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.

Introduction

The non-avian theropod dinosaur clade Deinonychosauria includes the clades Dromaeosauridae and Troodontidae. Most deinonychosaurians 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). Deinonychosaurians 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 deinonychosaurians around the Jurassic–Cretaceous boundary (Xing et al. 2009).
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...
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

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

<table>
<thead>
<tr>
<th>Specimen number</th>
<th>Tracks</th>
<th>Directions</th>
</tr>
</thead>
<tbody>
<tr>
<td>GSLTZP-S1-T101</td>
<td>4</td>
<td>N</td>
</tr>
<tr>
<td>GSLTZP-S2-TA</td>
<td>8</td>
<td>E to SE</td>
</tr>
<tr>
<td>GSLTZP-S2-TB</td>
<td>10</td>
<td>E to NW</td>
</tr>
<tr>
<td>GSLTZP-S2-TC</td>
<td>21</td>
<td>N</td>
</tr>
<tr>
<td>GSLTZP-S2-TD</td>
<td>10</td>
<td>NW to N</td>
</tr>
<tr>
<td>GSLTZP-S2-TE</td>
<td>12</td>
<td>NW</td>
</tr>
<tr>
<td>GSLTZP-S2-TF</td>
<td>6</td>
<td>NW</td>
</tr>
</tbody>
</table>
Shandong Province (Li et al. 2007) although it is closer in size to Dromaeosaurus from Korea (Kim et al. 2008, 2012). The apparent absence of a heel in Dromaeosaurus hamanensis and the recently-named Dromaeosaurus 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 Dromaeosaurus (no heel trace, small divarication angle, lack of clear claw impressions; Kim et al. 2012). Thus the Yanguoxia tracks share similarities to both ichnogenera, making unequivocal assignments; Kim et al. 2012). The Yanguoxia tracks share similarities to both ichnogenera, making unequivocal assignments; Kim et al. 2012). Thus the Yanguoxia tracks share similarities to both ichnogenera, making unequivocal assignments; Kim et al. 2012). Thus the Yanguoxia tracks share similarities to both ichnogenera, making unequivocal assignments; Kim et al. 2012). 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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 ichnوتaxa 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 Morocco tracks lack any impression of digit II. These differences support *Dromaeosauripus yongjingensis* as a new ichnospecies.

### 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-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.

Deinonychosaurians often have been inferred to be speedy predators. As yet, the only ichnological example for a speedy deinonychosaurian is a trackway of *Dromaeosauripus yongjingensis* 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 deinonychosaurians 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 *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.
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-

![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.](https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Aug 2020 Terms of Use: https://bioone.org/terms-of-use)
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* (this study), *E. Dromaeosauripus hamanensis* (Kim et al. 2008), *F. Dromaeopus* (Li et al. 2007), *G. Paravius* (Mudroch et al. 2010). *H. Morocco didactyl track* (based on Ishigaki and Lockley 2010).

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