don Nesbitt, Mark Turner and some of the authors on multiple prospecting trips of Quality Creek Canyon. One notable discovery was of a very large natural cast of an ornithopod pes (PRPRC 2001.01.001) which was carried up a steep cliff by CWH and volunteers using a stretcher. An isolated natural cast pes of a large theropod displaying a possible pathology (PRPRC 2002.01.001) (Fig. 2.92), and a latex mould of a partial theropod natural cast pes with skin impressions (PRPRC 2003.02.002M and MC) (Rylaarsdam et al., 2006, fig. 13) were also recovered on separate expeditions.

Fig. 2.92: Isolated natural cast block (PRPRC 2002.01.001) of a medium-sized theropod print with a possible pathology in digit III. Specimen is from the Kaskapau Formation, of northeastern British Columbia. Scale = 10 cm.

Other vertebrate track localities have been discovered in exposures of the Kaskapau Formation for which the exact ages (late Cenomanian or early – middle Turonian) are uncertain. Dinosaur tracks were recently discovered by Daniel Helm in yet another nearby creek. Ankylosaur tracks (cf. *Tetrapodosaurus* ichnosp.) (Fig. 2.93) are the most conspicuous on at least four stream bank exposures along this creek, although theropod tracks and some form of non-dinosaurian reptile (possibly turtle) prints are present as well. Recently, prospecting in this area by CWH, RTM, LGB and Mr. Daniel Helm led to the discovery of a lengthy trackway of a quadrupedal dinosaur (cf. *Tetrapodosaurus* ichnosp.). This find inspired further prospecting and discovery of more ankylosaur tracks (about thirty trackways over a stretch of three kilometers), as well as a natural cast of a turtle trackway (Fig. 2.94).

Fig. 2.93: One of several recently discovered *in situ* track sites with thyreophoran (anklosaur - pes) prints from the Kaskapau Formation of northeastern British Columbia.

Fig. 2.94: A natural cast of a turtle trackway on an isolated slab from the Kaskapau Formation of northeastern British Columbia. Scale in cm.

Well preserved natural cast pes prints of large ornithopods also have been recently recovered from another creek near Tumbler Ridge (PRPRC 2011.10.001 – 003). CWM and some volunteers recently discovered and recovered a few exquisite tridactyl natural casts of large ornithopod pedal prints (Fig. 2.95).

Fig. 2.95: A natural cast of a large ornithopod pes print from the Kaskapau Formation of northeastern British Columbia. Scale = 10 cm.

CARDIUM FORMATION (LATE CRETACEOUS: LATE TURONIAN - EARLY CONIACIAN)

The Cardium Formation spans the late Turonian and part of the early Coniacian, and while a small number of tracks have been found in Alberta (Currie, 1989), there is only one report from British Columbia to date (see below). The only terrestrial facies present lie above the shoreface sandstone of the lithostratigraphic Ram Member (Stott, 1963) and constitute the Moosehound Member of Stott (1963). The Moosehound Member represents lagoonal and coastal plain environments. Although distinct dinosaur tracks have not been identified, both core and outcrop sections reveal horizons of intense deformation in thinly-bedded lacustrine and lagoonal deposits. Deformation is most probably attributable to dinosaur trampling in subaqueous and/or saturated, unconsolidated sediment.

Natural cast tridactyl prints and natural cast prints attributable to ornithischians have been found at the Tepee Falls locality, near Tumbler Ridge, British Columbia (Fig. 2.96).

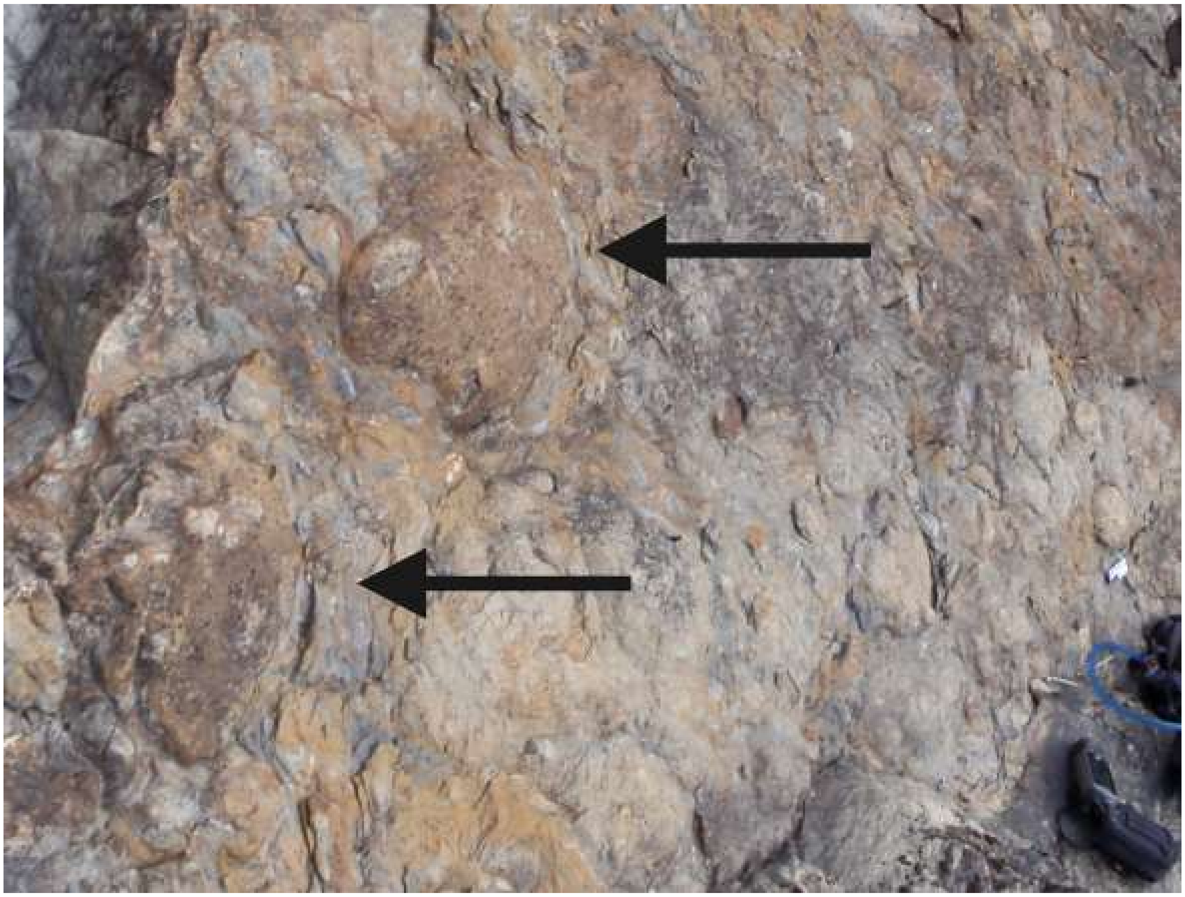

Fig. 2.96: Natural casts of large tridactyl prints (arrowed - presumed ornithopods) from the Cardium Formation, Teepee Falls locality of northeastern British Columbia. GPS unit in lower right corner for scale.

MARSHYBANK FORMATION (LATE CRETACEOUS: LATE CONIACIAN)

Like the Cardium, the Marshybank Formation is of dominantly marine aspect. However, in the far western part of the basin, in British Columbia, a thin wedge of coastal plain deposits (unit G of Plint, 1990) is preserved. The best exposure of unit G is on Belcourt Creek where crevasse splay sandstones preserve numerous examples of dinosaur undertracks. Unfortunately, detailed observation of these tracks was not made at the time of the stratigraphic study

(1988). Possible other tracks are preserved in unit G at Calliou Creek, British Columbia.

PUSKWASKAU FORMATION

Chungo Member (Late Cretaceous: Late Santonian)

The Chungo Member is primarily a marine shoreface sandstone, although a few meters thickness of coastal plain deposits are present in the most westerly thrust sheets. Lagoonal, lacustrine, swamp and channel deposits were observed in the most westerly section of the Chungo Member on Thistle Creek, Alberta. Deformation structures in swamp and lagoonal deposits might represent dinoturbation of very water-logged sediment, but no definitive tracks were observed.

OLDMAN FORMATION (LATE CRETACEOUS: LATE CAMPANIAN)

Therrien et al., (in press) describe the first occurrence of a hadrosaur trackway from the Milk River Natural Area (MRNA) of southern Alberta.

BELLY RIVER GROUP (FORMERLY JUDITH RIVER GROUP, CRETACEOUS: CAMPANIAN)

Since the late 19th century dinosaur and other vertebrate fossils have been found in abundance from several localities in the area that is now Dinosaur Provincial Park. Until recently no fossil vertebrate tracks had been recognized in the park area in spite of the amount of palaeontological research conducted over more than a century.

Two natural casts of footprints have been collected to date, one *in situ* specimen (RTMP 1981.034.0001) from near a bone quarry identified by McCrea (2005b) as an ornithopod print, but which is almost certainly a large theropod (tyrannosaur) print, and the other (a theropod print, RTMP 1993.036.0282) that was discovered out of context in a rock garden. In the last few years additional track finds have been made at other localities, many of which were of much-weathered *in situ* specimens near bone quarries. A brief footprint prospecting trip early in 2003 led to the discovery of a locality with several natural casts of dinosaur footprints. These finds demonstrate that there is potential for further footprint discoveries within Dinosaur Provincial Park (Currie, 1989a & b; McCrea et al., 2005b).

HORSESHOE CANYON FORMATION (LATE CRETACEOUS: LATE CAMPANIAN)

Several years ago, a medium-sized, mud-cracked block with numerous small, natural mould, tridactyl vertebrate tracks (Fig. 2.97) was discovered by RTMP resident artist Donna Sloan. The specimen was examined in detail by the late W.A.S. Sarjeant, but no publication was forthcoming due to the difficulty in interpreting the details of these small tracks. The specimen has languished in the RTMP collections for a dozen years since. It is possible that the tracks are of chelonian affinity and a re-study of this enigmatic track specimen is currently underway.

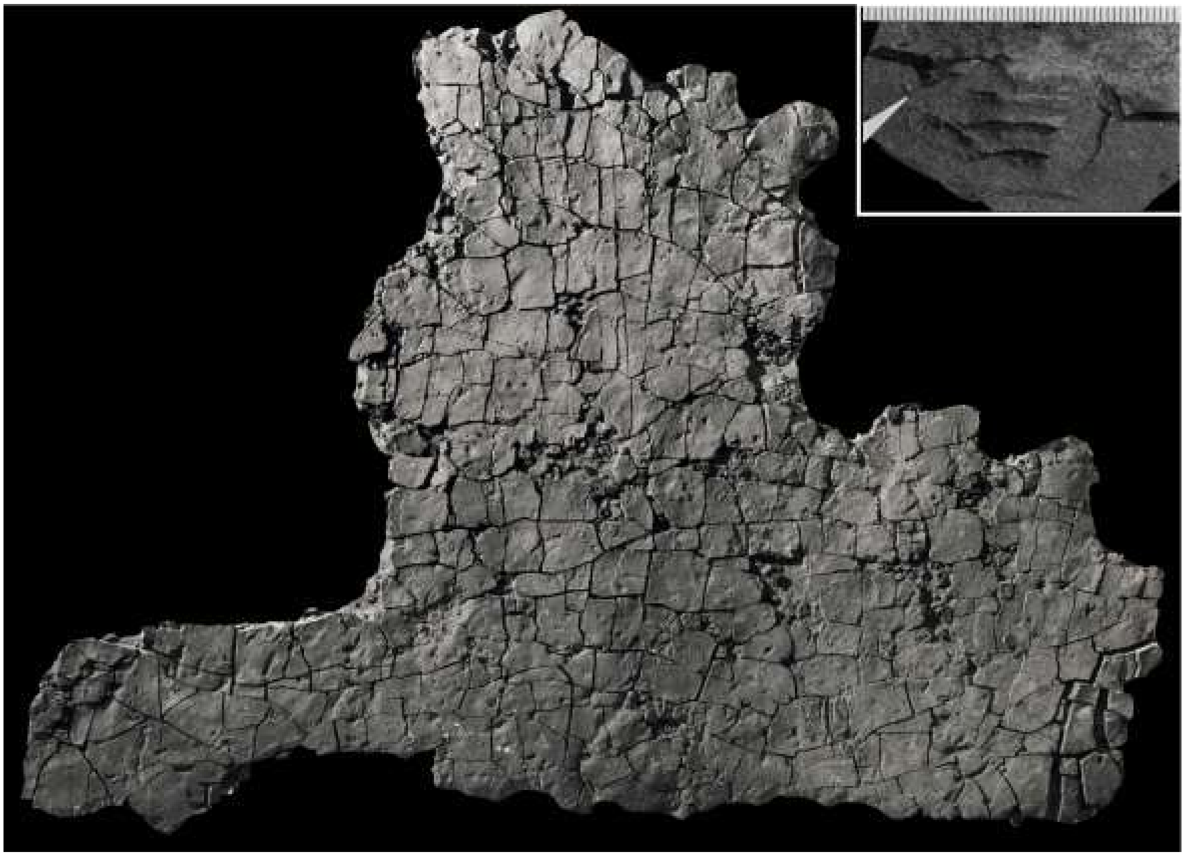

Fig. 2.97: Large, mud-cracked slab of a few m^2 area from the Horseshoe Canyon Formation. Inset: An enlarged view of one of the small, enigmatic tracks. Scale for inset is in mm.

More recently a natural cast of a hadrosaur track was found by RTMP technician Jim McCabe very close to the museum. It is very likely that this specimen was unearthed during the construction of the museum.

EDMONTON GROUP

St. Mary River Formation (Late Cretaceous: Campanian)

The vertebrate ichnofauna of southern Alberta is poorly known even though some scientific papers have been published on the ichnofauna of this region. The field sites are located along unstable river banks and are usually only accessible through ranch or reserve land. To date the ichnofauna is known to contain the prints of large and juvenile hadrosaurs, one probable tyrannosaur print, a trackway of three prints very similar in morphology to *Ornithichnites*, ichnosp. (Sternberg, 1926) (Fig. 2.98), and two avian track blocks (Fig. 2.99 a and b) (Currie, 1989; Currie et al., 1991; Langston, 1960; Lockley et al., 2004; Nadon, 1993; McCrea et al., 2001). Some of the best hadrosaur track skin impressions found to date are from the St. Mary River Formation (Currie et al., 1991; Lockley et al., 2004; Nadon, 1993).

Fig. 2.98: A fibreglass replica cast of three small theropod tracks (cf. *Ornithichnites* ichnosp.) from the St. Mary River Formation of southern Alberta. Scale = 10 cm.

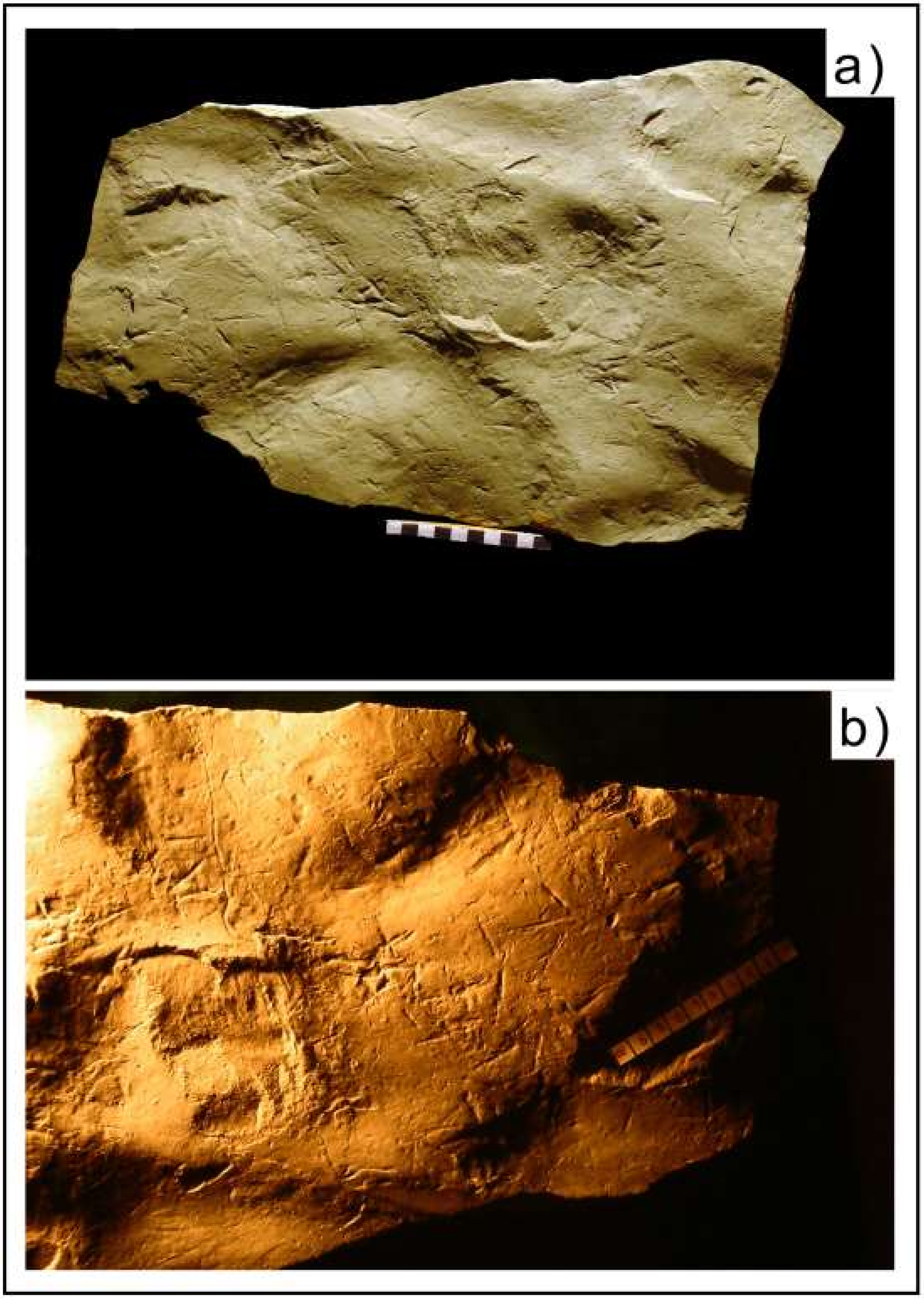

Fig. 2.99: a) Original natural mould slab with avian prints collected from the St. Mary River Formation of southern Alberta; b) image – closeup of a portion of the track slab. Scale on left image is in cm.

WAPITI FORMATION (LATE CRETACEOUS: LATE CAMPANIAN - EARLY MAASTRICHTIAN)

The track record of the Wapiti Formation in Alberta is becoming better known since the initial reports of Currie (1989a) and Tanke (2004). Single prints and partial trackways are not uncommon, and recent large-scale tracksites are being discovered in the Grande Prairie area. In Alberta the vertebrate ichnofauna includes tracks of small- to medium-sized theropods, hadrosaurs, ankylosaur or ceratopsian tracks and even possible small mammal or reptile tracks (Tanke, 2004; Fanti et al., in press).

No tracks were reported from the Wapiti Formation of British Columbia until the fall of 2004 when a hunter came across a single natural cast track of a large theropod near a forest service road. This track specimen (PRPRC 2004.08.001) exhibited skin impressions and slide marks produced by skin tubercles. The size of the track indicates a track-maker of impressive proportions and is almost certainly that of a tyrannosauroid (Farlow et al., 2009). This slab was removed to the PRPRC in December, 2004 with the help of Burlington Resources who provided the use of a large, flatbed truck with a very large crane.

A number of indistinct dinosaur tracks occur on a small area of shelving sandstone layers less than 100 metres from a PRPRC hadrosaur excavation site in British Columbia (McCrea and Buckley, 2010; 2011a; 2011b).

In the fall of 2010 a series of PRPRC - led prospecting trips in an area near the Alberta/B.C. border (exact localities are on file in the collections of the PRPRC) which resulted in the discovery of a large natural cast tridactyl track in the bed of a small creek which has been identified as a pes print of a hadrosaur (Fig. 2.100), referable to *Hadrosauropodus* ichnosp. of Lockley et al., (2004). Downslope in the same creek a natural cast of a large manus print was discovered which could be that of either an ankylosaur or a ceratopsian (Fig. 2.101). The third prospecting trip to this area in 2010 occurred in October and led to the discovery of a large, isolated block with a single, natural cast hadrosaur pes print with a large rib fragment lying close to it (Fig. 2.102). On the same trip a partial tridactyl natural cast print (theropod?) was found at a much higher elevation near the top of a valley.

Fig. 2.100: A natural cast of a large ornithopod pes track (cf. *Hadrosauropodus* ichnosp.) from the Wapiti Formation of northeastern British Columbia.

Fig. 2.101: A natural cast of a large manus (ankylosaur or ceratopsian) from the Wapiti Formation of northeastern British Columbia. Scale = 10 cm.

Fig. 2.102: Natural cast of a large ornithopod pes print with a small section of dinosaur rib near the lower left corner of the photograph. Specimen is from the Wapiti Formation of northeastern British Columbia. Scale = 10 cm.

A few *in situ* hadrosaur tracks with pedal and manual impressions were found during a prospecting trip by raft in August, 2011. An isolated natural cast block of small tridactyl prints, probably of a small theropod, was also found and recovered (PRPRC 2011.08.001) (Fig. 2.103a and b). Natural moulds of medium-sized theropod tracks were found near this same locality.

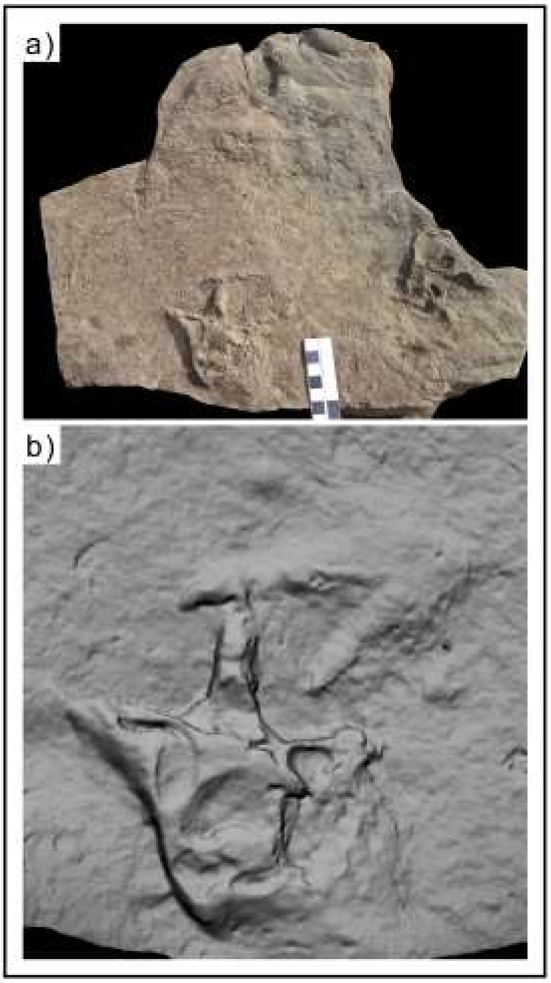

Fig. 2.103: a) A natural cast block (PRPRC 2011.08.001) with three small tridactyl prints collected from the Wapiti Formation of northeastern British Columbia – Scale = 10cm; b) Surface laser scan of two of the prints from the same slab.

A local guide/outfitter, Mr. Aaron Fredlund, discovered a tracksite in the vicinity of Tumbler Ridge. This tracksite is approximately 50 meters long by 2-3 meters wide containing natural mould tracks of medium-sized (Fig. 2.104) and large-sized theropods (Fig. 2.105), and large hadrosaur tracks with excellent skin impressions (McCrea et al., 2012) (Fig. 2.106 a and b). Three, theropod trackways with tracks that measure 65 cm in length are currently being described. The medium-sized theropod tracks are referable to *Saurexallopus*, but they are morphologically distinct from the other two described ichnotaxa (*S. lovei* and *S. zerbsti*) to warrant them being place within a new ichnotaxon described below (SYSTEMATIC ICHNOLOGY). There are compelling arguments that the *Saurexallopus* ichnosp. track-makers were likely oviraptosaurs (Lockley and Gierlinski 2009; Gierlinski and Lockley 2012; in press).

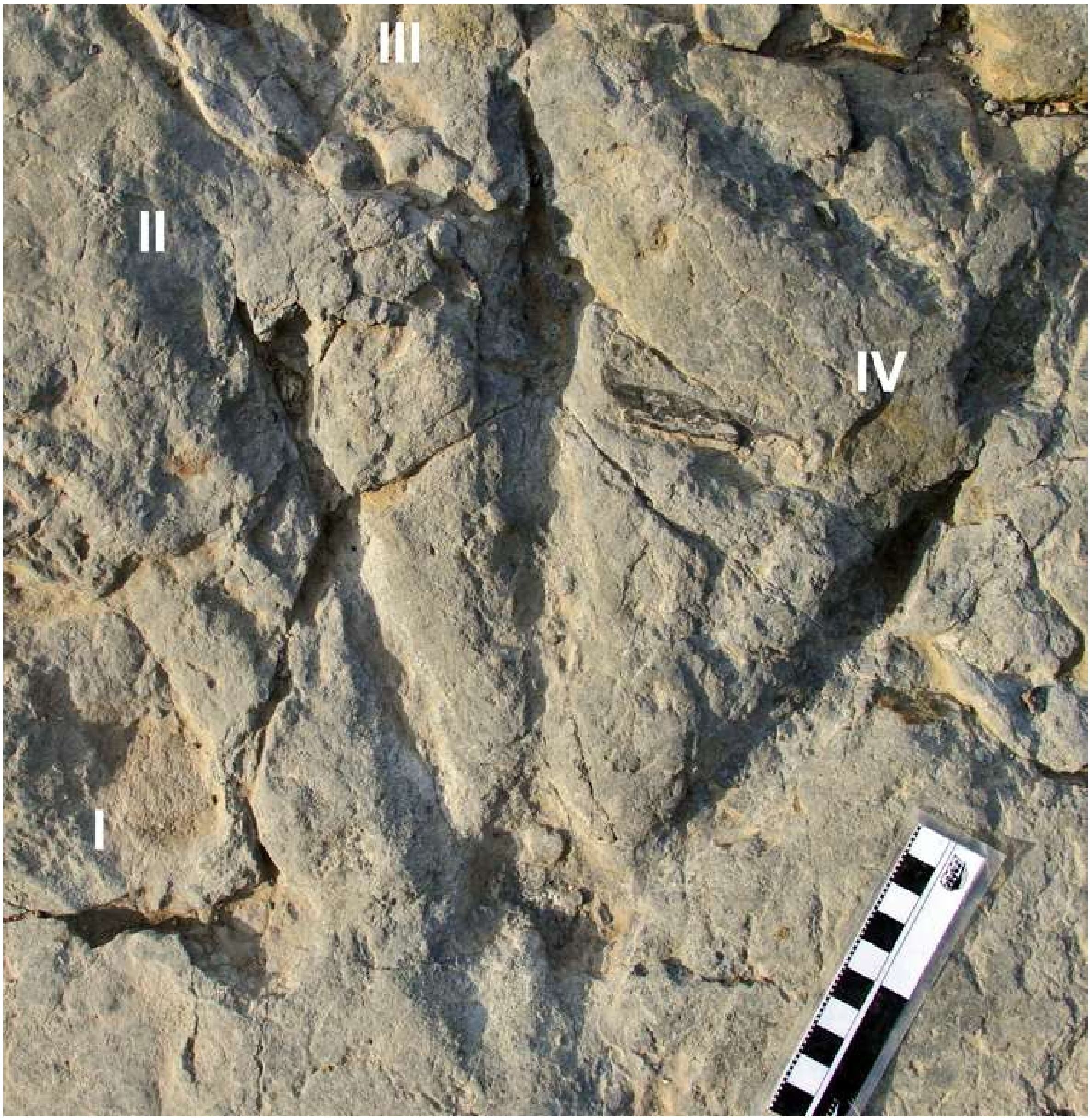

Fig. 2.104: Photograph of the holotype print of *Saurexallopus cordata* (McCrea et al., herein). The specimen is a natural mould from an *in situ* track site from the Wapiti Formation of northeastern British Columbia. Scale = 10 cm.

Fig. 2.105: A natural mould of a very large theropod track (right) from an *in situ* track site from the Wapiti Formation of northeastern British Columbia. Scale = 10 cm.

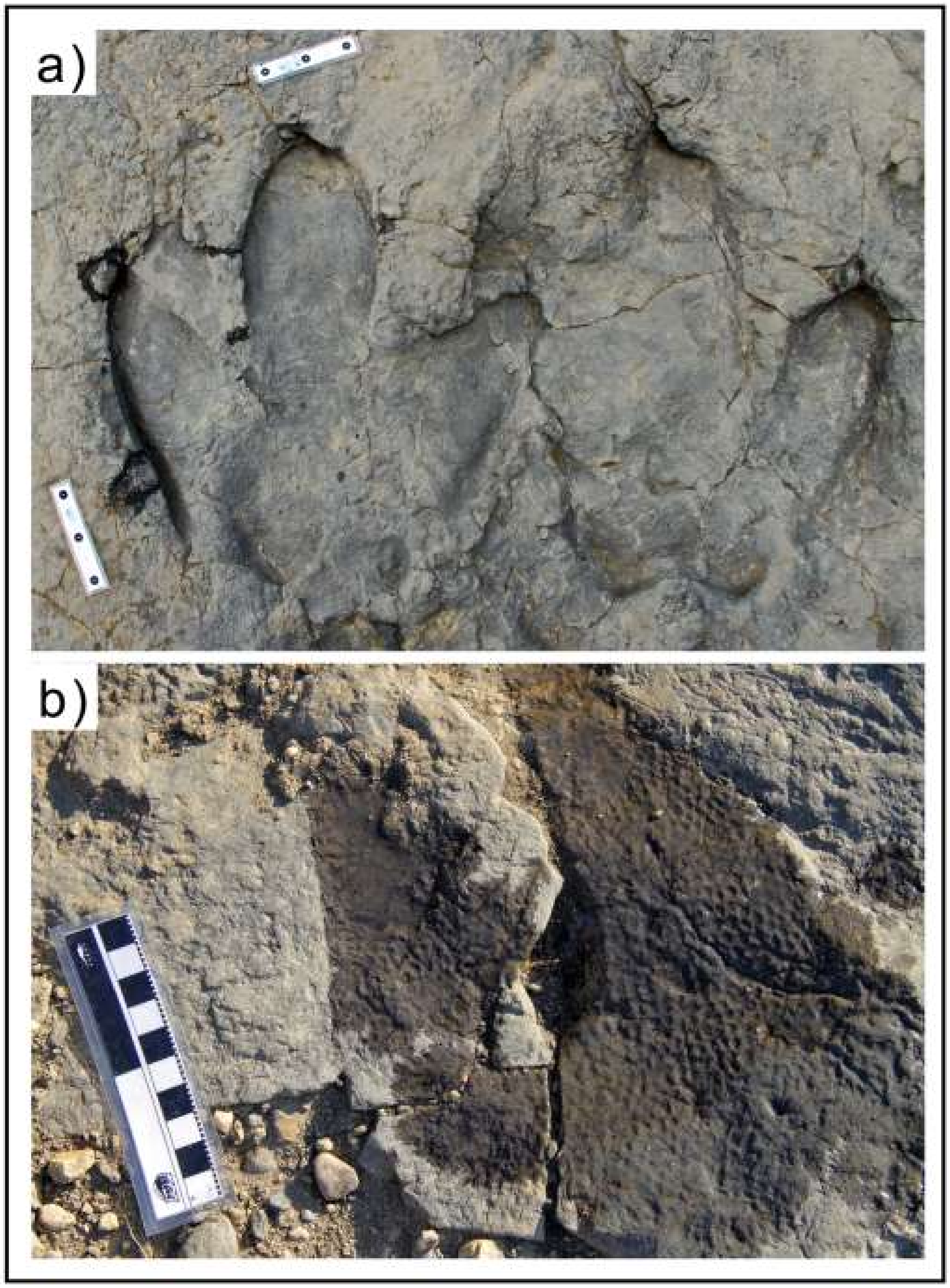

Fig. 2.106: Left image: two natural mould prints of *Hadrosauropodus* ichnosp. – the centers of each circle on the photogrammetry targets are 10cm apart. Right image: One of many examples of skin impressions from the *Hadrosauropodus* ichnosp. specimens

The hadrosaur tracks are referable to *Hadrosauropodus* ichnosp. and there are at least two trackway sequences with three prints each. This single, track-bearing layer was preserved by an overlying layer of kaolinitic clay over thirty centimeters thick.

The surface outcrop and subsurface occurrence of the Wapiti Formation has been recently studied with the result that this stratigraphically thick and undivided formation now has defined divisions that can be recognized and correlated over long distances (Fanti, 2007; Fanti and Canuneau, 2009; 2010). These research results should prove useful for determining the stratigraphic position of tracksites as far west as northeastern British Columbia and as far east as Edmonton where natural cast track slabs of large hadrosaurs (*Hadrosauropodus* ichnosp.) have been found within the last two decades. It is certain that continued exploration in British Columbia and Alberta will yield new tracksite discoveries in the future.

PASKAPOO FORMATION (PALEOCENE: MIDDLE TIFFANIAN)

Rutherford and Russell (1928) described a short natural cast trackway of a quadrupedal animal on a displaced sandstone block from the Paskapoo Beds. The track slab (UALVP 134) was discovered on the banks of the Red Deer River just to the west of the town of Red Deer, Alberta. Russell (1930) made a detailed description of the tracks and ascribed them to a mammalian track-maker. The trackway consists of a series of fore- and hind-foot impressions: the forefoot is digitigrade with at least three clawed digits, and the hindfoot is semidigitigrade and again with three clawed digits. In the earlier paper (Rutherford and Russell, 1928) the footprints were thought to be those of an unknown creodont or condylarth. Eventually, Russell (1930, p. 220) decided instead that they were those of a small condylarth.

However, McCrea et. al. (2004) described this track specimen (UALVP 134) and named a new ichnogenus, *Albertasuchipes*, ascribing these prints to a crocodylian track-maker rather than a mammalian one. A single, small turtle track was also identified adjacent to the crocodylian trackway. McCrea et al. (2004) recognized the likelihood that the UALVP 134 trackway was made subaqueously by a bottom-walking crocodylian and is thus, a crocodylian swimming trace). A new ichnospecies, *Albertasuchipes russelli*, was described in the same paper in recognition of Russell's original work on the specimen.

The *Albertasuchipes russelli* pes prints are similar in form to modern alligator walking prints figured by Farlow and Elsey (2010): however, they are also strikingly similar to the crocodylian swim track (pes) illustrated in Lockley et al., (fig. 10 – this volume) and a modern crocodylian swim track (pes) in Kumagi and Farlow (2010, fig. 6b)

Another new crocodylian trackway ichnotaxon (*Borealosuchipus hanksi*) was described by Erickson (2005) from the Lower Paleocene of North Dakota. According to Erickson (2005), the trackway shows evidence of associated belly drag marks similar to modern crocodylian traces when they have walked on land (several figs. in Farlow and Elsey, 2010). The *Borealosuchipus hanksi* tracks are markedly different from *Albertasuchipes russelli*, although McCrea et al., (2004) and Erickson (2005) commented on the presence of Paleocene aged *Borealosuchus* sp. in their study areas. McCrea et al., (2004) and Erickson (2005) both speculated about the possibility that a *Borealosuchus*-like specimen could have produced the *Albertasuchipes russelli* trackway from Alberta and the *Borealosuchipus hanksi* from North Dakota (a swim trace and a walking trace respectively).

To date, these are the only two Paleocene crocodylian trackways that have been reported, and are among the very few Paleocene vertebrate tracks known in the world.

PORCUPINE HILLS FORMATION (PALEOCENE: LATE TORREJONIAN-EARLY TIFFANIAN)

Six decades after the discovery of the Paleocene tracks from the Red Deer River, a large slab with natural casts of dog-like tracks (Fig. 2.107) was unearthed in Calgary's Signal Hill district in 1990 during excavation of basements for a new residential subdivision. The track slab (RTMP 1990.131.0001) was recovered by the RTMP and the mammalian identification was reaffirmed by later research (McCrea et al., 2003; 2004). The manus prints are more deeply impressed than those of the pes, making it possible to describe the morphology of both manus and pes prints from this specimen. The manus impressions are tetradactyl, with some digits carrying a single distinct phalangeal pad. A metacarpal pad impression is present in several of the manual traces, and is reminiscent of canid metacarpal pads. The pes is pentadactyl with some digits also possessing a single phalangeal pad. There are acuminate claw impressions on some of the digits of the manus and pes. McCrea et al. (2003; 2004) proposed that a creodont track-maker would be the most likely candidate for producing this trackway. This trackway was described as a new ichnotaxon *Sarjeantipes whitea* under the newly erected ichnofamily Sarjeantipodidae (McCrea et al., 2004).

Fig. 2.107: The unusual and distinct manus/pes set (6th and final in this trackway) of *Sarjeantipes whitea* recovered from the Porcupine Hills Formation in Calgary, Alberta. Scale = 10 cm.

SYSTEMATIC ICHNOLOGY

Class Aves

Ichnofamily Limiavipedidae

McCrea et al. nov.

Diagnosis: Trackway of a large, long-legged avian track-maker. Functionally tridactyl pes tracks with no obvious webbing. No hallux impression. Digits with sharp triangular claws. Digital pad impressions with 2-3-2 phalangeal formula. Total digit divarication over 100^{o}. Pes width greater than length. Pace and stride short compared to similar-sized theropod ichnotaxa, but long compared to other avian ichnotaxa. Strong rotation of the footprints toward the midline of the trackway. Average pace greater than 20 cm, average stride greater than 38 cm.

Discussion: There are many differences between the ichnofamilies Limiavipedidae and Avipedidae, but the inferred track makers are fundamentally different. The animals responsible for producing the ichnotaxa within Avipedidae are short-legged birds likely with many characteristics in common with modern shorebirds such as plovers. The track makers responsible for producing the ichnotaxa within Limiavipedidae are long-legged birds whose characteristics are more similar to modern wading birds such as herons, or cranes. Ichnotaxa within Limiavipedidae are as Buckley et al., (in review) observed, group separately from ichnotaxa in all other currently established Cretaceous avian ichnofamilies.

Type Ichnogenus: *Limiavipes* ichnosp. McCrea et al., herein.

Ichnogenus *Limiavipes* ichnogen. nov.

Limiavipes

McCrea et al., nov.

Derivation of name: Limi – Latin for “mud”; avi – “bird”, pes – “foot”

Diagnosis: Large, avian track with three, moderately thick, functional pedal digits; no hallux impression. Digits II and IV approximately equal in length; digit III is longer than digits II and IV. Sharp, triangular claw on each digit. Divarication between digits II and IV greater than 100° Footprint width greater than length. Pace and stride normally short. Individual footprints show a strong rotation towards the midline of the trackway.

Referred Specimens: PRPRC 2005.07.002, two footprints forming a trackway from the Gething Formation (Aptian), Gaylard Member of Gibson (1992) near Elisabeth Creek (exact locality information on file at the PRPRC).

Discussion: We no longer regard the emendations made by McCrea and Sarjeant (2001) to Currie’s (1981) original diagnosis of *Aquatilavipes* to be valid and reassign specimens of *A. curriei* to the newly described ichnogenus above. The footprints assigned to *Limiavipes* are much larger than those remaining within *Aquatilavipes*. Additionally, the digits of specimens within *Aquatilavipes* are slender, while those assigned to *Limiavipes* are much more robust. Specimens under *Aquatilavipes* have digit IV is longer than digit II creating an asymmetry with outer digit lengths. The outer digits lengths of *Limiavipes* specimens are nearly equivalent creating a symmetrical print.

This reassignment also has substantial quantitative justification. In applying multivariate analyses as suggested by Buckley et al. (2012) we have found strong statistical support for removing *A. curriei* from the ichnogenus *Aquatilavipes* even after size was removed as a factor.

Limiavipes curriei comb. nov.

(Fig. 2.48 a and b)

Derivation of name: We retain the original specific name defined by McCrea and Sarjeant (2001).

Holotype: Specimen RTMP 1998.089.0011; cast of isolated left pes taken from Grid H/G16 (McCrea, 2000). Deposited in the Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta.

Paratype: Specimen no. RTMP 1998.089.0010; cast of trackway (figs. 31.5 and 31.6 in McCrea and Sarjeant, 2001). Same repository as above.

Type Locality: Located on the footwall of 12 Mine South, W3 Main site footwall, about 21km northwest of Grande Cache, Alberta

Type Horizon: Holotype and paratype: Grande Cache Member of the Gates Formation, early Albian (Lower Cretaceous) below the No. 4 coal seam (Langenburg et al., 1987).

Diagnosis: As for ichnogenus.

Description **(corrected and emended from McCrea and Sarjeant, 2001):** Holotype (by standard measurement) overall length 7.9 cm, overall breadth 9.5 cm; length of digits II, 4.5 cm: III, 6.7 cm: IV, 5.0 cm. (Measurements taken to the anterior of the metatarsal pad (see p. 461-466 and text-figs. 31.4a and b). An ichnotaxon of avian affinity of moderately large size, the thickness of the digits being around 10% of their length. Digits terminate in narrow, sharp claws, those of digits II and IV inclined slightly axially towards digit III. Total interdigital span varies between 120º and 135º according to original substrate conditions, the angle between digits II and III on average greater than between digits III and IV. Digital pads often visible — three on digit III, two on digits II and IV. The center of each digit impression may show a groove, continuous or discontinuous; this may not be evident in shallower imprints. Based on orientation of digit III the footprints are rotated slightly inward towards the center of the trackway; the trackway is quite broad and the pace and stride, though variable, consistently short (average 23.5 cm and 48.4 cm, respectively).

There are distinct differences between *Limiavipes curriei* and all other currently named ichnospecies within *Aquatiliavipes*. There are significant differences between the footprint length of *A. curriei* (mean = 80.2 mm) and *A. swiboldae* and *A. izumiensis* (combined mean = 34.6 mm, *p*(same) = $1.17 \text{ X } 10^{-06}$). This difference is largely size-dependent, so a discriminant analysis was performed on a combination of $\log_{10}$-transformed linear (FL, footprint width, digit lengths II-IV) and on divarication data (DIVII-III, DIVIII-IV, and total divarication) for *L. curriei*, *A. swiboldae*, and *A. izumiensis*. This analysis shows that, even with the size component removed, there is still a significant difference between the *L. curriei* group and the *A. swiboldae* - *A. izumiensis* group (*p*(same) = $6.49 \text{ X } 10^{-19}$, with 95.7% of individual prints correctly placed in their ichnospecific groups).

Discussion: Ten trackways and more than 750 individual footprints of this ichnospecies were studied. The paratype slab (illustrated in McCrea and Sarjeant, 2001 – figs. 5-6) shows that two birds were moving at moderate speed in opposite directions, with a moderately long stride. A second trackway (McCrea and Sarjeant, 2001 - figs. 9-10) shows a meandering pattern of imprints, probably indicating a search for food along the edge of a drying-up pool.

One print, number A6 on the paratype trackway (McCrea and Sarjeant, 2001 –figs. 7-8) shows crater-like ‘swellings’, at left on digit III and at right on the metatarsal pad. These are comparable to the pathological effects produced by “bumblefoot” in living poultry, but it is more likely that they result from the activity of infauna in the sediment, the burrows of which are identical to the above features and are very common on these surfaces.

Table 31.1 in Sarjeant and McCrea (2001) gives correct measurements, but in the diagnoses of *A. curriei* the dimensions are reduced by an order of magnitude through the consistently incorrect placement of a period. This mistake has been corrected in the above description.

Dinosauria Owen, 1841
Theropoda Marsh, 1881
Ichnogenus *Saurexallopus* Harris et al., 1996; Harris, 1997
Saurexallopus cordata
McCrea et al., ichnosp. nov.
(Fig. 2.104)

Derivation of name: cordata – Latin for “heart-shaped”, referring to the shape of the metatarsal pad impression.

Diagnosis: As for *Saurexallopus* (Harris et al., 1996; Harris, 1997 and Lockley et al., 2004), but with prints possessing distinctly heart-shaped metatarsal pads forming a bi-lobed “heel” impression.

Holotype: *In situ* specimen (natural mould) of a right footprint and also replica silicone mould (PRPRC 2012.04.001M) and fiberglass reinforced (FGR) plaster cast PRPRC.2012.04.001MC curated at the Peace Region Palaeontology Research Centre (PRPRC) collection, Tumbler Ridge, British Columbia.

Type Locality: Northeastern British Columbia. Precise locality on file at the PRPRC, Tumbler Ridge, British Columbia, Canada.

Type Horizon: Upper Cretaceous (Campanian-Maastrichtian) Wapiti Formation, Unit 4 (Fanti and Catuneau, 2009).

***Description*:** The holotype print has a footprint length of 28.5 cm and a footprint width of 21.4 cm. Digit length dimensions are: digit II 18.2 cm, digit III 28.5 cm, and digit IV 21.7 cm. Digit divarications are: I-II 57 °, II-III 23 °, III-IV 34 °; total 114°. The holotype print shows evidence of distinct phalangeal pad impressions for digits II-III (?-2-3-3-x) and long, slender, acuminate claw impressions. Holotype print has a narrow, heart-shaped metatarsal pad with a bi-lobed "heel", which is different in character from that found in *S. lovei* or *S. zerbsti*.

Remarks: PRPRC 2012.04.001M and PRPRC 2012.04.001MC. The holotype *S. cordata* (Fig. 2.104) and two other medium-sized theropod prints from the above locality have a morphology almost identical to that of *Saurexallopus* (Harris, et al,. 1996; Harris, 1997; Lockley, 1998; Lockley and Peterson, 2002; Lockley et al., 2004) in displaying four digit impressions from what must have been four functional digits. We refer the Wapiti Formation specimens to *Saurexallopus* as their physical characteristics fit the diagnosis for this ichnogenus. Specimens of *Saurexallopus* ichnosp. from the Wapiti Formation are similar to the *S. lovei* (Harris et al., 1996; Harris 1997) in that the hallux is not reversed as opposed to *S. zerbsti* (Lockley et al., 2004) where the hallux is directed posteriorly.

Referred Specimens: Print #4 from PRPRC 2011.11.001.004M and PRPRC 2011.11.001.004MC from the same locality and same bedding horizon.

DISCUSSION

The Mesozoic record of western Canadian vertebrate tracks is confined almost exclusively to the Cretaceous, however the ichnological record for this geological period is one of the most continuous and complete in the world. Every terrestrial geological formation that has been investigated for tracks has yielded positive results. Furthermore, the majority of this track record is located in formations deposited within the Western Canadian Foreland Basin and so have a common link with the evolution of this basin and its depositional history.

To date, formations with large scale, *in situ* track surfaces are generally uncommon (Mist Mountain Formation, Gorman Creek Formation, Gething Formation, Gates Formation and Wapiti Formation). The record of the majority of vertebrate track-bearing formations consist of isolated track blocks, or small exposed *in situ* sites of only a few meters to tens of meters in area.

The track record of western Canada needs to be studied to understand the change of terrestrial vertebrate faunas through time. The body fossil record of the terrestrial Mesozoic of western Canada is among the richest in the world, but it is temporally restricted (primarily Campanian – Maastrichtian) making it impossible to track long-term regional faunal turnover and evolutionary changes. These trends can be inferred from the vertebrate track record which has a greater temporal range and is relatively complete through the Cretaceous (Fig. 2.1).

We offer a simplified first view of western Canadian vertebrate ichnofaunal change through time in order to present perceived trends within the data we currently possess (Fig. 2.108). Only dinosaurs (non-avian theropods) are included, since many non-dinosaurian tracks (except for birds, or avian theropods) are still relatively uncommon and their identity and affinity can be difficult to determine. Most small- to medium-sized dinosaur tracks (with the exception of the small quadrupedal ornithopods) were not included for similar reasons.

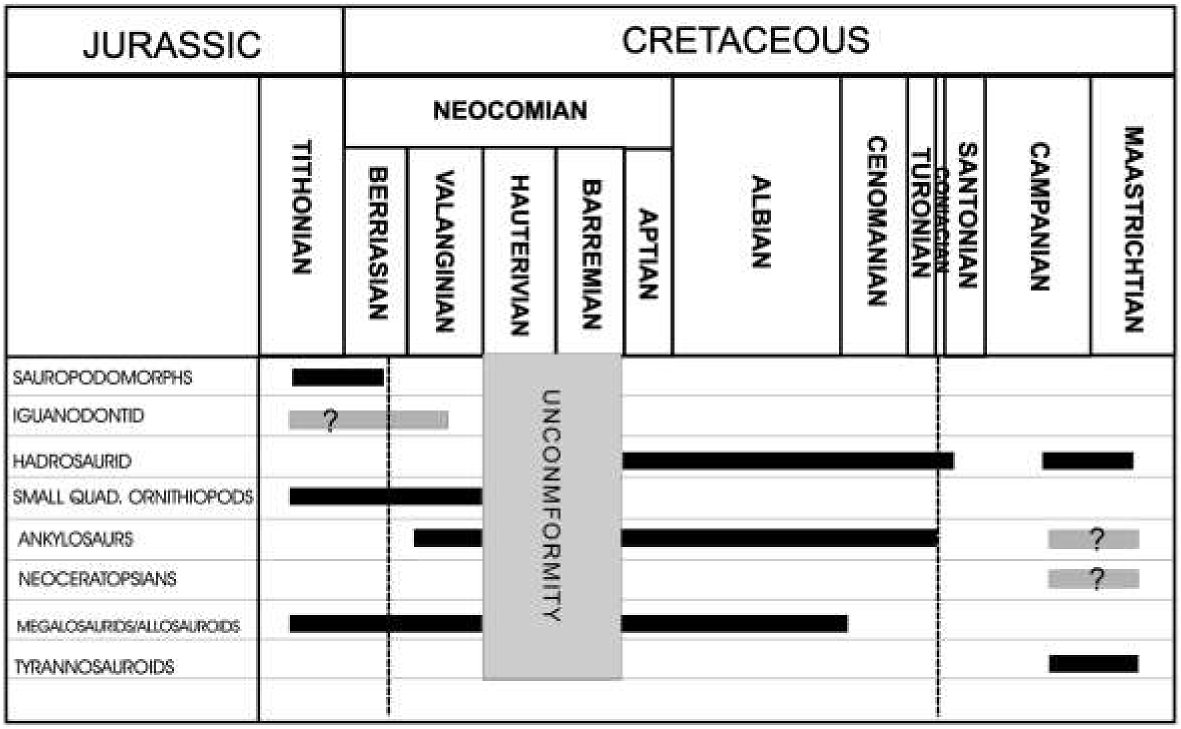

Fig. 2.108: Trends in western Canadian Mesozoic ichnofaunal turnover.

There are at least three regional ichnofaunal categories that can be recognized, which roughly correspond to three of the “footprint biochrons” established by Lucas (2007), which are, from oldest to youngest: Middle-Late Jurassic, Early Cretaceous, and Late Cretaceous.

Ichnofaunal Category 1 is the earliest division, and is based on the known temporal range of sauropods in western Canada which is from a single formation (Mist Mountain) that is thought by some (Gibson and Poulton, 1994) to straddle the Jurassic-Cretaceous boundary (however see Stott, 1998 for alternative viewpoint). There is an unconformity below this formation so we can not know what type of environment preceded that represented by the Mist Mountain Formation. However, it is possible that this first vertebrate ichnofaunal category was the twilight era of a Jurassic palaeoenvironment (typified by the presence of sauropods) that disappeared sometime in the Berriasian. However, some ichnofaunal elements from this category persisted beyond the Berriasian (allosauroids until the Albian and small quadrupedal ornithopods and large ornithopods - possibly iguanodontids - until the Valanginian). This category corresponds to the “Middle-Late Jurassic” footprint biochron of Lucas (2007) in which sauropod prints are abundant.

Ichnofaunal Category 2 is characterized by the ubiquitous presence of ankylosaurs (*Tetrapodosaurus* ichnosp.) which normally dominate ichnofaunas, particularly in the Valanginian and from the Albian into the Cenomanian. Although ankylosaurs are present in the Aptian of the Gething Formation, they are not the dominant component of the vertebrate ichnofauna. Instead it is the large ornithopods which are dominant in the Aptian. In the large-scale tracksites of the Albian Gates Formation, the ankylosaurs surge back to near complete dominance of the vertebrate ichnofauna. To date, not one large ornithopod track has been found in the Gates Formation which is a bit of a puzzle due to their previous dominance in the Aptian (Currie, 1983; 1989, 1995; Currie and Sarjeant, 1979) and their presence in the Cenomanian Dunvegan Formation and probable dominance in the Late Cenomanian-Turonian Kaskapau Formation.

The first observations on the association of *Tetrapodosaurus* ichnosp. tracks with wetland environments were made only recently (McCrea and Currie, 1998, McCrea, 2000; 2003; McCrea and Buckley, 2005b, 2006, 2007, 2008; McCrea et al., 2001) and to some extent support the palaeoenviromental observations made based on the ankylosaur osteologic record (Carpenter,1997).

The large and growing evidence that *Tetrapodosaurus* prints are found in proximity to low energy, high-organic content deposits (such as coal swamps, well-vegetated coastal plains and lake shores, etc.) is a reliable (and thus predictable) association that puts them in stratigraphic proximity to coal seams. These observations satisfy the criteria proposed by Lockley et al. (1994) for recognizing a distinct vertebrate ichnofacies (although see Hunt and Lucas, 2007 and Santi and Nicosia, 2008 for differing approaches to the concept and definition of what may or may not constitute an "ichnofacies"). We propose the "*Tetrapodosaurus* ichnofacies," taking the recommendation of Lockley et al. (1994) in naming this new ichnofacies after the dominant ichnotaxon (ichnogenus). There are over thirty ichnocoenoses (two from the Gorman Creek Formation, over twenty from the Gates Formation, one from the Pasayten(?) Group, at least ten from the Dunvegan Formation and a minimum of six from the Kaskapau Formation) in western Canada that support the establishment of the *Tetrapodosaurus* ichnofacies. The presence of ankylosaur tracks in the Dakota Group was reported by McCrea et al. (2001); however, recent finds of numerous ankylosaur tracks have been made in western Colorado and are found in sedimentary deposits indicating well-vegetated coastal plains (Lockley et al., in press). Some sites within the Dakota Formation, especially in the carbonaceous facies of western Colorado may also be included in the *Tetrapodosaurus* ichnofacies (Lockley et al. this volume).

The ornithopod-dominant Gething Formation appears to be assignable to the *Caririchnium* ichnofacies defined by Lockley et al. (1994), although in this case tracks of the ichnogenus *Amblydactylus* are the dominant feature. The Peace River Canyon tracksites occur in the Gaylard Member, the lower-most of three members comprising the Gething Formation; however, in some regions the Gething Formation is composed of the Gaylard Member alone (Gibson, 1992). The base of the Gaylard Member overlies the Cadomin Formation either gradationally or abruptly (Gibson, 1992). The facies are variable in the Gething Formation which is generally interpreted as a deltaic depositional environment (Gibson, 1992). This wide variability in sedimentary facies could have influenced the presence of the track-makers. Recent observations on Gething Formation sites have confirmed the predicted dominance of *Amblydactylus* ichnosp. at some of the Gething Creek and Elizabeth Creek localities. No low energy, high-organic content track-bearing sediments were found in Elizabeth Creek, and *Tetrapodosaurus* tracks (one or two natural casts in vertical section) were found at only one site along Gething Creek within a few centimeters of a coal seam. A small number of *Tetrapodosaurus* ichnosp. tracks were found together with large and small theropod tracks at the newly-reported Carbon Creek tracksite, but no *Amblydactylus* tracks have yet been reported. The sediments of the new Carbon Creek site are dark, indicating a fair amount of organic content, but the matrix is competent sandstone. Although at a preliminary stage, these observations appear to indicate that both *Tetrapodosaurus* and *Caririchnium* ichnofacies are present within the Gething Formation, with the *Caririchnium* ichnofacies being the most commonly encountered.

Taken together, the tracks of megalosaurids/allosauroids are numerous from the Valanginian into the Albian, but few tracks of large theropods (>35 cm FL) are found between the late Albian and Campanian. There is only one theropod track with a 50 cm footprint length (Fig. 2.109) and another with a 35 cm footprint length both of which are from the Dunvegan Formation (Cenomanian) of northeastern British Columbia (Scott, 2000). This category corresponds to the "Lower Cretaceous" footprint biochron of Lucas (2007), although instead of tracksites dominated by sauropods (in the southern U.S.) and ornithopods, the western Canadian sites are alternately dominated by ankylosaurs (Valanginian, Albian-Cenomanian) and ornithopods (Aptian and Turonian).

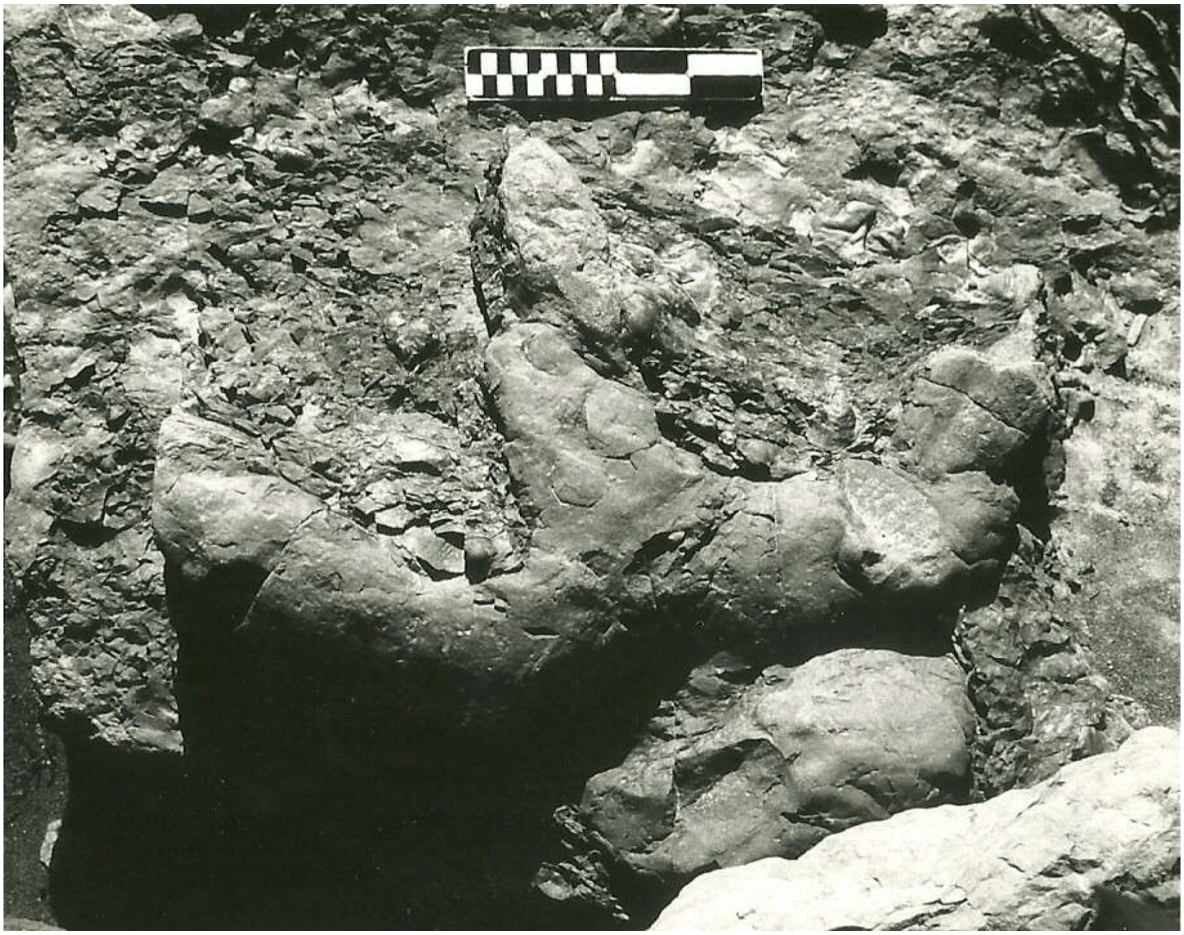

Fig. 2.109: Scarce large theropod track from the Dunvegan Formation of northeastern British Columbia. Scale in cm.

Ichnofaunal Category 3 is based on a handful of tracksites, but is characterized by the dominance of hadrosaur prints, and the low number of ankylosaurs and/or the possible presence of ceratopsians. The most striking aspect of this category is the presence of large (>60 cm FL) tyrannosaur footprints which make their first appearance in the late Campanian of western Canada (Alberta and British Columbia).

CONCLUSIONS

From the material summarized in this paper it is evident that a great deal of vertebrate ichnology research remains to be done in western Canada.

There are large regions in the mountainous interior of British Columbia that have not been investigated for fossil tracks. It is likely that, with the continued quest for natural resources (exploration similar to the beginnings of geological exploration in the Bowser Basin), additional fossil vertebrate tracks will be discovered. Mesozoic terrestrial deposits with economic coal deposits exist on Vancouver Island, but no tracks have been discovered there yet, although this will probably change if or when these coal deposits are exploited.

Northern Alberta has a few formations (Dunvegan, Grand Rapids, and McMurray) that should be investigated for fossil vertebrate tracks. As described above, central and southern Alberta already have yielded many fossil tracks, but many areas (even where there is active vertebrate palaentological research) have not specifically been investigated for tracks. It is probable that future directed efforts to finding tracks in central and southern Alberta will yield substantial results.

As of the time of writing there have been no reports of fossil vertebrate tracks (Mesozoic or early Cenozoic) from Saskatchewan and Manitoba. Saskatchewan has terrestrial deposits from the Late Cretaceous and well into the Early Cenozoic. It may be that the exposed sediments are not consolidated enough for tracks to survive if they were ever present. It is also possible that small outcrops of *in situ* or eroded track blocks do occur in Saskatchewan, but that they have not been noticed. Manitoba is unlikely to yield fossil vertebrate tracks of this age since there are no terrestrial deposits of appropriate age in outcrop.

Early Cenozoic tracks are restricted to a small record from the Paleocene of Alberta, and no Early Cenozoic tracks have been discovered in British Columbia to date. There is an impressive record of Eocene tracks in the Cascade Range just south of the Canada-US border in northwestern Washington State (Mustoe, 1993; 2002; Patterson and Lockley, 2004; Mustoe et al., 2012). There may be a potential for similar finds in southern British Columbia.

The diversity of tetrapod track types from western Canada is large. There is an abundance of some ichnotaxa that are generally rare, or at best scarce elsewhere in the world (e.g., tracks of ankylosaurs and tyrannosaurs). Some of the unusual associations and behaviors inferred from these tracksites make the vertebrate ichnological record of western Canadian significant on a global scale.

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3.0 REPLICATION AND DESCRIPTION OF A LARGE THEROPOD AND LARGE ORNITHOPOD TRACKWAY FROM THE UPPER MINNES GROUP (LOWER CRETACEOUS: VALANGINIAN) OF THE PEACE REGION OF NORTHEASTERN BRITISH COLUMBIA, CANADA

This chapter was formatted from a paper of the same title published in the New Mexico Museum of Natural Sciences, Bulletin 62, pp. 269-277 in 2014. This paper was a result of a collaborative effort and in order of priority these are: Richard T. McCrea and Tammy S. Pigeon. This project was conceived by the candidate who wrote the majority of the paper (>90%).

Institutional Abbreviations: PRPRC - Peace Region Palaeontology Research Centre

INTRODUCTION

Sediments of the Minnes Group of northeastern British Columbia are roughly equivalent in age to those of the Kootenay Group (Stott, 1998) (see fig 1, McCrea et al., this volume). Aside from a few track sites known from Narraway River and Kakwa Provincial Park localities from the Gorman Creek Formation (Currie, 1989; Sampson and Currie, 1996; McCrea and Buckley, 2005; 2006;

2007; 2008; McCrea, 2011; McCrea et al., this volume) few tracks have been found in the Minnes Group (Currie, 1989).

In the fall of 2004 a large track slab was uncovered and overturned by a Young's Mills, (a construction company), while creating a road for Canfor, (a logging company), on the side of a mountain south west of Chetwynd (1214 metres elevation, N 55^o 24' W122^o 5', Datum - NAD 27). One of us (RTM) visited the site on November 12, 2004 on the logging road where the track slab was discovered. At that time no tracks were evident on any of the other excavated rocks, but the potential for more finds in the area is good. The only track-bearing block found to date contains two natural cast trackways, each consisting of three tridactyl prints each (see fig. 21 - McCrea et al., this volume). The approximate dimensions of the block were measured (4.7m long x 2.5m wide x 0.4m thick) and from this a rough estimate of slab's mass was made (~9500 kg). Deteriorating weather conditions typical for the time of year and elevation prevented any further research at this site, but the block was deemed important enough to recover. The recovery of the trackslab was accomplished by local industry and was temporarily stored in a gated compound by Spectra Energy. The slab was later donated by Spectra Energy to the District of Chetwynd with the purpose of eventual public display. The District of Chetwynd realized that it was more appropriate to transfer responsibility of the care of this important specimen to the PRPRC in exchange for assistance in developing an outdoor exhibit with a high-fidelity replica of the track slab. This was a generous act from the District of Chetwynd, as well as a good recognition of the professional reputation of the decade-old PRPRC.

GEOLOGICAL CONTEXT

A surficial geology map (Stott, 1982: fig. 3a) indicates that Minnes Group strata is the only possible source for the track slab, but while precise locality data exists for the specimen it has proven difficult to determine from which formation (youngest to oldest: Bickford, Monach, Beattie Peaks, or Monteith formations) it originated due to forest and extensive ground cover in this area. In the Peace Region the exposed strata are youngest at the eastern edge of the foothills and get progressively older westward toward the Hart Ranges. The tracks were found on the extreme eastern edge of the Minnes Group surface outcrop, just over half a kilometer from the western edge of the Cadomin Formation which stratigraphically overlies the Minnes Group. It is likely that the track specimen originated from the upper part of the Minnes Group in this area. Stott (1998 – table 4) shows that the Bickford, Monach, Beattie Peaks, or Monteith formations are likely present in the Minnes Group of this area. It is reasonable to suppose that the tracks came from either the Monach or Bickford Formations which comprise the upper half of the Minnes Group both of which are thought to be of Valanginian age and are roughly contemporaneous with the Gorman Creek

Formation which is also of the Minnes Group, but recognized as a distinct mappable unit further to the southeast.

According to Stott (1998) the Bickford Formation is not widely distributed or exposed south of the Pine River. The Bickford Formation directly underlies the conglomerates of the Cadomin Formation and is composed of carbonaceous mudstone, siltstone and sandstone with thin coal seams. The Bickford Formation strata overlie the coarser, quartzose sandstones of the Monach Formation. The Monach Formation is present south of the Pine River at Mount Le Hudette (Stott, 1998), but east of Mount Le Hudette the Monach disappears due to erosion followed by the deposition of the sediments of the Cadomin Formation. This track slab was found approximately 10 km southeast of Mount Le Hudette so the Monach Formation is likely not present in the area of the track site.

With these considerations the Beattie Peaks Formation should be considered the most likely source for the tracks. It is unlikely that the lowermost Montieth Formation could have been the source for the tracks as this formation is predominantly composed of large successions of shale interbedded with thin layers of sandstone.

CREATING THE REPLICA MOULD, CAST AND COUNTER-MOULD

The original trackslab specimen (PRPRC 2012.01.001) was delivered to the PRPRC on January 30, 2011 (Fig. 3.1), however, the slab was too large and heavy to be stored inside the museum, so it was temporarily stored out of doors on museum property.

Fig. 3.1. Delivery of PRPRC 2012.01.001 on January 30, 2012.

The track slab was given some protection from the elements by a large canvas tent that was erected over it (Fig. 3.2). PRPRC staff immediately set about preparing to create a replica mould of the specimen as part of a collaboration with the District of Chetwynd to construct an outdoor exhibit showcasing the dinosaur trackways in concrete. It was decided that it would be desirable for the public to view the replicated tracks as natural moulds. As mentioned above the original tracks are preserved as natural casts which required museum technicians to make an initial latex mould of the original specimen. The latex mould would then have to be moulded in silicone in order to produce the desired natural mould replica.

Fig. 3.2. A canvas tent which covered PRPRC 2012.01.001 during itspreparation and moulding.

However, the slab had been stored outdoors in temperatures well below freezing in Chetwynd prior to its delivery to the PRPRC. Latex is unable to be stored, and will not cure under such conditions. The trackslab had to be warmed to a temperature that would allow latex to cure properly.

Within the large canvas tent a tarp was suspended several centimeters above the track surface. Two propane heaters were set up to circulate warm air under the tarp. The presence of the suspended tarp allowed the propane heaters to be more effective since a much smaller volume of air between the track surface and the overlying tarp had to be heated. The tarp also trapped the warm air near the surface of the track slab. A set of two 500W halogen lights and two electric space heaters were also employed, further increasing the heat focused on the trackslab. It took several days for the trackslab to become warm enough to begin latex moulding.

During the time the trackslab was thawing, museum technicians and volunteers worked on preparing the track surface for moulding. Even though the individual footprints were exposed natural casts, the natural mould surface was still in place over a large portion of the track surface (though not on the tracks themselves). This natural mould layer had the effect of reducing the true relief of the natural cast tracks and this layer obscured the margins of some of the tracks (Fig. 3.3). In most places this natural mould layer could be easily removed by careful prying with a chisel. Sometimes a hammer and chisel was employed, but if the layer was too resistant to remove it was left in place (Fig. 3.4). This preparation had a dramatic effect on the degree of vertical relief of the tracks. Some areas of the track surface had to be stabilized with Vinac during preparation, but the slab showed few signs of serious deterioration.

Fig. 3.3. Overview of the trackslab showing the remnants of the original natural mould track layer surrounding the natural cast tracks.

Fig. 3.4. Prying and chiseling the natural mould layer away to expose the true relief of the natural cast tracks prior to moulding with latex (February 2, 2012).

It took approximately a week to complete the latex mould which included four separate latex layers (the third layer reinforced with cheesecloth) and the reinforcing of high relief areas around the tracks with latex/vermiculite “plugs”. Due to the cold conditions the latex took longer than usual to set up, and from time to time uncured areas were pricked open and sprayed with a small solution of household-strength vinegar (~6% acetic acid) which is known to accelerate the curing of latex peels (Hamley and Thulborn, 1993).

When the latex layer had cured, a plaster/fiberglass support jacket was constructed (Fig. 3.5). It was necessary to make the support jacket in three interlocking sections so that when the track surface was de-moulded (Fig. 3.6), the replica mould and the support jacket could fit and be reassembled inside of the museum’s moulding and casting lab (Fig. 3.7a and b). The resulting latex mould was a perfect replica of the original PRPRC2012.01.001 slab, but with the prints appearing as [replicated] natural moulds instead of natural casts.

Fig. 3.5. Construction of the three-section FGR plaster and fibreglass matt support jacket (February 16, 2012).

Fig. 3.6. De-moulding the tracklab (February 17, 2012).

Fig. 3.7. a) Assembly of the three-section support jacket. b) Completed latex peel of the tracklab sitting on the support jacket.

One of the most time-consuming aspects of this project was the creation of a silicone production mould for the Chetwynd outdoor exhibit. A series of silicone (Smooth-Sil 940) mould tests were made upon expendable (low ammonia) latex moulds to see what effect silicone moulding on a latex surface would have on the curing ability of the silicone. These tests demonstrated that our silicone would not set up in the presence of latex, possibly due to the presence of sulpher within the latex mould. Further tests were made to see if coatings of acrylic spray would be a sufficient separator that would allow the silicone to cure. In these tests, several coats of acrylic spray (Krylon Crystal Clear acrylic clear coat) were found to give the desired effect.

Seven layers of clear coat were applied to latex mould (PRPRC 2012.01.001M) which expended three cans (approximately 350mL) of clear coat per layer, for a total of 21 cans (7.35 Litres) of clear coat. With the separator layer in place four layers of silicone (Smooth-Sil 940) were used to construct the production mould. Silicone was chosen for its long-shelf life and for its high tolerance for heat, necessary for casting in concrete. The silicone mould was completed near the end of April (Fig. 3.8), and was also given a support jacket to help the mould keep its shape during the concrete casting process. The total time required to date for this project was estimated to be 186.5 hours and involved four staff and volunteers. The completed silicone mold and support jacket were delivered to the District of Chetwynd in May, 2012.

Fig. 3.8. The completed silicone production mould shortly after de-moulding from the PRPRC 2012.01.001M.

Concrete casting of the framed mould (Fig. 3.9) was accomplished by District of Chetwynd public works staff, near the end of August, 2012. The support jacket provided for the mould was not employed for the concrete casting procedure. The completed replica of this track slab (reproduced as a natural mould surface) is currently on display with complete interpretive signage in Cedar Park, an outdoor area within the town of Chetwynd, northeastern British Columbia (Fig. 3.10).

Fig. 3.9. Wood frame constructed for the silicone mould in preparation for concrete casting at Cedar Park, Chetwynd, British Columbia (August 23, 2012).

Fig. 3.10. Dinosaur trackslab replica with interpretive signage at Cedar Park, Chetwynd, northeastern British Columbai (September 19, 2012).

METHODS AND DESCRIPTION

Both the original natural cast specimen (PRPRC 2012.01.001) and replica mould (PRPRC 2012.01.001M) were used for the scientific study of the two trackways. All measurements were taken from the replica mould (Fig. 3.11). A trackway map (Fig. 3.12) was produced from a tracing of the latex mould and compares well with photogrammetric images (Fig. 3.13) taken from the mould.

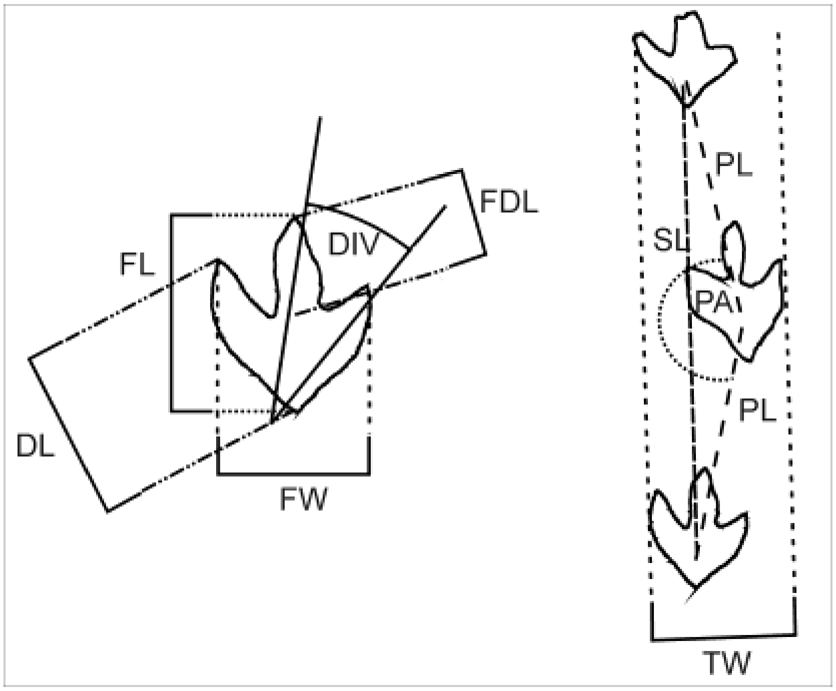

Fig. 3.11. Methods of footprint and trackway measurements used in this study.

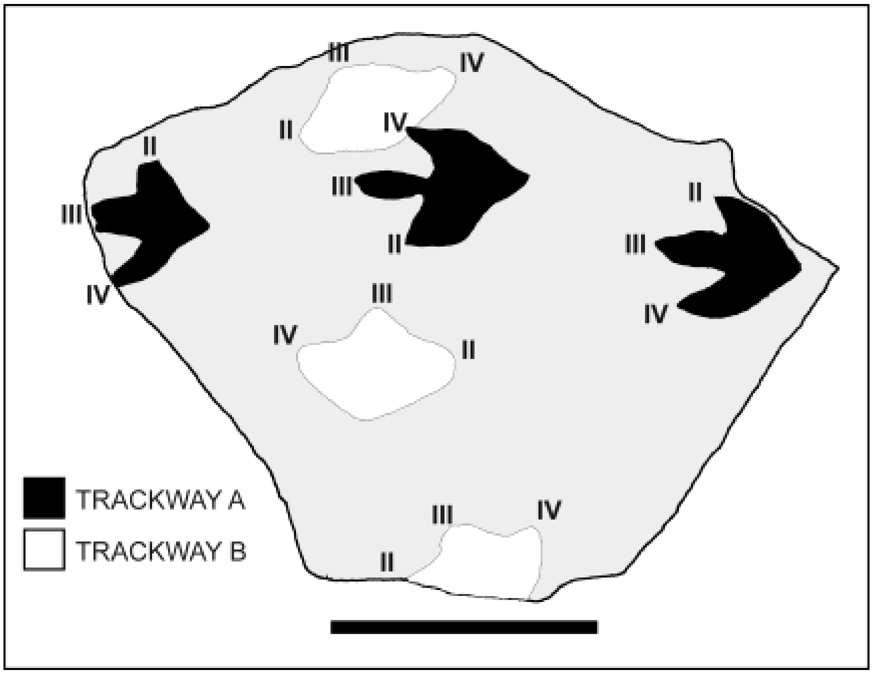

Fig. 3.12. Trackway map of PRPRC 2012.01.001M (Scale Bar = 1 metre). Trackway A was produced by a large theropod and Trackway B was produced by a large ornithopod.

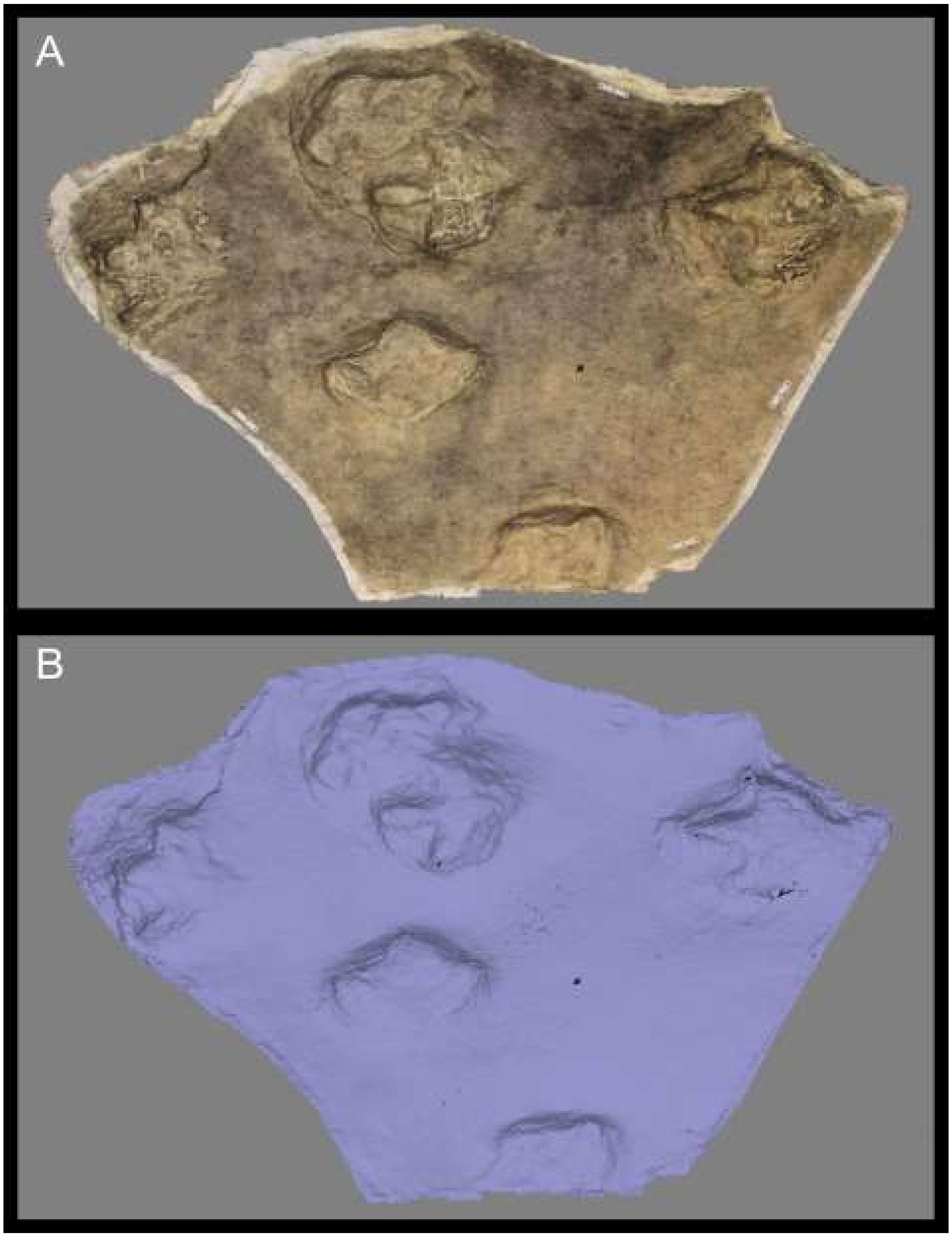

Fig. 3.13. Photogrammetric images of PRPRC2012.01.001M for comparison with the trackway map in Fig. 3.12 (herein). Top image is natural-shaded, the bottom image is a neutral shade generated by the program (Agisoft Photoscan Professional).

Studies of the three footprints of the theropod trackway show they are just under 60 cm long and that the animal's pace was approximately 1.2 meters with a 2.34 meter stride (Table 3.1). These footprint specimens are very large with robust digit impressions (though still showing faint phalangeal pad impressions), differing in general form from *Irenesauripus mclearni* and *I. acutus* tracks of Sternberg, (1932). These prints are similar in many aspects to *Megalosauripus* (*sensu* Lockley et al., 1998) as the short trackway segment preserved in this trackslab display a wider than normal trackway width and correspondingly low pace angulation value (68.5 cm and 158^{o} respectively) which is consistent with observations on other *Megalosauripus* trackways (Lockley et al., 1998). These unusual (for other large theropod trackways) pace and pace angulation values could also be correlated to the substrate consistency which, given the depth of the prints must have been quite soft. The constriction at the base of digit III (post-imprint sediment collapse) of print two, Trackway A, and the wide slide mark feature in digit II of the same print support the supposition of soft substrate conditions. We acknowledge the caution advised by Bates et al., (2013) after their preliminary conclusions of their studies on walking dynamics and substrate properties as related to footprint depth: that several factors may influence the depth to which an animal’s foot penetrates the substrate.

	Print #	FL	FW	FR	DL			FDL			DW			DIV			D/MPD				TW	PL	SL	PA
					II	III	IV	II	III	IV	II	III	IV	II-III	III-IV	Total	II	III	IV	MP				
TRACKWAY A	1(L)	59.5	48.0	6°	45.0	59.5	49.7	14.0	30.9	24.5	12.0	15.0	13.8	30°	33°	66°	10.3	12.1	8.2	9.8		-	-	-
	2	56.7	46.2	4°	45.2	56.7	44.0	17.7	29.9	18.6	16.4	11.5	11.5	34°	31°	65°	10.6	12.5	10.4	11.8		126.6	-	-
	3	-	50.0	3°	44.7	-	48.8	-	-	19.0	9.1	14.7	13.1	33°	30°	63°	9.8	11.8	9.7	10.4		117.5	234.2	158°
	$\bar{X}$	58.1	48.1	4°	45.0	58.1	47.5	15.9	30.4	20.7	12.5	13.7	12.8	32°	31°	65°	10.2	12.1	9.4	10.7	68.5	122.1	234.2	158°
TRACKWAY B	1(R)	-	-	26°	-	-	-	-	8.8	8.5	11.7	12.1	-	59°	-	-	-	5.6	5.3	4.2		-	-	-
	2	45.7	55.3	17°	41.9	45.7	39.8	16.5	11.9	16.7	12.5	20.0	14.4	39°	44°	83°	8.3	8.7	9.0	7.7		94.0	-	-
	3	-	61.2	21°	35.6	38.5	37.8	11.7	6.8	13.0	13.0	17.5	13.0	47°	77°	124°	5.6	5.4	5.2	6.7		107.0	187.0	143°
	$\bar{X}$	45.7	58.3	21°	38.8	42.1	38.8	14.1	9.2	12.7	12.4	13.7	13.7	48°	61°	104°	7.0	6.6	6.5	6.2	83.5	100.5	187.0	143°

Table 3.1. Footprint and trackway measurements from PRPRC 2012.01.001M (units in cm)- FL: Footprint Length; FW: Footprint Width; FR: Footprint Rotation; DL: Digit Length; FDL: Free Digit Length; DW: Digiti Width; DIV: Divarication; D/MPD; Digit/Metatarsal Pad Depth; TW: Trackway Width; PL: Pace Length; SL: Stride Length; PA: Pace Angulation.

The dimensions of the PRPRC2012.01.001 large theropod prints (footprint length and width) are within the range defined by Lockley et al., 1998 for *Megalosauripus*. We note that the occurrence of the PRPRC 2012.01.001 theropod trackway is outside the stratigraphic interval within which *Megalosauripus* ichnosp. is generally restricted (Lockley et al., 1996; 1998). It is worth noting that previous *Megalosauripus* ichnosp. occurrences are mainly from Europe and central Asia. It could be possible that similar track-makers were present for a longer stratigraphic interval in North America though Lockley (2000) expressed doubts that *Megalosauriupus* track-makers could have extended into the Cretaceous at all.

The PRPRC 2012.01.001 theropod prints are also quite similar in many respects to *Bueckeburgichnus* ichnosp. which are more age-appropriate being described from the Lower Cretaceous (Berriasian) of Germany (Lockley, 2000). Lockley's (2000) reported digit widths of *Bueckeburgichnus maximus* are much smaller values than those observed with the British Columbia specimen. However, there is no noticeable hallux with the British Columbia material which casts doubt on an identification of these prints as *Bueckeburgichnus* given the depth of the PRPRC 2012.01.001 theropod prints.

In order to avoid adding to the complexity and confusion surrounding the ichnotaxomony of large theropod prints we tentatively refer the PRPRC 2012.01.001 Trackway A prints to *Megalosauripus* ichnosp. until further material is discovered in western Canada that may help resolve the question of identification.

The supposed large ornithopod trackway also has three footprints, which are wider than long with three digit impressions with rounded, hoof-like terminations. No manual impressions are evident with this trackway, but it is possible that they were overprinted by the much larger pedal impressions (though see Schulp and Al-Wosabi, 2012, and references therein for discussions on the difficulty in discriminating between ornithopod and theropod tracks. The ornithopod pes impressions are 45 cm long with a 95 cm pace and a 186 cm stride. The overall morphology and dimensions of the Minnes Group ornithopod prints appears to agree better with an *Iguanodontipus* ichnosp. (Sarjeant et al., 1998) identification rather than with the other three large ornithopod ichnotaxa recognized that are commonly used (Hunt and Lucas, 2006; Diaz-Martinez et al., 2012) which are *Amblydactylus* (Sternberg, 1932), *Caririchnium* (Leonardi, 1984; Lockley, 1987) which are also likely to have been produced by Early Cretaceous iguanodontid track-makers and *Hadrosauropodus* (Lockley et al., 2004) from probable hadrosaurid tracks from the Upper Cretaceous. It is significant to note that the Minnes Group ornithopod trackway fills a small temporal gap in the large ornithopod track record of western Canada. Large ornithopod prints are present in the vertebrate ichnofauna of the Mist Mountain Formation (Tithonian-Berriassian) of southeastern British Columbia, but so far they are absent from the Gorman Creek Formation (Valanginian) ichnofauna, which is nearly contemporaneous with the Minnes Group strata where this specimen originated (McCrea et al., this volume).

The features of the tracks in both trackways suggest the ground on which the animals were walking was soft and wet, and that they were compelled to walk slowly. This is also suggested by the width of the trackways. The trackway width for large theropods is typically narrow, and there is a straight line of footprints with the individual tracks being oriented nearly parallel to the midline of trackway. The footprints of the PRPRC 2012.01.001 trackways are not in a straight line (low pace-angulation); they are staggered and the individual tracks are not parallel to the midline (see McCrea et al., this volume). The prints of the theropod trackway are rotated inward more than is typically seen when compared with most other track sites. As indicated by McCrea et al., (this volume) the record of Earliest Cretaceous tracks in northeastern British Columbia is sparse, but there is great potential for further finds in the near future.

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The senior author would like to thank Ben Bealak for finding and reporting this track specimen and for taking the time to take me to the specimen before it was moved from its original location. Thank you to Spectra Energy for their efforts over several years that ensured the safety of the trackslab while it was in their care.

The Tumbler Ridge Museum Foundation and the PRPRC are grateful to the District of Chetwynd for the donation of this significant track specimen. In particular I would like to thank Ellen Calliou (Economic Development Officer for the District of Chetwynd) for her efforts to get the slab donated to the PRPRC as well as for her vision and logistical support to create the wonderful outdoor interpretive exhibit. Many District of Chetwynd staff were involved in organizing and constructing the outdoor exhibit and I am pleased to acknowledge their efforts.

PRPRC head technician Tammy Pigeon and a small group of museum technicians and volunteers executed the various challenging moulding tasks associated with the exhibit project, and accomplished them in exemplary fashion. Nadine Secord donated her time and effort to assist with the outdoor preparation of the track slab for moulding during the middle of the winter. Thank you also to Matteo Belvedere with his helpful insights in photogrammetry techniques.

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4.0 VERTEBRATE ICHNITES FROM THE BOULDER CREEK FORMATION (LOWER CRETACEOUS: MIDDLE TO ?UPPER ALBIAN) OF NORTHEASTERN BRITISH COLUMBIA, WITH A DESCRIPTION OF A NEW AVIAN ICHNOTAXON, PAXAVIPES BABCOCKENSIS, ICHNOGEN. ET, ISP. NOV

The contents of this chapter have been re-formatted from a published paper of the same title published in the journal *Cretaceous Research*, Volume 55, pp. 1-18 on January 20, 2015. This paper was a result of a collaborative effort by several authors, and in order of priority these are: Richard T. McCrea, Lisa G. Buckley, A. Guy Plint, Martin G. Lockley, Neffra A. Matthews, Tommy Noble, Lida Xing and Jessica R. Krawetz. The candidate conceived this project and wrote the majority of the paper (>60%).

Keywords: Avian trackways; Theropod tracks; Ornithopod track; Skin impressions; Boulder Creek Formation; Albian; British Columbia; Cretaceous.

Institutional abbreviations: BCPM, Royal British Columbia Museum, Victoria, British Columbia, Canada; CVM, Cowan Vertebrate Museum, University of British Columbia, Department of Zoology, Vancouver, British Columbia, Canada; **PRPRC**, Peace Region Palaeontology Research Centre, Tumbler Ridge, British Columbia, Canada; **TMP**, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada;

MCF, Museo Municipal “Carmen Funes”; **UAMZ**, University of Alberta Museum of Zoology, University of Alberta, Department of Biological Sciences, Edmonton, Alberta, Canada;

INTRODUCTION

The first fossil footprints recovered from the Boulder Creek Formation were discovered in August, 2005 by Curtis Lettely (then a Ph.D. student of the Ichnology Research Group at the University of Alberta) during the course of a preliminary geological investigation in the Boulder Gardens recreational area south of Tumbler Ridge, British Columbia (Fig. 4.1). This area is within the boundaries of the recently established Tumbler Ridge Global Geopark which is part of the Global Geoparks Network, supported by UNESCO. The slab was discovered embedded vertically and partially buried in the talus and soil at the base of a short, steep cliff. Most of the rocks in the Boulder Gardens recreational area are covered with lichen colonies as was also the case for a portion of the track face of this slab. At the time of discovery only the most distinct avian tracks and two theropod tracks were visible (see fig. 2 of Buckley and McCrea, 2009).

The track slab was removed to the PRPRC via helicopter on October 4, 2005 and accessioned into the collections (PRPRC 2005.15.001). However, before the tracks could be studied a considerable growth of lichen on the track surface first had to be removed (see Methods below). From observations of the replica cast and the original trackslab (Fig. 4.2) a trackway map was prepared (Fig. 4.3). Seventy-two avian prints, three theropod, and one small ornithopod dinosaur prints were mapped. Five avian trackways were discernable with between three to six footprints per trackway (Fig. 4.3 & 4.4). The avian prints are unusual in that digit II-III impressions exhibit higher divarications than that observed for digits III-IV, a characteristic that is also found in *Barrosopus slobodai* from Argentina (Coria et al., 2002).

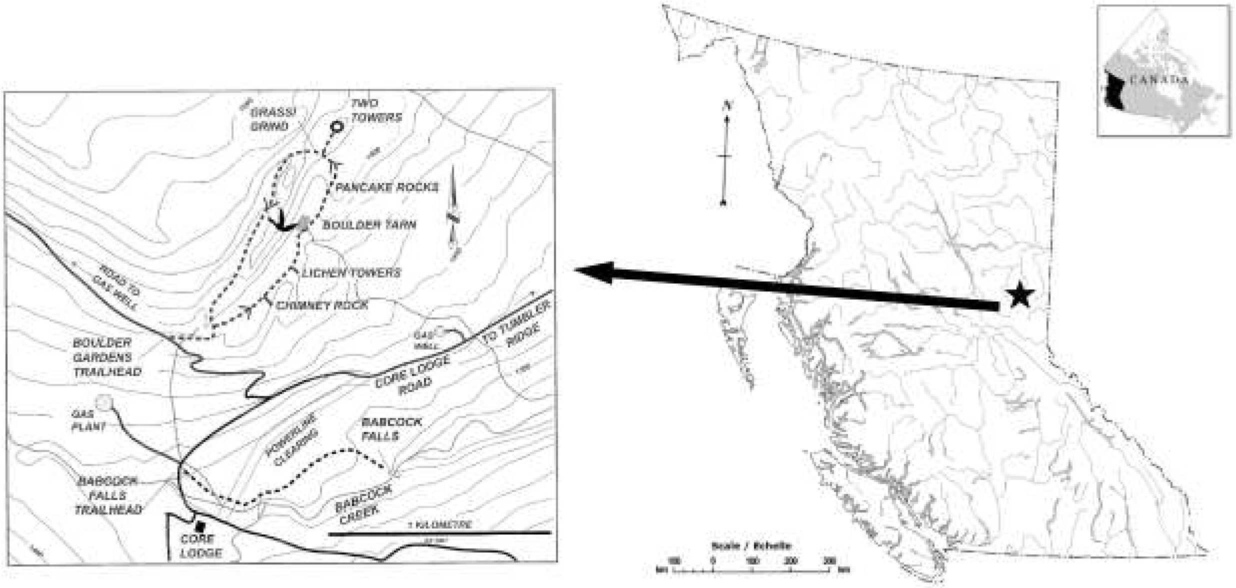


Fig. 4.1. Map showing the locality (bird track symbol) where the PRPRC 2005.15.001 slab was discovered. Provincial map modified from The Atlas of Canada website (http://atlas.gc.ca/site/html) made freely available via open government licence (http://open.canada.ca/en/open-government-licence-canada). The Boulder Garden trail map was modified from Helm, (2008) with written permission of the author.

Fig. 4.2. A view of a portion of PRPRC 2005.15.001, after cleaning, showing two small, tridactyl theropod tracks (*Irenichnites gracilis* PRPRC 2015.001.073 & 074) and many small tridactyl prints of avian affinity. Scale bar = 10cm. Numbers correlate to those in the trackway map (Fig. 4.3).

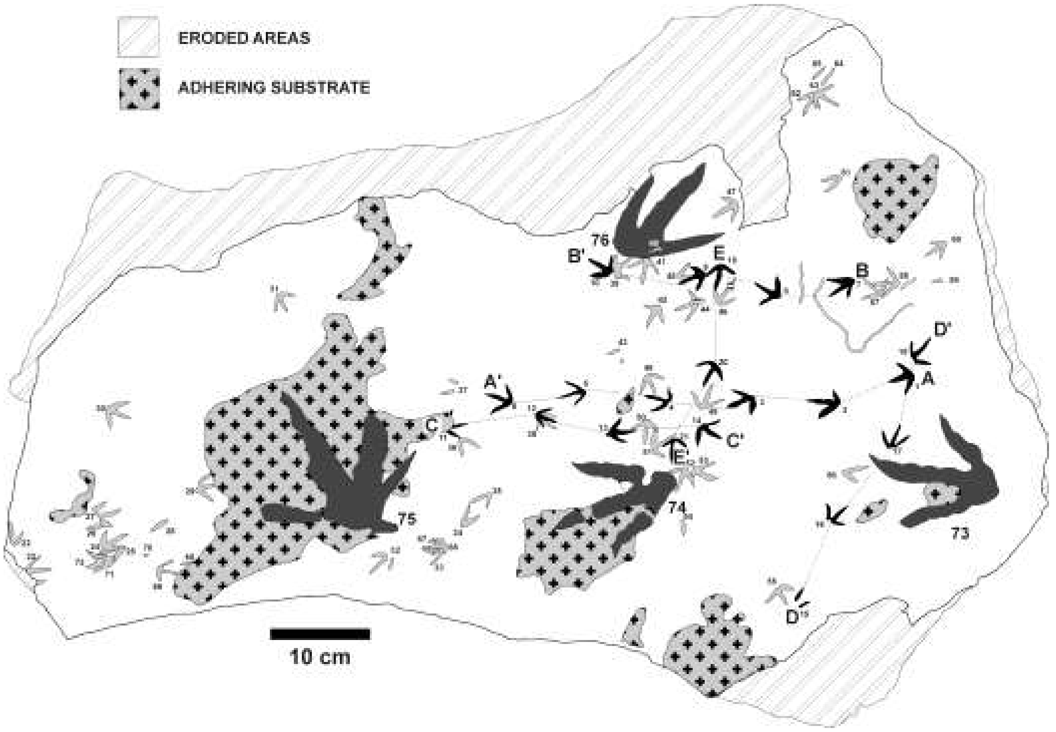


Fig. 4.3. Trackway Map of PRPRC 2005.15.001. Avian trackways (A-E) are indicated by black shading and connecting lines. The beginning of each trackway is indicated by an uppercase letter (e.g. A). The end of a trackway is indicated with an uppercase letter with an apostrophe (e.g. A'). All footprints are numbered.

The dinosaur footprints are small and at least two of them (Fig. 4.5) are identified as *Irenichnites gracilis*, originally described by Sternberg, (1932). One of the prints of *Irenichnites gracilis* (PRPRC 2005.15.001.074) displays skin impressions on the proximal ends of the digit and the metatarsal pad traces (Fig. 4.6). A slightly larger tetradactyl ornithopod print (PRPRC 2005.15.001.075) also has skin impressions with larger skin tubercles.

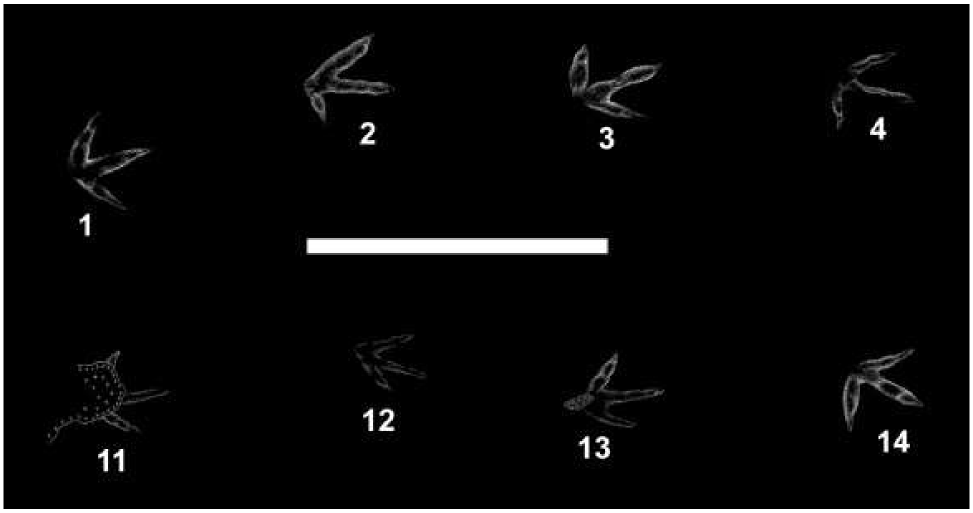


Fig. 4.4. Illustration of footprints within two avian trackways from PRPRC 2005.15.001. Top: Footprints from trackway A (Fig. 4.2). Bottom: Footprints from trackway C (Fig. 4.2). Scale = 10cm. Numbers correspond to those in Fig. 4.2.

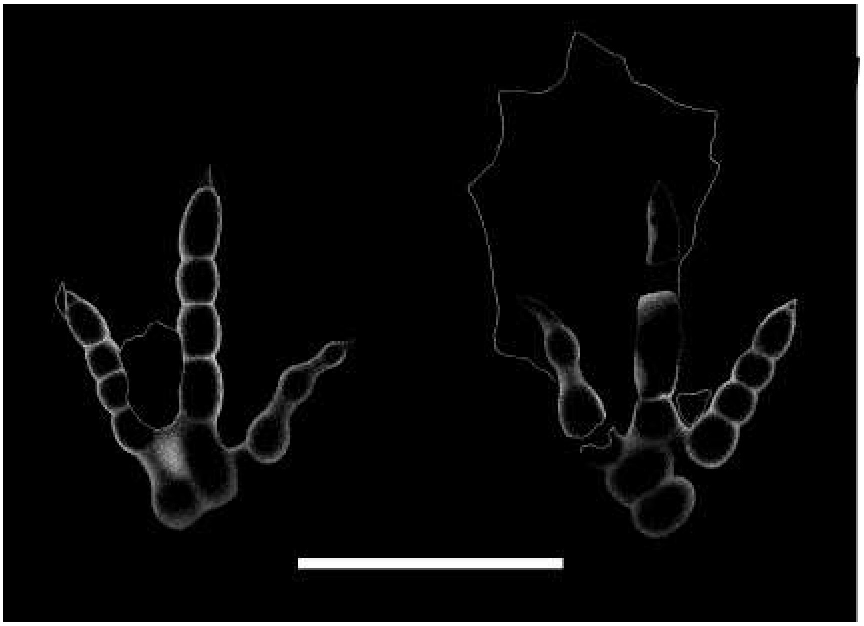


Fig. 4.5. Illustration of PRPRC 2005.15.001.073 (left image), and PRPRC 2005.15.001.074 (right image). Scale = 10 cm.

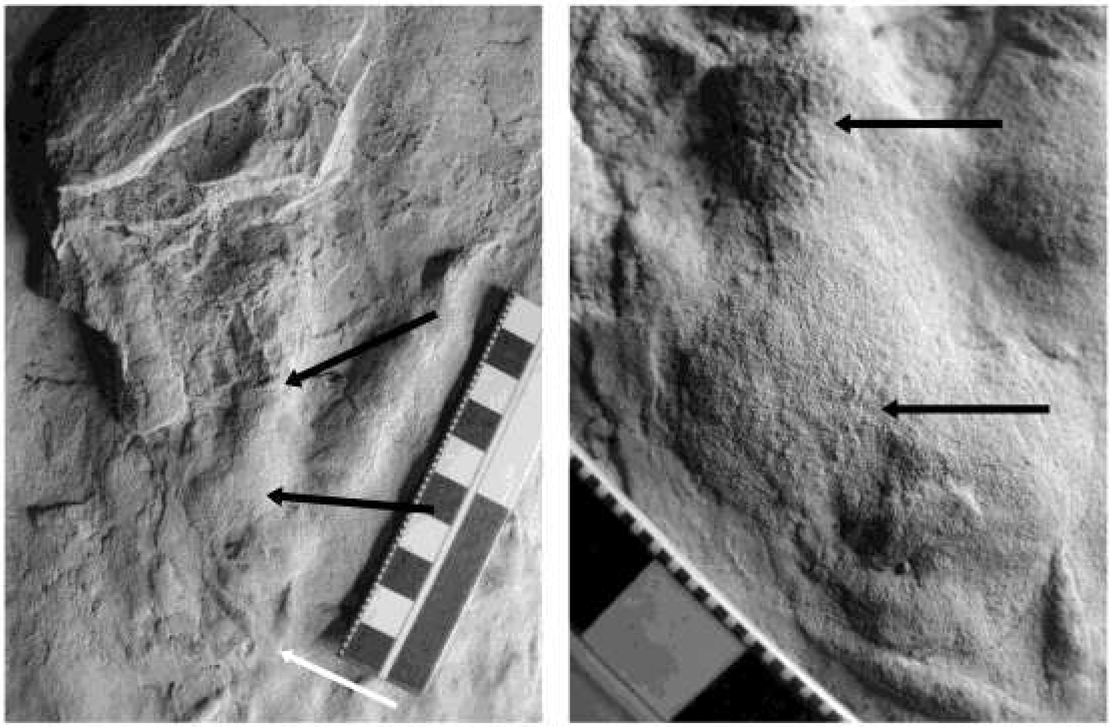


Fig. 4.6. Left: PRPRC 2005.15.001.074, cf. *Irenichnites gracilis* (10 cm scale with mm divisions). Dark arrows indicate areas with skin impressions. Avian print PRPRC 2005.15.001.052 indicated by a white arrow, is visible adjacent to the posterior portion of the metatarsal pad impression. Right:Magnified view of proximal digit III and metatarsal pad area with skin impressions of PRPRC 2005.15.001.074. Arrows indicate areas with skin impressions. Avian footprint partially visible on the bottom of photograph. Scale in cm and mm.

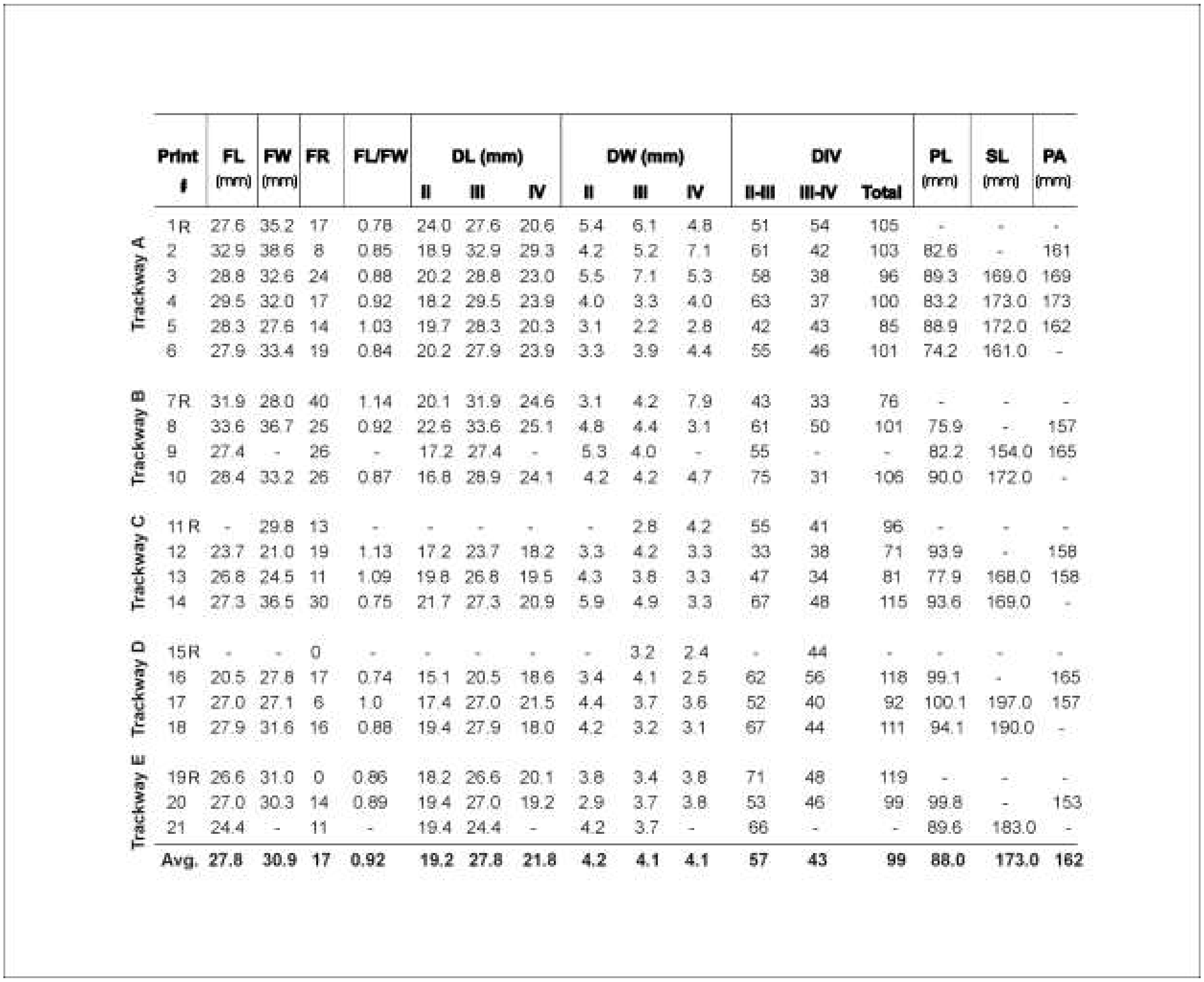
MATERIALS AND METHODS

Preparation and Replication

Extant lichen colonies encrusting the original track specimen were removed using a chemical technique reported by Buckley and McCrea (2007; 2009). Once the lichen had been removed, a latex ‘master’ mould of the track surface was made (PRPRC 2005.15.001M), and from this a master cast composed of FGR (fibre-glass reinforced) plaster was prepared (PRPRC.2005.15.001MC).

Measurements

Measurements (Tables 4.1 and 4.2) were taken following the methods of Leonardi (1987) with measurements of footprint length/footprint width (FL/FW) after McCrea and Sarjeant (2001) (Fig. 4.6). Preparation of the specimen to remove extant lichen colonies was described in Buckley and McCrea (2009).



	Print #	FL (mm)	FW (mm)	FR	FL/FW	DL (mm)			DW (mm)			DIV			PL (mm)	SL (mm)	PA (mm)
						II	III	IV	II	III	IV	II-III	III-IV	Total			
Trackway A	1R	27.6	35.2	17	0.78	24.0	27.6	20.6	5.4	6.1	4.8	51	54	105	-	-	-
	2	32.9	38.6	8	0.85	18.9	32.9	29.3	4.2	5.2	7.1	61	42	103	82.6	-	161
	3	28.8	32.6	24	0.88	20.2	28.8	23.0	5.5	7.1	5.3	58	38	96	89.3	169.0	169
	4	29.5	32.0	17	0.92	18.2	29.5	23.9	4.0	3.3	4.0	63	37	100	83.2	173.0	173
	5	28.3	27.6	14	1.03	19.7	28.3	20.3	3.1	2.2	2.8	42	43	85	88.9	172.0	162
	6	27.9	33.4	19	0.84	20.2	27.9	23.9	3.3	3.9	4.4	55	46	101	74.2	161.0	-
Trackway B	7R	31.9	28.0	40	1.14	20.1	31.9	24.6	3.1	4.2	7.9	43	33	76	-	-	-
	8	33.6	36.7	25	0.92	22.6	33.6	25.1	4.8	4.4	3.1	61	50	101	75.9	-	157
	9	27.4	-	26	-	17.2	27.4	-	5.3	4.0	-	55	-	-	82.2	154.0	165
	10	28.4	33.2	26	0.87	16.8	28.9	24.1	4.2	4.2	4.7	75	31	106	90.0	172.0	-
Trackway C	11 R	-	29.8	13	-	-	-	-	-	2.8	4.2	55	41	96	-	-	-
	12	23.7	21.0	19	1.13	17.2	23.7	18.2	3.3	4.2	3.3	33	38	71	93.9	-	158
	13	26.8	24.5	11	1.09	19.8	26.8	19.5	4.3	3.8	3.3	47	34	81	77.9	168.0	158
	14	27.3	36.5	30	0.75	21.7	27.3	20.9	5.9	4.9	3.3	67	48	115	93.6	169.0	-
Trackway D	15R	-	-	0	-	-	-	-	-	3.2	2.4	-	44	-	-	-	-
	16	20.5	27.8	17	0.74	15.1	20.5	18.6	3.4	4.1	2.5	62	56	118	99.1	-	165
	17	27.0	27.1	6	1.0	17.4	27.0	21.5	4.4	3.7	3.6	52	40	92	100.1	197.0	157
	18	27.9	31.6	16	0.88	19.4	27.9	18.0	4.2	3.2	3.1	67	44	111	94.1	190.0	-
Trackway E	19R	26.6	31.0	0	0.86	18.2	26.6	20.1	3.8	3.4	3.8	71	48	119	-	-	-
	20	27.0	30.3	14	0.89	19.4	27.0	19.2	2.9	3.7	3.8	53	46	99	99.8	-	153
	21	24.4	-	11	-	19.4	24.4	-	4.2	3.7	-	66	-	-	89.6	183.0	-
	Avg.	**27.8**	**30.9**	**17**	**0.92**	**19.2**	**27.8**	**21.8**	**4.2**	**4.1**	**4.1**	**57**	**43**	**99**	**88.0**	**173.0**	**162**

Table 4.1. Measurements of avian trackways A-E PRPRC 2005.15.001 (see Fig. 4.2).

Print #	FL (mm)	FW (mm)	FL/FW	DL (mm)			DW (mm)			DIV		
				II	III	IV	II	III	IV	II-III	III-IV	Total
24R	30.3	25.5	1.20	19.8	30.3	23.5	5.6	4.4	3.8	47	24	71
30 L	27.2	31.8	0.86	19.7	27.2	23.1	7.2	4.5	4.4	59	36	95
31 R	19.7	24.7	0.80	16.2	19.7	18.1	3.8	2.8	3.2	56	37	93
41 L	25.6	28.2	0.91	18.4	25.6	18.1	2.8	3.3	3.1	53	48	101
42 L	25.2	26.7	0.94	17.7	25.2	18.2	3.9	4.5	3.4	55	41	96
44 L	26.4	30.6	0.86	15.4	26.4	21.7	4.3	3.1	3.3	69	42	111
46 R	31.3	27.5	1.14	18.5	31.3	19.2	3.7	3.1	3.5	51	41	92
47 L	29.7	28.0	1.06	19.0	29.7	21.7	4.5	5.0	4.3	54	37	91
48 R	22.9	29.5	0.78	18.0	22.9	21.7	2.5	3.4	3.7	50	42	92
49 R	28.0	35.7	0.78	24.2	28.0	22.4	3.9	3.8	3.1	57	44	101
50 L	25.3	29.0	0.87	20.2	25.3	18.0	4.4	3.7	3.9	53	46	99
51 L	28.5	30.0	0.95	16.0	28.5	19.3	5.3	4.3	5.3	68	50	118
52 L	28.1	30.5	0.92	19.3	28.1	21.9	3.9	3.8	4.1	52	43	95
55 L	21.9	33.0	0.66	20.1	21.9	18.6	4.6	4.4	4.7	63	51	114
57 L	25.5	37.9	0.67	22.0	25.5	21.1	5.5	4.7	3.3	68	57	125
58 L	24.8	34.4	0.72	21.0	24.8	22.0	4.5	3.4	2.9	67	43	110
60 R	25.7	20.6	1.25	17.7	25.7	16.9	3.3	4.5	3.2	40	35	75
62 R	27.9	26.7	1.04	17.6	27.9	20.7	3.3	3.1	3.2	48	42	90
63 L	27.7	30.5	0.91	15.3	27.7	19.7	3.2	3.0	3.1	64	52	114
Avg.	**26.4**	**29.5**	**0.91**	**18.7**	**26.4**	**20.3**	**4.2**	**3.8**	**3.7**	**57**	**43**	**99**

Table 4.2. Measurments of (isolated?) prints PRPRC 2005.15.001 (see Fig. 4.2)

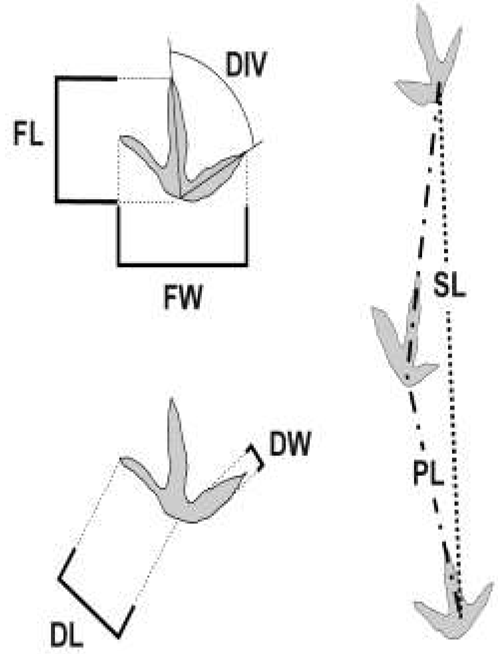


Fig. 4.7. Methods of trackway and footprint measurements used in this study.

DIV, digit divarication; DL, digit length; FL, footprints length; FW, footprint width; PL, pace length; SL, stride length.

Ichnology specimens and data

Multivariate analyses were conducted on track and trackway data collected by the authors for *Paxavipes babcockensis*, nov. ichnogen. nov. isp. (PRPRC 2005.15.001), and on data collected by the authors and Coria et al. (2002) for *Barrosopus slobodai* (MCF-PVPH-SB 415-17c). Data presented in Azuma et al. (2002) for *Aquatilavipes izumiensis*, and by McCrea and Sarjeant (2001) for *Aquatilavipes swiboldae* (holotype TMP 1979.023.0037, and specimens TMP 1998.089.0021, TMP 1998.089.0020, and TMP 1990.030.0001) were used as representatives of ichnofamily Avipedidae to compare with the proposed new ichnofamily Paxavipedidae.

Multivariate analysis materials and methods

Univariate and multivariate (discriminant and canonical variate analyses) were conducted using PAleontological STatistics (PAST) software, version 2.19 (Hammer et al., 2001). Footprint length to footprint width ratio (FL:FW) and total divarication (DIVTOTAL) were not included in analyses so as not to exaggerate the variation contributed to the dataset by FL, FW, and divarication, respectively.

Discriminant analysis projects a multivariate dataset to maximize the separation of two *a priori* determined groups in one dimension (Hammer and Harper, 2006), and is a useful tool for testing hypotheses of morphologic similarity. Using the available data, the analysis attempts to separate individual specimens: in this case, individual footprints from both *Paxavipes babcockensis* and *Barrosopus slobodai*, into the *a priori* determined groups. A 90% or greater correct identification of the individual prints into the two *a priori* categories is sufficient support for the presence of two morphologically distinct groups (Hammer and Harper, 2006). Discriminant analysis was conducted on both isolated tracks and tracks from trackways separated into the ichnotaxonomic groups, *Paxavipes* and *Barrosopus*, respectively. Canonical variate analysis (CVA) performs the same analysis as that of discriminant analysis, but on three or more *a priori* separated groups. Hotelling's t^2 results (the multivariate version of a t-test) were provided to show the level of significance of the separations. Significance for both analyses is measured at $p \geq 0.05$.

Osteology specimens and data

Angles for intertrochlear and plantar displacement were measured from digital photographs taken with a Sony α350 SLR 12.1 megapixel digital camera. Images were edited and angles were measured using Adobe Photoshop 7.0. Intertrochlear angles were measured from the long axes of the intertrochlear grooves of distal metatarsals II and IV, each measured from the intertrochlear groove of metatarsal III, as viewed from the distal end of the tarsometatarsus. Plantar angles were measured from the extensor end of the intertrochlear grooves of distal metatarsals II and IV as viewed from the distal end of the tarsometatarsus, and each angle for metatarsals II and IV were measured from the extensor end of the intertrochlear groove of metatarsal III. Tarsometatarsi were measured for *Charadrius vociferus* (BCPM 00978, BCPM 10760; UAMZ 4931, UAMZ 5663, UAMZ 5751, UAMZ 5752, UAMZ 6787) and *Charadrius semipalmatus* (BCPM 17454, BCPM 23807; CVM 14485) for Charadriidae, and *Actitis macularia* (BCPM 23257; UAMZ 5335, UAMZ 6879), *Caladris alba* (BCPM 18305; UAMZ 6770), and *Caladris melanotos* (CVM 14484, CVM 14556) for Scolopaciidae.

Interspecific vs. ontogenetic variation in foot size

Discriminant and canonical variate analyses were run with unadjusted linear data. This was done for two reasons. First, there are no visible size classes among the trackways for each ichnotaxon, so we can assume that all the footprints within each separate ichnotaxon were produced by track-makers that were approximately the same size and/or ontogenetic stage. Therefore, any difference in size between two ichnotaxa is not likely to be ontogenetic. Second, although shorebird young are precocial and their young mature at a slower rate relative to birds with altricial young (Gill, 2007), the young of shorebirds reach maturity quickly: young of *Charadrius vociferus* (Killdeer) leave the nest within 24 hours of hatching, and at day 17 the growth curve of chicks asymptotes (Bunni, 1959; Jackson and Jackson, 2000), and the young of *Actitis macularia* (Spotted

Sandpiper) reach 82% of their adult wing-tip to wing-tip length at day 15 (Oring et al., 1997). Unless two different size classes of footprints are documented within the sample in question, it is parsimonious to assume that the track-makers of each ichnotaxon are of adult or approaching adult-size. Two avian ichnotaxa that exhibit a significant difference in size may reflect two separate track-making species.

There is a dearth of documentation on postnatal development in digit length, foot length, and allometric growth of pes elements (i.e. phalangeal size) for extant shorebirds. However, postnatal hind limb development (except for pes phalanges) has been documented for both extant (ostrich, emu, rhea, kiwi) and extinct palaeognathes (*Aepyornis* sp., *Dinornis* sp.). *Aepyornis* sp. shows accelerated hind limb growth relative to forelimb development (Balanoff and Rowe, 2007), and Turvey and Holdaway (2005) show that the ossification rates and growth of the hind limbs of *Dinornis* sp. and the growth and ossification of the tarsometatarsii closely follows that of the femorae, which also exhibit accelerated relative hind limb development. Whether extant shorebirds exhibit relatively accelerated pes growth with respect to body size remains to be documented. The rapid attainment of adult body size by many extant shorebirds allows us to assume that, given the equal investment in both cursorial and aerial locomotory modes (Dial, 2003), hind limb and foot length of both extant and extinct shorebirds reached adult body size within several days of leaving the nest.

GEOLOGICAL SETTING, ENVIRONMENT AND PALEONTOLOGY

There are three terrestrial formations of Albian age in the Peace Region of British Columbia. In ascending order these are the Gates, Boulder Creek and Goodrich Formations. The vertebrate ichnofauna of the middle Albian Gates Formation (western Alberta, and northwestern British Columbia) is well-known (McCrea et al., 2014 and references therein), and although vertebrate tracks have previously been observed in the Boulder Creek and Goodrich Formations (McCrea et al., 2014) they are less well-known. The Gates and Boulder Creek Formations are separated by marine sediments of the Hulcross Formation. The Boulder Creek and Goodrich formations are separated by marine sediments of the Hasler Formation.

Stratigraphic relationships and age of the Walton Creek Member of the Boulder Creek Formation

In the foothills of British Columbia, the Albian Boulder Creek Formation was defined by Stott (1982) as a sandstone-rich succession that conformably overlay marine mudstone of the Hulcross Formation. Gibson (1992) subsequently divided the Boulder Creek Formation into a lower marine sandstone named the Cadotte Member, and an upper nonmarine unit called the Walton Creek Member. The top of the Cadotte Member is marked by a sharp but commonly pedogenically modified surface, above which lie alluvial and lacustrine deposits of the Walton Creek Member. The Hulcross and Boulder Creek Formations can be traced from the Foothills for > 300 km eastward into the subsurface of BC and Alberta, where they are equivalent to the Peace River Formation, the latter being divided into the Harmon, Cadotte and Paddy members in ascending order (Fig. 4.8).

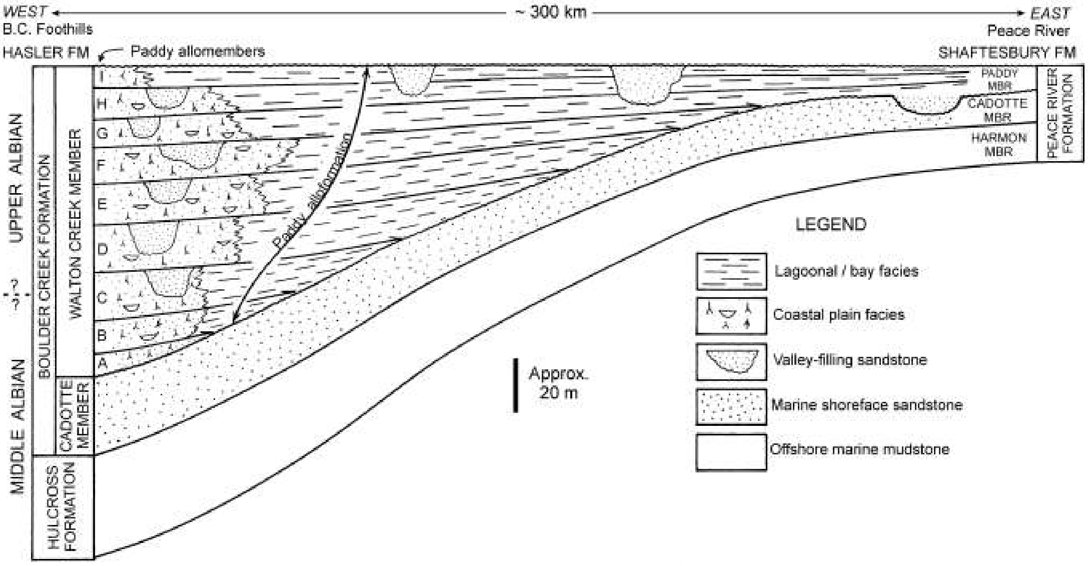


Fig. 4.8. Summary of stratigraphic relationships between Albian strata in the Rocky Mountain Foothills and the adjacent Plains to the east, Roca et al., (2008).

A recent regional allostratigraphic and sedimentological analysis, incorporating both outcrop and subsurface data (Rylaarsdam, 2006; Roca et al., 2008, Buckley and Plint, 2013), showed that the Cadotte and Paddy members of the Peace River Formation (the Cadotte and Walton Creek members of the Boulder Creek Formation) represent two distinct tectono-stratigraphic episodes (Plint et al., 2012). The Cadotte Member is of broadly tabular geometry and records the northward progradation of an ENE-WSW-trending strandplain during a period when the basin was experiencing a relatively low rate of flexural subsidence. In contrast, the Paddy/ Walton Creek member forms a strongly wedge-shaped body that thins from about 125 m thick in the BC Foothills to less than 10 m to the north and east of the town of Peace River, some 300 km to the East.

In subsurface, the Paddy Member was divided into nine allomembers (labelled A-I) on the basis of marine, brackish and lacustrine flooding surfaces (Rylaarsdam, 2006; Roca et al., 2008). Paddy allomembers onlap progressively eastward onto the top of the underlying Cadotte Member. This stratigraphic relationship indicates a temporal break between the top of the Cadotte and the base of the overlying Paddy Member. The magnitude of the stratigraphic hiatus increases eastwards to encompass most of the time represented by the Paddy. Thus, in the vicinity of the town of Peace River, the Cadotte Member is directly overlain by the Paddy allomember G, lower allomembers having lapped out further to the west (Roca et al., 2008).

Roca et al., (2008) concluded, on the basis of subsurface correlations, that the basal transgressive surface of the marine Joli Fou Formation erosively overlay the top of the Paddy Member. However, correlations were not unequivocal, and it is possible that the uppermost few metres of the Paddy Member are laterally intergradational with the basal few metres of the Joli Fou Formation.

The Hulcross Formation is dated as early middle Albian based on the presence of *Pseudopulchellia pattoni* and *Haplophragmoides multiplum,* whereas the overlying

Cadotte Member contains *Gastroplites kingi*, *Gastroplites allani*, and *Ammobaculites* sp., which are indicative of a late middle Albian age (Caldwell et al., 1993). Because diagnostic marine fossils are largely absent from the Walton Creek and Paddy strata, their age is not well-constrained. Near the town of Peace River, strata high in the Paddy Member (Paddy allomember PH in the allostratigraphic scheme of Roca et al*.,* 2008), contain *Inoceramus comancheanus* (Leckie and Singh, 1991). This bivalve is also common in the Joli Fou Formation, and is indicative of an early late Albian age. By inference therefore, the age of the Walton Creek and Paddy strata therefore ranges from late middle Albian to early late Albian (Fig. 4.8).

Facies and depositional environments of the Paddy / Walton Creek Member

As this paper is concerned solely with outcrop material, we refer the track-bearing rocks from the Boulder Gardens to the Walton Creek Member, although Roca et al., (2008) used the term ”Paddy Member” to encompass both outcrop and subsurface rocks. Space permits only a very brief summary of the main facies and depositional environments, based on results in Rylaarsdam et al., (2006).

In broad terms, the Walton Creek Member is primarily of non-marine aspect in the British Columbia Foothills, with only minor evidence of brackish and tidal conditions. Towards the east, in subsurface, the Walton Creek/Paddy rocks show progressively more evidence of deposition in shallow, brackish-water bays and low-energy deltaic environments. This lagoonal/deltaic association grades northward into sandstones suggestive of a marine shoreface environment, which in turn passes further northward into offshore mudstones and sandstones with abundant hummocky cross-stratification indicative of significant storm wave influence (Buckley, 2011; Buckley and Plint, 2013).

In the British Columbia foothills, dark grey to black, laminated, non-bioturbated mudstone, in places interbedded with thin beds of fine-grained siltstone or sandstone, forms upward-coarsening units up to 5 m thick. Plant debris, logs of wood and centimetre-scale bands of siderite concretions are common. This facies probably represents shallow vegetated floodplain lakes in which upward-coarsening reflects gradual shallowing. Diffuse punch-down structures are present in this facies, usually near the top of the succession and can be attributed to dinosaurs walking in very soft, non-cohesive sediment (Fig. 4.9).

Fig. 4.9. Dinosaur punch-down structure in thinly-bedded, unconsolidated lacustrine mudstone. Bedded units highlighted. Quintette mine access road, scale bar = 20 cm.

Lacustrine mudstones are commonly interstratified with units of dark grey silty clay to siltstone that may be well-laminated, poorly-laminated or massive, the latter having a fine, blocky-weathering appearance. Units are typically 1-3 m thick and can extend hundreds of metres laterally. Upper and lower contacts are usually gradational. Carbonaceous roots are sparse to abundant, but few well-developed paleosols are present. Nodular and spherulitic siderite is also very common. Coals, typically <50 cm thick, are associated with this facies but are not common. This facies represents poorly-drained, vegetated, rapidly-aggrading floodplains (McCarthy and Plint, 1999; McCarthy et al., 1999). Abundant spherulitic siderite indicates bacterially-mediated reducing conditions within the sediment, and a high ground-water table. Rare, sandstone-filled cracks attest to periods of lowered water table and desiccation.

Sheet-like units of very fine- to medium-grained sandstone, typically 10-50 cm thick and 50 to >100 m in lateral extent are interstratified with floodplain mudstone. Sandstone sheets typically have an abruptly gradational or sharp basal contact, and are commonly current-rippled or, rarely, cross-stratified. Roots are ubiquitous, and plant debris, including well-preserved leaves of both angiosperms (magnolia/tulip tree) and gymnosperms (ginkgo) is locally abundant. In some instances these sheet sandstones can be traced to the margins of lenticular, channel-filling sandstones and hence can readily be interpreted as crevasse splay deposits. Splay sandstones are commonly organized in groups of 3-15, separated by centimetre to decimetre thick mudstone beds. Dinosaur tracks impressed into floodplain mudstone are commonly preserved as natural casts on the basal surfaces of crevasse sandstones (Fig. 4.10). In other instances, crevasse sandstone beds are punched downward into coaly floodplain mudstone (Fig. 4.11).

Fig. 4.10. Large tridactyl track impressed into floodplain mudstone and preserved as a natural cast at the base of a crevasse splay sandstone. Bedded units highlighted.

Mount Spieker, scale bar = 20 cm.

Fig. 4.11. An intensely deformed crevasse splay sandstone that has been punched downward into an underlying coaly mudstone. The deformed bed is erosively overlain by an undeformed, current-rippled crevasse-splay sandstone. Bedded units highlighted. Whatley Creek, scale bar = 20 cm.

Lenticular, erosive-based bodies of fine- to coarse-grained, current rippled and cross-bedded sandstone are typically 2-5 m thick and <20 m wide. The basal surface is scoured and overlain by a lag of mudstone intraclasts, pebbles and logs. These units are readily interpreted as channel-fills. The channel-fills show little evidence of lateral migration, in the form of lateral-accretion surfaces, and are interpreted as the fills of non-migrating, possibly anastomosed rivers. Anastomosed rivers typify alluvial plains of extremely low gradient (Makaske, 2001; Lumsdon-West and Plint, 2005). Rarely, channel-fills show well-developed lateral-accretion surfaces and are interpreted as meandering river deposits, suggestive of somewhat steeper alluvial gradients.

The background suite of alluvial facies described above is locally replaced by bodies of medium-grained sandstone to fine-grained conglomerate that are up to 25 m thick, a few hundred to a few kilometres wide, that have a strongly erosive base and are recognizable both in outcrop and in well-log cross-sections. These sandstone bodies are typified by decimetre to metre-scale cross-bedding, numerous internal erosion surfaces and large-scale accretion surfaces. These large sandstone bodies are interpreted to have been deposited by braided rivers confined to paleo-valleys.

The preponderance of sideritic and carbonaceous floodplain deposits, shallow lakes and immature paleosols provide evidence that the Walton Creek/Paddy rocks were deposited primarily under conditions of rapid tectonic subsidence that favoured development of a low-gradient alluvial plain characterized by shallow lakes, poorly-drained floodplain soils and rapid aggradation resulting from frequent overbank flooding. Abundant roots and detrital plant material indicate that the alluvial plain was heavily vegetated, providing food and habitat for dinosaurs, birds, and other vertebrates (turtles, crocodilians, etc.). The pronounced south-westerly thickening wedge shape of the Walton Creek/Paddy rocks provides clear supporting evidence of strongly asymmetrical subsidence adjacent to the Cordilleran fold and thrust belt. In contrast to the fine-grained floodplain deposits, sandstones and conglomerates filling paleo-valleys suggest phases of alluvial incision, possibly related to tectonic uplift, increased fluvial discharge, and/or sea-level fall.

Context and characteristics of the track-bearing block (PRPRC 2005.15.001)

Specimen PRPRC 2005.15.001 was recovered from the Boulder Gardens recreational area at the base of a cliff on the southeastern slope of Mount Babcock, 24 kilometres south of the town of Tumbler Ridge, British Columbia. The original track slab (PRPRC 2005.15.001) is a natural cast (counter slab) and only small portions of the original, track-bearing surface still adhere to this specimen (Fig. 4.3). From observations based on the surviving counter slab, the original surface on which the tracks were registered was evidently fine-grained, organic-rich sand covered with a fine organic-rich mud drape. The surface was not uniform in topography at the time the tracks and trackways were registered. There are distinct undulations observable on the surface, which indicate that the sedimentary surface had original topography, as opposed to being the result of post-depositional effects. Original areas of high topography were drier and mud-cracked, and the surface sediments were relatively hard. In contrast, the sediment surface areas of original low topography were damper, softer, and the footprints are more deeply impressed, (Fig. 4.12).

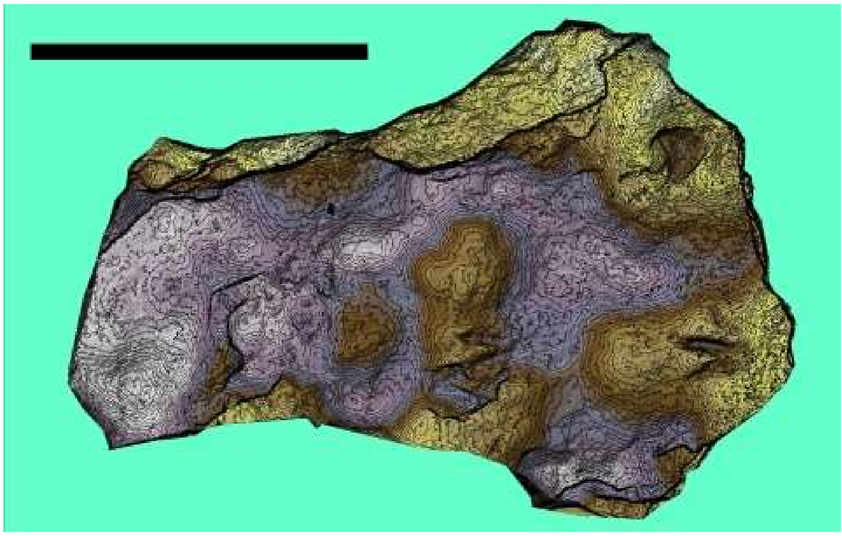


Fig. 4.12. Photogrammetric image of the PRPRC 2005.15.001 track block showing variation in topography of the track-bearing surface. Note that this image is of a natural cast and so the types of relief (low to high) were reversed on the original track surface. Scale = 50 cm. Contour interval is 1 mm.

These undulations are unlikely to be due to post-depositional processes as evidenced by observations of the sediments themselves and by the distribution and preservation of the footprints. The regions of the track slab that preserve evidence of relatively low topography (preserved as high-topography on the counter slab) are where the most deeply-impressed and best-preserved avian prints are found. Conversely, the topographically higher areas (preserved as topographically low areas on the counter slab) possess avian footprints that are only faintly impressed and are less well-preserved. This difference in depth of impression between the topographically high (shallow prints) and low (deep prints) areas of the track slab has been observed within single avian trackways (A, C & E). Topographically low regions also show evidence of sinusoidal invertebrate traces (repichnia, *Cochlichnus* isp.) –probably made by nematode worms (Figs. 4.3 and 4.13), whereas topographically high areas do not. Additionally, the sedimentary surface in the topographically high areas show small, but distinct desiccation cracks, features that are absent in the topographic lows. From these observations it is evident that, prior to burial, the original track surface possessed topography, possibly ripple-marks. The sediments in the original topographically high areas were dewatered to the point that mud cracks formed and the surface became more resistant to registering avian footprint impressions. The sediments in the topographic lows were either partially saturated with water or even sub-aqueous, possibly forming small pools. The sediments in the topographic low areas were not resistant to registering avian footprint impressions or even very small worm traces referable to *Cochlichnus* isp. (Hitchcock, 1858).

Fig. 4.13. Possible nematode worm trace (*Cochlichnus* isp.) to the left of a faint avian (*Paxavipes babcockensis* nov. ichnogen. nov. isp.) print (PRPRC 2005.15.001.008). Scale in cm and mm.

The track slab was discovered out of context at the base of a cliff face many tens of metres high and could have originated from any point on that face. Most of the sediments in the immediate area are massive, medium-grained sandstones with little organic content. They differ considerably from the sediments that form the track slab. However, exploration along the accessible areas of the cliff face showed small lenses of fine-grained organic-rich sediments within the predominantly coarse-grained sediments. It is possible that the track slab may be a remnant of such a lens.

ICHNOTAXONOMY

Class Aves

Subclass uncertain

Ichnofamily Paxavipedidae ichnofam. nov.

Description. Small tridactyl avian footprints with digit traces united proximally with the metatarsal pad and lacking webbing and hallux. Divarication between digit II and digit III traces greater than that between digit III and digit IV. Trackway characters consistent with a small, short-legged track-maker.

Type Ichnogenus. Paxavipes McCrea et al., herein

Referred specimens. Barrosopus slobodai, Coria et al., 2002.

Ichnogenus *Paxavipes* ichnogen. nov.

Derivation of name. Pax = peace [region], for the Peace Region of British Columbia where the specimen was discovered; avi-, bird, -pes, suffix identifying this as a trace.

Holotype. PRPRC 2005.15.001.014 and PRPRC 2005.15.001.014MC, single natural cast print and trackway C (PRPRC.15.001.011-014 inclusive), *Paxavipes babcockensis* McCrea et al., herein. Lower Cretaceous (middle Albian) of northeastern British Columbia, Canada.

Paratypes. Trackway A PRPRC 2005.15.001.001-006 inclusive, Trackway B PRPRC 2005.15.001.007-010 inclusive, Trackway D PRPRC 2005.15.001.016-018 inclusive.

Included ichnospecies. The ichnogenus is only known from the type ichnospecies.

Type Locality. Boulder Creek Formation: The Walton Creek Member (Lower Cretaceous: middle to ?late Albian), Mount Babcock, south of Tumbler Ridge. Precise locality on file at the Peace Region Palaeontology Research Centre.

Diagnosis. Trackway of a biped consisting of small tridactyl prints, without webbing and hallux. Individual footprints are generally wider than long (FL ~ 27 mm; FW ~ 30 mm); FL/FW ratio approximately 0.91. Divarication between digit traces II-III consistently greater than that between digits III-IV. Inward rotation of pes pronounced.

Description. Trackway of a small biped lacking hallux or web traces, and with divarication angles between traces of digits II and III averaging 57° and greater than the divarication angles between digits III and IV which average 43°. Tracks averaging 2.7 cm long and 3.0 cm wide (range 2.0 cm - 3.4 cm and 2.1 cm - 3.9 cm, respectively). All digit traces are narrow (around 4 mm thick) approximately 22% of the length of digit II, 15% of length of digit III and 19% of digit IV length. Digital pads are evident on some tracks, but are not consistently preserved. There is pronounced inward rotation of prints towards the midline of the trackway. The trackway is narrow with short pace and stride.

Ichnospecies *Paxavipes babcockensis* isp. nov.

Derivation of name. The specific name refers to Mount Babcock where the type specimen was discovered.

Holotype. The fourth footprint of trackway C (PRPRC 2005.15.001.014) of the original block and PRPRC 2005.15.001.014MC, the fibreglass reinforced (FGR) plaster replica. Lodged at the Peace Region Palaeontology Research Centre, Tumbler Ridge, British Columbia.

Paratypes. Trackway A PRPRC 2005.15.001.001-006 inclusive, Trackway B PRPRC 2005.15.001.007-010 inclusive, Trackway D PRPRC 2005.15.001.016-018 inclusive. Prints in trackways A, B C as above located on PRPRC 2005.15.001MC, the fibreglass reinforced (FGR) plaster replica.

Type Locality. as for ichnogenus

Diagnosis. as for ichnogenus

Description. as for ichnogenus

Remarks. Paxavipes babcockensis nov. ichnogen. nov. isp. trackways were evidently produced by a small short-legged bird. *Paxavipes babcockensis* prints are produced by short-legged birds with only three pedal digits with no webbing evident and greater divarication between digits II and III than that between digits III and IV (characters shared with *Barrosopus slobodai*).

Paxavipes babcockensis is similar to *Barrosopus slobodai* (Coria et al., 2002) in many respects, including general size and especially in the high divarication between digits II and III as compared with III and IV. However, *Paxavipes babcockensis* digits are joined proximally via a metatarsal pad which is absent in specimens of *Barrosopus slobodai*, although this may be due to circumstances of preservation.

Barrosopus slobodai footprints show a significantly higher total divarication and trackways have slightly greater pace and stride lengths than those of *Paxavipes babcockensis*. Digit widths of *Paxavipes babcockensis* are more uniform (all close to 4 mm) than those of *Barrosopus slobodai* prints. The outer digits of *Barrosopus slobodai* and *Paxavipes babcockensis* are both shorter than the middle digits, however, the outer digits of *Paxavipes babcockensis* have a greater equality in length than those of *Barrosopus slobodai* where digit IV is longer than digit II and almost as long as digit III.

Barrosopus slobodai and *Paxavipes babcockensis* are similar enough to both be included within the same ichnofamily, but are distinct enough to merit discrimination at the ichnogeneric level. They are among the smallest avian tracks known from the Mesozoic, although in the size range of *Koreanaornis* (Kim, 1969). However, *Koreanaornis* sometimes registers a small hallux trace, and different divarication morphology (Lockley et al., 1992, 2012)

Barrosopus slobodai and *Paxavipes babcockensis* prints can be distinguished from all other described avian ichnotaxa based on the trait they share in having consistently higher divarication between digits II and III than is found between digits III and IV while lacking visible webbing and hallux impression. There are avian ichnotaxa that do display a consistently higher divarication between digits II and III than digits III and IV; however, these ichnotaxa also display a prominent digit I (*Ignotornis yangi* Kim et al., 2006; *Ignotornis gajiensis* Kim et al., 2012) or display prominent webbing and are larger than *Paxavipes* and *Barrosopus* (*Gyeongsangornipes lockleyi* Kim et al., 2013).

The record of fossil avian tracks and the number of avian ichnotaxa has increased considerably in the past few years, particularly in Asia (Matsukawa et al., 2006; Lockley and Harris, 2010: Lockley et al., 2012). There are now several described avian ichnotaxa from Mesozoic and Cenozoic deposits worldwide. Where trackways exist these can be generally divided in to morphotypes indicating long-legged and short-legged ichnotaxa, each of which can be further sub-divided into categories based on numbers of digits, divarication between digit traces and the presence or absence of webbing. However presence or absence of webbing may be influenced by substrate: for example, traces of extant *Branta canadensis* (Canada Goose, replicas PRPRC NI2009.009, PRPRC NI2014.004) display webbing traces in those prints made in soft, water saturated substrate, while on firm or drier sediment webbing traces are not preserved. As the presence of webbing is highly variable due to substrate conditions we do not consider this a reliable character; however, there are some exceptions. In the case of a few distinctive ichnotaxa such as *Uhangrichnus* isp., and *Presbyornithiformipes* isp*.,* clear web traces have been consistently documented (see Lockley and Harris, 2010 for summary). Likewise, the webbing preserved in some ichnotaxa, such as *Sarjeantopodus* (Lockley et al., 2004) is diagnostic (contra Falkingham et al., 2009) and cannot be dismissed as unusual extramorphological preservation. In short, webbing is a useful character when present, but given its tendency to be inconsistently preserved it should not be the sole character used to differentiate among avian ichnotaxa.

The diagnoses of new ichnotaxa are sufficiently detailed to enable researchers to discriminate between two morphologically similar ichnotaxa. However, some of the earliest diagnoses of avian ichnotaxa are too general (i.e. *Avipeda* isp.) and are in need of future emendation, a task which is beyond the scope of this study. (Buckley et al., 2012; Buckley et al., in press; Lockley and Harris, 2010; McCrea et al., 2014).

Nearly all tridactyl semipalmate avian ichnotaxa described to date either possess nearly equal divarications between digits II-III and III-IV, or have higher divarications between digits III-IV and lower divarications between digits II and III (Buckley et al., 2012; Buckley et al., in press). The proportionally higher divarications between digits II-III consistently found in *Barrosopus* and *Paxavipes* prints make it obvious to distinguish these avian ichnotaxa from others that have been described to date. The high divarication between digits II-III observed in *Barrosopus* and *Paxavipes* may be due to the presence of a distinct osteological feature that is unique to the track-maker of these ichnogenera. Observationally, prints of *Paxavipes* are remarkably similar to those produced by extant members of Charadriiformes, particularly those of the modern Killdeer (*Charadrius vociferous*) (Elbroch and Marks, 2001; see Ichnomorphology and osteology).

Comparing Paxavipes to Barrosopus

A reported ichnotaxon with similar divarication to that of *Paxavipes babcockensis* nov. ichnogen. nov. isp. is *Barrosopus slobodai* from the Cretaceous (Campanian) Argentina (Coria et al., 2002). *Paxavipes babcockensis* possesses a significantly larger divarication between digits II-III than between digits III-IV ($p < 0.0001$). This divarication condition is similar to that of *Barrosopus slobodai* of Argentina (the sample of which is too small to test for a significant difference between digit divarications), although it is not temporally equivalent to *Paxavipes babcockensis* (Early Cretaceous: Albian).It is necessary to determine whether there is a significant quantitative morphologic difference between the *Paxavipes babcockensis* and *Barrosopus slobodai* tracks, as well as establishing the ichnofamily Paxavipedidae as distinct from ichnofamily Avipedidae. Multivariate analyses were used to test the qualitative separation between tracks of *Paxavipes babcockensis* and *Barrosopus slobodai*, and to demonstrate quantitative support for the novel ichnofamily Paxavipedidae as distinct from Avipedidae.

Discriminant analysis

Discriminant analyses on linear (footprint length and width, digits II-IV lengths and widths, pace and stride lengths) and angle data (digit divarication II-III and III-IV, pace angulation, footprint rotation) demonstrates that footprint groups formed by *Paxavipes babcockensis* and *Barrosopus slobodai* are significantly different ($p_{\text{same}} = 1.72 \times 10^{-03}$) with a 91.9% correct placement of individual footprints into the *a priori* groups of "*Paxavipes*" and "*Barrosopus*" (Fig. 4.14). Separate discriminant analyses on linear footprint and trackway data ($p_{\text{same}} = 6.14 \times 10^{-05}$; 91.8% separation) reveals a similar significant separation, while analysis on divarication and footprint angle data alone (p_{same} = 0.618; 56.3% separation) do not show significant separation between the prints of *Paxavipes babcockensis* and *Barrosopus slobodai*.

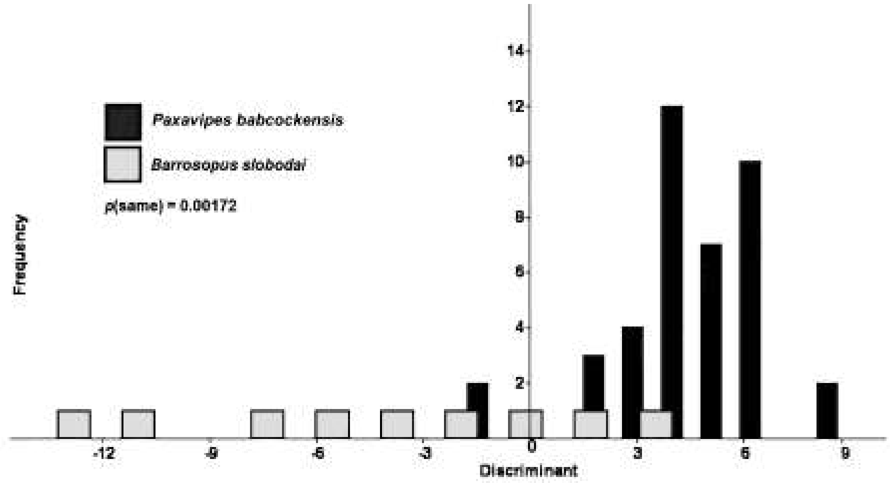


Fig. 4.14. Discriminant analysis comparing *Paxavipes babcockensis* (black) with *Barrosopus slobodai* (grey) using data from footprint length, footprint width, digit lengths, digit widths (D-II, D-III, D-IV), divarication (DIV II-III, DIV III-IV), pace length, stride length, pace angulation, and footprint rotation. The percentage of individual footprints correctly assigned to *Paxavipes babcockensis* and *Barrosopus slobodai* is 91.8%, indicating that the two track morphologies are distinct.

Separating Paxavipedidae and Avipedidae

The establishment of the ichnofamily Paxavipedidae is supported with both discriminant (Paxavipedidae vs. Avipedidae) and canonical variate (all ichnospecies separate) analyses. Discriminant analyses comparing Paxavipedidae (*Paxavipes babcockensis* and *Barrosopus slobodai*) to Avipedidae (*Aquatilavipes swiboldae,* *Aquatilavipes izumiensis*) show that 91.7% of all footprints were correctly identified to their assigned ichnofamilies and are significantly different (p_{same} = 1.98 X 10^{-26}, Fig. 4.15).

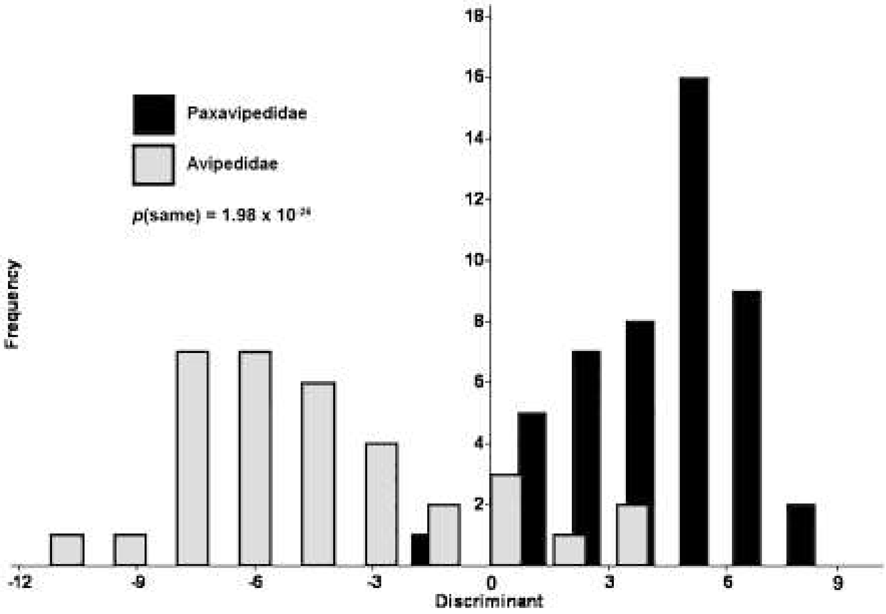


Fig. 4.15. Discriminant analysis on Avipedidae (*Aquatilavipes swiboldae*, *Aquatilavipes izumiensis*, grey) and the proposed Paxavipedidae (*Paxavipes babcockensis*, *Barrosopus slobodai*, black), using footprint length, footprint width, digit lengths (D-II, D-III, D-IV), and digit divarication (DIV II-III, DIV III-IV). Trackway measurements were excluded given the large amount of missing or unreported data. The two groups are significantly different (p_{same} = 1.98 X 10^{-26}), and 91.6% of individual footprints were correctly assigned to either Paxavipedidae or Avipedidae, respectively.

Canonical variate analyses (CVA) on data from the four ichnotaxa (excluding pace and stride measurements due to a large amount of missing data) shows that all four ichnotaxa are significantly different (Table 4.3, Fig. 4.16). Interestingly, *Aquatilavipes izumiensis* is almost isolated in morphospace from *Aquatilavipes swiboldae*, *Barrosopus slobodai*, and *Paxavipes babcockensis*. Examination of the data reveals that *Aquatilavipes izumiensis* has a much larger mean DIVIII-IV relative to DIVII-III when compared to *Aquatilavipes swiboldae*, *Barrosopus slobodai*, and *Paxavipes babcockensis* (Table 4.4).

	Paxavipes	*Barrosopus*	*A. swiboldae*	*A. izumiensis*
Paxavipes	-	1.49×10^{-03}	1.01×10^{-11}	8.45×10^{-22}
Barrosopus	1.49×10^{-03}	-	0.0211	2.31×10^{-06}
A. swiboldae	1.01×10^{-11}	0.0211	-	4.38×10^{-11}
A. izumiensis	8.45×10^{-22}	2.31×10^{-06}	4.38×10^{-11}	-

Table 4.3. Canonical variate analysis p_{same} results for footprint length (FL), footprint width (FW), digit lengths (DLII, DLIII, DLIV) and divarications (DIVII-III, DIVIII-IV) of *Paxavipes babcockensis*, *Barrosopus slobodai*, *Aquatilavipes swiboldae*, and *Aquatilavipes izumiensis*. All ichnospecies are significantly different from one another, although visually *Aquatilavipes swiboldae* groups more closely in morphospace with *Barrosopus slobodai* and *Paxavipes babcockensis* (**Fig. 16**): this is due to the much larger DIVIII-IV than DIVII-III in *Aquatilavipes izumiensis* (**Table 4**).

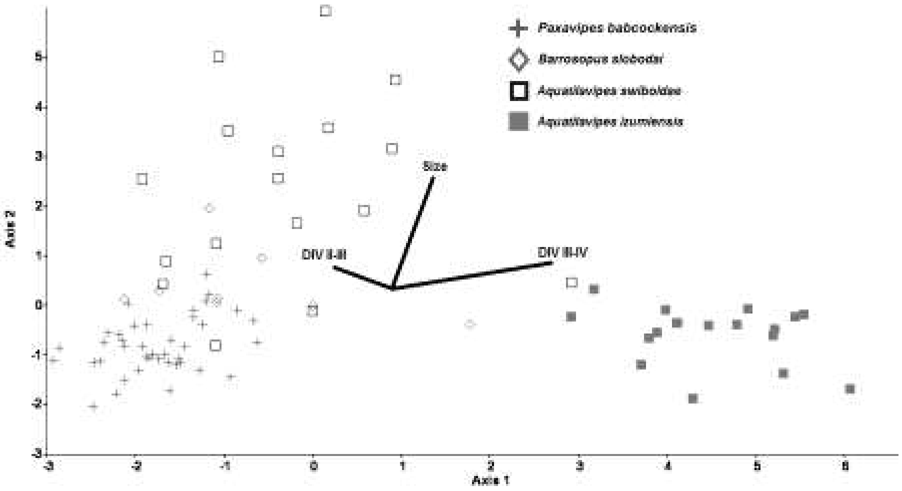


Fig. 4.16. Canonical variate analysis comparing *Paxavipes babcockensis* nov. ichnogen. nov. isp. (cross), *Barrosopus slobodai* (diamond), *Aquatilavipes swiboldae* (empty square), and *Aquatilavipes izumiensis* (solid square), using footprint length, footprint width, digit lengths (D-II, D-III, D-IV) and digit divarication (DIV II-III, DIV III-IV). In this analysis, axis 1 represents the relationship between the relative sizes of divarication between digits II – II and digits III - IV, and axis 2 represents footprint size. Treating the four ichnospecies separately in the analysis reveals that a) both *Paxavipes* and *Barrosopus* are smaller than *Aquatilavipes swiboldae*, and b) that the large difference between DIV II-III and DIV III-IV in *Aquatilavipes izumiensis* (DIV III-IV is larger) is greater than that seen in *Aquatilavipes swiboldae*: this is represented by the large DIV III-IV vector. This has the effect of “pushing” *Aquatilavipes swiboldae* over into the morphospace occupied by footprints of *Paxavipes* and *Barrosopus* that have a subequal DIV II-III vs. DIV III-IV, as *Aquatilavipes swiboldae* has DIV II-III that is almost equal to DIV III-IV (Table 4). Also, there are some footprints of *Aquatilavipes swiboldae* that display a DIV II-III that is larger than DIV III-IV: this is likely due to natural variation in digit divarication, or possibly a misidentification of “left” versus “right” prints, as no trackways were described by Currie (1981).

Ichnotaxon	Mean DIVII-III	Mean DIVIII-IV
Aquatilavipes izumiensis	52.8	67.3
Aquatilavipes swiboldae	58.1	58.6
Barrosopus slobodai	65.7	49.3
Paxavipes babcockensis	56.7	42.7

Table 4.4. Comparison of the mean divarications DIV II-III and DIV III-IV of *Aquatilavipes* (*Aquatilavipes izumiensis*, **Azuma *et al.* 2002**; *Aquatilavipes swiboldae*, **McCrea and Sarjeant 2001**) to *Barrosopus slobodai* **(Coria *et al.* 2002)** and *Paxavipes babcockensis* nov. ichnogen. nov. ichnosp. The mean divarication values show the main difference between the prints of Avipedidae and Paxavipedidae: that DIV II-III in Paxavipedidae is larger than DIV III-IV, while the opposite is seen in ichnospecies of the ichnogenus *Aquatilavipes*.

ICHNOMORPHOLOGY AND OSTEOLOGY

Digit divarication and osteology

One of the diagnostic characters of both *Paxavipes babcockensis* and *Barrosopus slobodai* (Paxavipedidae) is the possession of a much larger digit divarication II-III than that of III-IV. Because this feature is consistent among all footprints of *Paxavipes babcockensis*, this particular divarication condition is probably due to the morphology and relative position of distal metatarsals II, III, and IV, rather than an artifact of sediment-digit interaction. The mediolateral width of the intertrochlear notches between the distal ends of metatarsals II–III and III–IV (incisurae intertrochlearis medialis et lateralis, Baumel and Witmer, 1993), and the degree of plantar displacement of the distal ends of metatarsals II and IV from the saggital plane of the tarsometatarsus, should influence digit divarication.

Extant shorebirds provide modern analogs to investigate a possible osteological explanation for digit divarication in fossil avian footprints. However, unless there are observable differences between the tracks of extant shorebirds, it is fruitless to hypothesize on osteological causes of digit divarication conditions for extant shorebirds. Elbroch and Marks (2001) field guide to modern bird tracks and traces includes line drawings of the tracks of several species of modern shorebird. Using the same techniques to measure digit divarication as were used to document the tracks of *Paxavipes babcockensis* nov. ichnogen. nov. isp., digit divarications were measured from the line images of tracks of plovers (Charadriidae) and sandpipers (Scolopaciidae) (Elbroch and Marks, 2001; Table 4.5), and show that there is a significant difference in digit divarications II-III for the tracks of plovers, but not for sandpipers (Table 4.5). Although a small sample, it is sufficient to justify examining a hypothesized osteological cause for differences in digit divarication.

Taxon	**DIV II-III**	**DIV III-IV**
Piping Plover	71	71
Semipalmated Plover	62	62
Killdeer, trackway 1	72	51
Killdeer trackway 2	76	50
Black-bellied Plover	72	52
p_{same} = 0.027		
Least Sandpiper	58	51
Sanderling	65	45
Spotted Sandpiper	59	46
Dunlin #1	43	47
Dunlin trackway #2	57	58
Ruddy Turnstone	49	51
Lesser Yellowlegs	56	63
p_{same} = 0.361		

Table 4.5. Digit divarications measured from line drawings of individual tracks figured in Elbroch and Marks (2001) to test the observation that plovers (Charadriidae) have a significantly larger DIV II-III compared to DIV III-IV than do sandpipers (Scolopaciidae). Although the sample size is small, it does show that plover tracks have a significantly larger DIV II-III than DIV III-IV, whereas in sandpipers the DIV II-III and DIV III-IV are not significantly different. “Killdeer trackway 1” refers to the left trackway figured in Elbroch and Marks (2001:p.110), and “Killdeer trackway 2” refers to the right trackway figured in Elbroch

and Marks (2001:p.110); “Dunlin #1” refers to the left footprint figured in Elbroch and Marks (2001:p.109), while “Dunlin trackway #2” refers to the right prints figured in Elbroch and Marks (2001:p.109).

Examination of osteology specimens of the tarsometatarsi of species of extant shorebirds with a semipalmate foot morphology reveals two ways in which the distal ends of metatarsals II and IV are deflected from the midline of the tarsometatarsus (long axis of metatarsal III, Fig. 4.17, also see Falk et al., 2011), and how this deflection may potentially contribute to digit divarication in avian footprints. One form is the angle difference (herein referred to as the intertrochlear angle) between the trochlear groove of metatarsal II and IV, and the trochlear groove of metatarsal III (Fig. 17A). This angle captures both the medio-lateral length of the intertrochlear notch and the degree of latero- and medioplanter rotation of the distal ends of metatarsals II and IV, respectively. The second form is the medio- and latero-ventral displacement angle (hereon referred to as the plantar angle) from the distal ends of metatarsal III of the trochlear ends of metatarsals II and IV, respectively (Fig. 17B). Relatively large intertrochlear and plantar angles are hypothesized to result in a large digit divarication for the digits in question.

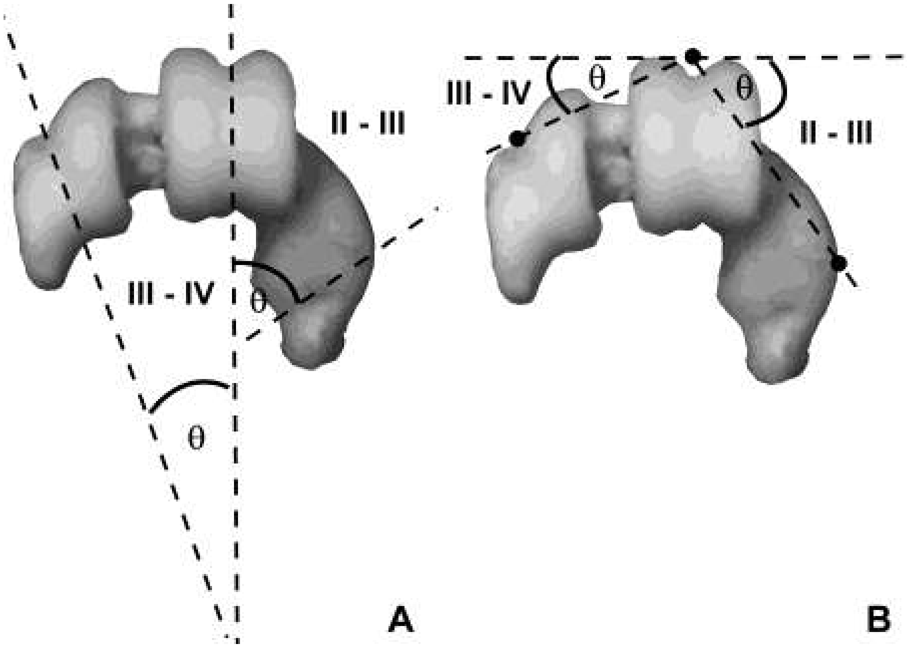


Fig. 4.17. Schematic diagram using *Caladris alba* BCPM 18305 showing measurements taken for intertrochlear angle (A) and plantar angle (B), both of which contribute to the orientation of attached pedal phalanges (digits) during foot registration. The measurements are based on the trochlear grooves of the metatarsals, which will provide not only a consistent and obvious landmark, but also provide the natural "midpoint" of the digit, as there is natural variation in the degree to which pedal phalanges can move medio-laterally.

Examination of the distal metatarsals of extant specimens of both Charadriidae (*Charadrius vociferus*, Killdeer; *Charadrius semipalmatus*, Semipalmated Plover) and the Scolopacidae (*Actitis macularia*, Spotted Sandpiper; *Calidris melanotos*, Pectoral Sandpiper; *Calidris alba*, Sanderling), show there is variation in the arrangement in the distal metatarsals on both specific and familial taxonomic levels (Figs. 18-19). All four study specimens have different intertrochlear and plantar displacement angles II-III, but intertrochlear angle II-III is larger for Charadriidae than Scolopacidae (Fig. 17). Also, there is little variation in intertrochlear angle III-IV among the four study specimens (Fig. 18). Discriminant analysis of Charadriidae and Scolopaciidae shows that they are significantly different based on their intertrochlear and plantar displacement angles (p_{same} = 3.38 X 10^{-04}, Fig. 19). The results are comparable with the observations made on the trackways depicted in Elbroch and Marks (2001).

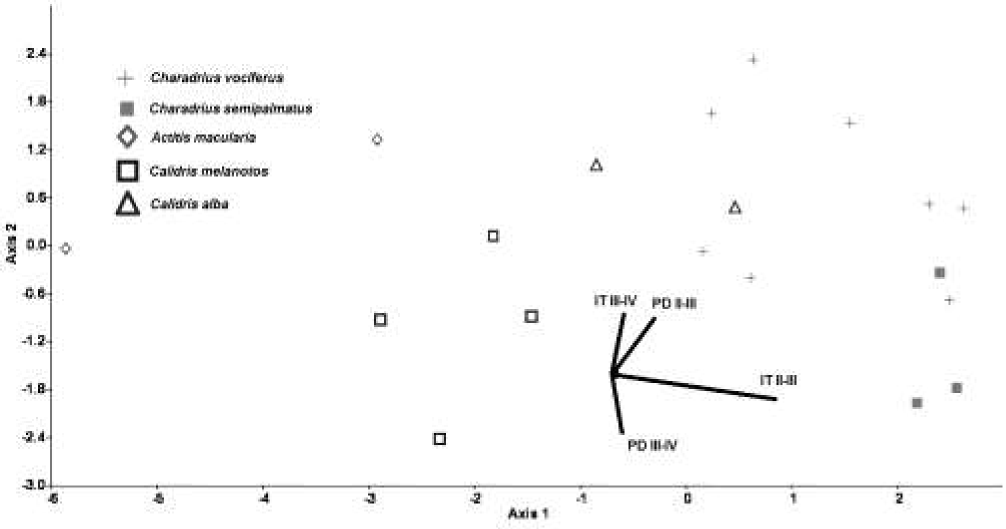


Fig. 4.18. Canonical variate analysis on extant Charadriidae (*Charadrius vociferus*, cross; *Charadrius semipalmatus*, filled square) and Scolopacidae (*Actitis macularia*, diamond; *Calidris melanotos*, empty square; *Calidris alba*, triangle) on intertrochlear (IT(Fig. 17A) and plantar displacement (PD) (Fig. 17B) angles measured from the distal tarsometatarsi of osteology specimens, with axis 1 representing the size of the angle of IT angle between digits II and III, and axis 2 representing the relationship between the relative sizes of the PD angle of digits II – III and IT angle of III – IV with the PD angle of digits III - IV. The specimens separate largely along the metatarsal II-III intertrochlear angle (axis 1), with both *Charadrius vociferus* and *Charadrius semipalmatus* having larger IT II-III than do the sampled scolopaciids. While it is not a large vector, Charadriidae separate from the Scolopacidae along the pedal displacement axis:

Charadriidae have a relatively larger pedal displacement angle II-III than Scolopaciidae. Larger IT and PD angles possibly contribute to the larger digit divarication (DIV) II-III relative to DIV III-IV observed in modern Charadriidae, and may also explain the larger DIV II-III seen in the track-maker of *Paxavipes*.

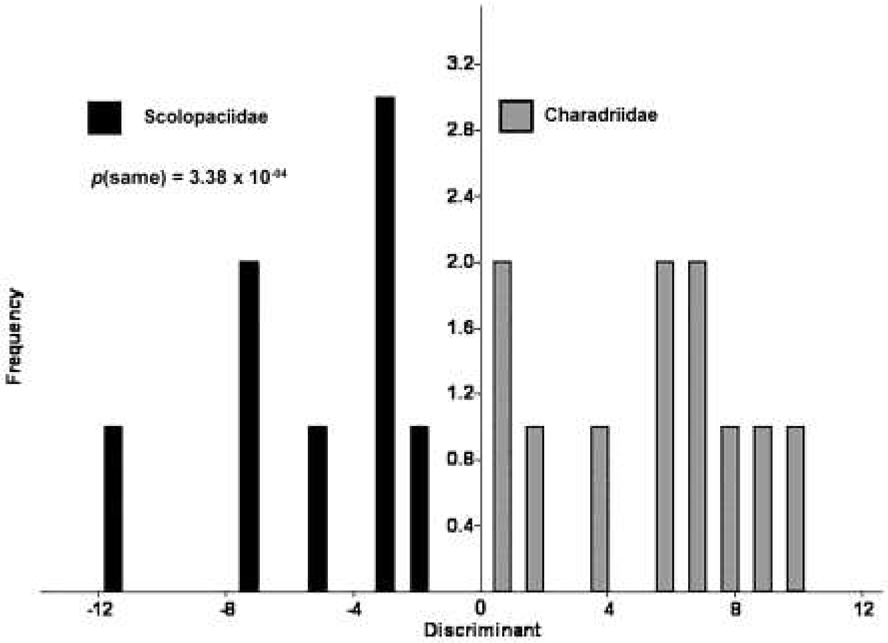


Fig. 4.19. Discriminant analysis graphical results comparing intertrochlear angle (IT, Fig. 17A) and plantar displacement angle (PD, Fig. 17B) data collected on the distal tarsometatarsii of extant Scolopaciidae (*Actitis macularia*, *Calidris melanotos*, *Calidris alba*), and Charadriidae (*Charadrius vociferus*, *Charadrius semipalmatus*). Charadriidae and Scolopaciidae are significantly different ($p_{\text{same}} = 3.38 \text{ X } 10^{-04}$), and there was 100% correct identification of each specimen to its *a priori* grouping of either Scolopacidae or Charadriidae. The arrangement of the distal tarsometatarsus appears to correlate the larger digit divarication II-III seen in the measured Charadriidae as compared to the measured Scolopaciidae.

DISCUSSION

Separation of Paxavipes babcockensis and Barrosopus slobodai

Multivariate analyses reveal that, despite the similarity in morphology, *Paxavipes babcockensis* and *Barrosopus slobodai* are discrete morphotaxa, supporting the assignment of *Paxavipes babcockensis* to a novel ichnogenus and ichnospecies. Although multivariate analyses are useful tools to support or refute the erection of a novel ichnotaxon, they cannot be the sole support for the new ichnotaxon.

Separation of Avipedidae and Paxavipedidae

Multivariate analyses reveal that there is statistical support for the erection of the novel ichnofamily Paxavipedidae as distinct from the existing ichnofamily Avipedidae based on comparisons with Cretaceous Avipedidae (*Aquatilavipes*).

Osteology and footprint morphology

Although the sample size in this study is small, there is an indication that some ichnological features, such as digit divarication, are the direct result of osteologic characteristics (see Falk et al., 2011 for ecomorphologic groupings.) Furthermore, the osteologic characters (i.e. intertrochlear angle and intertrochlear notch size) that result in ichnological differences may correlate to systematic differences. In this small study, intertrochlear angle II-III is much larger compared to intertrochlear angle III-IV in the specimens of Charadriidae (plovers) than in Scolopacidae (sandpipers). While the authors are not suggesting the track-makers of *Paxavipes babcockensis* were Early Cretaceous charadriids (Baker et al., 2007 show through multigene Bayesian analysis that Charadriidae diverged during the Late Cretaceous), the results suggest that we can predict that the morphology of the distal tarsometatarsus of the Early Cretaceous shorebird track-maker of *Paxavipes babcockensis* may be similar to that seen in extant plovers. The correlation of pedal osteology, ichnology, and systematics in extant shorebirds is currently being examined by LGB and RTM.

Dinosaur prints and skin Impressions

There are four non-avian prints on PRPRC 2005.15.001, three of which are produced by theropod track-makers, and one by an ornithopod track-maker. Two of the smaller theropod prints (PRPRC 2005.15.001.073 and 074) are referred to *Irenichnites gracilis*. Sternberg (1932) described *Irenichnites gracilis* as having a consistent separation between digit II and the rest of the print. The second digit impression of PRPRC 2005.15.001.073 is almost separate from the rest of the print. It is likely that all *Irenichnites gracilis* prints would exhibit some degree of digit II separation, depending on the qualities of the track-bearing substrate. The third theropod track (PRPRC 2005.14.001.076) is not sufficiently preserved to allow assignment to a particular ichnotaxon. The other non-avian track (PRPRC 2005.14.001.075) is a tetradacyl pes, probably of an ornithopod.

There are a small, but growing, number of reports of skin impressions from Cretaceous dinosaur footprints. To date these have been reported for hadrosaurs (Currie et al., 1991; Herrero and Farke, 2010; McCrea et al., 2014), ankylosaurs (McCrea et al., 2001; 2014), sauropods (Kim et al., 2010) and medium-sized theropods (Rylaarsdam, et al., 2006; Noe et al., 2014). Track specimens PRPRC 2005.15.001.074 and PRPRC 2005.15.001.075 possess skin impressions in the posterior part of the print (metatarsal pads and proximal digital pads). The skin impressions on the *Irenichnites gracilis* print (PRPRC 2005.15.001.074) are the first record of Early Cretaceous skin impressions on small theropod prints of which the authors are aware: see Noe et al. (2014) for a recent report of a 'mid' Cretaceous example from Colorado. The individual tubercles in the Canadian specimen are found on the metatarsal pad, as in the Colorado specimen, and on the proximal digital pads of some digits. The tubercles are small (>1 mm) and are ellipsoidal in shape (approximately 0.7 mm x 0.5 mm) (Fig. 4.6). The pattern of tubercles is not individual or random; rather, they are sequentially arranged in linear or wavy patterns reminiscent of friction ridge patterns present on the skin surface of other types of vertebrates, including humans.

The skin impressions on PRPRC2005.15.001.075 are on a tetradactyl ornithopod pes print (Fig. 4.20), similar to *Neoanomoepus* ichnosp (Lockley et al, 2009). However, PRPRC 2005.15.001.075 is partially covered by adhering sediment that obscures details necessary for precise ichnotaxonomic identification. The ornithopod print is significantly larger than the two *Irenichnites gracilis* prints (PRPRC 2005.15.001.073 and 074). The morphology of the individual tubercles present on PRPRC 2005.15.001.075 is distinct from those of the *Irenichnites gracilis* print (PRPRC 2005.15.001.074) in that the ornithopod tubercles are noticeably larger with an overall sub-round to elliptical shape (approximately 2.0 mm maximum dimension and up to 1.5 mm minimum dimension), and are variably polygonal (hexagonal, pentagonal, etc.) (Fig. 4.20).

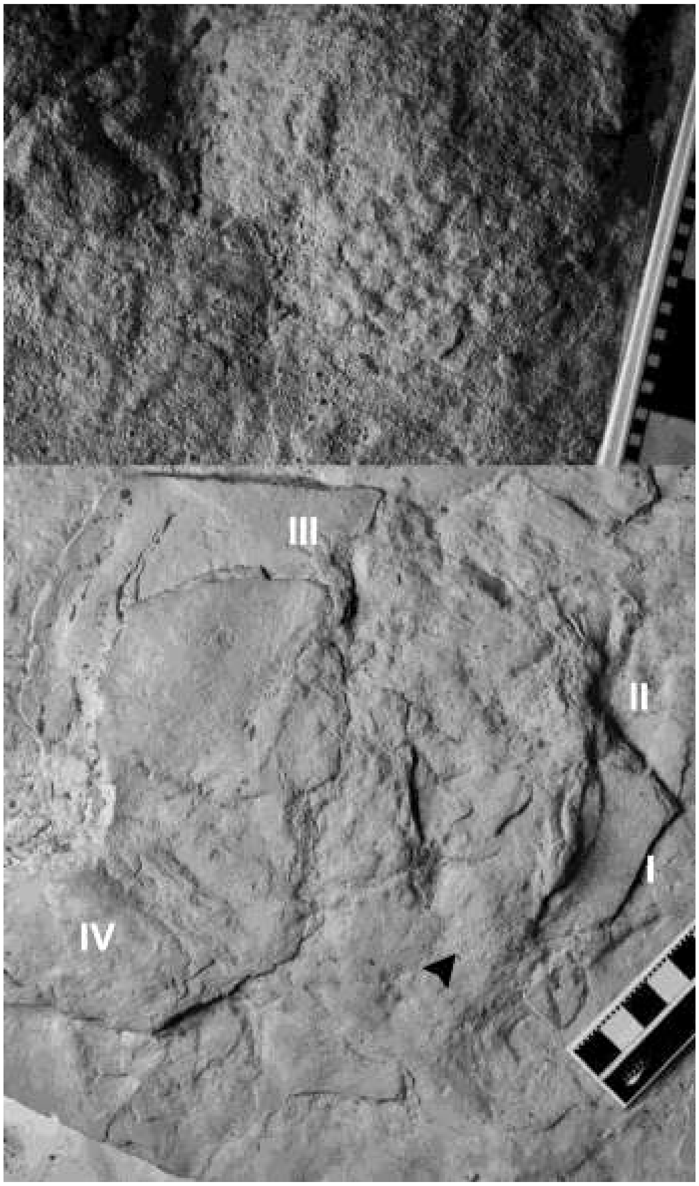


Figure 4.20. Top: Magnified view of skin impressions from the base of digit **II** of PRPRC 2005.15.001.075. Scale = 10 cm. Bottom: View of the tetradactyl print PRPRC 2005.15.001.075 with digits numbered. A black arrow shows the location of skin impression. Scale = 10 cm.

CONCLUSTIONS

The number of fossil vertebrate tracks found in the Boulder Creek Formation is sparse compared to many other track-bearing formations in western Canada (McCrea et al., 2014). Even with such a small sample of specimens which were described in this paper, several significant observations were made, especially in regards to the possibility of identifying osteological characters reflected in avian footprints. The number of avian prints on such a small track slab is great, yet the relative uniformity of these ichnites indicates a rather sparse avian diversity. Because this track slab has a surface area of only about 0.5 m2 it is unlikely that the record of the vertebrate ichnofauna preserved on it is a complete representation of the vertebrate diversity from this time.

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5.0 VERTEBRATE ICHNOLOGY

The contents of this chapter have been re-formatted from the chapter "21. Vertebrate Ichnology" which was published in the book "Dinosaur Provincial Park: a spectacular ancient ecosystem revealed" in 2005. This paper was a result of a collaborative effort and in order of priority these are: Richard T. McCrea, Philip J. Currie, S. George Pemberton. The candidate conceived this project and wrote the majority of the paper (>90%).

INTRODUCTION

The vertebrate fauna of Dinosaur Provincial Park is among the best known and best-studied in the world, with a history of research spanning two centuries (Coy, 1997; Spalding, 1988). Numerous dinosaur skeletons and extensive bonebed discoveries were made during this time, but virtually no fossil vertebrate tracks were reported within the area that is now Dinosaur Provincial Park. It was only in the last two decades of the twentieth century that the first fossil footprints were discovered in Dinosaur Provincial Park. Two isolated footprints were collected on two separate occasions; one *in situ* near a bone quarry, and another that was out of context. Recent observations near bone quarries have revealed the presence of additional *in situ* prints. A brief footprint prospecting trip early in 2003 led to the discovery of a locality with several natural casts of dinosaur footprints. These finds suggest that there is some potential for further footprint discoveries within Dinosaur Provincial Park.

The sediments of the Judith River Group (upper Campanian) are well exposed and contain the remains of many fossil vertebrates (Currie, 1989a; Eberth, 1997; Ryan and Russell, 2001), including the dinosaurs for which the park is named. Vertebrate skeletal remains are well known from the Oldman and Dinosaur Park Formations of the Judith River Group, but the record of fossil vertebrate footprints from Dinosaur Provincial Park is almost non-existent in the literature. However, fossil vertebrate footprints do occur in Dinosaur Provincial Park (Currie, 1989a, 1989b; Danis, 1986), though they have not been found in the type of sediments where footprints are typically preserved, nor have they yet been found as part of long trackways. To date, all of the fossil footprints found in Dinosaur Provincial Park were produced by dinosaur track-makers. Both theropod and ornithopod dinosaur tracks have been collected, though several ornithopod footprint specimens remain *in situ*.

The first fossil footprint reported from Dinosaur Provincial Park was found in 1981 (Currie, 1989b). The specimen (TMP 81.34.1), a natural cast, was discovered *in situ* (Fig. 5.1), adjacent to Quarry 155 (Currie, 1989b; Danis, 1986). The specimen was excavated (Fig. 5.2), jacketed and removed, and is now on display at the Dinosaur Provincial Park field station (Fig. 5.3). A second incomplete specimen was found *in situ* less than two meters from TMP 81.34.1, both likely part of the same trackway (Currie, 1989b), though no further prints were found in the area at that time. Specimen TMP 81.34.1 is a natural cast of a large, tridactyl footprint (Fig. 5.4), but with such a paucity of specimens it is prudent to resist referring this specimen to any existing ichnotaxon.

Fig. 5.1. A natural cast of a tridactyl dinosaur footprint (TMP 81.34.1) found *in situ* near Quarry 155 (rock hammer for scale). PN 81.15.01 courtesy of the Royal Tyrrell Museum of Palaeontology and Alberta Community Development.

Fig. 5.2. Excavating TMP 81.34.1 near Quarry 155. PN 81.15.13 courtesy of the Royal Tyrrell Museum of Palaeontology and Alberta Community Development.

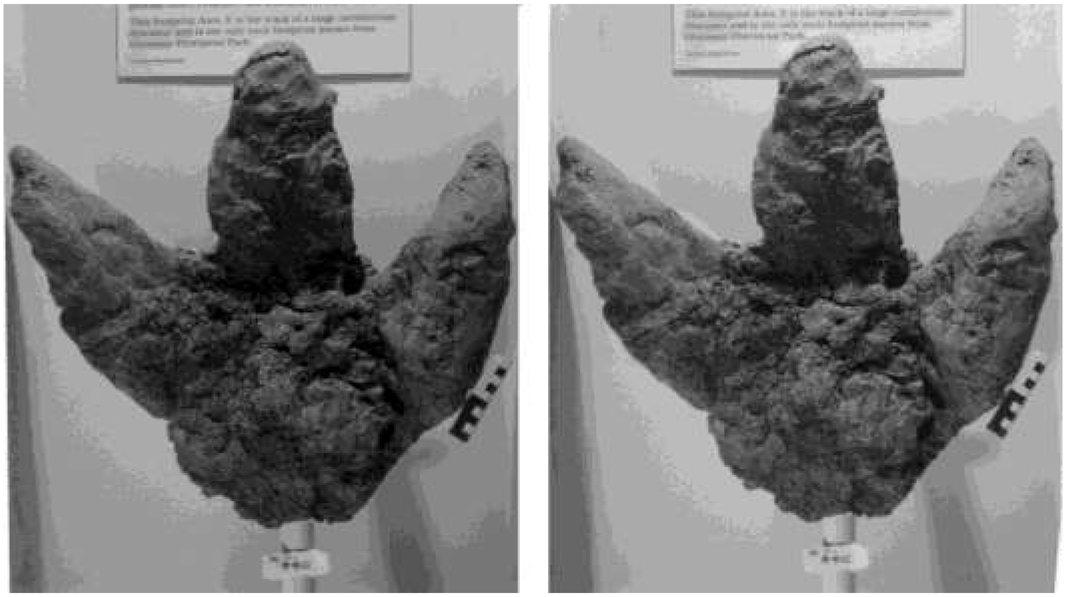


Fig. 5.3. Stereo pair of TMP 81.34.1 (10 cm scale).

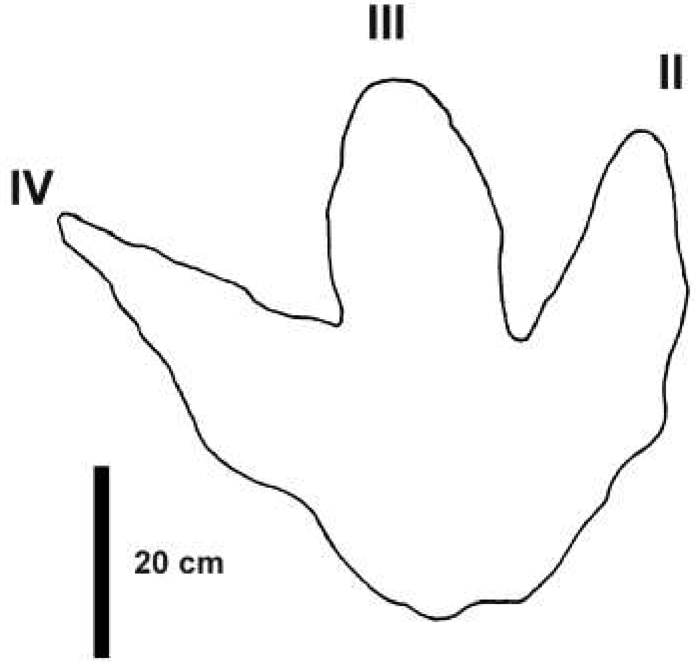
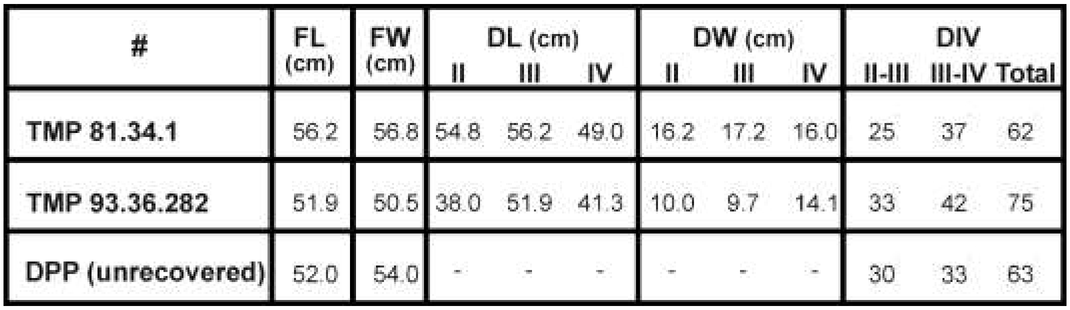


Fig. 5.4. Outline drawing of TMP 81.34.1.

There are similarities between TMP 81.34.1 and ichnotaxa such as *Amblydactylus* and *Caririchnium*, which are both attributed to large ornithopods. The dimensions of TMP 81.34.1 (Table 5.1) are consistent with that of a large ornithopod footprint, probably a hadrosaur, a group whose skeletal remains (representing many species) are commonly found in Dinosaur Provincial Park (Ryan and Russell 2001). The subequal lengths of digits II and IV and the two indentations in the heel of TMP 81.34.1 are characteristic of ornithopod prints. The measurements of digit divarication indicate that the print is likely a natural cast of a right print, based on the criteria that digits II and III are usually closer together than digits III and IV.



#	FL (cm)	FW (cm)	DL (cm)			DW (cm)			DIV		
			II	III	IV	II	III	IV	II-III	III-IV	Total
TMP 81.34.1	56.2	56.8	54.8	56.2	49.0	16.2	17.2	16.0	25	37	62
TMP 93.36.282	51.9	50.5	38.0	51.9	41.3	10.0	9.7	14.1	33	42	75
DPP (unrecovered)	52.0	54.0	-	-	-	-	-	-	30	33	63

Table 5.1. Dimensions of some Dinosaur Provincial Park footprint specimens. Specimen “DPP (unrecovered)” is the ornithopod print from Fig. 5.12.

The composition of TMP 81.34.1 is primarily an iron-rich sediment, typical of the many concretions found in Dinosaur Provincial Park. The rusty coloration of the footprint is different from the sediment layers immediately above or below it. The preservation of this specimen does not seem to be due to a simple infill of sediment, but is rather the product of a chemical reaction or reactions that concentrated iron minerals to form a concretion-like footprint cast. The action of the track-making dinosaur making the original impression in the substrate may have produced conditions favorable for the concentration and consolidation of the iron minerals that form the footprint cast.

More than a decade later, an eroded natural sandstone cast of a large tridactyl footprint (TMP 93.36.282), was found within a rock garden adjacent to the Dinosaur Provincial Park field station (Figure 5.5 and 5.6). The exact provenance is unknown, though it is certain that the rocks in the rock garden were native to Dinosaur Provincial Park. Phalangeal pad features are present on the digits, but are most obvious on digit III (Figure 5.7). The different lengths of digits II and IV, the indentation on the inner side of the print, along with the slenderness of the digits, the greater overall length to width proportions of the print, and the presence of sharp claws (Figure 5.7) suggest a theropod affinity for the track-maker (Table 5.1).

Fig. 5.5. A natural cast of a tridactyl dinosaur footprint (TMP 93.36.282) found in the rock garden near the DPP field station (10 cm scale).

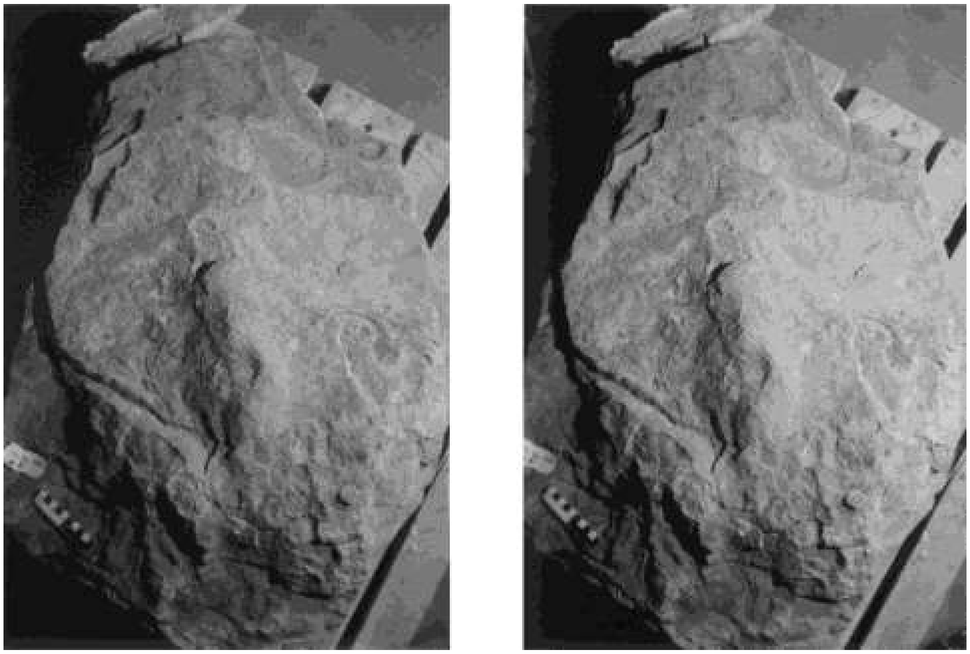


Fig. 5.6. Stereo pair of TMP 93.36.282 (10 cm scale).

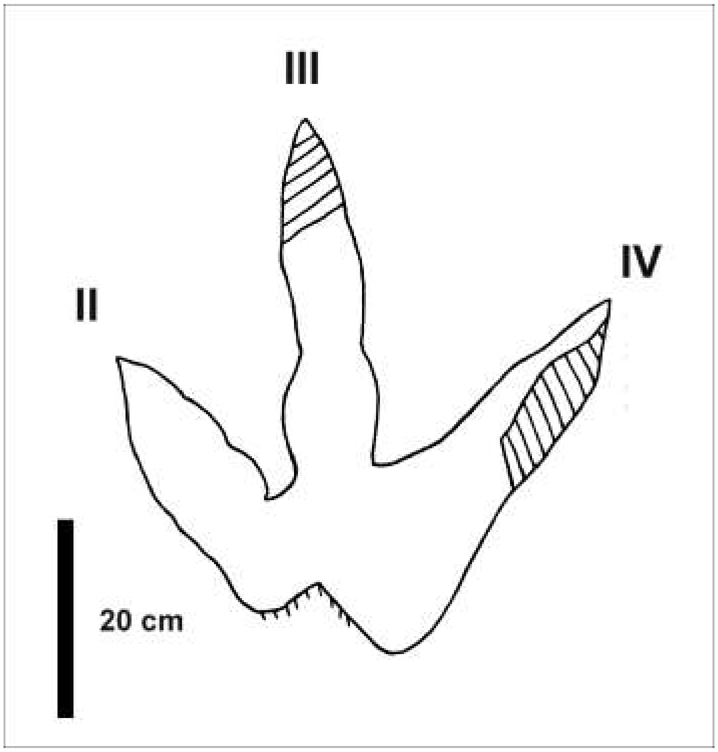


Fig. 5.7. Outline drawing of TMP 93.36.282.

The preservation of TMP 93.36.282 is evidently the result of an infill of sediment into the track-maker's original footprint which eventually became lithified to make the natural cast. While this type of preservation is typical of many fossil footprint localities, TMP 93.36.282 is, currently, the only specimen preserved in this way from Dinosaur Provincial Park. The rest of the known fossil footprints are either concretionary in nature, or are in sediments that are not consolidated enough to survive any length of exposure to the elements.

At this time, TMP 81.34.1 and TMP 93.36.282 are the only two footprints that have been collected from Dinosaur Provincial Park, though additional finds have recently been made. At Quarry 155, where TMP 81.34.1 and a partial print were previously found (Currie 1989b; Danis 1986), the second author found a tridactyl footprint eroding out of the sediment (Figure 5.8 and 5.9). This print is similar in lithologic composition to TMP 81.34.1 and likely formed in the same way. Only two well-preserved digits are exposed, while the tip of a third digit has just barely begun to erode out of the substrate. Though most of the footprint is still covered it appears to be the print of a large ornithopod, but a more reliable identification would only be possible once the specimen is excavated completely.

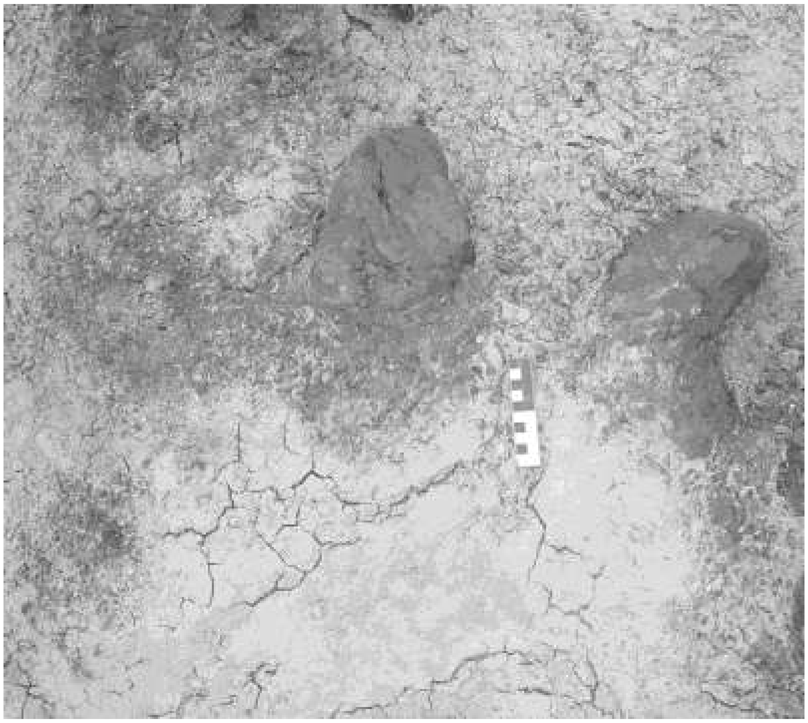


Fig. 5.8. Top, posterior view of an *in situ* tridactyl print eroding out of sediment at DPP Quarry 155 (10 cm scale).

Fig. 5.9. Top, anterior view of an *in situ* tridactyl print eroding out of sediment at DPP Quarry 155 (10 cm scale).

A second tracksite near Quarry 4 yielded the heavily weathered remnants of a few *in situ* prints (Figure 5.10 and 5.11). These prints were of similar preservation to those from Quarry 155, but were either less well consolidated, or had been exposed to the elements for a much longer time before being recognized. Only a faint outline is left of the few prints at Quarry 4 (Figure 5.11), and no confident identification can be made from the remains.

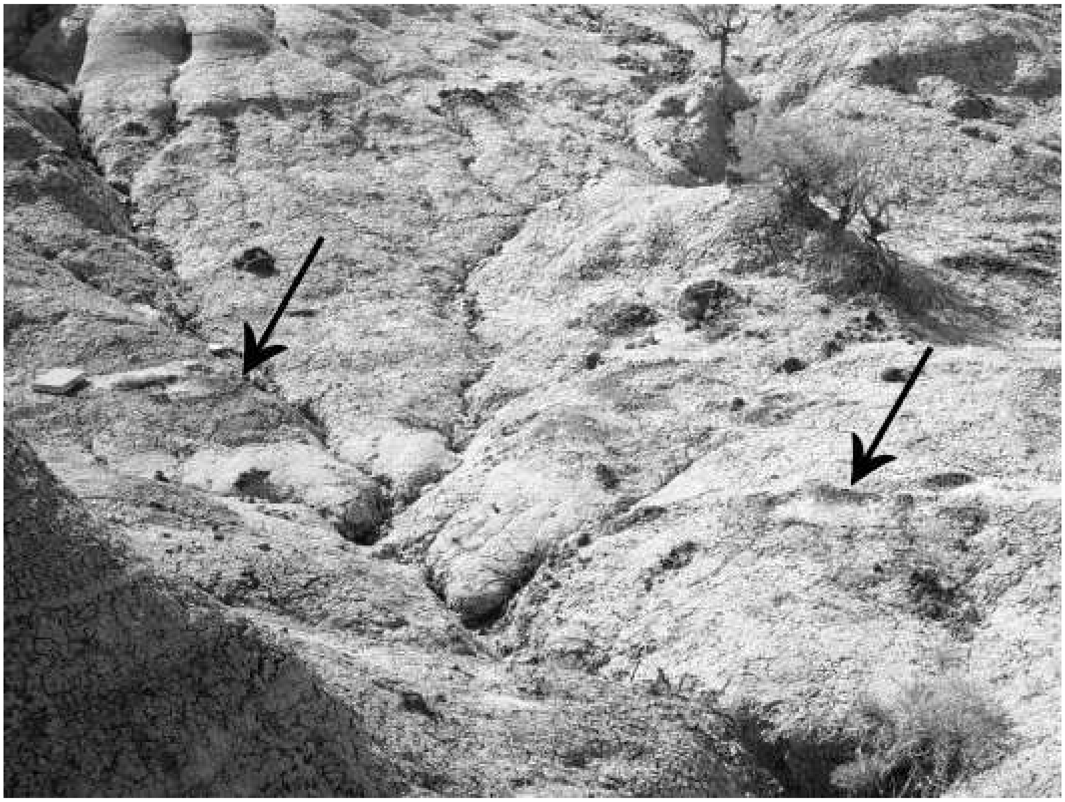


Fig. 5.10. *In situ* prints (arrowed) from DPP Quarry 4 (field notebook in left side for scale - 19 cm long).

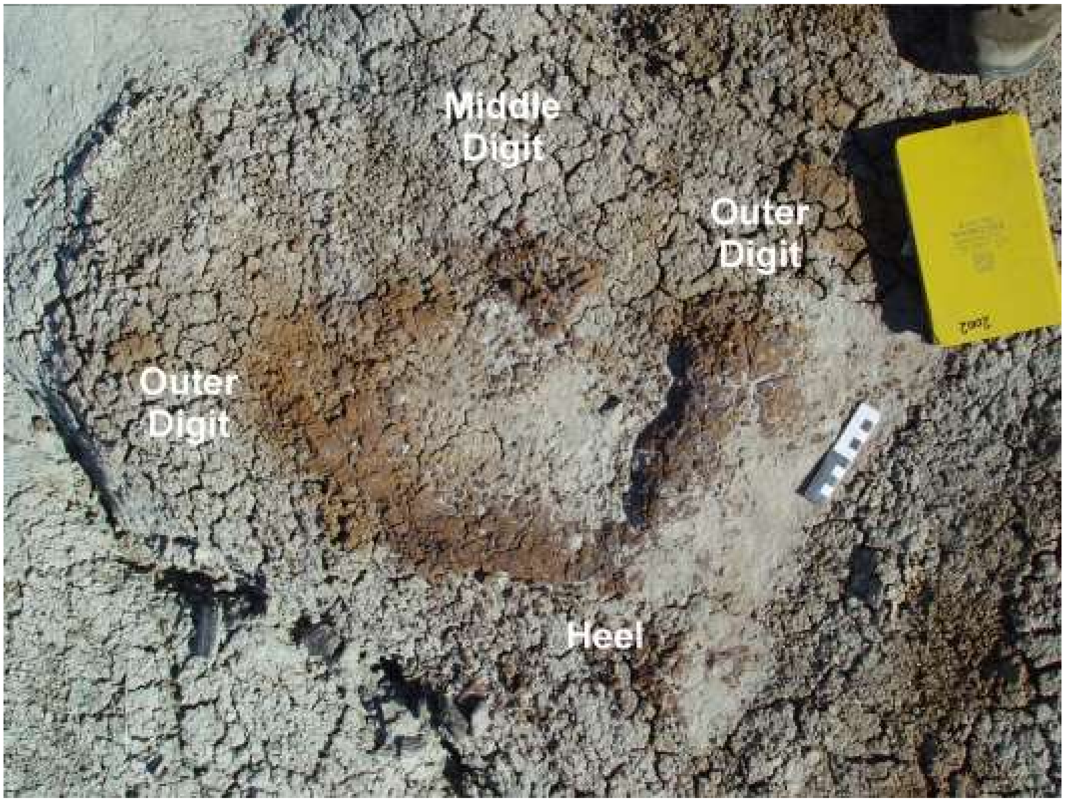


Fig. 5.11. A badly eroded print from DPP Quarry 4 (10 cm scale).

A third tracksite, found near the *Corythosaurus* interpretive station of Dinosaur Provincial Park early in 2003, consists of at least eight *in situ* footprint casts of concretion-like composition (similar to those from Quarries 4 and 155). These prints were found over a relatively large area and have been wholly uncovered by erosion (presumably wind and water). Only two were easily identifiable as footprints (Figures 5.12 and 5.13), the rest had fallen to pieces from exposure (Figure 5.14), but still had recognizable features including general outline, or fragments of digits (Figure 5.14 - upper left). The two good quality footprints specimens (Figures 5.12 and 5.13) appear to have been produced by large ornithopods. The dimensions of the best preserved print (Figure 5.12) also supports a large ornithopod designation. No trackway pattern could be discerned from this site at the time of its discovery. There are plans to return to this site to fully document it.

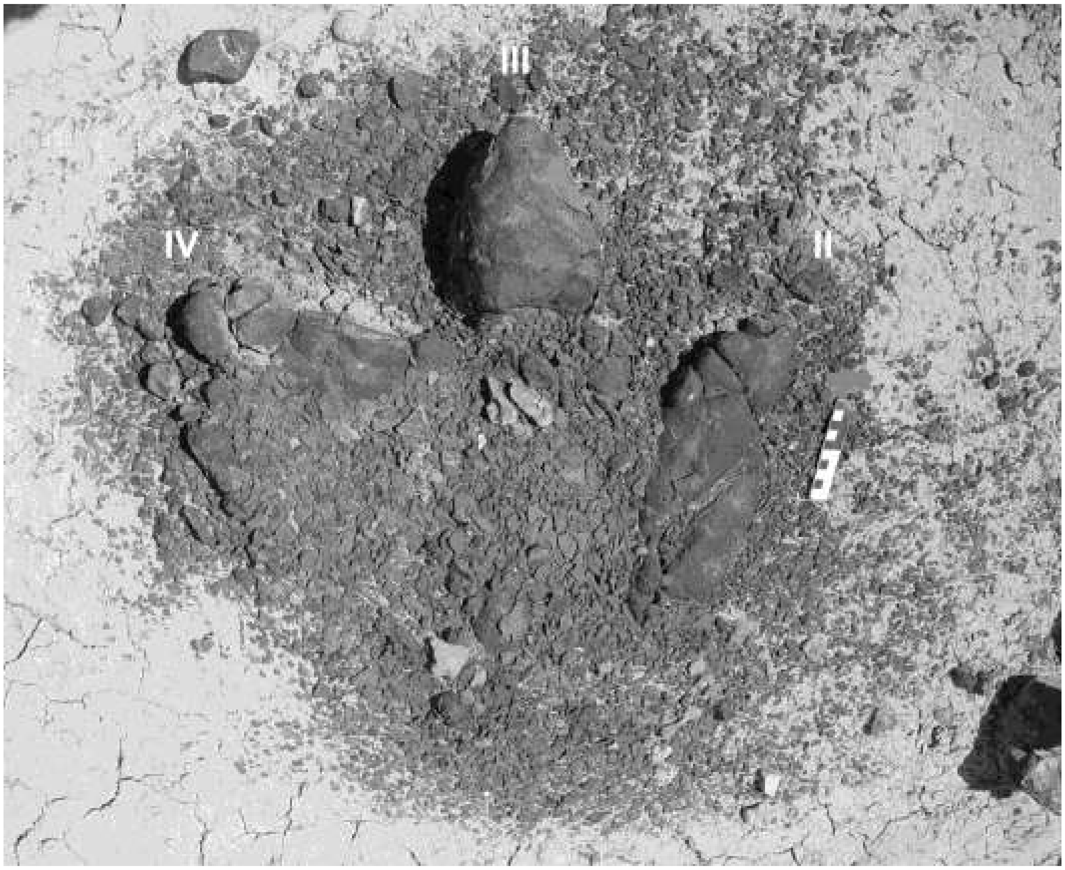


Fig. 5.12. A single large ornithopod footprint cast (presumed left print) found *in situ* near the *Corythosaurus* interpretive station in Dinosaur Provincial Park (10 cm scale).

Fig. 5.13. A second specimen of a large ornithopod footprint cast (partially eroded) found *in situ* near the *Corythosaurus* interpretive station in Dinosaur Provincial Park.

Fig. 5.14. Eva Koppelhus and the second author taking notes at new tracksite (the black arrow is pointing at complete footprint from Fig. 5.13, and the white arrows indicate locations of badly eroded footprint remnants).

DISCUSSION

Vertebrate ichnology research in Dinosaur Provincial Park is in a preliminary stage. The finds reported above suggest that there may be additional fossil footprint finds in the future. The concretion-like composition of many of the Dinosaur Provincial Park footprints appears to be the dominant mode of preservation for the prints found to date. This is a type of preservation that is not typical of most of the better known tracksites around the world, and as a result such tracks are not readily recognizable. Fossil footprints are often overlooked in the best of circumstances, or go unrecognized because of their sedimentological nature. Palaeontologists and geologists adopt specific search patterns suited for their particular field of endeavor and may unintentionally overlook such subtle fossils like footprints. The majority of footprints found to date appear so similar to the non-descript concretions that are commonly found in Dinosaur Provincial Park that it is hardly surprising so few prints and tracksites have been found in spite of the long history of research in the park. It is hoped that this writing will make other researchers more aware of the mode of preservation of Dinosaur Provincial Park’s fossil footprints, improve their search image, and make them look a little more closely at the shapes of concretions they encounter in the future.

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6.0 A ‘TERROR OF TYRANNOSAURS’: THE FIRST TRACKWAYS OF TYRANNOSAURIDS AND EVIDENCE OF GREGARIOUSNESS AND PATHOLOGY IN TYRANNOSAURIDA

The contents of this chapter have been re-formatted from a paper of the same title published in the journal *PLOSONE*, Volume 9, pp. 1-13 on July 30, 2014. This paper was a result of a collaborative effort and in order of priority these are: Richard T. McCrea, Lisa G. Buckley, James O. Farlow, Martin G. Lockley, Philip J. Currie, Neffra A. Matthews, and S. George Pemberton. This project was conceived by the candidate who wrote the majority of the paper (>70%).

INTRODUCTION

Reports of footprints attributable to tyrannosaurids are rare (Lockley et al., 2011) and although footprints of tyrannosaurids occur in Mongolia (Currie et al., 2003), the western United States (Lockley and Hunt, 1994; Lockley et al., 2004; 2011) and western Canada (Currie et al., 1991; McCrea et al., 2005; Farlow et al., 2009; Fanti et al., 2013), they were only known from single footprint occurrences. The lack of trackways attributable to tyrannosaurids left a conspicuous gap in locomotor and behavioral data for this group. Hypotheses on locomotion (Farlow et al., 1995; Paul, 1998; Hutchinson and Garcia, 2002; Henderson, 2003; Gatesy et al., 2009) and behavior (Currie, 1998; Currie and Eberth, 2010) of tyrannosaurids have been based solely on osteological material. There has never been an opportunity to test these hypotheses against a preserved record of tyrannosaurid movement, including possible group behavior. Here, we describe the first trackways (as opposed to rare and controversial isolated footprints) attributable to tyrannosaurids, as a new ichnotaxon (ichnogenus and ichnospecies) within a newly established ichnofamily. These trackways occur in the Upper Cretaceous (upper Campanian - lower Maastrichtian) Wapiti Formation in northeastern British Columbia. Three trackways (Fig. 6.1) occur on a 60 m x 3 m bedding plane exposure along with individual prints of large ornithopods (*Hadrosauropodus* isp.) and smaller theropods (*Saurexallopus cordata*) (McCrea et al., 2014). The track-layer is composed of fine-grained silty-sandstone with significant clay content and visible carbonized plant fragments. It is likely that the high clay content of the substrate allowed sediment displaced by the large theropod feet to be compacted rather than extruded to form sediment rims around the footprint, which can obscure footprint features. The compaction of the clay was probably an important factor in preventing deeply impressed tyrannosaurid prints from collapsing after the removal of the track-makers' feet.

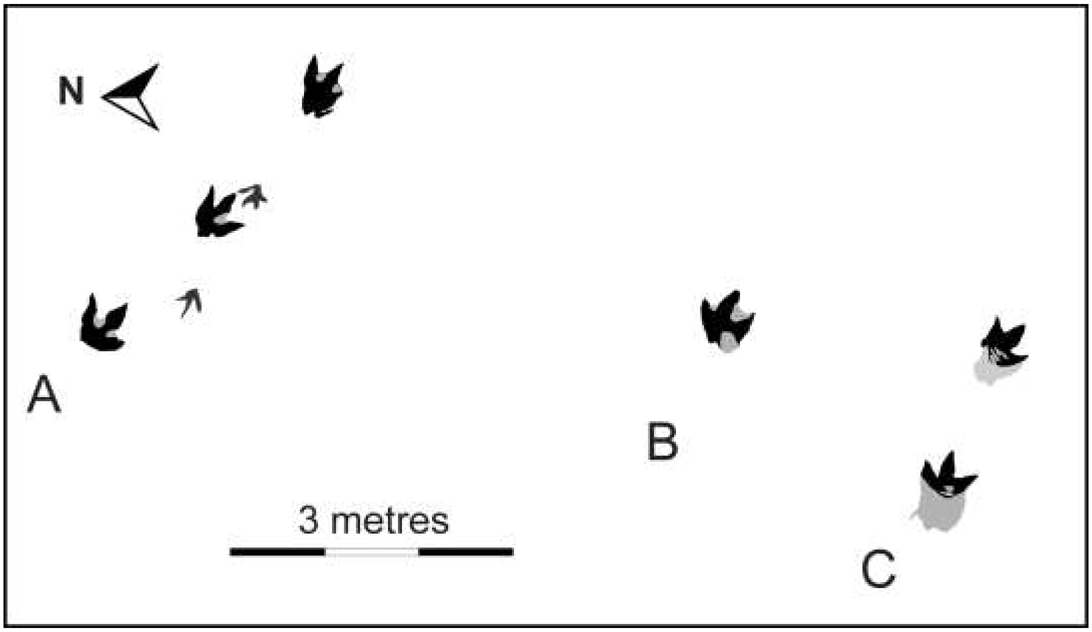


Fig. 6.1. Trackway map. A portion of the tracksite showing three parallel trackways of *Bellatoripes fredlundi* and a partial trackway of a smaller theropod *Saurexallopus cordata*. Trackway A: PRPRC 2011.11.001; Trackway B: PRPRC 2012.04.002; Trackway C: PRPRC 2012.04.003. This trackway map was produced by tracings taken from the site, but outlines of the prints were produced by studying the silicone moulds of all the trackways at the Peace Region Palaeontology Research Centre (PRPRC). Trackway B has two tracks (only the first one is figured, the second is a pace length in front), but a debris slide covered the second print shortly after discovery at the end of the field season.

Despite the large size of the footprints of the track-makers, there were only minor disturbances of sediment between digit impressions, and no detectable development of displacement rims around the tracks. The track-bearing substrate was the original surface as evidenced by the presence of skin impressions (consisting of small, indistinctly-shaped tubercles) and striations in several of the tyrannosaurid tracks. Skin impressions also occur in some of the *Hadrosauropodus* isp. tracks on the same surface several meters away. The track-bearing bed was observed to be overlain by a 30 cm thick layer of kaolinite. At present it is unclear if this kaolinite layer is uniformly distributed over the entire track-bearing surface.

The first two prints of Trackway A were discovered in early October, 2011 by Mr. Aaron Fredlund, a local guide-outfitter. The third print was excavated by Peace Region Palaeontology Research Centre (PRPRC) staff and volunteers in late October of the same year (Fig. 6.2). Trackway A consists of three large tridactyl footprints with several characteristics that allow identification of the track-maker as a large theropod. These include large terminal claw impressions, FL (footprint length) > FW (footprint width), the three digit impressions extending roughly the same distance distally from the footprint heel (but with III longest and IV generally longer than II), presence of a clawed hallux impression on one of the prints, as well as having long pace and stride with a high pace angulation. Two additional trackways (Trackway B and C) were discovered by excavating in the area immediately south of Trackway A in August, 2012 (Fig. 6.3).

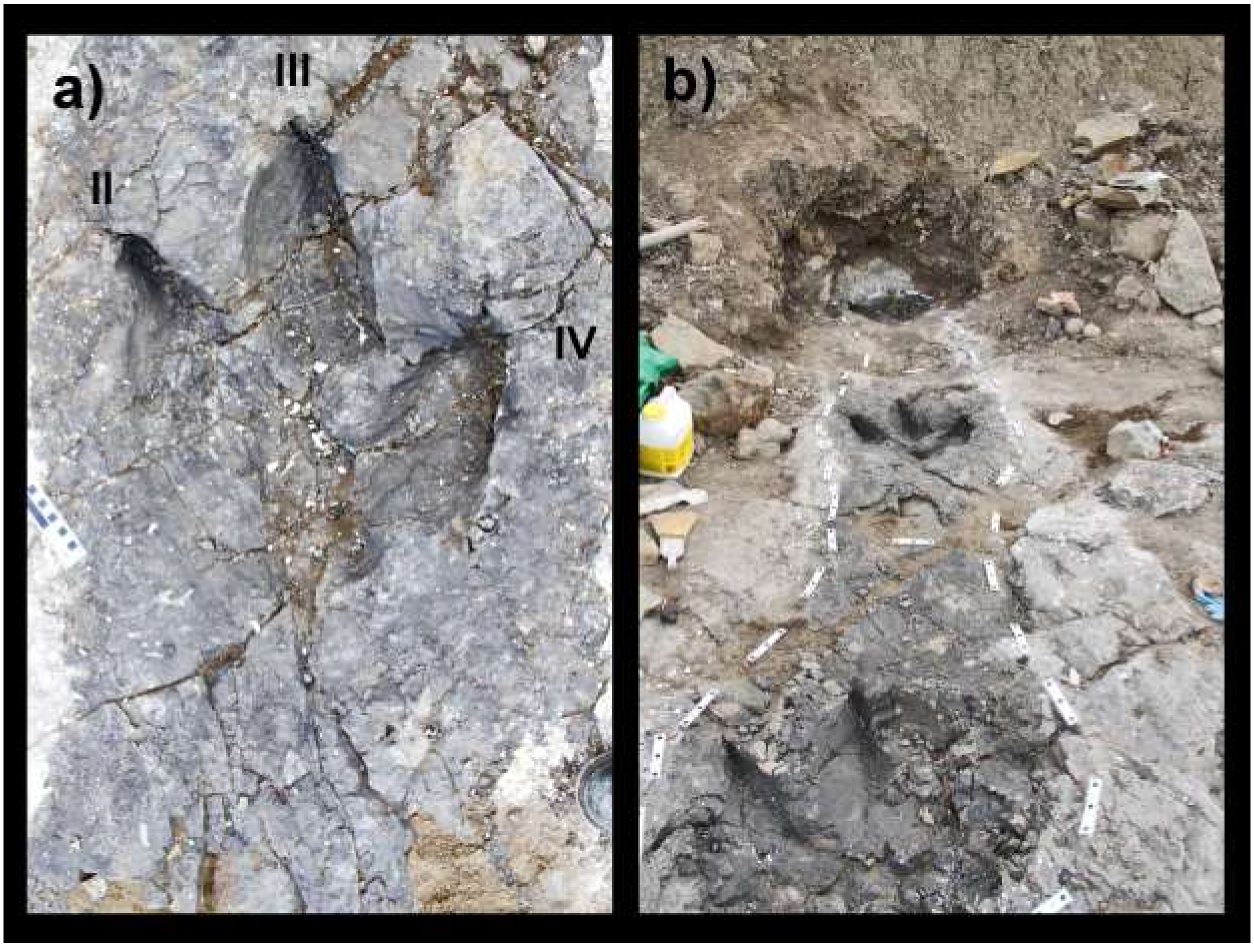


Fig. 6.2. *In situ* Trackway A images. a) Print #2 of Trackway A (*in situ*) - PRPRC 2011.11.001 (right); b) Trackway A (*in situ*) view to the east of prints #1-3. Note the thick layer of kaolinite in the freshly excavated area in front of print #3.

Fig. 6.3. Excavation of Tracksites (A: Trackway A; B: Trackway B; C: Trackway C). View toward the north from near Trackway C (foreground with LGB excavating and silicone mould of print #1 at the bottom of the figure), Trackway B is located in the center of the image and the silicone mould of Trackway B, print #1 is visible. Trackway A is covered in a green tarp near the top left of the image. The headings of the trackways are from left to right with other tracks likely buried by sediments forming a steep cliff.

MATERIALS AND METHODS

Molding and Measurements

No permits were required for this study. The original ‘Trackway A’ (PRPRC 2011.11.001) was molded (PRPRC 2011.11.001M) using platinum-cure silicone reinforced with a sectional plaster support jacket constructed at the site. A 1:1 replica of the trackway was cast (PRPRC 2011.11.001MC) using fiberglass-reinforced plaster (FGR 95). Linear and angle data were compiled from measurements taken directly from the silicone mold (Fig. 6.4). Measurements were taken of the original *in situ* trackway, but due to the degree to which the digit impressions undercut the track-bearing surface, these measurements were not accurate. The most accurate measurements were made possible through the study of the replica mold (PRPRC 2011.11.001M), where all track morphologies and trackway features are accessible to workers. Measurements of Trackways B and C were made from their silicone molds (PRPRC 2012.04.002M and PRPRC 2012.04.003M, respectively).

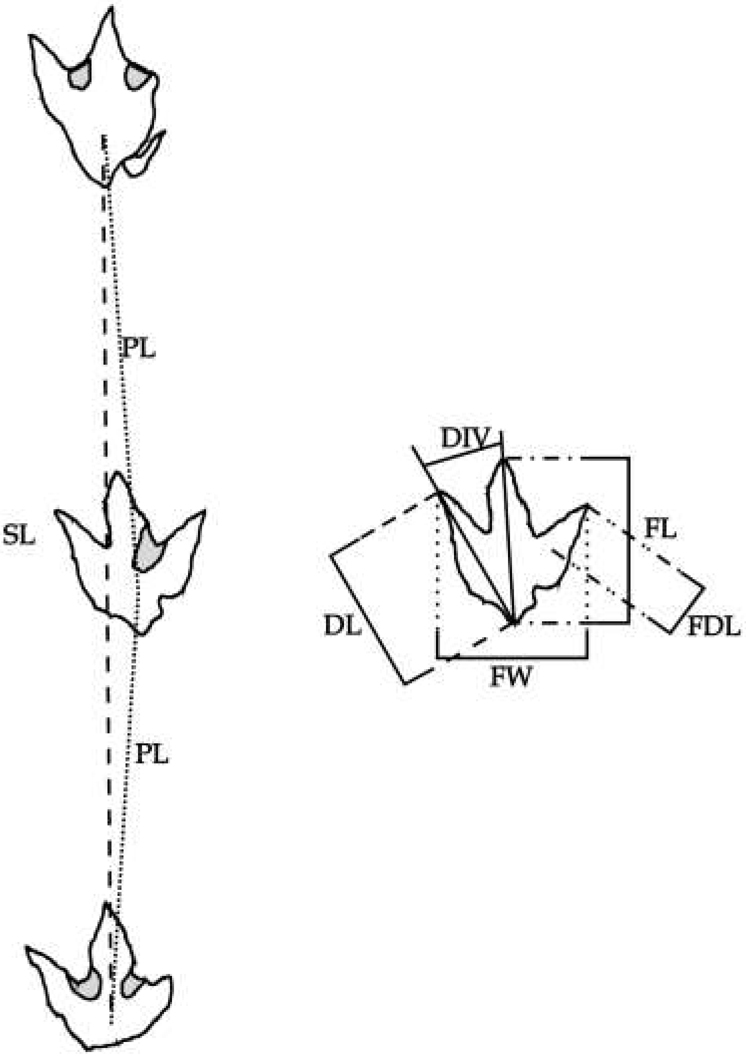


Fig. 6.4. Methods of trackway and footprint measurements used in this study. **DIV**, digit divarication; **DL**, digit length; **FDL**, free digit length; **FL**, footprint length; **FW**, footprint width; **PL**, pace length; **SL**, stride length.

Images for photogrammetric analysis were obtained with a Canon EOS 7D. Resulting image files were processed in Agisoft Photoscan Professional (v 1.0.4) and Cloud Compare (v 2.5.3).

A new quantitative method for comparing the robustness of tracks was developed by manually measuring the area (cm^2) of individual footprints (excluding the hallux impression and extra-morphological features, e.g. caudal-lateral drag-marks, etc.), and calculating a ratio (Footprint Area to Length Ratio; units in cm) by dividing the footprint area (cm^2) by its length (cm). Creating an area to length ratio allows for quantitative comparisons of the overall robustness of tracks of similar morphology (i.e. tridactyl tracks) of all sizes. The Footprint Area to Length Ratio uses Thulborn's (1990) track surface area calculation while accounting for the track surface area occupied per linear track length, which can be compared across dinosaurian ichnotaxa.

Calculations of Track-Maker Velocity and Age

Relative velocities of the track-makers were calculated using formulae from Thulborn and Wade (1984) and Alexander (1976) using the formula

(1) $S \simeq 3.60(0.783\lambda^{1.67}h^{-1.17})$ (km/h),

with λ as stride length in centimeters, and *h* as height at the hip, or pelvic limb length, in centimeters.

Thulborn and Wade (1984) refined the methodology used to calculate height at the hip (*h*) of bipedal dinosaurs for use in calculating relative velocity after Alexander (1976), who suggests that hip height (h) $\simeq 4.0X_{\text{footprint length(FL)}}$; however, see Alexander (1976) and Coombs (1978) for variations of this ratio. Thulborn and Wade (1984) account for allometry in large-sized theropods by using linear regression analyses of osteometric data to solve for h using footprint length (FL) for large theropods (their “carnosaurs”):

$$(2) \quad h \simeq 4.15\mathrm{MT} + 28.52 \text{ (cm)},$$

with metatarsus proximodistal length (MT) considered a proxy for footprint length (FL) in large theropods.

There are sufficient osteometric data available to tailor this hip height equation specifically for tyrannosaurids. This provides the opportunity to customize the existing equations to determine the relative size and velocity of the late Campanian - early Maastrichtian tyrannosaurid track-makers, including the track-makers of *Bellatoripes fredlundi*, as well as estimate the approximate age (Erickson et al., 2006) of the track-makers by determining the relationship between their femur lengths and footprint lengths.

Following the methodology of Thulborn and Wade (1984), and Currie (2003), hindlimb data (Currie, 2003) from specimens of *Albertosaurus sarcophagus*, *Gorgosaurus libratus*, and *Daspletosaurus torosus* were graphed to find the best fit line for the data. Data were not $\log_{10}$ transformed (Thulborn and Wade, 1984). Least-squares regression was used to find the best-fit lines for the bivariate comparisons of data. The power equation ($y = ax^b$) produced the line that best fit the data with the highest coefficient of determination (R^2) value (Figs. 6.5-6.6) for all graphs.

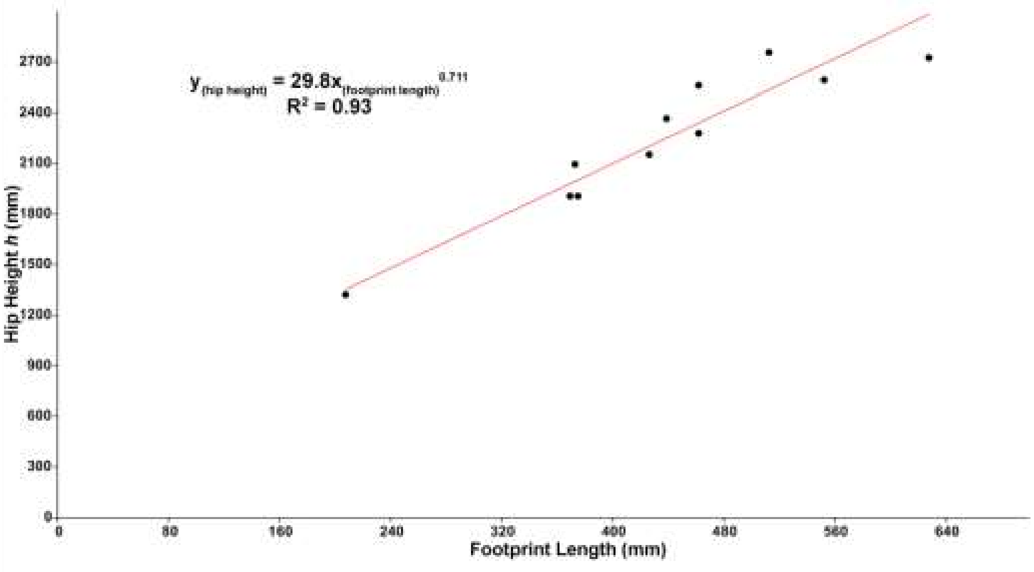


Fig. 6.5. Footprint length (digit III) versus hip height (*h*, leg length) of *Albertosaurus*, *Gorgosaurus*, and *Daspletosaurus*. Graphical results and best-fit regression line for footprint length (FL, calculated at the proximodistal lengths of digit III phalanges) compared to leg length as calculated from the sum of the proximodistal femur, tibia and astragalus, and metatarsal III lengths of late Campanian - early Maastrichtian tyrannosaurids *Albertosaurus*, *Gorgosaurus*, *Daspletosaurus* (Erickson et al., 2006; Myhrvold, 2013). All data are in millimeters (mm), and are unadjusted (Thulborn and Wade, 1984). Five percent was added to all totaled lengths to account for anatomical unknowns. Standard error for footprint length +/- 33.3 mm; hip height +/- 129 mm.

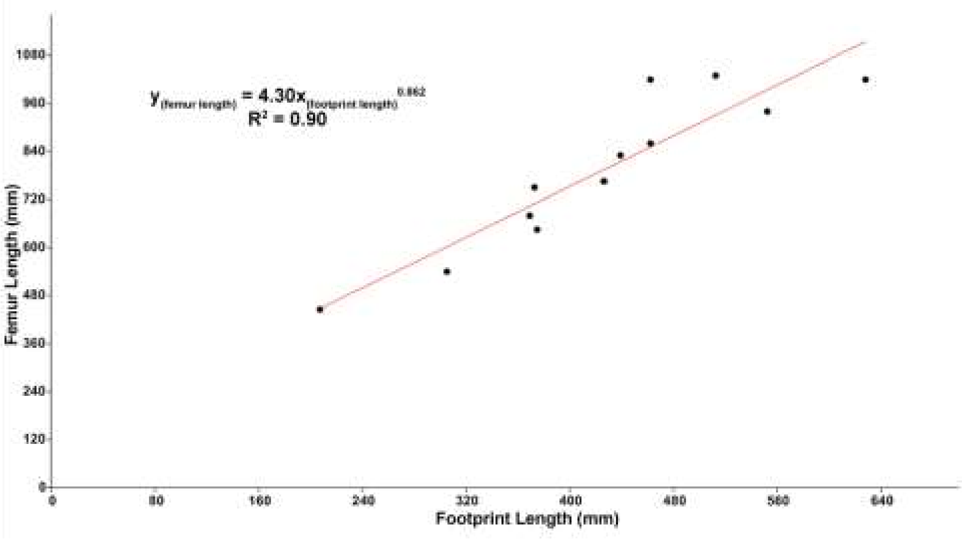


Fig. 6.6. Digit III length versus femur length for *Albertosaurus*, *Gorgosaurus*, and *Daspletosaurus*. Graphical results and best-fit line for comparing footprint length FL (digit III length, as calculated by totaling the proximodistal lengths of digit III phalanges and adding 5% to the total length to account for anatomical unknowns) to osteologic femur length (*y*) for late Campanian - early Maastrichtian tyrannosaurids *Albertosaurus*, *Gorgosaurus*, *Daspletosaurus* (Currie, 2003). The calculated *y* can then be used to estimate age of the track-maker using the methods of Erickson *et al.* (2006) and Myhrvold (2013). All data are in millimeters (mm), and are unadjusted (Thulborn and Wade, 1984). Standard error for footprint length +/- 32.3 mm; femur length +/- 55.7 mm.

Thulborn and Wade (1984) address the addition of anatomical unknowns (e.g. cartilage, tendons, keratinous sheaths, and other soft tissues such as distal metatarsal pad impressions) to limb length, but do not account for them in their calculations on the basis that these unknowns would not greatly alter the general conclusions. However, since footprints and trackways are a result of the combination of osteology and these anatomical unknowns, these unknowns need to be considered before using an ichnologic specimen to derive *h*, relative velocity, or estimated age. Thulborn (1982) cites Lambe's (1917) observations on a specimen of *Gorgosaurus libratus* to determine that adding 5% to the length obtained from measuring the bones of the hind limb reasonably accounts for the anatomical unknowns in large theropods. The regression was calculated to determine the quantitative relationship between footprint length and height at the hip (leg length) of *Albertosaurus*, *Gorgosaurus*, and *Daspletosaurus*. First, we consider the osteologic FL of digit III (which includes the straight line end-to-end measurements of phalanges III-1, III-2, III-3, and III-4 plus 5% of the total) as a proxy for ichnologic FL as measured from the footprint (Fig. 6.5). Digit III length is calculated by summing the lengths of the pedal phalanges and adding 5% to the total:

$$(3)\qquad \left(\sum_{i=\text{III-1}}^{\text{III-4}} x_i = \text{III-1} + \text{III-2} + \text{III-3} + \text{III-4}\right) \times 1.05 = \text{Digit III length} \cong \text{FL (mm)}.$$

Next, the regression was made between digit III length and leg length, calculated by adding the proximodistal lengths of the femur (F), tibiotarsus (T), and metatarsus (MT). Tibia and astragalus length was measured as the proximodistal length of the tibia and the astragalus combined. The proximodistal length of the metatarsus (Currie, 2003), which was measured from the proximal end of the metatarsus to the distal end of metatarsal III, was used for MT when calculating leg length. Anatomical unknowns were accounted for by adding 5% to the total measured lengths of the hind limbs.

$$(4)\qquad y_{(\text{hip height})} = 29.8x_{(\text{footprint length})}^{0.711}\ (\text{mm}),\ R^2 = 0.93\ (\text{Fig. 6.5})$$

Tests of this equation using known lengths of hind limb bones of tyrannosaurids (Currie, 2003) yielded results between 95% - 111% of the known lengths.

To determine the estimated age of the track-makers, the quantitative relationship between FL and osteologic femur length was determined using linear regression between the proximodistal length digit III plus 5% and femur lengths:

(5) $y_{(\text{femur length})} = 4.30x_{(\text{footprint length})}^{0.862}$ (mm), $R^2 = 0.90$ (Fig. 6.6)

Femur length (y) can then be entered into Erickson *et al.*'s (2006) equation to calculate age:

(6) $y_{(\text{age})} = 0.033x_{(\text{femur length})} - 9.765.$

At this time we are satisfied with Erickson *et al.*'s (2006)calculations, as the accuracy of the alterations made by Myhrvold (2013) has yet to be assessed.

Nomenclatural Acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new names contained herein are available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix "http://zoobank.org/". The LSID for this publication is: urn:lsid:zoobank.org:pub:0D77CC19-3DC9-4F8D-ADA0-59B3F9D9580C. The electronic edition of this work was published in a journal with an ISSN, and has been archived and is available from the following digital repositories: PubMed Central and LOCKSS.

SYSTEMATIC ICHNOLOGY

Dinosauromorpha Benton, 1984

Dinosauriformes Novas, 1992

Dinosauria Owen, 1841

Theropoda Marsh, 1881;

Coelurosauria Gauthier, 1986;

Tyrannosauroidea Walker, 1964;

Tyrannosauridae Osborn, 1905

Ichnofamily Tyrannosauripodidae ichnofam. nov.

(urn:lsid:zoobank.org:act:C2F3EC7D-71A5-4A50-9AE7-62500EDB2000)

Diagnosis

Large functionally tridactyl, mesaxonic tracks with distal metatarsal pad impression; may have craniomedially-directed hallux impression; footprint length greater than width; robust footprint with thick digits; generally lacking distinct digital pad impressions. Digit impressions thickened proximally, strongly tapering distally and terminating in acuminate claw impressions. Trackway narrow with slight inward rotation of pes towards midline; pace length close to 175 cm or greater; stride length close to 350 cm or greater.

Type ichnogenus

Tyrannosauripus Lockley and Hunt (1994**)**.

Referred specimens

Tyrannosauripus pillmorei Lockley and Hunt (1994) (CU-MWC225.1), unnamed print from Nemegt Formation MPD 100F/12 (Currie et al., 2003) print TMP 81.34.1 from the Belly River Group in Dinosaur Provincial Park, Alberta (McCrea et al., 2005) and large theropod tracks from the Campanian - Maastrichtian Wapiti Formation of British Columbia (PRPRC 2004.08.001, PRPRC 2011.11.001, PRPRC 2011.11.001M, PRPRC 2011.11.001MC, PRPRC 2012.04.002, PRPRC 2012.04.002M, PRPRC 2012.04.003, PRPRC 2012.04.003M) described by McCrea *et al.*, herein.

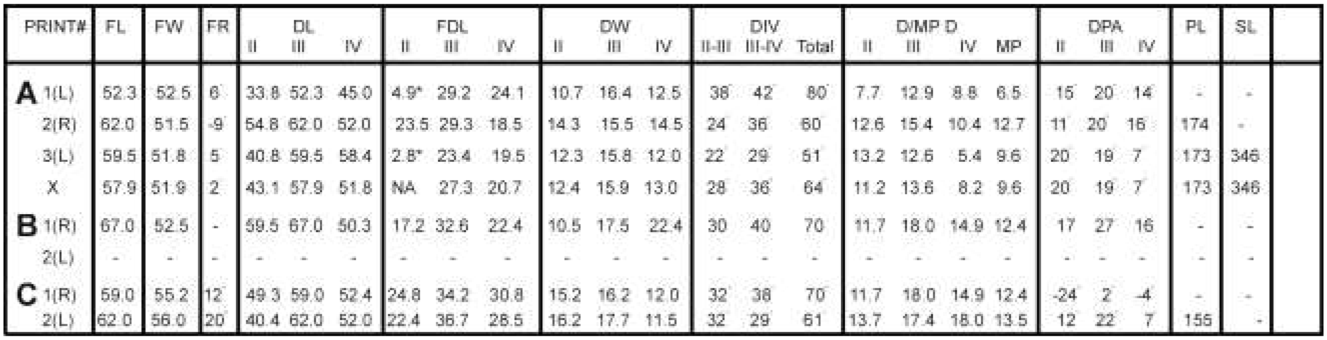
Bellatoripes fredlundi ichnogen. et ichnosp. nov. (Figs. 6.1-6.3, 6.7-6.9)
(urn:lsid:zoobank.org:act:B64813F7-B142-4DB1-8DEF-0542E8D1E7DA)

Etymology

Bellatoripes, bellatorius, Latin for “warlike”, “martial”, “pugnacious”; pes, Latin for “foot”; *fredlundi*, Latinized name in honor of Mr. Aaron Fredlund, who discovered and reported the type specimen in 2011.

Diagnosis

Bipedal trackway of a large, functionally tridactyl, digitigrade track-maker. Footprints longer than wide with footprint length (FL) over 50 cm. Footprint Area to Length Ratio greater than 20 cm^2:1 cm. Prints are mesaxonic and digits II and IV are of similar length. Digit impressions are wide, lacking obvious digital pad impressions. Digits are thick proximally and taper strongly distally. The free digit length (FDL) of digit III is short compared to the length of the footprint. Total divarication is variable, but is generally no greater than 80 °. Divarication between digits III and IV is normally greater than between digits II and III. Metatarsal pad impression present with a wide caudal margin. Pace length nearing 175 cm; stride length nearing 350 cm. Footprints in trackway are in line, with a pace angulation nearing 180°. Trackway width is narrow, with footprints overlapping the midline of the trackway. Footprint rotation is slight, but generally toward the trackway midline (Table 6.1).



PRINT#	FL	FW	FR	DL			FDL			DW			DIV			D/MP D				DPA			PL	SL	
				II	III	IV	II	III	IV	II	III	IV	II-III	III-IV	Total	II	III	IV	MP	II	III	IV			
A 1(L)	52.3	52.5	6	33.8	52.3	45.0	4.9*	29.2	24.1	10.7	16.4	12.5	38	42	80	7.7	12.9	8.8	6.5	15	20	14	-	-	
2(R)	62.0	51.5	-9	54.8	62.0	52.0	23.5	29.3	18.5	14.3	15.5	14.5	24	36	60	12.6	15.4	10.4	12.7	11	20	16	174	-	
3(L)	59.5	51.8	5	40.8	59.5	58.4	2.8*	23.4	19.5	12.3	15.8	12.0	22	29	51	13.2	12.6	5.4	9.6	20	19	7	173	346	
X	57.9	51.9	2	43.1	57.9	51.8	NA	27.3	20.7	12.4	15.9	13.0	28	36	64	11.2	13.6	8.2	9.6	20	19	7	173	346	
B 1(R)	67.0	52.5	-	59.5	67.0	50.3	17.2	32.6	22.4	10.5	17.5	22.4	30	40	70	11.7	18.0	14.9	12.4	17	27	16	-	-	
2(L)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
C 1(R)	59.0	55.2	12	49.3	59.0	52.4	24.8	34.2	30.8	15.2	16.2	12.0	32	38	70	11.7	18.0	14.9	12.4	-24	2	-4	-	-	
2(L)	62.0	56.0	20	40.4	62.0	52.0	22.4	36.7	26.5	16.2	17.7	11.5	32	29	61	13.7	17.4	18.0	13.5	12	22	7	155	-	

Table 6.1. Footprint and trackway data for trackways A, B, and C of *Bellatoripes fredlundi*. Linear measurements in cm. Data collected from PRPRC 2011.11.001M (Trackway A), PRPRC 2012.04.002M (Trackway B), PRPRC 2012.04.003M (Trackway C). DIV, digit divarication; FDL, free digit length; DD, digit depth; DL, digit length; DPA, digit plunge angle; DW, digit maximum width; FL, footprint length; FR, footprint rotation; FW, footprint width; L, left print; MP, metatarsal pad; MPD, metatarsal pad depth; R, right print; T, total divarication. PA, pace angulation; PL, pace length, PRPRC, Peace Region Palaeontology Research Centre; R, right; SL, stride length. * denotes digit lengths that are considered incomplete due to pathology. NA denotes mean data that is not available due to pathology.

Holotype

In situ specimen PRPRC 2011.11.001 (Trackway A) natural mould with three pes prints (two left, one right); also replica silicone mold (PRPRC 2011.11.001M, Fig. 6.7) and fiberglass reinforced (FGR 95) plaster cast (PRPRC 2011.11.001MC) stored at the Peace Region Palaeontology Research Centre (PRPRC) collection, Tumbler Ridge, British Columbia. Print #2 (right) is designated as the holotype footprint.

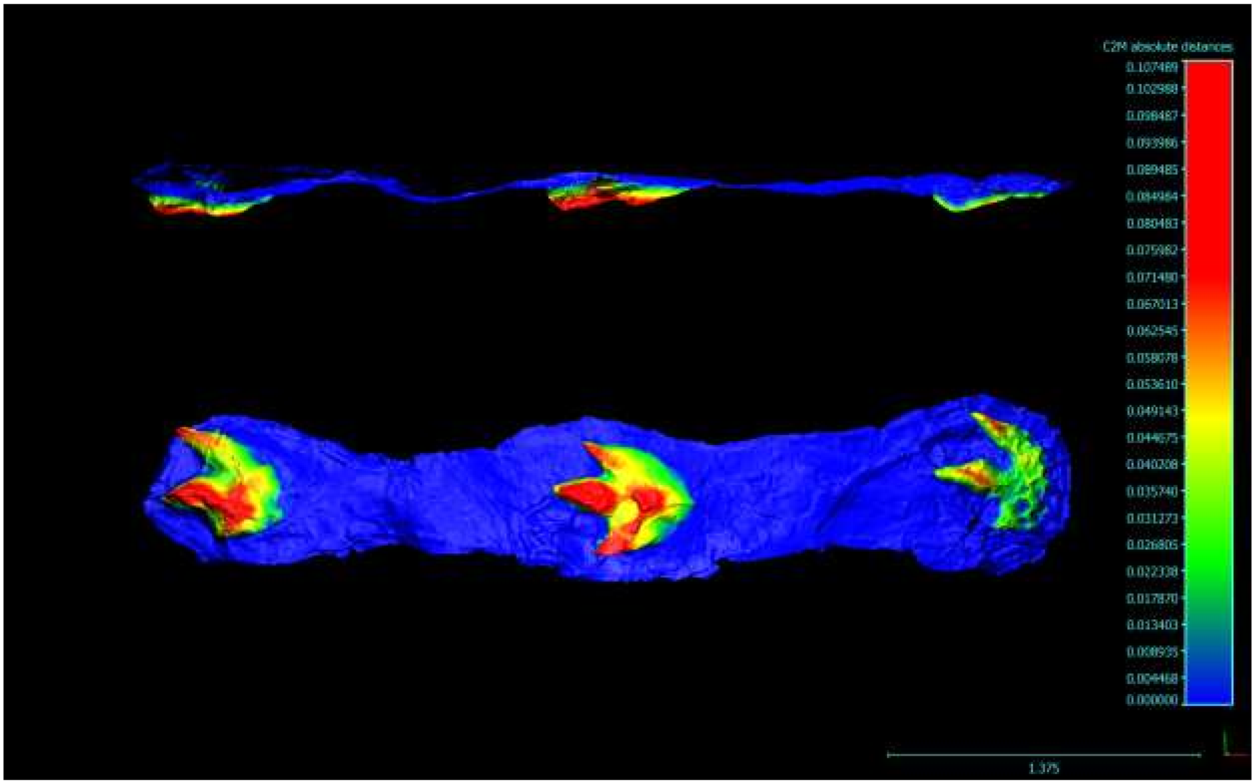


Fig. 6.7. Photogrammetic image of *Bellatoripes fredlundi* Holotype (Trackway A). Figure rendered from images of the silicone mould (PRPRC 2011.01.001M). Lateral view (top) and plan view (bottom). Note that the topographic profile for the lateral view is reversed in this orientation. Topographic profile scale and linear scale are in meters.

Paratypes

In situ specimens PRPRC 2012.04.002 (Trackway B, Figs. 6.9a-b); replica silicone mould (PRPRC 2012.04.002M) and PRPRC 2012.04.003 (Trackway C, Fig. 6.9c) and silicone mould (PRPRC 2012.04.003M).

Referred Specimens

Print TMP 81.34.1 from the Belly River Group in Dinosaur Provincial Park, Alberta McCrea et al., (2005) and PRPRC 2004.08.001 from the Wapiti Formation of British Columbia (Farlow et al., 2009).

Type locality

Northeastern British Columbia, east of Tumbler Ridge. Precise locality on file at the Peace Region Palaeontology Research Centre, Tumbler Ridge, British Columbia, Canada.

Type horizon

Upper Cretaceous (Campanian - Maastrichtian) Wapiti Formation, Unit 4 (Fanti and Catuneanu (2009).

Remarks

PRPRC 2011.11.001 is a 4 meter long trackway with three footprints (two left and one right) (Figs. 6.1-6.2, 6.7-6.8). The two left footprints each have an obviously truncated second digit, indicating pathology. The right footprint possesses three complete digit impressions (II-IV) and is designated as the holotype. Entry striations and skin tubercle impressions have been found in each footprint. Striations and some skin tubercle impressions are found along one or both sides of digit III on all prints, and skin tubercle impressions are found in the metatarsal pad area of print #3. The presence of skin impressions indicates that these are true tracks, rather than undertracks.

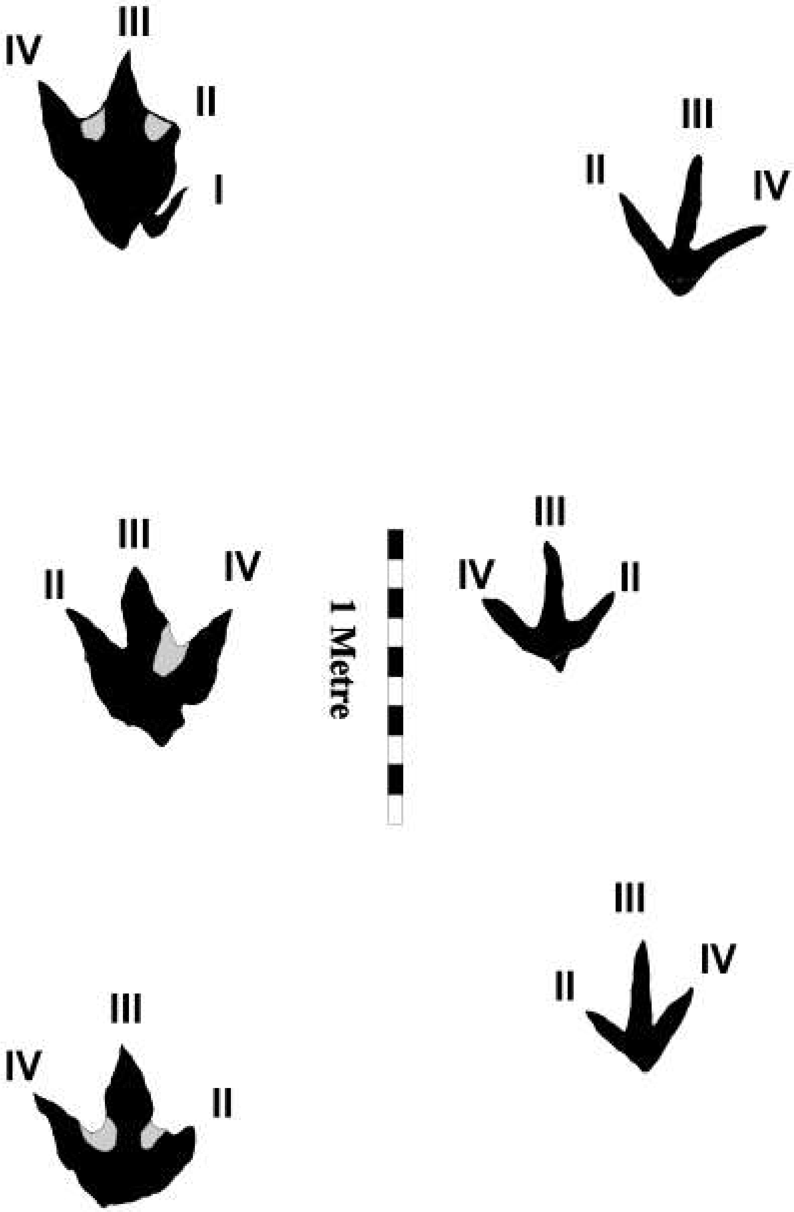


Fig. 6.8. Comparison of (Footprint Area to Length Ratio). *Bellatoripes fredlundi* holotype, Trackway A, Print # 2 PRPRC 2011.11.001 (left) Footprint Area to Length Ratio = 24.3 cm^2:1 cm. *Irenesauripus mclearni* track from the Gates Formation **(right)** Footprint Area to Length Ratio = 8.4 cm^2:1 cm.

A list of synapomorphies that are potentially observable in footprints was proposed by Carrano and Wilson (2001). Features present in the *Bellatoripes fredlundi* tracks and trackways, such as bipedal trackway, narrow gait, lack of metatarsal prints, and a laterally divergent digit IV indicate that *Bellatoripes fredlundi* shares some features in common with Dinosauromorpha, Dinosauriformes and Dinosauria. The presence of clawed digit impressions with prints reflecting mesaxonic, functionally tridactyl pedes indicates the track-makers belong to Theropoda. There are no recognized feather traces associated with the *Bellatoripes fredlundi* tracks, which is presently the only synapomorphy that could support inclusion of this ichnotaxon within Coelurosauria (Carrano and Wilson, 2001). Tyrannosauroidea and Tyrannosauridae synapomorphies (Holtz, 2004) do not include features of the feet that could be reflected in tracks. Farlow *et al.* (2013) comment that in order for many of the synapomorphies listed by Carrano and Wilson (2001) to be impressed in a substrate the track-maker would have to sit on the ground. The argument for the identification of *Bellatoripes fredlundi* tracks being made by tyrannosaurids is of necessity based on footprint size, overall morphology (although lacking presently known synapomorphies of Tyrannosauroidea and Tyrannosauridae) as well as stratigraphic and geographic occurrence. These observations reasonably exclude any other theropod clade as potential track-makers for *Bellatoripes fredlundi*. Furthermore, *Bellatoripes fredlundi* tracks, in common with other footprints, are impressions of feet that possessed skin, muscle, tendons and other tissues supported by a skeletal framework. Soft tissue anatomy is only very rarely preserved with body fossils, thus synapomorphies of Tyrannosauroidea and Tyrannosauridae are, out of necessity, based on skeletal features. The characteristic of digits impressions thickened proximally and strongly tapering distally in Tyrannosauripodidae is a reflection of the soft tissue anatomy of the foot of the track-maker and is unique to this ichnofamily and the included ichnotaxa.

If the identification of ichnotaxa within Tyrannosauripodidae as tyrannosaurid ichnotaxa stands the test of time and scientific consensus, some of the characteristics of this ichnofamily may become synapomorphies of Tyrannosauroidea and Tyrannosauridae.

Farlow *et al.* (2013) indicate the difference in the greater free length of digit IV compared with digit II as having potential for a tyrannosaurid-specific feature that could be preserved in tracks. This feature was observed by Farlow *et al.* (2013) in tracks from Alberta described by McCrea *et al.* (2005). Specimens of *Bellatoripes fredlundi* show equivocal results for this proposed character. Out of a population of six measured footprints (Table 6.1) only four prints were useful due to a repetitive pathology of digit II of prints #1 and #3 for Trackway A. The intact print #2 of Trackway A displays a digit II with longer free digit length (FDL) than digit IV. Digit IV has a free digit length greater than that of digit II in the single measured print of Trackway B. Digit II free digit length measurements of both prints of Trackway A were greater than the digit IV measurements. This osteological character may simply be masked by the soft tissues of the track-makers' feet.

COMPARATIVE ICHNOLOGY

Morphological characteristics of *Bellatoripes fredlundi* tracks and characteristics of their trackways are markedly distinct from other previously described large theropod ichnotaxa. *Tyrannosauripus pillmorei* (Lockley and Hunt, 1994), almost certainly a track of *Tyrannosaurus rex*, is the only ichnotaxon that is comparable to *Bellatoripes fredlundi*, as it is similarly robust with digit impressions that are wide proximally and taper strongly distally. *Tyrannosauripus pillmorei* prints are substantially longer (40%) and wider (20%) than those of *Bellatoripes fredlundi*. *Tyrannosauripus pillmorei* also has indistinct digital pad impressions and a hallux that is directed medially, whereas *Bellatoripes fredlundi* has no digital pad impressions and a cranially-directed hallux impression. Trackway characteristics of *Tyrannosauripus pillmorei* are unknown as the only specimen is a single natural cast footprint from the Raton Formation (Upper Cretaceous-Paleocene) several meters below the Cretaceous/Paleogene boundary.

A few tracks from Alberta have been identified as those of tyrannosaurids (McCrea *et al.***,** 2005; Fanti et al., 2013; Farlow et al., 2013). One of these (TMP 81.34.1, fig. 21.4 in McCrea *et al.***,** 2005) was initially identified as an ornithopod print, but later identified as a tyrannosaurid print (Farlow et al., 2013; McCrea et al., 2014). TMP 81.34.1 is quite similar to *Bellatoripes fredlundi*, with a 56.2 cm length and proximally wide digits (digit widths: II-16.2 cm, III-17.2 cm, IV-16.0 cm, table 21.1 in McCrea *et al.*, 2005) which taper to points. This specimen has been referred to *Bellatoripes fredlundi*. Other prints (TMP 93.36.282) described by McCrea *et al.* (2005) and UALVP 53475 reported by Fanti *et al.*, 2013) are large and were probably produced by tyrannosaurids. These specimens (TMP 93.36.282 – figs. 21.5-21.7 in McCrea *et al.*, 2005, and UALVP 53475 fig. 5 in Fanti *et al.*, 2013) lack the robustness of *Bellatoripes fredlundi*, as well as possessing noticeable digital pad impressions which are absent in both *Bellatoripes fredlundi* and *Tyrannosauripus pillmorei*. These prints are smaller than *Bellatoripes fredlundi* (TMP 93.36.282 is 51.9 cm; and UALVP 53475 is 49.0 cm) with digit widths nearly half that reported for *Bellatoripes fredlundi*, and may represent an earlier ontogenetic stage of the tyrannosaurids that were likely the makers of tracks of

Bellatoripes fredlundi. Calculations estimating femur length from the length of the type footprints (see Materials and Methods, Figs. 6.5-6.6) suggest the approximate ages of the tyrannosaurid track-makers of *Bellatoripes fredlundi* Trackways A, B, and C were 26, 29, and 25 years (+/-2 years), respectively. The estimated age for the maker of Trackway B is near the upper age-limit estimated for tyrannosaurids (Erickson et al., 2004; 2006; 2010), indicating the track-maker was fully adult, although such age-limits may be minimum estimates (Woodward et al., 2011). The track-maker of TMP 93.36.282 is calculated have been approximately 21 years of age and the track-maker of the smaller UALVP 53475 was approximately 20 years of age. These smaller tyrannosaurid tracks (UALVP 53475 and TMP 93.36.282) have a greater overall similarity to many track types that have been identified as allosaurid from older sedimentary deposits. This observation fits with observations (Erickson et al.,2004; 2010) that juvenile tyrannosaurs were much more gracile than adult tyrannosaurs. Juvenile tyrannosaurids may have retained a gracile body form to a certain age, after which they fleshed-out to a robust adult form. There are much more specimens and data that need to be collected before an attempt is made to construct an ontogenetic series for tyrannosaurids based on footprints, but it is possible that the timing of this transition from gracile juvenile to robust adult may be found by studying tyrannosaur footprints. In the meantime, it would be prudent to be cautious about naming new ichnotaxa based on track material that may have been produced by juvenile tyrannosaurids.

Tracks of *Irenesauripus mclearni* (Sternberg, 1932) are much less robust than those of *Bellatoripes fredlundi*. The surface area of print #2 of Trackway A of

Bellatoripes fredlundi was calculated as 1509 cm^2. When divided by footprint length (62.0 cm), the Footprint Area to Length Ratio was calculated as 24.3 cm^2:1 cm. For comparison, a large theropod print (*Irenesauripus mclearni*, a presumed allosauroid) from the Gates Formation (Lower Cretaceous: Albian) was found to have a surface area of 483 cm^2. When divided by its footprint length (57.5 cm) the Footprint Area to Length Ratio of the *Irenesauripus mclearni* print is 8.4 cm^2:1 cm, which is substantially less than the ratio calculated for print #2 of *Bellatoripes fredlundi*. The Footprint Area to Length Ratio quantitatively demonstrates that the track of *Bellatoripes fredlundi* is more robust than the print of *Irenesauripus mclearni* (Fig. 6.8).Tracks of the *Irenesauripus mclearni* holotype (CMN 8548) possess no hallux impressions, and no hallux impressions have been observed to date in any other tracks that have been attributed to *Irenesauripus mclearni* from western North America. Digital pad impressions for this ichnotaxon are usually well-developed on the comparatively long and slender digit impressions. The *Irenesauripus mclearni* holotype specimen is significantly smaller (FL: 38 cm) than those of *Bellatoripes fredlundi*, although some prints identified as *Irenesauripus mclearni* from western Canada are up to 50 cm length. *Irenesauripus mclearni* trackways have much shorter pace (94 cm for the holotype trackway) and stride values with lower pace angulation. Furthermore, they frequently show greater footprint rotation towards the midline than the *Bellatoripes fredlundi* holotype, but usually less footprint rotation than observed in the *Bellatoripes fredlundi* paratype (Trackway C).

The holotype of *Irenesauripus acutus* (CMN 8549) is much larger (FL: 53.5 cm) than the *Irenesauripus mclearni* holotype (Sternberg, 1932) and is similar in size to some tracks of *Bellatoripes fredlundi*. However, *Irenesauripus acutus* tracks have not been observed to have hallux impressions. The footprints of *Irenesauripus acutus* are proportionally longer and more slender than those of *Irenesauripus mclearni*, and though not evident in Sternberg's (1932) figure 2 illustration, *Irenesauripus acutus* tracks possess well-developed digital pad impressions as evidenced by a photograph of an *Irenesauripus acutus* track on pg. 81, Plate 3 of Sternberg (1932). The measured pace of the *Irenesauripus acutus* holotype is 173 cm, which is within the range found with *Bellatoripes fredlundi* trackways.

Prints of *Bueckeburgichnus maximus* described from the Lower Cretaceous of Germany (Kuhn, 1953; Lockley, 2000) are similar in size (FL: 56 cm) to *Bellatoripes fredlundi*. *Bueckeburgichnus maximus* digit impressions are not as robust as those of *Bellatoripes fredlundi* and the digit impressions possess traces of digital pads, although Lockley (2000) noted that digit II of *Bueckeburgichnus maximus* was similar to that of *Tyrannosauripus pillmorei* in being broad and well-padded. *Bueckeburgichnus maximus* tracks have a proportionally short, medially-directed hallux impression. A *Bueckeburgichnus maximus* track also possesses a narrow caudal margin of the metatarsal pad area (the heel) whereas *Bellatoripes fredlundi* tracks have a much wider metatarsal pad trace, sometimes with two or three lobe-like impressions (Fig. 6.9b). As *Bueckeburgichnus maximus* was described from a single print (Kuhn, 1953; Lockley, 2000), its trackway characteristics are unknown.

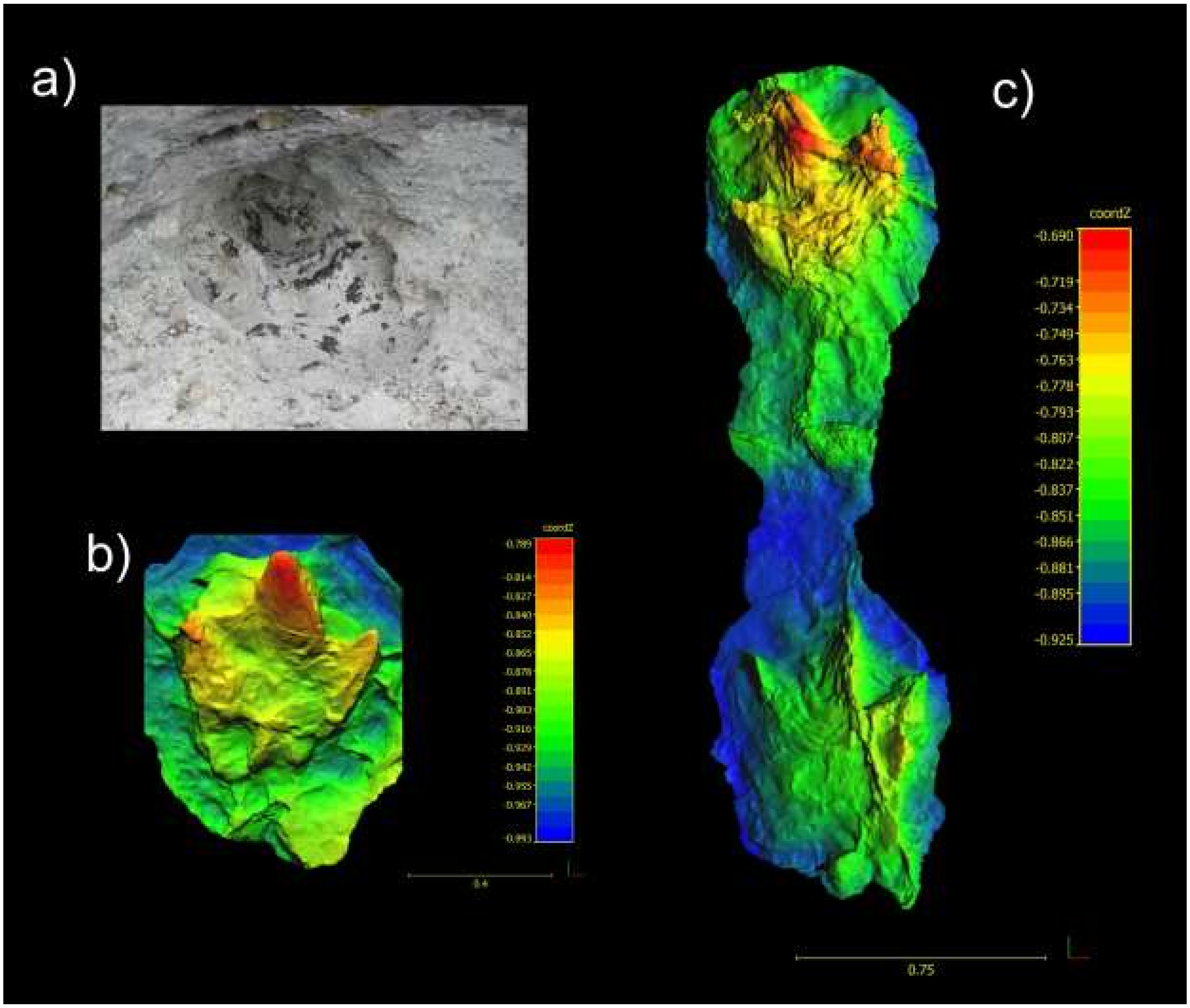


Fig. 6.9. Trackway B of *Bellatoripes fredlundi*. a) Partially excavated print #2 of Trackway B (not mapped or moulded); b) Photogrammetric image of Trackway B, print #1 from its silicone mould (PRPRC 2012.04.002); c) Photogrammetric image of Trackway C, prints #1 and 2 from its silicone mould (PRPRC 2012.04.003). Topographic profile scales and linear scales are in meters.

A description of *Megalosauripus* (*Megalosauripus uzbekistanicus*, *Megalosauripus teutonicus* and other specimens assigned to this ichnogenus) by Lockley *et al.* (1998) shows that these are large theropod tracks (FL: 40-77 cm) with a wide global and stratigraphic (Upper Jurassic to Lower Cretaceous) distribution. A *Megalosauripus* track differs considerably from a *Bellatoripes fredlundi* track in having observable digital pad impressions (although not observed in *Megalosauripus teutonicus*), and a narrow, elongate heel impression. Where present, hallux impressions are proportionally short and directed caudomedially to craniomedially. *Megalosauripus* trackway characteristics are distinctly irregular and variable, and generally display low pace angulation, although some *Megalosauripus* trackways from North America are known to have high pace angulation values (175^{o}) (Lockley *et al.*, 1998).

Eutynichnium lusitanicum is a large theropod ichnotaxon (FL: 37-40 cm excluding hallux) described from the Late Jurassic of Portugal (Lockley *et al.*, 1998). Digit impressions II-IV are wide, but do not taper, differing from those of *Bellatoripes fredlundi* which are wide and taper strongly to acute points. Digital pad impressions are not clearly defined, which is somewhat similar to *Bellatoripes fredundi* specimens where they are absent. A *Eutynichnium lusitanicum* print had a hallux impression that is directed craniomedially, similar to that of *Bellatoripes fredlundi* when present. The caudal margin of the metatarsal pad impression of *Eutynichnium lusitanicum* is narrow compared to that of *Bellatoripes fredlundi*. *Eutynichnium lusitanicum* has a relatively short pace (100 cm) compared with *Bellatoripes fredlundi* where the pace varies between 155 cm (Trackway C) and 174 cm (Trackway A). The difference in size between the track-makers of *Eutynichnium lusitanicum* and *Bellatoripes fredlundi* may account for some of the difference in pace length; however, the pace lengths observed in *Eutynichnium lusitanicum* are shorter than those observed in similar sized theropod footprints such as *Irenesauripus mclearni* (Sternberg, 1932).

Eubrontes (Hitchcock, 1845) is an ichnogenus of tracks from the Lower Jurassic, attributable to large theropods, with maximum footprint lengths just over 40 cm. *Eubrontes* tracks, unlike *Bellatoripes fredlundi*, often possess obvious digital pad impressions (Lull, 1915; 1953), as well as narrow caudal margins of the metatarsal pad area. Recently described specimens identified as *Eubrontes* from the Lower Jurassic of Utah show a craniomedially-directed hallux impression (Milner et al., 2006), although hallux traces are not evident in many previously described and figured specimens. *Eubrontes* trackways tend to have a maximum pace length of just over 1.2 meters with footprint rotations varying between 0° and 10° towards the midline of the trackway (Lull, 1953).

Gigandipus (Hitchcock, 1855; 1858) is a large theropod ichnogenus described from the Lower Jurassic that differs from *Bellatoripes fredlundi* in possessing well-defined digital pad impressions, a more medially-directed hallux impression and a narrow caudal margin of the metatarsal pad trace. The footprint length of *Gigandipus* is just under 45 cm (Lull, 1915; 1953). Lull (1953) gave a pace value of just over one meter for *Gigandipus* and footprint rotations varying between 0°-10° towards the midline of the trackway (Lull, 1953). From the diagram of a *Gigandipus* trackway (fig. 52 from Lull, 1953) the pace angulation appears to be close to 180°, similar to that described for Trackway A of *Bellatoripes fredlundi*.

Inferred track-maker

The only specimens of theropods recovered from Upper Cretaceous (upper Campanian - lower Maastrichtian) deposits of western Canada with pedes large and robust enough to produce tracks of *Bellatoripes fredlundi* are those of tyrannosaurids, (the albertosaurines *Albertosaurus* or *Gorgosaurus*, and the tyrannosaurine *Daspletosaurus* - Holtz, 2004). Given the present osteological record, it is unlikely that these traces were made by an as yet unreported large Upper Cretaceous non-tyrannosaurid theropod, such as giant ornithomimosaurians or oviraptorosaurians. Giant ornithomimosaurians are reported from the Early Cretaceous of China but were likely functionally tetradactyl (Mackovichy et al., 2009), and those reported from North America (Cullen et al., 2013) are too small to have made these tracks. Many specimens of oviraptorosaurians possess a comparatively long digit I (Osmolska, 2004) and were likely functionally tetradactyl (Harris, 1996; Gierlinski and Lockley, 2012). Large-bodied oviraptorosaurians described to date from North America (Lamanna, 2014) are also too small (~ 3.50 m body length) to be a potential track-maker of *Bellatoripes fredlundi*.

Unusual Features

There is an inferred pathology associated with digit II of the left footprint (seen in prints #1 and #3 of PRPRC 2011.11.001, Trackway A), reducing the length of digit II by at least 14 cm (Table 1; Figs. 6.4, 6.7-6.8). The pathology may have involved the loss of the distal and penultimate phalanges (II-2, II-3), or it may be a trace of a deformation or dislocation that prevented the distal portion of digit II from contacting the substrate. The rough, uneven margin of the distal ‘nub’ of the digit II impression is consistent with a wound that would have involved a loss of tissue and bone.

The pathology on digit II (left prints) of Trackway A does not appear to have significantly impaired the track-maker’s locomotion. Stride, pace and pace angulation values indicate a normal and efficient gait for a large theropod. The pes rotation of the second print (right) is the opposite of what is normally expected (outward rather than inward rotation from the midline of the trackway), and is consistent with compensation for this injury or deformity. This specimen is an interesting addition to the growing literature of dinosaur footprint pathology (Tanke and Rothschild, 2002) and to the literature of tyrannosaurid-specific pathologies (Molnar, 2001; Tanke and Rothschild, 2002).

Locomotion and behavior

The individual footprints in PRPRC 2011.11.001 (Trackway A), the first print of PRPRC 2012.04.002 (Trackway B) and the second print of PRPRC 2012.04.003 (Trackway C) undercut the original surface of the track-bearing layer to a considerable degree. The skin impressions provide information on foot movement (Gatesy, 2001) and in addition are evidence of true tracks that are not compromised by poor preservation. Two areas of lengthy (7.2 cm and 12.0 cm lengths), parallel striations (4 striations per cm width perpendicular to the long-axis of the striations) are present on shallow drag marks leading up to the caudal edge of print #2, Trackway C (Fig. 6.10). Both sets of impressions are parallel to the direction of travel (7^{o} toward digit II in relation to the central axis of digit III with a 10° plunge in the direction of travel). They are interpreted as being the result of the caudal portion of the foot making shallow contact with the substrate (pre-touch-down phase) as the foot moved forward towards the area where the foot begins to settle (touch-down phase) prior to the animal putting its full weight down (weight-bearing phase). The footprint cycle ends with the kick-off phase (Thulborn and Wade, 1989) leading towards the next touch-down phase. These striations are therefore identified as entry striations.

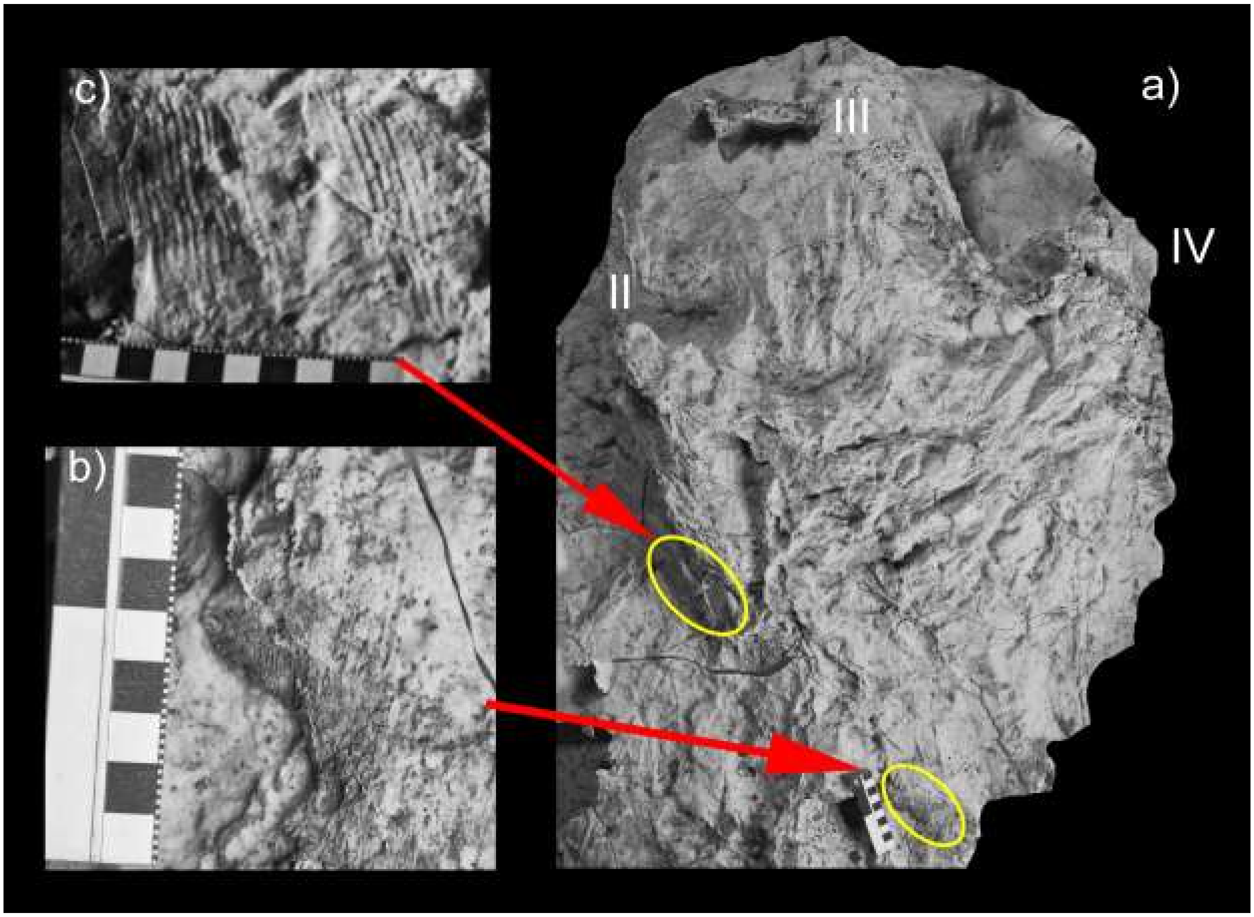


Fig. 6.10. Striations on *Bellatoripes fredlundi* paratype track. a) Photograph of silicone mold of print #2 Trackway C (PRPRC 2012.04.003), arrows pointing to areas with striations; b) photograph of striations on caudal drag marks leading up to print #2; c) photograph of striations on the outer margin of digit II print #2 Trackway C.

A third area of striations (4 striations/cm width) is present on the same footprint, but occurs along a 27 cm long portion of the outer edge of digit II. In relation to the rest of the footprint these striations extend from the surface of the substrate and run in an anterior (7.3 cm) and downward (6.2 cm) direction, representing a 50^{o} plunge angle, 35^{o} towards digit IV in relation to the central axis of digit III. The striations are deeply incised into the substrate on the caudal portion of the digit II impression, but become less distinct toward the cranial portion of this digit. These are interpreted as entry-striations recording the trajectory of the foot entering the substrate and quickly penetrating to the deepest point of the weight-bearing phase (Thulborn and Wade, 1989). As the foot settled it slipped forward and away from the midline of the trackway. Alternatively, the digit II striation impressions could be interpreted as exit striations recording the trajectory of the foot as it is withdrawn backwards and slightly towards the trackway midline. The process of limb movement we propose below likely fits with this latter interpretation.

The foot movements deduced by study of the *Bellatoripes fredlundi* tracks contrasts with published observations of trackways of Triassic (Gatesy et al., 1999), Jurassic (Avanzini et al., 2012), and Cretaceous (Pérez-Lorente and Herrero Gascón, 2007) theropods in which the footprints indicate that the track-makers' feet were dragged cranially out of the substrate after registering during the kick-off phase (Thulborn and Wade, 1989). This could be explained as a function of the depth of the substrate compared to the size of the animals involved. The difference may also be related to the consistency of the substrate: the substrate consistency for the reported Triassic prints (Gatesy et al., 1999) may have influenced the movement of the limbs such that caudal withdrawal of the pedes from the substrate was not possible, in contrast to the reported prints of Jurassic and Late Cretaceous theropod tracks (Huerta et al., 2012; Romero-Molina 2003). In the extant *Struthio camelus*, flexion and extension of the intertarsal and metatarsophalangeal joints are assisted by the elastic energy storage/release by ligaments, and tendons of the gastrocnemius and digital flexor muscles (Rubenson et al., 2007): during a full-motion cycle, flexion of the intertarsal joint occurs automatically with tarsometatarsal abduction, while extension results in adduction (Rubenson et al., 2007) (the passive engage-disengage mechanism of Schaller *et al.* (2009). The track-makers of *Bellatoripes fredlundi*, while utilizing hip-driven rather than knee-driven locomotion (Gatesy, 1990; Farlow et al., 2000) may have consequently withdrawn their pedes during intertarsal flexion enough to retract the digits and remove them from the footprint caudally**,** instead of dragging the digits cranially through the substrate (Fig. 6.11). The claw impressions of several of the *Bellatoripes fredlundi* tracks from the British Columbia site undercut the substrate and were not disturbed by the withdrawal of the feet. This is consistent with the interpretation of the withdrawal of the foot caudally from the footprint during the take-off phase of the footprint cycle.

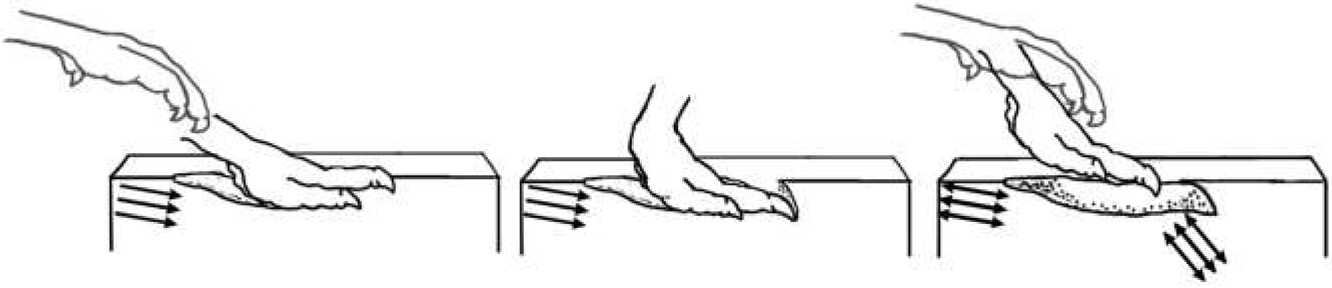


Fig. 6.11. Hypothesized pes movement of the track-maker for *Bellatoripes fredlundi*. The digits were not dragged cranially through the substrate as previously described in theropods footprints (Gatesy et al., 1999; Avanzini et al., 2012; Pérez-Lorente and Herrero Gascón,2007). The pes and digits were retracted from the substrate along an opposite trajectory of their entry prior to the pes moving forward in the next step cycle. Arrows indicate trajectory of the foot of Trackway C, print#2 as deduced from entry striations at the point of pes entry (left frame) and exit (center frame) into the substrate.

In recent years, the evidence for gregarious behaviour in some species of theropod dinosaurs has substantially increased (Currie, 1998; Tanke and Currie, 1998; Currie and Eberth, 2010; McCrea and Buckley, 2011). This evidence takes the form of osteological signaling features, pathologies that show interactions between individuals, and analysis of monodominant bonebeds (Currie and Eberth, 2010). Although tyrannosaurid footprints are rare, it is significant that the first reported tyrannosaurid trackways represent three individuals moving in the same direction (roughly southeast: Trackway A -116°, Trackway B -120°, and Trackway C -128°, unadjusted) in close proximity (just over 5.5 meters between Trackways A and B, and just over 2.5 meters between Trackways B and C). Given that tyrannosaurids normally make up only five percent of the faunal composition (Currie and Russell, 2005), the probability of three unassociated tyrannosaurids walking in parallel (8.4 m between the two individuals that are farthest apart) is low. The preservation (depth of impression, lack of compression uplifts, evidence of skin impressions and striations) of the footprints in all three trackways suggests that they were made at approximately the same time, and increases the likelihood that these track-makers were associated. Tracks and trackways of smaller theropods and large ornithopods at this tracksite do not follow the same bearing as the tyrannosaurid trackways. In fact, the non-tyrannosaurid trackways are random in regards to compass bearing, which rules out a geographic barrier that might have compelled the tyrannosaurids to walk in the same direction and in close association. The inference that these three animals were moving as a social group is the most parsimonious interpretation based on current data (Currie and Eberth, 2010) and provides the first trackway evidence showing gregarious behaviour in tyrannosaurs.

In calculating the relative velocity for the track-maker of *Bellatoripes fredlundi*, for Trackway A the estimated *h* of the track-maker is 2.87 m (+/- 1.30 cm). It is worth pointing out that *h* calculated using the general large theropod equation (Thulborn, 1990) is 2.80 m. While the *h* for tyrannosaurids may not be significantly different from results obtained from the original equation (Thulborn and Wade, 1984; Thulborn, 1990), the opportunity exists to determine the hip height to footprint length relationship for other taxa of both small and large theropods, which may be of use in studies that combine both computer simulations and known trackways.

One issue with using *h* to calculate relative velocity as per Thulborn and Wade (1984) is that it only takes into account a completely straight hind limb, which is not anatomically accurate. The straight-leg hip height provides a lower limit to the velocity of the track-maker of *Bellatoripes fredlundi*. Taking into account a flexion of the knee of 110° and a flexion at the ankle of 140° (Hutchinson and Garcia, 2002a; 2002b) an estimated hip height of 2.30 m is obtained. Using both values for *h* results in a range of relative velocities from 6.40 km/hr to 8.50 km/hr (+/- 0.40 km/hr) for the maker of Trackway A, with a stride length (λ) to *h* ratio of 1.69 at the lower end of the range. This correlates with the hypothesized energetically optimal walking gait as determined for large bipedal dinosaurs (Thulborn, 1982), although the concept of such an optimum has been disputed (Farlow et al., 2000). Trackway A likely represents the optimal gait that the tyrannosaurid track-makers habitually used for general locomotion. While there is the need for caution in using footprint length in calculating track-maker velocities (Manning, 2008), the *Bellatoripes fredlundi* trackways comprise true tracks which are the least susceptible to erroneous velocity estimates.

The locomotory capabilities of tyrannosaurids have been studied and discussed at length in numerous articles (Gatesy, 1990; Alexander, 1996; Paul, 1998; Farlow et al., 2000; Biewener, 2002; Henderson and Snively, 2004; Hutchinson et al., 2005; Hutchinson and Gatesy, 2006; Sellers and Manning, 2007; Paul, 2008; Brusatte et al., 2010; Persons and Currie, 2011; Hutchinson et al., 2011) mostly addressing their speed and agility (specifically that of *Tyrannosaurus rex*). The calculated relative velocity of the tyrannosaurid track-maker of Trackway A of *Bellatoripes fredlundi* shows an animal that was moving at a typical walking gait, and does not provide insight into the top speed of the carnivorous track-maker. However, the trackways of *Bellatoripes fredlundi* provide the first record of the walking gait of tyrannosaurids. If tyrannosaurids were capable of higher-velocity gaits these would likely be at higher velocities than 8.50 km/h. Future models testing the potential velocity and gait of a tyrannosaurid will have the opportunity to incorporate the preserved track record of this group as an analytical control.

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7.0 NEW ICHNOTAXA OF MAMMAL AND REPTILE TRACKS FROM THE UPPER PALEOCENE OF ALBERTA

The contents of this chapter have been re-formatted from a paper of the same title published in the journal *Ichnos*, Volume 11, pp. 323-339 in 2004. This paper was a result of a collaborative effort and in order of priority these are: Richard T. McCrea, S. George Pemberton, and Philip J. Currie. The candidate conceived this project and wrote the majority of the paper (>90%).

Keywords: mammal trackway; crocodylian trackway; Paskapoo Formation; Porcupine Hills Formation; upper Paleocene

INTRODUCTION

The first fossil footprints from the Paleocene of Alberta were described in a short note by Rutherford and Russell (1928) and again in a more detailed treatment by Russell (1930). The recovered trackway was on an isolated block found along the banks of the Red Deer River, a short distance west of the town of Red Deer (Fig. 7.1). UALVP 134 (University of Alberta Laboratory for Vertebrate Paleontology) is a short segment of a trackway preserved in sandstone as a natural cast. The block had fallen from its original "…, in legal subdivision 1, section 18, township 38, range 27, west of the 4th meridian", (Russell, 1930), but Rutherford and Russell (1928) were confident that they had correctly identified the layer of strata from which it had originated. The footprint block was in two pieces when it was found; fortunately there was a small area of contact between the two sections which made it possible to restore the slab with the footprints in their original spatial context (Rutherford and Russell, 1928; Russell, 1930).

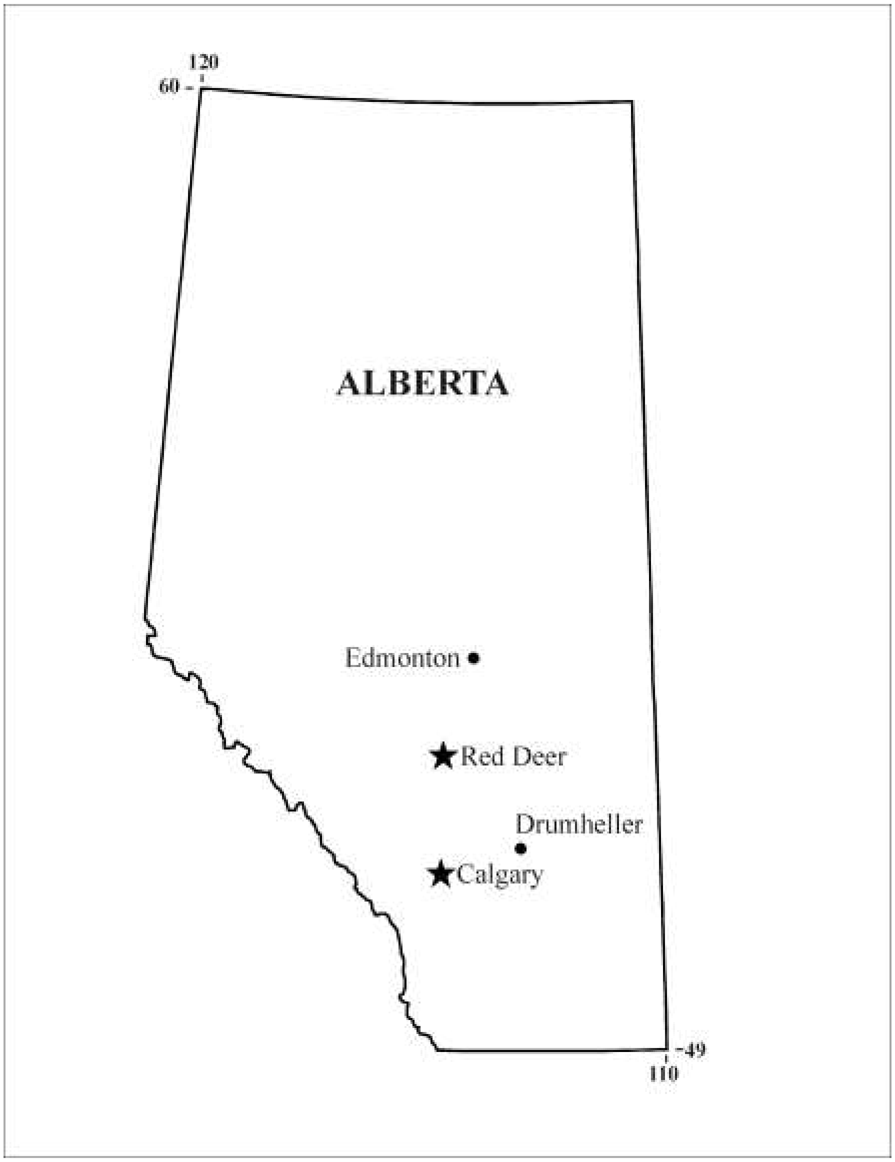
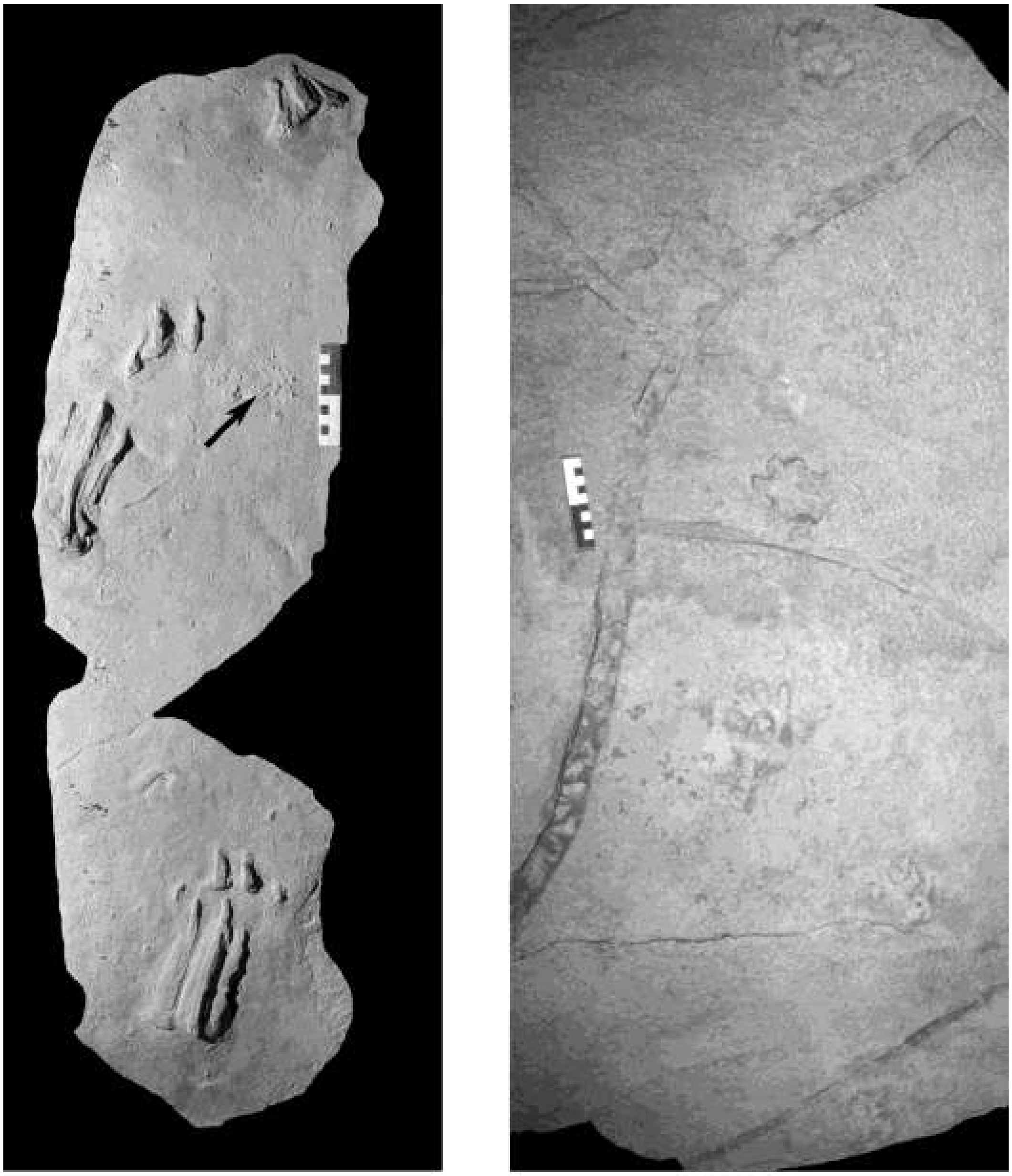


Fig. 7.1. Map of Alberta showing general localities from where the UALVP 134 (Red Deer) and TMP 90.131.01 (Calgary) trackslabs were discovered.

UALVP 134 displays five reasonably large footprints (three pedal, two manual) preserved as natural casts on the underside of a sandstone block (Fig. 7.2). Rutherford and Russell (1928) and Russell (1930) refer to the type of preservation as a ‘natural mould’. However, using the standardized terminology set out by Leonardi (1987), these prints would be considered as natural casts because they are the infillings of the original tracks. Russell (1930) speculated that the original footprints were likely made in finer-grained substrate, an interpretation this paper agrees with. The original muddy substrate with footprint impressions was later filled in with coarse sandstone. When the footprint layers were finally exposed, the fine-grained substrate was quickly eroded, leaving behind the more resistant sandstone infill.



UALVP 134 **TMP 90.131.01**

Fig. 7.2. Photographs of trackslabs UALVP 134 (replica cast) and TMP 90.131.01 (original). Scale bars = 10 cm. Note that the black arrow on the UALVP 134 photograph is pointing to a single tridactyl trace attributed to a swimming turtle.

The trackway is narrow and there is considerable heteropody between the pes and the manus prints, with the pes prints being much larger than those of the manus (Figs. 7.2

& 7.3). The manus prints are in a position just anterior to the pes prints in the two complete manus/pes sets. This trackway was initially described as being made by a functionally tridactyl, digitigrade animal (Rutherford and Russell, 1928). The manus prints are certainly digitigrade, and the pes prints (which lack a heel) could be considered semi-digitigrade.

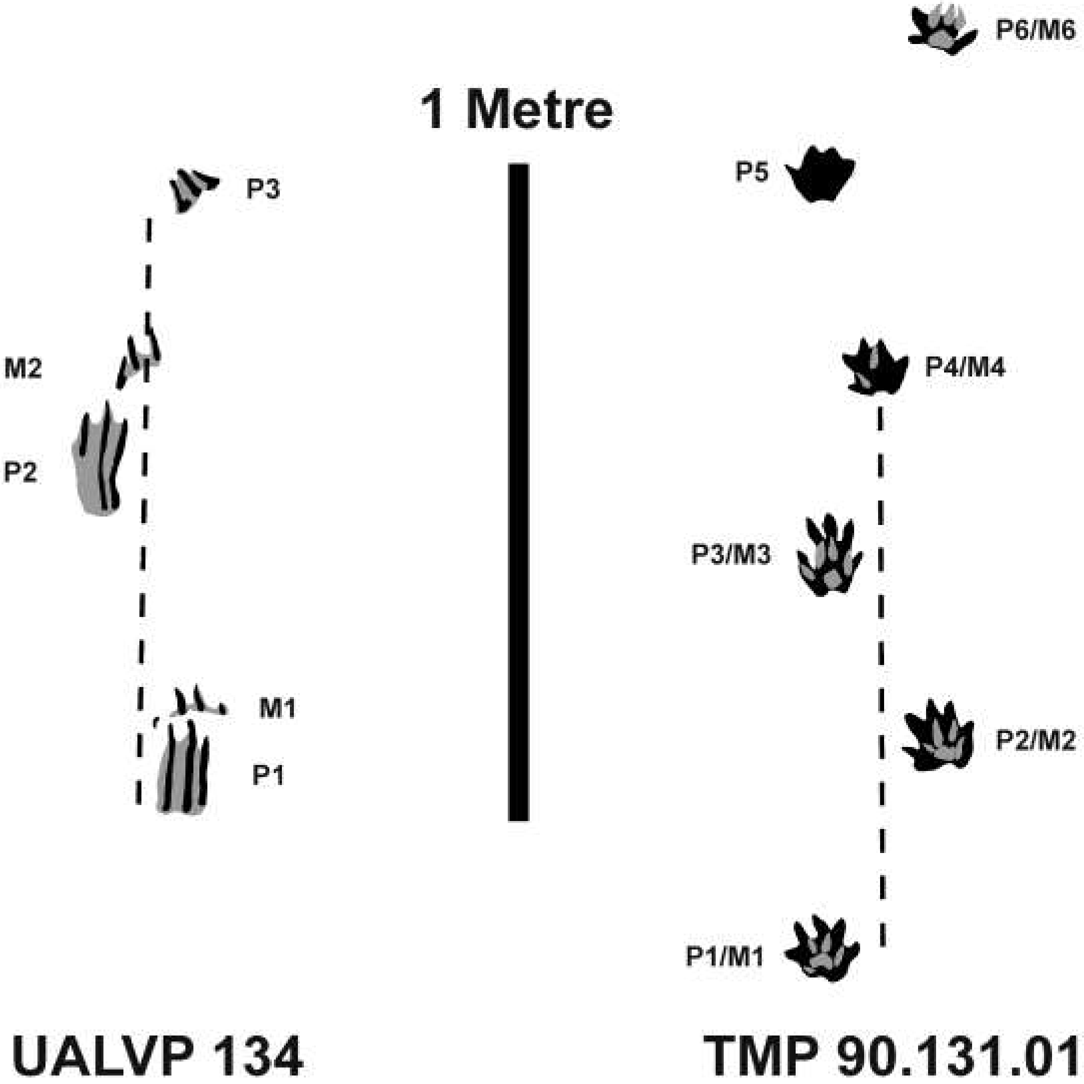


Fig. 7.3. Trackway maps of UALVP 134 and TMP 90.131.01 (dashed line indicates midline of trackways).

Russell (1930) reasoned that due to the size of the tracks the only possible track makers could have been mammals and dinosaurs. The age of the tracks exclude a dinosaurian track maker, though Rutherford and Russell (1928), and Russell (1930) admitted that there was no known Paleocene mammal that could have made such prints. They speculated that the trackway could have been produced by some undiscovered form of condylarth or creodont, which is quite reasonable. Crocodylians were not mentioned as possible track-makers, possibly due to the absence of tail drag and/or body impressions. Russell (1930) did remark that the trackway must have been made by a quadrupedal animal that was capable of keeping its body off the ground while it was walking. This statement may have caused him to exclude crocodylians and the tracks were attributed to mammals.

This paper disagrees with the mammalian origin of the UALVP 134 specimen as it possesses characters that closely resemble a reptilian track-maker. As discussed below, these prints bear a striking resemblance to modern crocodylian tracks and the many fossil tracks that have been attributed to crocodylians. The specimen UALVP 134 displays many non-mammalian characters and its original designation as a mammal trackway must be cast in doubt. The tracks are almost certainly that of a crocodylian reptile of respectable proportions rather than a mammal.

A second Paleocene fossil footprint block was discovered in October, 1990 at a locality near Signal Hill within the city of Calgary, Alberta (Fig. 7.1). The footprint find was reported to the Royal Tyrrell Museum of Palaeontology in Drumheller by Mr. Gordon White, a stone mason and landscaper who was involved with preparations for a new subdivision on the west side of Signal Hill. A great quantity of in situ stone was encountered during the excavation of basements for the new houses that would become part of the Signal Hill and Signature Park communities (Gordon White, pers. comm. 2003). The slabs of rock removed during the basement excavations were put in a pile near the base of the hill. Workers noticed some dog-like tracks on a portion of a slab that was exposed in the rock pile and this find was duly reported to the museum. Mr. White (pers. comm., 2003) recollected that the excavation from which the track-bearing slabs originated was from an area just below a group of stones that had been set in a pattern to represent numbers. These stones had been put in place by Canadian Armed Forces regiments that trained in the area during World War I; the numbers indicate particular regiments (Gordon White, pers. comm., 2003). Mr. Darren Tanke, a technician at the Tyrrell Museum, visited the site and confirmed that the prints were genuine. The large slab was delivered by Mr. White to the Royal Tyrrell Museum in November, 1990 (Gordon White, pers. comm., 2003; Darren Tanke, pers. comm., 2003).

TMP 90.131.01 (Royal Tyrrell Museum of Palaeontology), displays a single trackway of 12 prints (6 pedal, 6 manual) preserved as natural casts on a mud-cracked substrate (Figs. 7.2 & 7.3). The tracks are about the size of those that a medium-sized dog would make. The manus prints do look dog-like although the pes prints do not. There is considerable heteropody, the manual prints being half the size of the pes prints. Unlike the UALVP 134 footprint block, the TMP 90.131.01 trackway shows complete overprinting of all manual prints by the pedal prints. The TMP 90.131.01 trackway is quite narrow and the morphology of the digital and pedal pads (described below) indicate a mammalian track-maker. The nature of the claws suggest that it was a predator. The specimen TMP 90.131.01, displays many distinctly mammalian footprint and trackway characters. The track-maker was a mammal of possibly creodont affinity and these mammals were a significant group of predators early in the Tertiary.

METHODS

Measurements (Table 7.1) were taken following Leonardi (1987), but additional explanation is required for some of the methods of measurement (Fig. 7.4) that appear in Table 7.1. All measurements except for divarication (DIV) are in millimeters. Measurement values that appear in bold type in Table 7.1 are estimates. All measurements were taken from replicated casts of the original slabs for ease of access, and that allowed manipulation for lighting purposes.

Spec #	Print #	FL (mm)	FW (mm)	FR	FD (mm)	DL (mm)					DW (mm)					DIV					TW (mm)		PL (mm)	SL (mm)	PA (mm)
						I	II	III	IV	V	I	II	III	IV	V	I-II	II-III	III-IV	IV- V	Total	TM	TMe			
TMP 90.131.01	P1(R)	99.0	110.0	0°	5.0	73.0	91.5	93.0	90.0	67.0	21.0	20.0	23.0	25.0	20.0	25°	27°	16.5°	33°	101.5°	15.0	231.0	-	-	-
	P2(L)	109.0	111.0	+5°	15.0	64.5	95.0	100.5	94.0	79.0	13.0	20.0	17.0	11.0	17.0	31°	25°	17°	27°	100°	-	-	343.5	-	-
	P3(R)	122.5	96.0	+6°	8.0	73.0	110.0	115.0	114.0	78.5	6.5	17.0	19.0	17.0	13.0	22°	18°	16°	23°	79°	-	-	319.0	602.0	130°
	P4(L)	91.0	101.0	+6.5°	14.0	45.0	77.5	83.5	79.5	69.0	11.0	17.0	16.0	10.0	18.0	38.5°	27°	18°	39°	122.5°	-	-	311.0	577.5	148.5°
	P5(R)	84.0	105.0	0°	4.0	-	76.5	80.0	82.0	75.5	-	18.5	12.0	14.0	13.0	-	29°	20°	37.5°	-	-	-	306.5	596.5	123°
	P6(L)	-	105.0*	-9°	13.0	48.0	71.5	-	-	64.5	10.0	21.0	-	-	16.5	40°	-	-	-	136°	-	-	291.0	530.0	-
	M1(R)	51.0	68.0	+22°	-	-	(33.5) 44.5	(28.5) 50.0	(26.0) 46.0	(19.0) 27.0	-	9.5	11.0	9.5	7.5	-	36.5°	37°	76.5°	150°	66.0	200.0	-	-	-
	M2(L)	63.5	64.0	+2.5°	-	-	(20.0) 41.5	(42.0) 63.0	(33.0) 62.0	(38.0) 46.0	-	8.0	13.0	10.0	8.5	-	39°	26°	26.5°	91.5°	-	-	340.0	-	128
	M3(R)	78.0	78.5	+8°	-	-	(40.0) 64.5	(37.0) 78.0	(42.5) 72.0	(30.0) 59.0	-	13.0	14.0	13.5	11.0	-	27°	10°	42.5°	79.5°	-	-	317.5	601.0	-
	M4(L)	-	-	-14.5°	-	-	32.0	35.0	-	-	-	13.0	10.0	-	-	-	-	-	-	-	-	-	-	-	-
	M5(R)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	M6(L)	68.5	-	-	-	-	(39.5) 66.0	(33.0) 67.0	(36.5) 67.5	-	-	16.0	16.0	14.5	-	-	14°	8°	-	-	-	-	-	-	-
UALVP 134	P1(L)	143.0	69.0	-8°	17.0	-	135.0	143.0	104.5	-	-	[6.5] 22.0	[6.0] 27.0	-	-	-	12°	11.5°	-	23.5°	122.0	245.0	-	-	-
	P2(R)	162.0	69.0	+13°	19.0	-	-	160.0	-	-	-	[9.0] 20.0	[8.0] 30.0	[7.5] 24.0	-	-	11°	11°	-	22°	-	-	492.0	-	-
	P3(L)	49.0	79.0	+38°	12.0	-	-	49.0	-	-	-	-	[7.5] 19.0	-	-	-	-	-	-	-	-	-	511.5	929.5	133°
	M1(L)	45.0	88.0	+11°	8.0	-	40.0	37.0	19.0	-	-	[9.0] 25.0	[12.0] 15.0	[8.0] 21.0	-	-	43°	72°	-	115°	-	-	-	-	-
	M2(R)	63.0	76.0	-10°	11.0	-	58.0	60.0	-	-	-	[10.0] 16.0	[8.0] 26.0	16.0	-	-	30°	30°	-	60°	-	-	540.0	-	-

Table 7.1. TMP 90.131.01 and UALVP 134 footprint and trackway measurements.

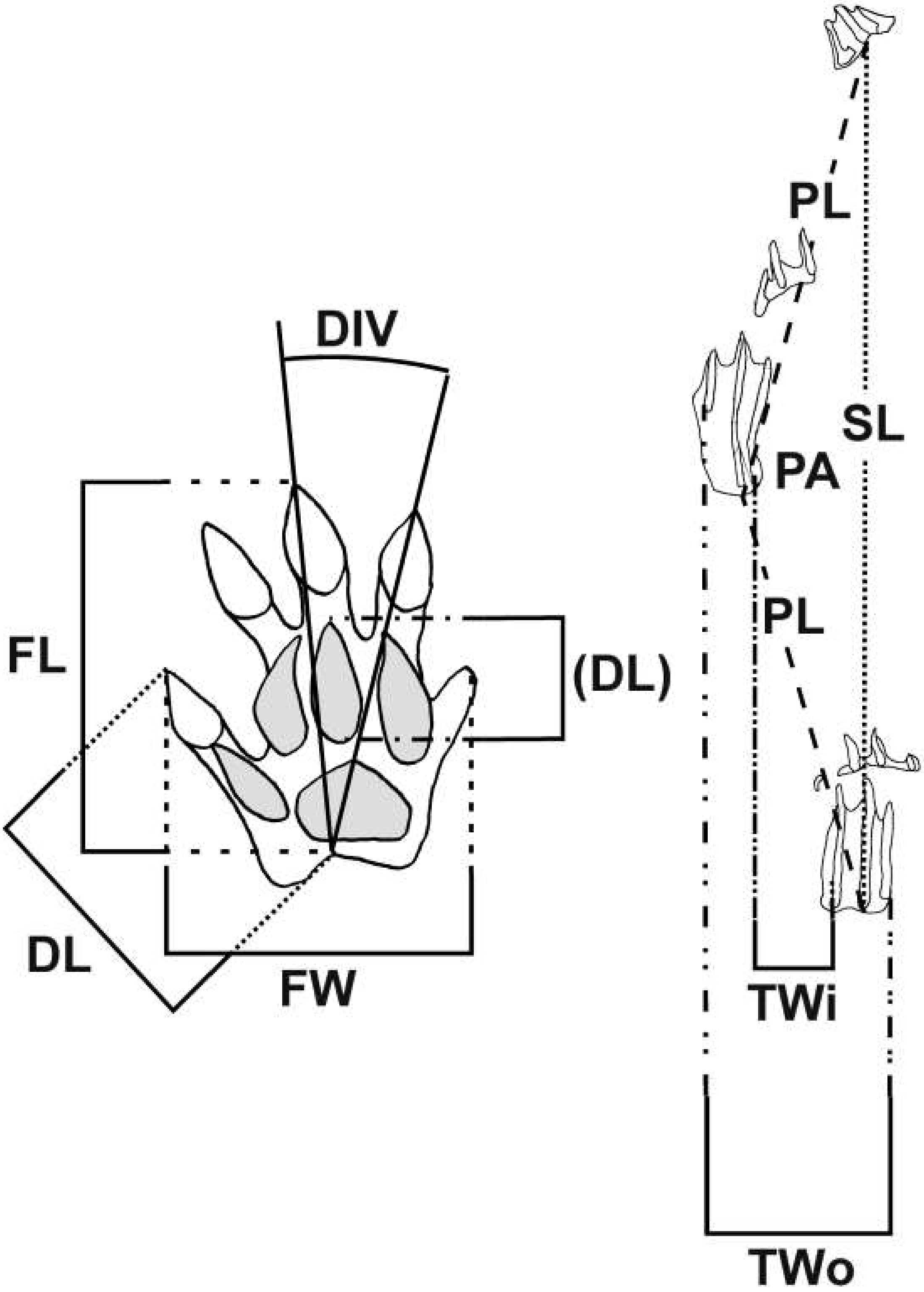


Figure 7.4. Methods of footprint and trackway measurements used in this study.

Print #: Ichnites are numbered in the presumed order in which the track-making animal produced them. Designated as pes (P) or manus (M). The left (L) or right (R) orientation of the print is also indicated.

FL (Foot Length): The length of the foot is measured from the base of heel to tip of main digit. For pes prints of specimen TMP 90.131.01 this measurement was taken from the posterior edge of the pes behind the long axis of digit III (Fig. 7.4). For pes prints of specimen UALVP 134, this measurement was taken from the base of the third digit to the tip as there was no heel impressed.

FW (Foot Width): Foot width is the tip to tip distance between the two outermost digits of the print (Fig. 7.4). In Table 7.1 (*) = the tip to tip distance between digits I-IV.

FR (Footprint Rotation): After Leonardi (1987).

FD (Footprint Depth): Footprint depth is measured in the region with the greatest relief. The values recorded for TMP 90.131.01 are the greatest depth of the manual prints because they impressed more deeply than the pedal impressions that overprinted them.

DL (Digit Length): Method one is the distance between base of heel and tip of digit (Fig. 7.4), whereas Method two is the distance between the posterior portion of the last visible phalangeal pad and the tip of digit (Fig. 7.4). These measurements are in brackets ( ) in Table 7.1.

DW (Digit Width): Measurements taken across widest point of digit, perpendicular to the long axis of the digit. Measurements in brackets [ ] for UALVP 134 are for the width of the claw impressions.

TW (Trackway Width): TWi is the inner trackway width (Figure 7.4); TWo is the outer trackway width (Fig. 7.4).

DIV (Divarication): Angles are taken from the base of footprint behind the principle digit (Fig. 7.4).

PL & SL (Pace Length and Stride Length): Taken from the base of the heel for pes prints of TMP 90.131.01, and from base of digit **III** of UALVP 134 (Fig. 7.4).

PA (Pace Angulation): After Leonardi (1987), (Fig. 7.4).

GEOLOGICAL SETTING, ENVIRONMENT AND PALEONTOLOGY

Specimen UALVP 134 was recovered from the Paskapoo Formation near Red Deer, Alberta. The Paskapoo Formation is the last of six clastic wedges recognized in the Alberta foreland basin (Cant and Stockmal, 1989) and the last of the three clastic wedges that comprise the Upper Cretaceous to Lower Tertiary, Upper Zuni Sequence (Leckie, 1989). The sediments of the unconformity-bounded Paskapoo Formation are non-marine, consisting of shales, sandstones and conglomerates (Cant and Stockmal, 1989; Leckie, 1989), and contain economic coal seams (Demchuck, 1990). The Paskapoo Formation is regarded as early-late Tiffinian (North American Tertiary Land Mammal Age) based on fossil mammal remains (Fox, 1990). The strata that UALVP 134 originated belong to the Lacombe Member of the Paskapoo Formation (Demchuk and Hills, 1991) which outcrops in this area. The mammal localities in closest proximity to the UALVP 134 site along the Red Deer River are mid-Tiffinian in age (Krause, 1978; Fox, 1990).

Specimen TMP 90.131.01 was recovered from the Porcupine Hills Formation. A proposed northward extension of the boundaries of the Porcupine Hills Formation, (Carrigy, 1970; 1971) encompassed fossil vertebrate sites in the Calgary area previously thought to be within the Paskapoo Formation (Krause, 1978). These sites are now considered to be a part of the Porcupine Hills Formation (Krause, 1978; Fox, 1990). Caliche deposits in the Porcupine Hills Formation in southern Alberta indicate semi-arid conditions (Leckie, 1989; Lecki and Smith, 1992), but the climate to the north in west-central Alberta was much more humid (Jerzykiewicz and Sweet, 1988). The Porcupine Hills Formation is considered to be late Torrejonian to early Tiffinian, based upon fossil mammal remains (Fox, 1990). Fossil mammals at sites closest to the TMP 90.131.01 locality are late Torrejonian in age (Fox, 1990).

Body fossils of tetrapods including mammals, (Simpson, 1927; Krause, 1978; Fox, 1984; 1990) and aquatic freshwater vertebrates (Wilson, 1980; Wilson and Williams, 1991; Murray, 1996) have been found in the Paskapoo Formation. Fossil plants, insects and a variety of freshwater molluscs have also been described (Wilson and Williams, 1991). Fox (1984; 1990) lists tetrapods that have been found in the Paskapoo and Porcupine Hills Formations. Included among small mammals are larger mammals such as pantodonts, condylarths and creodonts. Present also are amphibians, turtles, champsosaurs, lacertilians, and crocodylians (Fox, 1984).

Both footprint specimens (UALVP 134 and TMP 90.131.01) were discovered as isolated slabs and so this paper can not go into precise details of their stratigraphic context. Both track slabs are natural casts with no vestige of the original footprint substrate adhering to them, though the original footprint substrate was likely fine-grained. Both trackways were overlain and infilled by much coarser grained sediment, a product of a higher energy environment than the original substrate the tracks were made upon. Given the alluvial and lacustrine nature of the sediments that occur in the Paskapoo Formation (Leckie and Smith, 1992; Murray, 1996), and the Porcupine Hills Formation (Lerbekmo and Sweet, 2000), these higher energy deposits could have been caused by flooding events along the banks of rivers or streams (Murray, 1996), or perhaps near the mouth of stream that was emptying into the shallow margin of a lake.

SYSTEMATIC ICHNOLOGY

CLASS REPTILIA

ORDER CROCODYLIA

Ichnofamily: Batrachopodidae (Lull, 1904)

Ichnogenus *Albertasuchipes* ichnosp.

McCrea, Pemberton, and Currie, nov.

Included Ichnospecies: The ichnogenus is only known from the type ichnospecies

Type Ichnospecies: *Albertasuchipes russellia* McCrea, Pemberton, and Currie herein. late Paleocene (middle Tiffanian), Alberta.

Etymology: Alberta, for the name of the Canadian province in which the type specimen was discovered; Greek suchus, crocodile; -ipes, suffix identifying this as a trace.

Diagnosis: Trackway of quadruped with pronounced heteropody. Manus: tridactyl, digitigrade, approximately one-third length of pes. Impressions wider than long (FLẋ = 54.0 mm; FWẋ = 82.0 mm); FL/FW ratio approximately 0.66. Manual digits range in thickness between 16.0 mm and 26.0 mm. Manus digits are nearly parallel to axis of print and spaced approximately 20 mm apart. No digital pads. Digits II and III longest, Digit IV less than half length of digits II and III; claw impressions robust (6.0 - 12.0 mm thick) and terminate in obtuse to acuminate points; pace of manual prints 540 mm. Placement of manus typically, immediately anterior to pes. Pes: tridactyl and semi-digitigrade. Impressions longer than wide (FLẋ= 152.5 mm; FWẋ = 69.0 mm); FL/FW ratio 2.21. Digits nearly parallel to main axis of print with slight curve of digits towards midline of trackway, starting at position half to three-quarters of length of the footprint and extending anteriorly to tips. Digits spaced approximately 20 mm apart and range in thickness between 19.0 and 30.0 mm. No digital pads. Digit III longest in pes; digit II longer than digit IV. Digits terminate in robust (6.0 - 9.0 mm thick), obtuse claws. No true heel impression, posterior portion of print roughly truncate. Pace length (pes) approximately 500 mm (3 times pes length); stride length just over 900 mm (6 times pes length); pes pace angulation approximately 130^{o} degrees. Trackway narrow (pes: TWi = 122.0 mm; TWo = 245.0 mm), with inner margin of pes tracks near trackway midline, manus tracks overlapping trackway midline or just lateral to it. Manus rotation variable. Pes rotation variable, but usually towards midline.

Albertasuchipes russellia

McCrea, Pemberton, and Currie, ichnosp. nov.

Figs. 7.2, 7.3, 7.5A-C and 7.6A-C

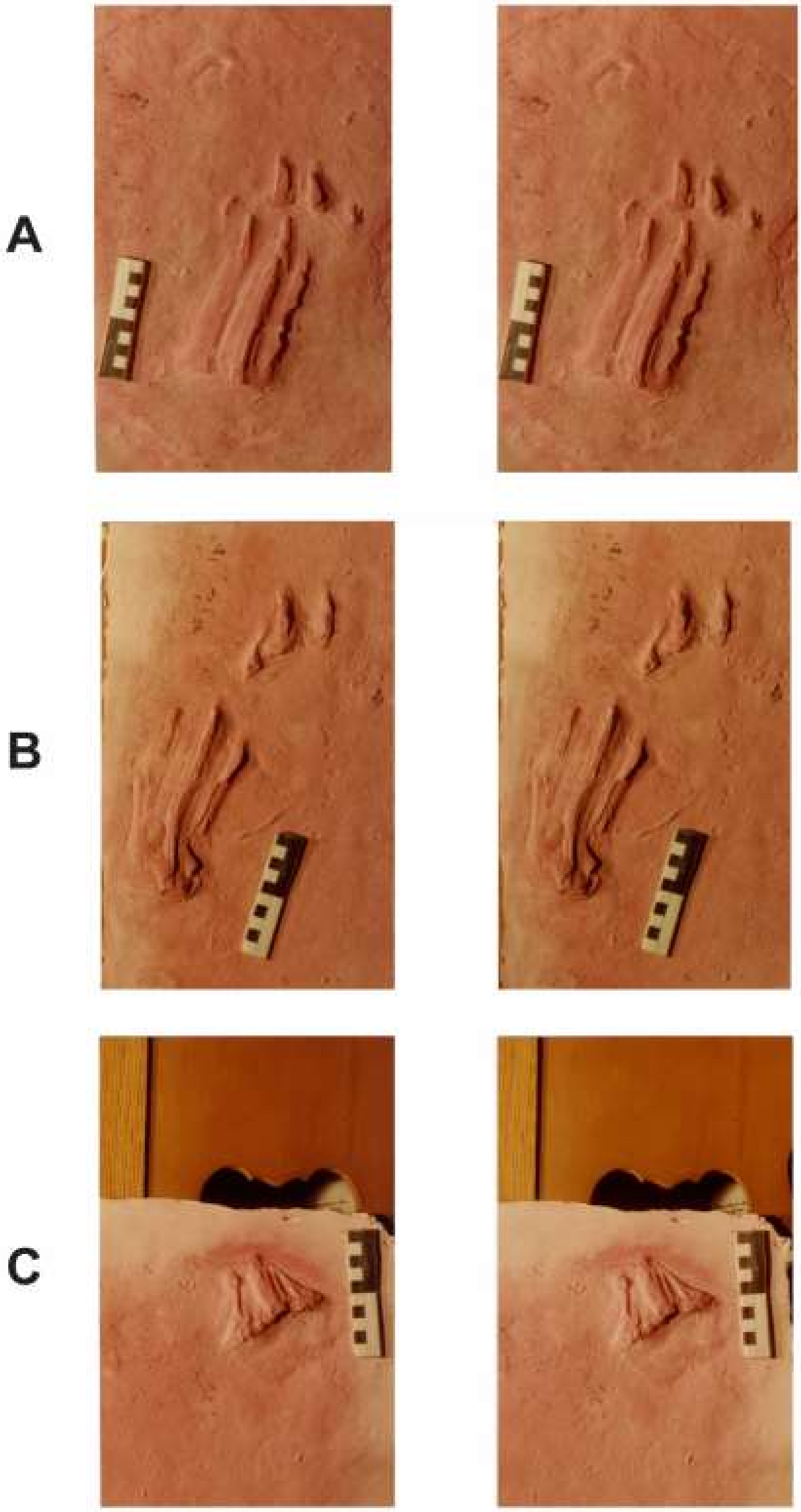


Fig. 7.5. Stereo pairs of tracks from UALVP 134 (replica cast). Scale bar = 10 cm. A manus/pes set 1 (left), B manus/pes set 2 (right), C pes 3 (left).

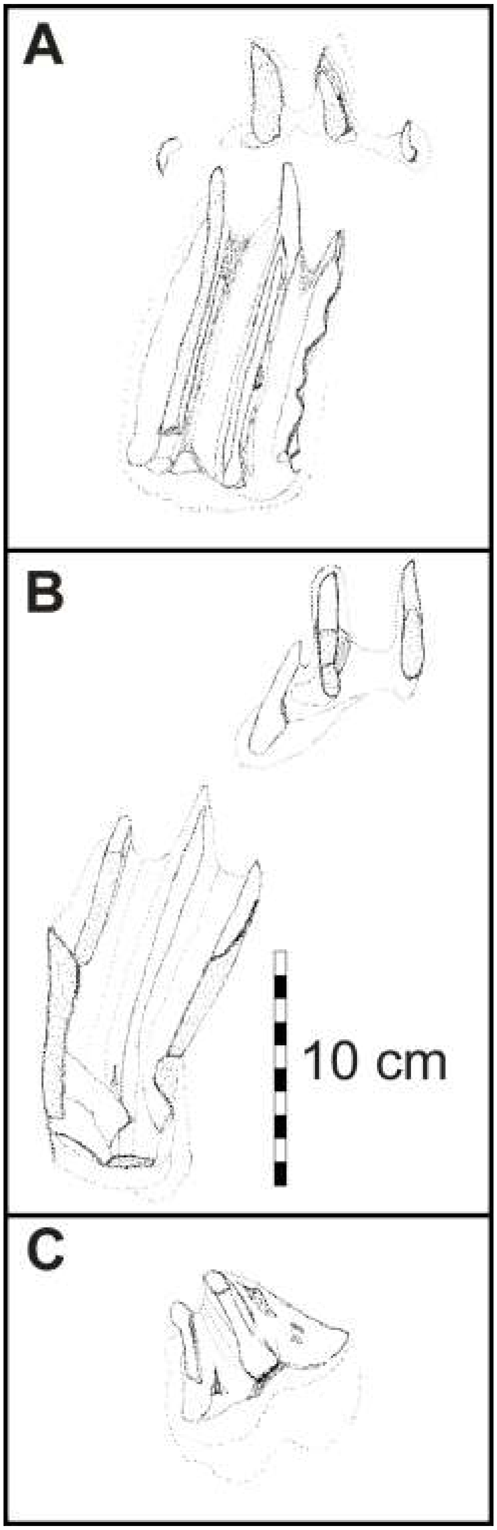


Fig. 7.6. Illustrations of footprints of UALVP 134. A. manus/pes set 1 (left), B. manus/pes set 2 (right), C. pes 3 (left).

Holotype: UALVP 134; natural cast of a trackway with 3 pes prints (two left; one right) and two manus prints (one left; one right). Curated at the University of Alberta, Laboratory for Vertebrate Paleontology, Edmonton, Alberta.

Etymology: In honour of Loris S. Russell's original work on this and many other palaeontological specimens from the Paleocene of western Canada.

Diagnosis: As for ichnogenus.

Horizon and Locality: Paskapoo Formation (late Paleocene: middle Tiffinian), Red Deer River, about 1 km west of Red Deer, Alberta.

Remarks: The tracks of UALVP 134 were initially described as mammalian, (Rutherford and Russell, 1928; Russell, 1930) possibly of condylarthian affinity. Recently, this specimen was still regarded as mammalian, with the track-maker being either a creodont (Scrivner, and Bottjer, 1986) or an amphicyonid (Sarjeant, et al., 2002). Sarjeant et al., (2002) found similarities between their newly described mammalian ichnotaxon, *Hirpexipes alfi* (Order Carnivora; Family Amphicyonidae) and the UALVP 134 prints, but also cited many differences in the number and nature of the digits (including claws), and the degree of heteropody (less pronounced in *H. alfi*). There are no phalangeal, metacarpal or metatarsal pads present on any of the *Albertasuchipes russellia* tracks, characters that are usually present in modern and fossil terrestrial mammal tracks except ungulates (Jaeger, 1948; Murie, 1974; Stokes and Stokes, 1986; Sarjeant and Wilson, 1988; Rezendes, 1992; Sarjeant and Langston, 1994; Halfpenny, 1998; Kaler, 1998; Remeika, 1999; Sarjeant, et al., 2002). We found that *Albertasuchipes russellia* prints are morphologically similar to modern crocodylian tracks and trackways (Jaeger, 1948; Demathieu and Haubold, 1974; Reineck and Howard, 1978; Padian and Olsen, 1984; Olsen and Padian, 1986; Zug, 1974) as well as fossil tracks and trackways attributed to crocodylians and crocodylomorphs (Haubold, 1971; 1974; Padian and Olsen, 1984; Olsen and Padian, 1986; Bennett, 1992; Demathieu and Sciau, 1992; Lockley and Hunt, 1995a; Coombs, 1996; Fuentes Vidarte and Meijide Calvo, 1999; Lockley and Meyer, this volume).

Padian and Olsen (1984) recorded the trackway characteristics of a modern caiman (*Caiman sclerops*) to compare with a *Pteraichnus saltwashensis* trackway from the Morrison Formation of Arizona. Lockley et al., (1995) observed that the manus prints of the caiman trackway were always anterior to the pes, or are just slightly overlapped by them, a feature that is seen in the UALVP 134 specimen. Overall, there is a good deal of similarity between the *Caiman* sp. trackway and the *A. russellia* trackway, with the exception of a tail drag impression which is usually associated with crocodylian tracks produced during a high walk (Zug, 1974; Lockley et al., 1995). Although this significant feature is lacking in the UALVP 134 specimen, it does not necessarily negate the identification of the track-maker as a crocodylian. Sometimes animals whose tails are long and heavy in proportion to their bodies, including salamanders (Peabody, 1959), and lizards (Leonardi, 1975), do not always leave tail impressions. Reasons for the absence of tail drag marks in such animals have been attributed to behavior, gait, and consistency of the substrate. If the footprints were made underwater, then the tail may also have been floating above the substrate. The presence of a single turtle track (Fig. 7.7) may indicate that the UALVP 134 tracks were produced in subaqueous conditions, an interpretation that is discussed below. The absence of a tail impression should not be considered diagnostic for identifying the trace-maker, although when it is present it could be quite helpful.

Fig. 7.7. Photograph of single turtle print on UALVP 134 (scale bar = 10 cm).

There are faint, convex impressions (anteriorly oriented) that are associated with the anterior regions of some of the pes and manus digits, and these interconnect adjacent digits. These markings may represent inter-digital webbing which crocodylians do possess, but may just represent displaced sediment caused by the weight of the animal. The pes tracks of UALVP 134 correspond well to the morphology of modern and fossil crocodylian and crocodylomorph tracks with the exception that one digit (possibly digit V) left no impression. The proportions of the digits that did impress, the near parallel nature of the impressions, and the possible presence of webbing are quite similar to that of the modern *Alligator ?mississipiensis* illustrated by Olsen and Padian (1986). The manus tracks of UALVP 134, are also similar to the *A. ?mississipiensis* track of Olsen and Padian (1986) with the lack of impressions of digits I and II which are in a posterior attitude while digits III-V are facing forward. There may be a trace of manus digit II associated with the first manus track on the *A. russellia* trackway, (Russell, 1930) just anterior and to the inside of the inner pes digit (Figs. 7.5a and 7.6a). We speculate that because the manus tracks of UALVP 134 are positioned immediately anterior to the pes prints that the impressions of manus digits I and II may have been overprinted by the pes if the manus was placed in the same position as the manus of *A. ?mississippiensis* illustrated by Olsen and Padian (1986). There certainly are digit impressions not represented on the trackway of the UALVP 134 trackway, but these are minor features that can be included in an emended description if a more complete specimen is discovered in the future.

We find that *A. russellia* shares some similarities with *Champsosaurichnus parfeti* (Lockley and Hunt 1995a), as both possess characteristics of crocodylomorph reptiles. However, *C. parfeti* prints are smaller than those of *Albertasuchipes russellia*, and there is a greater degree of heteropody between the manus and pes impressions in the *A. russellia* specimen because Lockley and Hunt, (1995a) were unable to distinguish whether the holotype print of *C. parfeti* was a manual or pedal print. There is not the same degree of symmetry observed in the *A. russellia* prints as there is in *C. parfeti* prints. Based on the above differences we cannot attribute *A. russellia* prints to the action of a champsosaur reptile.

Lockley and Meyer (this volume) discuss the status of two vertebrate ichnofamilies Batrachopodidae (Lull, 1904), and Crocodylopodidae (Fuentes Vidarte and Meijide Calvo, 1999), which together contain several crocodylomorph ichnotaxa. Emended diagnoses of these two ichnofamilies by Lockley and Meyer (this volume) show that they are quite similar. The Batrachopodidae essentially contains ichnotaxa that are "stout-toed" forms with narrow digit divarication and the Crocodylopodidae are composed of ichnotaxa of "slender-toed" forms with wide digit divarication (Lockley and Meyer, this volume). A comparison of *A. russellia* with ichnotaxa of both of these ichnofamilies suggests that *A. russellia* has more in common with the Batrachopodidae and should be placed within that ichnofamily. The digits of *A. russellia* are quite robust in outline and lack the degree divarication seen in the Crocodylopodidae. *A. russellia* prints differ from those of *Batrachopus* ichnosp. and allies (see Olsen and Padian, 1986) in that there are no visible digital pad impressions, but this may be a preservational difference since several specimens attributed to *Batrachopus* ichnosp. lack digital pad impressions and not all digits were impressed in some specimens (Olsen and Padian, 1986).

Distinct differences exist between *A. russellia* and the two ichnotaxa (*Antipus flexiloquus* Hitchcock 1858 and *Crocodylopodus meijidei* Fuentes Vidarte and Meijide Calvo 1999) assigned to Crocodylopodidae. Both *A. flexiloquus* and *C. meijidei* are slender-toed forms with wide digit divarication (Lockley and Meyer, this volume). Given the differences between *A. russellia* and the two ichnotaxa currently within Crocodylopodidae it seems best not to place *A. russellia* within Crocodylopodidae, but rather with the more similar ichnotaxa under Batrachopodidae.

No direct comparisons were made between Paleocene crocodylian fossils and the UALVP 134 trackway though crocodylian skeletal taxa such as *Borealosuchus* sp., (Wu et al., 2001; Brochu, 2000) and *Leidyosuchus* sp., (Brochu, 1997) are known to occur in Paleocene deposits in western Canada. It would be interesting to eventually make comparisons between these crocodylian skeletal taxa and the UALVP 134 trackway to see if they match up

CLASS MAMMALIA

ORDER CREODONTA

Ichnofamily Sarjeantipodidae

McCrea, Pemberton and Currie, nov

Diagnosis: Trackway of a medium-sized mammalian predator, with digitigrade to plantigrade footprints. Manus one-half to two-thirds size of pes. Manus prints are partially or completely overprinted by pes prints. Manus tetradactyl, pes pentadactyl (digit I impression reduced or absent). Pes digit II-IV are of similar length; pes digit V is shorter than digits II-IV and digit I (if present) is the shortest. Manus digits III and IV are of similar length and are the longest, with digit II being only slightly shorter; manus digit V is the shortest. Manus digits II-V and pes digits

II-V each with a single phalangeal pad with a rounded posterior margin. Acuminate claw impressions may be present on the manus, but are not always obvious. Total divarications of the digits for both the manus and pes are just over 100 degrees. There is a good deal of variability of divarication between digits of the manus and pes, although the variability is less in the pes. The metacarpal pad is roughly triangular to pentangular in shape with rounded margins; the metatarsal pad not always visible due to overprinting, but is similar to the metacarpal pad where present. There is a space between the digit impressions and the metacarpal and metatarsal pads. Pace length of pes, approximately one-third of a meter; stride length just over one-half meter. Pes pace angulation approximately 130 degrees.

Type Ichnogenus: *Sarjeantipes* ichnosp., McCrea, Pemberton and Currie, herein

Other Included Ichnogenera: *Quirtipes* ichnosp., Sarjeant, Reynolds and Kissell-Jones, 2002.

Ichnogenus *Sarjeantipes* ichnosp.
McCrea, Pemberton, and Currie, nov.

Etymology: In honour of William A.S. Sarjeant, who made many substantial contributions to the field of vertebrate ichnology; -ipes to identify this as a vertebrate ichnotaxon.

Diagnosis: Trackway of quadruped with pronounced heteropody; manus tetradactyl, semi-digitigrade and about 2/3 length of pes. Manus impressions with distinct triangular to pentangular main pad. Manus digits II - V and pes digits II-V with single distinct phalangeal pads with rounded posterior margins. Phalangeal pads of manus separated by space from metacarpal pad. Manus digit impressions terminating in acuminate claws. Manus slightly wider than long. Pes pentadactyl, plantigrade with distinctly concave, bi-lobed heel. Pes digits terminating in rounded claw impressions. Pes slightly wider than long with distinct phalangeal pads. Metatarsal pad not seen due to overprinting. Pes digits II and IV approximately 5% shorter than digit III. Pes digit V is short, being only 80% of the mean length of digit III. Pes digit I is the shortest, only 65% of the length of digit III. Digits III and IV are longest in manus, with digit II only slightly shorter than digit IV. Digit V shortest in manus, 70-80% of lengths of digits III and IV respectively. Total divarications of digits for both manus and pes are approximately 108 degrees. Good deal of variability of divarication between digits of manus and pes, although more so in manus. Pace length of pes, approximately one-third meter and stride length just over one-half meter. Trackway narrow, about one pes width; pes pace angulation approximately 130 degrees. Inner margin of pes tracks near trackway axis; pes rotation low ($\dot{x}$= +1.4 degrees; outward) based on alignment of digit III (longitudinal axis), in relation to trackway midline. Placement of the manus is to outside of trackway midline; manus rotation is variable.

Type Ichnospecies: *Sarjeantipes whitea* McCrea, Pemberton, and Currie herein. Paleocene (Torrejonian), Alberta.

Sarjeantipes whitea

McCrea, Pemberton, and Currie, ichnosp. nov.

Figs. 7.2, 7.3, 7.8 A-F, 7.9 A-F and 7.10

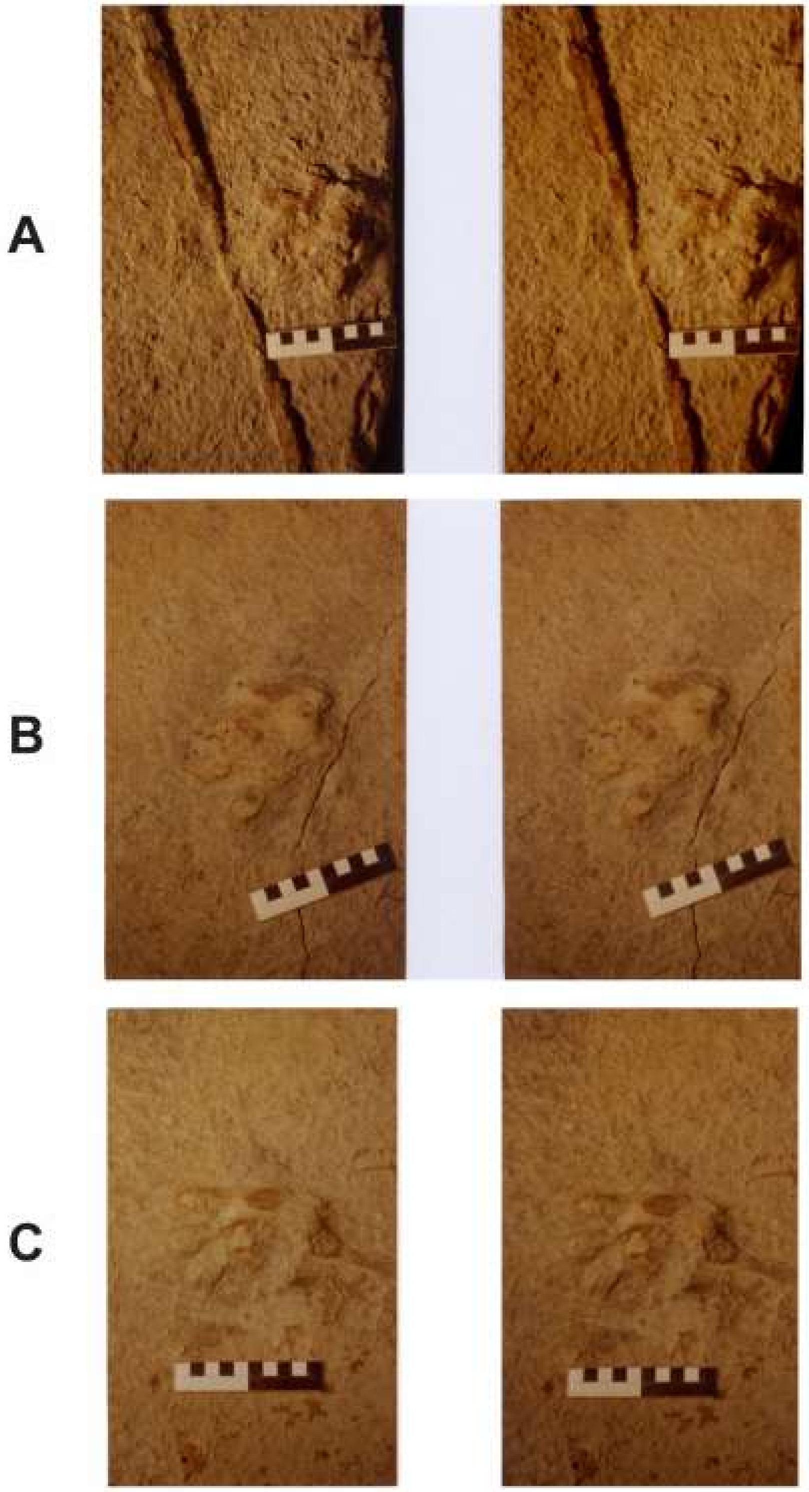

A
B
C

Fig. 7.8. Stereo pairs of tracks from TMP 90.131.01 (original). Scale bar = 10 cm. A. manus/pes set 1 (right), B. manus/pes set 2 (left), C. manus/pes set 3 (right), D. manus/pes set 4 (left), E. manus/pes set 5 (right), F. manus/pes set 6 (left).

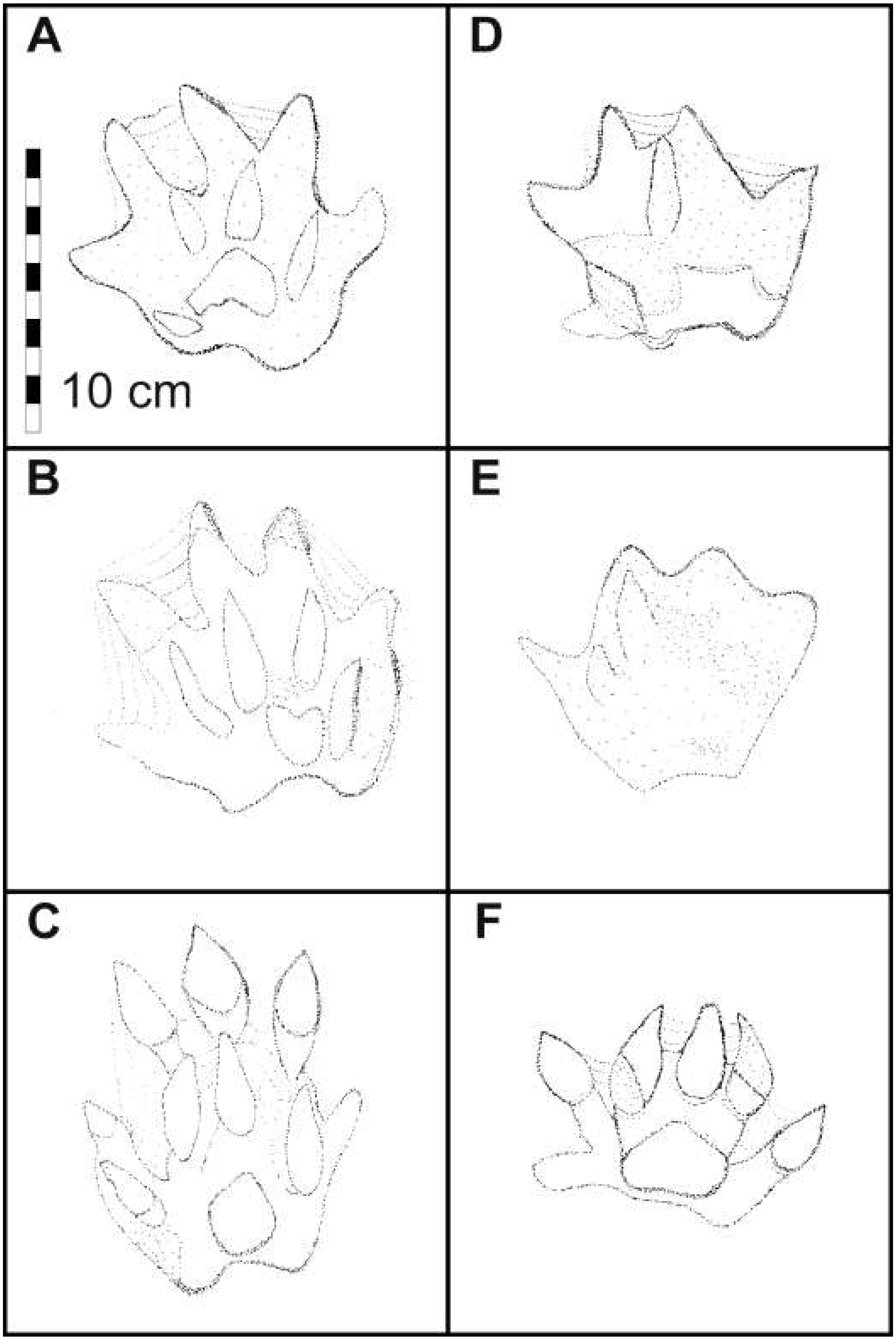


Fig. 7.9. Illustrations of footprints of TMP 90.131.01. A. manus/pes set 1 (right), B. manus/pes set 2 (left), C. manus/pes set 3 (right), D. manus/pes set 4 (left), E. manus/pes set 5 (right), F. manus/pes set 6 (left).

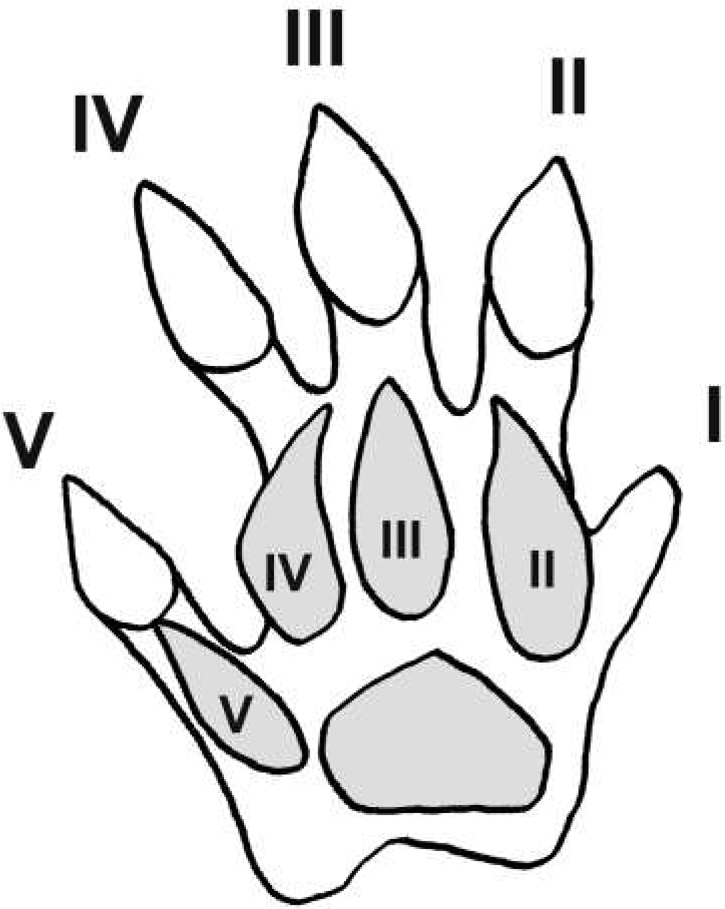


Fig. 7.10. Composite drawing (outline) based on TMP 90.131.01 track specimens.

Etymology: In recognition of Gordon White, who participated in the discovery and recovery of the footprints.

Diagnosis: As for ichnogenus.

Holotype: Specimen TMP 90.131.01; natural cast of a trackway with 6 pes prints (3 left; 3 right) and 6 manus prints (3 left; 3 right). Curated by the Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta.

Dimensions (Table 7.1): Average manus length is 65 mm, average manus width is 70 mm. Manus print rotation is somewhat more variable than that of the pes. The average pes pace is 314 mm, and stride is 577 mm. The average pes pace angulation is 134 degrees. The average manus pace is 329 mm, stride is 601 mm and pace angulation is 128 degrees. Average pes length is 101 mm, average pes width is 105 mm. Pes digit divarication approximately 108 degrees. Divarication of pes digits I-II and IV-V are approximately 30 degrees. Divarication between pes digits II-III is approximately 25 degrees, between digits III-IV is 18 degrees. Pes impressions completely overlap those of the manus. There is generally little rotation of the pes prints in relation to the midline of the trackway. Inner trackway width (TWi) for the manus tracks it is 66 mm and for the pes tracks is 15 mm; the outer trackway width (TWo) of the manus was 200 mm and 231 mm for the pes. Gleno-acetabular dimension measured as 57.5 mm (Pes 1 and 2 and manus 3 and 4).

Horizon and Locality: Porcupine Hills Formation (Upper Paleocene: late Torrejonian), Community of Signature Park, Calgary, Alberta: exact legal land description unknown.

Remarks: The *Sarjeantipes whitea* trackway was produced by a short-bodied animal walking in a straight line in the first part of the trackway. The tracks indicate that the animal made a slight turn of 20 degree to the left at the midpoint in the trackway. The trackway ends soon after the turn was completed.

S. whitea differs from *Quiritipes impendens* Sarjeant, Reynolds and Kissell-Jones, 2002, in that the manual prints of *S. whitea* are nearly half the size of the pes prints (pronounced heteropody) while the pes prints of *Q. impendens* are only, "…somewhat larger…" than the manus prints (Sarjeant, et al., 2002). In most manus/pes sets, *S. whitea* manual prints are positioned between the heel and digital hypex region of the overlying pes prints. The pes of *S. whitea* possesses five digits in most of the footprints studied, while *Q. impendens* appears to have only four pes digits impressed in all cases. However, Sarjeant et al., (2002) attribute *Q. impendens* tracks to creodonts, a group that they acknowledge as having retained five pes digits until the time of their extinction in North America in the late Oligocene.

S. whitea pes prints are semi-plantigrade to plantigrade. The manual prints could be considered semi-digitigrade. However, morphological details of the posterior regions of the manus prints are difficult to distinguish due to primary overlap of the pes prints. The pes digits of *S. whitea* are more divergent than those of *Q. impendens*, although this may be merely a consequence of substrate consistency and gait. The heel of the *S. whitea* pes is distinctly bi-lobed with no indication of the longer, sub-rounded heel seen in the *Q. impendens* prints.

With FL/FW ratios of 0.97 and 0.93 for the pes and manus respectively of *S. whitea*, compared to FL/FW ratios of 1.70 and 1.63 (pes and manus) for *Q. impendens* (calculated using measurements given by Sarjeant, et al., 2002), there is sufficient grounds for designating a separate ichnotaxon at the ichnogeneric level for the TMP 90.130.1 trackway. *Q. impendens* prints lack claw impressions (Sarjeant et al., 2002), but this may be a preservational issue. The morphology of *Q. impendens* prints accords well enough with *S. whitea* prints in many other aspects, which justifies its inclusion within the Ichnofamily Sarjeantipodidae.

Quirtipes ichnosp. was not selected as the type ichnogenus for Sarjeantipodidae because of the lack of trackway data (pace, stride, pace-angulation) due to the track-bearing slabs not being assembled properly (Sarjeant et al., 2002). The trackway of *Sarjeantipes* ichnosp. is on a single well-consolidated block which makes trackway measurements much more reliable for the purpose of characterizing this new ichnofamily. Lockley and Meyer (2000) mention a vertebrate ichnotaxon *Hyaenodontipus* sp. from the upper Eocene of France described by P. Ellenberger in the early 1980's. The name *Hyaenodontipus* sp. implies a hyaenodontid creodont track-maker, and these prints may be similar enough to be included in Sarjeantipodidae.

It is possible that the makers of *Quirtipes* ichnosp. and *Sarjeantipes* ichnosp. tracks were of similar morphology to hyaenodontid creodonts such as *Prolimnocyon atavus*, figured by Gebo and Rose (1993). Gebo and Rose (1993) speculated that some creodonts could have had a "scansorial" habit, being equally proficient walking on the ground or climbing trees.

DISCUSSION

Other Paleocene track records

There are only a few Paleocene track sites reported from North America with no certain reports of footprints from any other continent. The Paleocene of Europe has produced no footprints as yet (Lockley and Meyer, 2000). The Paleocene track record of South and Central America appears to be little better. Although many Tertiary tracksites are poorly dated, most appear to be mid-late Tertiary in age (Leonardi, 1994). We are unaware of Paleocene tracks being reported from any other continent. Lockley and Meyer (2000) refer to the global vertebrate track record of the Paleocene as "impoverished the world over" so perhaps this is not surprising. The bulk of reliably dated Paleocene tracks are from north-western North America. Gilmore (1928) described a new ichnotaxon of amphibian tracks from Montana, *Ammobatrachus montanensis*, from the Fort Union Formation (early Paleocene) which were later renamed *Ambystomichus montanensis*, by Peabody (1954). Johnson (1986) documented amphibian tracks and two types of bird tracks from the Fort Union Formation of Wyoming, but did not name any of them. Lockley and Hunt, (1995b) mention the existence of bird and small mammal tracks only 60 cm above the K/T iridium layer at a locality in Colorado within the Raton Formation. Lockley and Hunt (1995b) also describe bird and "dog-like" tracks and trackways of creodonts from a site near Baggs, Wyoming (no formation name given) that they claimed to be of Paleocene age. These creodont track specimens were reported by Lockley and Hunt (1995b) to be on display in the Raymond Alf Museum in Claremont, California. Although Lockley and Hunt (1995b) did not mention any specimen numbers, the creodont tracks appear to be the same specimens recently described and named *Quirtipes impendens* by Sarjeant, et al., (2002). However, Sarjeant et al., (2002) claim that the *Q. impendens* slabs are from the Eocene (Wasatchian) Muddy Creek Formation, not the Paleocene as Lockley and Hunt (1995b) reported.

Other fossil mammal footprints from western Canada

Sarjentipes whitea prints were not the first mammal footprints to be described from pre-Quaternary strata of western Canada, but they are by far the most complete and convincing. The earliest report of fossil mammal prints from western Canada was a single manus/pes set (BCPM 1222), possibly from the mid-Cretaceous Gething Formation of northeastern British Columbia. This was introduced as a new ichnotaxon (*Duquettichnus kooli*) by Sarjeant and Thulborn (1986). Another mammalian ichnotaxon (*Tricorynopus? brinkmani*) was described from the mid-Cretaceous Gates Formation of western Alberta (McCrea and Sarjeant, 2001). The supposed mammalian prints were discovered on a small isolated piece of rock (TMP 98.89.20) which contained the natural molds of several avian prints. The number of prints identified as possible mammalian prints were very few and did not occur in a trackway. Sarjeant (2000) admits that the assignment of the purported mammalian prints from the Gates Formation to the Late Eocene mammal ichnotaxon *Tricorynopus* Sarjeant and Langston (1994), "…, is in the highest degree tentative". Two other slabs (TMP 2000.44.01 and TMP 2000.44.02) were reported by Sarjeant (2000) as possibly having mammalian tracks on them. Later examinations by the first author, of the original slabs as well as the photographs and figures from Sarjeant (2000) revealed the possibility that the "mammal" prints are most likely partial avian prints or are the result of two or more partial avian prints overlapping each other. The bedding plane from which the footprint slabs (TMP 98.89.20, 2000.44.01 and 2000.44.02) had originated was located by the first author and Martin Lockley (University of Colorado at Denver). Several slabs and counter slabs were collected (TMP 99.49.01) and were pieced together at the Royal Tyrrell Museum of Palaeontology in early February, 2001. Close inspection of these specimens by the first author in February, 2001 and May and December of 2002 failed to reveal any footprints other than those of avian origin.

Possible aquatic origin of UALVP 134 trackway

There are some indications that the *Albertasuchipes russellia* trackway (UALVP 134) may have been produced in very wet, possibly aquatic conditions. There are prominent longitudinal slip marks associated with the digits. Furthermore, the claw impressions of the first two pes prints are very long (Figure 7.5A-B), which likely occurred during the touch down and weight-bearing phase of the step cycle (Thulborn and Wade, 1989) when pressure was applied to the slippery substrate. There are indications of back-slipping of digit III of the first two pes prints (Figure 7.5A-B) where a deeper impression of the tips of these digits can be found approximately 20-40 mm behind the foremost impression of the same digits, and which were probably produced during the kick-off phase of the step cycle (Thulborn and Wade, 1989). This degree of back-slipping could be interpreted as the action of an animal on a very slippery substrate, or of an animal that was partially buoyed up by the water in an aqueous setting. The UALVP 134 trackway definitely does not exhibit the typical “trotting’ behavior described by Russell (1930). The manus impressions are placed in front of the pes impressions, perhaps with partial overlap, indicating an animal that was moving at a fairly low speed. If the animal were trotting we would expect to see the manus prints overlapped by the pes prints to a greater degree as in the modern *Caiman* sp. trackway produced by an animal in a rapid walk (Padian and Olsen, 1984).

One indication that the *A. russellia* trackway could have been produced in subaqueous conditions is the presence of a single tridactyl footprint with distinct claw impressions (Figure 7.2 and 7.7). This single impression resembles the morphology of some modern turtle tracks (Jaeger, 1948; Chamberlain, 1975; Stuart and Stuart, 1994) and also resembles the morphology seen in some of the fossil prints attributed to turtles (Bernier et al.,1982; Sarjeant and Langston, 1994; Foster et al., 1999). The existence of the small tridactyl print on the UALVP 134 specimen was not mentioned in Rutherford and Russell (1928) or Russell (1930). The original substrate would have been sufficiently fine-grained for this small reptile to have made other impressions if it had been walking in a fully terrestrial setting. The orientation of the print on the block is such that one would expect to see others in a line of progression if the substrate had been fully terrestrial. It is possible that this single print could have been produced by a swimming turtle that made brief contact with the substrate. Zug (1971) describes two distinct types of aquatic locomotion for turtles, true swimming, where the animal propels itself through the water without making contact with the substrate, and bottom walking, where the limbs are in contact with the substrate. The first author videotaped a fully aquatic turtle in an aquarium at the Royal Tyrrell Museum in February, 2002. Though the individual was exhibiting the true swimming locomotion described by Zug (1971), the animal occasionally made contact with the substrate with one or more limbs at a time. It is possible that this sort of swimming behavior could account for the single turtle track on the UALVP 134 slab. If this substrate was truly at the bottom of a shallow body of water the *A. russellia* track-maker could have been bottom walking as well. The tail may have made infrequent contact with the substrate if it made contact at all as the tail would have buoyed up by the water to some extent.

Russell (1930) records a 45° turn to the right by the track-maker recorded by the position of the last (left) pes impression. This pes impression certainly does have a different angle of rotation in relation to the midline than the two previous pes impressions. Russell (1930) considered the last pes impression as being partially incomplete as it is much shorter than the two previous pes impressions, and occurs near the edge of the slab. The last pes impression actually ends one to two centimeters before the edge of the trackslab. The surface between the last pes impression and the edge of the block is smooth, showing no signs of breakage. The pes track itself shows no sign of attenuation, though the pes digits are noticeably convergent and the pes is oriented downwards at an angle of 15 degrees. This naturally incomplete trace could be a record a different sort of locomotion than that which produced the previous two pes prints. Perhaps the animal shifted from a bottom walk to a full swim initiated by a kick that left a partial impression in the substrate. There is no way to be certain of this interpretation because the trackway ends at that point, so we are left with speculation, which may not be nearly as colorful as that of Russell (1930).

Future research

In the spring of 2001, a brief field excursion to the area along the Red Deer River valley where the UALVP 134 specimen was collected did yield up a single eroded block with natural casts of footprints on it. There were two or three vertebrate tracks of probable reptilian origin (possibly from a turtle or a small crocodylian) on the block. Plans are currently underway to survey the banks of the Red Deer River valley in this area for additional Paleocene footprint material. It is doubtful if any further footprint finds will be made in the Signal Hill area in Calgary due to the established residential areas whose construction brought about the first track discovery from this site. It is possible that future industrial or residential excavations in the Calgary area could uncover additional footprints, but it is far from certain that they would be recognized for what they are and be reported to the proper institution.

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8.0 VERTEBRATE ICHNOPATHOLOGY: PATHOLOGIES INFERRED FROM DINOSAUR TRACKS AND TRACKWAYS FROM THE MESOZOIC

The contents of this chapter were taken verbatim from a paper published by the journal *Ichnos* on September 11, 2015. This paper was a result of a collaborative effort by several authors, and in order of priority these are: Richard T. McCrea, Darren H. Tanke, Lisa G. Buckley, Martin G. Lockley, James O. Farlow, Lida Xing, Neffra A. Matthews, Charles W. Helm, S. George Pemberton, and Brent H. Breithaupt. The candidate wrote the majority of the paper (>60%)

Keywords: Dinosaur tracks, amputation; antalgic gait; compensated gait; Jurassic, Cretaceous; ichnopathology; laterality; irregular gait; limping gait; shuffling gait; waddling gait.

Institutional Abbreviations: FGM – Fraser-Ft. George Museum; **PRPRC** – Peace Region Palaeontology Research Centre; **TMP**- Royal Tyrrell Museum of Palaeontology; **UALVP** – University of Alberta Laboratory for Vertebrate Paleontology; **UCM** – University of Colorado Museum

INTRODUCTION

Over the course of the past few decades there has been a marked increase in the literature of pathology of dinosaurs (e.g. Tanke and Rothschild, 2002 and references therein). However, the literature on inferred pathology from dinosaur tracks and trackways (ichnopathology) has not seen a corresponding increase. Reports on ichnopathology in dinosaurs have been infrequent, with perhaps less than one paper published per decade since the beginning of modern studies of dinosaur traces in the early 19th Century. It is possible that reports of ichnopathology have not kept pace with reports of pathologies on osteological specimens due to the various influences of track-bearing substrate, the behaviour of the track-maker, as well as a range of taphonomic factors which make such interpretations difficult. The sparse publication record of ichnopathology may also be a reflection of the cautious approach ichnologists employ when interpreting phenomena related to tracks.

Even with a restrained approach toward footprint and trackway interpretation, some dinosaur tracks and trackways exhibit morphologies that have defied explanation by conventional behaviours of the track-maker, or by the physical and dynamic qualities of the track surface, both pre- and post-burial.

This paper discusses previous reports of dinosaur ichnopathology with reinterpretations where such is warranted. Several recent and new reports of dinosaur ichnopathologies are described, from sites in the Jurassic of China and the Cretaceous of North America. A number of criteria are proposed that will aid in the interpretation of ichnopathologies

MATERIALS AND METHODS

Series of overlapping photographic images were taken for photogrammetric imaging with a DSLR Camera (Canon EOS 7D) and rendered into 3D models using Agisoft Photoscan Professional (v 1.0.4) and Cloud Compare (v 2.5.3).

PREVIOUS REPORTS OF ICHNOPATHOLOGY

The literature of dinosaur ichnites and trackways demonstrating various pathological conditions was reviewed by Tanke and Rothschild (2002) and we summarize a few of these cases here. Hitchcock (1844) described a trackway as *Sauroidichnites abnormis*, a short trackway of four small, tridactyl prints from the Early Jurassic (Hitchcock, 1844, figs. 6, 7 and 8). Hitchcock (1844) thought that while the midlines of the two left prints were oriented toward the direction of travel, the two right prints were strongly rotated toward the trackway midline by nearly 45^o indicating an injury to the right foot. Upon examination of Hitchcock's illustration of the *Sauroidichnites abnormis* trackway (Hitchcock, 1844, fig. 8), it appears that the midline of print 1 (left) is oriented toward the direction of travel as Hitchcock initially described. Print 2 (right) of this trackway is strongly in turned toward the midline of the trackway as is print 4 (right). However, print 3 (left) is noticeably rotated toward the trackway midline, not as strongly as prints 2 and 4 though. It is likely that this trackway is one of the first described examples of ichnopathology.

Fourteen years later, Hitchcock (1858) reported on fossil tracks from the Early Jurassic of Connecticut and illustrated a trackway of a quadrupedal animal (pl. 36, fig. 8 and pl. 48, fig. 10) that exhibited only two digit impressions on the forefoot (Fig. 8.1) which he described as *Antipus bifidus*. In his description of *Antipus bifidus,* Hitchcock (1858) expressed confusion about the bifid footprint with associated tail impression, which seemed to be characteristic of ‘lizards’, but he was unable to reconcile the two digit prints with the anatomy of any known ‘lizard’. In his description of *Antipus bifidus* Hitchcock (1858) did not entertain the possibility that this print might have been from a track-maker that was missing a digit. Lull (1953) mentions the didactyl character of *Antipus bifidus*, but aside from referring to it as “a very questionable species” he did not consider the possibility of this print being pathological. As an entire lateral digit impression (possibly digit II if the probable tail impression belongs to the same track-maker) is missing it is likely that this could be the first legitimate example of an ichnopathology.

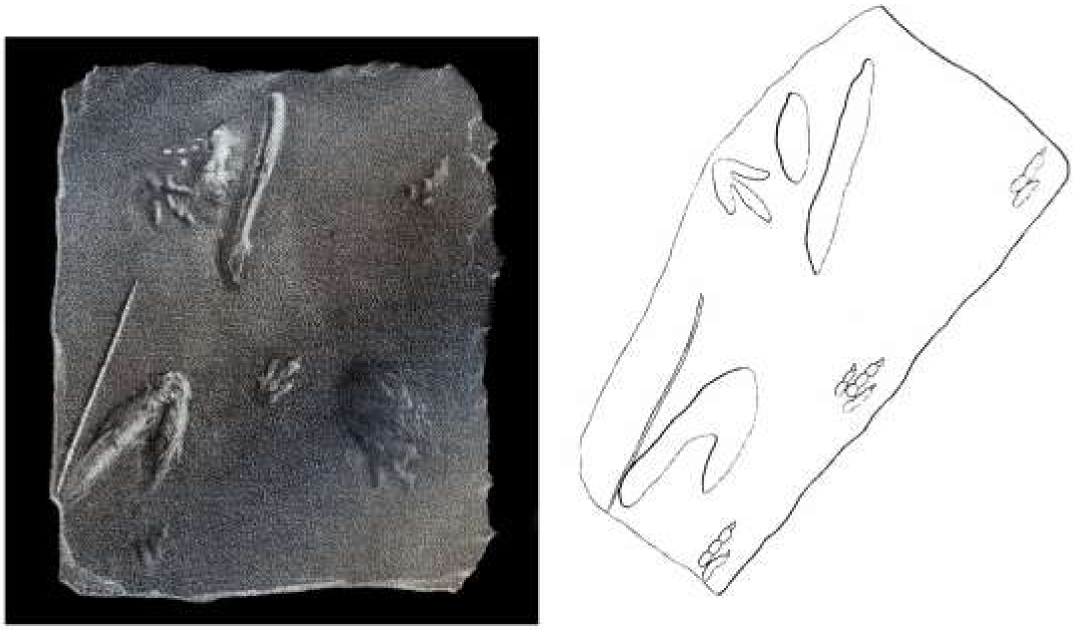


Figure 8.1. *Antipus bifidus* trackway with missing digit from the Early Jurassic of Connecticut. Left image modified from Hitchcock,1858 plate 48, figure 10. Right image modified from Hitchcock, 1858, plate 36, fig. 8. The right image has been scaled and rotated to match the orientation of the left image.

Inferred pedal digit loss in the right foot of an otherwise normal *Eubrontes* trackway from the Newark Supergroup (Late Triassic - Early Jurassic) was reported by Abel (1935). The missing digit impression was repeated in the trackway (Fig. 8.2) making this a convincing example of ichnopathology.

Figure 8.2. A Late Triassic – Early Jurassic *Eubrontes* isp. trackway from the Newark Supergroup with a missing digit (Abel, 1935). Figure modified from Lockley, 1991. Scale bar = 1 metre.

We suggest that trackways with one or more visible, repetitive pathologies, but with a nearly normal gait (no, or minimal trace of a limp), such as the *Eubrontes* trackway reported by Abel (1935) be classified as examples of *Compensated Gait*. Such trackways demonstrate that the track-making animal has adapted to, or compensated for the visible injury and its locomotion is very close to normal.

Tucker and Burchette (1977 p. 198) described prosauropod (*Anchisauripus*) ichnites from the Triassic (Norian) of south Wales with a "....distinctive malformation of digit III...." This specimen manifests strong angulation of the distal end of the toe impression which was repeated in several tracks, confirming this is not a normal substrate interaction. Tucker and Burchette (1977) did not report that the *Anchisauripus* trackway values (pace, stride, etc.) were abnormal so this trackway may be identified as an example of a compensated gait.

Jenny and Josen (1982) and Ishigaki (1986a, fig2,; 1986b; 1988) briefly described and figured a mid-Jurassic small theropod trackway from the Aganane Formation of Morocco exhibiting pathology that caused one of the toes to be abnormally positioned. This compelling example showed signs of both limping, (as defined by Dantas et al., 1994) and a malformed foot. Instead of the tridactyl foot having the toes more or less equally spread, digits III and IV are closely appressed (Fig. 8.3). An artistic rendering of the trackway and potential theropod track-maker was published as the front piece for the first chapter in Lockley's (1991) dinosaur tracks book. This trackway is classified as exhibiting a limping gait, with a visible and repetitive ichnopathology of a digit.

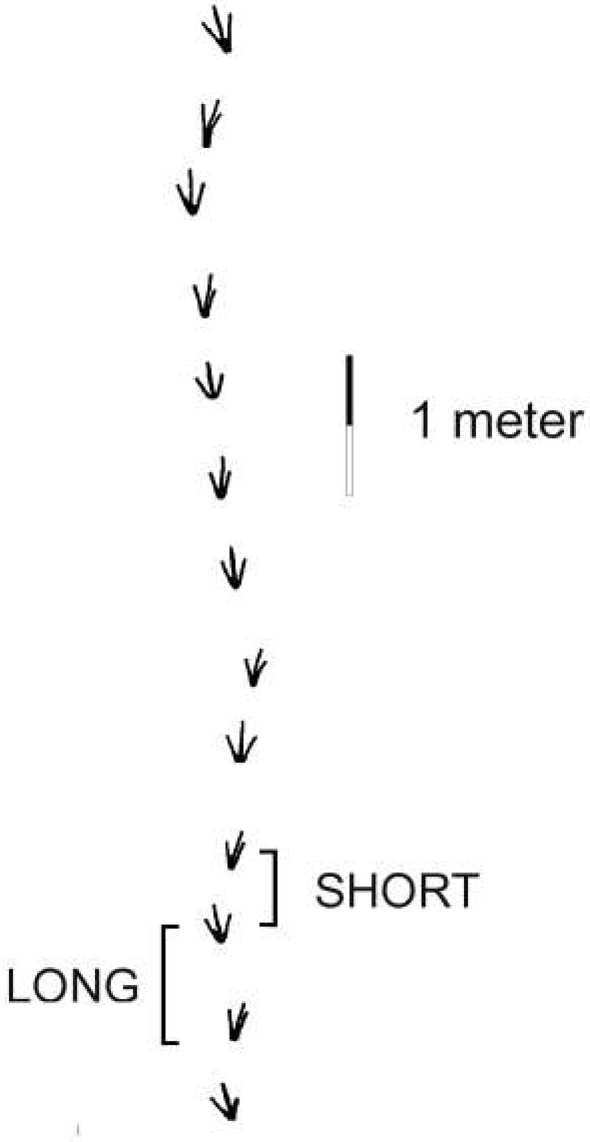


Figure 8.3. Irregular gait of a large theropod trackway with a repetitive impression of an abnormal digit II of the left footprint from the Middle Jurassic Aganane Formation of Morocco. Modified from Lockley et al., 1994.

Dantas et al. (1994) described a limping theropod and sauropod from Cabo Espichel and defined "limping" as follows: "…, an irregular gait in which one leg or foot is favoured over the other, resulting in consistent differences in the length of alternate steps". As there was no visible ichnopathology observed in any of the footprints, Dantas et al. (1994) considered that the trackways from Cabo Espichel may have been from animals with injuries on other parts of the body, or perhaps there was a congenital condition that affected the track-makers' locomotion. Dantas et al. (1994) also speculated that these trackways may be examples of gaits of healthy animals which were simply favouring one side over another. Furthermore Dantas et al. 1994 postulated that many such irregularities in otherwise normal trackways would become apparent if scrutinized.

Lockley et al. (1994) summarized a number of trackway occurrences of irregular gait, many of which appear herein and with the exception of the theropod trackway from Morocco (Jenny and Josen, 1982; Ishigaki,1986a; 1986b; 1988) these trackways are likely all examples of irregular gaits of healthy animals, rather than pathologically influence limping behaviour. We include a photogrammetric image of a large theropod trackway showing irregular gait from the Morrison Formation of Utah (Fig. 8.4).

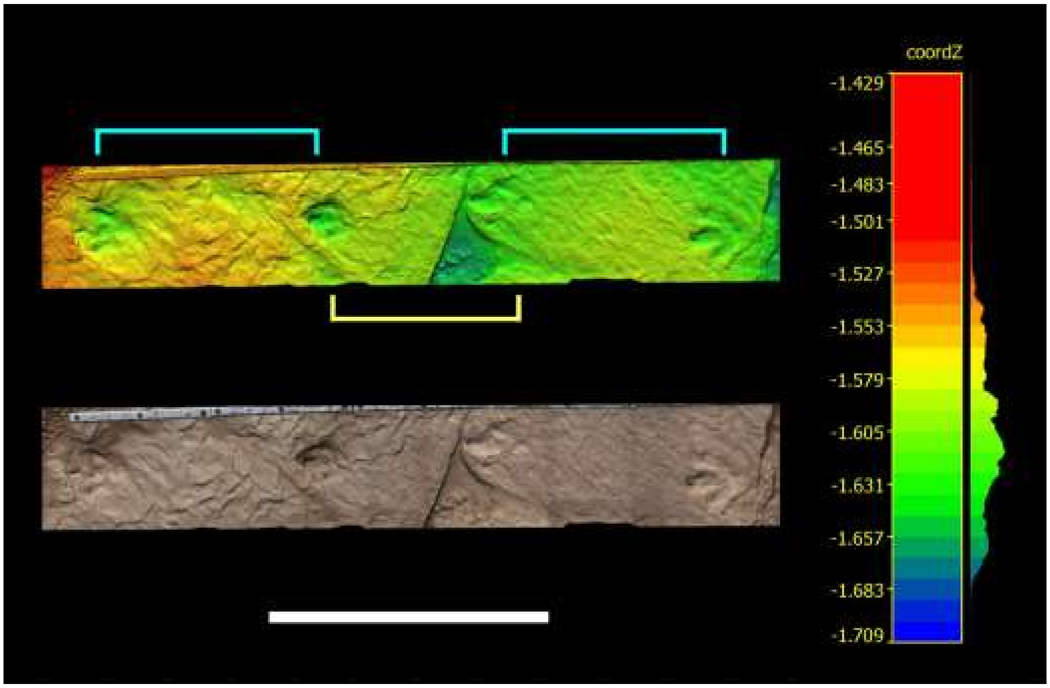


Figure 8.4. Photogrammetric images of a large theropod trackway showing an example of inequal gait. This trackway is from the Copper Ridge locality, near Moab Utah from the Upper Jurassic Morrison Formation and corresponds to part of the trackway from Lockley et al. (1994 fig. 3b). White scale bar = 2 meters. Vertical scale in meters.

Currie et al. (2003 – fig. 7e) reported an uncollected, single hadrosaur footprint from a locality in Mongolia that exhibited a bulbous expansion under the fourth digit impression that might be interpreted as soft tissue swelling. However, the authors wisely cautioned that this feature could just as easily be the product of the track-maker shifting its weight on the track surface during locomotion. If this is an ichnopathology, it adds to a very small record of known hadrosaur pedal pathologies (Tanke and Rothschild, 2014).

Avanzini et al. (2008) reported a possible pathology associated with a trackway of a large theropod with four consecutive prints from the Late Jurassic of Asturias, Spain. The ichnopathology involved digit IV and was seen on both right footprints in the trackway. The digit impression was oriented almost perpendicular to the midline of both of the right footprints resulting in a III-IV divarication value of 80^{o}, over 40^{o} greater than observed from the III-IV divarication values of the left prints in the same trackway. Avanzini et al. (2008) observed normal pace and stride length values for this trackway and this can be an example of a compensated gait.

RECENT AND NEW REPORTS

Lufeng Formation (Early Jurassic)

Few records of osseous abnormalities in Chinese dinosaurs have been documented. Formal reports include possible bacterial infection in the fibula of the basal ceratopsian *Psittacosaurus* (Lü et al., 2007), osteoarthritis in the theropods *Caudipteryx*, *Confuciusornis* and *Microraptor* (Rothschild et al., 2012), healed bite marks in *Sinraptor* (Tanke and Currie, 2000), and a healed fracture in the theropod *Yangchuanosaurus* (Xing et al., 2009). Possible palaeopathological phenomena have also been reported in the sauropods *Fusuisaurus* and *Mamenchisaurus*, although these were not described in detail (Xing et al., 2009). In addition, Xing et al. (2013a) reported a remodelled alveolus in the maxilla of the Early Jurassic theropod *Sinosaurus* as the first confirmed example of pathological or traumatic loss of teeth in a dinosaur. Xing et al. (in press) also describe two instances of pathological vertebral fusion in two genera of sauropodomorph dinosaurs (*Lufengosaurus huenei* and an unnamed basal sauropod) from the Early Jurassic Lufeng Formation in Yunnan, China. Both pathologies are consistent with spondyloarthropathy and represent the earliest known occurrence of that disease in dinosaurs. These two specimens affirm that early dinosaurs suffered from the same bone diseases as living vertebrates.

Reports of footprints or trackways from China bearing evidence of pathology are also very recent (Xing et al., 2009; Xing et al., 2012, Lockley et al., 2013; Xing et al., 2014).Two large theropod track specimens from Lufeng County in Yunnan Province of China referred to *Eubrontes pareschequier* (Lockley et al., 2013; Xing et al., 2014; formerly *Changpeipus pareschequier* Xing et al., 2009) may be examples of ichnopathology (Fig. 8.5). We are also aware that such relatively minor irregularities in footprint morphology could be due to the vagaries of preservation.

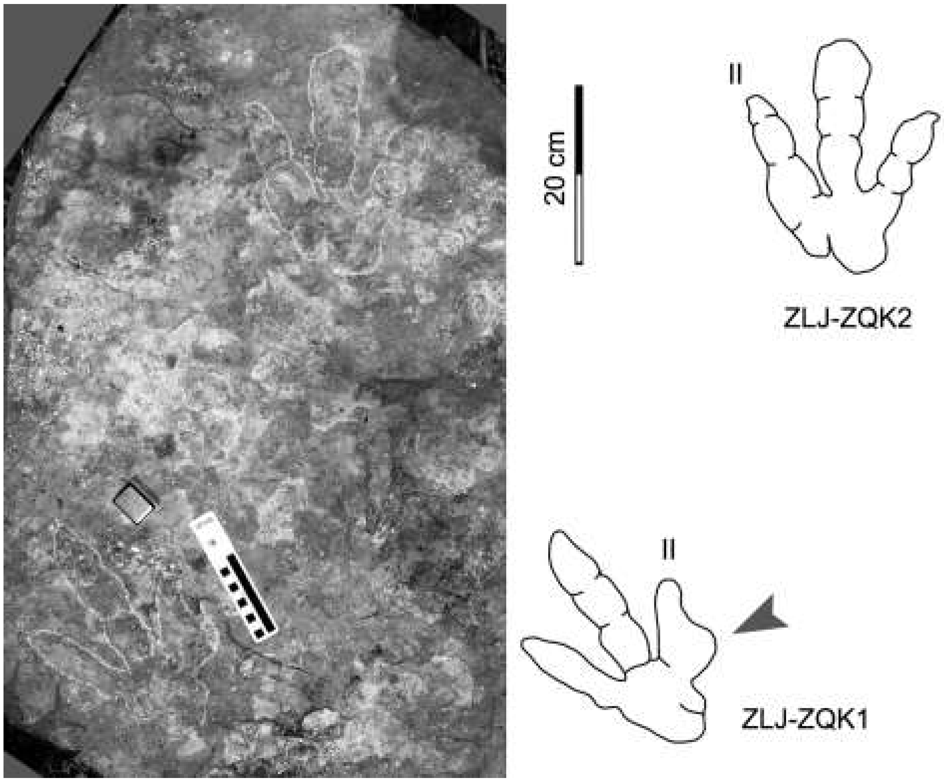


Figure 8.5. Two tracks of *Eubrontes pareschequier* with possible pathologies from the Lufeng Formation (Early Jurassic) Lufeng County, Yunnan Province, China. Left: photograph of trackslab with footprints outlined in chalk. Scale bar in cm. Right: outline drawing of the same footprints with ZLJ-ZQK2 showing absence of the terminal portion of the digit III impression, and ZLJ-ZQK1 exhibiting a swelling on the medial edge of the digit II impression.

Track specimen ZLJ-ZQK1 (Fig. 8.5) is a *Eubrontes pareschequier* track that exhibits a possible swelling feature that at the posterior-medial end of the track that is absent in ZLJ-ZQK2. Xing et al., (2009) interpreted this prominence as an oddly shaped or oddly distorted metatarsophalangeal pad. Xing et al. (2009) speculated that it could also represent pathology on the foot of the track-maker, constituting osteogenic tissue and bone marrow that were replaced by a hyperplasic mass of fibrous tissue. ZLJ-ZQK2 (*Eubrontes pareschequier*) is complete with the exception of the absence of the distal end of digit III (Fig. 8.5) which may represent the amputation or severe dislocation of the terminal end of this digit. These footprints were not found in context within trackways so the above interpretations of ichnopathology are speculative.

Laiyang Group (Early Cretaceous)

A single theropod track reported by Xing et al. (2012) from Jimo City, Shandong Province exhibits an unusually shortened digit II which may indicate an injury or congenital deformation on the foot of the track-maker (Fig. 8.6). As it is a single track it is possible that the missing digit could simply be an extra-morphological variant created by a particular behaviour of the track-maker, substrate interactions, or both (Xing et al., 2012).

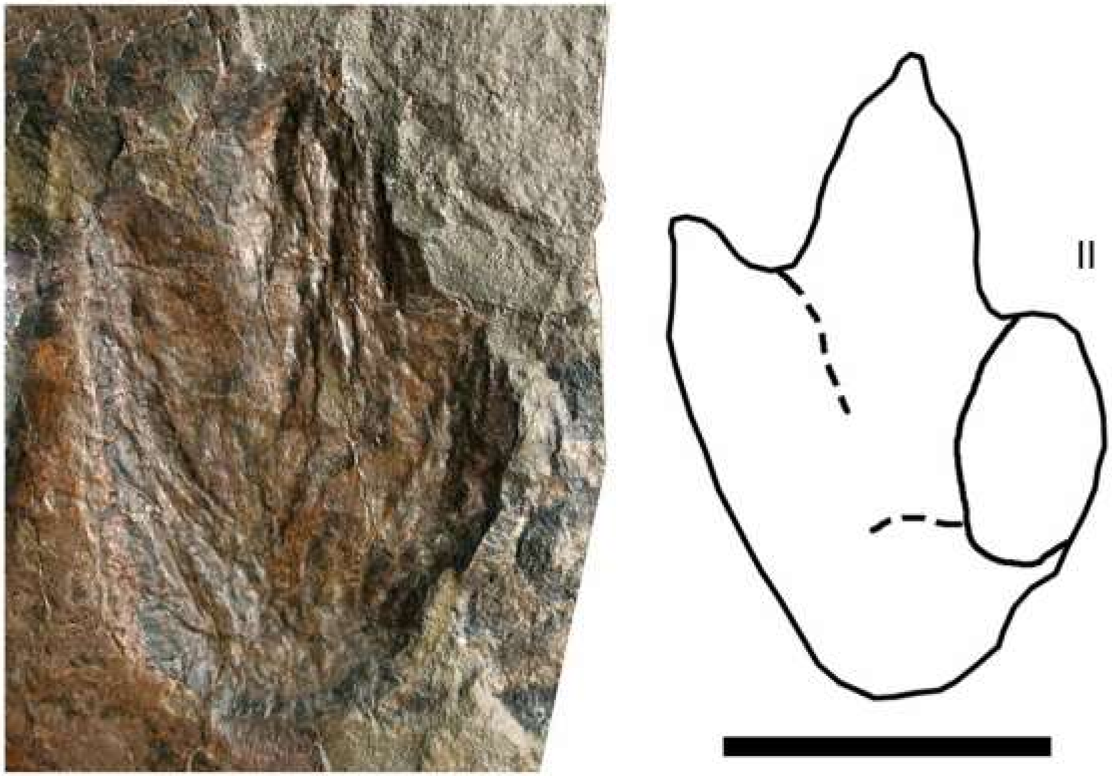


Figure 8.6. Left: Photograph of a theropod track with possible ichnopathology of digit II from the Early Cretaceous Laiyang Group, Shandong Province, China. Right: Interpretive outline drawing of track specimen. Scale bar = 10 cm.

Gates Formation (early Albian)

McCrea et al. (2014a) reported the existence of a large *in situ* track surface exposed on a steeply dipping wall exposed, in the fall of 2011, during road construction near a coal mine in the Falling Creek area of northeastern British Columbia. The vertebrate ichnofauna was comprised of a number of trackways with large, tetradactyl prints identifiable as *Tetrapodosaurus borealis*, as well as a single unusual trackway, possibly referable to *Irenesauripus mclearni*, made by a large bipedal theropod. The footprints in Falling Creek

Irenesauripus mclearni trackway exhibit an extremely short pace and stride (relative scale provided from lens cap in picture); so much so that McCrea et al. (2014a) speculated that the trackway might have been the product of two large theropod track-makers, one following the other using the same midline. Closer examination of the tracksite and the photographs (Fig. 8.7) and a brief re-examination of the site by RTM in 2014, revealed that the two large theropod scenario is unlikely as the footprints, particularly the left prints, exhibit strikingly similar morphology, and as well as being consistently, strongly rotated toward the midline of the trackway. Some of the right prints are rotated inward as well, but not to the same degree.

Figure 8.7. Falling Creek theropod trackway (cf. *Irenesauripus mclearni*) from the Early Cretaceous Gates Formation of northeastern British Columbia, Canada. Camera lens cover for scale is 6.6 cm diameter.

Although the track surface had deteriorated substantially since exposure, spalling into small shards, the gross morphology of the individual footprints was evident, and exhibited no noticeable abnormalities. It is possible that the track-maker may have had an injury to the soft tissue (muscle, tendon, ligament, etc.) of the foot.

However, in two reported cases of trackways exhibiting amputation of digits (Abel, 1935; McCrea et al., 2014b) even such an extreme injury did not affect the pace or stride noticeably, and only had a marginal effect on footprint rotation. In the case of a tyrannosaur trackway reported by McCrea et al. (2014b) it was the uninjured foot that exhibited a very slight outward rotation. If the Falling Creek large theropod was injured it is more likely that the injury was manifested above the level of the feet, somewhere between the ankles and the hips. However, injuries to the lower leg are more likely to affect the animal’s ability to make a step only in the affected leg. Injuries to the upper leg, including the hip joint and sacral area would not only limit the range of movement of the affected leg or side, but would also limit the range of movement of the leg on the uninjured side as well.

It is worth considering whether the unusual Falling Creek theropod trackway might have been produced due to substrate conditions rather than being a result of injury to the track-maker. The track-bearing substrate is very fine-grained (low energy) with substantial organic content and is dominated by *Tetrapodosaurus borealis* trackways. McCrea (2000; 2001; 2003a) previously observed that such low energy, high-organic content tracksites almost always reveal a vertebrate ichnofauna that is dominated by quadrupeds to the near exclusion of bipedal track-makers, especially when these substrates possessed high water content. McCrea et al., (2014a) defined the *Tetrapodosaurus* ichnofacies based on over thirty vertebrate ichnocoenoses of low energy depositional environments with high organic content. At rare sites where theropods venture onto such wet, fine-grained, organic substrates, or other sites that were wet (discussed below) the substrate conditions were observed to affect the morphology of the footprints as well as the gait of the bipedal track-makers. For theropods, in addition to the main functional digits II-IV being impressed, the hallux (digit I) and a portion of the metatarsus may also be impressed due to the depth the feet penetrated the wet substrate, examples of which are discussed below (under the heading "*Qualities of the substrate*"). Pace and stride is greatly reduced and there is pronounced inward and generally equal rotation of left and right footprints toward the midline.

Footprint depth and morphology are good indicators of the water content of a track-bearing substrate. Neither the *Tetrapodosaurus borealis*, nor the cf. *Irenesauripus mclearni* tracks are deeply impressed. No hallux or metatarsus impressions were evident in the Falling Creek cf. *Irenesauripus mclearni* trackway. As mentioned above, pace and stride is greatly reduced, but the degree of rotation of the left and right prints is consistently unequal. The substrate at the Falling Creek site was comparatively firm at the time the tracks were made, making it unlikely that the condition of the substrate could account for the unusual appearance of this large theropod trackway. This trackway is one of a very few suggesting a pathology-induced limp, without a visible deformity in the footprints.

The Falling Creek theropod trackway is an example of a *Pigeon-Toed Waddling Gait* characterized by a comparatively wide stance, with one or more footprints strongly in turned, short pace and stride where left and right footprints are side by side, or are nearly so, but with no marks indicating foot dragging. Pigeon-toed Waddling Gait is very different from a slow walk which can be produced by the activities of a healthy animal. For example, a large theropod trackway from the Lark Quarry exhibits typical pace and stride and pace angulation values for this a large theropod. However, the distal portion of the trackway shows short pace and stride values of an animal that slowed down considerably (Thulborn and Wade, 1979; 1984).

A large theropod from the Narraway River site in the Gorman Creek Formation (Cretaceous: Valanginian) exhibited typical pace, stride, and pace angulations values, but the track-maker slowed and came to a halt before making a nearly 90 degree turn (Sampson and Currie, 1996; McCrea et al., 2014a fig. 23). At no point did the track-maker's footprints exhibit similar features to that produced by the Falling Creek large theropod.

Dakota Group (Albian – early Cenomanian)

A single, natural cast of a right theropod footprint was collected from the Club Gulch tracksite in western Colorado. One of the outer digit impressions exhibits a strong curve towards the digit III impression (Fig. 8.8). The curved digit impression also appears to be unusually thickened compared to the other two digit impressions. This thickening begins slightly anterior to the hypex and expands strongly toward the end of this digit, but excludes the claw impression.

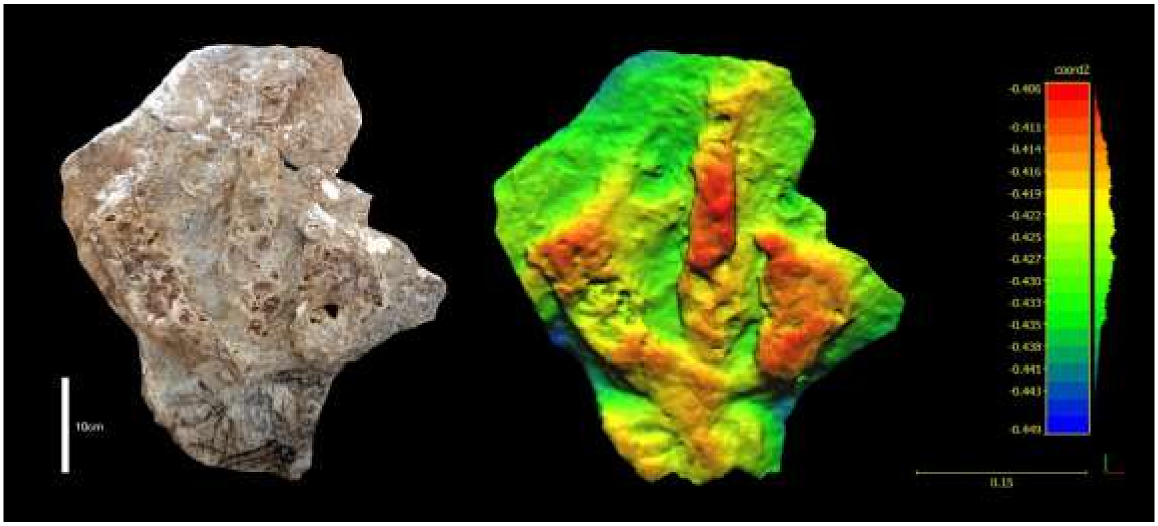


Figure 8.8. Photograph (left) and photogrammetric (right) images of a natural cast theropod track (UCM 207.123) from the Cretaceous (Albian-Cenomanian) Dakota Formation of western Colorado exhibiting unusual swelling and dramatic inward curve of digit II. Values for the vertical and horizontal scales for the right image are in meters.

The affected digit impression is identified as being digit II based on the comparative lengths of all the digits and the curvature of the claw impression of digit III toward the affected digit. While it is acknowledged above that identifying ichnopathology from a single print is difficult, it is also difficult to ascribe the combination of the swelling and curvature of digit II to the vagaries of preservation, substrate condition, or post-depositional effects. If UCM 207.123 is an example of ichnopathology, it is likely that the track-maker suffered a significant dislocation of digit II with resultant swelling of the soft tissues which are reflected in this footprint.

A direct plaster replica of a modern Canada Goose (*Branta canadensis*) trackway was collected for the PRPRC's neoichnology collection by LGB in the summer of 2014, from a mudflat along the Pine River, close to Pyramis Peak west of Chetwynd in northeastern British Columbia. At the time of collection nothing unusual was observed about the trackway. However, once the specimen was cleaned, a swelling on digit IV of both right footprints was noticed and a slight curve of the anterior portion of this digit toward digit III (Fig. 8.9). This swelling is similar to that of UCM 207.123, but occurring on digit IV and without such a pronounced curvature.

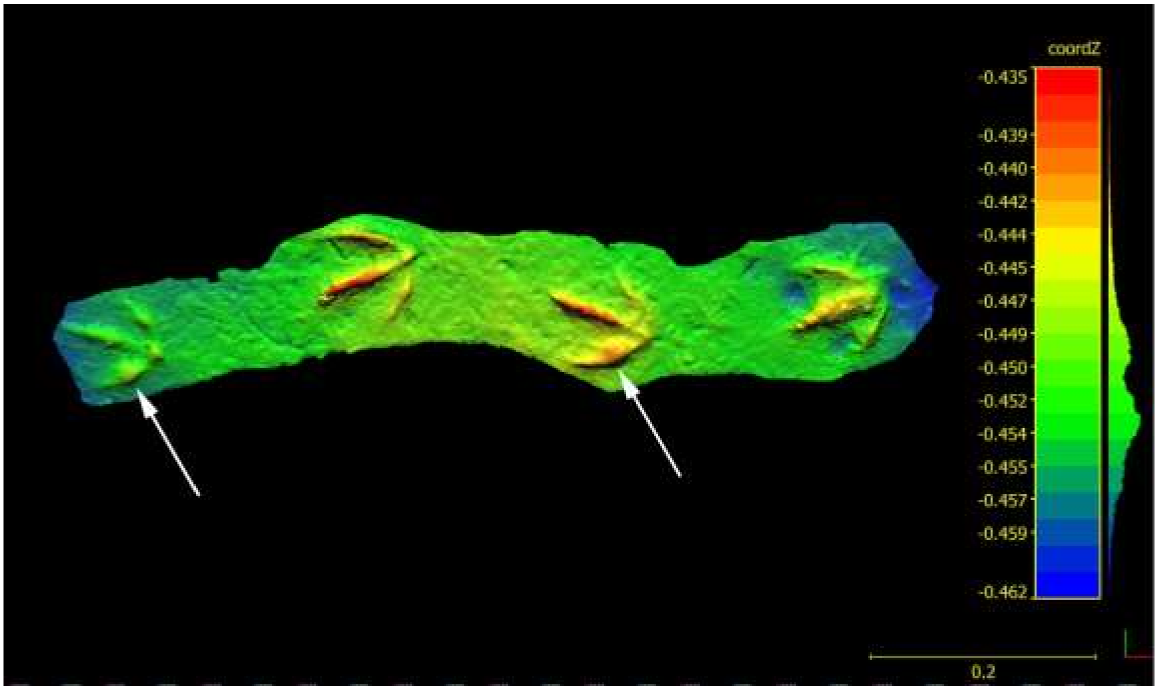


Figure 8.9. Direct plaster replica (natural cast) of modern Canada Goose (*Branta canadensis*) trackway (PRPRC NI2014.004) showing repetitive pathological swelling of digit IV of the right print. Horizontal and vertical scales in metres.

Kaskapau Formation (late Cenomanian – early Turonian)

The Kaskapau Formation is a nearly kilometre thick sequence of marine deposits in the Western Canada Foreland Basin, dominated by mudstones of marine origin. However, there are thin terrestrial wedges, often only a few metres thick, which have been found to contain bones and tracks of terrestrial vertebrates, including dinosaurs (Ryalaarsdam et al., 2006; McCrea et al., 2014a).

Extensive surveys along river and creek exposures by RTM and volunteers in 2001- 2002 and RTM and LGB from 2003 - present, revealed a great potential for footprint discoveries. Most of the footprint finds were of fallen natural cast blocks, mainly of isolated prints. The natural casts are generally formed of coarse-grained, well-consolidated sandstones that were deposited over the finer-grained and less consolidated organic-rich sediments upon which the dinosaurs walked. There were very few *in situ* tracksites and those that were found were small in surface area. Many of the prints were made in soft sediments, such as paleosols, which are very friable upon exposure (Rylaarsdam et al., 2006; McCrea et al., 2014a). Upon exposure the fine-grained paleosols erode swiftly, while the sandstone sediments that infilled the original footprints are much more resistant to erosion. As a result, natural mould footprints are rarely observed while natural casts are the most common type of footprint preservation currently known from Kaskapau Fm. exposures.

PRPRC 2002.01.001 is a single, natural cast on an isolated boulder found by CWH and volunteer Larry White in Quality Creek Canyon near the town of

Tumbler Ridge, British Columbia (Helm, 2002; McCrea 2003b; McCrea et al., 2014a). This footprint was reported by McCrea et al. (2014a) as an example of a possible pathology due to the severe curvature of digit III as well as the very high splay of both outer digits (Fig. 8.10). The inferred primary pathology on middle digit III appears to be a severe lateral dislocation similar to the specimen described by Tucker and Burchette (1977). As there is no swelling associated with this trace, the footprint was probably made after the injury had healed.

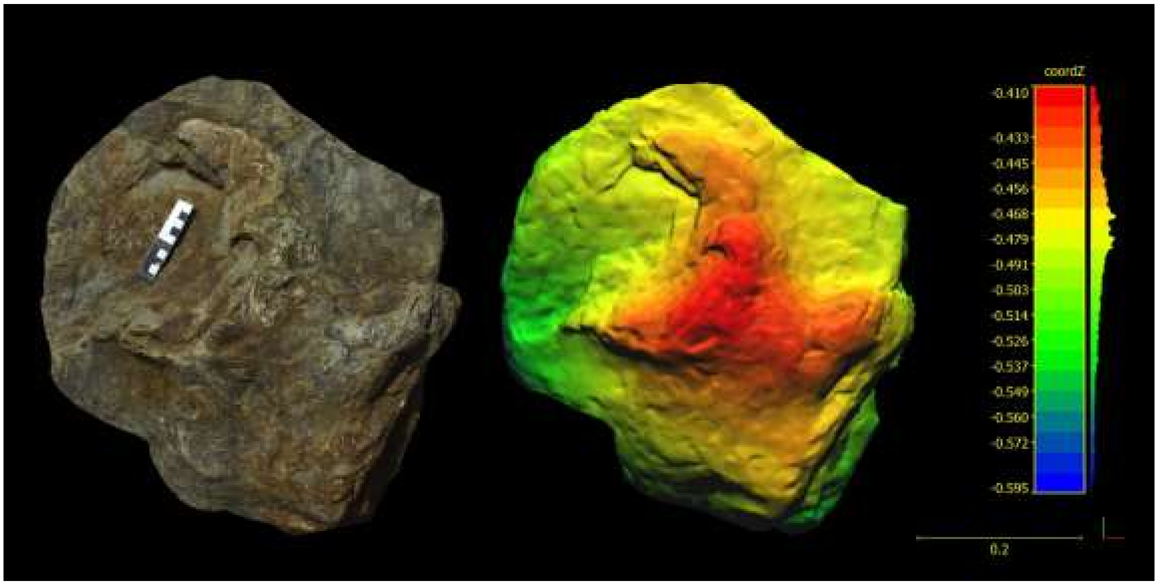


Figure 8.10. PRPRC 2002.01.001. Photograph (left – scale = 10 cm) and 3D photogrammetric imaging (right – vertical and horizontal scales in meters) of a natural cast theropod print from the Late Cretaceous (Turonian) Kaskapau Formation of northeastern British Columbia with a pronounced curve of digit III. Vertical and horizontal scales are in meters.

The outer digits display an exceedingly high total divarication (149^{o} degrees). Due to the deformation visible in the digits of this footprint it is difficult to identify the second and fourth digits with certainty. The degree of severity of this print's deformity precludes the assumption that the curvature of the third digit is toward the midline and inner digit (digit II) when it could actually have been bent (from injury) in the opposite direction. Divarications of the outer digits were taken as angles diverging from the main axis of digit III (Fig. 8.11). The digit impression that the third digit impression curves towards diverges at a 90^{o} angle from this axis. The digit impression that the third digit curves away from diverges at an angle of 59^{o} from the long axis of digit III. It is the free length of the third digit that displays features which indicate that it was the location of the primary injury. Digit III's free length is 27.2 cm. However, only the proximal portion of this digit impression (15.1 cm) is straight. At the end of the proximal portion of digit III it begins to curve away from the digit's central axis at an angle of 45^{o} (Fig. 11). The digit impression continues another 6.5 cm distally at which point another divergence begins. This next divergence angles away a further 58^{o} from the central axis for the final 5.6 cm (Fig. 11). The total divergence of the distal end of the digit III impression, which is almost half of the free length of this digit, is 103^{o}.

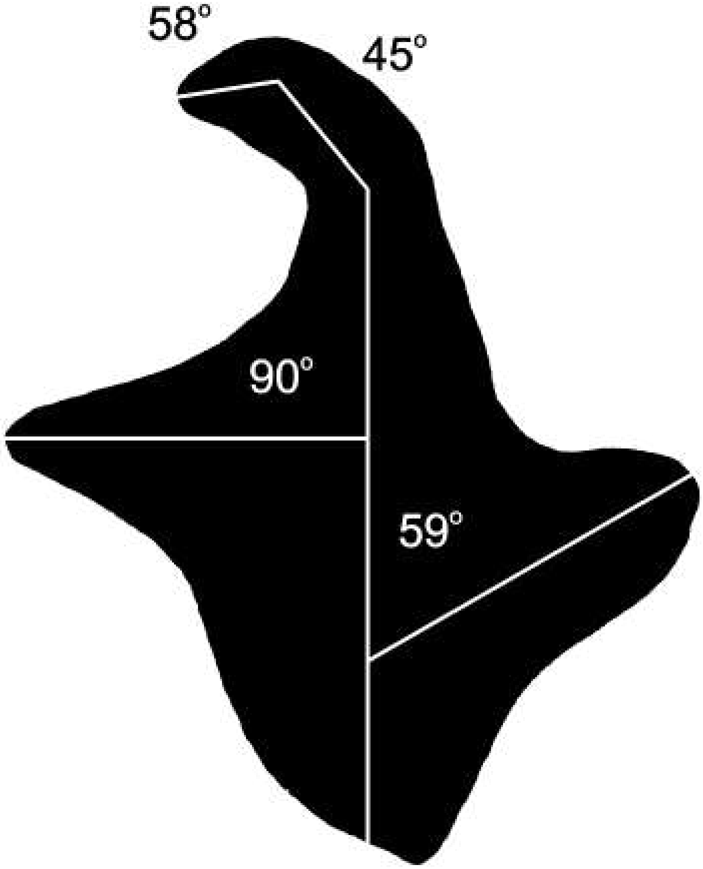


Figure 8.11. Schematic of divarication measurements of lateral digits from the central axis of digit III (white). Degree of divergence of distal end of digit III impression from the central axis of digit III (black).

It is difficult to judge whether the basal areas of all digit impressions and the metatarsal pad impression are disproportionally thickened as a result of the injury to the track-maker's third digit, or are simply due to the vagaries of preservation. It is likely that the extreme divarication between the outer digits, (but primarily between digit III and the outer digit it curves toward) may be the result of the track-maker's foot compensating for the primary pathology (dislocations on the distal portion of digit III). If so, this is an example of a secondary pathology which involved both outer digits of the foot. It is difficult to imagine the track-maker's gait not being affected by this ichnopathology, but with only a single print it is impossible to infer a tertiary pathology (see section below "Interpretation and Classification of Ichnopathologies").

The Kaskapau Formation is known to contain dinosaur skeletal fossils, (McCrea, 2003b, Ryalaarsdam et al., 2006) often in fragmentary condition. The relatively large size of the ichnite (PRPRC 2002.01.001) suggests a top predator was the track-maker. Presently, no comparative material of large theropods has been recovered from this formation and the identity of the specific track-maker is unknown. Turonian-aged theropods are poorly known worldwide.

Wapiti Formation (Campanian/Maastrichtian) Nose Mountain

An unusual large theropod track was discovered at the base of the east side of Nose Mountain, about 90 km southwest of Grande Prairie, Alberta by Royal Tyrrell Museum summer staff in 1989 (Fig. 8.12). The specimen consisted of a single, natural cast on a large white sandstone slab. The original track surface consisted of soft grey clay, which was subsequently infilled by sand. Palynomorphs recovered from the upper and lower parts of the exposed Wapiti Fm. section at Nose Mountain were correlated with the *Porosiportis porosus* Zone of Sweet et al., (1989), giving it an early late Maastrichtian age, laterally correlated with the base of the Battle River Fm. of the central Alberta Plains (Dawson et al. 1989, 1994; Braman and Sweet, 1999).

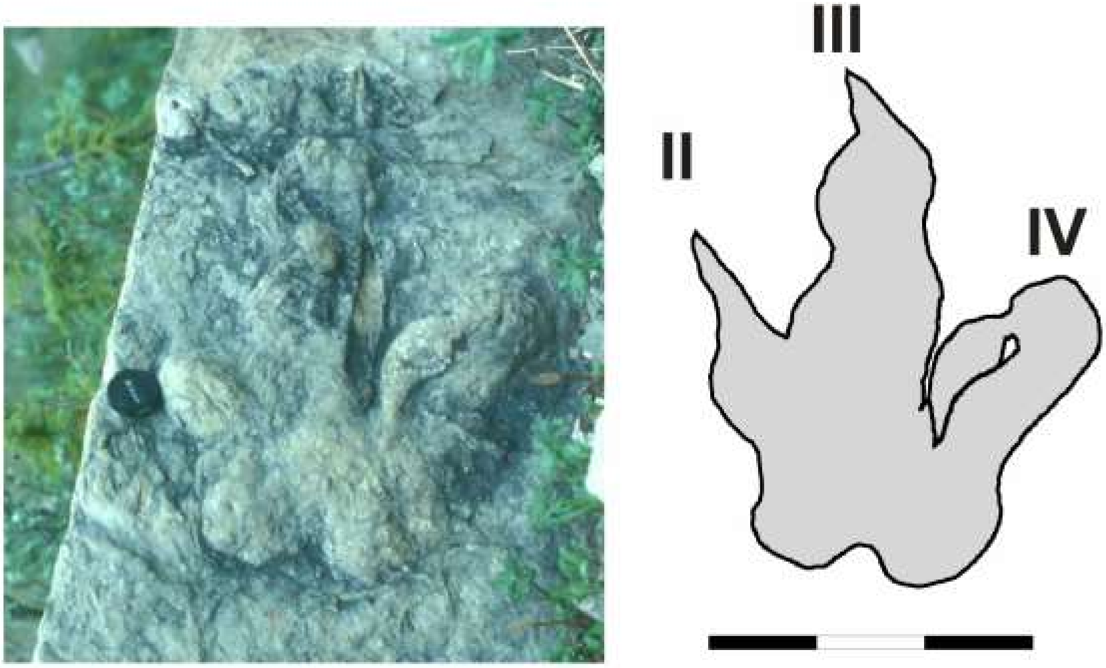


Figure 8.12. Left: Natural cast of a large theropod track from the Late Cretaceous (Campanian-Maastrichtian) Wapiti Formation from a locality on the east side of Nose Mountain, Alberta exhibiting an extreme dislocation of the distal end of digit IV involving the distal two pedal phalanges. The pedal claw impression is visible in lateral profile. The camera lens cover is 52 mm diameter. Right: Outline drawing of the Nose Mountain theropod track composed from the image to the left. Scale bar = 30 cm.

At time of discovery, the specimen was photographed with the intentions of returning later to make a replica cast and/or collect the specimen. When colleagues reinvestigated the area in 1990, it was discovered that a massive landslide had buried the specimen and it could no longer be relocated. Therefore, the following description is based solely on the photograph (Fig.

8.12). Approximate measurements are extrapolated from a 52 mm diameter camera lens cap used for scale in the photograph. Based on this scale the footprint length is 49 cm. The length of the affected ungual was measured as 11.2 cm, taken as a straight line from the middle of the base to the tip.

The morphology of the Nose Mountain theropod track conforms well to tyrannosaur prints described by McCrea et al. (2014b), although due to its size and presence of digital pad impressions the track-maker was probably not fully adult. This tyrannosaurid track is approximately the same length as another tyrannosaurid track (UALVP 53475) from the Grande Prairie area reported by Fanti et al. (2013) which McCrea et al. (2014b) estimated the track-maker to be almost 20 years of age.

The pathology is on presumed digit IV that appears to show severe rotational twisting, so that nearly half of the digit was folded underneath itself and the anterior portion of the metatarsal pad. Most striking in its appearance is the three-dimensional preservation of the claw impression which is an impression of the lateral surface rather than the normal ventral surface. The claw appears expanded proximally and steadily tapering distally to a point, as seen in examples of tyrannosaurid pedal claws in Tyrrell collections (Fig. 8.13) Tyrannosaurid pedal claws are a remarkably good match in regards to size, curvature and general morphology.

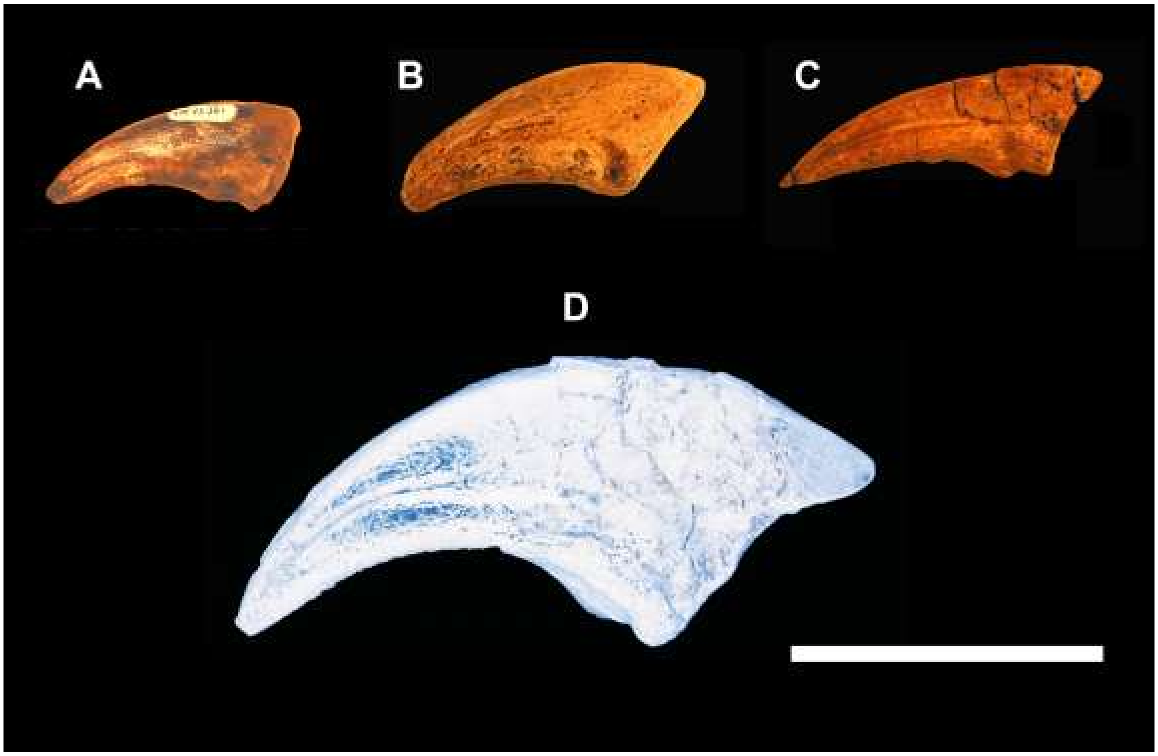


Figure 8.13. Lateral views of pedal claws from a variety of tyrannosaurids. A. TMP 1973.030.0001 – tyrannosaurid from Dinosaur Provincial Park, Alberta; B. TMP 1991.036.0703 – water-worn tyrannosaurid claw from Dinosaur Provincial Park, Alberta; C. TMP 2000.045.0011 – *Albertosaurus* ungual from the *Albertosaurus* bonebed, Dry Island Buffalo Jump Provincial Park, Alberta; D. TMP 1981.006.0004 - *Tyrannosaurus rex* from the Crowsnest Pass, Alberta is presented as a photographic negative to make it visible in this figure as the original specimen was black in colour. Scale bar = 10 cm.

This unique specimen likely represents a record of a relatively recent injury to the track-maker because the affected claw retains its normal shape in spite of being dislocated beneath the foot. The claw does not appear abraded or worn, suggesting the injury had been incurred shortly before the footprint was made. However, the caudal portion of the claw impression in the area that articulates with the rest of the digit appears to be very narrow in comparison with the rest of the digit. With such a dramatic dislocation it is possible that the soft tissues of this joint had atrophied due to constriction of the blood supply. The ichnopathology may not have been a freshly incurred dislocation at the time this track was made, but the injury would not have been very old. It seems likely that such an injury would have eventually resulted in necrosis of the soft tissues, and may have led to the loss of a portion of this track-maker's digit.

Wapiti Formation (Campanian/Maastrichtian) Northeastern British Columbia

A recent report on tyrannosaur trackways from the Wapiti Formation of northeastern British Columbia (McCrea et al., 2014b) included a trackway (PRPRC 2011.11.001) with three prints, (two left and one right), of which the two left prints both exhibit a dramatically truncated digit II impression. McCrea et al., (2014b – figs. 1 and 7) compared the length of the affected digit II impression of both left prints with the length of the corresponding digit impression in the intact right print of this trackway (Fig. 8.14). The left digit II impressions were shorter than the right digit II impression by at least 14 cm and likely involved the loss of the distal and penultimate phalanges on that digit (II-2 and II-3). This is a rare example of a repetitive pathology within the same trackway and provides evidence that this is a true pathology and not simply a preservational artefact.

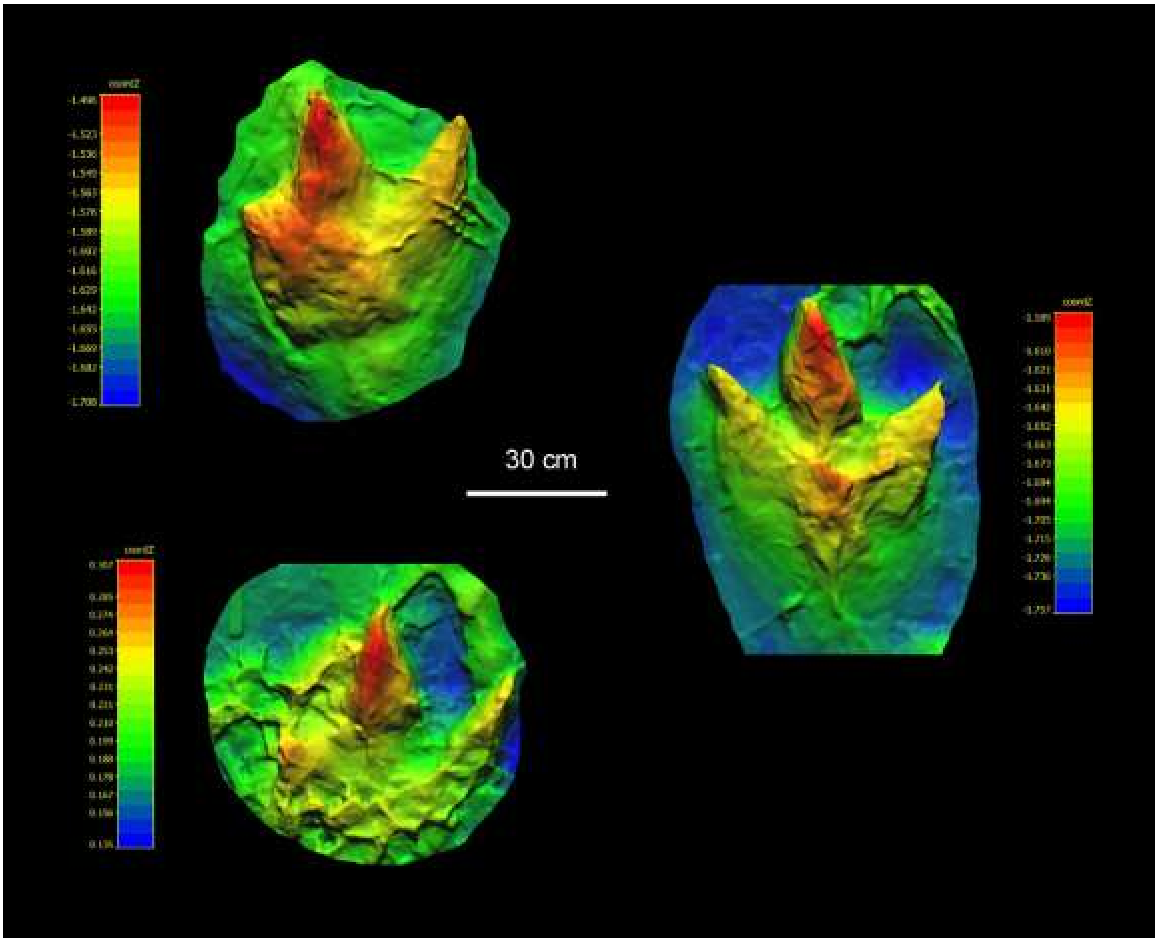


Figure 8.14. Photogrammetric images of tracks from PRPRC 2011.01.001M (silicone mould of a natural mould trackway). Bottom left is print #1 (left); Top left is Print #3 (left); Right is print #2 (right - reversed). Prints #1 and #3 display an extremely truncated digit II impression, leaving just a small nub remaining. The reversed image of the intact print #2 shows a lengthy digit II as contrast. Vertical and horizontal scales are in meters.

McCrea et al. (2014b) observed nearly identical pace lengths for (PRPRC 2011.11.001) with a barely perceptible outward rotation of the right pes which was not affected by a visible pathology. As striking as this ichnopathology is, it did not appear to affect the locomotion of this animal and thus we identify it as an example of a ‘compensated gait’.

Interpretation and Classification of Ichnopathologies

The fossil record is replete with dinosaur ichnites and trackway occurrences providing us with details of locomotion, speed, biomechanics, soft tissues and behaviour. However, ichnites or trackways with indications of osseous or soft tissue pathology which may have negatively influenced locomotion (gait and trackway patterns) of the affected animal are rare (Tanke and Rothschild, 2002). The identification of footprint morphology or trackway quality as being produced by an injured animal can be somewhat tenuous. There are a number of important factors that can influence footprint morphology and trackway quality that can be either contemporaneous or post-depositional in origin (Schulp, 2002; Schulp and Brokx, 1999).

Biological factors include the action of the animal itself (over-printing, shifting the foot to make a double impression, turning, change in gait, etc.,) All of these can produce “anomalies” in the tracks of animals, but are not the result of injury and therefore cannot be considered evidence of an ichnopathology. An ichnopathology may develop as a result of a trauma to the foot that has produced an osseous deformation which is capable of being recognised in a footprint or trackway. Examples of such deformations include footprints manifesting missing, broken or deformed digits possibly associated with a trackway showing “limping” (Lockley, et al., 1994). Other bodily injuries, bone fractures or soft tissue pathology more proximal to the body that would also affect the normal progression are harder to quantify. For example, an animal with a fractured fibula would be expected to limp; yet the individual footprints within its trackway would appear normal.

Identifications of true ichnopathology can come from the descriptions of abnormal trackways, such as those that show repetitive atypical morphology, or inconsistency of gait. Less confident designations of ichnopathology involve identifications based on isolated footprints which would show unusual morphologies including partially, or completely missing digit impressions. In these cases there is no trackway providing a context to show whether these footprint morphologies are repetitive. In such cases confident identifications of ichnopathology are difficult.

There are a number of primary factors that may cause pathologies affecting the morphology and ultimately the locomotory function of an animal's limbs, however most of these fit into the five following categories:

I Congenital abnormalities: these are deformations arising from birth and early development, possibly influencing gait.

II Biomechanical injury: defects due to physical damage to the body, possibly affecting the movement of the limb and its elements.

III Brain or spinal injury: resulting in nerve damage possibly causing abnormal gait.

IV Sickness: this includes defects due to infection or diseases such as cancer among others.

V Age-related: degeneration due to age that may affect gait.

It is likely that only biomechanical injury defects are identifiable from tracks, but congenital and disease induced defects have been observed from skeletal specimens (Tanke and Rothschild, 2002 and references therein). These inferred primary pathologies may have caused secondary morphological abnormalities when the animal was alive, such as swellings and/or extreme splaying of digits. Possible tertiary effects are the influences of the primary and/or secondary pathologies on the gait of the affected track-makers. Most or all of the above effects likely would have been painful to the track-makers and it is certainly possible that the effects on the track-makers' locomotion may have been a result of both the biomechanical effects of the injury itself and the animals' motivation to avoid or minimize the pain of the injury. As such, most pathologies could have produced gaits influenced by pain, termed *'antalgic gaits'*. However, it is prudent to simply describe the biomechanical aspects of suspected ichnopathologies rather than their potential causes. It is also best to avoid terminology for ichnopathologies that imply diagnoses to a single cause since there are potentially many different causes for each type of ichnopathology with little chance for a clinical (post-mortem) examination of the afflicted track-maker.

It should be recognized that it is difficult or nearly impossible to ascertain just how dire an injury reflected by an ichnopathology was to the track-maker. Amputations, deformations and severe limping observed in tracks and trackways that were probably unpleasant and painful to the track-maker, may not have been life-threatening. Indeed, inferring severe amputations of pedal digits from fossil trackways with otherwise normal trackway configurations (e.g. little or no limping) shows that these animals were quite resilient in their recovery from their injuries. The probability of discovering the trackway of a grievously wounded, pre-terminal track-maker, is very remote.

Distinguishing True Trace Pathologies From Non-Pathological Traces

When making inferences of pathologies from footprints and trackways (ichnopathology) it is prudent to be aware of other factors that may produce ichnites that falsely appear to manifest signs of pathology.

Limping: Previous descriptions of limping dinosaurs (eg. Dantas et al., 1994; Lockley et al., 1994; Avanzini et al., 2008) are a bit more controversial if identified as being from the result of pathology. Farlow (pers comm. in Dantas et al., 1994), pointed out that inconsistency of gait may simply be an indication of a healthy animal favouring one side over the other and that this is seen in the gaits of modern healthy animals (even professional athletes).

The question of whether limping in dinosaurs is due to pathology, rather than slightly favouring one side of the body over the other may be a question of degree. We agree that irregular gaits are likely not uncommon in healthy animals, but the term “limping” implies abnormality and possibly pathology. It would be advisable to make a distinction between minor, if consistent, irregularities in pace and stride values which we can define as “*irregular gaits*”, and the more extreme examples that are more likely to be cases of ichnopathology which may be properly referred to as “*limping gaits*”. We propose the term “*limping gait*” to identify trackways where there is a visible pathology associated with an obvious limp. A limping gait may also be used to identify ichnopathologies in trackways where no ichnopathology is visible in the footprints, but where extremely unequal gaits, and/or unusual footprint rotations or other footprint features (i.e. foot drag traces - shuffling) are exhibited.

Preference for one foot over its contralateral counterpart has been demonstrated in activities related to object (including food) manipulation and foraging in mammals, birds, and even amphibians (Rogers and Workman, 1993; Bisazza et al., 1996; Pike and Maitland, 1997; Andrew and Rogers 2002; Csermely 2004; Quaranta et al., 2004; Izawa et al., 2005; Robins and Rogers 2006). Laterality has also been demonstrated in the preferred hindfoot on which galloping racehorses land (Williams and Norris, 2007), and the foot on which some (but seemingly not all) species of waterfowl and waders prefer to stand while resting (Randler, 2007). Standing ostriches do so on both feet, but prefer to stand with the right foot forward, and the right foot is also the preferred foot with which ostriches begin moving (Baciodonna et al., 2010).

Footedness is only one manifestation of a more general tendency toward laterality in vertebrates. Other examples include a preference for the use of the right eye over the left when moving toward a food source that has to be manipulated (Andrew et al., 2000; Tommasi and Andrew, 2002), a preference for rightward movements by cetaceans chasing after prey (MacNeilage, 2014), and the common tendency for humans walking across a landscape without landmark cues to move in circles (Bestaven et al., 2012).

Whether asymmetry could be expected to occur in step (pace) lengths in healthy, uninjured bipedal animals is uncertain. Although some features of left/right gait asymmetry do occur in human locomotion, this does not include step length (Hirokawa, 1989; Sadeghi et al., 2000; Gunderson et al., 1989; Titianova et al., 2004; Zverev, 2006), at least as commonly measured in human studies (heel to heel, parallel to the direction of progression, rather than obliquely to it (cf. Zverev 2006: fig. 1). We are unaware of any comparable studies of ground birds.

From 1988 through 1995 JOF measured pace lengths (obliquely from the tip of the digit III impression of one print to the tip of the digit III impression of the following contralateral footprint) in trackways of emus (*Dromaius novaehollandiae*, both captive birds and wild individuals in Queensland, Australia), as part of larger study of intraspecific footprint shape variability in this species, the details of which will be published elsewhere. Data were obtained for at least 30 individual birds; uncertainty of the number of animals is due to the fact that the trackways of wild birds were measured in the absence of their makers.

For six individual emus in this study (Table 8.1) there were enough pace lengths measured to allow meaningful comparison of the ratio of the pace beginning with a footprint to the preceding pace ending in that footprint, between footprints where the beginning (stepping-off) footprint was a left as opposed to a right. In two of these birds, the beginning pace/ending pace ratio was significantly larger when the beginning footprint was a right as opposed to a left. The same result was seen in a comparison of right versus left stepping-off beginning/ending pace ratios in the pooled sample of pace lengths of all other emus besides the six birds examined individually (Table 8.1), and for all of the paces of all of the birds (Fig. 8.15).

Bird	Stepping-Off Print Symmetry	Pace Beginning in Footprint / Pace Ending in Footprint				
		Minimum	Maximum	Median	Mean	Number of Measurements
1988 Fort Wayne Zoo Adult 3	Left	0.835	1.432	0.968	1.021	16
	Right	0.740	1.244	0.967	0.996	16
1988 Fort Wayne Zoo Adult 5	Left	0.750	1.256	1.009	0.998	25
	Right	0.829	1.542	0.987	1.012	23
1988 Fort Wayne Zoo Adult 6	Left	0.742	1.248	0.961	0.942*	17
	Right	0.971	1.284	1.061	**1.065***	19
1988 Fort	Left	0.751	1.307	1.043	1.019	10

Wayne Zoo Juvenile 4	Right	0.706	1.357	0.926	0.947	7
1989 Fort Wayne Zoo Juvenile A	Left	0.382	1.279	0.894	0.848	12
	Right	0.625	1.814	1.007	1.055	10
1989 Fort Wayne Zoo Juvenile C	Left	0.526	1.458	0.789	**0.801***	20
	Right	0.703	2.033	0.993	1.149*	16
All Other Emus Pooled	Left	0.545	1.757	0.975	0.958*	62
	Right	0.586	2.367	1.036	1.056*	66

Table 8.1. Laterality (or lack thereof) in the ratio of the pace beginning with a footprint (the stepping-off print) to the preceding pace ending in the same footprint, where the stepping-off footprint is a left or a right, in captive and wild emus (*Dromaius novaehollandiae*). Number of individual birds in the "all other emus pooled" treatment is at least 24; uncertainty in the number is due to the impossibility of knowing how many individuals were responsible for trackways measured in the wild in Australia. In comparisons marked with an asterisk, the mean ratio is significantly different (independent samples t-test; $p < 0.05$) between cases when the stepping-off print (the print with which the pace begins) is a left as opposed to a right. If the mean ratio for a left or a right foot step-off also significantly differs from 1 (i.e., ending pace = beginning pace; one-sample t-test $p < 0.05$), the mean ratio is indicated in bold.

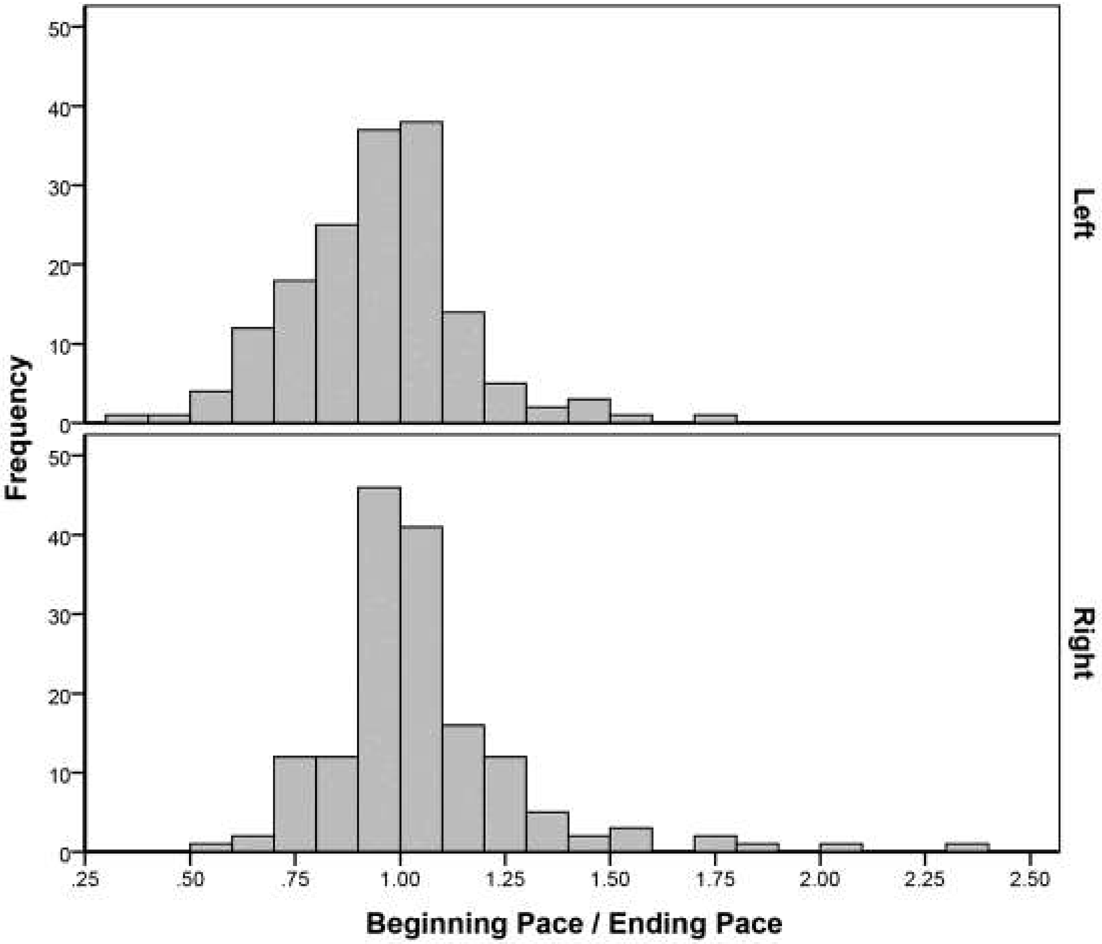


Figure 8.15. Frequency distribution of the ratio of the pace beginning with a footprint to the pace ending with a footprint, across all paces of all emus in the sample. Top: Pace begins with a left footprint (minimum = 0.38, maximum = 1.76, median = 0.948, mean = 0.945, N = 162). Bottom: Pace ends with a right footprint (minimum = 0.59, maximum = 2.37, median = 1.004; mean = 1.049, N = 157).

These results are suggestive rather than conclusive, but the fact that emus may take longer paces when stepping off from the right as opposed to the left foot seems consistent with the preferred right-footedness observed in ostriches (Baciodonna et al., 2010). The possibility that pace asymmetry in ground bird and non–avian bipedal dinosaur trackways is often due to laterality rather than injury must therefore be considered. Such laterality might take the form of footedness, but it also might reflect step length adjustments associated with the preferred use of one eye (or even ear) over the other when the animal is monitoring its surroundings while walking (L. Tommasi, personal communication).

A systematic examination of the step lengths among dinosaur trackways could prove of considerable interest. If pace lengths within single trackways are commonly observed to be slightly larger when beginning with one foot (the right- though very rarely do we see the true beginning of a trackway) rather than the other, this would suggest that laterality rather than injury is the more likely explanation. Further, one would intuitively expect pace asymmetry to be more common if it is usually due to laterality as opposed to injury. Finally, one might also expect pace asymmetry to be less extreme if it is due to laterality as opposed to injury.

Reduction or Retraction of Digits: Not all track impressions with missing digits are due to pathology (e.g. amputation or dislocation). Certain taxa of ankylosaurs are known to have reduced the number of pedal digits from four to three (loss of pedal digit I) in the Late Cretaceous (e.g. *Euoplocephalus* sp., Vickaryous et al, 2004), which therefore has a chance of being observed in the track record. McCrea et al. (2001; 2014a) reported on ankylosaur tracks and trackways from the Dunvegan Formation (Cenomanian) where pedal digit I was significantly reduced in comparison with pedal digits II-IV. There are a number of trackways with deeply impressed footprints from the Dunvegan Formation that show no trace of digit I on any of the preserved tracks (McCrea, 2014a).

The Dromaeosauridae are thought to have had the ability to retract their lengthy and robust pedal digit II (Ostrom, 1969a, b). Trackways of dromaeosaurs would therefore exhibit only a partial digit II impression in all footprints in a trackway (Li et al., 2007; Kim et al., 2008; 2012; Lockley et al., 2004; Cowen et al., 2010; Xing et al., 2013b, Lockley et al., 2014). There is the potential to mistake single footprints that might be attributable to dromaeosaurs as possessing an amputated digit II. The converse is also possible, a single footprint with a missing or truncated second digit could be a true pathology, but could be mistaken for a dromaeosaur footprint. It is also possible that registration of partially retracted digits, as in ichnogenus *Evazoum* (Lockley and Lucas, 2013) could be misinterpreted as a pathology.

Descriptions and figures of digit II impressions for *Velociraptorichnus* (fig. 2 in Zhen et al., 1994) and *Dromaeopodus* (fig 2. in Li et al., 2007) indicate that only a portion of digit II was impressed, leaving a short and distinctly rounded impression near the antero-medial margin of the heel pad impression. The rounded morphology of the shortened digit II impression described from tracks attributed to dromaeosaurs contrasts to the, "… rough and uneven margin of the distal 'nub' of the digit II impression,…", observed in a tyrannosaur trackway from the Wapiti Formation of British Columbia (McCrea et al., 2014b: p. 10). Footprints of animals that have lost pedal digits (or manual digits if quadrupedal) would be unlikely to exhibit the rounded morphology observed in digit II impressions attributed to dromaeosaurs. It is more likely that any loss of digits would have left irregular and uneven stumps which could be used to identify such ichnopathologies, even in single tracks.

Troodontidae were also subject to a reduction and modification of digit II (Makovicky and Norell, 2004) which could also be mistaken for pathology in single tracks, although few tracks attributabed to troodontids have been reported to date (Van der Lubbe et al., 2009; Mudroch et al., 2011). The digit II impression of *Paravipes didactyloides* is superficially somewhat similar in morphology to digit II impressions of dromaeosaur tracks as they are rounded or oval in shape (fig. 5 Mudrock et al., 2011; Lockley et al., in press a). Clearly, reasonably well-preserved trackways provide the best chance to avoid misidentification of pathologies or evolutionary digit reductions or habitual digit retractions.

Polydactyly: The presence of supernumerary digits in vertebrates is mainly a congenital condition, but the record of pedal polydactyly in the osteologic and ichnologic record for dinosaurs appears to be non-existent. However, because dinosaurs left a great many more tracks than bones, there is a chance that eventually true pedal polydactyly reflected in dinosaur tracks may be discovered. Reports of polydactyly in modern birds is not uncommon: Tabin, (1992) included a figure of a chicken foot with an extra pedal digit due to a genetic abnormality involving the Hox genes.

The possibility exists to mistake normal footprint morphologies as being polydactylous, especially with certain theropod and small ornithopod tracks. The majority of theropod clades have three functionally weight-bearing digits (II-IV) and a digit I (hallux) that is reduced to a certain degree depending on the taxon (Thulborn, 1990). In almost all theropods, digit V is absent or was reduced to a short splint. In such taxa the hallux was attached more proximally than digits II-III, and thus was non-functional for locomotion. However, if the substrate consistency was such that the foot impressed deep enough to impress digit I, an "extra" digit would appear to be present (see below in "*Qualities of the substrate"*).

Therizinosaurids (Clark et al., 2004) and oviraptorids (Osmolska et al., 2004) have been found to have four functional (likely weight-bearing), pedal digits (I-IV) instead of the typical three (II-III) of most other theropods. Tracks and trackways attributable to oviraptorids have been described (*Saurexallopus* isp.) and these tracks display four slender and lengthy digit impressions (Fig. 8.16). Three ichnospecies have been described to date, *Saurexallopus lovei* (Harris, et al., 1996; Harris, 1997) *Saurexallopus zerbsti* (Lockley et al., 2004) and *Saurexallopus cordata* (McCrea et al., 2014a). A single, tetradactyl pes print from the Upper Cretaceous Cantwell Formation in Alaska has been put forward as a therizinosaur by Fiorillo and Adams (2012), but this print was assigned by these authors to *Saurexallopus*, which have recently been ascribed to oviraptors (Lockley and Gierlinski, 2009; Gierlinski and Lockley, 2013).

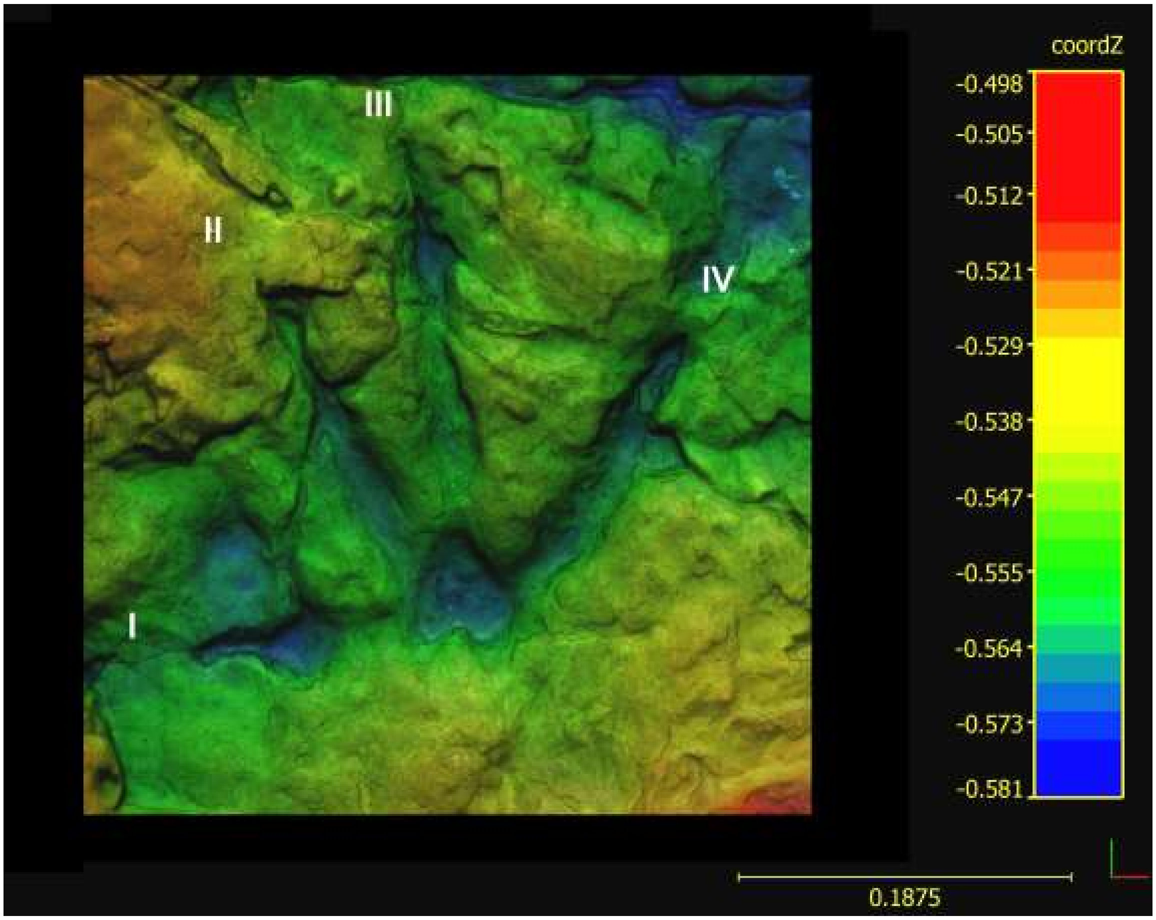


Figure 8.16. Photogrammetric image of the holotype print of *Saurallexopus cordata* (McCrea et al., 2014a) from northeastern British Columbia.

Lockley et al. (2009) described *Neoanomoepus perigrinatus*, tracks identified as being the product of a small quadrupedal ornithopod with four functional pedal digits and five manual digits. McCrea et al. (2014a, fig. 29) also reported cf. *Neoanomoepus* isp. track and trackway specimens from another locality in the Gorman Creek Formation of northeastern British Columbia. Thulborn (1990) observed that digit I of the pes of the basal ornithopod *Hypsilophodon* sp. was long enough to make contact with the ground. The *Hypsilophodon* sp. manus is pentadactyl and its body size compares favourably to *Neoanomoepus* isp. tracks and trackways. Basal ornithopods seem to be likely candidates for *Neoanomoepus* isp. and similar trackways that have been identified as the product of small quadrupedal ornithopods. However, Norman et al. (2004) counter that digit I in known basal ornithopods, including *Hypsilophodon* sp., was not long enough to have made contact with the ground, much less be functionally weight-bearing during locomotion.

Some basal Iguanodontia, such as *Tenontosaurus* sp., exhibit a well-developed and functional digit I (Forster, 1990, fig. 22; Norman, 2004) that would have been long enough to contact the substrate during locomotion. *Tenontosaurus* sp. adults were too large to make *Neoanomoepus* isp. tracks, however it is probable that some form of basal ornithopod or basal iquanodontid was responsible for making *Neoanomoepus* isp. and similar tracks, and that the observed tetradactyl pes prints are a reflection of normal anatomy of small, quadrupedal ornithopods.

A rather more mundane cause of apparent polydactyly from fossil tracks may simply be the result of two or more tracks overlapping (Lockley, 1991 p. 14; McCrea et al., 2004; 2014a, p. 39). The resulting trace can appear to be a single footprint with an unusually high number of digits, but is probably just a double-print. Likewise, digit traces may be duplicated where separate entrance and exit traces are preserved.

Perhaps the best chance of recognizing true polydactyly in the ichnological record of dinosaurs is from the tracks, and preferably trackways of dinosaur groups that have been well-studied, but also which have exhibited prominent digit impressions. Polydactyly in tracks and trackways of large ornithopods (hadrosaurs and iguanodontids), large theropods (tyrannosaurids, allosaurids and megalosaurids) would be the easiest to recognize. Polydactyly in tracks and trackways of ankylosaurs might be slightly less obvious. Polydactylous sauropod tracks would likely be very difficult to identify, as extra-digit impressions would be small in relation to the size of the footprint and might be mistaken for extra morphological features.

Pre- and Post-Impression Effects

There are a number of factors that may influence the morphology and preservation of footprints. Some of these factors, such as substrate consistency, are present before a track-maker traverses an impressionable substrate. Other factors may come into play after footprints have been made and can include partial erosion, foreign objects and active invertebrate infauna present in the track-bearing substrate, or present in the sediments which have been deposited over a track surface (post-burial).

Qualities of the substrate: There are numerous examples of footprints and trackways that display the effects of deformation due to substrate condition (sediment consistency, sediment collapse, etc.), but one in particular can have a great effect on the final morphology of the footprint. If a substrate has a very high moisture content, and/or lacks the composition (e.g. low to no clay content) to sufficiently maintain the initial morphology of a track after the track-maker’s foot is withdrawn, the print is likely to be subject to a degree of sediment collapse (Fig. 8.17) causing the footprints and especially long digit impressions to appear pinched-in (Matsukawa et al., 2014; McCrea et al., 2014a). Theropod prints from the Paluxy River of Texas have also been observed with this type of preservation (Kuban, 1989; Farlow, et al., 2012, fig. 17).

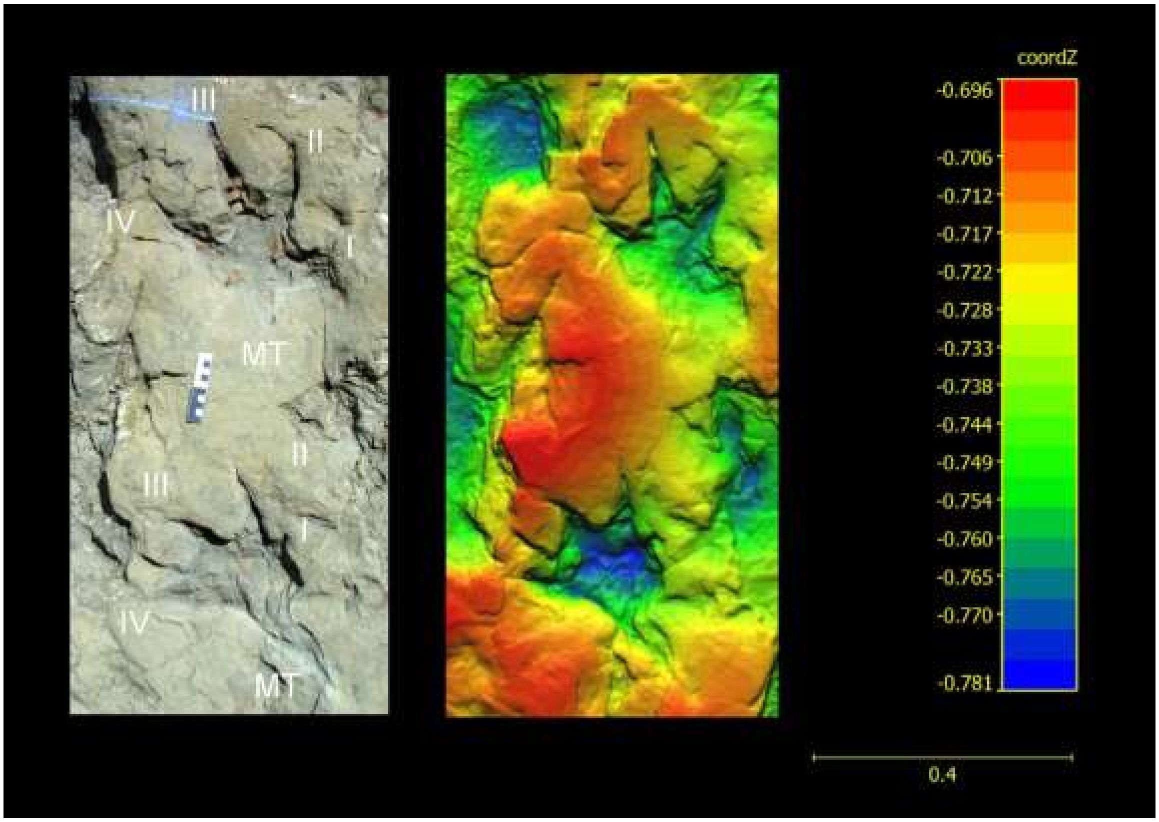


Figure 8.17. A pair of theropod tracks (both left prints) from the Kaskapau Formation (late Cenomanian – early Turonian) from Flatbed Creek near Tumbler Ridge, British Columbia showing pinching of digits I-III due to sediment collapse after the foot was removed. MT = metatarsus impression. Scale in left image = 10 cm; horizontal and vertical scales in right image are in metres.

If the substrate that a track-maker was walking on was soft, its feet would have penetrated deeply into the substrate, allowing the non-functional hallux to impress along with digits II-IV, and possibly an impression of the metatarsus as well (Fig. 8.17-8.19). Theropod hallux impressions are not common, but they do occur and have been reported in the literature (Lockley and Hunt, 1994; Harris et al., 1996; Harris; 1997; McCrea, 2000; Lockley et al., 2004; Nouri et al., 2011; Xing et al., 2013c; McCrea et al., 2014a, b; Xing et al., 2014). The recognition of a small digit trace medial to the weight-bearing digits is sufficient to identify the impression as the hallux, a normal occurrence and not an example of polydactyly.

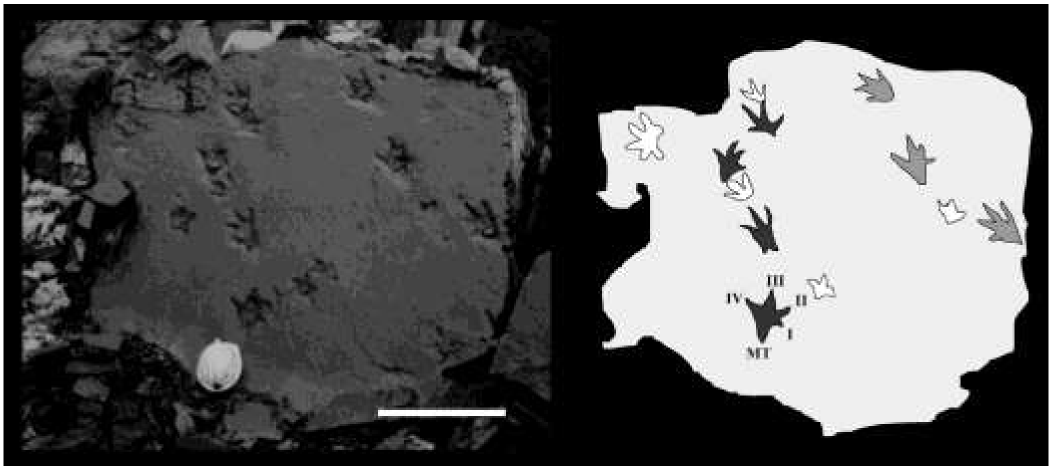


Figure 8.18. Photograph and interpretive drawing of a trackslab with "five-toed" theropod footprints from the South-Pit Lake site (TMP1990.027.0001). Digits I-IV and the lower portion of the metatarsus (MT) are labelled on the drawing. Scale bar on photograph = 1 metre.

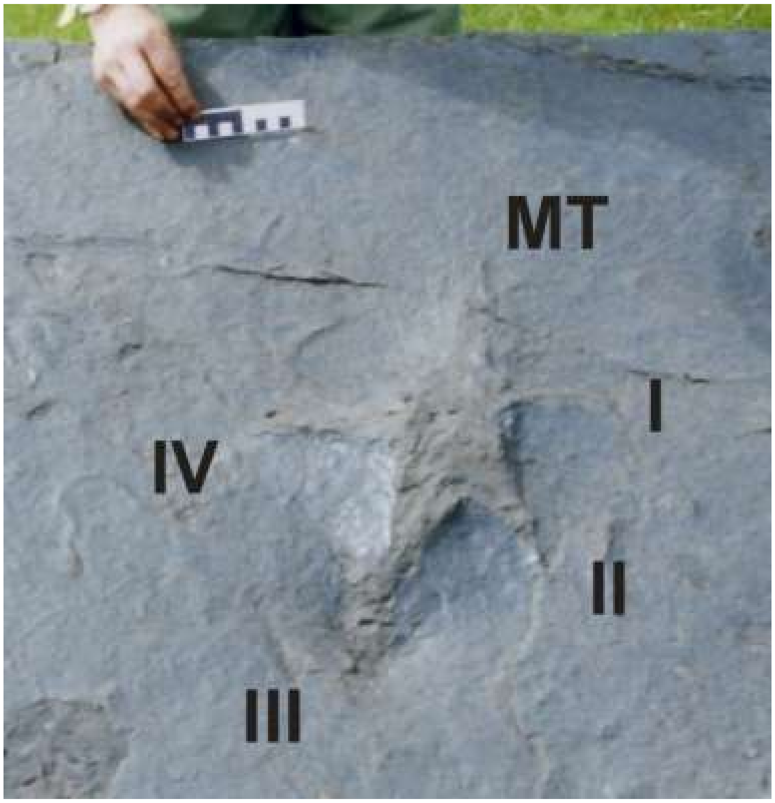


Figure 8.19. Theropod tracks from the Mist Mountain Formation (Tithonian-Berriasian) of southeastern British Columbia. Scale = 10 cm.

Metatarsus impressions are somewhat less common (Kuban, 1989; Perez-Lorente, 1993) but they appear as posteriorly-oriented traces almost directly in line with the long axis of the footprint (Fig. 8.17-8.19). If the substrate is soft enough, the feet of dinosaurs may sink in deeply, and anatomical features of the foot and lower leg may be impressed that otherwise would not normally make contact with the substrate. In addition to the impression of the non-functional hallux of many theropods there may appear a lengthy, backward-directed impression that sometimes has the same proportions as the other (digit) impressions. It is unlikely that this is an extra digit, but rather is the impression of the metatarsus of the track-maker. These types of traces may appear to be pentadactyl, but they are instead “tetradactyl” with impressions of digits I-IV with the addition of the digit-like metatarsus impression. Fig. 8.17 shows this feature in two theropod tracks from Flatbed Creek near Tumbler Ridge, British Columbia (McCrea, 2014a), but this has also been observed in small- to medium-sized theropod tracks from the Gates Formation (Albian) of northwestern Alberta (Fig. 8.18) as well as from the Mist Mountain Formation (Tithonian-Berriasian) of southeastern British Columbia (Fig. 8.19).

Mechanical disturbance (current, over-printing, slickensides, etc.): Ankylosaur tracks in a trackway from the 12 Mine South, A-Pit site near Grand Cache, Alberta appeared to be smeared as a result of the directional flow of water (McCrea and Currie, 1998, fig.4). Such changes to track morphology were likely made shortly after the footprints were made, but before they were buried.

Tracks may also be deformed by a number of post-burial effects, including the result of the development of undertracks from track-makers traversing a sediment surface that was deposited above them (Lockley et al., in press b). Tracks may also be deformed hundreds, thousands or even millions of years after they were made as a result of small- or large-scale tectonic effects which cause sedimentary layers to slip, developing slickenside features. Slickenside influences on tracks have often been observed from a number of tracksites (Thulborn, 1998; Parker and Rowley, Jr., 1989; RTM pers. obsv.).

Influence/introduction of foreign objects: An example of non-pathology as a result of a foreign object comes from a single tyrannosaur print (PRPRC

2004.08.001) *Bellatoripes fredlundi* from British Columbia (Farlow et al., 2009; McCrea et al., 2014a, b) that exhibits an abnormality with the distal portion of digit III (Fig. 8.20). This abnormality gives the appearance of a truncated digit III impression which could easily be interpreted as an ichnopathology (amputation). Upon close examination the digit III anomaly was found to be caused by the introduction of a foreign body (a thick segment of a tree branch) during the burial of the original, natural mould footprint. The wood fragment settled (along with coarse sands) into the footprint along the long axis of digit III and is exposed for a few centimetres at the distal end of this digit impression.

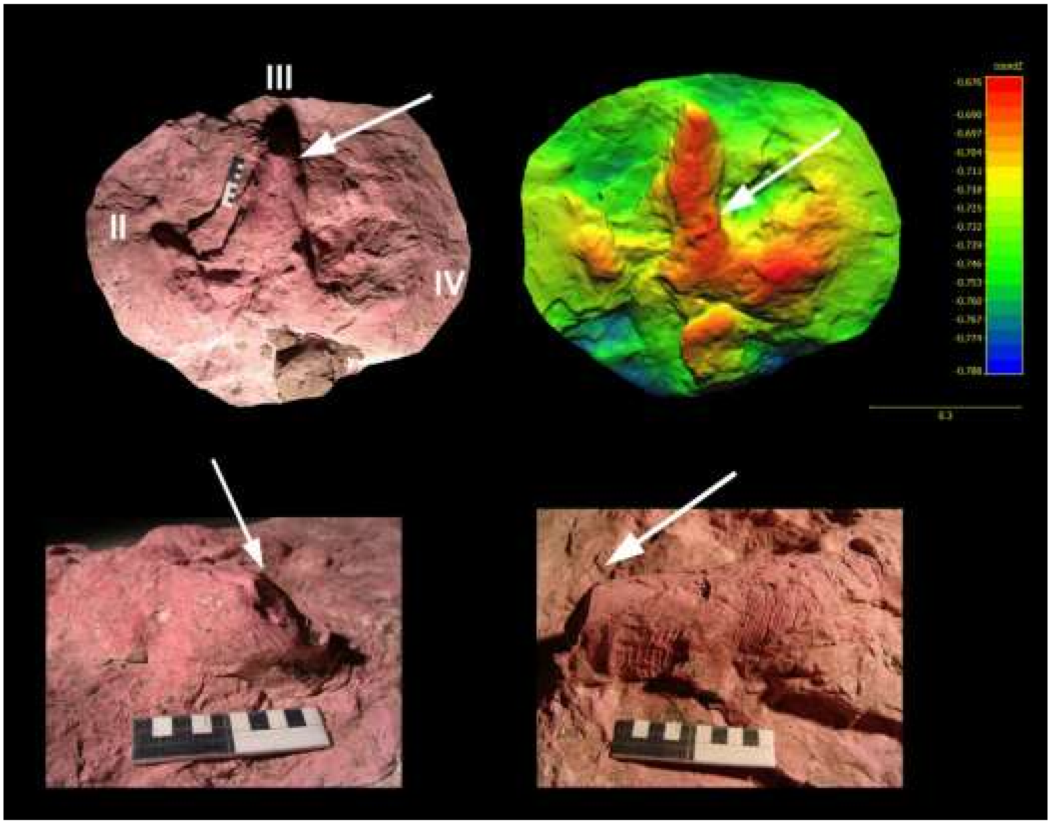


Figure 8.20. PRPRC 2004.08.001 (All images are from PRPRC 2004.08.001MC, a replica cast painted light red for research purposes). Top left: view of whole natural cast footprint (left) with arrow indicating position of wood fragment visible at the distal end of the digit III

impression. Top right: photogrammetric image of PRPRC 2004.08.001MC (horizontal and vertical scales in metres) with arrow pointing at the bottom of two partial invertebrate U-burrows. Bottom left: anterio-lateral view of the distal end of the digit III impression with wood fragment visible (indicated by an arrow). Striations from skin tubercles are visible lateral to the wood fragment. Bottom right: medial view of the digit III impression with the wood fragment visible (indicated by an arrow). Skin tubercles and striations are visible along the medial edge of the digit III impression. Scale bars = 10 cm.

Influence of infauna: A cautionary example involving a possible avian ichnopathology was described and illustrated in McCrea and Sarjeant (2001, fig. 31.7 and 31.8). McCrea and Sarjeant (2001) reported that one left footprint in a large avian trackway “showed a craterlike swelling on the left side of digit III and on the right side of the metatarsal pad”. The possibility of these swellings being pathological (i.e. “bumblefoot”) was entertained, but since this was the only left print in a trackway of nine prints (with five left prints) that was associated with these “swellings” it was conceded that these marks were more likely the result of the action of infaunal invertebrates whose traces (identical to the marks associated with the *Limiavipes curriei* print) are extremely abundant all over that particular track-bearing bedding-plane.

A further example of the action of infauna occurs on the base of digit III of a tyrannosaur footprint, PRPRC 2004.08.001, where there are two, thick semi-circular structures (Fig. 8.20, upper right) which could be misinterpreted as pathological swellings on this digit. Instead they are the ventral surfaces of two U-shaped burrows, lined with faecal pellets, not unlike that found in *Ophiomorpha* isp. The invertebrate burrows were made after the original natural mould footprint had been filled with sediment. These invertebrate traces end at the interface between the sediments of the original, track-bearing substrate, and that of the infilling substrate. It is likely that burrowing invertebrates responsible for these U-traces were unable to penetrate far into the track-bearing substrate due to the prior compaction of the track surface caused by a combination of the mass and velocity of the tyrannosaur that made the footprint.

A similar circumstance was observed in a natural cast sauropod pes print (original - FGM 2001.13.1 and replica PRPRC 2000.01.001MC) from the Mist Mountain Formation of southeastern British Columbia (McCrea et al., 2014a). A lengthy invertebrate trace convex hyporelief (150 mm long x 4 mm wide) is visible on the plantar area of the sauropod track, near the base of digits I and II (Fig. 8.21). The invertebrate trace-maker had burrowed in the uncompacted sediments infilling the sauropod pes track, but could not penetrate the compacted sediments caused by the sauropod's passage. Instead the invertebrate trace-maker progressed along the interface between the sediments of the original track surface and those that covered it. Large track-makers create greatly compacted sediments which are impassable to some invertebrate infauna. This type of invertebrate trace has the potential for being mistaken for pathological growth, or swelling on the plantar surface of the track-maker's foot.

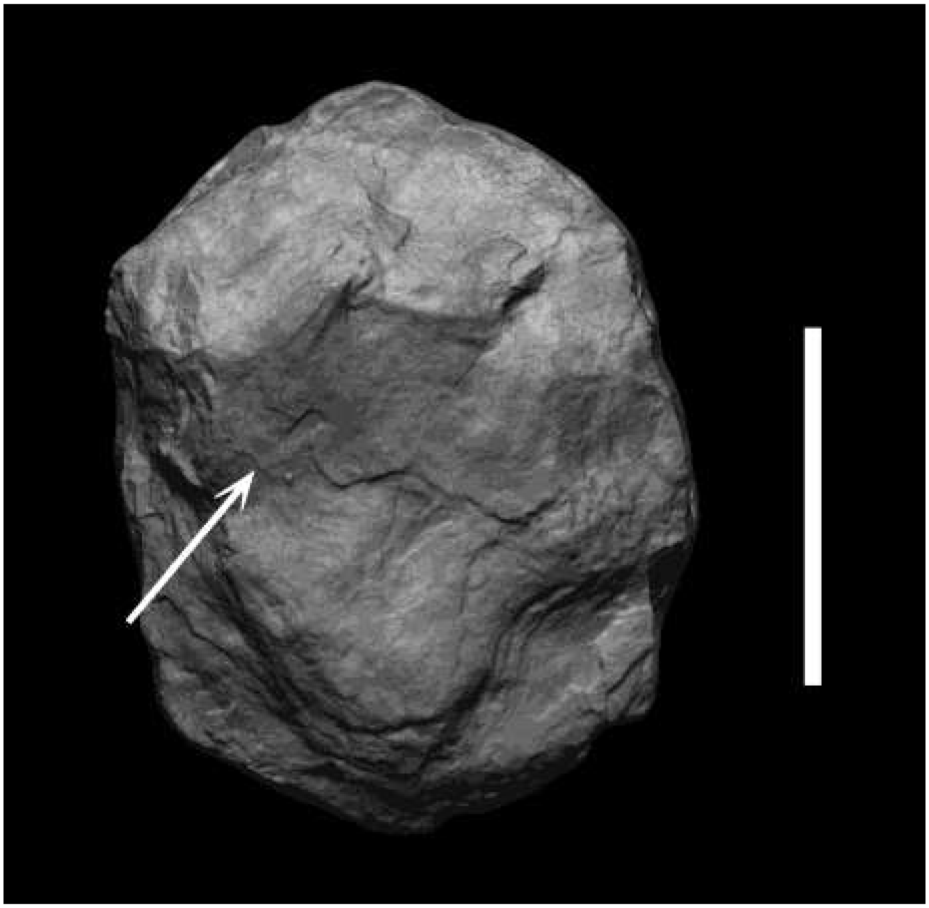


Figure 8.21. Natural cast of a right sauropod pes with an arrow pointing to an invertebrate trace made along the substrate interface (scale = 50 cm).

DISCUSSION

Out of the 14 tyrannosaurid footprints reported to date, four of which are from Alberta (McCrea et al., 2005. Fanti et al., 2013, McCrea et al., 2014b), eight from British Columbia (Farlow et al., 2009, McCrea et al., 2014b), one from the United States (Lockley and Hunt, 1994), and one from Mongolia (Currie et al., 2003), three footprints from two individuals exhibit remarkable pathologies. This amounts to 21% of individual tyrannosaur footprints with pathologies so far, or 14% of individual track-makers.

Pedal pathologies, and pathologic tracks, in theropods are not common. A theropod track either isolated or in a trackway, exhibits a characteristic preservation: the medial edge of the foot (digit II) impresses deeper than the lateral edge (digit IV). Digit II is inferred to have relatively more of the animal's body weight supported on it than digit IV, with digits II and III being the primary weight-bearing digits (Hopson 2001). Likewise, Lockley (2000, 2007) noted that digit II is typically, shorter, wider and more anteriorly located than digit IV. During the avian step cycle, the subphalangeal pads of all digits contact the substrate simultaneously (Senter 2009). Assuming the theropod foot moved in a similar manner to that of an extant bird foot (although Farlow et al. 2000 show differences in theropod and avian gait), it is unlikely that the injuries to the digits are the result of normal locomotion. In other words, theropods likely did not contact the ground preferentially with one digit, which might have increased the likelihood of differential stress or injury. It is unlikely that these pathologies were caused by scavenging. It is reasonable to suppose that wounds like this would be caused by restraining large, struggling prey, or fighting with other predators (Tanke and Currie, 2000).

Pedal injuries of such severe natures invites speculation as to their etiologies. A number of factors could lead to the ichnopathologies seen here. As in extant wild vertebrates, bone fractures are the most common disorder of the dinosaur skeleton (Tanke, 1989; Rothschild and Tanke, 1992; Rothschild and Martin, 1993; Rothschild, 1997; Tanke and Rothschild, 2002), and are observed across many diverse families. However, true examples of fractured and healed weight-bearing pedal elements among larger theropods (and other large bipeds) are rare (Molnar, 2001). Stress-related fractures on specimens of *Allosaurus* reported by Rothschild et al. (2001) show a distribution of 3% medial (digit II) and 10% on middle (digit III) and lateral (digit IV) digits, respectively. Where osteopathy affecting large theropods in this critical area is observed, it is typically in the form of simple osteophytes of possible infectious (non-traumatic) origins. Osteomyelitis with extra (sometimes exuberant) overriding bone growth has also been observed (Hanna, 2002; Farke and O'Connor, 2007) as well as stress-related abnormalities to pedal phalanges (Bell, 2010). This extra bone should not be confused with a fracture callus, which can superficially appear similar, especially if there are associated infectious complications. Fractures of weight-bearing pedal elements may be so severely detrimental to the affected animal that the odds of recovery and long-term survival are low. In a review of stress fractures in theropods, Rothschild et al. (2001, table 23.1) observed that healed stress fractures range from 0.3% (*Albertosaurus*), 1.2% (*Tyrannosaurus*), 2.4% (*Saurornitholestes*), 5.9% (*Chirostenotes*), 6% (*Allosaurus*), and 100% (*Ceratosaurus*, although the sample size for this observation was N = 1). As a consequence, pedal phalanx fractures among larger theropods are accordingly rare in the fossil record.

Extant volant raptors may not be the ideal analog for non-avian theropods in terms of foot use, as non-avian theropods are cursorial (and, in many of the examples provided, are large animals), and large theropods lack the well-developed flexor tubercles on their pedal phalanges (Fig. 8.13), that are possessed by extant birds of prey. However, there have been many studies on digit use with respect to prey handling in extant volant raptors, and these studies provide useful data on digit use in theropods. There is much opportunity to examine digit use in cursorial non-raptorial extant birds in future studies.

The low frequency of pedal injury in theropod traces is similar to that seen in extant birds of prey (excluding the injuries caused by anthropogenic means, such as leg snares, captivity, etc.) Bedrosian and St. Pierre (2007) saw a 14% (1/7) and 4% (4/86) pelvic injury rate (missing talons, missing digits, missing feet, or missing legs) in wild American Kestrals and Red-tailed Hawks, respectively. The specific pedal digit is not always identified in field reports of pedal digit injury, but Bedrosian and St. Pierre (2007) make specific mention of a broken talon (phalanx II-3) and a missing digit II on a Red-tailed Hawk and an American Kestral, respectively. A fractured left phalanx III-2 was reported by Gempton and Wheeldon (1983) on an adult female Australian Harrier. In these reports the affected birds were either of regular weight or slightly underweight (with body weight used as an indicator of overall health). Injury of pedal digits I and II have the potential to be detrimental to extant birds of prey: digits I and II oppose one another and apply the most power when handling and restraining prey (Einoder and Richardson, 2007; Fowler et al., 2009; 2011), and the talons of digits I and II are often the largest, with large flexor tubercles (Mosto and Tambussi, 2014). In non-raptorial birds, published information on the injuries to the legs and feet shows that injuries are also anthropogenic in origin, and these do not provide accurate data on natural pes digit injury for cursorial birds.

Congenital defects are another possibility. Extant chickens (*Gallus*) and other avians can develop curled toes (Pourlis, 2011). Dislocations are a final consideration. Dislocations of the pes among theropod dinosaurs are rarely noted. Tanke and Currie (2000) described a possible dislocation of a digit III ungual in a subadult specimen (TMP 1991.036.0500) of the Late Cretaceous tyrannosaurid *Gorgosaurus* (Fig. 8.22).

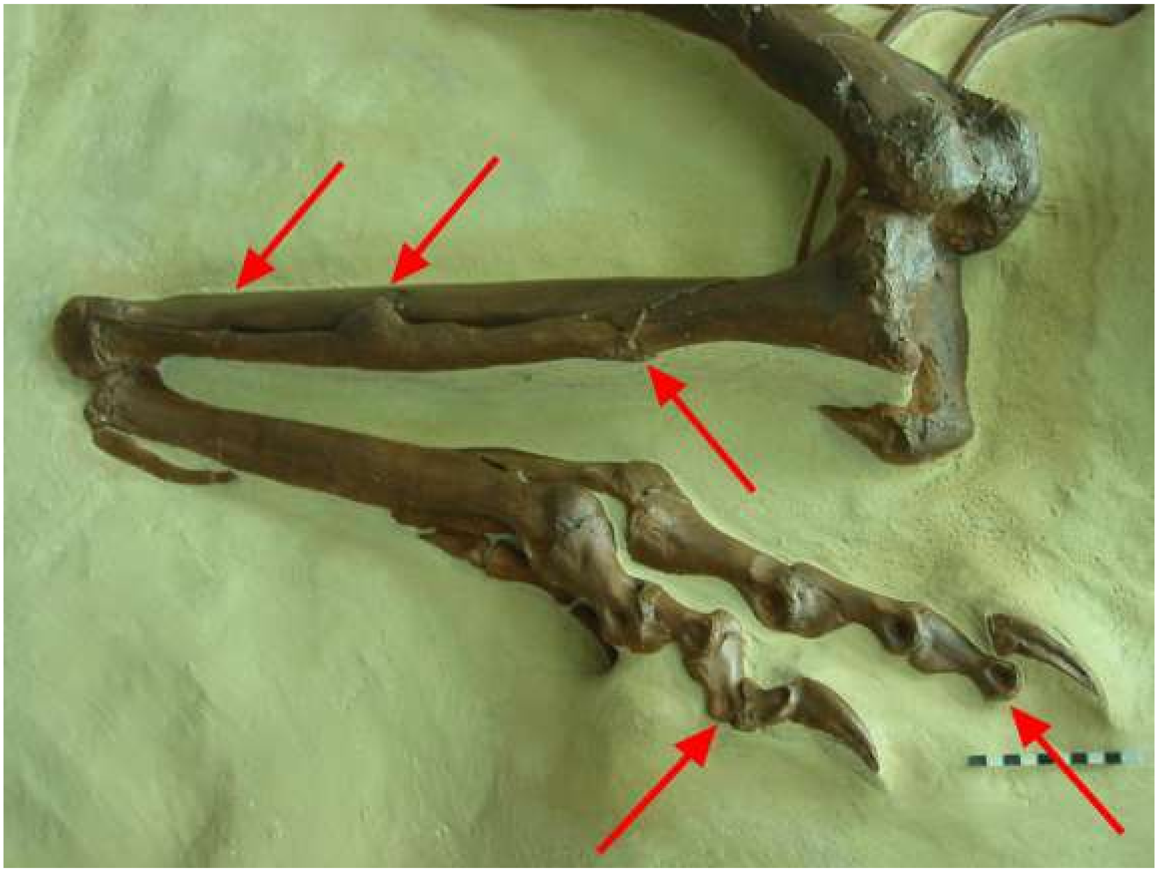


Figure 8.22. Articulated *Gorgosaurus* specimen TMP 1991.036.0500 right lower limb showing fractures to the fibula (fracture callus with bone spur at mid-length) which were in the process of healing, contacting tibia as well as a dislocated pedal claw on digit three (phalanx III-4) and possible dislocations of phalanges on digit IV. Scale in cm.

The ungual had over-thrust the penultimate phalanx over half of the latter's length. If correctly diagnosed, this animal would have left footprints with a shortened digit III. Supporting the dislocation hypothesis are associated osteopathies affecting the same limb. These consist of a fibula with a partially healed fracture at mid-length and a prominent distally-directed mushroom-like growth affecting the anteromedial fovea region of digit II-2. This lesion is suggestive of an avulsion (muscle tear) as have been observed in other tyrannosaurids (Carpenter and Smith, 2001; Brochu, 2003). Given the associated limb and phalanx osteopathy, limping in this individual seems likely and possibly contributing factors in this subadult's premature death.

Documented skeletal pathologies in pedal phalanges in *Allosaurus* and other theropods (Lambe, 1917; Ostrom, 1976; Rothschild et al., 1997; Hanna, 2002; Tanke and Rothschild, 2002; Farke and O'Connor, 2007; Bell, 2010; Bell et al., 2011, McCrea et al., 2014a, 2014b), show that, while the sample size of pathologic digits is small (and indeed, paleopathologies are relatively rare, Rothschild and Tanke, 2005) damaged phalanges appear to be evenly distributed among the three digits. The small sample size shows that there are more injuries to digits II and III than to digit IV (Table 8.2).

Pedal digit	Pedal phalanx	Pathologies documented	Digits affected total	Including track pathologies
II	II-1	3	6	7
	II-2	1		
	II-3 (ungual)	2		
III	III-1	4	5	7
	III-2	1?*		
	III-3	1		
	III-4 (ungual)	1+		
IV	IV-1	2	4	5
	IV-2	2		
	IV-3	0		
	IV-4	0		
	IV-5 (ungual)	0		

Table 8.2. Osteopathologies documented (see review in Rothschild and Tanke, 2005) in theropod track-makers for *Allosaurus* (Hanna, 2002), *Majungasaurus* (Farke and O'Connor 2007), Tyrannosauridae (Lambe 1917; Bell 2010; McCrea et al. 2014a, 2014b), and Dromaeosauridae (Ostrom 1976). While the sample size is small, there are more documented injuries in digits II and III than in digit IV.

The pathological phalanges range in inferred severity of injury, from responses to stress or repetitive use injuries (e.g. Bell, 2010), to bony growths on joint surfaces (e.g. Hanna, 2002), to callouses from healed fractures (e.g. Ostrom, 1976), to dislocated (Figs. 8.8, 8.10, 8.12), and amputated digits (Figs. 8.1, 8.2, 8.5, 8.6, 8.14) (McCrea et al., 2014b; Abel, 1935). There is a large degree of speculation involved when inferring how much discomfort these paleopathologies would have presented to the animals. While some of the paleopathologies seen in pes elements and tracks could represent a large range of discomfort (e.g. for cases of exostosis), there are some pathologies that would cause more discomfort, and potentially have more likelihood of producing enough discomfort to alter the regular use of the injured element, than others (Fig. 8.23). Some disarticulated Late Cretaceous hadrosaur and ornithomimid pedal phalanges in Royal Tyrrell Museum collections are so severely pathological as to suggest premortem sloughing off of the affected distal portion.

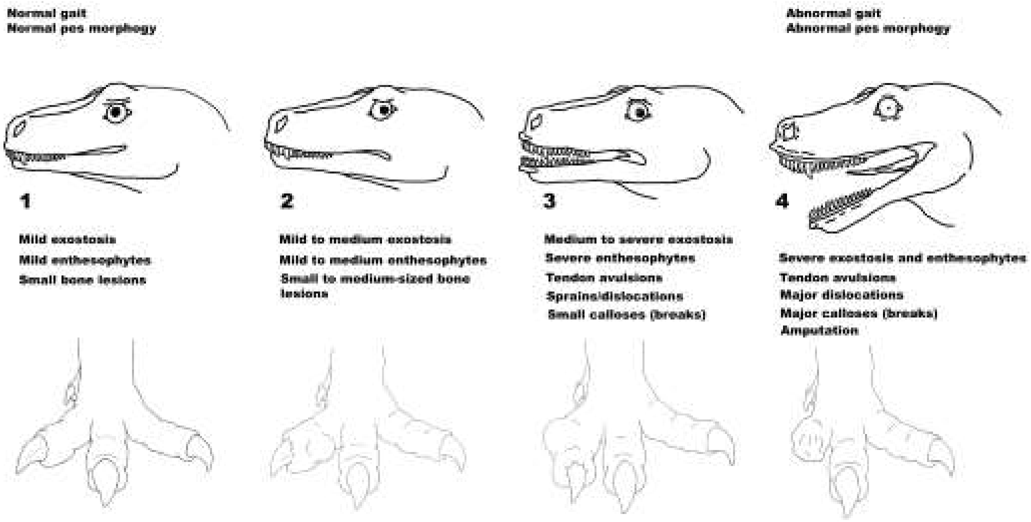
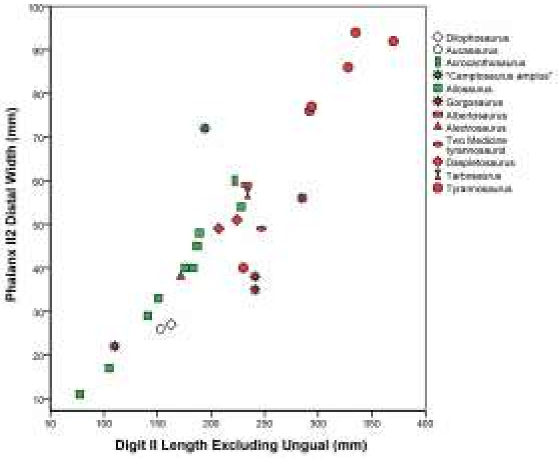
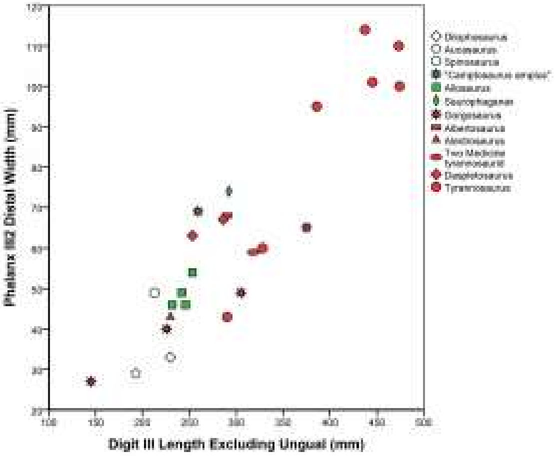


Figure 8.23. A simplified scale for injuries from mild to severe, the inferred degree of pain scale is speculative.

The occurrences of true traumatic ichnopathology among the Dinosauria are still largely restricted to theropods or those groups with elongate digits. This could be related to the more delicate morphology of the foot, inherent potential accidents (i.e. falling) related to bipedalism (Farlow et al., 1995) and a more active lifestyle involving the use of the foot as a raptorial weapon. The protruding toes in theropods are long and narrow and exposed to potential injury, although from footprints at least it seems that digit II is disproportionally prone to injury. It is possible that the medial digits are more susceptible to injury which may be related to how long these digits are in relation to their width (Fig. 8.24). It seems reasonable to assume that long, relatively thin digits may be structurally weak and more vulnerable to injury. However, the comparatively long and thin bones of tyrannosaurids (Fig. 8.24) were also surrounded by substantial soft tissue (flesh, muscle and sinew) as evidenced by their tracks (McCrea et al., 2014b). These tissues certainly would have provided a degree of protection and ameliorated the effects of the forces that must have been exerted on the feet during life of these animals.


Phalanx II2 Distal Width (mm)
Digit II Length Excluding Ungual (mm)
10
20
30
40
50
60
70
80
90
100
50
100
150
200
250
300
350
400
Dilophosaurus
Aucasaurus
Acrocanthosaurus
"Camptosaurus amplus"
Allosaurus
Gorgosaurus
Albertosaurus
Alectrosaurus
Two Medicine tyrannosaurid
Daspletosaurus
Tarbosaurus
Tyrannosaurus


Phalanx III2 Distal Width (mm)
Digit III Length Excluding Ungual (mm)
20
30
40
50
60
70
80
90
100
110
120
100
150
200
250
300
350
400
450
500
Dilophosaurus
Aucasaurus
Spinosaurus
"Camptosaurus amplus"
Allosaurus
Saurophaganax
Gorgosaurus
Albertosaurus
Alectrosaurus
Two Medicine tyrannosaurid
Daspletosaurus
Tyrannosaurus

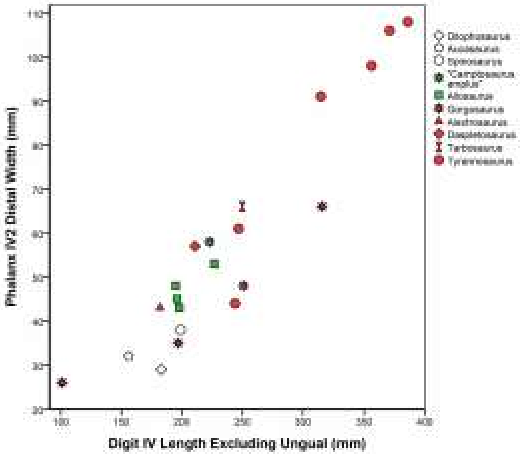

Phalanx IV2 Distal Width (mm)
Digit IV Length Excluding Ungual (mm)
20
30
40
50
60
70
80
90
100
110
100
150
200
250
300
350
400
Dilophosaurus
Aucasaurus
Spinosaurus
"Camptosaurus amplus"
Allosaurus
Gorgosaurus
Alectrosaurus
Daspletosaurus
Tarbosaurus
Tyrannosaurus

Figure 8.24. Graphs plotting digit lengths to phalanx width for several dinosaur taxa. Top: digit II length to phalanx II2 distal width. Middle: Digit III length to phalanx III2 width. Bottom: Digit IV length to phalanx IV width.

The presumed active lifestyle of theropods can, and probably did occasionally, lead to manual and pedal traumatisms related to running, intraspecific strife, prey capture and killing (Marshall et al., 1998; Sullivan et al., 2000; Carpenter and Smith, 2001; Rothschild et al., 2001).

The potential range of motion of pedal phalanges may also, when examined in the context of an active bipedal lifestyle, contribute to the rate of injury in theropod pedes. Examination of the range of extension and flexion of digits in theropods with non-specialized pedal digits (*Allosaurus*, *Dilophosaurus*, *Chirostenotes*, and *Mononykus*, data presented in Senter, 2009) reveals there is considerable overlap in the potential range of motions of digits II, III, and IV with respect to the most proximal phalanges II-1, III-1, and IV-1. Examination of the ranges of the individual phalanges within digits shows that different taxa have differing maximum ranges of digit hyperextension and flexion. In the large theropods *Allosaurus* and *Dilophosaurus*, digit II shows the least amount of hyper extension in phalanges (II-3), with correspondingly small amounts of hyperextension in phalanges III-4, and IV-1 (of *Allosaurus*) and IV-5 (of *Dilophosaurus*).

The least amount of flexion was observed in phalanges II-1, III-1 (of *Dilophosaurus*) and III-4 (of *Allosaurus*), IV-2 (of *Dilophosaurus*) and IV-1 (of *Allosaurus*). There are no striking differences in phalangeal joint flexibility of the large theropods studied by Senter (2009) that could account for an individual digit that would be more prone to damage than others. The unguals of digits II and III, and phalanx IV-1 seem to have the lowest degree of extension, while phalanges II-1, III-1, IV-1 and IV-2 seem to have the lowest degree of flexion.

An active lifestyle in large pterosaurs has been implicated in a number of traumatic osteopathies in that group (Bennett, 2003). Feet of most contemporaneous herbivores such as sauropods, stegosaurs, ankylosaurs and ceratopsians (and hadrosaurs to a lesser extent) were more elephantine-like in morphology, with shorter stubby toes encased in a thickly padded foot (Lockley, 2007). Feet with this compact and cushioned morphology, despite their massive weight-bearing function would have been less vulnerable to external damage from contact with injurious objects in the environment, which could show in footprints. Well-documented examples of stress fractures among Late Cretaceous ceratopsians (Rothschild, 1988; Rega et al., 2010; Tanke and Rothschild, 2010) pertain to bones enveloped in tissue. Thus, such damage or pathology would not obviously be expressed in track or trackway abnormalities or irregularities, unless indirectly through modifications to gait.

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09 CONCLUSIONS

This study focused primarily on track sites within Alberta and British Columbia; provinces with combined areas in excess of 1.5 million km2 which is a great deal larger than many countries. Field sites were scattered over a large area from southern Alberta and southeastern British Columbia, to northeastern British Columbia, and as far west as Lillooet, B.C. Many sites were exposed naturally along the banks of creeks and rivers (sometimes in rivers), or on anticline limbs near the tops of mountains. On the other hand, a number of track sites were found in industrial locations including coal mines, gaswell sites, and seismic cutlines. Transportation to sites was as varied as the location of the sites themselves. A variety of road vehicles, ATV's, helicopters, bicycles, river rafts, or just plain hiking were employed to visit the sites so they could be studied.

The first objective of this study was to undertake a comprehensive survey of track-bearing formations in western Canada (British Columbia and Alberta). This was done in order to establish the foundation of knowledge that would provide the context necessary to make sense of data gathered from so many sites from so many formations. As a result of this study a number of formations were recognized for the first time as possessing vertebrate traces. Western Canada has also been recognized as possessing the most stratigraphically complete record of vertebrate ichnofaunas in the world for the Cretaceous **(Lockley and Lucas, 2014)**. Regardless of the value the rest of this study is deemed to have, there now exists a substantial framework of published research which will greatly assist future endeavors in this field.

The recently published record of vertebrate ichnology of western Canada has filled a large temporal gap left by the absence of body fossils for most of the stages of the Cretaceous **(Chapter 2 – McCrea et al., 2014a)**. What is now known about the 90 million year long history of terrestrial vertebrates from the Late Jurassic to the Early Paleocene in western Canada was largely made possible through this study. The data from this study allows us to recognize differences and similarities between the composition of regional vertebrate ichnofaunas and whether they change through time and/or environment **(Chapter 2 - McCrea et al., 2014a)**. As a result we are now able to relate the significance of western Canada's vertebrate track record to the larger global context with observations on palaeoecology, palaeogeography, and extinction or extirpation.

During the course of this research a careful, conservative approach to ichnotaxonomic identification was employed. Even so, this research has led to the description of four new vertebrate ichnofamilies, six new ichnogenera, and seven new ichnospecies:

Albertasuchipes russellia ichnogen. et., isp. nov. **(McCrea et al., 2004)**.

Sarjeantipodidae ichnofamily nov. **(McCrea et al., 2004)**.

Sarjeantipes whitea ichnogen. et., isp. nov. **(McCrea et al., 2004)**.

Neoanomoepus perigrinatus ichnogen. et., isp. nov. **(Lockley et al., 2009)**.

Limiavipedidae ichnofamily nov. **(McCrea et al., 2014a)**.

Limiavipes curriei ichnogen. et. **(McCrea et al., 2014a)**.

Saurexallopus cordata isp. nov. **(McCrea et al., 2014a)**.

Tyrannosauripodidae ichnofamily nov. **(McCrea et al., 2014b)**.

Bellatoripes fredlundi ichnogen. et., isp. nov. **(McCrea et al., 2014b)**.

Paxavipedidae ichnofamily nov. **(McCrea et al., 2015)**.

Paxavipes babcockensis ichnogen. et., isp. nov. **(McCrea et al., 2015)**.

Even though a number of vertebrate groups have very conservative pes and manus anatomies the taxonomy of the track-makers was identified as completely as possible. Synapomorphies involving the pes or manus have not generally been identified for diagnosis to lower level taxonomic groupings (Carreno and Wilson, 2001; Farlow et al., 2013; McCrea et al., 2015) and so did not play a significant part in the majority of this study. Stratigraphic and palaeogeographic context and comparisons were used as additional support for track-maker identifications that had already been made from anatomical comparisons to vertebrate ichnites.

Interpretations of the habitats of the track-makers and characteristics of the palaeoenvironment were based on palaeoecological observations of many of the track sites reported in this study. This research has defined the new ‘Tetrapodosaurus Ichnofacies’ **(Chapter 2 - McCrea et. al., 2014a)**, characterized by the strong association of *Tetrapodosaurus* isp. tracks and trackways with low energy, high-organic content substrates which are often found in proximity to coal seams.

This study of vertebrate traces has also led to revelations about the behaviors, biology and biomechanics of extinct animals that were not possible, or were only hinted at from studies of osteological specimens. For example the description of a track site with trackways of large tyrannosaurids **(Chapter 6 - McCrea et al., 2014b)** provided very strong evidence for gregariousness of this group which had been postulated by others based on the analyses of sites with preserved osteological remains. Also, interpretations of injuries inferred from footprints **(Chapter 8 – McCrea et al., in press)** provided evidence of the difficult and dangerous lives dinosaurs (particularly large theropods) lived, and how they may have coped with serious injuries.

This research has had a direct impact on the conservation of fossil track sites in western Canada. The designation of the Grande Cache, Alberta tracksites as a Provincial Historic Resource **(Spivak et al., 2006)** is one of the highest protective designations for vertebrate track sites in Canada. This research has also been behind the province of British Columbia's current drive to implement protective and management legislation for vertebrate trace fossils.

The Peace Region Palaeontological Research Centre in Tumbler Ridge, British Columbia was brought into being due to this thesis project. This institution now has one of largest collections of vertebrate ichnites in the world and has led to the establishment of the UNESCO supported Tumbler Ridge Global Geopark in the fall of 2014, which is the second Global Geopark in North America.

Ongoing and Future Work

Chapter 2 **(McCrea et al., 2014a)** was a comprehensive summary of the ichnological record of western Canada. Fig. 2.108 illustrated the general trends of occurrence of track-makers through time, but this was (with the exception of tracks of small quadrupedal ornithischians) mostly composed of occurrences of tracks from large dinosaurs. Small- and medium-sized theropod tracks occurrences were not included in this figure due to sometimes highly variable preservation and problematic identification. Non-dinosaurian track occurrences were not included in this figure because these track types are the least reliably preserved due to their size (preservation bias), or are generally restricted to depositional environments that do not favour large-scale exposure, or are found on substrates that do not survive long after exposure. The exclusion of the above track types from Fig. 2.108 did not diminish the ability to identify regional vertebrate ichnofaunal categories for western Canada. Their absence in the most recent version of the ichnological record may not, and in many cases likely did not, reflect the absence of the track-makers.

Fig. 9.01 presents all of the occurrences of all of the track-types (and their implied makers) that have been recognized to date from western Canada. This figure includes currently unpublished temporal extensions of some groups (e.g. Sauropodomorphs, Megalosaurids/Allosauroids, avians) and temporal reductions for others (e.g. Mammalia, for reasons explained in Chapter 2 – McCrea et al., 2014a).

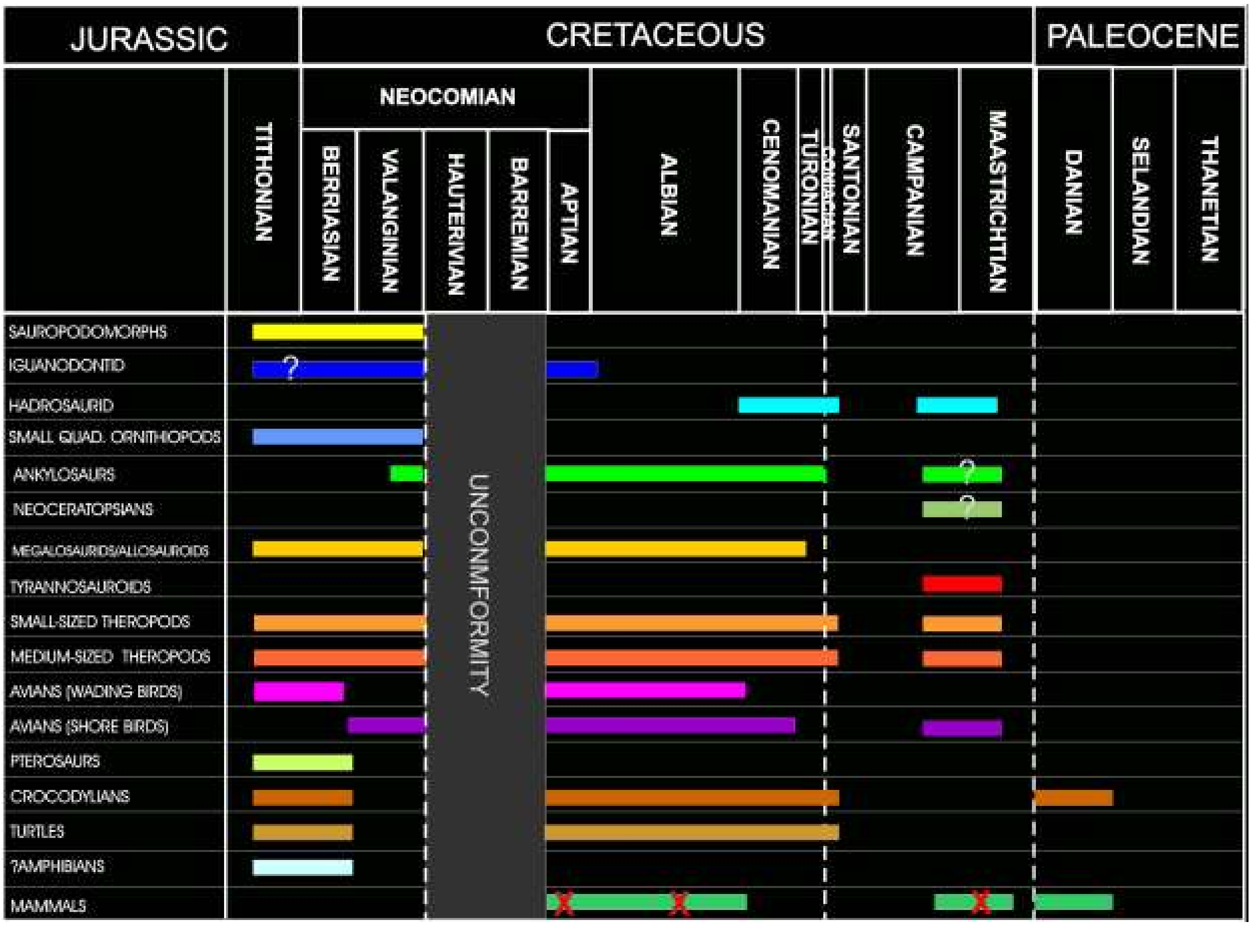

Fig. 9.01. The record of vertebrate ichnology of Western Canada.

The Megalosaurid/Allosauroid extension was based on a single large theropod print from the Dunvegan Formation (Cenomanian) from Chapter 2, (Fig. 2.109), and McCrea et al., (2014a).

The recent focus of vertebrate ichnology research on the Minnes Group strata has led to the discovery of a number of track sites, especially in the vicinity of Mt. Reesor, in northeastern British Columbia. A recent discovery and collection of an *ex situ* natural cast of a pes print (Fig. 9.02) in Minnes Group strata by this candidate considerably extends the northward range of Sauropodomorphs in North America from a present day latitude of 49° 50’ for the first sauropod track discoveries in the Mist Mountain Formation of the Elk Valley Coal District (McCrea et al., 2014) to 55° 0’.

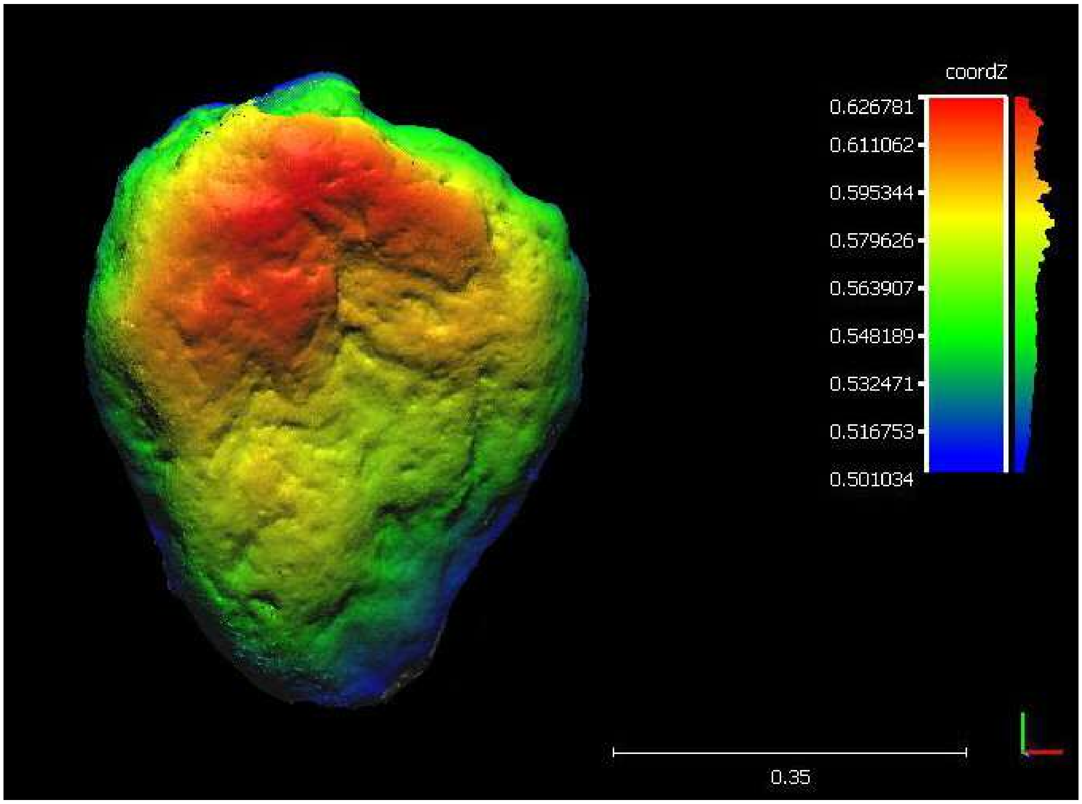

Fig. 9.02. A recently discovered sauropod pes (natural cast of a right pes) from the Minnes Group from Tim’s Creek located on the southeast flank of Mt. Reesor, northeastern British Columbia.

The ichnological record of shorebirds in western Canada was also extended back to the Valanginian with the recent discovery from Minnes Group strata from the same area that the sauropod print was found (Fig. 9.03).

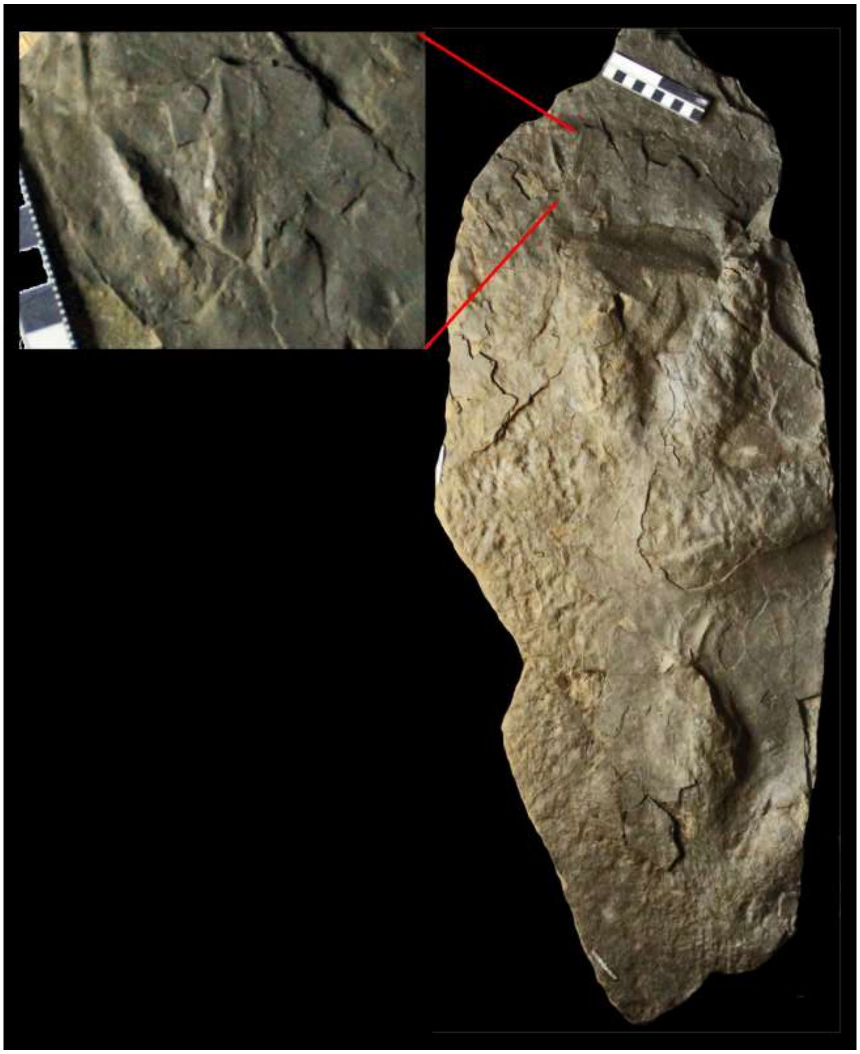

Fig. 9.03. Natural cast slab with medium-sized theropod and avian ichnites from the Minnes Group of northeastern B.C.

A large, vertical track surface area from a drainage area on Mount Reesor was recently discovered and is currently under study (Fig. 9.04). So far it is known to contain the tracks of large iguanodontids, and small to very large (FL = 65 cm+) theropods.

Fig. 9.04. Closeup of a large-scale, vertical track surface from the Minnes Group with tracks of large quadrupedal ornithopods and large bipedal theropods visible.

Chapter 2 (McCrea et al., 2014a) serves the purpose of a comprehensive survey of vertebrate ichnological occurrences in western Canada. It was not intended to go into detail in regards to the specific descriptions or treatments of individual track sites, or ichnofaunas. Descriptions of almost every track-bearing formation in western Canada which were provided in Chapter 2 (McCrea et al., 2014a) could easily be elaborated upon, some of which to a very large degree. The Mist Mountain Formation, Minnes Group, Gething Formation, Gates Formation and Dunvegan Formations have been found to possess huge numbers of tracks or track surfaces which individually would spawn a great number of scientific publications or large monograph style treatments. Continued work on the vertebrate ichnofauna of the Gething Formation is particularly important from a global perspective because Sternberg’s (1932) publication was the world’s first description of a Cretaceous vertebrate ichnofauna.

In addition to the continued production of scientific descriptions of western Canada’s vertebrate ichnofaunas is the need for detailed comparisons to other regional ichnofaunas from around the world. These comparisons are underway and more are planned for the future. This will allow the integration of western Canada’s vertebrate ichnofauna into the global track record.

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