

Behavioral and faunal implications of Early Cretaceous deinonychosaur trackways from China

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Abstract Deinonychosaurian theropods, the dinosaurian sister group of birds, are characterized by a large raptorial

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claw borne on a highly modified second digit that was thought to be held in a retracted position during locomotion. In this study, we present new trackway evidence for two coeval deinonychosaurian taxa from the Early Cretaceous of Shandong, China that indicate a hitherto unrecognized body size diversity for this period and continent. These fossil tracks confirm diversity and locomotory patterns implied by phylogeny and biogeography, but not yet manifested in the body fossil record. Multiple parallel and closely spaced trackways generated by the larger track maker provide the best evidence yet discovered for gregarious behavior in deinonychosaurian theropods.

Keywords Deinonychosaur · Cretaceous · Footprint · Gregariousness · China · Locomotion

Introduction

Deinonychosaurian theropod dinosaurs, such as *Troodon*, *Velociraptor*, and *Microraptor*, have long sustained both popular and scientific interest for numerous reasons, including their close phylogenetic relationship to birds (Makovicky and Norell 2004) and the unusual structure (Currie and Dong 2001; Norell and Makovicky 1997; Ostrom 1969; Xu and Norell 2004) and use (Barsbold 1998; Carpenter 1998) of their sickle-clawed feet. But despite these studies, little direct evidence yet bears on issues of the in vivo morphology of the feet of these dinosaurs (Lockley et al. 2004; Zhen et al. 1994) and how they were maintained during locomotory behavior. Similarly, deinonychosaurs have often been portrayed as gregarious (e.g., Ostrom 1990), although evidence presented in support of this is ambiguous. In this study, we report the discovery of multiple trackways of both a large and a small species of

Early Cretaceous deinonychosaur from Junan County, Shandong Province, China. These trackways are extensive, well preserved, and reveal excellent details of foot morphology. In addition to confirming that the sickle claw of digit II was held retracted during locomotion, the presence of multiple parallel and closely spaced trackways on a single bedding plane allow an analysis of gait and provide strong evidence for gregarious behavior. When combined with the small coeval dromaeosaurids known from body fossils, these trackways increase the known diversity of the Early Cretaceous, Asian deinonychosaurian fauna to include taxa of substantially larger body size. The presence of large deinonychosaurians in this fauna has been predicted by phylogeny and biogeography but is not yet documented by the body fossil record.

Materials and methods

The trackways occur in Lower Cretaceous rocks of the Tianjialou Formation (Fig. 1) and form part of a rich vertebrate ichnofauna of more than 300 tracks on 12 different stratigraphic levels pertaining to at least eight named and unnamed ichnotaxa, including zygodactyl avian *Shandongornipes muxiai* (Li et al. 2005a, b; Lockley et al. 2007b) and tiny *Minisauripus* (Lockley et al. 2007a) theropod tracks. Among these tracks are 18 large (foot

length up to 28.5 cm) deinonychosaurian footprints (Table 1) assigned to *Dromaeopodus shandongensis* ichnogen. et ichnosp. nov., plus two smaller deinonychosaurian footprints (foot length ~10 cm) in a single trackway attributed to the poorly known *Velociraptorichnus sichuanensis* (Zhen et al. 1994) (Fig. 2). Because of its excellent fidelity and diversity of unique or very rare tracks, such as *Dromaeopodus*, *Velociraptorichnus*, and *Shandongornipes*, this locality, still under investigation, is one of the most important and most diverse ichnological sites in Asia.

All originals of tracks and trackways discussed herein remain in situ at Houzuoshan Dinosaur Park. Measurements and tracings were taken directly from the track surfaces. Molds were also made from these surfaces that were later used to generate the holotype and paratype casts discussed below.

Description of specimens

Ichnotaxonomy

Dromaeopodidae ichnofam. nov.

Type ichnogenus and ichnospecies

Dromaeopodus shandongensis ichnogen. et ichnosp. nov.

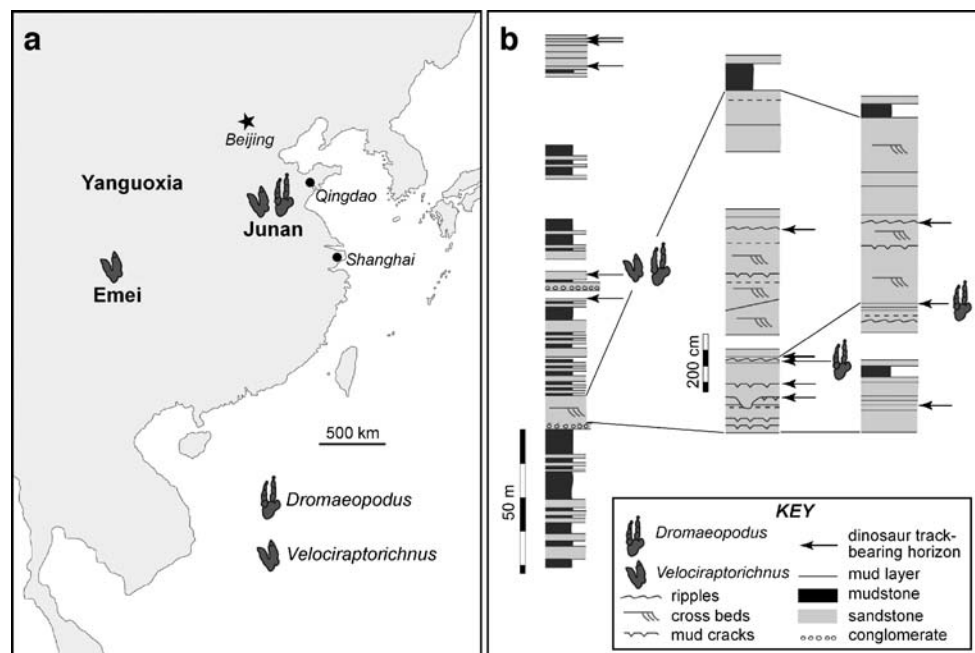


Fig. 1 Occurrences of deinonychosaur tracks. **a** Didactyl deinonychosaur tracks have been reported from three Cretaceous dinosaur tracks sites in East Asia: Junan (this paper), Emei (Zhen et al. 1994), and Yanguoxia (Li et al. 2006). By comparison, the large number of Asian, Cretaceous dinosaur tracksites underscores the scarcity of deinonychosaurian tracks. **b** Stratigraphic occurrence of deinonychosau-

rian tracks within the Tianjialou Fm. at Junan; empty spaces represent covered intervals. The section is composed of sandstone beds deposited in river channels and intervening mudstones deposited in floodplain environments. Dinosaur tracks, including those referred to the Dromaeopodidae, occur in thin mud layers draped on thicker sandstone beds, indicating they were impressed shortly after flooding events

Table 1 Distribution of left and right footprints, pes length and width, step and stride length, and pace angulation for eight trackways of *D. shandongensis*

Trackway number	Left/right prints	Pes length (cm)	Pes width (cm)	Step length (cm)	Stride length (cm)	Pace angulation
1	–/1	28	12.5	–	–	–
2	–/1	(26)	(12.5)	–	–	–
3	1/–	(24)	12.5	–	–	–
4	1/–	–	–	–	–	–
5	2/2	26	9.5	103	–	–
6	3/2	26.5	12.5	103	–	–
7	2/2	28.5	12.5	93	186	170°
8	–/1	–	–	–	–	–

Trackway 7 is the holotype (Fig. 2e). Values in parentheses are estimates from incomplete tracks.

Diagnosis

Narrow, didactyl tracks of a biped with digit III only slightly longer than IV, and digit II represented by a short, round impression posteromedial to free part of digit III.

Known distribution

Early Cretaceous of eastern Asia and western North America.

Referred ichnotaxa

Velociraptorichnus sichuanensis (Zhen et al. 1994) and *Dromaeopodus shandongensis* ichnogen. et ichnosp. nov.

Dromaeopodus shandongensis ichnogen. et ichnosp. nov.

Etymology

From the Greek *dromaeus*, “runner,” and *pous*, “foot,” referring to probable taxonomic affinities of track maker. The specific epithet refers to the holotype locality in Shandong Province.

Holotype and paratype

The holotype is a University of Colorado at Denver (CU) replica of a trackway consisting of four footprints (CU 214.111) (Fig. 2e; Table 1: trackway 7). The paratype is CU 214.112, replica of a left pes (Table 1: trackway 8). The original tracks and trackways remain in the field.

Horizon and locality

Barremian–Aptian Tianjialou Formation, uppermost member of the Dasheng Group, Houzuoshan Dinosaur Park,

Junan County, Shandong Province, China. The Tianjialou Formation has been assigned an Early Cretaceous, and most likely Barremian–Aptian, age based on its fossils of *Psittacosaurus* spp. as well as conchostracans (*Yanjiestheria* spp.) known to be of this age elsewhere in China (Li et al. 2005a).

Known distribution

Early Cretaceous of eastern Asia.

Diagnosis

Tracks made by a biped that are functionally didactyl, elongate, and exhibit the following characteristics: digit III and IV traces subparallel, subequal in length, displaying laterally convex curvature, and possessing both three toe pads each as well as sharp claw impressions; suboval heel pad forming about one-third of the posterior length; proximal portion of digit II impressed as a large, hemispherical depression medial to the anterior margin of the heel pad and posteromedial to the margin of digit III; step lengths from 92–103 cm in the three preserved trackways; pace angulation high (170°; Fig. 3; Table 1); digit III axis shows slight inward rotation (~10°) relative to sagittal plane.

The curved digits of *Dromaeopodus* distinguish the ichnotaxon from the smaller *Velociraptorichnus*, which has straight digits. In both, though less prominently in *Velociraptorichnus*, the proximal portion of digit II is represented by a large hemispherical depression medial to the anterior margin of the heel pad and posteromedial to the margin of digit III (Fig. 2; Supplementary Movie S1). None of the footprints are deep enough to have captured digit I or metatarsus impressions (Gatesy et al. 1999).

Discussion

Foot morphology and track maker

Three features of *Dromaeopodus* tracks are consistent with the anatomy of articulated deinonychosaur foot fossils to the exclusion of those of any other bipedal Mesozoic taxon: the abbreviated impression of digit II, indicating retraction of its claw; the subequal lengths of digits III and IV; and their nearly parallel orientation and slight inward curvature (Currie and Dong 2001; Norell and Makovicky 1997; Ostrom 1969; Xu and Norell 2004). Some basal birds (e.g., *Rahonavis*) may also have adopted a functionally didactyl posture (but see Makovicky et al. (2005)), but are all far too small to have made *Dromaeopodus* or *Velociraptorichnus* tracks and no East Asian, Early Cretaceous candidates are

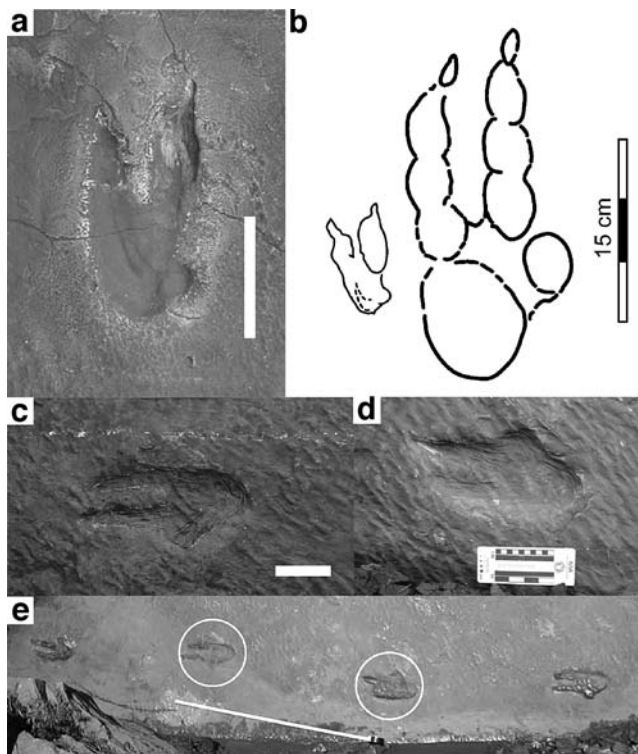


Fig. 2 **a** *Velociraptorichnus* and **c–e** *Dromaeopodus* tracks from Junan. The comparative schematic (**b**) illustrates the relative size and anatomical differences between the smaller *Velociraptorichnus* (left) and larger *Dromaeopodus* (right) prints. Close-ups of the middle right (**c**) and left (**d**) prints, respectively, are from the holotype trackway (**e**). Scale bars: **a** 5 cm, **c** 10 cm and **e** 1 m

known. The only other described didactyl archosaur tracks are Late Triassic in age (Gaston et al. 2003) and otherwise unique in toe pad morphology and thus both temporally and anatomically incongruent with a deinonychosaurian origin.

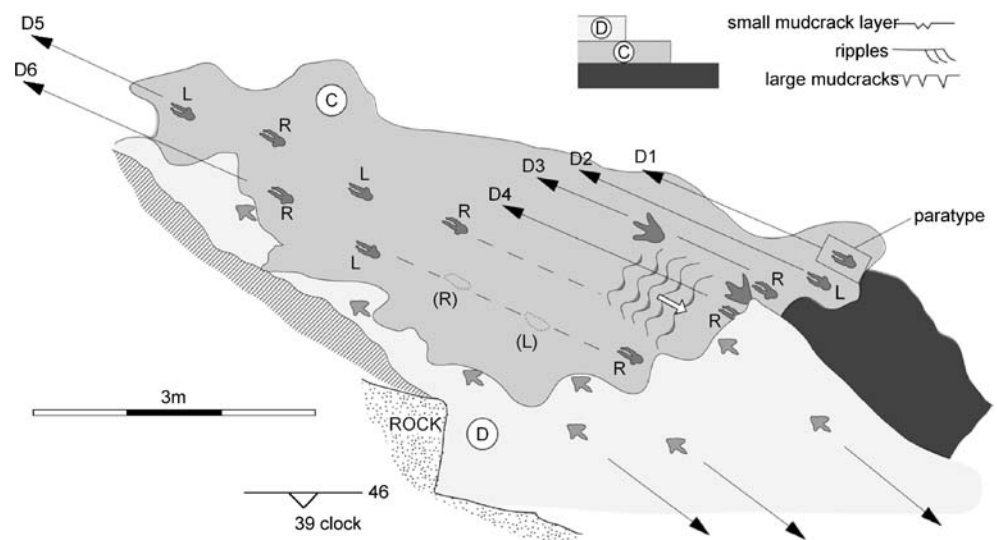
A diverse assemblage of deinonychosaurs is known from the Early Cretaceous of Asia (for reviews, see Makovicky and Norell (2004); Norell and Xu (2005); Turner et al.

(2007)), further supporting our identification of the track maker as a deinonychosaur. With the exception of the original report of *Velociraptorichnus* from the Early Cretaceous of Sichuan (Zhen et al. 1994), unnamed tracks from South Korea (MGL, personal observation), and unnamed ichnites of dubious quality from the Early Cretaceous of Utah (Lockley et al. 2004) and Gansu Province, China (Li et al. 2006), confirmed deinonychosaurian tracks have been notably absent from the ichnological record. The identification of tracks that are quite unique in the track record, and both anatomically and temporally consistent with having been made by deinonychosaurians, warrants placing *Dromaeopodus shandongensis* and *Velociraptorichnus* within their own ichnofamily.

The Deinonychosauria comprises two clades, the Troodontidae and Dromaeosauridae. Basal members of both lineages are remarkably small animals (Makovicky et al. 2005; Xu and Norell 2004; Xu et al. 2002), but large dromaeosaurids, with body lengths in excess of 3 m, are known from the Early Cretaceous of North America (Kirkland et al. 1993) and from the early Late Cretaceous of Mongolia (Perle et al. 1999), whereas large bodied troodontids only occur in Campanian–Maastrichtian sediments on either continent, and even then are not known to attain dimensions necessary to qualify as potential *Dromaeopodus* track makers (Makovicky and Norell 2004). Therefore, the *Dromaeopodus* track maker was most parsimoniously a large dromaeosaurid as inferred from both phylogenetic understanding of body size evolution (Turner et al. 2007b) and consideration of geological age and paleobiogeography.

Anatomical investigation of the hypertrophied second digits of deinonychosaurs, with their expanded interphalangeal joints, led to the interpretation of these animals as being functionally didactyl (Ostrom 1969). In many well-preserved specimens of both dromaeosaurs and troodontids,

Fig. 3 Map of sedimentary bed surface with six parallel and closely spaced trackways of *Dromaeopodus* indicating simultaneous passage of a structured group of at least six similarly sized individuals. Individual trackways are enumerated (numbers beginning with “D”) and directions of travel are indicated by long arrows with black heads. Current direction, as determined by ripples on the surface, is denoted by small white arrow



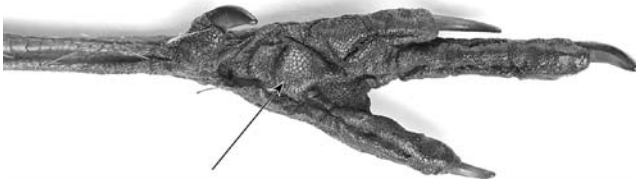


Fig. 4 Left foot of a seriema (*Cariama cristata*) in plantar view, exhibiting a large heel pad (arrow) below the metatarsal–phalangeal joints. This specimen was defleshed and dried, so the heel pad would have been larger in life

the second pedal digit is indeed preserved in a retracted position (Currie and Dong 2001; Norell and Makovicky 1997; Russell and Dong 1993), supporting the prediction that footprints of these animals would only register a partial impression of digit II (Ostrom 1969). *Dromaeopodus* and *Velociraptorichnus* trackways, representing multiple individuals of two discreet taxa from different time horizons, provide incontrovertible evidence that the large digit II claw was consistently held in a retracted position, with only the proximal part of digit II involved in weight-bearing during locomotion.

Footprints often reveal anatomical features that cannot be inferred from skeletal anatomy. The unexpectedly large, hemispherical impression demonstrates that a toe pad cushioned the basal part of digit II (Fig. 2) in the large *Dromaeopodus* and, to a lesser extent, smaller *Velociraptorichnus* track makers at the Junan tracksites. A larger heel pad cushioned the base of the foot below the metatarsal–digital articulations in *Dromaeopodus*. Such heel pads have been observed in trackways of sauropods and other graviportal dinosaurs, but are unusual in nonavian theropod tracks. Moderately large heel pads and toe pads are observed in ratites such as the emu (*Dromaius*) and cassowary (*Casuaris*). Seriemas (*Cariama* spp.), which are mid-size South American “gruiform” birds with enlarged, trenchant claws on digit II analogous to those of deinonychosaurs, also possess single, remarkably large heel pads below their metatarsophalangeal joints (Fig. 4).

Behavior

The *Dromaeopodus* sample resolves into eight trackways from three stratigraphic levels (Figs. 1, 2, and 3; Table 1). The clear imprints of full foot lengths and the lack of toe drag marks extending anterior to the footprints indicate that all of the individuals that generated the trackways were walking rather than running. Trackways 1–4 and 8 are represented by isolated footprints of moderate depth (1–2 cm) displaying clear pad and claw impressions. Trackways 5–7 each represent 3–4 consecutive steps, allowing for measurements of stride and pace angulation (Table 1).

Trackways 1–6 occur together on a single bedding plane (Fig. 3); all are closely spaced and indicate an identical direction of travel. The bedding plane, a thin layer of sandstone (Fig. 3), is covered with an irregular mud drape and ripple marks. The absence of desiccation cracks indicates the footprints were emplaced within a very short time span. The overlying sandstone layer also bears footprints made by other dinosaurs running parallel, but opposite, to the deinonychosaurian trackway directions, suggesting that the tracks were emplaced parallel to a “physically controlled” landscape feature such as shoreline or drainage that was subject to episodic flooding (Ostrom 1972). Current ripples preserved along with the *Dromaeopodus* tracks (Fig. 3) suggest that a water body or waterway of some sort was indeed present; site sedimentology suggests a river channel complex.

Dromaeosaurids have been portrayed as both solitary and gregarious, and tracks provide a means of testing both hypotheses by preserving evidence of living behavior. Tenuous evidence previously advanced in support of hypothesized gregarious behavior in dromaeosaurids has consisted solely of taphonomic interpretation of four partial, largely disarticulated skeletons of *Deinonychus* alongside a skeleton of the ornithomimid *Tenontosaurus* and the occurrence of more shed *Deinonychus* teeth at one *Tenontosaurus* carcass than could be expected from a single individual (Maxwell and Ostrom 1995; Ostrom 1969, 1990). Such discoveries could also result from distinct, time-averaged death or scavenging events, however, and are subject to alternative interpretations, such as chance occurrence of an opportunistic feeding frenzy (Brinkman et al. 1998), perhaps with agonistic behavior between individuals competing for limited resources (Roach and Brinkman 2007).

The discovery of six parallel, closely spaced *D. shandongensis* trackways provides compelling, independent evidence for at least occasional gregarious (“pack” or family group) behavior in the track-making animals, comparable to what has been demonstrated in other dinosaurs (Lockley 1989; Ostrom 1972). The tracks do not overlap, footprint size is almost uniform between trackways, and “inter-trackway” spacing (Lockley 1989) is regular and less than a single stride length, all of which strongly suggest that they were registered by a group of six individuals moving together as a coherent group, regardless of possible physiographic “control.” Because the sedimentology indicates a relatively rapid emplacement and subsequent burial of the trackways, a scenario in which six similarly sized individuals independently generated parallel, regularly spaced, nonoverlapping trackways is highly unlikely.

Whether such an aggregation of similarly sized individuals represents a common or rare (or perhaps seasonal) event cannot be determined from a single find, but it indicates that dromaeosaurids in fact engaged in some type

of group behavior. Whether this behavior was specifically hunting cannot be ascertained from the present track sample, but Roach and Brinkman (2007) claimed that cooperative hunting arises secondarily from group maintenance and that extant animals that maintain social groupings typically do so for primary reasons other than hunting. Thus, the fact that the *Dromaeopodus* track makers behaved gregariously implies that cooperative hunting cannot be ruled out. Primarily solitary hunting tactics for dromaeosaurs were proposed by Roach and Brinkman (2007) based on phylogenetic bracketing of diapsid behaviors combined with taphonomic interpretation and evidence of intraspecific aggression in *Deinonychus*. Roach and Brinkman (2007) proposed that trackway data previously presented in support of gregarious nonavian theropods are perhaps better interpreted as coincidental instances of normally solitary individuals converging on a common point (e.g., food source). While we agree that some footprint associations may have been misinterpreted as gregarious, many convincing examples remain (see Lockley and Matsukawa (1999) for review). Group behavior more parsimoniously explains their numbers and diversity through the Mesozoic than does postulating that all such occurrences coincidentally represent parallel trackway segments of otherwise divergent trackways. Furthermore, the regularity and narrow intertrackway spacing of the *Dromaeopodus* group trackways are comparable to data that Roach and Brinkman (2007, p. 127) agree are supportive of hypothesized gregarious behavior in herbivorous dinosaurs. Thus, the probably dromaeosaurid *Dromaeopodus* track makers were apparently capable of nonagonistic group behaviors comparable to those inferred for some herbivorous dinosaurs (Lockley 1989), and not limited to random, agonistic encounters between individuals, as in Komodo dragons (contra Roach and Brinkman 2007).

Paleobiogeography

Footprint size, varying between 26 and 28.5 cm in the better preserved *Dromaeopodus* tracks, is consistent with a track maker comparable to *Achillobator* (Perle et al. 1999) in size (Table 1; see S2, S3, and S4 for formula and measurements), providing the first evidence that such animals were locally abundant in the Early Cretaceous of East Asia. Whereas the sizeable *Utahraptor* (Kirkland et al. 1993) is known from roughly contemporaneous deposits of North America (Kirkland 2005), large dromaeosaurid fossils are unknown in Asia until the Santonian–Campanian Bayn Shire Formation of Mongolia that yielded *Achillobator* (Perle et al. 1999). Recent phylogenetic research confirms that dromaeosaurids of this size are monophyletic (Norell et al. 2006; Senter 2007; Senter et al. 2004; Turner et al. 2007) and that the clade of Barremian–Maastrichtian,

Laurasian dromaeosaurids originated in Asia. The inferred Barremian–Aptian age of the track-bearing Tianjialou Formation indicates that the taxonomic diversity, and at least two orders of magnitude in body size disparity (Turner et al., unpublished data) of Laurasian dromaeosaurs, appeared almost simultaneously in the Asian and North American fossil records, very soon after the earliest-known occurrences of primitive members of this lineage in the Yixian Formation of Liaoning (Norell and Xu 2005).

Coupled with current phylogenetic hypotheses in which Asia appears to be the center of origin for Laurasian dromaeosaurids (Norell et al. 2006; Senter 2007), the footprint component of the diverse, Early Cretaceous, Asian dromaeosaurid fauna lends some support to the prediction that this continent served as a source of biogeographic dispersal of large (*Utahraptor*) and medium-sized (*Deinonychus*) dromaeosaurids to North America during or shortly before the Barremian. This could have occurred across a Beringian land bridge (Plafker and Berg 1994), as indicated by some other dinosaurs (Carpenter et al. 2002; Kirkland et al. 1997, 2005), albeit earlier than previously hypothesized (Cifelli et al. 1997); alternatively, exchange occurred across a Eurasian–eastern North American route (Chinnery et al. 1998; Kirkland 2005). Determination of which scenario is better supported awaits further discoveries; the tracks described in this study suggest that the trace fossil record has the potential to contribute further information in this regard.

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