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A new deinonychosaurian track from the Lower Cretaceous Hekou Group, Gansu Province, China

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Herein we describe deinonychosaurian (Dinosauria: Theropoda) tracks in the Lower Cretaceous Hekou Group at sites I and II of Liujiaxia Dinosaur National Geopark, Gansu Province, China. The site preserves 71 didactyl tracks, the largest concentration of deinonychosaurian tracks in Asia. The tracks pertain to a new dromaeopodid ichnospecies: *Dromaeosauripus yongjingensis* ichnosp. nov., which is diagnosed by: a digital pad formula of x-1-3-4-x and a mean divarication angle between digits III and IV of 19°, and having the proximal portion of digit II contacting the anterior margin of a large, rounded metatarsophalangeal pad. Six *Dromaeosauripus* trackways from site II comprise at least two, and possibly three, turning trackways in which the track maker(s) turned without slowing down. None of the *Dromaeosauripus* trackways are parallel or closely spaced, suggesting that they were made by solitary track makers. Estimates of dromaeopodid track-maker sizes are between 61–300 cm, well within the size range established by body fossils of both dromaeosaurids and troodontids.

Key words: Dinosauria, Theropoda, Deinonychosauria, *Dromaeosauripus yongjingensis*, Cretaceous, Hekou Group, China.

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Introduction

The non-avian theropod dinosaur clade Deinonychosauria includes the clades Dromaeosauridae and Troodontidae. Most deinonychosaurs were functionally didactyl, possessing highly modified second pedal digits (Makovicky and Norell 2004; Norell and Makovicky 2004; Longrich and Currie 2009) that were held off the ground during cursorial locomotion (Zhen et al. 1994; Li et al. 2007; Xing et al.

2009). Deinonychosaurs attract a great deal of attention because of their close phylogenetic relationship with birds (Currie 1997; Xu et al. 2009, 2010). The coincidental and fortuitous discoveries of numerous deinonychosaurian tracks (Ichnofamily Dromaeopodidae), beginning in 1994, promoted study of deinonychosaurian locomotion and behaviour and provided new evidence for the existence and distribution of deinonychosaurs around the Jurassic–Cretaceous boundary (Xing et al. 2009).



Fig. 1. Photograph of Liujiaxia Dinosaur National Geopark sites I and II.

Dromaeopodid tracks were first discovered, and are particularly common, in China. The first dromaeopodid tracks, *Velociraptorichnus sichuanensis*, were from the ?Early Cretaceous of E'mei, Sichuan Province (Zhen et al. 1994). After a hiatus of more than a decade, a mass of new dromaeopodid track discoveries in China closely followed one another, including unnamed, Early Cretaceous dromaeosaurid tracks from Yanguoxia, Yongjing County, Gansu Province (Li et al. 2006), new specimens of *Velociraptorichnus*, the new ichnotaxon *Dromaeopodus shandongensis* from the Early Cretaceous of Junan, Shandong Province (Li et al. 2007), and *Menglongipus sinensis* from the Jurassic–Cretaceous boundary of Chicheng, Hebei Province (Xing et al. 2009). Reports outside China include unnamed ichnites from the earliest Cretaceous of Germany (Richter et al. 2007), unnamed ichnites of dubious quality from the Early Cretaceous of Utah (Lockley et al. 2004), *Dromaeosauripus hamanensis* and the recently-erected *Dromaeosauripus jinjuensis* from South Korea (Kim et al. 2008, 2012), *Paravipus didactyloides* from the Middle Jurassic of Niger (Mudroch et al. 2010), and unnamed tracks from possibly the Early Jurassic of Morocco (Ishigaki and Lockley 2010). Dromaeosaurid tracks have also been confirmed from the Late Cretaceous of Utah (Cowen et al. 2010).

Here we present a detailed description of dromaeopodid tracks from Yongjing County, China, which represent the largest-known accumulation and some of the best-preserved didactyl tracks anywhere in the world. This site was first reported by Li et al. (2006), who also noted the didactyl tracks and posited that they may represent a new ichnotaxon. We provide evidence to support this claim and examine the ramifications for *Dromaeosauripus* trackmaker foot morphology.

Institutional abbreviations.—GSLTZP, Fossil Research and Development Center of the Third Geology and Mineral Resources Exploration Academy of Gansu Province, China; HDT, Huaxia Dinosaur Tracks Research and Development Center, Gansu, China; LDNG, Liujiaxia Dinosaur National Geopark, Gansu, China.

Historical and geological background

In 2000, workers from the Research Center of Paleontology of the Bureau of Geology and Resource Exploration of Gansu Province discovered ten dinosaur track sites in the Hekou Group, Yanguoxia, Gansu Province (Du et al. 2001; Li et al. 2002). Zhang et al. (2006) reported a preliminary exploration of this and other, associated sites that had not yet been fully exposed in 2002, but their report did not include dromaeopodid tracks. Two subsequent Sino-Japanese and Sino-Japanese-Korean joint expeditions worked at the Yanguoxia dinosaur track sites in 2002 and 2004, which was followed by a preliminary report on two of the sites (Li et al. 2006) including the first report of dromaeopodid tracks at the locality. Beginning in 2004, the senior author was invited by the Fossil Research and Development Center, Third Geology and Mineral Resources Exploration Academy, Gansu Provincial Bureau of Geo-exploration and Mineral Development and the Geological Museum of Gansu to study dinosaur tracks in exposures of the Yanguoxia Formation (Hekou Group) in Liujiaxia Dinosaur National Geopark, Yanguoxia, Gansu Province (Fig. 1). During this study, new didactyl trackways were discovered and are described herein.

Liujiaxia Dinosaur National Geopark lies 54 km west of the city of Lanzhou, on the north shore of Taiji Lake (Yanguoxia Reservoir), Yongjing County, Linxia Hui Autonomous Prefecture, Gansu Province. The track locality sits at the southeastern edge of the Lanzhou-Minhe Basin. Specifically, the locality lies in the southeastern part of the Zhoujiatai low-uplift portion of the basin and occurs in the Yanguoxia Formation (Cai et al. 1999). Dinosaur footprints mainly occur in the ninth layer of fine sandstone-siltstone. The geological setting of the tracksite has been previously mentioned by researchers (Zhou et al. 2005; Li et al. 2006; Zhang et al. 2006).

Systematic ichnology

Dromaeopodidae Li, Lockley, Makovicky, Matsukawa, Norell, Harris, and Liu, 2007

Genus *Dromaeosauripus* Kim, Lockley, Yang, Seo, Choi, and Lim, 2008

Type species: *Dromaeosauripus hamanensis*, Early Cretaceous Haman Formation of Namhae area, Korea.

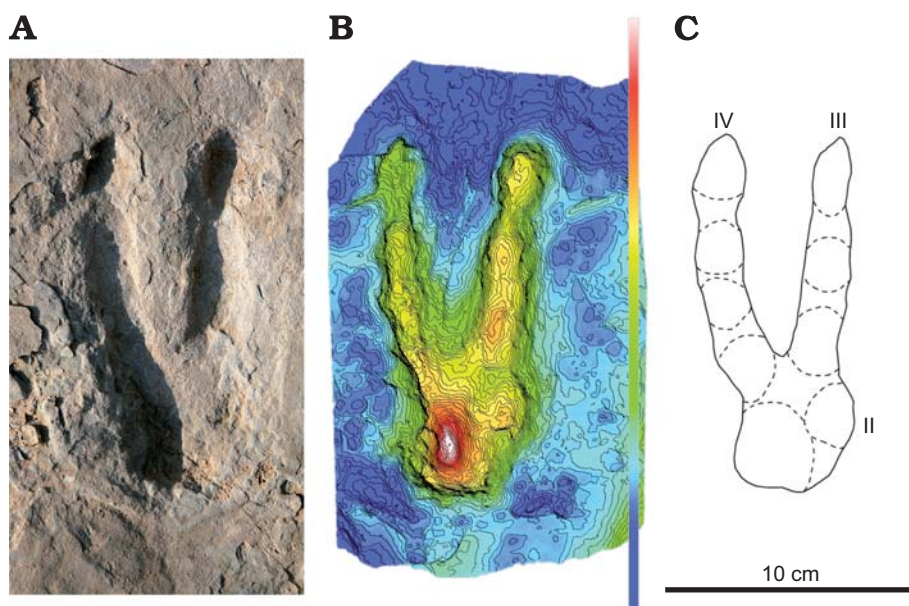
Dromaeosauripus yongjingensis ichnosp. nov.

Figs. 2–5.

Etymology: Ichnospecies name after the locality of the fossil site in Yongjing County, Gansu Province.

Type material: Holotype: A complete natural mould of a left pes print, cataloged as GSLTZP-S2-TE4L (Figs. 2, 3), from Yanguoxia track site II (S2). (“L” and “R” appended to the ends of specimen numbers indicate left and right pedes, respectively.) An artificial mold of the track is

Fig. 2. Deinonychosaurian track *Dromaeosauripus yongjingensis* ichnosp. nov. holotype GSLTZP-S2-TE4L from the Early Cretaceous Yanguoxia track site, Gansu, China. **A.** Photograph. **B.** Computerized photogrammetry, with 0.2 mm contour lines; color banding reflects topography (blue-green, highest; red-white, lowest). Based on the photogrammetric maps from Xing et al. (2009: fig. 6). **C.** Outline drawing.



stored at the Huaxia Dinosaur Tracks Research and Development Center, Geological Museum of Gansu, where it is cataloged as HDT.3. The original track remains in situ at LDNG. Paratypes: The paratype specimens, GSLTZP-S2-TA1-8, comprise eight natural molds in a second trackway. Of the paratypes, TA4L (Li et al. 2006: fig. 8B) is the best preserved. Artificial molds of tracks GSLTZP-S2-TA1R-6L are stored at the Huaxia Dinosaur Tracks Research and Development Center, where they are cataloged as HDT.4–9. All of the original tracks remain in the field at LDNG.

Type locality: Yanguoxia track site, Yongjing County, Gansu Province, China.

Type horizon: Yanguoxia Formation, Lower Cretaceous.

Other material.—Other specimens occur in trackways GSLTZP-S2-TB, TC, TD, TE, and TF. Including the holotype specimens, there are 67 tracks preserved at LDNG site II (Table 1). In addition, there are 4 didactyl footprints (GSLTZP-S1-T101) in a trackway at LDNG site I (S1), 120 m southeast of S2, but they are heavily weathered: only four specimens remain identifiable.

Diagnosis.—Medium-sized (~14.8 cm long and ~6.4 cm wide), didactyl theropod tracks. Digital pad impressions well-developed and with a formula of x-1-3-4-x; sharp claw impressions absent; proximal portion of digit II contacts the anterior margin of a large, rounded metatarsophalangeal pad;

mean divarication angle between digits III and IV is 19°; step lengths range from 35.7–37.5 cm and pace angulations from 143–180°.

Description.—All 71 didactyl theropod tracks from LDNG are extremely similar in morphology. All lack manus and tail traces. The length:width ratio of the holotype is 2.34. The short, round impression of digit II lies in direct contact with, and protrudes barely at all medially from, the anterior margin of the metatarsophalangeal pad. The nearly parallel (mean divarication angle 19°) impressions of digits III and IV are directed forward; digit III is slightly shorter than digit IV. Digit III has three pads, while digit IV has four pads. The metatarsophalangeal pad is deep, large, and suboval (3.3 × 3.1 cm).

The best-preserved 19 specimens, including the holotype and paratypes (Fig. 3), have an average length:width ratio of 2.27. The impression of digit II always lies posteromedial to the impression of digit III, at a variable distance from its long axis; the differences may be functions of individual variation and/or varying foot-substrate interactions. Across trackways GSLTZP-S2-TA and -TB, the mean step length is 36.6 cm (35.7 in TA and 37.5 in TB) and the pace angulations range from 143–180°.

Remarks.—The functional didactyly of the Yanguoxia tracks strongly supports their interpretation as deinonychosaurian. Li et al. (2006) suggested that the Yanguoxia didactyl track maker was probably a dromaeosaurid and that the tracks were readily distinguished from *Velociraptorichnus sichuanensis* and probably a new ichnotaxon. However, they did not provide sufficient detail or description of the tracks to establish an ichnotaxon. Shortly thereafter, other didactyl theropod ichnotaxa were erected from other localities, necessitating further comparison of the Yanguoxia specimens.

In the presence of a distinct heel, *Dromaeosauripus yongjingensis* is morphologically similar to *Dromaeopodus* from

Table 1. Number of tracks in and directions of *Dromaeosauripus yongjingensis* trackways from Liujiaxia Dinosaur National Geopark sites I (S1) and II (S2).

Specimen number	Tracks	Directions
GSLTZP-S1-T101	4	N
GSLTZP-S2-TA	8	E to SE
GSLTZP-S2-TB	10	E to NW
GSLTZP-S2-TC	21	N
GSLTZP-S2-TD	10	NW to N
GSLTZP-S2-TE	12	NW
GSLTZP-S2-TF	6	NW

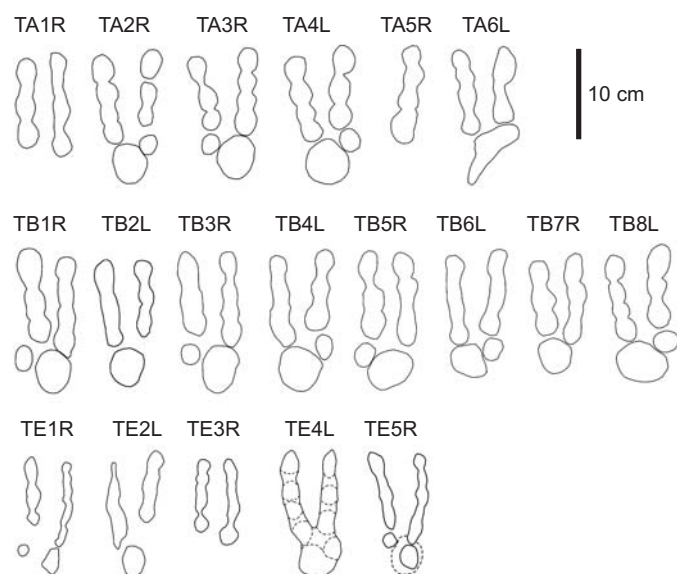


Fig. 3. Outline drawings of 19 of the best preserved *Dromaeosauripus yongjingensis* specimens (specimen numbers begin with GSLTZP-S2-) from Liujiaxia Dinosaur National Geopark site II, Early Cretaceous, including the holotype (TE4L).

Shandong Province (Li et al. 2007) although it is closer in size to *Dromaeosauripus* from Korea (Kim et al. 2008, 2012). The apparent absence of a heel in *Dromaeosauripus hamanensis* and the recently-named *Dromaeosauripus jinjuensis* (Kim et al. 2012) is likely due to behaviour (i.e., digitigrade), preservation, and/or substrate consistency as several *D. yongjingensis* tracks (TA1R, TE3R; Fig. 3) closely resemble those of Korean *Dromaeosauripus* (no heel trace, small divarication angle, lack of clear claw impressions; Kim et al. 2012). Thus the Yanguoxia tracks share similarities to both ichnotaxa, making unequivocal assignment to either of these ichnotaxa difficult. Although *Dromaeopodus* preserves a suboval metatarsophalangeal pad, similar to *D. yongjingensis*, *Dromaeopodus* tracks are almost twice as large as the Yanguoxia tracks (Li et al. 2007; Table 2) and preserve distinct, sharp claw impressions, which are lacking in *D. yongjingensis*. While we recognize the subjectivity inherently involved in ichnotaxonomy (owing to the subtle relationships between behaviour, substrate composition, preservation, and the resultant track), we err on the side of caution in assigning the Yanguoxia tracks to *Dromaeosauripus* (based on the aforementioned shared traits) rather than attempting to synonymize the preexisting species of *Dromaeosauripus* but erect a new ichnospecies to accommodate the observed differences between those ichnotaxa (see following discussion).

The divarication angles (mean: 19°) between digits III–IV in *D. yongjingensis* are greater than in *Dromaeopodus* (~5°; Li et al. 2007), *Paravipus* (5–15°; Mudroch et al. 2010), *Dromaeosauripus hamanensis* (5–10°; Kim et al. 2008), *Dromaeosauripus jinjuensis* (8–14°; Kim et al. 2012), and the unnamed Morocco didactyl tracks (16°; Ishigaki and Lockley 2010), but less than in *Velociraptorichnus* (21–28°; Zhen et al.

1994; Xing et al. 2009) and *Menglongipus* (41–44°). One of the most striking differences is the digital pad formula: the x-1-3-4-x digital pad formula of *D. yongjingensis* differentiates it from other *Dromaeosauripus* (formula x-1-4-4-x; Kim et al. 2008, 2012), *Dromaeopodus* (formula x-1-3-3-x; Li et al. 2007), and *Menglongipus* (formula x-1-2-1-x; Xing et al. 2009); *Velociraptorichnus* and *Paravipus* lack distinct digital pads.

Dromaeosauripus yongjingensis provides new information of the morphology of the *Dromaeosauripus* pes. In previously described didactyl tracks, digit III is characteristically subequal in length to digit IV. The average ratios of the lengths of digit III:digit IV are: Sichuan *Velociraptorichnus* tracks (0.90; Zhen et al. 1994; Xing et al. 2009), the unnamed Morocco didactyl tracks (1.08; Ishigaki and Lockley 2010), *Dromaeopodus* (1.0; Li et al. 2007), the Junan *Velociraptorichnus* tracks (1.2; Li et al. 2007), *Dromaeosauripus hamanensis* (1.23; Kim et al. 2008), and *Dromaeosauripus jinjuensis* (1.06; Kim et al. 2012). Only *Menglongipus* (2.36; Xing et al. 2009) differs significantly from this ratio. Although the lengths of digits III and IV are subequal (as measured from the posterior edge of the heel to the anterior tips of the digits) in *D. yongjingensis*, the proximal part of digit III did not make contact with the substrate in most tracks resulting in a relatively shorter digit III impressions (average ratio = 0.88; 0.91 in the holotype as measured from the distal tip to

Table 2. Measurements (in cm) of the best-preserved *Dromaeosauripus yongjingensis* tracks from Liujiaxia Dinosaur National Geopark site II. Abbreviations: LD III, length of digit III; LD IV, length of digit IV; ML, maximum length; MW, maximum width between the tips of digits III and IV; III–IV, angle between digits III and IV.

Specimen number GSLTZP-S2-	ML	MW*	LD III	LD IV	III–IV	ML/MW
TA1R	—	5.96	9.94	11.55	—	—
TA2L	15.02	7.56	8.51	10.01	24°	1.99
TA3R	14.48	7.65	8.41	9.69	25°	1.89
TA4L	15.47	7.74	9.27	9.57	22°	2.00
TA5R	—	—	—	10.84	—	—
TA6L	15.75	6.92	8.52	9.51	—	2.28
TB1R	16.07	6.51	10.45	11.00	15°	2.47
TB2L	14.18	6.32	8.29	9.54	17°	2.24
TB3R	16.00	6.41	9.32	10.45	16°	2.50
TB4L	15.80	7.01	9.03	10.04	20°	2.25
TB5R	15.39	6.09	9.62	10.29	13°	2.53
TB6L	14.30	6.60	9.49	9.76	20°	2.17
TB7R	13.37	5.96	8.20	9.95	19°	2.25
TB8L	15.17	7.15	9.12	9.72	21°	2.12
TE1R	13.26	5.13	7.56	9.38	17°	2.58
TE2L	14.16	5.59	8.01	9.59	20°	2.53
TE3R	—	4.35	8.03	9.48	—	—
TE4L	14.01	6.00	9.28	10.18	19°	2.34
TE5R	13.80	6.28	8.82	10.05	22°	2.20

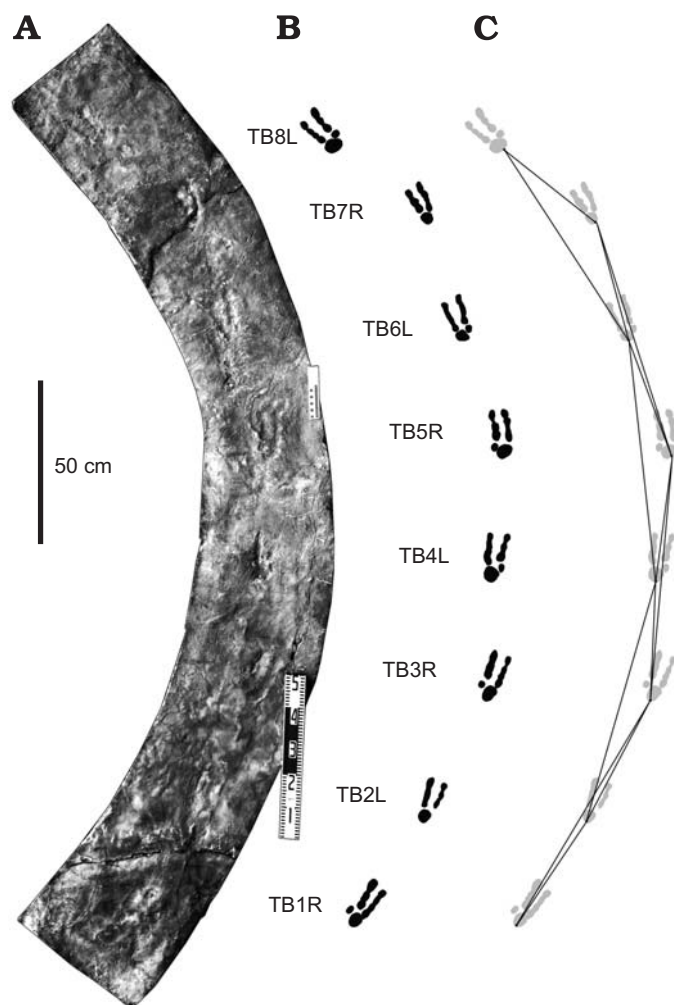


Fig. 4. Turning trackway of *Dromaeosauripus yongjingensis* GSLTZP-S2-TB at Liujiaxia Dinosaur National Geopark site II, Early Cretaceous. A. Photograph. B. Outline drawing. C. Pace angulations.

the proximal margin of the digits). In other words, there is a significant gap between the proximal margin of digit III and the metatarsophalangeal pad. However, there is variation in this configuration resulting in similarities to the Korean *Dromaeosauripus* tracks (Kim et al. 2008, 2012) suggesting gait and/or substrate consistency play a significant role in the morphology of *Dromaeosauripus* tracks. If the similarities (and differences) between *Dromaeosauripus* tracks were due solely to gait, then the digital pad formula would be expected to overlap among the three ichnospecies. But this is not the case as even the most complete tracks of *D. yongjingensis* (i.e., those that preserves the most information about the shape of the pes; Fig. 3) retain three digital pads on digit III (compared to four in *D. hamanensis* and *D. jinjuensis*).

Dromaeosauripus yongjingensis also differs from other *Dromaeosauripus* and *Paravipus* most prominently by possessing a metatarsophalangeal pad, which the latter two ichnotaxa lack (Kim et al. 2008; Mudroch et al. 2010; Kim et al. 2012). *D. yongjingensis* differs from *Velociraptorichnus* (Zhen et al. 1994; Li et al. 2007; Xing et al. 2009) in that

Velociraptorichnus has relatively wide digit impressions and sharp claw impressions, which are the opposite of the condition in *D. yongjingensis*. *Dromaeosauripus yongjingensis* also differs from the unnamed Morocco didactyl tracks (Ishigaki and Lockley 2010) in that Morocco tracks lack any impression of digit II. These differences support *Dromaeosauripus yongjingensis* as a new ichnospecies.

Stratigraphic and geographic range.—*Dromaeosauripus hamanensis* from the Early Cretaceous Haman Formation of Korea, *Dromaeosauripus jinjuensis* from the Early Cretaceous Jinju Formation of Korea, *Dromaeosauripus yongjingensis* from the Early Cretaceous Yanguoxia Formation of China.

Discussion

Turning trackway and walking velocities.—The six *Dromaeosauripus yongjingensis* trackways at LDNG S2 are comprised of at least two, and possibly three, turning trackways. Trackway GSLTZP-S2-TA turns 29° from E to SE. Trackway GSLTZP-S2-TB makes the most pronounced turn: 88° from E to NW. If GSLTZP-S2-TC-TF were made by the same track maker (see 6.2, below), then they collectively represent an individual making three turns: 41° from N to NW, then 30° from NW to N, and then 75° from N to NW.

Many theropod trackways appear to have extremely high pace angulations (nearing 180°) and stride lengths (Lockley 1991). As the velocity of a track maker decreases, pace angulations should decrease concurrently (Day et al. 2002). The first eight footprints of the GSLTZP-S2-TB trackway are the best preserved and the most continuous (Fig. 4). The pace angulations from GSLTZP-S2-TB1R-TB8L are 173°, 154°, 176°, 152°, 172°, and 143° (Fig. 4C). Using the equation of Alexander (1976), the walking velocity of the track maker decreases slightly along the trackway: 0.79 m/s, 0.73 m/s, 0.74 m/s, 0.75 m/s, 0.76 m/s, and 0.71 m/s. The slight decrease corresponds to the turn in the trackway, but is so slight that the track maker clearly made the turn without a marked drop in velocity.

Deinonychosaurs often have been inferred to be speedy predators. As yet, the only ichnological example for a speedy deinonychosaurian is a trackway of *Dromaeosauripus* from Korea that suggests a velocity of 4.86 m/s (Kim et al. 2008). All other known trackways indicate relatively slow, presumably walking, locomotory modes. The velocities calculated for *Dromaeosauripus yongjingensis* tracks are slower than those calculated for *Paravipus* (1.67 m/s, 3.61 m/s; Mudroch et al. 2010) and *Dromaeopodus* (1.63 m/s; Li et al. 2007; Kim et al. 2008).

Behaviour.—Body fossil evidence of gregariousness in deinonychosaurs has been ambiguous. The occurrence of more shed *Deinonychus* teeth at one *Tenontosaurus* carcass than could be expected from a single individual has been used to infer gregarious, possibly pack-hunting behaviour for

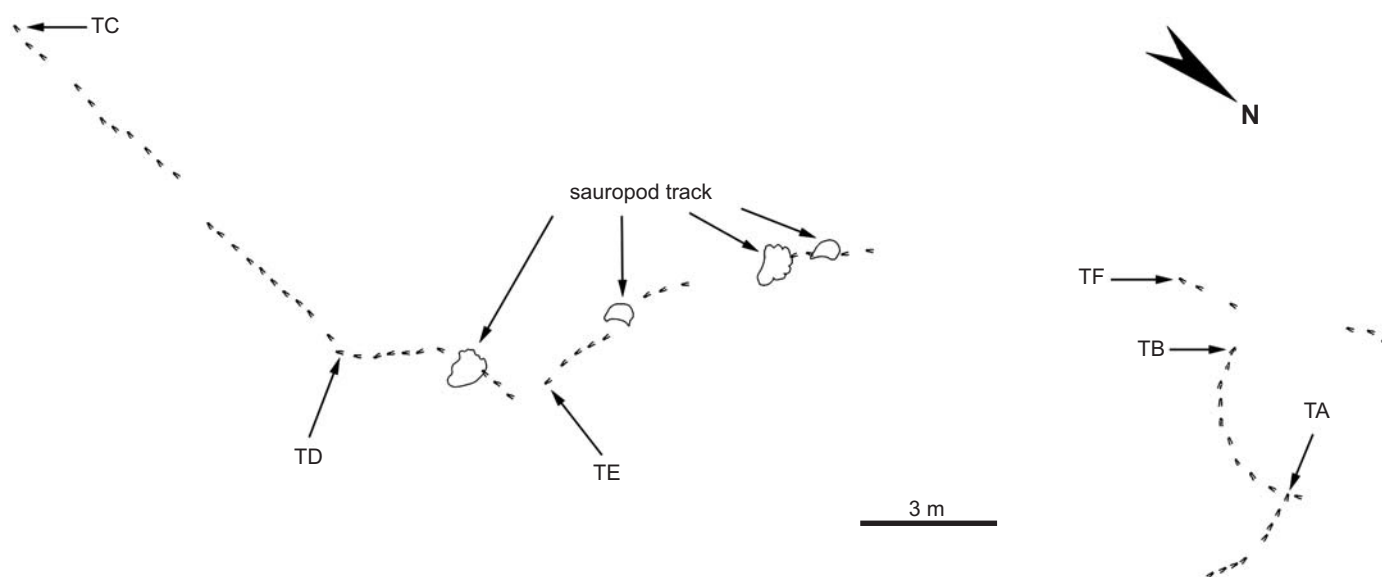


Fig. 5. Schematic map of the relative positions of six *Dromaeosauripus yongjingensis* trackways (GSLTZP-S2-TA to TF) at Liujiaxia Dinosaur National Geopark site II, Early Cretaceous.

Deinonychus (Maxwell and Ostrom 1995; Ostrom 1990). However, Roach and Brinkman (2007) interpreted this evidence as indicating that *Deinonychus* had a Komodo dragon- or crocodile-like feeding strategy in which individuals are usually solitary hunters but may be drawn in groups to carcasses, resulting in intraspecific agonism. In contrast, the famous “fighting dinosaurs” specimen (Carpenter 1998) suggests that a single, individual dromaeosaurid was capable of hunting on its own, without a pack.

Trackways, in contrast to body fossils, provide compelling evidence of deinonychosaurian group behaviour. Li et al. (2007) documented six parallel, closely spaced *Dromaeopodus* trackways that suggest at least occasional gregarious behaviour in the track-making animals. For *Dromaeosauripus yongjingensis*, the single trackway at LDNG site I is uninformative with respect to gregariousness. The six trackways at LDNG S2 (Fig. 5), however, provide a better sample to analyze gregariousness in deinonychosaurians (Table 1). Trackways GSLTZP-S2-TC, -TD, and -TE all may have

been left by the same track maker: a portion of the track series has been obliterated by sauropod tracks made after the *Dromaeosauripus yongjingensis* tracks (Fig. 5), making interpretation ambiguous. Tracks in discontinuous trackway GSLTZP-S2-TF have the same walking orientation and were therefore most likely left by the same track maker. None of the six *Dromaeosauripus yongjingensis* trackways are parallel or closely spaced, suggesting that the track makers were, at least at the time the tracks were registered, solitary.

Dromaeosaurid or Troodontid?—Based on body fossils, members of the Deinonychosauria (Dromaeosauridae + Troodontidae) span one of the largest size ranges in Theropoda: the largest members, such as *Utahraptor* (Dromaeosauridae), approached 7 m in length (Kirkland et al. 1993), while the smallest, such as *Anchiornis* (Troodontidae), measured just 34 cm in length (Xu et al. 2009). The largest troodontid currently known is *Saurornithoides*, which approached 2.5–3 m in length (Norell et al. 2009). The size range of deinonycho-

Table 3. Comparison of the foot lengths and estimated track-maker body lengths of dromaeopodid ichnospecies. *calculated using the average hip height to body length ratio of 1:2.63 (Xing et al. 2009) and the formula: hip height = $3.983x + 69.453$; where x is the length of digit III (Li et al. 2007). Note, only those taxa with length of digit III reported were calculated.

Ichnospecies	Authors	Foot length (cm)	Digit III length (cm)	Body length* (cm)
<i>Velociraptorichnus sichuanensis</i>	Zhen et al. 1994; Xing et al. 2009	10.7	6.2	247.6
Shandong <i>Velociraptorichnus</i>	Li et al. 2007	10.0	?	?
<i>Dromaeopodus shandongensis</i>	Li et al. 2007	28.5	?	?
<i>Dromaeosauripus hamanensis</i>	Kim et al. 2008	15.5	15.5	345.1
<i>Dromaeosauripus jinjuensis</i>	Kim et al. 2012	9.3	9.3	280.1
<i>Dromaeosauripus yongjingensis</i>	this study	13.4–16.1	7.56–10.45	261.9–292.1
<i>Menglongipus sinensis</i>	Xing et al. 2009	5.8–6.7	5.2–5.8	237.2–243.5
<i>Paravipus didactylodes</i>	Mudroch et al. 2010	27.5	27.5	470.8
Morocco didactyl track	Ishigaki and Lockley 2010	~27.0	?	?

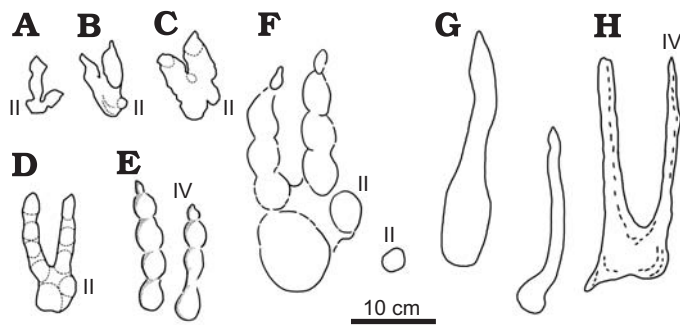


Fig. 6. Schematic diagrams of dromaeopodid ichnotaxa to the same scale. **A.** *Menglongipus* (Xing et al. 2009). **B.** *Shandong Velociraptorichnus* (Li et al. 2007). **C.** *Velociraptorichnus* (Zhen et al. 1994; Xing et al. 2009). **D.** *Dromaeosauripus yongjingensis* (this study). **E.** *Dromaeosauripus hamanensis* (Kim et al. 2008). **F.** *Dromaeopodus* (Li et al. 2007). **G.** *Paravipus* (Mudroch et al. 2010). **H.** Morocco didactyl track (based on Ishigaki and Lockley 2010).

saurians based on the track record is concordant with that of the body fossil record. Estimates of track-maker sizes for all currently known dromaeopodid ichnotaxa (Fig. 6, Table 3), including *Dromaeosauripus yongjingensis*, fall between 61–300 cm, well within the size range established by body fossils of both dromaeosaurids and troodontids, although the largest tracks are at the uppermost end of the troodontid range. Furthermore, Lubbe et al. (2009, 2011) argued on osteological grounds that dromaeosaurids would produce tracks subequal lengths between digits III and IV whereas troodontids possess a relatively shorter digit IV. Based on this distinction, we contend that *Dromaeosauripus yongjingensis* (and probably all *Dromaeosauripus* tracks) were likely made by a dromaeosaurid.

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References

Alexander, R.M. 1976. Estimates of speeds of dinosaurs. *Nature* 261: 129–130.
 Cai, X.F., Li, C.A., Zhan, C.S., and Gu, Y.S. 1999. The construction and significance of the Yanguoxia Formation on the southern margin of the Minhe Basin, Gansu. *Sedimentary Facies and Palaeogeography* 19 (3): 16–20.
 Carpenter, K. 1998. Evidence of predatory behaviour by theropod dinosaurs. *Gaia* 15: 135–144.

Cowan, J., Lockley, M.G., and Gierlinski, G. 2010. First dromaeosaur trackways from North America: new evidence, from a large site in the Cedar Mountain Formation (early Cretaceous), eastern Utah. *Journal of Vertebrate Paleontology* 30: 75A.
 Currie, P.J. 1997. Dromaeosauridae. In: P.J. Currie and K. Padian (eds.), *Encyclopedia of Dinosaurs*, 194–195. Academic Press, San Francisco.
 Day, J.J., Norman, D.B., Upchurch, P., and Powell, H.P. 2002. Biomechanics: dinosaur locomotion from a new trackway. *Nature* 415: 494–495.
 Du, Y., Li, D., Peng, B.L., and Bai, Z. 2001. Dinosaur footprints of Early Cretaceous in Site 1, Yanguoxia, Yongjing County, Gansu Province. *Journal of China University of Geosciences* 12: 2–9.
 Ishigaki, S. and Lockley, M.G. 2010. Didactyl, tridactyl and tetradactyl theropod trackways from the Lower Jurassic of Morocco: evidence of limping, labouring and other irregular gaits. *Historical Biology* 22: 100–108.
 Kim, J.Y., Kim, K.S., and Lockley, M.G. 2008. New didactyl dinosaur footprints (*Dromaeosauripus hamanensis* ichnosp. et ichnosp. nov.) from the Early Cretaceous Haman Formation, south coast of Korea. *Palaeogeography, Palaeoclimatology, Palaeoecology* 262: 72–78.
 Kim, J.Y., Lockley, M.G., Woo, J.O., and Kim, S.H. 2012. Unusual didactyl traces from the Jinju Formation (Early Cretaceous, South Korea) indicate a new ichnospecies of *Dromaeosauripus*. *Ichnos* 19: 75–83.
 Kirkland, J.I., Burge, D., and Gaston, R. 1993. A large dromaeosaur (Theropoda) from the Lower Cretaceous of Utah. *Hunteria* 2 (10): 1–16.
 Li, D.Q., Du, Y.S., and Gong, S.Y. 2000. New discovery of dinosaur footprints of the Early Cretaceous from Yanguoxia, Yongjing County, Gansu Province. *Earth Sciences Journal of China University of Geosciences* 25: 498–525.
 Li, D., Azuma, Y., Fujita, M., Lee Y.-N., and Arakawa, Y. 2006. A preliminary report on two new vertebrate track sites including dinosaurs from the early Cretaceous Hekou Group, Gansu province, China. *Journal of the Paleontological Society of Korea* 22: 29–49.
 Li, R.H., Lockley, M.G., Makovicky, P.J., Matsukawa, M., Norell, M.A., Harris, J.D., and Liu, M.W. 2007. Behavioural and faunal implications of Early Cretaceous deinonychosaur trackways from China. *Naturwissenschaften* 95: 185–191.
 Lockley, M.G. 1991. *Tracking Dinosaurs—A New Look at an Ancient World*. 238 pp. Cambridge University Press, Cambridge.
 Lockley, M.G., White, D., Kirkland, J., and Santucci, V. 2004. Dinosaur tracks from the Cedar Mountain Formation (Lower Cretaceous), Arches National Park, Utah. *Ichnos* 11: 285–293.
 Longrich, N.R. and Currie, P.J. 2009. A microraptorine (Dinosauria—Dromaeosauridae) from the Late Cretaceous of North America. *Proceedings of the National Academy of Sciences, U.S.A.* 106: 5002–5007.
 Lubbe, T. van der, Richter, A., and Böhme, A. 2009. *Velociraptor's* sisters: First report of troodontid tracks from the Lower Cretaceous of northern Germany. *Journal of Vertebrate Paleontology* 29 (Supplement 3): 194A.
 Lubbe, T. van der, Richter, A., Böhme, A., Sullivan C., and Huhner, T.R. 2011. Sorting out the sickle claws: how to distinguish between dromaeosaurid and troodontid tracks. *Dinosaur Track Symposium in Obernkirchen, Germany. April 14–17, 2011, Abstracts volume*, 18–19. Georg-August-Universität Göttingen, Göttingen.
 Makovicky, P.J. and Norell, M.A. 2004. Troodontidae. In: D.B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*, Second Edition, 184–195. University of California Press, Berkeley.
 Maxwell, W.D. and Ostrom, J.H. 1995. Taphonomy and paleobiological implications of *Tenontosaurus*–*Deinonychus* associations. *Journal of Vertebrate Paleontology* 15: 707–712.
 Mudroch, A., Richter, U., Joger, U., Kosma, R., Idé, O., and Maga, A. 2010. Didactyl tracks of paravian theropods (Maniraptora) from the ?Middle Jurassic of Africa. *PLoS ONE* 6 (2): e14642 (1–10).
 Norell, M. A. and Makovicky, P. J. 2004. Dromaeosauridae. In: D.B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*, Second Edition, 196–209. University of California Press, Berkeley.
 Norell, M.A., Makovicky, P.J., Bever, G.S., Balanoff, A.M., Clark, J.M.,

- Barsbold, R., and Rowe, T. 2009. A review of the Mongolian Cretaceous dinosaur *Saurornithoides*. *American Museum Novitates* 3654: 1–63.
- Ostrom, J.H. 1990. Dromaeosauridae. In: D.B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*, 269–279. University of California Press, Berkeley.
- Richter, U., Richter, A., and Lehmann, J. 2007. Fährten sucher auf der Dinospur in den Rehburger Bergen. *Fossilien* 1: 11–20.
- Roach, B.T. and Brinkman, D.L. 2007. A reevaluation of cooperative pack hunting and gregariousness in *Deinonychus antirrhopus* and other nonavian theropod dinosaurs. *Bulletin of the Peabody Museum of Natural History* 48: 103–138.
- Xing, L.D., Harris, J.D., Sun, D.H., and Zhao, H.Q. 2009. The earliest known deinonychosaur tracks from the Jurassic–Cretaceous boundary in Hebei, China. *Acta Palaeontologica Sinica* 48: 662–671.
- Xu, X., Ma, Q., and Hu, D. 2010. Pre-*Archaeopteryx* coelurosaurian dinosaurs and their implications for understanding avian origins. *Chinese Science Bulletin* 55: 3971–3977.
- Xu, X., Zhao, Q., Norell, M., Sullivan, C., Hone, D., Erickson, G., Wang, X., Han, F., and Guo, Y. 2009. A new feathered maniraptoran dinosaur fossil that fills a morphological gap in avian origin. *Chinese Science Bulletin* 54: 430–435.
- Zhang, J., Li, D., Li, M., Lockley, M., and Bai, Z. 2006. Diverse dinosaur, pterosaur and bird-track assemblages from the Hakou Formation, Lower Cretaceous of Gansu Province, northwest China. *Cretaceous Research* 27: 44–55.
- Zhen, S.N., Li, J.J., Chen, W., and Zhu, S. 1994. Dinosaur and bird footprints from the Lower Cretaceous of Emei County, Sichuan. *Memoirs of the Beijing Natural History* 54: 105–120.
- Zhou, X.G., Li, D.Q., and Peng, C. 2005. Analysis of paleoenvironment and fossil formation based on Yanguoxia dinosaur tracks from Yongjing County, Gansu province. *Gansu Science and Technology* 21 (11): 114–117.