Tetradactyl Theropod Ichnotaxa and their Trackmakers

by

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We acknowledge and respect the Lək̓ʷəŋən (Songhees and Esquimalt) Peoples on whose territory the university stands, and the Lək̓ʷəŋən and W̱SÁNEĆ Peoples whose historical relationships with the land continue to this day.

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Abstract

While most theropod dinosaurs would have left behind tridactyl (three-toed) footprints, there are rare occurrences of tetradactyl (four-toed) theropod footprints in the palaeoichnological record. Previously, diagnostic criteria between the tetradactyl theropod ichnogenera *Saurexallopus* and *Ordexallopus* were poorly defined. Systematic revision of ichnotaxonomy now separates these two ichnotaxa on the basis of digit I orientation. The trackmaker for *Saurexallopus* has been debated since the ichnogenus was first described. Arguments were split between Oviraptorosauria and Therizinosauria. Based on morphological observation and multivariate comparison of measurements for skeletal and footprint material, an Oviraptorosaurian affinity is preferable. The discovery of a novel ichnospecies of *Saurexallopus*, *S. neesowatchiensis*, from the Aptian-Albian Gething Formation of northeastern British Columbia, Canada has implications for an earlier appearance of gigantic oviraptorosaurs in North America and an earlier appearance of Oviraptorosauria in Canada.

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Acknowledgements

The Neeso-Watchie Dinosaur Tracksite is on Treaty 8 territory, and I would like to acknowledge and respect the Saulteau First Nation and the Tse'khene, Métis, Dene, and Tsa'tinne peoples upon whose traditional territory the tracksite lay.

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Dedication

This thesis is dedicated to my parents David and Cheryl Dickson, who have always supported me in all my endeavors and to my chosen family who show nothing but love and support. In pursuit of the dream.

In loving memory of Josie, my dear friend, family, mentor, and knight. A bright and special soul taken from this world far too soon.

Introduction

Palaeoichnology is the study of trace fossils. These include anything left behind as a result of the activity of some living organism such as coprolites (fossilized feces) or ichnites (fossilized footprints). In relation to dinosaurs, the study of dinosaur footprints is particularly important as it can fill gaps in the skeletal fossil record. Because an animal leaves behind only one body but can produce many footprints during its lifetime, there is a higher chance of its tracks being preserved than the animal itself (Lockley & Hunt, 1995). By identifying what dinosaurs produced tracks at a given site, we can expand the faunal composition to include taxa for which no bones have been found. This is especially important in British Columbia as only a handful of dinosaur bones have been found, thus far limited to the Late Cretaceous (Arbour & Evans, 2019; Cross & Arbour, 2024; McCrea & Buckley, 2004). Dinosaur footprints, however, have been found as far back as the Jurassic/Cretaceous boundary (McCrea et al., 2014).

The Early Cretaceous Neeso-Watchie Dinosaur Tracksite near Hudson's Hope in northeastern British Columbia preserves a highly diverse assemblage of dinosaurs including small to medium theropods, small to medium ornithopods, sauropods, and two large tetradactyl theropod tracks. Some publications have sought to ascribe a trackmaker for similar tetradactyl theropod tracks, but there is no current consensus. Fiorillo & Adams (2012) proposed that such tracks were created by therizinosaurs – herbivorous theropods with sickle-shaped claws; Gierliński & Lockley (2013) argued that they were created by oviraptorosaurs – bird-like omnivorous theropods. The tetradactyl footprints found at the Neeso-Watchie tracksite are described here. In Chapter 1, I establish their systematic relationship to other tetradactyl theropod footprints. In Chapter 2, I attempt to identify what kind of dinosaur could leave behind these unusual tracks.

1.1 Ichnotaxonomy

Identifying dinosaur trackmakers comes with its own challenges because many dinosaurs had a similar tridactyl (three-toed) foot shape. This makes it nearly impossible to ascribe a footprint to a specific dinosaur species. As a result, a separate naming system was established based on footprint morphology so that ichnites (fossilized footprints) of similar types could be associated with one another throughout time and space with the implication being that similar morphologies are made by the same type of animal, even though we are not sure what dinosaur it was specifically. The naming system works similarly to the taxonomic system used for identifying living organisms using binomial nomenclature; the same ranks are used but with the prefix ichno- (e.g. ichnogenus). This concept was established by Edward Hitchcock in the mid-1800s (Hitchcock, 1836).

Currently six tetradactyl theropod ichnogenera are recognized as valid: *Macropodosaurus* (Sennikov, 2021), *Xiangxipus* (Xing et al., 2016), *Picunichnus* (Calvo and Rivera, 2018), *Boutakioutichnium* (Nouri et al., 2011), *Ordexallopus* (Lockley et al., 2018a), and *Saurexallopus* (Harris et al., 1996). With this recent rise in interest in the field and quality of data, a review of the literature is necessary as there seems to be little consensus on what constitutes a significant difference in morphology. By analyzing the literature, we can confirm that the morphological features observed in new footprints like those described herein (Ch. 1) are either comparable to previously described ichnotaxa or have significant differences that warrant the erection of a new name. In order to definitively assign the Neeso-Watchie footprints, I delve into the literature and amend ichnotaxonomic diagnoses to clarify differences between the established tetradactyl theropod ichnogenera and reclassify previously described occurrences.

1.2 Trackmaker Identification

Having identified the Neeso-Watchie footprints as a new ichnospecies of *Saurexallopus*, I seek to then identify what kind of dinosaur might have produced these enigmatic footprints and resolve the debate between *Saurexallopus* as either an oviraptorosaurian or therizinosaurian ichnogenus (Gierliński & Lockley, 2013; Fiorillo & Adams, 2012). In order to achieve this goal, I compare *Saurexallopus* footprints with skeletal fossils of the feet of potential trackmaker groups. I include both of the proposed groups as well as basal Neornithischia and Leptoceratopsidae. The latter are not theropods and thus have been ignored as potential trackmakers for *Saurexallopus*. Unlike other ornithischians, however, these two groups do not have the blunt hooves typical of larger ornithischians. Rather, they have four relatively slender toes ending in triangular unguals that could theoretically leave behind sharp claw-marks. Their feet are also in the general size range of most known *Saurexallopus* tracks. The inclusion of Leptoceratopsidae was based largely on the Denali National Park '*Saurexallopus'* sp., which are broader, thicker, and less widely divaricated than other *Saurexallopus* ichnospecies (Fiorillo & Adams, 2012; Fiorillo et al., 2018).

I use both morphological observations and multivariate analysis to identify the trackmaker for *Saurexallopus*. Multivariate analyses are carried out using linear measurements of digit and foot lengths and widths as well as interdigital angular data. Principal component analyses are performed to determine if these measurements could confidently be used to identify trackmaker groups from their feet and if footprints can be associated with those trackmaker groups. Linear discriminant analyses are performed on the datasets to see if footprints entered as belonging to an unknown group could be classified into one of the potential trackmaker groups.

Finally, landmark analysis is performed on the arc of the distal metatarsals to test if the observation made by Fiorillo et al. (2018) that therizinosaurs have a shallower arc can be used to identify potentially therizinosaurian footprints.

Chapter 1: Description of a new dinosaur ichnospecies from the Lower Cretaceous Gething Formation, British Columbia, Canada and a reassessment of tetradactyl theropod ichnotaxa

1.1 Introduction

The Peace Region of northeastern British Columbia, Canada has historically shaped the understanding of the dinosaurs that roamed the region during the Early Cretaceous by preserving a large and diverse assemblage of dinosaur footprints. The presence of these trace fossils in the Peace River Canyon was first reported by Frank McLearn (1922), which then spurred research led by Charles Sternberg for the National Museum of Canada (now the Canadian Museum of Nature). This research led to the erection of several new ichnogenera representing a diverse dinosaurian fauna of theropods, ornithopods, and ankylosaurs (Sternberg, 1932). During the 1970s, the area was revisited by a crew from the Provincial Museum of Alberta (now the Royal Alberta Museum) as the construction of the W.A.C. Bennett and Peace Canyon dams would eventually submerge the tracksites (Currie, 1981, 1983; Currie & Sarjeant, 1979). These expeditions yielded a small avian ichnogenus (Currie, 1981). When the Peace Canyon Dam construction was completed in 1979, these vast and significant tracksites became largely lost to science except for the specimens collected during the 1970s expeditions. Since the completion of the dams, the Gething Formation has mostly been found as small exposures like the Ninesting Creek tracksite, at which the tracks of another medium-sized avian theropod and a tetradactyl non-avian theropod have been reported (Lockley et al., 2022).

In 2008, a new large tracksite of the same formation in the Hudson’s Hope area was reported by Barry Mireau to the Peace Region Palaeontology Research Centre (now Tumbler

Ridge Museum), and a TRM crew began work on the site in 2016 (McCrea, 2017). This site, the Neeso-Watchie Dinosaur Tracksite (previously referred to as the Six Peaks Dinosaur Tracksite) revealed an even more diverse dinosaurian fauna than previously known for the region, including tracks of a tetradactyl theropod (McCrea, 2017). As of 2023, ongoing research by the Royal British Columbia Museum continues excavation and documentation of this extensive tracksite.

Here I identify and describe a new ichnospecies of the tetradactyl theropod ichnogenus *Saurexallopus* based on tracks at the Neeso-Watchie tracksite. These tracks are noteworthy for being morphologically distinct from previously described examples of this ichnogenus and provide new insights on the faunal composition of Early Cretaceous western Canada. I also review the systematics of *Saurexallopus* and other similar tetradactyl theropod tracks.

1.2 Geological setting

The Neeso-Watchie tracksite is located just west of Hudson's Hope in the Peace Region of northeastern British Columbia (Figure 1.1). Unlike the historical Peace River Canyon sites, this tracksite is not along a river and is thus not at risk of flooding and is not exposed to the same level of erosion. The tracksite, accessible via forestry roads, is relatively flat. Approximately 700 m^2 is currently exposed with in excess of 1000 tracks, the majority of which are ichnogenera previously documented in the region including *Irenesauripus* and *Columbosauripus* (theropods) and *Amblydactylus* and *Gypsichnites* (ornithopods).

The track surface is preserved in the Gaylard Member of the Gething Formation (McCrea, 2017). The Gaylard Member is comprised of coal-bearing fine-grained sandstone, carbonaceous mudstone with plant fragments, and occasional conglomerates (Stott, 1971). This member fines and thins northward, with interspersed channel deposits containing ripple laminae and carbonaceous debris (Stott, 1971). Among the plants identified within the Gaylard Member are cycads, ginkgoes, conifers, and ferns, which suggest a coastal swamp palaeoenvironment (Stott, 1971). The combination of alluvial and swampy features corresponds with the southward transgression of the Clearwater/Moosebar boreal sea onto an alluvial plain or deltaic complex during the Early Cretaceous (Gibson, 1992). Further evidence that supports this environmental interpretation is the occurrence of marine to brackish bivalves—the presence of which dates the Gaylard Member to the Aptian-Albian (Gibson, 1992).

Figure 1.1: Map displaying the location of the Neeso-Watchie Dinosaur Tracksite. Created with ArcGIS Online. Basemap by Esri Canada (2019)

1.3: Materials and methods

Two footprints sharing distinctive tetradactyl morphology are preserved in epirelief as natural moulds at the Neeso-Watchie tracksite (Figure 1.2). These tracks most likely represent shallow undertracks as the overlying layer is thin, fissile, and where still present at the tracksite contains footprints. All footprints remain *in situ* at the tracksite. Silicone moulds (RBCM P2023.107.0003 and RBCM P2023.107.0005) were made in the field using Smooth-On Rebound 25 and 40, supported by plaster and burlap shells. Another silicone mould was independently made for storage at the Tumbler Ridge Museum by the Peace Region Palaeontology Research Centre team at an earlier date. I examined casts and original specimens with similar morphologies held at the University of Colorado, the Tumbler Ridge Museum, the Denver Museum of Nature and Science, and the Perot Museum of Nature and Science to help with the identification of the Neeso-Watchie footprints.

I created 3D models of the specimens using photogrammetry. Photographs were taken using a Nikon D3200 and processed using Agisoft Metashape Version 2.0.0 (2023). False-color depth and contour maps were generated in CloudCompare v2.12.4 (2023) to better visualize the footprint outlines (Figure 1.3).

Figure 1.2: Photographs of the holotype (left) and paratype (right) footprints of Saurexallopus neesowatchiensis

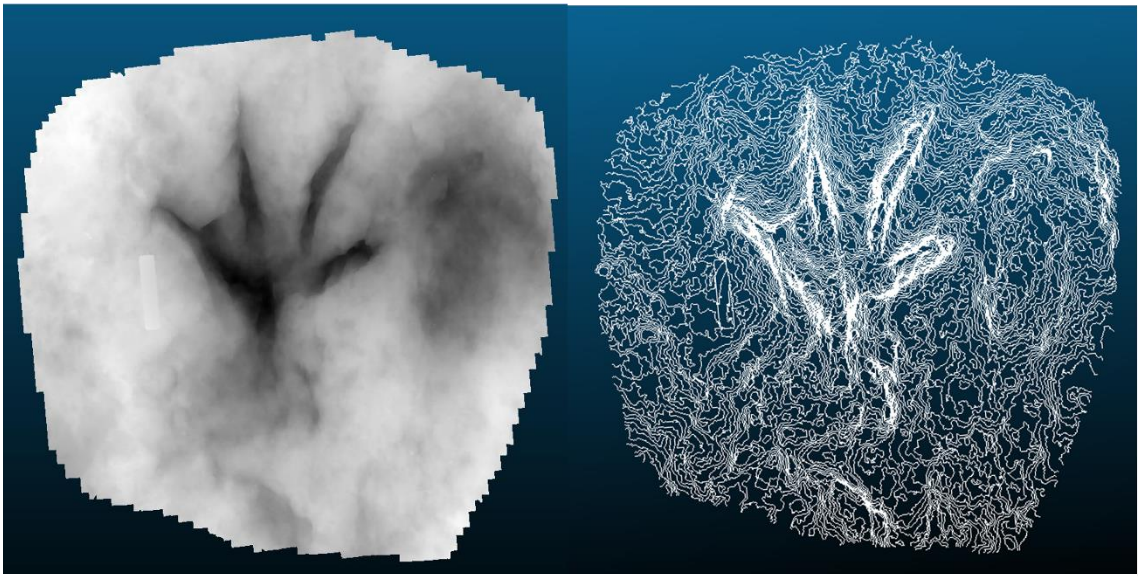

Figure 1.3: False-colour depth map (left) and contour map (right) of the holotype Saurexallopus neesowatchiensis track generated in CloudCompare v2.12.4 (2023)

I took linear measurements (Figure 1.4) including footprint lengths and widths in the field using a measuring tape. Footprint length was measured along digit III starting at a point where the midlines of all digits intersected, and footprint width was measured perpendicular to length. Digit II and III lengths were measured along the digit from a point midway between the hypices on either side, while digit I and IV lengths were measured from the point where the midline is perpendicular to a line tangent to the single hypex. All digital widths were measured at half the length of the digit. Angular measurements including interdigital angles were taken digitally from photographs using ImageJ 1.53t (Schneider et al., 2012). Interdigital angles were taken between digit midlines at a single point where all midlines converged.

Abbreviations

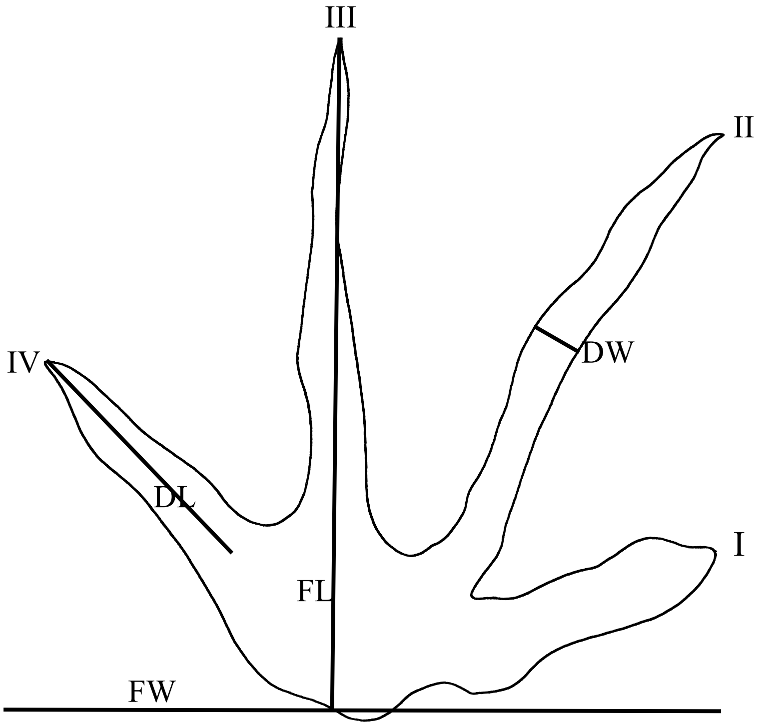

Figure 1.4: Diagram of linear measurements on footprints drawn on Saurexallopus neesowatchiensis holotype track. Digits labeled I-IV. FL – footprint length, FW – footprint width, DL – free digit length, DW – digit width

Institutional Abbreviations—CEUM, Utah State University Eastern Prehistoric Museum, Price, Utah, U.S.A.; **DMNS**, Denver Museum of Nature and Science, Denver, Colorado, U.S.A.; **Muz. PIG**, Geological Museum of the Polish Geological Institute, Warsaw, Poland; **DMNH**, Perot Museum of Nature and Science, Dallas, Texas, U.S.A.; **RBCM**, Royal British Columbia Museum, Victoria, British Columbia, Canada; **TRMF**, Tumbler Ridge Museum, Tumbler Ridge, British Columbia, Canada; **UCM**, University of Colorado Museum of Natural History, Boulder, Colorado, U.S.A.

Anatomical Abbreviations—FL, footprint length; **FW**, footprint width; **DL**, free digit length; **DW**, middle digit width

1.4 Systematic ichnology

THEROPODA Marsh, 1881

ORDEXALLOPUS Lockley, Li, Xing, Guo, and Matsukawa, 2018

Original Diagnosis—From Lockley et al. (2018a): "tetradactyl theropod track with unusually long hallux directed postero-medially for between half and a third of track width from center of metatarso-phalangeal digit IV heel pad. Tridactyl portion of track almost as wide as long with II-IV digit divarication (~80-90˚)".

Revised Diagnosis— Apparently bipedal track with four long, slender functional pedal digits. Digit I postero-medially oriented and straight to curved. Tridactyl portion of track approximately as wide as long with II-IV digit divarication (~80-90˚). Digit III longest digit; digits II and IV subequal in length. Distal metatarsal impression well-rounded. Digit I usually not connected proximally.

Type ichnospecies—*Ordexallopus zhanglifui* Lockley et al., 2018

Referred material—Three *Ordexallopus* sp. trackways (C – four footprints, D – four footprints, E – five footprints) preserved in concave epirelief from the Gething Formation (Aptian-Albian), Ninesting Creek tracksite, near Tumbler Ridge, British Columbia, Canada (Lockley et al., 2022). Of the thirteen tracks seven do not preserve clear digit I impressions, however, they occur in trackways in which postero-medially oriented and curved digit I impressions are present making them referable to *Ordexallopus* under the revised diagnosis.

Muz. PIG 1704.II.4, preserved in concave epirelief, from the Młynarka Mount (Upper Campanian), Roztocze Hills, Poland (50˚30.790’N, 023˚03.784’E) (Gierliński, 2009, 2015).

Trackway CEUM 405 (three footprints), preserved in concave epirelief, from the Blackhawk Formation (Campanian), Meetinghouse Canyon locality 1 (UCM Locality #815), near Castle Dale, Utah (Lockley et al., 2018b)

ORDEXALLOPUS ZHANGLIFUI Lockley, Li, Xing, Guo, and Matsukawa, 2018

Holotype—Trackway T1 at Chabu site 8D: UCM tracing T 1440

Paratypes—Trackways T2 and T11 at Chabu site 8D: UCM tracing T 1440

Diagnosis——As for *Ordexallopus* (Lockley et al., 2018a)

Locality and Age—Chabu dinosaur tracksite 8D, Jingchuan Formation, Lower Cretaceous (Barremain), Inner Mongolia, China (Lockley et al., 2018a)

ORDEXALLOPUS ZERBSTI Lockley, Nadon, and Currie, 2003 comb. nov.

Holotype—UCM 224.2

Original Diagnosis——From Lockley et al. (2003) “Tetradactyl track with very slender toe impressions, and prominent hallux trace extended medially. Holotype 35 cm long including hallux and 30 cm wide. Length 30 cm excluding hallux. Metapodial impressions sub-triangular and slightly asymmetric with anterior apex converging with distal portion of digit three, and posteromedial corner oriented toward hallux impression: posterolateral corner of metapodial impression connects proximally with digit IV, whereas digit II connects distally, resulting in a much deeper posterior recess (hypex) for the interdigital angle between III and IV than between II and III. Trackway narrow with relatively short step (78 cm). Foot length/pace length ratio about 1:2.5”.

Revised Diagnosis——Tetradactyl track with slender digits. Digit I poster-medially oriented and curved posteriorly. Tridactyl portion as wide as long with II-IV digit divarication (~80˚). Digit III longest; digits II and IV subequal in length. Subangular metapodial impression.

Locality and Age—Zerbst Ranch, Lance Formation, Late Cretaceous (Maastrichtian), Niobrara County, Wyoming (Lockley et al., 2003)

SAUREXALLOPUS Harris, 1997

Exallopus lovei Harris et al., 1996

Original Diagnoses——From Harris et al. (1996): "Apparently bipedal tracks with four long, slender functional pedal digits. Average divarication between outermost digits (I and IV) is 111.4˚. Footprint width greater than length. Digits II and IV subequal in length; both shorter than digit III. Digit I shortest digit, and not a reversed hallux. Impression of distal end of metatarsals impressed deeper than the digits and is semicircular in shape. Claw marks compressed laterally.

Track maker apparently bipedal, although possibility exists that pes prints completely overlie manus prints." Amended by Lockley et al. (2003) to include that digit I extends "medially to postero-medially. Formula for digital pad impressions is 2,2,3,?4 corresponding to digits I–IV, respectively. Metapodial impressions subtriangular and slightly asymmetric with anterior apex converging with proximal portion of digit three. Digit IV connected to metapodial proximally, whereas digit II connects distally. Trackway narrow with relatively short step."

Revised Diagnosis——Apparently bipedal tracks with four long, slender functional pedal digits. Average divarication between outermost digits (I and IV) is 111˚. Digits II and IV subequal in length; both shorter than digit III. Digit I shortest digit. Digit I straight and medially oriented, not a reversed hallux. Impression of distal end of metatarsals impressed deeper than the digits and is semicircular in shape. Claw marks compressed laterally.

Type ichnospecies—*Saurexallopus lovei* Harris, 1997

Referred material— One *Saurexallopus* sp. trackway (CEUM 9119 – two footprints) and one isolated *Saurexallopus* sp. (UCM 225.9) preserved in concave epirelief from the Blackhawk Formation (Campanian), Meetinghouse Canyon locality 1 (UCM Locality #815), near Castle Dale, Utah (Lockley et al., 2018b). Four *Saurexallopus* sp. (UCM 225.16-225.19) preserved in concave epirelief from Meetinghouse Canyon locality 2 (UCM Locality #816), also in the Blackhawk Formation near Castle Dale, Utah (Lockley et al., 2018b).

SAUREXALLOPUS LOVEI Harris, 1997

Holotype—DMNS 5989

Paratype—DMNS 5996

Plesiotypes—DMNS 5990, 5992, 5993, 5994, 5995, 5997

Diagnosis—— As for *Saurexallopus* (Harris et al., 1996; Harris, 1997)

Locality and Age—DMNS Locality #443 "Bridger-Teton Wilderness on the east side of Whetstone Creek, 1067 m upstream from confluence of Whetstone and Pacific Creeks, at an elevation of 2304 m (NW 1/4 of NE 1/4 of SW 1/4 of Sec. 10, T46N, R113W; 43˚57'54"N, 110˚24'39"W" (Harris et al., 1997). Whetstone Falls Member, Harebell Formation, Upper Cretaceous (Maastrichtian).

SAUREXALLOPUS CORDATA McCrea, Buckley, Plint, Currie, Haggart, Helm, and Pemberton, 2014

Holotype—From McCrea et al. (2014): "*In situ* specimen (natural mould) of a right footprint and also replica silicone mould (TRM 2012.04.001M) and fiber glass reinforced (FGR) plaster cast TRM 2012.04.001MC"

Diagnosis——As for *Saurexallopus* "but with prints possessing distinctly heart-shaped metatarsal pads, forming a bi-lobed "heel" impression" (McCrea et al., 2014)

Locality and Age—Along the banks of the Redwillow River east of Tumbler Ridge, British Columbia. Precise locality data on file at the TRM and the RBCM. Wapiti Formation, Unit 4, Upper Cretaceous (Campanian-Maastrichtian) (McCrea et al., 2014).

SAUREXALLOPUS NEESOWATCHIENSIS Dickson et al., 2024, ichnosp. nov.

(Fig. 1.2)

Holotype— *In situ* natural mould of a left foot (map grid number Y5-1) and RBCM P2023.107.0003 (silicone mould of same track)

Etymology— From Neeso-Watchie (Cree), the name used by the family of Saulteau First Nations member Tom Aird for the area in which the tracksite is located.

Paratype— *In situ* natural mould of a left foot (map grid number O11-1) and RBCM P2023.107.0005 (silicone mould of same track)

Diagnosis——Large (>35 cm) functionally tetradactyl footprints with slender digits (digit L/W >~5.5) radiating from a rounded distal metatarsal impression (differs from heart-shaped metatarsal impression in *S. cordata*). Digit I straight and medially oriented, not a reversed hallux (differs from reversed hallux in *Ordexallopus*). Laterally compressed claw marks. Digit III longest followed by digit II which is slightly longer than digit IV (differs from *S. lovei*). Digit I is the shortest.

Locality and Age—Neeso-Watchie tracksite south of Williston Lake and west of Hudson’s Hope, British Columbia, Canada; precise locality information is on file at the RBCM and TRM. Gaylard Member of the Gething Formation, Lower Cretaceous (Aptian-Albian).

Description—RBCM P2023.107.0003 has a length of 48.9 cm and a width of 50.3 cm, making it slightly wider than it is long. Excluding digit I, FW is 49.8 cm. Digit III is the longest at 38.0 cm, followed by digit II at 36.4 cm. Digit IV is shorter at 21.1 cm with digit I being the shortest at 18.5 cm. Total divarication from digits I-IV is 114.2˚ (78.7˚ from II-IV). The heel is not bilobed as in *S. cordata* (McCrea et al., 2014). *S. neesowatchiensis* appears most similar to the type ichnospecies *S. lovei* (Harris et al, 1996) though much larger, and digit IV is shorter than, instead of subequal to, digit II. No digital pads are visible. A partial metapodium impression is preserved on the holotype specimen. RBCM P2023.107.0003 is oriented 125˚ N within the tracksite and is preserved near tracks of *Irenesauripus* and *Gypsichnites*; another track, possibly from the same trackmaker, is identifiable posterior to RBCM P2023.107.0003 but is more poorly preserved and cannot be confidently referred to *S. neesowatchiensis*. A second isolated track with similar morphology, designated as the paratype for *S. neesowatchiensis*, is present ~10 meters to the east and is oriented at 33˚ N. RBCM P2023.107.0005 is slightly shorter than the holotype but nearly as wide (FL 40.0 cm and FW 49.6 cm). Without digit I FW=43.5 cm. Digit III is the longest at 25.5 cm, followed by digit II at 23.5 cm. Digit IV is 18.4 cm. Digit I is the shortest at 17.2 cm. Since this track is deeper, it is possible that the variation in digit length ratios is attributable to a wetter substrate. Total divarication is 123˚ (82.4˚ for the tridactyl portion of the footprint). Unlike in the holotype, no metatarsal impression is present.

Taxon	Specimen Number	Formation	Age	FL	DLI	DLII	DLIII	DLIV	WI	WII	WIII	WIV	Source	Elements Preserved
Saurexallopus neesowatchiensis	RBCM P2023.107.0003	Gething Formation	Aptian-Albian	48.9	18.5	36.4	38	21.1	4.4	4.1	3.9	3.7	This study	Original
Saurexallopus neesowatchiensis	RBCM P2023.107.0005	Gething Formation	Aptian-Albian	40	16.7	21.7	27.7	20.5	2	2	3	4.8	This study	Original
Saurexallopus cordata	TRMF 2012.04.001M	Wapiti Formation	Late Campanian	29.3	11.8	17.6	28.1	17.3	2.8	2.1	2.1	2.5	McCrea et al., 2014	Cast
Saurexallopus lovei	DMNS 5989	Harebell Formation	Maastrichtian	27.5	10.6	18.5	20.1	17.5	1.8	2.3	3.5	2.1	Harris et al., 1996	Original
Saurexallopus sp.	DMNH 2014-11-10	Cantwell Formation	Late Campanian	25.2	7.3	19	16	13	1.9	3.3	3.4	3.8	Fiorillo & Adams, 2012	Cast
Saurexallopus sp.	DMNH 2010-07-01	Cantwell Formation	Late Campanian	19.3	6.1	12.5	13.4	8.8	2.1	3.2	4.4	4.7	Fiorillo & Adams, 2012	Cast
Saurexallopus sp.	DMNH 2014-11-09	Cantwell Formation	Late Campanian	19.5	4.6	9.3	11.1	7.9	2.8	3.4	2.5	3.1	Fiorillo & Adams, 2012	Cast
Saurexallopus sp.	DMNH 2013-08-06	Cantwell Formation	Late Campanian	21.7	6.7	11.6	12.7	10.1	3.5	4.1	4.2	4.2	Fiorillo & Adams, 2012	Cast
Saurexallopus sp.	DMNH 2013-08-04	Cantwell Formation	Late Campanian	19.4	8	13.6	14.3	13.2	3.7	2.8	2.8	3	Fiorillo & Adams, 2012	Cast
Ordexallopus zerbsti	UCM 224.2	Lance Formation	Maastrichtian (Lancian)	28.7	11.3	15.8	21.5	17.8	3.9	3.9	3.3	4.2	Lockley et al., 2003	Cast

Table 1.1: Linear measurements of footprints in cm

Taxon	Specimen Number	Formation	Age	DI/WI	DII/WII	DIII/WIII	DIV/WIV	Source	Elements Preserved
Saurexallopus neesowatchiensis	RBCM P2023.107.0003	Gething Formation	Aptian-Albian	6.8	11.88	12.54	8.46	This study	Original
Saurexallopus neesowatchiensis	RBCM P2023.107.0005	Gething Formation	Aptian-Albian	12.05	15.52	13.35	6.5	This study	Original
Saurexallopus cordata	TRMF 2012.04.001M	Wapiti Formation	Late Campanian	5.43	10.95	13.38	8.4	McCrea et al., 2014	Cast
Saurexallopus lovei	DMNS 5989	Harebell Formation	Maastrichtian	8.37	10.75	7.83	11.29	Harris et al., 1996	Original
Saurexallopus sp.	DMNH 2014-11-10	Cantwell Formation	Late Campanian	7.37	8.55	7.41	5.45	Fiorillo & Adams, 2012	Cast
Saurexallopus sp.	DMNH 2010-07-01	Cantwell Formation	Late Campanian	6.19	6.34	4.39	3.15	Fiorillo & Adams, 2012	Cast
Saurexallopus sp.	DMNH 2014-11-09	Cantwell Formation	Late Campanian	6.02	5.88	5.04	3.88	Fiorillo & Adams, 2012	Cast
Saurexallopus sp.	DMNH 2013-08-06	Cantwell Formation	Late Campanian	3.55	4.89	5.2	4.7	Fiorillo & Adams, 2012	Cast
Saurexallopus sp.	DMNH 2013-08-04	Cantwell Formation	Late Campanian	3.26	6.01	7	5.67	Fiorillo & Adams, 2012	Cast
Ordexallopus zerbsti	UCM 224.2	Lance Formation	Maastrichtian (Lancian)	4.03	6.51	8.78	5.69	Lockley et al., 2003	Cast

Table 1.2: Digit length to width ratios of footprints

Taxon
Saurexallopus neesowatch
Saurexallopus neesowatch
Saurexallopus cordata
Saurexallopus lovei
Saurexallopus sp.
Saurexallopus sp.
Saurexallopus sp.
Saurexallopus sp.
Saurexallopus sp.
Ordexallopus zerbsti

Table 1.3: Interdigital angles for footprints

1.5 Discussion

While there are numerous other theropod footprints present at the Neeso-Watchie tracksite (*Columbosauripus* and *Irenesauripus*), the two *S. neesowatchiensis* specimens are not associated with any trackways of the former and have clear outlines showing that the first digit impressions are true and not double traces or the result of overprinting. They are referable to the ichnogenus *Saurexallopus* based on their slender tetradactyl morphology with digit I functional and medially oriented (Harris et al., 1997). The large tetradactyl footprints identified at the Neeso-Watchie tracksite can be differentiated from other previously described tetradactyl theropod footprints and are interpreted here as a new ichnospecies in *Saurexallopus* (Figs. 1.5 and 1.6). *Saurexallopus neesowatchiensis* differs from *S. cordata* based on the rounded, rather than bilobed, heel, and in *S. neesowatchiensis* digit IV is shorter than digit II compared to the subequal length of digit IV compared to digit II in *S. lovei*.

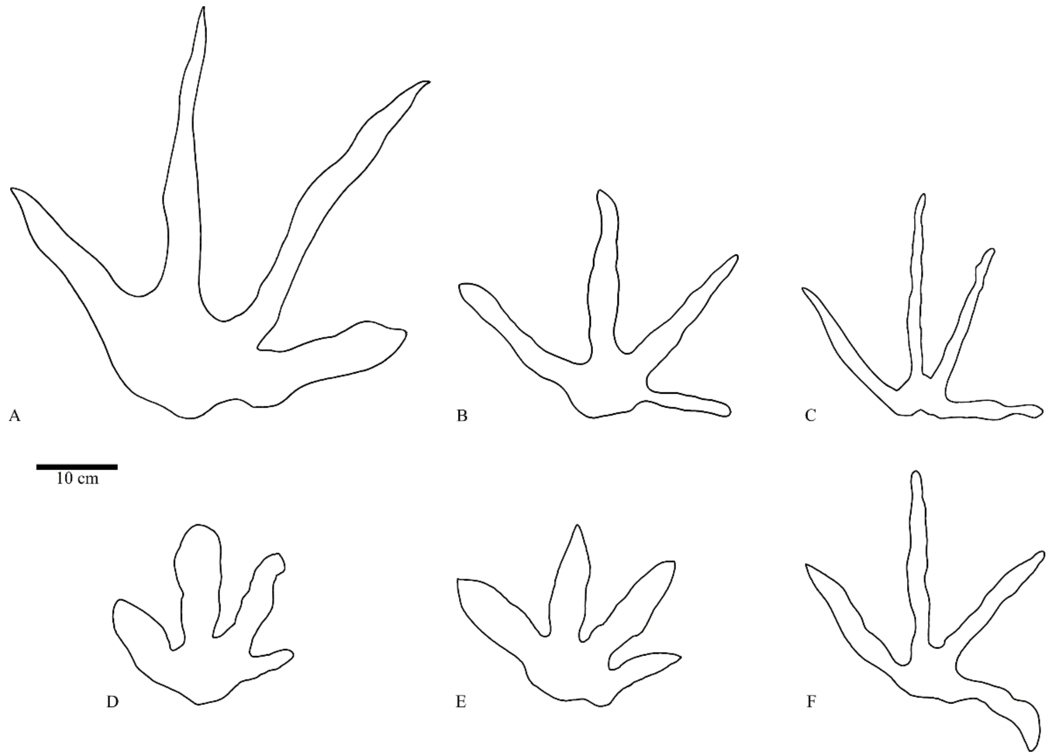

Figure 1.5: Comparison of outlines for different "Saurexallopus" specimens drawn to scale. A) S. neesowatchiensis (RBCM P2023.107.0003), B) S. lovei (DMNS 5989), C) S. cordata (TRM 2012.04.001MC), D and E) Denali "Saurexallopus" (DMNH 2010-07-01 and DMNH 2013-08-04), and F) Ordexallopus (previously *"Saurexallopus"*) *zerbsti (UCM 224.2). B and C represent right pes tracks and have been mirrored horizontally for better comparison.*

Figure 1.6: Photographs of different "Saurexallopus" specimens to scale. A) S. neesowatchiensis (in situ track represented by mould RBCM P2023.107.0003), B) S. lovei (DMNS 5989), C) S. cordata (TRM 2012.04.001MC), D and E) Denali "Saurexallopus" (DMNH 2010-07-01 and DMNH 2013-08-04), and F) "Saurexallopus" zerbsti (UCM 224.2). B and C represent right pes tracks and have been mirrored horizontally for better comparison.

Several other occurrences of *Saurexallopus* sp. have been reported, including one occurrence in Poland and several in Colorado and Utah (Gierliński, 2009; Gierliński & Lockley, 2013; Lockley et al. 2018b; Lockley et al., 2018c). Fourteen footprints referred to *Saurexallopus* sp. (T1.1, T1.2, T2.1, T2.2, T3-T7, T9-T10, T11[UCM 229.23], and T17-T18) were reported from the Laramie Formation (Maastrichtian) Cherryvale site near Marshall, Colorado (Lockley et al., 2018c). Moulds of T1.2, T3, and T17 were made to create replica specimens UCM 229.21-22 and UCM 229.27, respectively. Of the Cherryvale footprints, only the isolated track T17 preserves a digit I impression which is posteriorly rotated and curved, making it referable to *Ordexallopus* according to my revised diagnoses. Based on the tridactyl nature of the remaining thirteen tracks, I suggest that most *Saurexallopus* sp. from the Cherryvale site are not in fact referable to *Saurexallopus* and instead are from a tridactyl ichnogenus. Similarly, one trackway (UCM 225.24 – three footprints) and four individual footprints (UCM 225.5 T1-T2, UCM 225.8, and UCM 225.11) from the Blackhawk Formation (Campanian) Meetinghouse Canyon locality 1 (UCM Locality #815) near Castle Dale, Utah were referred to *Saurexallopus*, despite being tridactyl (Lockley et al., 2018b). While there were some *Saurexallopus* present at this locality, these occurrences do not display the diagnostic tetradactyl nature of *Saurexallopus*; as such, we suggest that these specimens are also not *Saurexallopus* but instead a tridactyl ichnogenus. UCM 225.6 preserves a reversed hallux, possibly as a result of the dinosaur stepping into deeper or wetter substrate.

While *Saurexallopus* has been reported throughout North America, there are two Chinese ichnotaxa comparable to *Saurexallopus* that I discuss further here – *Xiangxipus* and *Ordexallopus*. The first is the Aptian *Xiangxipus chenxiensis* (Xing et al., 2016; Zeng, 1982). While this ichnospecies is defined as tridactyl, there are apparently tetradactyl footprints within the holotype trackway, however, there is some argument about whether the digit I impressions are actually double traces of digit II (Xing et al., 2016; Lockley et al., 2013). With an average FL ~ 18.0 cm, *X. chenxiensis* may be equivalent to smaller *Saurexallopus* specimens if it is indeed a tetradactyl ichnotaxon. The posterior rotation of digit I (in the case that it is not a double trace) and the diagnostic wide divarication angles of *X. chenxiensis* nonetheless set it apart from *S. neesowatchiensis*.

Ordexallopus zhanglifui, also from the Early Cretaceous, is similar in size to *S. neesowatchiensis* (FL = 41.0-45.5 cm and FL = 48.9 respectively). The main distinguishing character between *Ordexallopus* and *Saurexallopus*, according to Lockley et al. (2018), is that *Ordexallopus* is larger with more robust digits. *S. neesowatchiensis* is comparable in size and bridges the gap in digital width between other *Saurexallopus* (~2 cm) and *Ordexallopus* (~7-9 cm), with an average digital width of ~4 cm. However, the orientation of digit I better distinguishes *Ordexallopus* from *Saurexallopus*. In *Ordexallopus*, digit I is postero-medially oriented and curved, whereas in all species of *Saurexallopus* except *S. zerbsti* (as originally described), digit I is medially oriented and straight. When *S. zerbsti* was first described, the diagnosis for *Saurexallopus* was modified to include a variable orientation for digit I, as either postero-medial or medial (Lockley et al., 2003). I thus propose that the diagnosis for *Saurexallopus* be reverted back to the original description given by Harris et al. (1996) in which digit I is medially oriented, thus differentiating *Saurexallopus* from *Ordexallopus*, which has a postero-medially oriented digit I. In revising the diagnosis of *Saurexallopus* to only include specimens with a medially oriented digit I, we propose the new combination *Ordexallopus zerbsti*, given that this species differed from all other *Saurexallopus* ichnospecies by its postero-medially oriented, curved first digit.

The *Saurexallopus* sp. track from Poland reported by Gierliński (2009) is tetradactyl, but has a postero-medial orientation of digit I. As such, I refer this track to *Ordexallopus* following my amended diagnoses.

Alaskan "*Saurexallopus"* tracks described by Fiorillo and Adams (2012) have thick digits with blunt claws. They are less widely splayed, having an average total divarication of 98.5˚. They are unlike other specimens referred to *Saurexallopus* and *Ordexallopus* and should not be referred to either ichnogenus at present.

The footprints at the Neeso-Watchie Dinosaur Tracksite are among the oldest representatives of *Saurexallopus*, as most other specimens are of Late Cretaceous age – the only exception being found elsewhere in the Peace Region in the Gething Formation near Tumbler Ridge (Lockley et al., 2022). The Ninesting Creek *Saurexallopus* tracks have a posteriorly directed hallux most similar to *S. zerbsti*; as such, we propose that the *Saurexallopus* found at Ninesting Creek are actually referable to *Ordexallopus*. Not only are they morphologically distinct, but the footprints at Ninesting Creek are significantly smaller than the Neeso-Watchie tracks described here, indicating that two different theropod groups capable of making functionally tetradactyl prints, but with highly differing body sizes, were present in western Canada during the Early Cretaceous. The identification of what dinosaur produced these rare tracks could significantly inform our understanding of the faunal composition for the tracksites at which they are found, especially in areas like British Columbia where the body fossil record is so poor.

Chapter 2: Interpreting trackmakers for tetradactyl theropod ichnogenera

2.1 Introduction

Dinosaur palaeoichnology plays a significant role in our understanding of faunal composition, especially in areas where there are gaps in the dinosaur body fossil record. Being able to identify what kind of dinosaur produced a particular type of track is, therefore, an important aspect of studying footprints. Identifying trackmakers comes with its own challenges, however, as most bipedal dinosaurs walked on three toes, producing tridactyl footprints. It is relatively easy to distinguish between theropod and ornithopod tracks: theropods generally had long, slender toes with sharp claws while ornithopods typically had thicker, shorter digits with either dull claws or hooves (Farlow and Chapman, 1997; Thulborn, 1990). Identifying trackmakers beyond this level can be difficult. Additionally, footprints reflect not only skeletal morphology, but also soft tissues and the interaction of the foot with the substrate (Falkingham et al., 2016).

There are some rare cases in which theropods produced tetradactyl (four-toed) tracks rather than the typical tridactyl tracks. First, a dinosaur may sink deeper into the substrate, impressing the hallux which is usually held high off of the ground (Gatesy et al., 1999). Second, the dinosaur may have a plantigrade stance where the toes and metatarsals are flat against the ground as opposed to the usual digitigrade posture common in theropods (Sennikov, 2021). The final way a fourth toe may appear is if digit I, which is usually held high off the ground, is positioned distally on the metatarsus and regularly makes contact with the surface (Nicosia et al., 2007). These last two are the result of a functionally tetradactyl theropod foot. These four-toed occurrences are far less common than tridactyl theropod footprints, and identifying what group(s) could have left behind such enigmatic traces can provide significant insight into the distribution of dinosaur taxa.

Currently, there are six tetradactyl ichnogenera attributed to theropods: *Macropodosaurus* (Sennikov, 2021), *Xiangxipus* (Xing et al., 2016), *Picunichnus* (Calvo and Rivera, 2018), *Boutakioutichnium* (Nouri et al., 2011), *Ordexallopus* (Lockley et al., 2018a), and *Saurexallopus* (Harris et al., 1996). These are easily distinguished from other tetradactyl dinosaur ichnogenera attributed to non-theropods. For example, *Tetrapodosaurus* is a quadrupedal (four-legged) ichnogenus attributed to ankylosaurs (armoured dinosaurs) (Thulborn, 1990). Other tetradactyl ichnogenera like *Navahopus* and *Otozoum* have been attributed to basal sauropodomorphs (‘prosauropods’). *Navahopus* represents a quadrupedal variety of prosauropods, preserving manus prints with a distinct medial “thumb” or digit I (Lockley and Hunt, 1995). *Otozoum* on the other hand appears to be the result of a bipedal posture in prosauropods (Lockley and Hunt, 1995). These bipedal tracks can still be differentiated from theropod tracks by the robust, nearly-parallel digits with blunt claw marks. The six ichnogenera attributed to theropods, however, display narrow, long digits with sharp claw marks and are never associated with manus impressions.

Since the ichnogenus *Saurexallopus* was first described by Harris et al. (1996, 1997), two different trackmakers have been proposed. Most palaeontologists prefer an oviraptorosaurian trackmaker for *Saurexallopus* (Gierliński, 2009; Gierliński and Lockley, 2013; Lockley et al., 2022). Based on an assemblage of *Saurexallopus* sp. from Denali National Park, Alaska, a therizinosaurian affinity has also been proposed for this ichnogenus (Fiorillo and Adams, 2012; Fiorillo et al., 2018). The discovery of two particularly large footprints attributable to *Saurexallopus* in the Early Cretaceous Neeso-Watchie tracksite in northeastern British Columbia, Canada inspired this research, thus this project seeks to investigate the differences between tetradactyl theropod tracks and identify their trackmakers, with the end goal of identifying what type of dinosaur produced the Neeso-Watchie tracks.

2.2 Materials and methods

I directly observed original, cast, or *in situ* tetradactyl theropod tracks from across North America (Tables 2.1 and 2.2). Linear measurements including footprint length taken along digit III from tip to heel, distal metatarsal width, digit lengths from tip to heel, free digit lengths, and digital widths were made using a tape measure (Fig. 2.1). In order to ensure reproducibility and consistency, all measurements of physical specimens were taken by me following the diagram in Fig. 2.1.

	Specimen Number	Locality	Age	FL	LM	WM	DLI	DLII	DLIII	DLIV	WI	WII	WIII	WIV	Elements Preserved	Measurement Source
	RBCM P2023.107.0003	Gething Formation, British Columbia	Aptian-Albian	489	109	160	185	364	380	211	44	41	39	37	Original	Direct measurement
	RBCM P2023.107.0005	Gething Formation, British Columbia	Aptian-Albian	400.4	123.4	172.6	167	217	277	205	20.4	20	30	47.8	Original	Direct measurement
ta	TRMF 2012.04.001M	Wapiti Formation, British Columbia	Late Campanian	293	12	72.3	118	176	281	173	28	21	21	25	Cast	Direct measurement
	DMNS 5989	Harebell Formation, Wyoming	Maastrichtian	275	74	115	106	185	201	175	17.8	23.3	35.1	21.2	Original	Direct measurement
	DMNH 2014-11-10	Cantwell Formation, Alaska	Late Campanian	252	92	102	73	190	160	130	19	33	34	38	Cast	Direct measurement
	DMNH 2010-07-01	Cantwell Formation, Alaska	Late Campanian	193	59	91	61	125	134	88	21	32	44	47	Cast	Direct measurement
	DMNH 2014-11-09	Cantwell Formation, Alaska	Late Campanian	195	84	92	46	93	111	79	28	34	25	31	Cast	Direct measurement
	DMNH 2013-08-06	Cantwell Formation, Alaska	Late Campanian	217	90	97	67	116	127	101	34.9	41.3	41.7	41.5	Cast	Direct measurement
	DMNH 2013-08-04	Cantwell Formation, Alaska	Late Campanian	194	51	97.4	80	136	143	132	36.5	27.6	27.7	30	Cast	Direct measurement
	UCM 224.2	Lance Formation, Wyoming	Middle Campanian-Maastrichtian	287	72	109.1	113	158	215	178	39	38.9	32.7	41.9	Cast	Direct measurement

Linear measurements of footprints in mm. Abbreviations are as follows: FL – foot length, LM – length of atarsal region, DL – free digit length, W – digit width

Taxon	Specimen Number	LI	LII	LIII	LIV
Saurexallopus neesowatchiensis	RBCM P2023.107.0003	299	487	489	313
Saurexallopus neesowatchiensis	RBCM P2023.107.0005	245.8	310.3	400.4	310.9
Saurexallopus cordata	TRMF 2012.04.001M	152	230	293	210
Saurexallopus lovei	DMNS 5989	149	250.5	275	239.3
Saurexallopus sp.	DMNH 2014-11-10	140	282	252	207
Saurexallopus sp.	DMNH 2010-07-01	130	203	193	148
Saurexallopus sp.	DMNH 2014-11-09	119	167	192	167
Saurexallopus sp.	DMNH 2013-08-06	124	202	217	195
Saurexallopus sp.	DMNH 2013-08-04	119	166	194	170
Ordexallopus zerbsti	UCM 224.2	157	253.1	287	238.6

Table 2.2: Digit lengths of footprints measured from tip to heel in mm. Abbreviations are as follows: L – digit length measured to heel

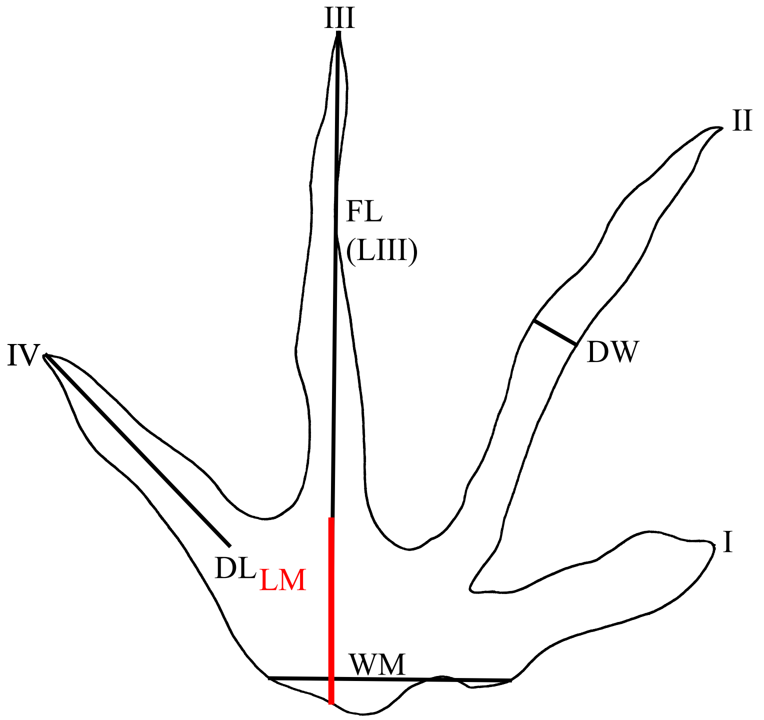

Figure 2.1: Linear measurements of footprints showing the distal metatarsal length in red, which is equal to digit III length to the heel minus free digit III length

Angular measurements including interdigital angles and total divarication were taken digitally using ImageJ 1.53t (Schneider et al., 2012). These angles were taken between digit tips from a single point at the heel where all digits converged. Most specimens were digitally modeled using photogrammetry; photographs were collected using a Nikon D3200 and models were created using Agisoft Metashape Version 2.0.0 (2023). Digital models were then processed in CloudCompare (2023) to produce false-colour depth maps and contour lines to make track outlines clearer.

I also directly observed original and cast pes fossils of various dinosaur groups that possessed a first digit long enough to produce tetradactyl tracks as opposed to the tridactyl footprints typically left behind by theropods (Table 2.3). This included therizinosaurs and oviraptorosaurs, both of which have previously been considered potential trackmakers for *Saurexallopus* (Fiorillo and Adams, 2012; Gierliński and Lockley, 2013). I also included several neornithischians, which have not previously been proposed as potential trackmakers since they are not theropods, but which have a foot morphology that could potentially leave tetradactyl tracks like those of *Saurexallopus* based on their long, narrow digits and narrow, sharply pointed or triangular unguals. I added leptoceratopsids to the dataset as a potential trackmaker group for the Denali S*aurexallopus* specimens, based on general morphological observations of the skeletal structure of leptoceratopsids and the morphology of these tracks. Linear measurements of digit lengths and widths as well as total foot lengths and widths were taken for each foot using manual calipers. Lengths were taken along the ventral side of each bone. Angular measurements were taken digitally from photographs of articulated pes fossils. Where possible, photogrammetry was also done so that 3D models of the feet could be produced. This dataset was then expanded upon by performing a literature review and including figured specimens with reported digit lengths. Any additional measurements not included in the literature (i.e. total foot measurements and digit widths) were taken from published figures using ImageJ.

Taxon	Specimen Number	I-II	II-III	III-IV
Thescelosaurus neglectus	CMN 9154	11.7	15.1	10.6
Parksosaurus warreni	ROM 804	9.3	9	15
Parksosaurus warreni	ROM 804	10.1	13.2	12
Hypsilophodon foxii	TMP P82.041.0001	6.2	15.3	11.7
Hypsilophodon foxii	TMP P82.041.0001	9.4	11.4	11.7
Anzu wyliei	ROM 55377A	38.3	33.8	30
Chirostenotes perigracilis	CMN 8538	17.1	20	20.9
Alxasaurus elesitaiensis	CMN 41835	6.7	7.8	8.5
Nothronychus graffami	UMNH VP 16420	7.9	8.3	6.7
Falcarius utahensis	UMNH VP composite	9.9	15.3	12.9
Falcarius utahensis	CEUM composite	17.1	13	15.5
Leptoceratops gracilis	CMN 8887	11.6	11.5	16.3
Cerasinops	MOR 300	18.3	21.9	25
Montanoceratops	MOR 542	13.8	17	15.1
Saurexallopus neesowatchiensis	RBCM P2023.107.0003	37.4	33.8	44.7
Saurexallopus neesowatchiensis	RBCM P2023.107.0005	37.8	42.8	39.7
Saurexallopus cordata	TRMF 2012.04.001M	58	36.6	45.4
Saurexallopus lovei	DMNS 5989	64	23.6	43.1
Saurexallopus sp.	DMNH 2014-11-10	31.3	30	41.2
Saurexallopus sp.	DMNH 2010-07-01	27.7	33.7	47.6
Saurexallopus sp.	DMNH 2014-11-09	31.5	33.8	27.7
Saurexallopus sp.	DMNH 2013-08-06	31.5	26.9	25.4
Saurexallopus sp.	DMNH 2013-08-04	31.9	28.2	47.8
Ordexallopus zerbsti	UCM 224.2	76.7	40.7	38.2

Table 2.3: Interdigital angles for footprints and articulated pes skeletons

Taxon	Specimen Number	Locality	Age	FL	LM	WM	DLI	DLII	DLIII	DLIV	WI	WII	WIII	WIV	Elements Preserved	Measurement Source
Thescelosaurus neglectus	CMN 9154	Lance Formation, Wyoming	Middle Campanian-Maastrichtian	233	60.9	126	70.9	132.1	172.1	135.8	15.3	22	33.1	17.1	Cast of USNM 7757, complete right pes	Direct measurement
Parksosaurus warreni	ROM 804	Horseshoe Canyon Formation, Alberta	Maastrichtian	238	74	104.5	92.6	134.2	164	153.2	14.6	17.9	18.9	16.4	Original, partial right pes; II-1, III-3, IV-1-3 and IV-U reconstructed	Direct measurement
Parksosaurus warreni	ROM 804	Horseshoe Canyon Formation, Alberta	Maastrichtian	213	53.5	99.5	86.5	134.4	159.5	141.6	13.4	19	19.9	17.1	Original, nearly complete left pes; II-2-U reonstructed	Direct measurement
Hypsilophodon foxii	TMP P82.041.0001	Wealden Group, Wessex Formation, England	Berriasian-Barremian	178	81.5	54	54.6	73.6	96.5	93.6	8.4	8.6	9.6	9.2	Cast of NHMUK PV R196, partial right pes; II-2, III-3, IV-3 and all unguals reconstructed	Direct measurement
Hypsilophodon foxii	TMP P82.041.0001	Wealden Group, Wessex Formation, England	Berriasian-Barremian	184	84.6	53.4	54.5	74.1	99.4	83.5	8.7	9.1	10.1	9.2	Cast of NHMUK PV R196, partial left pes; III-3-U reconstructed	Direct measurement
Anzu wyliei	ROM 55377A	Hell Creek Formation, South Dakota	Maastrichtian	464	123.4	169	107.7	228.6	340.6	284.1	15.2	21.9	23.1	25.1	Cast of CM78001, partial left pes; I, II, III-2, IV-1, IV-U, and metatarsals reconstructed	Direct measurement
Chirostenotes perigracilis	CMN 8538	Belly River Formation	Late Campanian	289	59.8	108	94.5	192.5	229.2	205	10.9	14	17.2	16.1	Original, nearly complete right pes; II-U reconstructed	Direct measurement
Caudipteryx zoui	BPM 0001	Yixian Formation, China	Early Cretaceous				25	58	76	46					Original specimen, complete pes	Zhou et al., 2000
Xingtianosaurus ganqi	IVPP V13390	Yixian Formation, China	Early Cretaceous				33.61	66.64	84.11	74.31					Original specimen, complete pes	Qui et al., 2019
Similicaudipteryx yixianensis	IVPP V12556	Jiufotang Formation, China	Barremian-Aptian				51	115	146	112					Original specimen, nearly complete pes; II-1 estimated	He et al., 2008
Oksoko avarsan	MPC-D 102/110.a	Nemegt Formation, Mongolia	Maastrichtian	159.29	48.89	51.18	38	85.4	110.4	83.2	7.32	12.25	13.11	11.07	Original specimen, complete pes	Funston et al., 2020
Oksoko avarsan	MPC-D 102/110.b	Nemegt Formation, Mongolia	Maastrichtian				39	79.3	107.2	82.6					Original specimen, complete pes	Funston et al., 2020
Oksoko avarsan	MPC 102/11	Nemegt Formation, Mongolia	Maastrichtian	149.57	41.37	50.67	31.4	80.8	108.2	80	6.09	12.08	12.28	8.87	Original specimen, complete pes	Funston et al., 2020
Oksoko avarsan	MPC-D 100/33	Nemegt Formation, Mongolia	Maastrichtian				44.9	92.8	112.2	84.3					Original specimen, complete pes	Funston et al., 2020
Elmisaurus rarus	ZPAL MgD-I/98	Nemegt Formation, Mongolia	Maastrichtian	177.4	37.4	49.05	49	110	140	113	6.67	9.64	12.49	6.07	Original specimen, complete pes	Osmólska, 1981
Caudipteryx dongi	IVPP V12344	Yixian Formation, China	Early Cretaceous	116.51	32.51	30.16	23	60	84	54	3.31	6.03	5.24	5.24	Original specimen, partial pes	Zhou & Wang, 2000
Alxasaurus elesitaiensis	CMN 41835	Bayin Gobi Formation, Mongolia	Aptian	307	66.3	152.5	116.5	185.5	240.7	238.8	17.5	18	20	19.2	Cast of IVPP 88501, nearly complete right pes; I-1-U and IV-3 reconstructed	Direct measurement

Nothronychus graffami	UMNH VP 16420	Tropic Shale Formation, Utah	Turonian	278.3		269	150.5	216.6	278.3	209	38.7	36.6	35	34.9	Original specimen, nearly complete right pes; missing unguals, partial III-2	Direct measurement, estimated III-2 from Smith & Gillette, 2024, unguals from Kirkland & Wolfe, 2001 *N. mckinleyi* based on size comparison by Hedrick et al., 2015
Falcarius utahensis	UMNH VP composite	Cedar Mountain Formation, Utah	Aptian-Albian	331.7	187.7	108.2	64.9	129.9	144	138.3	11.2	14.5	11.1	16.7	Original specimen, composite left pes, IV-4 estimated	Direct measurement
Falcarius utahensis	CEUM composite	Cedar Mountain Formation, Utah	Aptian-Albian	314.9	165.1	196.2	59.4	152.9	149.8	180.3	10.1	19.7	15.7	12.9	Original specimen, composite right pes	Direct measurement
Leptoceratops gracilis	CMN 8889	Scollard Formation, Alberta	Maastrichtian	150.94	0.03	130.08	99.07	128.96	150.91	151.15	18.37	22.26	22.07	19.11	Original specimen, complete left pes	Arbour & Evans, 2019
Leptoceratops gracilis	CMN 8887	Scollard Formation, Alberta	Maastrichtian	164.25	68.38	64.19	64.67	82.14	95.87	90.48	18.54	14.69	16.11	13.38	Cast, complete left pes	Arbour & Evans, 2019
Cerasinops	MOR 300	Two Medicine Formation, Montana	Campanian	173.38	12.16	154.46	115.79	149.42	161.22	150.85	16.6	21.19	23.15	18.1	Original, complete left pes	Arbour & Evans, 2019
Montanoceratops	MOR 542	St. Mary River Formation, Montana	Maastrichtian	130.53	14.07	54.07	81.87	98.4	116.46	120.56	14.99	17.13	18.56	15.37	Original, complete right pes	Arbour & Evans, 2019

Table 2.4 Linear measurements for skeletal materials. Abbreviations are as follows: FL – foot length; LM – length of distal metatarsal region, WM – width of metatarsals, DL- digit length, W – digit width

Once measurements were taken for all comparative materials, size was removed using the allometric vs. standard method using digit II length as the standard. Digit II length was chosen as it was the inner digit that did not affect total foot length (unlike digit III) and was a consistently measurable variable across trackmaker groups and footprints. This data was then log transformed. Several principal component analyses (PCAs) were performed on the transformed data using PAST 4.16 (Hammer et al., 2001) to establish which measurements represent the most significant differences between the taxa and if trackmaker groups and/or footprint morphologies can be identified based on the measurements taken. I ran separate PCAs using two different measurements for footprint digit length: lengths measured from the digit tip to the convergence point (the 'heel' of the footprint) as well as free digit lengths. Digit lengths for the pes skeletons were the same for all tests. Linear discriminant analyses (LDAs) were also performed in which footprints were entered as belonging to '?' group in order to test if they could consistently be classified as any of the trackmaker clades based on measurements alone. Significant differences were determined based on which principal components were retained using the broken-stick model. Further iterations were done excluding interdigital angles to determine if angular measurements provide any significant information about identification.

Fiorillo and Adams (2012) observed that therizinosaurs have a shallower arc across the distal metatarsal condyles compared to oviraptorosaurs and suggested that this could be used to identify potential therizinosaur tracks. I tested this hypothesis using a geometric morphometric landmark analysis. I chose the articulation point of each digit with the metatarsals as my landmarks to create an arc along the bases of the four digits. On footprints, these articulation points correlate to where the free digits connect to the distal metatarsal impression. I used tpsDig2 Version 2.32 (Rohlf, 2021) to plot landmarks on images of the specimens. This included a combination of my own images and published figures from the literature. I then imported the .tps files of both the pes skeletons and the footprints into MorphoJ Version 1.08.02 (Klingenberg, 2011), where I performed a Procrustes fit on the data, linked my landmarks to create a wireframe, and generated a covariance matrix. Using the matrix, I performed a PCA in MorphoJ to test if there was a relationship between the arc of the digits and dinosaur or footprint taxon.

Abbreviations

Institutional Abbreviations—**BPM**, Beipiao Paleontological Museum, Liaoning, China **CEUM**, Utah State University Eastern Prehistoric Museum, Price, Utah, U.S.A.; **CM**, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A.; **DMNH**, Perot Museum of Nature and Science, Dallas, Texas, U.S.A.; **DMNS**, Denver Museum of Nature and Science, Denver, Colorado, U.S.A.; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **MOR**, Museum of the Rockies, Bozeman, Montana, U.S.A. **MPC**, Institute of

Paleontology, Mongolia; **NHMUK**, Natural History Museum, London, England; **PVSJ**, Museo de Ciencias Naturales, San Juan, Argentina; **RBCM**, Royal British Columbia Museum, Victoria, British Columbia, Canada; **TRM**, Tumbler Ridge Museum, Tumbler Ridge, British Columbia, Canada; **UCM**, University of Colorado Museum of Natural History, Boulder, Colorado, U.S.A.; **USNM**, United States National Museum, Washington, D.C., U.S.A. **ZPAL**, Institute of Paleobiology, Polish Academy of Sciences, Warszawa, Poland

Anatomical Abbreviations—FL, footprint length; **ML**, length of distal metatarsals, **WM**, width of metatarsals; **L**, digit length to heel, **DL**, free digit length; **DW**, digit width; ***h***, height at the hip

2.3 Results

Morphology of tetradactyl theropod tracks

Tetradactyl theropod footprints can be grouped into three informal morphotypes based on digit divarication and shape. The first morphotype includes the ichnogenera *Picunichnus* and *Boutakioutichnium*, which have thick, highly elongated digits with narrow interdigital angles (Calvo and Rivera, 2018; Nouri et al., 2011). Digit I in both is very short and located at the back of the foot, directed either medially or posteriorly. The second morphotype is represented by *Macropodosaurus*. This ichnotaxon is also elongate with narrow divarication, however digit I is parallel to the other digits and positioned laterally. Most notably, this ichnogenus has a plantigrade nature with a short, wide, oval-shaped metatarsal impression (Sennikov, 2021). The third morphotype includes three ichnogenera (*Xiangxipus*, *Ordexallopus*, and *Saurexallopus*) which display widely divaricated digits. *Xiangxipus* is tridactyl, with long narrow digits widely splayed. If present, the first digit is rotated posteriorly (Lockley et al., 2022; Xing et al., 2016). *Ordexallopus* also has a posteriorly oriented but curved digit I (Lockley et al., 2018a).

Saurexallopus displays a large range of morphologies (Fig. 2.2), especially in relation to the orientation of digit I. The holotype ichnospecies *Saurexallopus lovei* possesses a medially oriented long, thin digit I. *Saurexallopus cordata* and *Saurexallopus neesowatchiensis* (the Neeso-Watchie tracks that inspired this study) exhibit similarly thin medial first digits. *Saurexallopus zerbsti* (reclassified as *Ordexallopus zerbsti*, Ch. 1) displays a postero-medially oriented, curved digit I. Most *Saurexallopus* sp. were tridactyl and were not associated with any tetradactyl footprints, so it is unlikely these actually represent occurrences of *Saurexallopus*. The Poland *Saurexallopus* sp. has a straight but posteriorly rotated digit I (Gierliński, 2009). The Denali *Saurexallopus* sp. footprints, referred to Therizinosauria by Fiorillo and Adams (2012), display a significantly different morphology to other *Saurexallopus*. They are narrower, with lower interdigital angles. Additionally, the digits are much broader and have lower digit length to width ratios (Table 2.5).

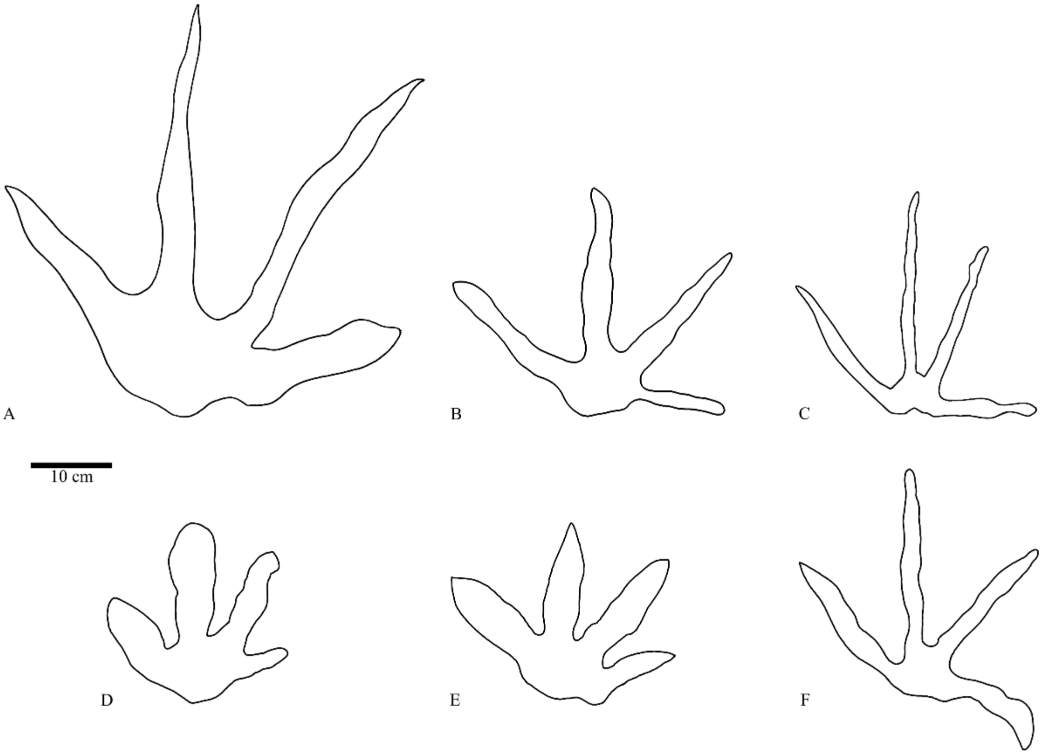

Figure 2.2: Comparison of outlines for different "Saurexallopus" specimens drawn to scale. A) S. neesowatchiensis (RBCM P2023.107.0003), B) S. lovei (DMNS 5989), C) S. cordata (TRM 2012.04.001MC), D and E) Denali "Saurexallopus" (DMNH 2010-07-01 and DMNH 2013-08-04), and F) Ordexallopus (previously *"Saurexallopus") zerbsti (UCM 224.2). B and C represent right pes tracks and have been mirrored horizontally for better comparison.*

Morphology of the pedal skeleton of potential tetradactyl trackmakers

The most significant difference observed in pes fossils for different potential tetradactyl trackmaker groups is the position and shape of metatarsal I (Fig. 2.3). In Therizinosauria, Neornithischia, and Leptoceratopsidae, metatarsal I is positioned parallel to the other metatarsals and is nearly as long as metatarsal II, with the exception of *Falcarius*, a small, basal therizinosaur. In the larger, more derived therizinosaurs all of the metatarsals are relatively short and wide. Metatarsal I in Oviraptorosauria, however, is much shorter than the other metatarsals and is positioned postero-medially toward the distal end of the metatarsus.

In addition to these differences, ratios of digit lengths and widths vary between potential trackmaker groups (Table 2.5). Oviraptorosaur pes skeletons have the highest digit length to width ratios, followed by therizinosaurs, then neornithischians; leptoceratopsids have the lowest digit length to width ratios. Ratios between the lengths of each digit vary highly within groups with no discernable trends and thus cannot confidently be used to attribute a footprint to a trackmaker.

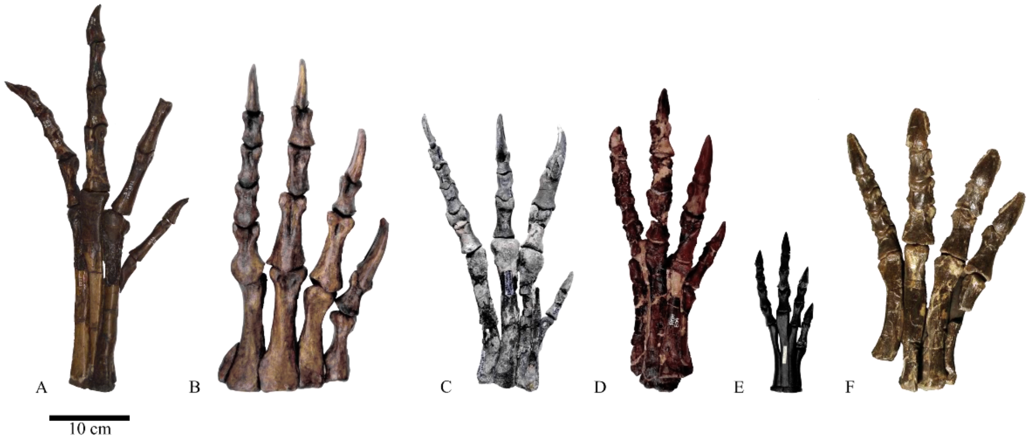

Figure 2.3: Representatives of potential trackmaker feet to scale: Oviraptorosauria A) Chirostenotes ROM 8538; Therizinosauria B) Alxasaurus CMN 41835 and C) Falcarius CEUM composite; Neornithischia D) Parksosaurus ROM 804 and E) Hypsilophodon TMP P82.041.0001; Leptoceratopsidae F) Montanoceratops MOR 542

Taxon	Specimen Number	DLI/WI	DLII/WII	DLIII/WIII	DLIV/WIV
Thescelosaurus neglectus	CMN 9154	4.63399	6.00455	5.1993958	7.94152047
Parksosaurus warreni	ROM 804	6.34247	7.49721	8.6772487	9.34146341
Parksosaurus warreni	ROM 804	6.45522	7.07368	8.0150754	8.28070175
Hypsilophodon foxii	TMP P82.041.0001	6.5	8.55814	10.052083	10.173913
Hypsilophodon foxii	TMP P82.041.0001	6.26437	8.14286	9.8415842	9.07608696
Anzu wyliei	ROM 55377A	7.08553	10.4384	14.744589	11.3187251
Chirostenotes perigracilis	CMN 8538	8.66972	13.75	13.325581	12.7329193
Caudipteryx zoui	BPM 0001				
Xingtianosaurus ganqi	IVPP V13390				
Similicaudipteryx yixianensis	IVPP V12556				
Oksoko avarsan	MPC-D 102/110.a	5.19126	6.97143	8.4210526	7.51580849
Oksoko avarsan	MPC-D 102/110.b				
Oksoko avarsan	MPC 102/11	5.15599	6.68874	8.8110749	9.01916573
Oksoko avarsan	MPC-D 100/33				
Elmisaurus rarus	ZPAL MgD-I/98	7.34633	11.4108	11.208967	18.616145
Caudipteryx dongi	IVPP V12344	6.94864	9.95025	16.030534	10.3053435
Alxasaurus elesitaiensis	CMN 41835	6.65714	10.3056	12.035	12.4375
Nothronychus graffami	UMNH VP 16420	3.88889	5.91803	7.9514286	5.98853868
Falcarius utahensis	UMNH VP composite	5.79464	8.95862	12.972973	8.28143713
Falcarius utahensis	CEUM composite	5.88119	7.76142	9.5414013	13.9767442
Leptoceratops gracilis	CMN 8889	5.39303	5.79335	6.8377889	7.90947148
Leptoceratops gracilis	CMN 8887	3.48813	5.59156	5.9509621	6.76233184
Cerasinops	MOR 300	6.9753	7.05144	6.9641469	8.33425414
Montanoceratops	MOR 542	5.46164	5.74431	6.2747845	7.84385166
Saurexallopus neesowatchiensis	RBCM P2023.107.0003	4.20455	8.87805	9.7435897	5.7027027
Saurexallopus neesowatchiensis	RBCM P2023.107.0005	8.18627	10.85	9.2333333	4.28870293
Saurexallopus cordata	TRMF 2012.04.001M	4.21429	8.38095	13.380952	6.92
Saurexallopus lovei	DMNS 5989	5.95506	7.93991	5.7264957	8.25471698
Saurexallopus sp.	DMNH 2014-11-10	3.84211	5.75758	4.7058824	3.42105263
Saurexallopus sp.	DMNH 2010-07-01	2.90476	3.90625	3.0454545	1.87234043
Saurexallopus sp.	DMNH 2014-11-09	1.64286	2.73529	4.44	2.5483871
Saurexallopus sp.	DMNH 2013-08-06	1.91977	2.80872	3.0455635	2.43373494
Saurexallopus sp.	DMNH 2013-08-04	2.19178	4.92754	5.1624549	4.4
Ordexallopus zerbsti	UCM 224.2	2.89744	4.0617	6.5749235	4.24821002

Table 2.5: Length to width ratios of digits for potential trackmaker feet and different 'Saurexallopus' morphologies

One final morphological feature that differs between the skeletons of the different trackmaker taxa is the shape of the claws. Theropods typically have very laterally compressed, sharp claws. Smaller ornithischians like *Hypsilophodon*, thescelosaurids, and leptoceratopsids have subangular claws unlike the hooves of larger ornithischians such as hadrosaurs or ceratopsids. While these types of claws are not as narrow or pointed as theropod claws, it is possible for the tips of digits to leave behind traces that are thinner, wider, longer, or shorter than the foot that produced them as a result of different sediment consistencies (Falkingham & Gatesy, 2014; Milàn & Falkingham, 2016). As such, even slightly blunter claws like those of the smaller ornithischians could still produce very narrow and laterally compressed claw marks like those preserved in *Saurexallopus*.

Statistical Analyses

All four PCAs produced similar results (Fig. 2.4). The two PCAs including angular data display the most separation between skeletal groups, indicating that interdigital angles contribute significant information to the dataset.

The PCA including interdigital angles where digit length is taken from the distal toe tip to the posterior edge of the heel (Test A) shows the most separation between potential trackmaker groups, with all skeletal groups forming distinct convex hulls (Fig 2.4A). There is only a slight overlap between Therizinosauria and Neornithischia. Test C, where digit lengths for footprints are the free digit lengths and the metatarsal region length and angular data are included, shows similarly separated convex hulls with slightly more overlap between Therizinosauria and Neornithischia (Fig 2.4C). Leptoceratopsidae also has a very slight overlap with Therizinosauria. In Tests A and C, total variance can be explained by two similarly loaded principal components. A table showing the loadings for each PCA test is located in the appendix. Test A PC1 (44.4%) and Test C PC1 (45.38%) show an inverse relationship between interdigital angles, which are positively correlated, and metatarsal width and digit IV length which pull negatively. Test A PC2 (40.48%) shows a positive correlation between digit widths, digit I length, and metatarsal width, inversely related to digit III length (essentially total foot length). Test C PC2 (26.64%) has these same loadings but also loads negatively on interdigital angles. Tests A and C plot Therizinosauria, Neornithischia, and Leptoceratopsidae, which all have wide metatarsals, low interdigital angles, and relatively long fourth digits in the upper left quadrant and Oviraptorosauria which have narrower, more widely splayed digits and relatively short fourth digits in the lower middle to right. In both of these analyses, the *Saurexallopus* hull overlaps with Oviraptorosauria and is distinct and separate from the Denali '*Saurexallopus*' and *Ordexallopus zerbsti*, which plot together but separately from all skeletal groups.

Tests B and D exclude angular data and display significantly more overlap between potential trackmaker groups. Test B, in which digit length is taken from tip to heel, shows that total variance can be explained by two principal components. PC1 (70.32%) is heavily loaded positively on digit widths, with a slight positive correlation of digit I length and metatarsal width and negative correlation with digit III length. PC2 (20.5%) is very heavily loaded positively to metatarsal width, showing a very slight positive relationship with digit IV length and inverse relationship with digit III and IV widths. Test B plots the wider, shorter pes skeletons of Therizinosauria and Leptoceratopsidae in the upper middle to right. Neornithischia plots centrally and slightly overlaps both Oviraptorosauria and Leptoceratopsidae. There is slight overlap between Therizinosauria and Oviraptorosauria. The Oviraptorosauria convex hull has a large vertical range, showing that metatarsal widths within the clade are highly variable and are likely not a significant variable for identification. In Test B, *Saurexallopus* and the Denali '*Saurexallopus'* again plot separately with *O. zerbsti* falling within the Denali hull. In this plot, *Saurexallopus* overlaps with Neornithischia but still plots close to the Oviraptorosauria hull. The Denali hull, while still separate, plots near Leptoceratopsidae.

Test D, in which digit length is free digit length and distal metatarsal length is included, has the most overlap between potential trackmaker groups. There is significant overlap between Oviraptorosauria, Therizinosauria, and Neornithischia. Additionally, only PC1 (64.49%), almost entirely loaded on distal metatarsal length, proved to be statistically significant using the broken-stick model. As such, I regard Test D as largely uninformative.

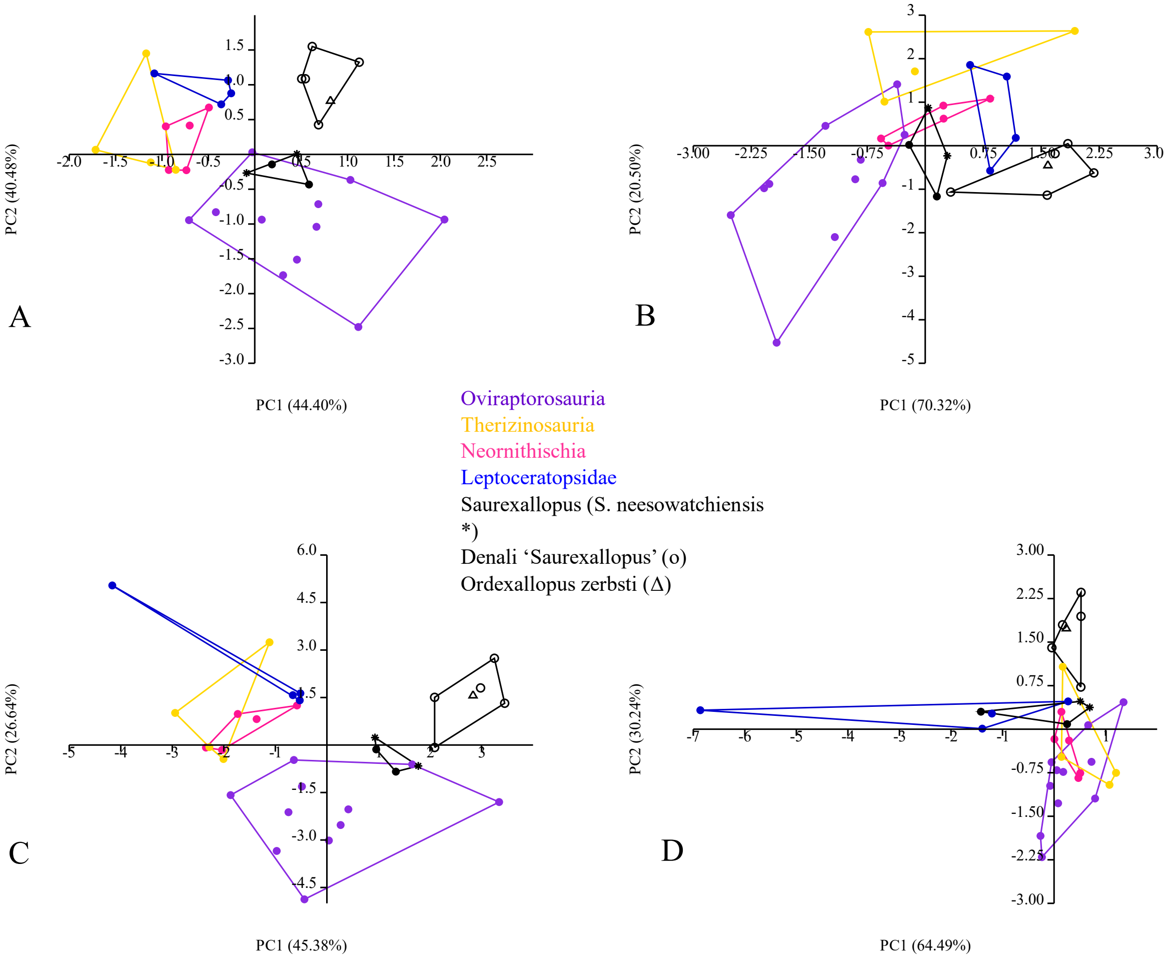

Figure 2.4: PCA scatter plots for footprint and skeleton measurements. A) digit length measured to heel with interdigital angles included, B) digit length measured to heel excluding interdigital angular data, C) free digit and distal metatarsal lengths with interdigital angles, and D) free digit and distal metatarsal lengths without interdigital angular data.

The LDAs for both types of digit length including interdigital angles identified more samples correctly than the datasets excluding angular data. The LDA for digit length measured to the heel (Test A) identified 83.33% of skeletal specimens correctly; the LDA for free digit length measurements (Test B) correctly identified 70.83%. Of the two datasets including angular data, the LDA where digit length was measured to the heel (Test C) correctly identified slightly more than the dataset with free digit lengths (Test D) (66.67% and 58.33% respectively). Classifications for the footprint specimens are shown in Table 2.6. The dataset for this analysis, while limited to 24 skeletal specimens, contained a wide range of sizes within each taxonomic group. The high percentage of correctly identified taxa indicates that not just size, but the relationships of the variables are different enough to distinguish between different dinosaur groups even with a smaller dataset. Still, it would be beneficial to expand the dataset to see if accuracy changes drastically.

Taxon	Specimen	LDA A	LDA B	LDA C	LDA D
Saurexallopus neesowatchiensis	RBCM P2023.107.00	Oviraptorosauria	Oviraptorosauria	Oviraptorosauria	Oviraptorosauria
Saurexallopus neesowatchiensis	RBCM P2023.107.00	Leptoceratopsidae	Neornithischia	Leptoceratopsidae	Neornithischia
Saurexallopus cordata	TRMF 2012.04.001M	Oviraptorosauria	Oviraptorosauria	Oviraptorosauria	Oviraptorosauria
Saurexallopus lovei	DMNS 5989	Leptoceratopsidae	Neornithischia	Leptoceratopsidae	Neornithischia
Saurexallopus sp.	DMNH 2014-11-10	Oviraptorosauria	Oviraptorosauria	Oviraptorosauria	Oviraptorosauria
Saurexallopus sp.	DMNH 2010-07-01	Leptoceratopsidae	Neornithischia	Oviraptorosauria	Oviraptorosauria
Saurexallopus sp.	DMNH 2014-11-09	Leptoceratopsidae	Leptoceratopsidae	Oviraptorosauria	Oviraptorosauria
Saurexallopus sp.	DMNH 2013-08-06	Leptoceratopsidae	Oviraptorosauria	Leptoceratopsidae	Oviraptorosauria
Saurexallopus sp.	DMNH 2013-08-04	Leptoceratopsidae	Therizinosauria	Oviraptorosauria	Oviraptorosauria
Ordexallopus zerbsti	UCM 224.2	Oviraptorosauria	Therizinosauria	Leptoceratopsidae	Therizinosauria

Table 2.6: LDA classifiers for 'Saurexallopus' specimens corresponding to Tests A-D.

Geometric morphometrics

The 2D landmark analysis performed on the digit to metatarsal joints proved less informative than the statistical analysis on linear measurements. The PCA conducted on the landmarks revealed that 87.79% of variance could be explained by just two principal components.

In the PC1-PC2 morphospace (Fig. 2.5), there is a high degree of overlap between the convex hulls for the pes skeleton trackmaker groups. There is also considerable overlap between the two *Saurexallopus* footprints, despite them being quite different morphologically and statistically based on the PCAs. Because of the significant overlap between trackmaker groups and separation of footprints from skeletal hulls, the arc created by digit to metatarsal articulation points is not a statistically significant observation for identifying footprint trackmakers.

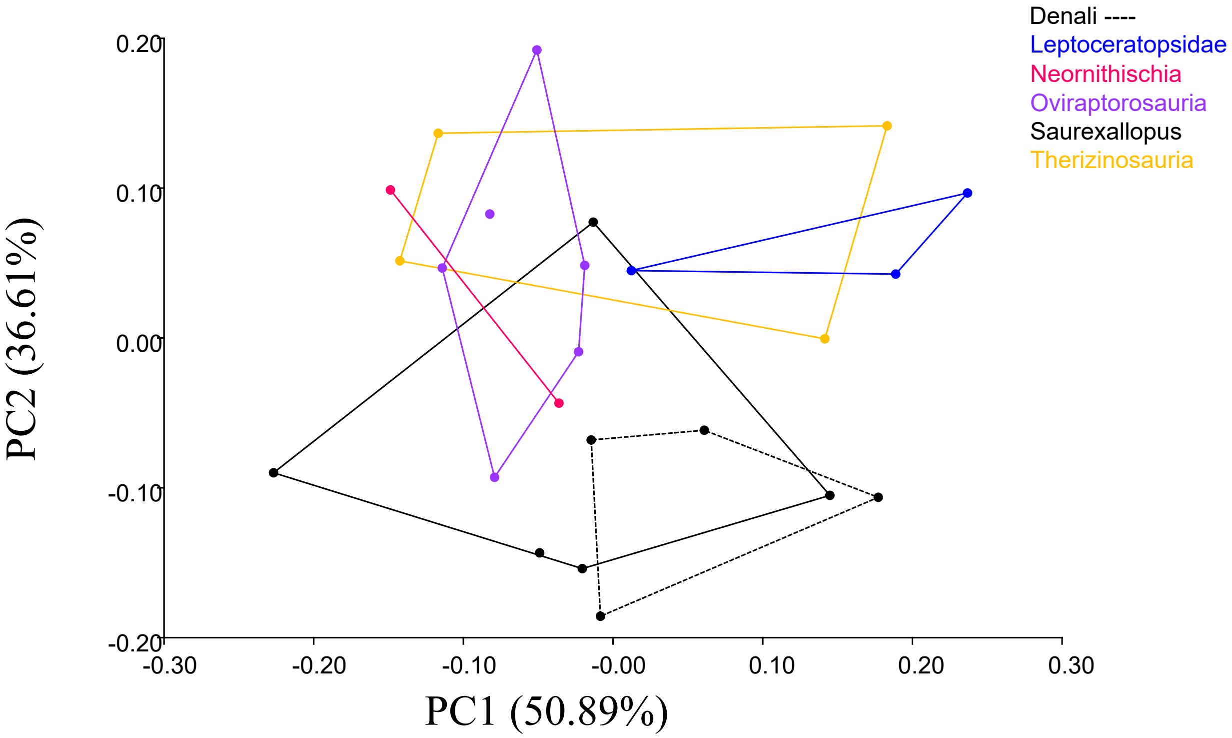

Figure 2.5: Landmark analysis PCA scatter plot showing convex hulls of potential trackmaker skeletons and footprints

2.4 Discussion

Saurexallopus tracks were likely made by an oviraptorosaur

The systematic ichnology of *Saurexallopus* was reviewed and revised in Chapter 1. *Saurexallopus* includes *S. lovei*, *S. cordata*, and the new taxon *S. neesowatchiensis*, and does not include *Ordexallopus zerbsti* (previously *S. zerbsti*) or '*Saurexallopus*' sp. from Denali National Park. *Saurexallopus* has four long, slender digits radiating from a rounded heel. Digit I is positioned medially and is nearly as long as digit IV. Interdigital angles for these tracks are high.

Two hypotheses have been proposed for the trackmaker of *Saurexallopus*: Oviraptorosauria and Therizinosauria. I also tested the hypothesis that *Saurexallopus* tracks could have been made by a thescelosaurid or other small bipedal ornithischian, or by a leptoceratopsid. All of these clades possessed long first digits that could have been in contact with the ground during regular movement. Morphologically, the pes skeletons of therizinosaurs had more parallel, wider digits whereas oviraptorosaurs possessed long, narrow, widely splayed digits. Neornithischians and leptoceratopsids similarly possessed more parallel digits, and metatarsal I was nearly equal in length and positioned parallel to metatarsal II. An oviraptorosaur affinity for *Saurexallopus* is preferred based on broad morphological observations of the tracks, i.e. on the long, narrow, widely splayed digits.

In the PCAs conducted on both measurements of digit length (Tests A and C), the *Saurexallopus* convex hull overlapped with the convex hull of Oviraptorosauria. In Test B, while not overlapping, *Saurexallopus* plotted very close to the oviraptorosaur hull. The overlap in two of the three significant PCAs lends support for an oviraptorosaurian trackmaker for *Saurexallopus*. On the other hand, *Saurexallopus* plots separately from the Therizinosauria hull in all three of the statistically significant PCAs. These results indicate that a therizinosaur trackmaker for *Saurexallopus* can be rejected, but that an oviraptorosaurian trackmaker cannot be rejected. In combination with the morphological observations discussed above, I conclude that *Saurexallopus* tracks were most likely made by an oviraptorosaur.

In the LDAs, *Saurexallopus cordata* and the holotype specimen for *Saurexallopus neesowatchiensis* were consistently classified as Oviraptorosauria, which could lend support for a likely oviraptorosaurian affinity for these tracks. The paratype for *S. neesowatchiensis* and *S. lovei*, on the other hand, were both classified by the LDAs including angular data as Leptoceratopsidae and by the LDAs excluding angular data as Neornithischia. These classifications may be the result of differences between data types as skeletal measurements do not take into account soft tissue or substrate interaction. The paratype for *S. neesowatchiensis* for example, which is certainly not attributable to a leptoceratopsid or neornithischian based on its large size and medially oriented digit I, does have slightly more robust digits II-IV and narrower, longer digit I compared to the holotype specimen. Additionally, digit II displays strong curvature at the distal end. This track is much deeper than the holotype specimen, and these morphological differences are possibly the result of a wetter substrate, resulting in slightly distorted proportions. External factors like soft tissue and substrate consistence are factors that cannot be accounted for by skeletal material alone, so while footprints largely reflect the skeletal anatomy of the foot, footprints do not entirely share the same morphospace. As such, in cases like these where footprints do not fit clearly with the skeletal data the LDA may just be pulling them into the closest group as opposed to reflecting a true association.

Evolutionary and palaeobiogeographical implications for the Neeso-Watchie *Saurexallopus*

The dinosaur body fossil record of British Columbia is very poor, with only a handful of bones being discovered, none of which are from the Early Cretaceous. However, the trace fossil record is excellent, particularly the trace fossil record of the Early Cretaceous. The Peace Region of northeastern BC has abundant tracksites with a wide range of morphologies showing a highly diverse dinosaur fauna that included small to large theropods and ornithopods as well as ankylosaurs, birds, and sauropods (McCrea et al., 2014). The construction of the Peace Canyon and W.A.C. Bennett Dams has submerged many of the historical Peace Region tracksites, making the Neeso-Watchie tracksite very important for palaeontology in the area because it is located well away from any water source. The two large *Saurexallopus* tracks found at the Neeso-Watchie tracksite, representing the new ichnospecies *S. neesowatchiensis* (Ch. 1), have significant implications for understanding Early Cretaceous dinosaur faunal composition in North America.

As with other *Saurexallopus*, these footprints were likely produced by a member of Oviraptorosauria, bird-like non-avian theropod dinosaurs. Oviraptorosauria includes the subclades Oviraptoridae and Caenagnathidae. The generally smaller oviraptorids are found only in Asia, whereas caenagnathids are present in Asia but are predominantly found in North America (Yu et al., 2018). Asian oviraptorosaurs tend to be found in formations representing dune environments while the North American species are usually found in fluvial deposits (Osmólska et al., 2004). These feathered dinosaurs had long necks and beaks with no teeth, indicating a possibly omnivorous or herbivorous diet as opposed to the carnivorous diet of most theropods (Omólska et al., 2004). Being Aptian-Albian in age (~125-100.5 Ma), the Neeso-Watchie footprints represent the oldest occurrence of this group of dinosaurs in Canada (Fig. 2.6). The only other North American Early Cretaceous oviraptorosaur is the small, primitive *Microvenator*, from the Cloverly Formation of Wyoming and Montana (Makovicky & Sues, 1998). This species, represented only by a probable juvenile, is among the smallest of non-avian theropods (Yu et al., 2018). All other Early Cretaceous oviraptorosaurs including

Similicaudipteryx yixianensis from the Aptian Jiufotang Formation (He et al., 2008) and *Caudipteryx dongi* from the Yixian Formation (Zhou & Wang, 2000) have been found in China.

Saurexallopus neesowatchiensis also likely represents a species of oviraptorosaur unknown in the skeletal fossil record based on its size. Using the equation for hip height ($h \approx 4FL$) established by Alexander (1976) and validated by Henderson (2003), the *S. neesowatchieensis* trackmaker would have been approximately 2 m at the hip. This measurement places it between the largest species of oviraptorosaur known from the body fossil record: *Gigantoraptor erlianensis* (3.5 m at the hip) from the Campanian-Maastrichtian Iren Dabasu Formation of China (Xu et al., 2007), *Anzu wyliei* (1.5 m at the hip) from the Maastrichtian of the United States (Lamanna et al., 2014), and *Hagryphus giganteus* (1.5 m) from the Campanian of the United States (Zanno & Sampson, 2005) (Fig. 2.7). Interestingly, the discovery of the dinosaur egg oogenus *Macroelongatoolithus* in the Albian-Cenomanian Wayan, Dakota, and Cedar

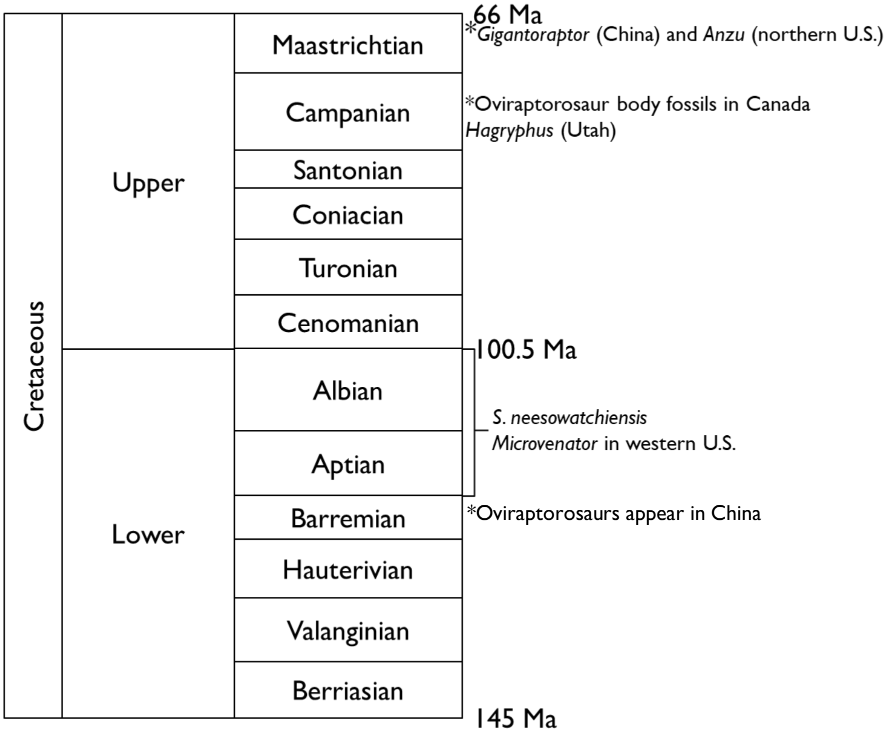

Figure 2.6: Geological time scale showing oviraptorosaurian presence in Asia and North America as well as the timing of large oviraptorosaurs

Mountain Formations of the United States provides support for the presence of a similarly large oviraptorosaur in North America during the mid-Cretaceous (Simon et al., 2018; Zelenitsky et al., 2000).

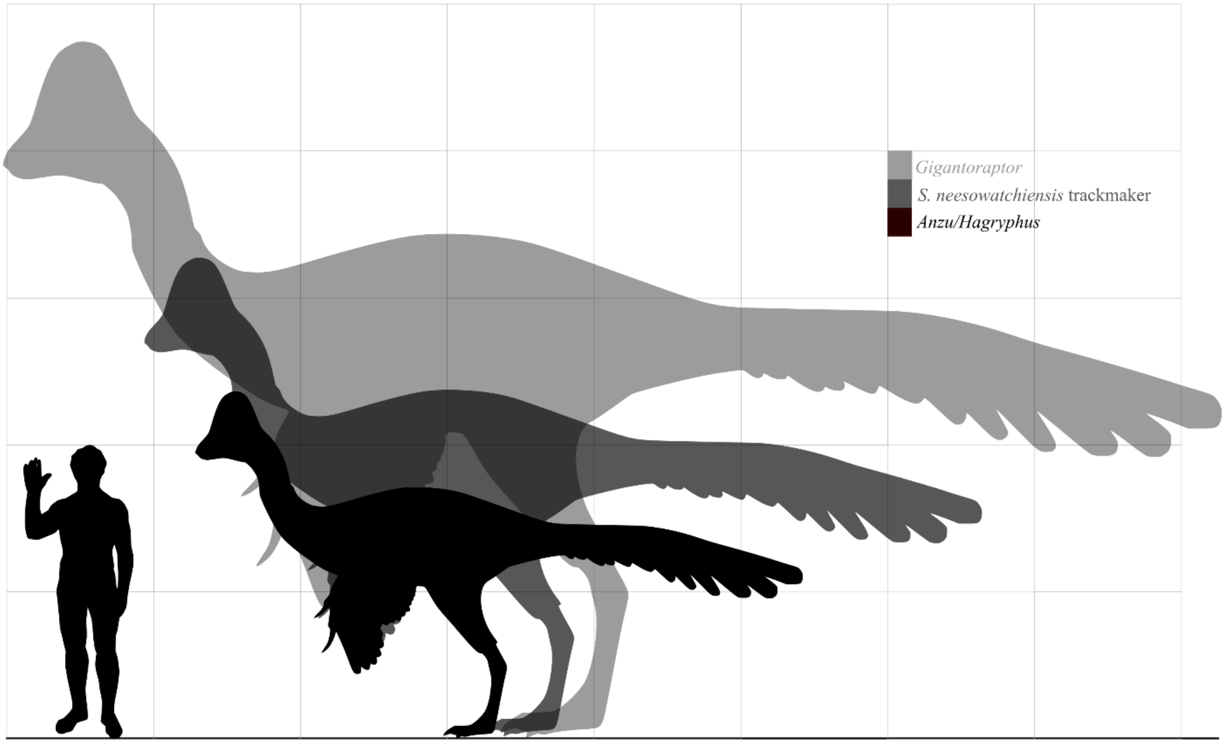

Figure 2.7: Size comparison of the potential S. neesowatchiensis trackmaker compared to other large oviraptorosaurs and a 2m tall human. Public domain silhouettes from phylopic.org. Homo sapiens by NASA and Anzu by Itai Fein

Potential trackmakers for other tetradactyl theropod tracks

Unlike *Saurexallopus*, *Ordexallopus* has a posteriorly oriented digit I. This rotation is likely associated with the reversal of the hallux in theropod feet. In the PCAs, *O. zerbsti* plots within the convex hull for the Denali '*Saurexallopus'* sp. based on lengths and interdigital angles, but based on the posterior rotation and curvature of *O. zerbsti*, they do not truly share the same morphospace. Additionally, *O. zerbsti* does not plot within or near any of the convex hulls for potential trackmakers. It is also not consistently classified by the LDAs, which I interpret as showing that the actual trackmaker may be absent from my dataset. Because the focus of my research was on *S. neesowatchiensis*, a large Early Cretaceous ichnogenus for which no known avian candidate exists, I did not include birds in my dataset. It is possible that, based on the widely splayed, narrow digits and reversed hallux, smaller *Ordexallopus* like *O. zerbsti* could have been produced by a bird (Lockley et al., 1992). Footprints similar to *O. zerbsti* have been discovered also within the Peace Region Gething Formation. These footprints, found at the Ninesting Creek tracksite, have previously been referred to *Saurexallopus* and were attributed to an oviraptorosaur. These footprints are also found in association with footprints of the avian ichnogenus *Wupus* (Lockley et al., 2022), documenting the presence of relatively large birds in the Early Cretaceous of western Canada. If the Ninesting Creek are indeed *Ordexallopus*, and if *Ordexallopus* can be attributed to birds, this may indicate the presence of more than one type of bird present during the Aptian-Albian of British Columbia. *Ordexallopus zhanglifui* tracks from the Early Cretaceous Jingchuan Formation of China, however, are both geologically older and larger, with more robust digits (Lockley et al., 2018a). Because of their reversed hallux, it is unlikely that they were made by any therizinosaur as all of the large therizinosaurs have broad, nearly parallel digits. There are no known large avian theropods present during the Early Cretaceous, the largest being *Sapeornis* with a FL ~4-5 cm (Zhou & Zhang, 2003), so it is unlikely that a bird produced these specific tracks. Large Early Cretaceous theropods are rare in East Asia's fossil record, but a trackmaker like the carcharodontosaurid *Kelmayisaurus petrolicus* from the Lianmugin Formation of China or the basal tetanuran *Siamotyrannus isanensis* from the Sao Khua Formation of Thailand is possible (Brusatte et al., 2010). Because digit I is not connected proximally in the majority of *O. zhanglifui* tracks, and the tracks appear deeply impressed, it is also possible that the digit I impression is actually a reversed hallux being imprinted as a result of the dinosaur sinking into a wet substrate. In this case, the trackmaker may not be functionally tetradactyl like that of the trackmaker for *Saurexallopus*. The identity of the trackmaker for these tracks requires further investigation.

The Denali National Park *Saurexallopus* tracks, identified as therizinosaur tracks by Fiorillo and Adams (2012) and Fiorillo et al. (2018), have considerably broader, blunter digits than *Saurexallopus* and *Ordexallopus*. Fiorillo et al. (2018) noted differences in the arc of the metatarsals and considered these footprints to be more similar to therizinosaurs than oviraptorosaurs in this regard; my landmark analysis did not show any significant differences between Oviraptorosauria, Therizinosauria, and Neornithischia. This suggests either that the arc is not taxonomically significant or that landmark analysis does not adequately capture this morphological feature. DMNH 2014-11-10 represents a different morphology with thinner and more widely splayed digits which could potentially be referred to *Saurexallopus*. In the LDAs presented here, this specimen was consistently identified as an oviraptorosaur while the remaining Denali footprints were variably classified as Oviraptorosauria, Neornithischia, or Leptoceratopsidae. The fact that this particular print was consistently identified while the others were not might support the presence of two morphotypes for the Denali '*Saurexallopus*' sp. with DMNH 2014-11-10 being a more gracile ichnospecies. The wider morphology represented by the majority of the Denali tracks has narrower interdigital angles. In the PCAs, the Denali footprints form their own convex hull distinct from *Saurexallopus*, indicating that they do not occupy the same morphospace and arguably should be assigned to a novel ichnogenus. Interestingly, in the LDAs only one of the Denali '*Saurexallopus'* is classified as belonging to Therizinosauria and only in the LDA where angular data is excluded and digit lengths are taken to the heel. Instead, the Denali footprints are variably classified as Oviraptorosauria, Neornithischia, or Leptoceratopsidae, rejecting the therizinosaurian affinity hypothesis proposed by Fiorillo and Adams (2012) and Fiorillo et al. (2018). One observation of note is that the LDA associated with the highest accuracy (where digit length is taken to the heel and interdigital angles are included) classifies the Denali '*Saurexallopus'* as belonging to Leptoceratopsidae, whose pes skeletons possess four subequal, narrowly splayed digits with subangular claws. Digit lengths and proportions for the Denali specimens align fairly well with those of the leptoceratopsids, lending support to this classification. While this is not proof that these footprints were produced by leptoceratopsids, it is interesting as leptoceratopsids have not previously been proposed as a potential trackmaker. If these footprints were indeed created by leptoceratopsids, they would represent a northwestern range extension for Laramidian leptoceratopsids. They would also be the first known occurrence of leptoceratopsids in the palaeoichnological record. One footprint, found in association with a skeleton, has been attributed to the closely related family Protoceratopsidae, but the Denali tracks display longer, more widely splayed digits (Niedźwiedzki et al., 2011). Additionally, as these footprints are not associated with manus prints, the Denali tracks could provide support for a bipedal stance in Leptoceratopsidae, which has been proposed before (Chinnery and Horner, 2007). Finally, based on Alexander's (1976) equation for hip height, the trackmaker for the Denali footprints would be approximately 0.9 m tall at the hip, within the size range of Leptoceratopsidae (Russel, 1970) and far smaller than known Maastrichtian therizinosaurs (Carrano, 2006).

One other tetradactyl theropod ichnogenus that has been ascribed to therizinosaurs is *Macropodosaurus*. These footprints have short, broad, parallel digits ending in sharp claws. These footprints preserve the entire metatarsal region behind the digits, representing a plantingrade stance (Sennikov, 2021). Based on the broad, flat, parallel metatarsals I observed on larger therizinosaur specimens, I agree that a plantigrade stance makes sense for this group of dinosaurs and that *Macropodosaurus* is attributable to Therizinosauria.

Xiangxipus is debatably a tetradactryl theropod ichnogenus. Lockley et al. (2022) regard it as having a postero-medially oriented digit I while Xing et al. (2016) dismiss the first digit as a double impression of digit II. Because of the doubts on its true morphology, a trackmaker cannot be identified with certainty beyond a small, unspecified theropod.

The remaining two tetradactyl theropod ichnogenera (*Picunichnus* and *Boutakioutichnium*) have significantly shorter first digits than the other tetradactyl theropod ichnogenera. Additionally, digit I is located near the back of the foot as opposed to a more forward position with the other digits (Calvo and Rivera, 2018; Nouri et al., 2011). As such, it is possible that these tracks do not represent dinosaurs that were functionally tetradactyl and instead are hallux impressions left behind due to the trackmaker sinking further into the substrate.

2.5 Conclusion

Tetradactyl theropod footprints are rare in the ichnological fossil record as most theropod dinosaurs walked on three functional digits. In some cases, where the substrate is wetter or deeper, the first digit, which is usually held high on the heel and off of the ground, may be impressed (Gatesy et al., 1999). In other cases, a particular group of theropods may have been functionally tetradactyl, walking with all four digits on the ground at all times. Functional tetradactyly may be the result of a plantigrade stance, in which the metatarsals are flat against the ground as in the presumed therizinosaur ichnogenus *Macropodosaurus* (Sennikov, 2021). In other cases, digit I may be positioned distally along the metatarsals as opposed to proximally. This appears to be the case for *Ordexallopus* and *Saurexallopus*, in which four long, widely-splayed digits radiate from a distal metatarsal pad (Harris et al., 1996; Lockley et al., 2018a). *Ordexallopus* has a reversed digit I (Lockley et al., 2018a); smaller specimens like *O. zerbsti* may represent the tracks of birds.

Saurexallopus is more gracile, with thin, narrow digits and a medially oriented digit I (Harris et al., 1996). Some specimens attributed to this ichnogenus from Denali National Park in Alaska had previously been attributed to *Saurexallopus* and therizinosaur trackmakers (Fiorillo & Adams, 2012; Fiorillo et al., 2018), however these tracks are not comparable statistically or morphologically to other known *Saurexallopus* and likely represent a new ichnogenus. Additionally, comparison with potential trackmakers including Oviraptorosauria, Therizinosauria, Neornithischia, and Leptoceratopsidae does not support a therizinosaurian affinity for the Denali tracks; statistical analysis instead indicates a potentially leptoceratopsid origin, or a trackmaker not sampled in this study. Most *Saurexallopus* were likely produced by Oviraptorosauria, a family of bird-like herbivorous or omnivorous theropods that originated in China during the Early Cretaceous. *Saurexallopus neesowatchiensis*, a new ichnospecies from the Aptian-Albian Gething Formation of British Columbia represents a previously-unknown gigantic oviraptorosaur present in North America during the Early Cretaceous.

Conclusions

This research began with two main questions: what are the large tetradactyl theropod footprints at the Neeso-Watchie Dinosaur Tracksite and what dinosaur made them.

The first question resulted in a systematic revision of tetradactyl theropod ichnogenera. Until now, there was little consensus on what truly distinguished *Saurexallopus* from *Ordexallopus*, another tetradactyl theropod ichnogenus with widely-splayed digits and a long digit I. *Ordexallopus* was previously diagnosed based almost entirely on size as *Ordexallopus zhanglifui*, the holotype ichnospecies, was considerably larger than previously described *Saurexallopus* (Lockley et al., 2018a). The discovery of the Neeso-Watchie specimens, which bridge the size gap between the two ichnogenera, brought that diagnostic character into question.

Through review of the literature and observation of *Saurexallopus* specimens throughout North America, I came to the conclusion that a much clearer diagnostic character that distinguished the two ichnogenera is the orientation of digit I. In *Ordexallopus*, digit I is posteriorly oriented. In the original diagnosis of *Saurexallopus* by Harris et al., 1996, *Saurexallopus* was diagnosed by a medially-oriented first digit. This diagnosis was amended by Lockley et al., 2003 who discovered a tetradactyl theropod footprint with a reversed hallux which they named *Saurexallopus zerbti*. As a result of my review, I have reverted the diagnosis for *Saurexallopus* back to the original medial orientation and have reclassified *S. zerbsti* as *O. zerbsti*, reflecting its posteriorly oriented first digit. With the diagnoses of these tetradactyl theropod ichnotaxa resolved, I was able to identify the large Neeso-Watchie footprints as a new ichnospecies of *Saurexallopus* – *S. neesowatchiensis*.

With the ichnotaxonomy of the footprints resolved, the question of trackmaker identity could be tackled. Until now, there has been heavy debate on the trackmaker for *Saurexallopus*.

Generally, arguments fell between two non-carnivorous maniraptoran theropod groups: Oviraptorosauria (Lockley et al., 2022; Gierliński & Lockley, 2013) and Therizinosauria (Fiorillo et al., 2018; Fiorillo & Adams, 2012). These attributions were based almost entirely on observations. I decided to apply a multivariate approach to more test hypotheses of *Saurexallopus* trackmaker identity.

I observed and measured pes skeletons for various dinosaurs within the potential trackmaker groups. This included Oviraptorosauria and Therizinosauria as well as the non-theropod Neornithischia and Leptoceratopsidae. While the latter two groups are not theropods, they do not have the typical blunt, wide hoof morphology of larger ornithischians. Instead, they have four rather narrow, long digits with subangular unguals.

Morphologically, I noted that oviraptorosaurs largely differ from the other three groups in having a shorter metatarsal I, positioned medially on the proximal end of metatarsal II. The other three potential trackmaker groups have significantly longer first metatarsals, positioned parallel to the rest. Principal component analyses conducted on several iterations of footprint and skeletal measurements largely produced the same results: *Saurexallopus* are created by oviraptorosaurs. The convex hulls for *Saurexallopus* frequently overlap with those of Oviraptorosauria. In contrast, *Saurexallopus* never overlap with Therizinosauria, thus rejecting the therizinosaurian trackmaker hypothesis. Interestingly, the '*Saurexallopus'* from Denali attributed to therizinosaurs plot separately from other *Saurexallopus*. In addition to the thicker, more robust morphology of the Denali tracks in comparison to other *Saurexallopus*, these results support the hypothesis that the Denali tracks are not actually referable to *Saurexallopus* but rather another tetradactyl ichnogenus.

If indeed *S. neesowatchiensis* can be attributed to an oviraptorosaurian trackmaker, as is suggested by their slender, long, widely divaricated morphology which resembles the skeletal morphology of Oviraptorosauria and supported by the statistical analyses conduced in this study, these footprints have a significant impact on our understanding of the palaeobiogeography and evolution of Oviraptorosauria. Firstly, these footprints represent the earliest occurrence of the group in Canada. Oviraptorosaurs do not appear in the skeletal fossil record of Canada until the Campanian of the Late Cretaceous (Osmólska et al., 2004). Additionally, the size of the *S. neesowatchiensis* trackmaker is noteworthy. Based on Alexander's equation for hip height (Alexander, 1976), the trackmaker for the Neeso-Watchie tracks would have stood about 2m tall at the hip. This places it among the larger of oviraptorosaurs, between *Gigantoraptor* from the Maastrichtian of China (Xu et al., 2007) and *Hagryphus* (Zanno & Sampson, 2005) and *Anzu* (Lamanna et al., 2014) from the Campanian and Maastrichtian of the United States, respectively. The size of *Saurexallopus neesowatchiensis* suggests a much earlier origin for large body size in oviraptorosaurians than is currently known from the body fossil record, but which is also supported by the fossil record of rare large oviraptorosaur eggs in the mid Cretaceous of North America (Simon et al., 2018; Zelenitsky et al., 2000)

Studying ichnofossils like the *Saurexallopus* at the Neeso-Watchie tracksite can provide us with insight we are not privy to if we only rely on the body fossil record for our understanding of past ecosystems. The footprints in this study are a prime example of the significance of palaeoichnology in understanding dinosaurian faunas. These two footprints alone expand the geographical presence of a rare theropod group into Canada nearly 50 million years prior to what we previously believed. In addition, they indicate an earlier evolution for the derived trait of gigantism in Oviraptorosauria.

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Appendix

Table 1: Loadings for PCA Test A – digit length measured to the heel with angles included

	PC1	PC2
WM	-0.40	0.13
LI	-0.12	0.29
LIII	-0.01	-0.39
LIV	-0.41	0.08
WI	0.13	0.42
WII	0.16	0.42
WIII	0.18	0.42
WIV	0.22	0.40
I-II	0.42	-0.11
II-III	0.43	-0.13
III-IV	0.42	-0.15

Table 1: Loadings for PCA Test B – digit length measured to heel, no angular measurements

	PC1	PC2
WM	0.09	0.94
LI	0.15	0.15
LIII	-0.07	-0.03
LIV	-0.01	0.25
WI	0.60	0.03
WII	0.47	-0.03
WIII	0.35	-0.10
WIV	0.50	-0.16

Table 2: Loadings for PCA Test C – free digit length with angular measurements included

	PC1	PC2
LM	0.11	-0.27
WM	-0.19	0.34
DLI	-0.08	0.37
DLIII	0.04	-0.22
DLIV	-0.25	0.17
WI	0.31	0.38
WII	0.33	0.34
WIII	0.35	0.31
WIV	0.37	0.28
I-II	0.38	-0.19
II-III	0.38	-0.24
III-IV	0.37	-0.27

Table 3: Loadings for PCA Test D – free digit lengths excluding angular data

	PC1	PC2
LM	0.99	0.01
WM	0.01	0.00
DLI	-0.12	0.06
DLIII	0.02	-0.02
DLIV	-0.03	-0.05
WI	-0.04	0.57
WII	0.01	0.47
WIII	-0.02	0.38
WIV	0.04	0.55