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# Vertebrate Ichnopathology: Pathologies Inferred from Dinosaur Tracks and Trackways from the Mesozoic

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Literature concerning dinosaur footprints or trackways exhibiting abnormal gait or morphology reflecting pathology (ichnopathology) is rare. We report on a number of Jurassic and Cretaceous occurrences of theropod footprints from western North America with unusual morphologies interpreted herein as examples of inferred pathologies, or *ichnopathologies*. The majority of ichnopathologies are primarily manifested in the digit impressions and include examples of swelling, extreme curvature, dislocation or fracture, and amputation. A number of occurrences are single tracks on *ex situ* blocks with substantial deformation (inferred dislocation or fracture), or absence of a single digit impression. Two occurrences are from *in situ* natural mould trackways, one of which is a lengthy trackway of a presumed allosauroid with no noticeable deformation of the digits or feet but with strong inward rotation of the left footprint toward the midline and a pronounced, waddling limp. The other is a tyrannosaurid trackway consisting of three footprints (one right, two left) with the two left prints exhibiting repetitive ichnopathology of a partially missing Digit II impression.

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**Keywords** Dinosaur tracks, Amputation, Antalgic gait, Compensated gait, Jurassic, Cretaceous, Ichnopathology, Laterality, Irregular gait, Limping gait, Shuffling gait, Waddling gait

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## INTRODUCTION

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

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

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



FIG. 1. *Antipus bifidus* trackway with missing digit from the Early Jurassic of Connecticut. Left image modified from Hitchcock, 1858 plate 48, figure 10. Right image modified from Hitchcock, 1858, plate 36, fig. 8. The right image has been scaled and rotated to match the orientation of the left image.

## MATERIALS AND METHODS

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

## PREVIOUS REPORTS OF ICHNOPATHOLOGY

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

Fourteen years later, Hitchcock (1858) reported on fossil tracks from the Early Jurassic of Connecticut and illustrated a trackway of a quadrupedal animal (pl. 36, fig. 8 and pl. 48, fig. 10) that exhibited only two digit impressions on the fore-foot (Fig. 1) which he described as *Antipus bifidus*. In his description of *Antipus bifidus*, Hitchcock (1858) expressed

confusion about the bifid footprint with associated tail impression, which seemed to be characteristic of “lizards,” but he was unable to reconcile the two digit prints with the anatomy of any known “lizard.” In his description of *Antipus bifidus* Hitchcock (1858) did not entertain the possibility that this print might have been from a track-maker that was missing a digit. Lull (1953) mentions the didactyl character of *Antipus bifidus*, but aside from referring to it as “a very questionable species” he did not consider the possibility of this print being pathological. Since an entire lateral digit impression is missing it is likely that this could be the first legitimate example of an ichnopathology.

Inferred pedal digit loss in the right foot of an otherwise normal *Eubrontes* trackway from the Newark Supergroup (Late Triassic–Early Jurassic) was reported by Abel (1935). The missing digit impression was repeated in the trackway (Fig. 2) making this a convincing example of ichnopathology.

We suggest that trackways with one or more visible, repetitive pathologies, but with a nearly normal gait (no, or minimal trace of a limp), such as the *Eubrontes* trackway reported by Abel (1935) be classified as examples of *Compensated Gait*.



FIG. 2. A Late Triassic – Early Jurassic *Eubrontes* isp. trackway from the Newark Supergroup with a missing digit (Abel, 1935). Figure modified from Lockley, 1991. Scale bar = 1 metre

Such trackways demonstrate that the track-making animal has adapted to, or compensated for the visible injury and its locomotion is very close to normal.

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

Jenny and Josen (1982) and Ishigaki (1986a, fig. 2, 1986b, 1988) briefly described and figured a mid-Jurassic small theropod trackway from the Aganane Formation of Morocco exhibiting pathology that caused one of the toes to be abnormally positioned. This compelling example showed signs of both limping, (as defined by Dantas et al., 1994) and a malformed foot. Instead of the tridactyl foot having the toes more or less equally spread, digits III and IV are closely appressed (Fig. 3). An artistic rendering of the trackway and potential theropod track-maker was published as the front piece for the first chapter in Lockley's (1991) dinosaur tracks book. This trackway is classified as exhibiting a limping gait, with a visible and repetitive ichnopathology of a digit.

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

Lockley et al. (1994) summarized a number of trackway occurrences of irregular gait, many of which appear herein and with the exception of the theropod trackway from Morocco (Jenny and Josen, 1982; Ishigaki, 1986a, 1986b, 1988) these trackways are likely all examples of irregular gaits of healthy animals, rather than pathologically influenced limping behavior. We include a photogrammetric image of a large theropod trackway showing irregular gait from the Morrison Formation of Utah (Fig. 4).

Currie et al. (2003, fig. 7e) reported an uncollected, single hadrosaur footprint from a locality in Mongolia that exhibited a bulbous expansion under the fourth digit impression that might be interpreted as soft tissue swelling. However, the authors wisely cautioned that this feature could just as easily

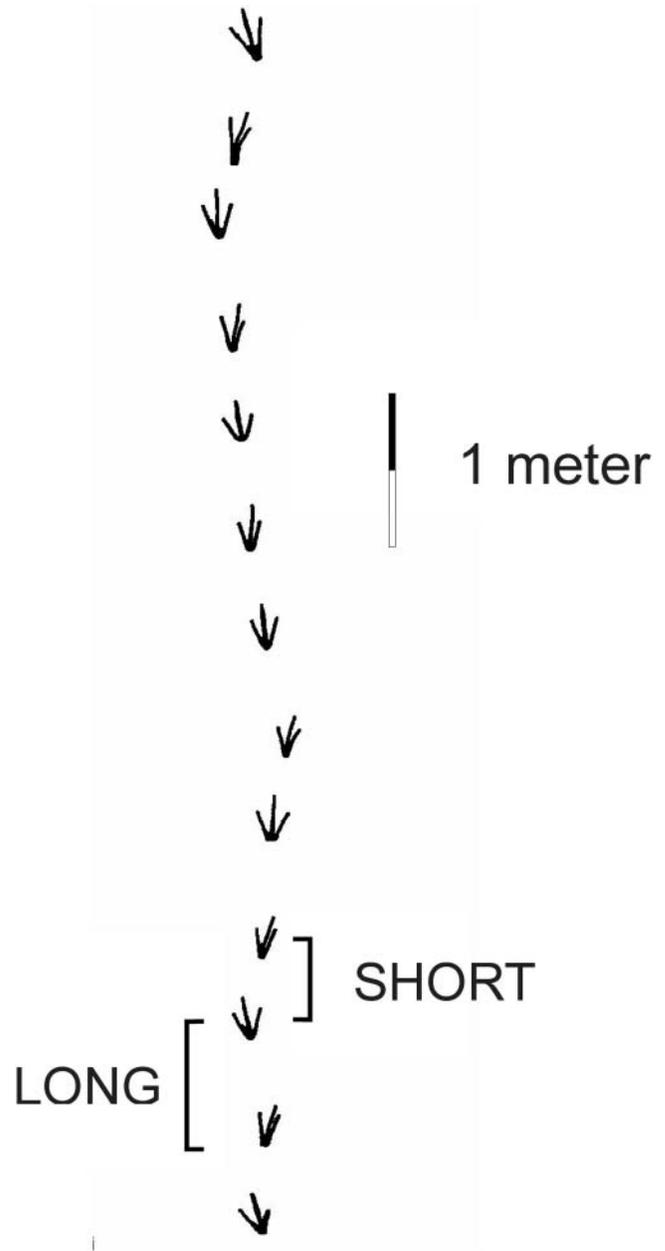


FIG. 3. Irregular gait of a large theropod trackway with a repetitive impression of an abnormal digit II of the left footprint from the Middle Jurassic Aganane Formation of Morocco. Modified from Lockley et al. (1994).

be the product of the track-aker shifting its weight on the track surface during locomotion. If this is an ichnopathology, it adds to a very small record of known hadrosaur pedal pathologies (Tanke and Rothschild, 2014).

Avanzini et al. (2008) reported a possible pathology associated with a trackway of a large theropod with four consecutive prints from the Late Jurassic of Asturias, Spain. The ichnopathology involved digit IV and was seen on both right footprints in the trackway. The digit impression was oriented almost perpendicular to the midline of both of the right footprints

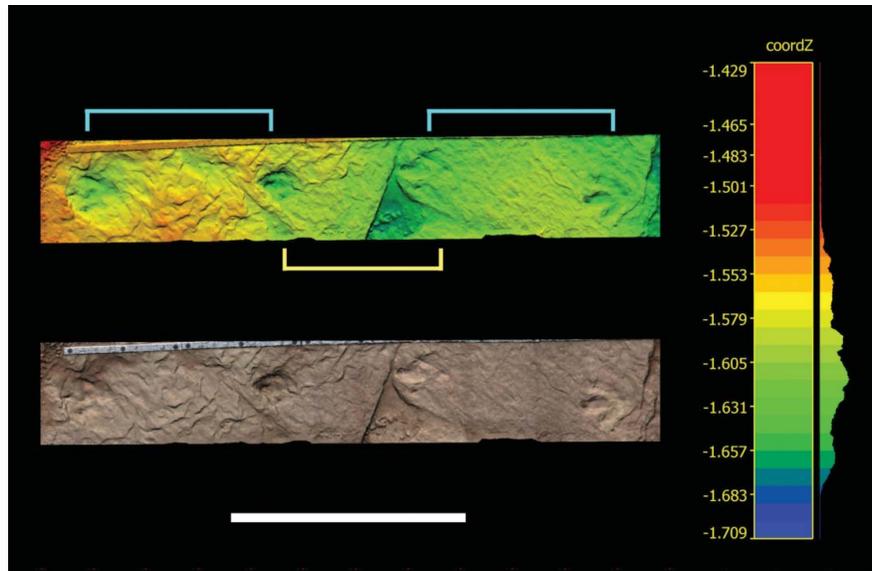


FIG. 4. Photogrammetric images of a large theropod trackway showing an irregular gait. Blue brackets = long pace, Yellow bracket = short pace. This trackway is from the Copper Ridge locality, near Moab Utah from the Upper Jurassic Morrison Formation and corresponds to part of the trackway from Lockley et al. (1994, fig. 3b). White scale bar = 2 meters. Vertical scale in meters.

resulting in a III–IV divarication value of  $80^\circ$ , over  $40^\circ$  greater than observed from the III–IV divarication values of the left prints in the same trackway. Avanzini et al. (2008) observed normal pace and stride length values for this trackway and this can be an example of a compensated gait.

## RECENT AND NEW REPORTS

### Lufeng Formation (Early Jurassic)

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

dinosaurs suffered from the same bone diseases as living vertebrates.

Reports of footprints or trackways from China bearing evidence of pathology are also very recent (Xing et al., 2009; Xing et al., 2012, Lockley et al., 2013; Xing et al., 2014). Two large theropod track specimens from Lufeng County in Yunnan Province of China referred to *Eubrontes pareschequier* (Lockley et al., 2013; Xing et al., 2014; formerly *Changpeipus pareschequier* Xing et al., 2009) may be examples of ichnopathology (Fig. 5). We are also aware that such relatively minor irregularities in footprint morphology could be due to the vagaries of preservation.

Track specimen ZLJ-ZQK1 (Fig. 5) is a *Eubrontes pareschequier* track that exhibits a possible swelling feature that at the posterior-medial end of the track that is absent in ZLJ-ZQK2. Xing et al. (2009) interpreted this prominence as an oddly shaped or oddly distorted metatarsophalangeal pad. Xing et al. (2009) speculated that it could also represent pathology on the foot of the track-maker, constituting osteogenic tissue and bone marrow that were replaced by a hyperplastic mass of fibrous tissue. ZLJ-ZQK2 (*Eubrontes pareschequier*) is complete with the exception of the absence of the distal end of digit III (Fig. 5), which may represent the amputation or severe dislocation of the terminal end of this digit. These footprints were not found in context within trackways so the above interpretations of ichnopathology are speculative.

### Laiyang Group (Early Cretaceous)

A single theropod track reported by Xing et al. (2012) from Jimo City, Shandong Province exhibits an unusually shortened digit II, which may indicate an injury or congenital deformation

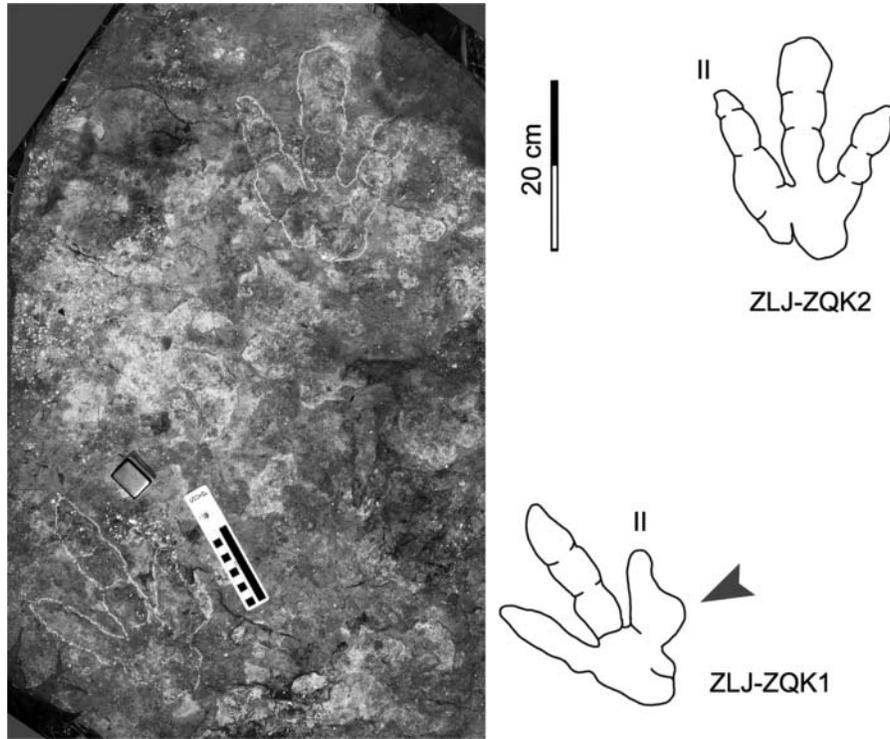


FIG. 5. Two tracks of *Eubrontes pareschequier* with possible pathologies from the Lufeng Formation (Early Jurassic) Lufeng County, Yunnan Province, China. Left: photograph of trackslab with footprints outlined in chalk. Scale bar in cm. Right: outline drawing of the same footprints with ZLJ-ZQK2 showing absence of the terminal portion of the digit III impression, and ZLJ-ZQK1 exhibiting a swelling on the medial edge of the digit II impression.

on the foot of the trackmaker (Fig. 6). As it is a single track it is possible that the missing digit could simply be an extra-morphological variant created by a particular behavior of the trackmaker, substrate interactions, or both (Xing et al., 2012).

**Gates Formation (early Albian)**

McCrea et al. (2014a) reported the existence of a large *in situ* track surface exposed on a steeply dipping wall exposed, in fall 2011, during road construction near a coal mine in the Falling Creek area of northeastern British Columbia. The vertebrate ichnofauna comprised a number of trackways with large, tetradactyl prints identifiable as *Tetrapodosaurus borealis*, as well as a single unusual trackway, possibly referable to *Irenesauripus mclearnii*, made by a large bipedal theropod. The footprints in the Falling Creek cf. *Irenesauripus mclearnii* trackway exhibit an extremely short pace and stride (relative scale provided from lens cap in picture), so much so that McCrea et al. (2014a) speculated that the trackway might have been the product of two large theropod trackmakers, one following the other using the same midline. Closer examination of the tracksite and the photographs (Fig. 7) and a brief re-examination of the site by RTM in 2014 revealed that the two large theropod scenario is unlikely as the footprints, particularly the left prints, exhibit strikingly similar morphology, and as well as being consistently, strongly rotated toward the

midline of the trackway. Some of the right prints are rotated inward as well, but not to the same degree.

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

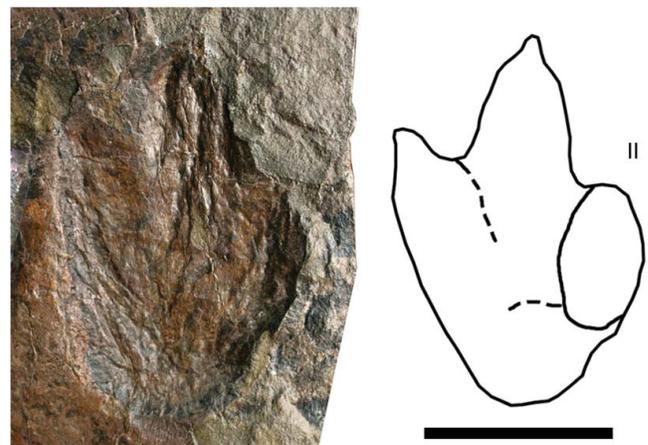


FIG. 6. Left: Photograph of a theropod track with possible ichnopathology of digit II from the Early Cretaceous Laiyang Group, Shandong Province, China. Right: Interpretive outline drawing of track specimen. Scale bar = 10 cm.



FIG. 7. Falling Creek theropod trackway (cf. *Irenesauripus mclearni*) from the Early Cretaceous Gates Formation of northeastern British Columbia, Canada. Camera lens cover for scale is 6.6 cm diameter.

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

It is worth considering whether the unusual Falling Creek theropod trackway might have been produced due to substrate conditions rather than being a result of injury to the trackmaker. The track-bearing substrate is very fine-grained (low

energy) with substantial organic content and is dominated by *Tetrapodosaurus borealis* trackways. McCrea (2000, 2001, 2003a) previously observed that such low energy, high-organic content tracksites almost always reveal a vertebrate ichnofauna that is dominated by quadrupeds to the near exclusion of bipedal track-makers, especially when these substrates possessed high water content. McCrea et al. (2014a) defined the *Tetrapodosaurus* ichnofacies based on more than 30 vertebrate ichnocoenoses of low energy depositional environments with high organic content. At rare sites where theropods venture onto such wet, fine-grained, organic substrates, or other sites that were wet (discussed below), the substrate conditions were observed to affect the morphology of the footprints as well as the gait of the bipedal track-makers. For theropods, in addition to the main functional digits II–IV being impressed, the hallux (digit I) and a portion of the metatarsus may also be impressed due to the depth the feet penetrated the wet substrate, examples of which are discussed below (under the heading “Qualities of the substrate”). Pace and stride is greatly reduced and there is pronounced inward and generally equal rotation of left and right footprints toward the midline.

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

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

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

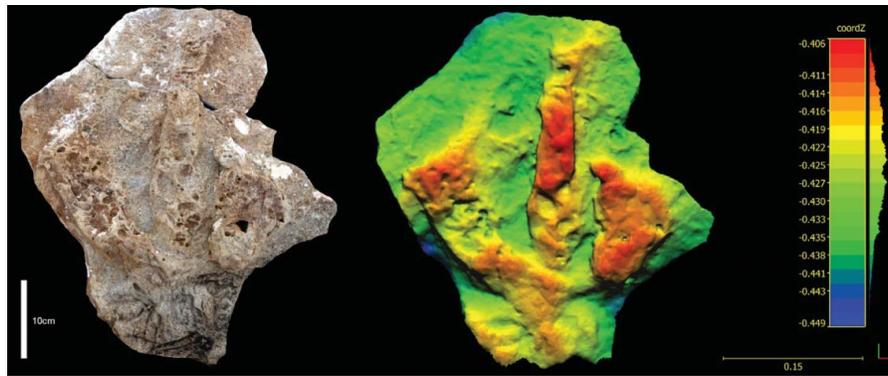


FIG. 8. Photograph (left) and photogrammetric (right) images of a natural cast theropod track (UCM 207.123) from the Cretaceous (Albian-Cenomanian) Dakota Formation of western Colorado exhibiting unusual swelling and dramatic inward curve of digit II. Values for the vertical and horizontal scales for the right image are in meters.

### Dakota Group (Albian–early Cenomanian)

A single, natural cast of a right theropod footprint was collected from the Club Gulch tracksite in western Colorado. One of the outer digit impressions exhibits a strong curve toward the digit III impression (Fig. 8). The curved digit impression also appears to be unusually thickened compared to the other two digit impressions. This thickening begins slightly anterior to the hypex and expands strongly toward the end of this digit but excludes the claw impression.

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

A direct plaster replica of a modern Canada Goose (*Branta canadensis*) trackway was collected for the Peace Region Palaeontology Research Centre's (PRPRC) neoichnology collection by LGB in summer 2014 from a mudflat along the Pine River, close to Pyramid Peak west of Chetwynd in northeastern British Columbia. At the time of collection nothing unusual was observed about the trackway. However, once the specimen was cleaned, a swelling on digit IV of both right footprints was noticed and a slight curve of the anterior portion of this digit toward digit III (Fig. 9). This swelling is similar to that of UCM 207.123, but occurring on digit IV and without such a pronounced curvature.

### Kaskapau Formation (late Cenomanian–early Turonian)

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

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

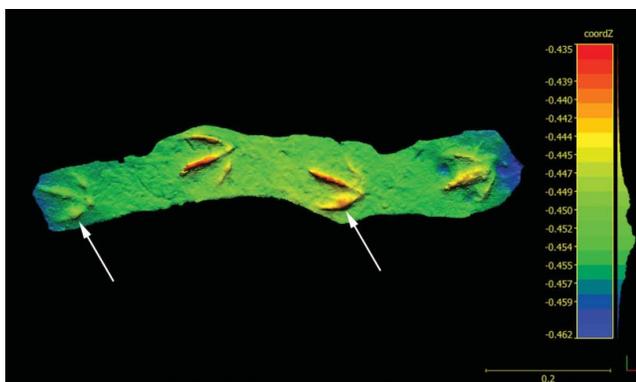


FIG. 9. Direct plaster replica (natural cast) of modern Canada Goose (*Branta canadensis*) trackway (PRPRC NI2014.004) showing repetitive pathological swelling of digit IV of the right print. Horizontal and vertical scales in metres.

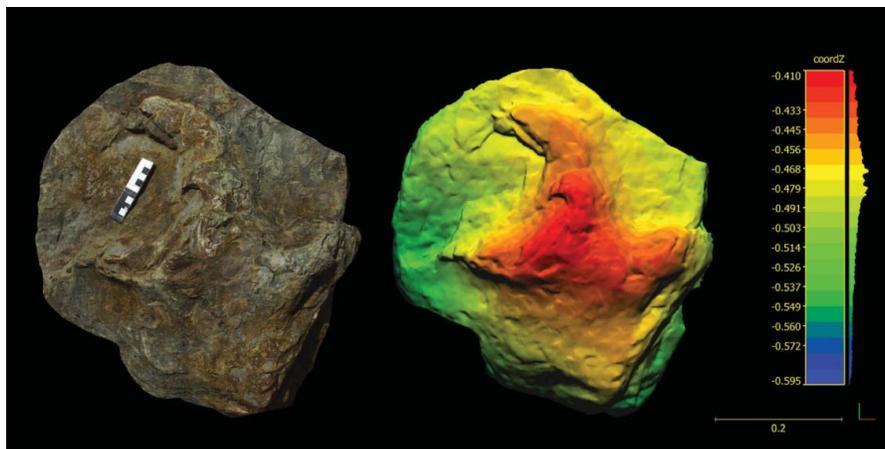


FIG. 10. PRPRC 2002.01.001. Photograph (left – scale = 10 cm) and 3D photogrammetric imaging (right – vertical and horizontal scales in meters) of a natural cast theropod print from the Late Cretaceous (Turonian) Kaskapau Formation of northeastern British Columbia with a pronounced curve of digit III.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

the most common type of footprint preservation currently known from Kaskapau Fm. exposures.

PRPRC 2002.01.001 is a single, natural cast on an isolated boulder found by CWH and volunteer Larry White in Quality Creek Canyon near the town of Tumbler Ridge, British Columbia (Helm, 2002; McCrea 2003b; McCrea et al.,

2014a). This footprint was reported by McCrea et al. (2014a) as an example of a possible pathology due to the severe curvature of digit III as well as the very high splay of both outer digits (Fig. 10). The inferred primary pathology on middle digit III appears to be a severe lateral dislocation similar to the specimen described by Tucker and Burchette (1977). As there is no swelling associated with this trace, the footprint was probably made after the injury had healed.

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

It is difficult to judge whether the basal areas of all digit impressions and the metatarsal pad impression are disproportionately thickened as a result of the injury to the trackmaker's

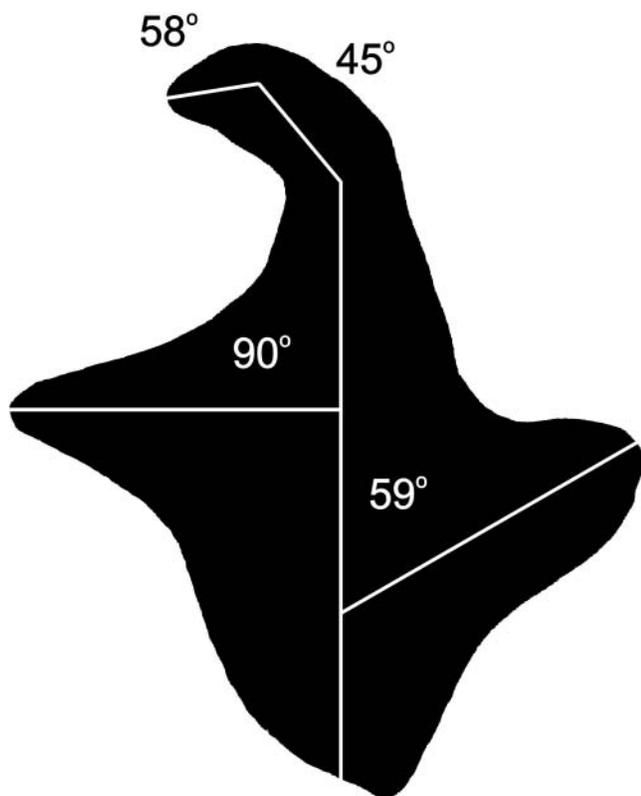


FIG. 11. Schematic of divarication measurements of lateral digits from the central axis of digit III (white). Degree of divergence of distal end of digit III impression from the central axis of digit III (black).

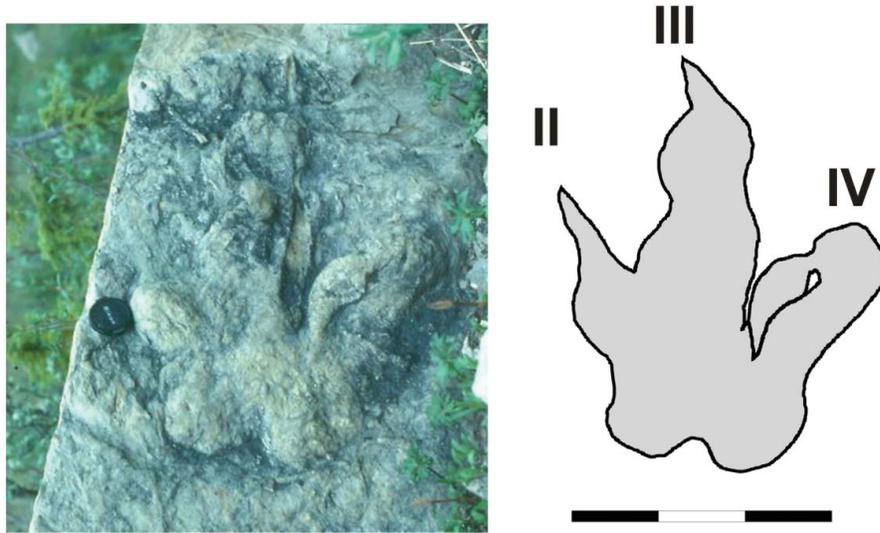


FIG. 12. Left: Natural cast of a large theropod track from the Late Cretaceous (Campanian-Maastrichtian) Wapiti Formation from a locality on the east side of Nose Mountain, Alberta exhibiting an extreme dislocation of the distal end of digit IV involving the distal two pedal phalanges. The pedal claw impression is visible in lateral profile. The camera lens cover is 52 mm diameter. Right: Outline drawing of the Nose Mountain theropod track composed from the image to the left. Scale bar = 30 cm.

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

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

### Wapiti Formation (Campanian/Maastrichtian) Nose Mountain

An unusual large theropod track was discovered at the base of the east side of Nose Mountain, about 90 km southwest of Grande Prairie, Alberta by Royal Tyrrell Museum summer staff in 1989 (Fig. 12). The specimen consisted of a single, natural cast on a large white sandstone slab. The original track surface was composed of soft grey clay, which was subsequently infilled by sand. Palynomorphs recovered from the upper and lower parts of the exposed Wapiti Fm. section at Nose Mountain were correlated with the *Porosiportis porosus* Zone of Sweet et al. (1989), giving it an early late

Maastrichtian age, laterally correlated with the base of the Battle River Fm. of the central Alberta Plains (Dawson et al. 1989, 1994; Braman and Sweet, 1999).

At time of discovery, the specimen was photographed with the intention of returning later to make a replica cast and/or collect the specimen. When colleagues reinvestigated the area in 1990, it was discovered that a massive landslide had buried the specimen and it could no longer be relocated. Therefore, the following description is based solely on the photograph (Fig. 12). Approximate measurements are extrapolated from a 52 mm diameter camera lens cap used for scale in the photograph. Based on this scale the footprint length is 49 cm. The length of the affected ungual was measured as 11.2 cm, taken as a straight line from the middle of the base to the tip.

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

The pathology is on presumed digit IV that appears to show severe rotational twisting, so that nearly half of the digit was folded underneath itself and the anterior portion of the metatarsal pad. Most striking in its appearance is the three-dimensional preservation of the claw impression which is an impression of the lateral surface rather than the normal ventral surface. The claw appears expanded proximally and steadily tapering distally to a point, as seen in examples of tyrannosaurid pedal claws in Tyrrell collections (Fig. 13). Tyrannosaurid

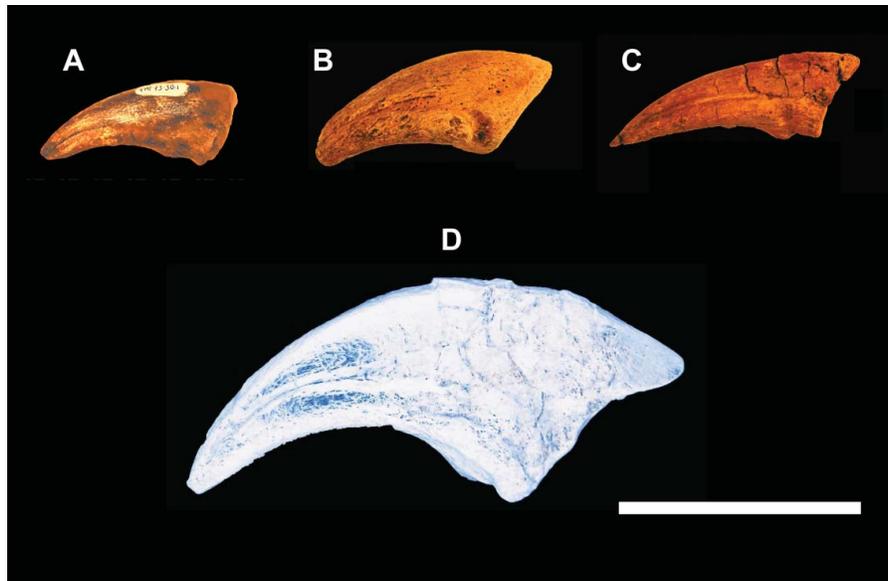


FIG. 13. Lateral views of pedal claws from a variety of tyrannosaurids. A. TMP 1973.030.0001 – tyrannosaurid from Dinosaur Provincial Park, Alberta; B. TMP 1991.036.0703 – water-worn tyrannosaurid claw from Dinosaur Provincial Park, Alberta; C. TMP 2000.045.0011 – *Albertosaurus* unguis from the *Albertosaurus* bonebed, Dry Island Buffalo Jump Provincial Park, Alberta; D. TMP 1981.006.0004 - *Tyrannosaurus rex* from the Crowsnest Pass, Alberta is presented as a photographic negative to make it visible in this figure as the original specimen was black in colour. Scale bar = 10 cm.

pedal claws are a remarkably good match in regards to size, curvature and general morphology.

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

#### Wapiti Formation (Campanian/Maastrichtian) Northeastern British Columbia

A recent report on tyrannosaur trackways from the Wapiti Formation of northeastern British Columbia (McCrea et al., 2014b) included a trackway (PRPRC 2011.11.001) with three prints, (two left and one right), of which the two left prints both exhibit a dramatically truncated digit II impression. McCrea et al. (2014b, figs. 1 and 7) compared the length of the affected digit II impression of both left prints with the length of the corresponding digit impression in the intact right

print of this trackway (Fig. 14). The left digit II impressions were shorter than the right digit II impression by at least 14 cm and likely involved the loss of the distal and penultimate phalanges on that digit (II-2 and II-3). This is a rare example of a repetitive pathology within the same trackway and provides evidence that this is a true pathology and not simply a preservational artefact.

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

#### Interpretation and Classification of Ichnopathologies

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

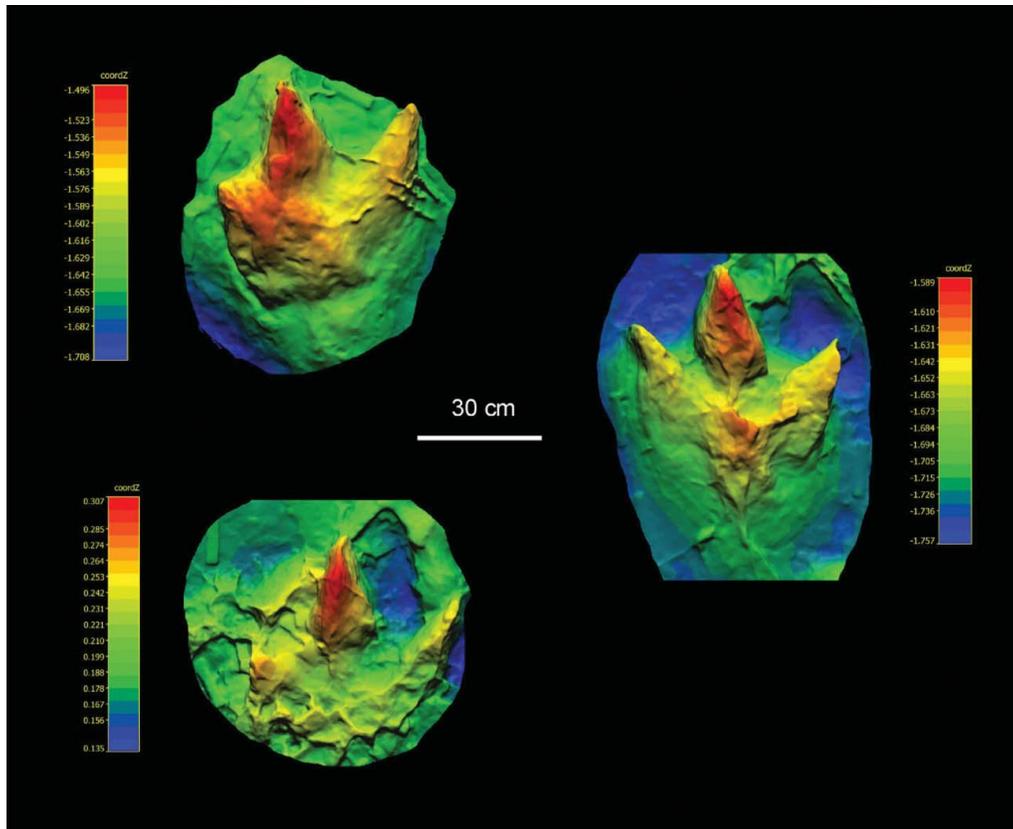


FIG. 14. Photogrammetric images of tracks from PRPRC 2011.01.001M (silicone mould of a natural mould trackway). Bottom left is print #1 (left); Top left is Print #3 (left); Right is print #2 (right - reversed). Prints #1 and #3 display an extremely truncated digit II impression, leaving just a small nub remaining. The reversed image of the intact print #2 shows a lengthy digit II as contrast. Vertical and horizontal scales are in meters.

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

Identifications of true ichnopathology can come from the descriptions of abnormal trackways, such as those that show repetitive atypical morphology or inconsistency of gait. Less confident designations of ichnopathology involve identifications based on isolated footprints which would show unusual morphologies including partially, or completely missing digit

impressions. In these cases there is no trackway providing a context to show whether these footprint morphologies are repetitive. In such cases confident identifications of ichnopathology are difficult.

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

- *I Congenital abnormalities*: these are deformations arising from birth and early development, possibly influencing gait.
- *II Biomechanical injury*: defects due to physical damage to the body, possibly affecting the movement of the limb and its elements.
- *III Brain or spinal injury*: resulting in nerve damage possibly causing abnormal gait.
- *IV Sickness*: this includes defects due to infection or diseases such as cancer among others.
- *V Age-related*: degeneration due to age that may affect gait.

It is likely that only biomechanical injury defects are identifiable from tracks, but congenital and disease-induced defects have been observed from skeletal specimens (Tanke and

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

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

### Distinguishing True Trace Pathologies from Non-Pathological Traces

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

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

The question of whether limping in dinosaurs is due to pathology rather than slightly favoring one side of the body over the other may be a question of degree. We agree that irregular gaits are likely not uncommon in healthy animals, but the term "limping" implies abnormality and possibly pathology. It would be advisable to make a distinction between minor, if consistent, irregularities in pace and stride values which we can define as "*irregular gaits*," and the more

extreme examples that are more likely to be cases of ichnopathology which may be properly referred to as "*limping gaits*." We propose the term *limping gait* to identify trackways where there is a visible pathology associated with an obvious limp. A limping gait may also be used to identify ichnopathologies in trackways where no ichnopathology is visible in the footprints, but where extremely unequal gaits, and/or unusual footprint rotations or other footprint features (i.e., foot drag traces—shuffling) are exhibited.

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

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

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

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

TABLE 1  
 Laterality ratios of captive and wild emus (*Dromaius novaehollandiae*)

| Bird                           | Stepping-Off<br>Print Symmetry | Pace Beginning in Footprint/Pace Ending in Footprint |         |        |               | Number of<br>Measurements |
|--------------------------------|--------------------------------|--|---------|--------|---------------|---------------------------|
|                                |                                | Minimum  | Maximum | Median | Mean          |                           |
| 1988 Fort Wayne Zoo Adult 3    | Left                           | 0.835  | 1.432   | 0.968  | 1.021         | 16                        |
|                                | Right                          | 0.740  | 1.244   | 0.967  | 0.996         | 16                        |
| 1988 Fort Wayne Zoo Adult 5    | Left                           | 0.750  | 1.256   | 1.009  | 0.998         | 25                        |
|                                | Right                          | 0.829  | 1.542   | 0.987  | 1.012         | 23                        |
| 1988 Fort Wayne Zoo Adult 6    | Left                           | 0.742  | 1.248   | 0.961  | 0.942*        | 17                        |
|                                | Right                          | 0.971  | 1.284   | 1.061  | <b>1.065*</b> | 19                        |
| 1988 Fort Wayne Zoo Juvenile 4 | Left                           | 0.751  | 1.307   | 1.043  | 1.019         | 10                        |
|                                | Right                          | 0.706  | 1.357   | 0.926  | 0.947         | 7                         |
| 1989 Fort Wayne Zoo Juvenile A | Left                           | 0.382  | 1.279   | 0.894  | 0.848         | 12                        |
|                                | Right                          | 0.625  | 1.814   | 1.007  | 1.055         | 10                        |
| 1989 Fort Wayne Zoo Juvenile C | Left                           | 0.526  | 1.458   | 0.789  | <b>0.801*</b> | 20                        |
|                                | Right                          | 0.703  | 2.033   | 0.993  | 1.149*        | 16                        |
| All Other Emus Pooled          | Left                           | 0.545  | 1.757   | 0.975  | 0.958*        | 62                        |
|                                | Right                          | 0.586  | 2.367   | 1.036  | 1.056*        | 66                        |

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

For six individual emus in this study (Table 1) there were enough pace lengths measured to allow meaningful comparison of the ratio of the pace beginning with a footprint to the preceding pace ending in that footprint, between footprints where the beginning (stepping-off) footprint was a left as opposed to a right. In two of these birds, the beginning pace/ending pace ratio was significantly larger when the beginning footprint was a right as opposed to a left. The same result was seen in a comparison of right versus left stepping-off beginning/ending pace ratios in the pooled sample of pace lengths of all other emus besides the six birds examined individually (Table 1), and for all of the paces of all of the birds (Fig. 15).

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

A systematic examination of the step lengths among dinosaur trackways could prove of considerable interest. If pace lengths within single trackways are commonly observed to be

slightly larger when beginning with one foot (the right- though rarely do we see the true beginning of a trackway) rather than the other, this would suggest that laterality rather than injury is the more likely explanation. Further, one would intuitively expect pace asymmetry to be more common if it is usually due to laterality as opposed to injury. Finally, one might also expect pace asymmetry to be less extreme if it is due to laterality as opposed to injury.

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

The Dromaeosauridae are thought to have had the ability to retract their lengthy and robust pedal digit II (Ostrom, 1969a, b). Trackways of dromaeosaurs would therefore exhibit only a partial digit II impression in all footprints in a trackway (Li et al., 2007; Kim et al., 2008, 2012; Lockley et al., 2004; Cowen et al., 2010; Xing et al., 2013b; Lockley et al., 2014).

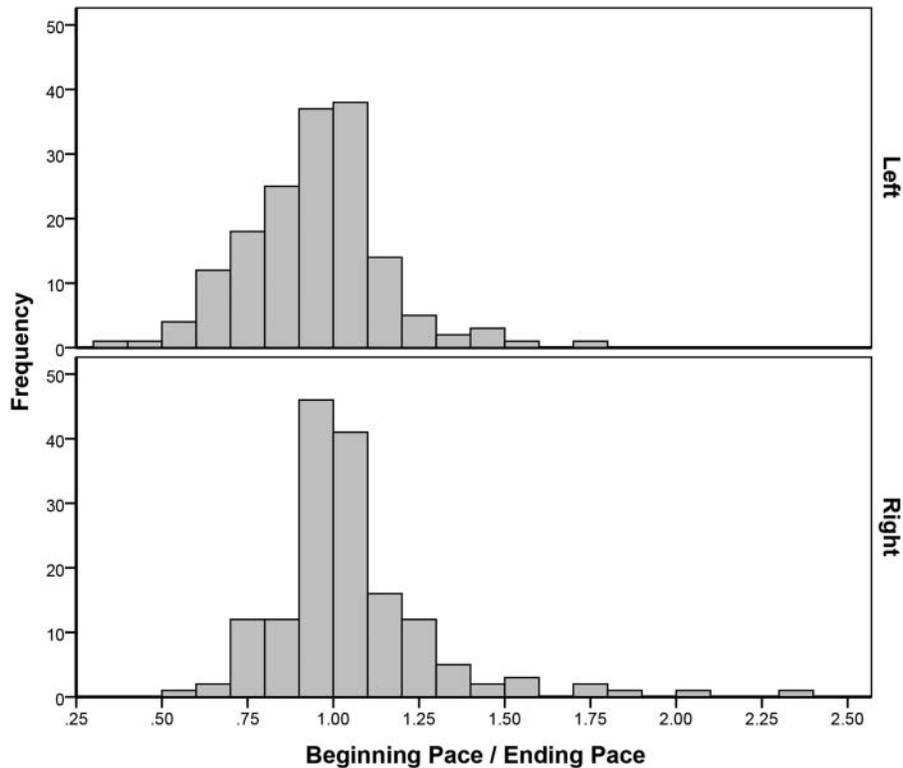


FIG. 15. Frequency distribution of the ratio of the pace beginning with a footprint to the pace ending with a footprint, across all paces of all emus in the sample. Top: Pace begins with a left footprint (minimum = 0.38, maximum = 1.76, median = 0.948, mean = 0.945,  $N = 162$ ). Bottom: Pace ends with a right footprint (minimum = 0.59, maximum = 2.37, median = 1.004; mean = 1.049,  $N = 157$ ).

There is the potential to mistake single footprints that might be attributable to dromaeosaurs as possessing an amputated digit II. The converse is also possible, a single footprint with a missing or truncated second digit could be a true pathology, but could be mistaken for a dromaeosaur footprint. It is also possible that registration of partially retracted digits, as in ichnogenus *Evazoum* (Lockley and Lucas, 2013) could be misinterpreted as a pathology.

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

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

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

The possibility exists to mistake normal footprint morphologies as being polydactylous, especially with certain theropod and small ornithopod tracks. The majority of theropod clades

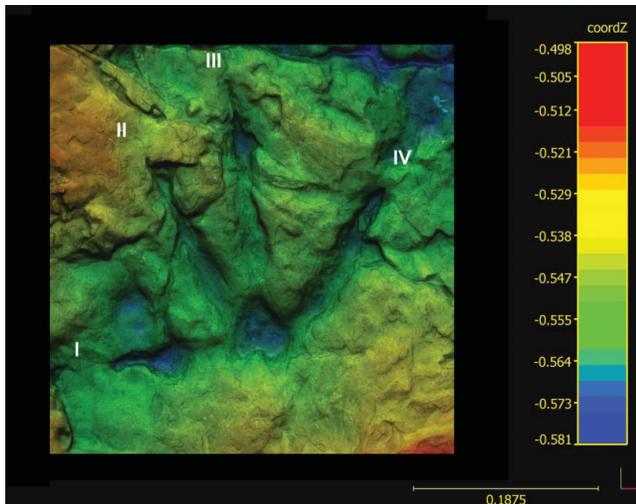


FIG. 16. Photogrammetric image of the holotype print of *Saurexallopus cordata* (McCrea et al., 2014a) from the Late Cretaceous (Campanian-Maastrichtian) Wapiti Formation of northeastern British Columbia.

have three functionally weight-bearing digits (II–IV) and a digit I (hallux) that is reduced to a certain degree depending on the taxon (Thulborn, 1990). In almost all theropods, digit V is absent or was reduced to a short splint. In such taxa the hallux was attached more proximally than digits II–III, and thus was nonfunctional for locomotion. However, if the substrate consistency was such that the foot impressed deep enough to impress digit I, an “extra” digit would appear to be present (see “Qualities of the substrate” section).

Therizinosaurids (Clark et al., 2004) and oviraptorids (Osmolska et al., 2004) have been found to have four functional (likely weight-bearing) pedal digits (I–IV) instead of the typical three (II–IV) of most other theropods. Tracks and trackways attributable to oviraptorids have been described (*Saurexallopus* isp.) and these tracks display four slender and lengthy digit impressions (Fig. 16). Three ichnospecies have been described to date, *Saurexallopus lovei* (Harris et al., 1996; Harris, 1997), *Saurexallopus zerbsti* (Lockley et al., 2004), and *Saurexallopus cordata* (McCrea et al., 2014a). A single, tetradactyl pes print from the Upper Cretaceous Cantwell Formation in Alaska has been put forward as a therizinosaur by Fiorillo and Adams (2012), but this print was assigned by these authors to *Saurexallopus*, which have recently been ascribed to oviraptors (Lockley and Gierlinski, 2009; Gierlinski and Lockley, 2013).

Lockley et al. (2009) described *Neoanomoepus perigrinatus*, tracks identified as being the product of a small quadrupedal ornithopod with four functional pedal digits and five manual digits. McCrea et al. (2014a, fig. 29) also reported cf. *Neoanomoepus* isp. track and trackway specimens from another locality in the Gorman Creek Formation of northeastern British Columbia. Thulborn (1990) observed that digit I of the pes of the basal ornithopod *Hypsilophodon* sp. was long

enough to make contact with the ground. The *Hypsilophodon* sp. manus is pentadactyl and its body size compares favorably with *Neoanomoepus* isp. tracks and trackways. Basal ornithopods seem to be likely candidates for *Neoanomoepus* isp. and similar trackways that have been identified as the product of small quadrupedal ornithopods. However, Norman et al. (2004) counter that digit I in known basal ornithopods, including *Hypsilophodon* sp., was not long enough to have made contact with the ground, much less be functionally weight-bearing during locomotion.

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

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

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

### Pre- and Post-Impression Effects

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

*Qualities of the substrate:* There are numerous examples of footprints and trackways that display the effects of

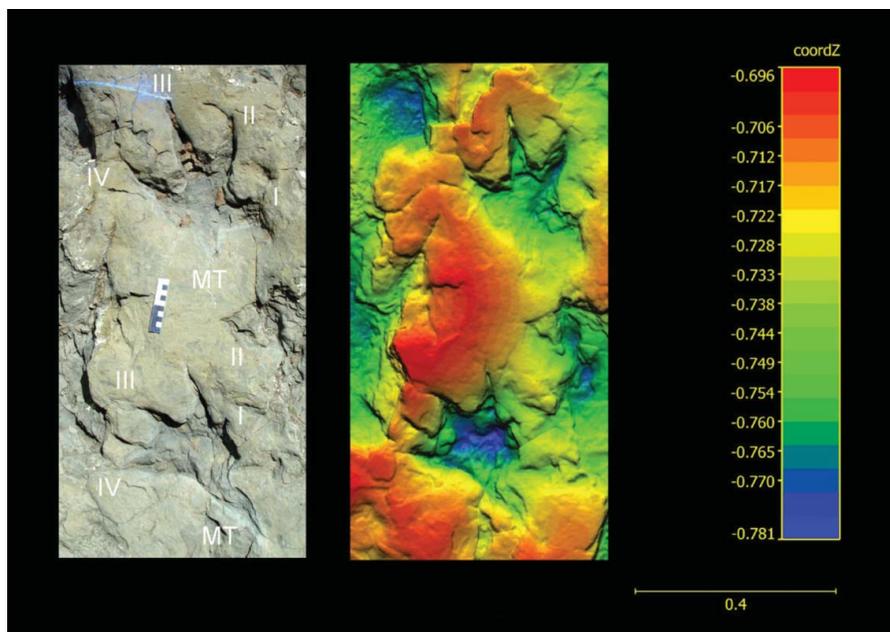


FIG. 17. A pair of theropod tracks (both left prints) from the Kaskapau Formation (late Cenomanian – early Turonian) from Flatbed Creek near Tumbler Ridge, British Columbia showing pinching of digits I–III due to sediment collapse after the foot was removed. MT = metatarsus impression. Scale in left image = 10 cm; horizontal and vertical scales in right image are in meters.

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

If the substrate that a track-maker was walking on was soft, its feet would have penetrated deeply into the substrate, allowing the nonfunctional hallux to impress along with digits II–IV, and possibly an impression of the metatarsus as well (Figs. 17–19). Theropod hallux impressions are not common, but they do occur and have been reported in the literature (Lockley and Hunt, 1994; Harris et al., 1996; Harris, 1997; McCrea, 2000; Lockley et al., 2004; Nouri et al., 2011; Xing et al., 2013c; McCrea et al., 2014a, b; Xing et al., 2014). The recognition of a small digit trace medial to the weight-bearing digits is sufficient to identify the impression as the hallux, a normal occurrence and not an example of polydactyly.

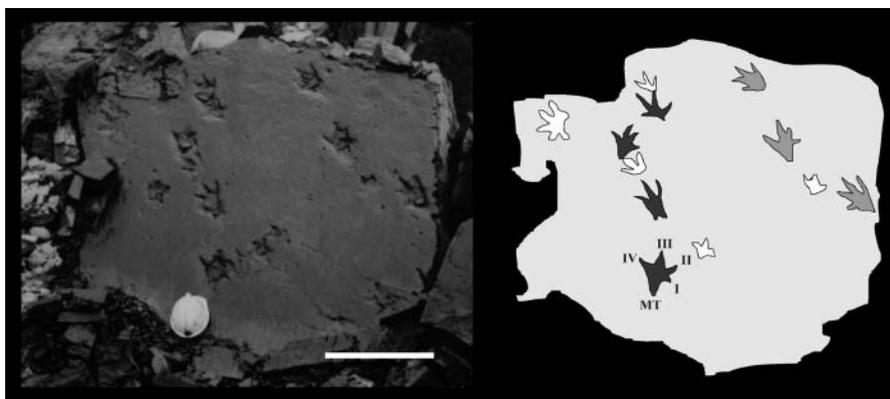


FIG. 18. Photograph and interpretive drawing of a trackslab (TMP1990.027.0001) with "five-toed" theropod footprints from the Early Cretaceous (Albian) Gates Formation, South-Pit Lake site near Grande Cache, Alberta. Digits I–IV and the lower portion of the metatarsus (MT) are labelled on the drawing. Scale bar on photograph = 1 meter.

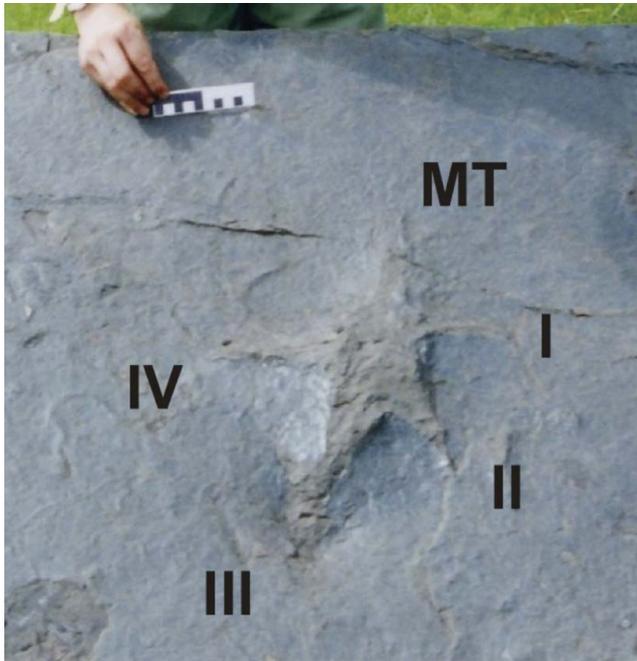


FIG. 19. Theropod track from the Mist Mountain Formation (Tithonian-Berriasian) of southeastern British Columbia. Scale = 10 cm.

Metatarsus impressions are somewhat less common (Kuban, 1989; Perez-Lorente, 1993), but they appear as posteriorly-oriented traces almost directly in line with the long axis of the footprint (Figs. 17–19). If the substrate is soft enough, the feet of dinosaurs may sink in deeply, and anatomical features of the foot and lower leg may be impressed that otherwise would not normally make contact with the substrate. In addition to the impression of the non-functional hallux of many theropods there may appear a lengthy, backward-directed impression that sometimes has the same proportions as the other (digit) impressions. It is unlikely that this is an extra digit, but rather is the impression of the metatarsus of the trackmaker. These types of traces may appear to be pentadactyl, but they are instead “tetradactyl” with impressions of digits I–IV with the addition of the digit-like metatarsus impression. Fig. 17 shows this feature in two theropod tracks from Flatbed Creek near Tumbler Ridge, British Columbia (McCrea et al., 2014a), but this has also been observed in small- to medium-sized theropod tracks from the Gates Formation (Albian) of northwestern Alberta (Fig. 18) as well as from the Mist Mountain Formation (Tithonian-Berriasian) of southeastern British Columbia (Fig. 19).

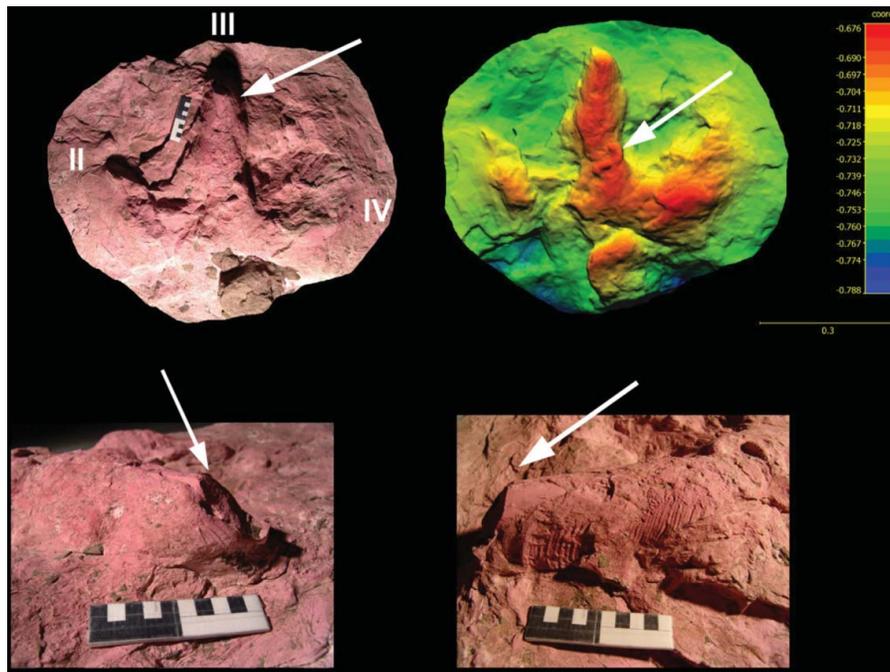


FIG. 20. A single, natural cast of a tyrannosaur print (All images are from PRPRC 2004.08.001MC, a replica cast painted light red for research purposes) from the Late Cretaceous (Campanian-Maastrichtian) Wapiti Formation of northeastern British Columbia. Top left: view of whole natural cast footprint (left) with arrow indicating position of wood fragment visible at the distal end of the digit III impression. The distal end of the digit III impression is missing due to the presence of the wood fragment. Top right: photogrammetric image of PRPRC 2004.08.001MC (horizontal and vertical scales in meters) with arrow pointing at the bottom of two partial invertebrate U-burrows. Bottom left: antero-lateral view of the distal end of the digit III impression with wood fragment visible (indicated by an arrow). Striations from skin tubercles are visible lateral to the wood fragment. Bottom right: medial view of the digit III impression with the wood fragment visible (indicated by an arrow). Skin tubercles and striations are visible along the medial edge of the digit III impression. Scale bars = 10 cm.

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

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

*Influence/introduction of foreign objects:* An example of nonpathology as a result of a foreign object comes from a single tyrannosaur print (PRPRC 2004.08.001) *Bellatoripes fredlundii* from British Columbia (Farlow et al., 2009; McCrea et al., 2014a, b) that exhibits an abnormality with the distal portion of digit III (Fig. 20). This abnormality gives the appearance of a truncated digit III impression which could easily be interpreted as an ichnopathology (amputation). Upon close examination the digit III anomaly was found to be caused by the introduction of a foreign body (a thick segment of a tree branch) during the burial of the original, natural mold footprint. The wood fragment settled (along with coarse sands) into the footprint along the long axis of digit III and is exposed for a few centimeters at the distal end of this digit impression.

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

A further example of the action of infauna occurs on the base of digit III of a tyrannosaur footprint, PRPRC 2004.08.001, where there are two, thick semi-circular structures (Fig. 20, upper right) which could be misinterpreted as pathological swellings on this digit. Instead they are the ventral surfaces of two U-shaped burrows, lined with faecal pellets, not unlike that found in *Ophiomorpha* isp. The invertebrate burrows were made after the original natural mould footprint had been filled with sediment. These

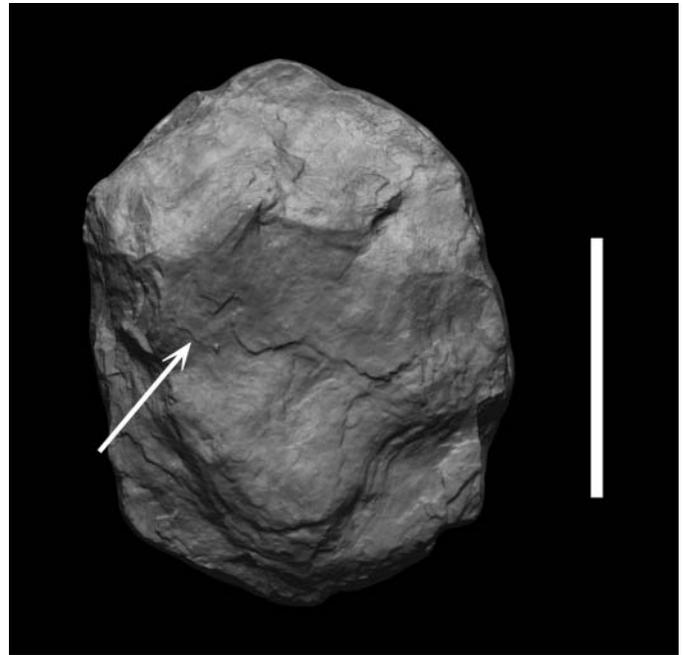


FIG. 21. Natural cast of a right sauropod pes from the Mist Mountain Formation (Tithonian-Berriasian) of southeastern British Columbia. An arrow indicates an invertebrate trace made along the substrate interface (scale = 50 cm).

invertebrate traces end at the interface between the sediments of the original, track-bearing substrate, and that of the infilling substrate. It is likely that burrowing invertebrates responsible for these U-traces were unable to penetrate far into the track-bearing substrate due to the prior compaction of the track surface caused by a combination of the mass and velocity of the tyrannosaur that made the footprint.

A similar circumstance was observed in a natural cast sauropod pes print (original - FGM 2001.13.1 and replica PRPRC 2000.01.001MC) from the Mist Mountain Formation of southeastern British Columbia (McCrea et al., 2014a). A lengthy invertebrate trace convex hyporelief (150 mm long  $\times$  4 mm wide) is visible on the plantar area of the sauropod track, near the base of digits I and II (Fig. 21). The invertebrate tracemaker had burrowed in the uncompacted sediments infilling the sauropod pes track, but could not penetrate the compacted sediments caused by the sauropod's passage. Instead the invertebrate tracemaker progressed along the interface between the sediments of the original track surface and those that covered it. Large trackmakers create greatly compacted sediments which are impassable to some invertebrate infauna. This type of invertebrate trace has the potential for being mistaken for pathological growth, or swelling on the plantar surface of the trackmaker's foot.

## DISCUSSION

Out of the 14 tyrannosaurid footprints reported to date, four of which are from Alberta (McCrea et al., 2005. Fanti et al.,

2013, McCrea et al., 2014b), eight from British Columbia (Farlow et al., 2009, McCrea et al., 2014b), one from the United States (Lockley and Hunt, 1994), and one from Mongolia (Currie et al., 2003), three footprints from two individuals exhibit remarkable pathologies. This amounts to 21% of individual tyrannosaur footprints with pathologies so far, or 14% of individual trackmakers.

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

Pedal injuries of such severe natures invites speculation as to their etiologies. A number of factors could lead to the ichnopathologies seen here. As in extant wild vertebrates, bone fractures are the most common disorder of the dinosaur skeleton (Tanke, 1989; Rothschild and Tanke, 1992; Rothschild and

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

Extant volant raptors may not be the ideal analog for nonavian theropods in terms of foot use because nonavian theropods are cursorial (and, in many of the examples provided, are large animals), and large theropods lack the well-developed flexor tubercles on their pedal phalanges (Fig. 13), that are possessed by extant birds of prey. However, there

TABLE 2

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

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

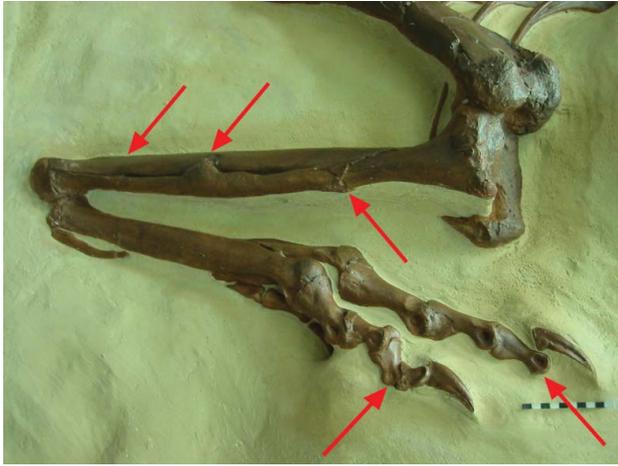


FIG. 22. Articulated *Gorgosaurus* specimen TMP 1991.036.0500 right lower limb showing fractures to the fibula (fracture callus with bone spur at mid-length) which were in the process of healing, contacting tibia as well as a dislocated pedal claw on digit three (phalanx III-4) and possible dislocations of phalanges on digit IV (red arrows). Scale in cm.

have been many studies on digit use with respect to prey handling in extant volant raptors, and these studies provide useful data on digit use in theropods. There is much opportunity to examine digit use in cursorial nonraptorial extant birds in future studies.

The low frequency of pedal injury in theropod traces is similar to that seen in extant birds of prey (excluding the injuries caused by anthropogenic means, such as leg snares, captivity, etc.) Bedrosian and St. Pierre (2007) saw a 14% (1/7) and 4% (4/86) pelvic injury rate (missing talons, missing digits, missing feet, or missing legs) in wild American Kestrels and Red-tailed Hawks, respectively. The specific pedal digit is not always identified in field reports of pedal digit injury, but Bedrosian and St. Pierre (2007) make specific mention of a broken talon (phalanx II-3) and a missing digit II on a Red-tailed

Hawk and an American Kestrel, respectively. A fractured left phalanx III-2 was reported by Gempton and Wheeldon (1983) on an adult female Australian Harrier. In these reports the affected birds were either of regular weight or slightly underweight (with body weight used as an indicator of overall health). Injury of pedal digits I and II have the potential to be detrimental to extant birds of prey: digits I and II oppose one another and apply the most power when handling and restraining prey (Einoder and Richardson, 2007; Fowler et al., 2009, 2011), and the talons of digits I and II are often the largest, with large flexor tubercles (Mosto and Tambussi, 2014). In nonraptorial birds, published information on the injuries to the legs and feet shows that injuries are also anthropogenic in origin, and these do not provide accurate data on natural pes digit injury for cursorial birds.

Congenital defects are another possibility. Extant chickens (*Gallus*) and other avians can develop curled toes (Pourlis, 2011). Dislocations are a final consideration. Dislocations of the pes among theropod dinosaurs are rarely noted. Tanke and Currie (2000) described a possible dislocation of a digit III ungual in a subadult specimen (TMP 1991.036.0500) of the Late Cretaceous tyrannosaurid *Gorgosaurus* (Fig. 22).

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

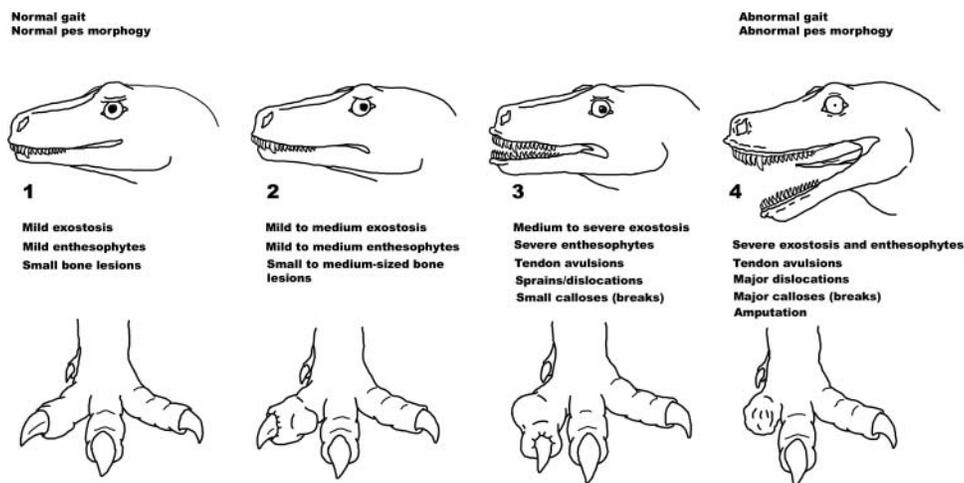


FIG. 23. A simplified scale for injuries from mild to severe, the inferred degree of pain scale is speculative.

Documented skeletal pathologies in pedal phalanges in *Allosaurus* and other theropods (Lambe, 1917; Ostrom, 1976; Rothschild et al., 1997; Hanna, 2002; Tanke and Rothschild, 2002; Farke and O'Connor, 2007; Bell, 2010; Bell et al., 2011, McCrea et al., 2014a, 2014b), show that, while the sample size of pathologic digits is small (and indeed, paleopathologies are relatively rare, Rothschild and Tanke, 2005) damaged phalanges appear to be evenly distributed among the three digits. The small sample size shows that there are more injuries to digits II and III than to digit IV (Table 2).

The pathological phalanges range in inferred severity of injury, from responses to stress or repetitive use injuries (e.g., Bell, 2010), to bony growths on joint surfaces (e.g., Hanna, 2002), to callouses from healed fractures (e.g., Ostrom, 1976), to dislocated (Figs. 8, 10, and 12), and amputated digits (Figs. 1, 2, 5, 6, and 14) (McCrea et al., 2014b; Abel, 1935). There is a large degree of speculation involved when inferring how much discomfort these paleopathologies would have presented to the animals. While some of the paleopathologies seen in pes elements and tracks could represent a large range of discomfort (e.g., for cases of exostosis), there are some pathologies that would cause more discomfort, and potentially have more likelihood of producing enough discomfort to alter the regular use of the injured element, than others (Fig. 23). Some disarticulated Late Cretaceous hadrosaur and ornithomimid pedal phalanges in Royal Tyrrell Museum collections are so severely pathological as to suggest premortem sloughing off of the affected distal portion.

The occurrences of true traumatic ichnopathology among the Dinosauria are still largely restricted to theropods or those groups with elongate digits. This could be related to the more delicate morphology of the foot, inherent potential accidents (i.e., falling) related to bipedalism (Farlow et al., 1995) and a more active lifestyle involving the use of the foot as a raptorial weapon. The protruding toes in theropods are long and narrow and exposed to potential injury, although from footprints at least it seems that digit II is disproportionately prone to injury. It is possible that the medial digits are more susceptible to injury which may be related to how long these digits are in relation to their width (Fig. 24). It seems reasonable to assume that long, relatively thin digits may be structurally weak and more vulnerable to injury. However, the comparatively long and thin bones of tyrannosaurids (Fig. 24) were also surrounded by substantial soft tissue (flesh, muscle, and sinew) as evidenced by their tracks (McCrea et al., 2014b). These tissues certainly would have provided a degree of protection and ameliorated the effects of the forces that must have been exerted on the feet during life of these animals.

The presumed active lifestyle of theropods can, and probably did occasionally, lead to manual and pedal traumatism related to running, intraspecific strife, prey capture, and killing (Marshall et al., 1998; Sullivan et al., 2000; Carpenter and Smith, 2001; Rothschild et al., 2001).

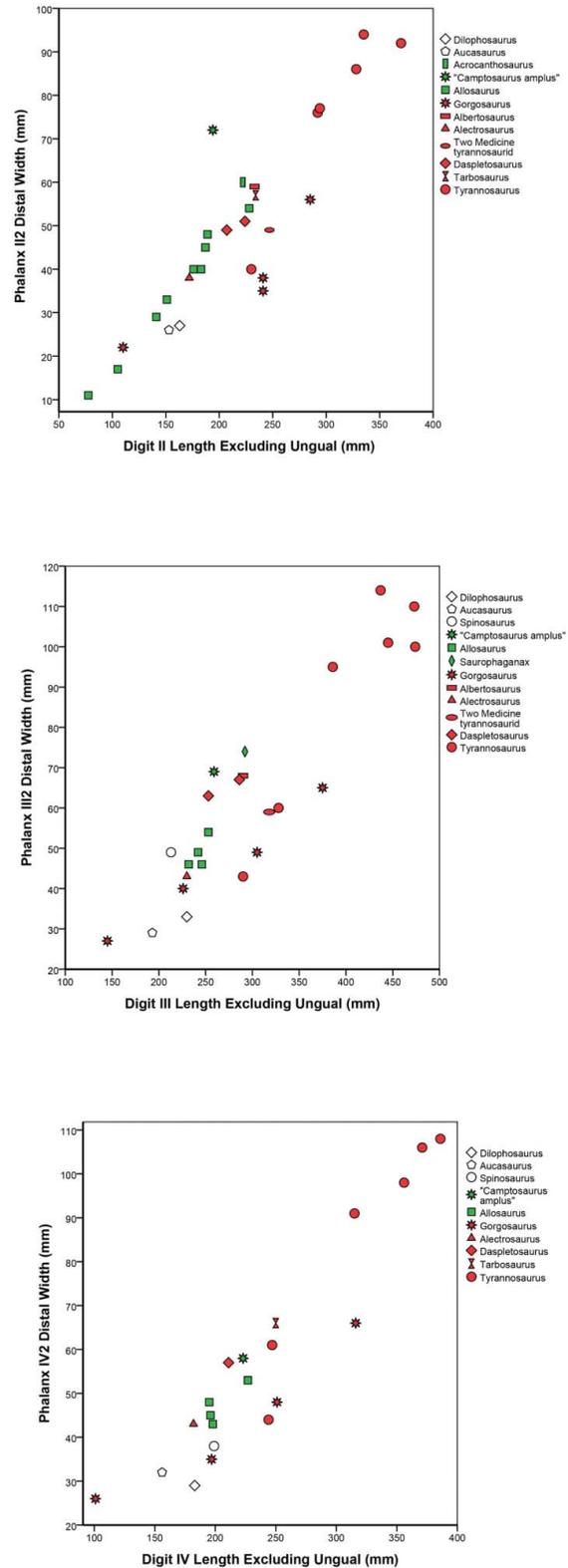


FIG. 24. Graphs plotting digit lengths to phalanx width for several dinosaur taxa. Top: digit II length to phalanx II2 distal width. Middle: Digit III length to phalanx III2 width. Bottom: Digit IV length to phalanx IV2 distal width.

The potential range of motion of pedal phalanges may also, when examined in the context of an active bipedal lifestyle, contribute to the rate of injury in theropod pedes. Examination of the range of extension and flexion of digits in theropods with non-specialized pedal digits (*Allosaurus*, *Dilophosaurus*, *Chirostenotes*, and *Mononykus*; data presented in Senter, 2009) reveals there is considerable overlap in the potential range of motions of digits II, III, and IV with respect to the most proximal phalanges II-1, III-1, and IV-1. Examination of the ranges of the individual phalanges within digits shows that different taxa have differing maximum ranges of digit hyperextension and flexion. In the large theropods *Allosaurus* and *Dilophosaurus*, digit II shows the least amount of hyperextension in phalanges (II-3), with correspondingly small amounts of hyperextension in phalanges III-4, and IV-1 (of *Allosaurus*) and IV-5 (of *Dilophosaurus*).

The least amount of flexion was observed in phalanges II-1, III-1 (of *Dilophosaurus*) and III-4 (of *Allosaurus*), IV-2 (of *Dilophosaurus*) and IV-1 (of *Allosaurus*). There are no striking differences in phalangeal joint flexibility of the large theropods studied by Senter (2009) that could account for an individual digit that would be more prone to damage than others. The unguals of digits II and III, and phalanx IV-1 seem to have the lowest degree of extension while phalanges II-1, III-1, IV-1, and IV-2 seem to have the lowest degree of flexion.

An active lifestyle in large pterosaurs has been implicated in a number of traumatic osteopathies in that group (Bennett, 2003). Feet of most contemporaneous herbivores such as sauropods, stegosaurs, ankylosaurs, and ceratopsians (and hadrosaurs to a lesser extent) were more elephantine-like in morphology, with shorter stubby toes encased in a thickly padded foot (Lockley, 2007). Feet with this compact and cushioned morphology, despite their massive weight-bearing function would have been less vulnerable to external damage from contact with injurious objects in the environment, which could show in footprints. Well-documented examples of stress fractures among Late Cretaceous ceratopsians (Rothschild, 1988; Rega et al., 2010; Tanke and Rothschild, 2010) pertain to bones enveloped in tissue. Thus, such damage or pathology would not obviously be expressed in track or trackway abnormalities or irregularities, unless indirectly through modifications to gait.

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