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The non-avian theropod track *Jialingpus* from the Cretaceous of the Ordos Basin, China, with a revision of the type material: Implications for ichnotaxonomy and trackmaker morphology

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Abstract

Deposits from the Ordos Basin of mid-western China are rich in body fossils and ichnofossils of Early Cretaceous vertebrates. Thousands of Early Cretaceous sauropod, theropod and bird tracks described since 1958 have been found at several localities in the basin. We report two new sites (Dijiaping and Bawangzhuang) in the Luohe Formation of the Ordos Basin, Shaanxi Province, which contain small theropod footprints that are here referred to the ichnogenus *Jialingpus*. The assignment is based on pad configurations including (1) the large metatarsophalangeal area positioned in line with the axis of digit III, (2) the subdivision of this part into a small pad behind digit II, which in some specimens is close to the general position of the hallux (digit I), and a large metatarsophalangeal pad behind digit IV, and (3) a distinct inter-pad space between metatarsophalangeal pads and proximal phalangeal pads of digits II and III. We re-describe the type material of the type ichnospecies *Jialingpus yuechiensis* from the Upper Jurassic Penglaizhen Formation of Sichuan Province, proposing a largely amended diagnosis for this ichnotaxon. The presence of a digit I trace in the holotype, indicating a relatively long hallux, and the large metatarsophalangeal area positioned in line with digit III distinguishes *Jialingpus* from the ichnogenus *Grallator* and similar tracks that all lack these features. The only difference between *Jialingpus* specimens from the Cretaceous of the Ordos Basin and those of the Jurassic Penglaizhen Formation is the larger digit divarication in the Cretaceous taxon. This is the fourth record of *Jialingpus* in China and the second in Cretaceous strata, with the first being those from the Huangyangquan locality in Xinjiang, China.
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Keywords: Early Cretaceous; Non-avian theropod tracks; Ordos Basin; Luohe Formation; *Jialingpus*

1. Introduction

1.1. Vertebrate tracks from the Ordos Basin

The Ordos Basin is the second largest sedimentary basin in China, spreading across Shaanxi, Gansu, and Shanxi provinces as well as the Ningxia and Inner Mongolia autonomous regions. It includes deposits of Jurassic and Early Cretaceous ages. A large number of body fossils are known from the Lower Cretaceous strata. The invertebrate fauna includes ostracods and estherians (*Cypridea*, *Eosestheria*) (Ma, 1998); the vertebrate fauna includes the fishes *Lycoptera* and *Sinamia* (Ma, 1998), the turtles *Ordosemys* (Brinkman and Peng, 1993a) and *Sinemys* (Brinkman and Peng, 1993b), the choristodere *Ikechosaurus* (Brinkman and Dong, 1993), the pterosaur *Huanhepterus* (Dong, 1982), the dinosaurs *Psittacosaurus* (Russell

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and Zhao, 1996), *Sinornithoides* (Russell and Dong, 1993), as well as stegosaurs (Dong, 1993), and the bird *Otogornis* (Hou, 1994).

Numerous Jurassic and Cretaceous vertebrate tracksites are also known from the Ordos Basin. The Chabu tracksites, discovered in the mid-west area of the basin, display thousands of sauropod, theropod and bird tracks from the Lower Cretaceous Jingchuan Formation (Lockley et al., 2002; Li et al., 2006, 2011). The Hailiutu tracksite from the north of the basin shows theropod, ornithopod, and crocodile tracks from the ?Lower–Middle Jurassic Shiguai Group (Li et al., 2010). Two Jurassic dinosaur tracksites were reported from the southwest margin of the Ordos Basin: the Shenmu tracksite (Teilhard de Chardin and Young, 1929; Kuhn, 1958; Li et al., 2012) in the northern area of Shaanxi Province, and the Tongchuan tracksite (Young, 1966) in central-western Shaanxi.

In 1935, three footprints (XYT7–9) were discovered by Mr. Zi-Feng Guo (a local peasant), near the Zhidang River, at Bawangzhuang Village (Xunyi County, Xianyang City, Shaanxi Province) (Fig. 1). In 1999, six footprints (XYT1–6) were found by Mr. Li-Xin Zhang (a local peasant) during the construction of a warehouse on a hill near his home, in Dijiaping Village, Xunyi County. All of these footprints were collected by the Xunyi Museum in December 2005 and March 2009, where they are currently curated. More recently, in May 2011, two of us (Li-Da Xing and Song-Mei Hu) were invited by the Xunyi Museum to study dinosaur tracks from the local museum, and during prospecting in the area, more tracks (described below as specimens DJP1–6) were discovered at exposures nearby.

1.2. Jialingpus yuechiensis *material*

Between 1940 and 2012, 63 tetrapod ichnospecies were erected based on Chinese type specimens. Lockley et al. (2013) reviewed these tracks and reduced the Jurassic theropod ichnotaxa among them from 23 to only 9 because most ichnogenera were considered subjective junior synonyms of *Grallator* and *Eubrontes*. Previous studies had already suggested this for some cases (Lockley et al., 2013 and references therein). However, all of these proposed synonymies affected Lower and Middle Jurassic theropod tracks, many of which were poorly preserved. In contrast to this overabundance of names, only three Late Jurassic theropod ichnogenera have been erected. *Jialingpus* is one of these, and was described based on several well-preserved tracks from the Upper Jurassic Penglaizhen Formation of Sichuan Province (Zhen et al., 1983, 1989; Yang and Yang, 1987). Lockley et al. (2013) retained *Jialingpus* as valid; nevertheless the ichnogenus is in need of detailed comparison with other ichnotaxa, and such an analysis is pending.

In recent years, *Jialingpus* was also reported from Middle Jurassic to Lower Cretaceous strata of other regions, including the Middle Jurassic of Morocco (Gierliński et al., 2009a), the Upper Jurassic of Poland and Spain (Gierliński et al., 2009b), the Lower Cretaceous Obernkirchen Sandstone of Germany (Gierliński et al., 2009b), and the Early Cretaceous Huangyangquan tracksites, Xinjiang, China (Xing et al., 2011). In this situation, and to allow for better comparisons, it is necessary to re-describe the holotype of *Jialingpus*; we did such a re-description in the systematics section below.

1.3. Institutional abbreviations

BNHM = Beijing Natural History Museum, Beijing, China; CU = University of Colorado Denver, USA; DJP = Dijiaping tracksite, Shaanxi, China; IVPP = Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; MGCM = Moguicheng Dinosaur and Bizarre Stone Museum, Xinjiang, China; XY = Xunyi Museum, Shaanxi, China. CU specimens were transferred to the University of Colorado Museum of Natural History (UCM) in 2012.

2. Geological setting

Xunyi County is located in central-western Shaanxi Province (Fig. 1), and geologically belongs to the southern margin of the Ordos Basin, where the Lower Cretaceous was divided by Hao et al. (1986) into the lower part of the Luohe Formation and the Huanhe-Huachi Formation, the upper part of the Luohandong Formation and the Jingchuan Formation (Fig. 2). Wu et al. (2007) subsequently recognized the Yijun Formation as an additional Lower Cretaceous unit below the Luohe Formation. The Ejinhoro Formation at the Chabu tracksites corresponds to the Jingchuan Formation (Li et al., 2006), although Wu et al. (2007) have also interpreted the Ejinhoro Formation as pertaining to the Huanhe-Huachi Formation.

The Dijiaping tracksite (GPS: 35°15′36″N, 108°36′4″E) was discovered in the Luohe Formation, in Dijiaping Village, Malan Town, Xunyi County (Fig. 1). The stratum containing the fossils has large cross-stratifications, which are typical for the formation (Ma, 1998). The tracks are preserved on brown-red sandstone associated with large mud cracks, ripple marks, and invertebrate traces. The Luohe Formation is approximately 200 to 500 m thick, and accounts for 2/3 of the surface area of this basin. It notably includes alluvial facies grit or weathered sandstone and fish remains (*Lycoptera*, Actinopterygii) (Yang et al., 2008).

The Bawangzhuang tracksite (Fig. 1) was discovered 28 km to the west of Bawangzhuang Village (Qiupotou Town, Xunyi County). The site had been lost after its discovery in 1935, and the precise location of the original find cannot be determined. However, the stratigraphy of the Zhidang River bank and the presence of fuchsia-colored siltstones similar to the slab in which the Bawangzhuang tracks were preserved indicates that it was probably also recovered from the Luohe Formation. Abundant invertebrate traces co-occur with the Bawangzhuang tracks.

3. Systematic ichnology

3.1. Dijiaping tracksite

Material. Six complete natural casts on three slabs without counterparts were given the field identification numbers DJP1–6 (Figs. 3–5; Table 1). These original tracks were not collected and are still in situ. Additionally, six natural casts on a single slab

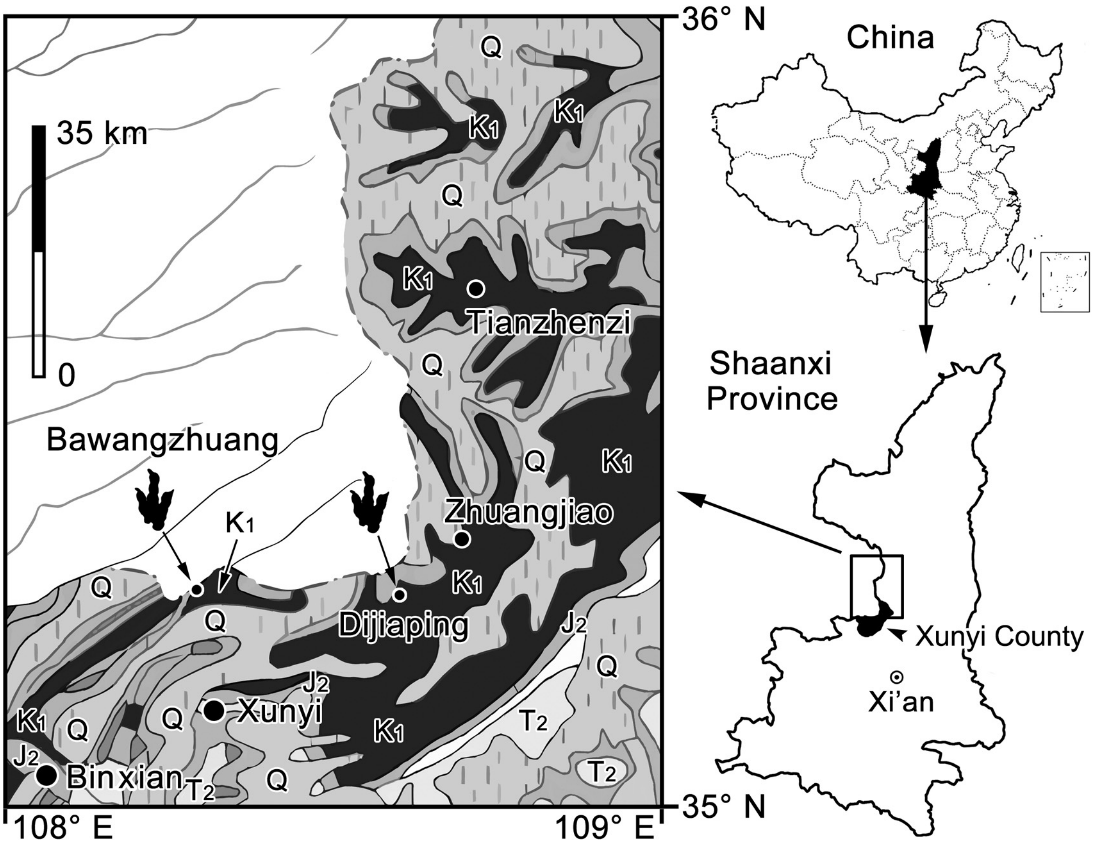

Fig. 1. Location of the Dijiaping and Bawangzhuang track localities (indicated by the footprint icon) in Shaanxi Province, China.

Table 1
Measurements (in cm) of *Jialingpus* tracks from China.

Specimen	ML	MW*	LD I	LD II	LD III	LD IV	II–III	III–IV	II–IV	ML/MW	M
DJP1	11.1	8.1	–	5.0	7.6	5.1	38°	30°	67°	1.4	0.63
DJP2	11.1	8.6	–	5.4	6.5	5.6	37°	33°	70°	1.3	0.60
DJP3	–	–	–	–	9.0	7.6	–	–	–	–	–
DJP4	17.1	11.7	–	8.0	12.7	7.5	30°	30°	60°	1.5	0.64
DJP5	15.7	14.8	–	9.3	9.5	11.6	42°	26°	68°	1.1	–
DJP6	14.0	–	–	–	8.8	7.0	–	27°	–	–	–
XYT1	12.6	8.8	–	5.9	9.7	7.0	37°	25°	62°	1.4	0.54
XYT2	11.6	9.3	–	5.8	7.9	6.4	38°	30°	68°	1.2	0.62
XYT3	13.8	–	–	–	8.6	4.8	–	27°	–	–	–
XYT4	>13.9	11.5	–	>9.4	>12.3	>7.5	–	–	–	–	–
XYT5	13.3	11.2	–	5.2	7.7	6.9	35°	33°	67°	1.2	–
XYT6	10.7	7.5	–	4.0	7.4	4.9	33°	27°	60°	1.4	–
XYT7	15.4	11.3	–	6.4	10.1	7.2	39°	26°	65°	1.4	0.68
XYT8	14.1	12.4	–	7.4	9.6	9.0	37°	30°	67°	1.1	0.56
XYT9	14.1	–	–	>2.9	9.7	6.8	–	28°	–	–	–
BNHM-SCFP 11	21.0	13.5	–	12.0	15.2	10.8	21°	27°	48°	1.6	0.70
BNHM-SCFP 21	19.7	10.5	4.7	8.4	13.9	8.0	22°	25°	47°	1.9	0.82
BNHM-SCFP 24	20.0	10.3	3.5	8.4	13.0	8.4	19°	28°	47°	1.9	0.75
IVPP DT 1	15.1	8.8	–	7.6	9.6	6.9	24°	32°	56°	1.7	0.75
IVPP DT 2	20.7	11.5	–	11.8	14.3	9.6	23°	21°	44°	1.8	0.93
IVPP DT 3	>17.2	10.8	–	10.5	13.0	9.2	23°	22°	45°	–	0.74
CU 199-31b	18.1	11.8	–	8.7	12.0	10.1	28°	22°	50°	1.5	–
CU 199-32	10.8	6.1	–	5.3	7.0	5.7	19°	28°	47°	1.8	–
CU 199-33	17.8	11.9	–	10.4	11.2	7.1	23°	21°	44°	1.5	–
CU 199-36	9.7	5.5	–	5.2	7.4	5.1	22°	25°	47°	1.8	0.76

Abbreviations: ML: maximum length; MW: maximum width*; LD I: length of digit I; LD II: length of digit II; LD III: length of digit III; LD IV: length of digit IV; II–III: angle between digits II and III; III–IV: angle between digits III and IV; II–IV: angle between digits II and IV; M: mesaxony (length/width ratio for the anterior triangle). * measured as the distance between the tips of digits II and IV.

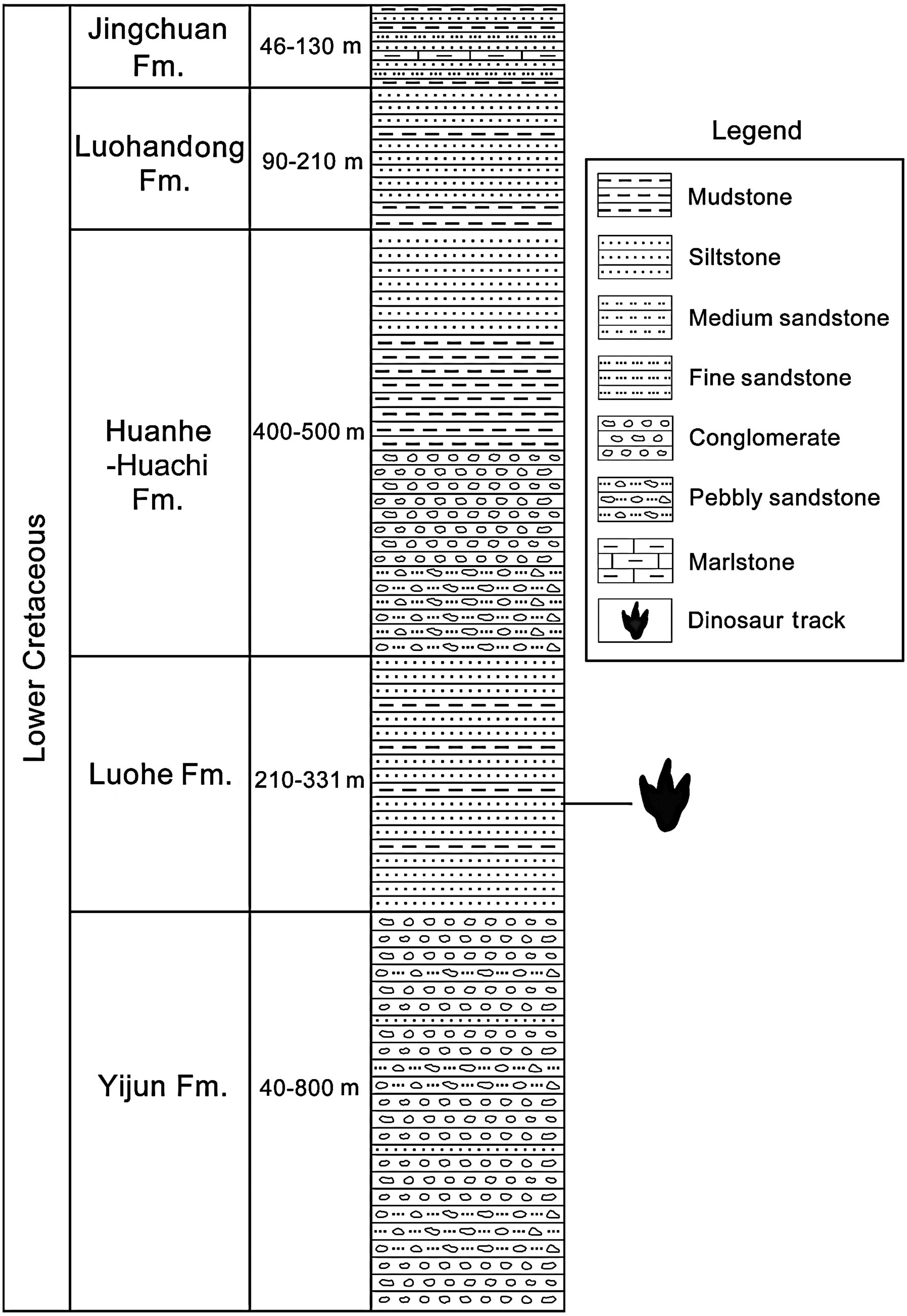

Fig. 2. Lower Cretaceous stratigraphy of Xunyi County, Shaanxi Province, China (based on Ma, 1998) with the position of the track-bearing horizon.

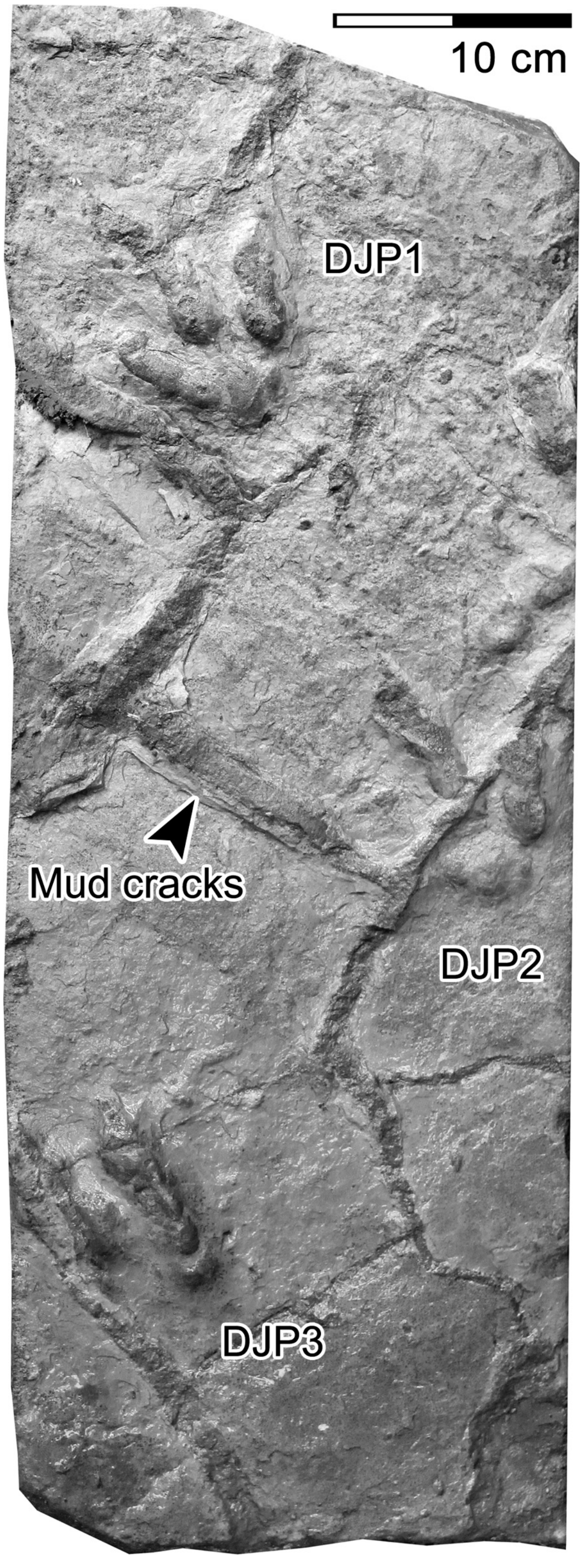

Fig. 3. Photograph of Dijiaping specimens DJP1–3.

were collected by the Xunyi Museum, and cataloged as XYT1–6 (T = theropod) (Figs. 4, 5; Table 1).

Locality and horizon. Dijiaping tracksite, Xunyi County, Xianyang City, Shaanxi Province, China. Luohe Formation, Lower Cretaceous.

Description. These twelve tracks are preserved on four slabs without counterparts. Mud cracks and invertebrate traces are also present, especially on the slab containing specimens DJP1–3 (Fig. 3). Aside from specimen DJP3, tracks are generally similar in morphology. Their size ranges between 10.7 cm and 17.1 cm in length, and between 7.5 cm and 14.8 cm in width. DJP1, 2, 4–6 and XYT1–6 are small-sized and tridactyl. The length:width (L/W) ratios range between 1.1 and 1.5. All of these tracks are isolated, lacking evidence of distinct trackways.

DJP4 is the biggest and best-preserved of these tracks. The impression of digit III is directed anteriorly and is the longest, whereas that of digit II is shorter than digit IV. Digit II possesses two digit pad traces; the impression of distal pad 2 is shallower due to weathering. Digits III and IV have three phalangeal pad traces, but although the margins of the first (proximal) pad are clear, the borders between pads 2 and 3 are more difficult to distinguish. Claw marks are sharp. The metatarsophalangeal area, where preserved, is positioned in line with the long axis of digit III in all tracks from the Dijiaping tracksite. Especially in the more complete specimens DJP1, DJP4, XYT1, and XYT2, two distinct metatarsophalangeal pad traces can be seen: a smaller one behind digit II and another larger one continuous with digit IV. There is a distinct metatarsophalangeal pad trace behind digit II which is oval in shape, and connected to the trace of the first pad of digit II via a short inter-pad space. This is the general position in which one would expect to find the trace of digit I (hallux) if present. It is tempting to interpret this part as the base or attachment of the hallux; however, as discussed below, it probably represents the metatarsophalangeal pad of digit II. The trace of the metatarsophalangeal pad of digit IV is extended proximally and round and blunt distally where it is connected to the first pad of the third digit by a large inter-pad space. The divarication angle between digits II and III is almost equal to the one between digits III and IV.

Specimens DJP1, DJP2, XYT1, and XYT2 are slightly smaller than DJP4, yet their overall morphologies are very similar. The divarication angles between the traces of digits II and IV of these tracks range between 61.8° and 69.8°, the divarication angles between digits II and III being much larger than those between digits III and IV. These tracks lack the inter-pad space connecting the traces of the metatarsophalangeal region with the proximal ends of digits II and III, which could be due to individual variation, the consistency of the substrate, or the lighter weights of the smaller track makers leaving shallower tracks. XYT3–6 are poorly preserved and shallower than XYT1 and XYT2. The divarication angle between the traces of digits II and III is significantly larger in DJP5 than in other tracks, which may have been influenced by a mud crack affecting the second digit. DJP6 and XYT3 are incomplete, both revealing poorly preserved impressions of digit II, represented only by faint traces. DJP3 is only preserved with two parallel digit impressions (III and IV), of which digit IV possesses four discernible digit pads, whereas those of digit III are indistinct. Both of these digit traces reveal sharp claw marks.

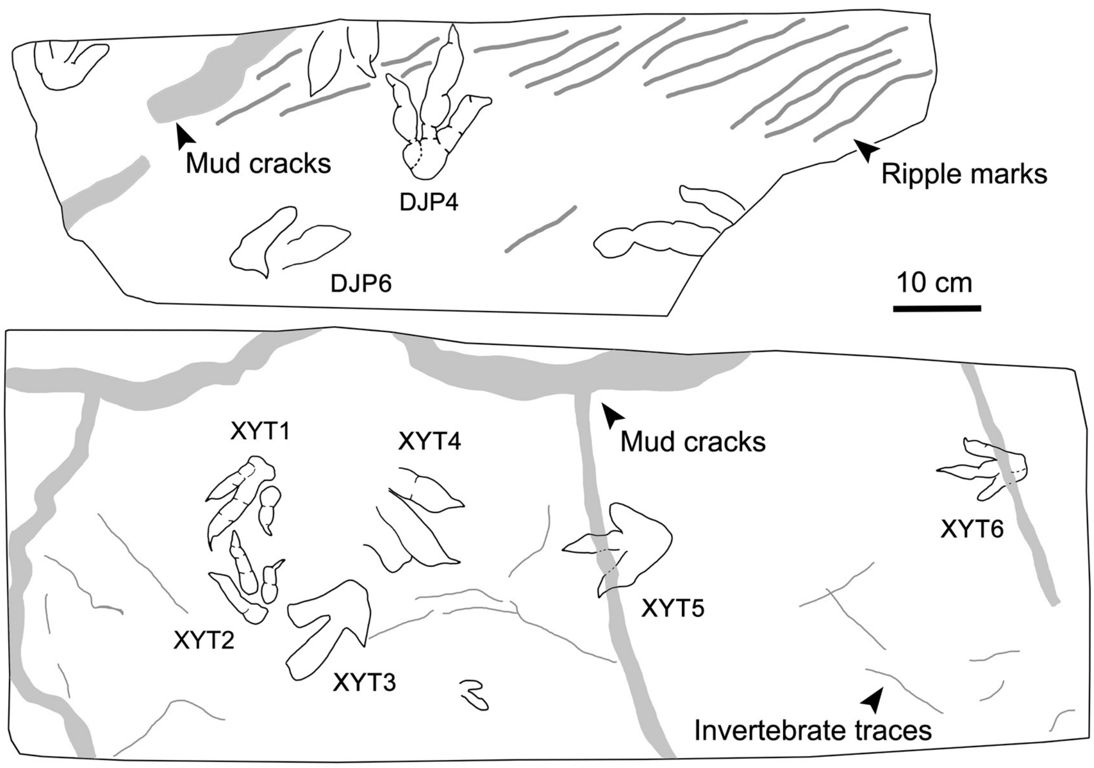

Fig. 4. Outline drawings of slabs with Dijiaping specimens DJP4 and 6 and XYT1–6.

3.2. Bawangzhuang tracksite

Material. Three complete natural casts on a single slab cataloged as XYT7–9 (Figs. 6, 7; Table 1).

Locality and horizon. Bawangzhuang tracksite, Xunyi County, Xianyang City, Shaanxi Province, China. Luohe Formation, Lower Cretaceous.

Description. All three tracks were preserved on a single slab associated with invertebrate traces. Their sizes range between 14.1 cm and 15.4 cm in length and 11.3 cm and 12.4 cm in width. XYT7 and XYT8 constitute a single pace (42 cm), and both are very similar to DJP4 in morphology. As in the latter, they show the characteristic metatarsophalangeal area in line with digit III consisting of a small metatarsophalangeal pad II and a large metatarsophalangeal pad IV separated by a crease. The divarication angles between digits II and IV range between 65.4° and 67.0°, with the divarication angles between digits II and III being much larger than those between digits III and IV. Specimen XYT9 is poorly preserved, but shares the same morphological characteristics as those of the other tracks.

3.3. Re-description of the type material of Jialingpus yuechiensis

Saurischia Seeley, 1888
Theropoda Marsh, 1881
Jialingpus Zhen et al., 1983

Amended diagnosis. Small- to medium-sized functionally tridactyl theropod tracks, with a hallux trace being occasionally present and with a phalangeal pad formula (including metatarsophalangeal pads II and IV) of 2-3-3-4-x and x-3-3-4-x respectively, if a hallux trace is absent. The L/W ratio ranges between 1.1 and 1.9, the divarication angles range between 44° and 70°, and the mean L/W ratio of the anterior triangle ranges between 0.70 and 0.93. An elongate and swollen metatarsophalangeal area consists of a larger metatarsophalangeal pad of digit IV and a smaller, medial metatarsophalangeal pad behind digit II, likely belonging to digit II. The proximal (metatarsophalangeal) area of the footprint is larger than any individual digital pad trace.

Type ichnospecies. *Jialingpus yuechiensis* Zhen et al., 1983.

Type locality and horizon. Yuechi County, Guang'an City, Sichuan Province, China. Penglaizhen Formation, Upper Jurassic.

Amended diagnosis. As for the ichnogenus.

Description. Specimens of *Jialingpus yuechiensis* (Fig. 8) are currently curated in the Beijing Natural History Museum (BNHM), the Chongqing Natural History Museum, and the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) in Beijing. Casts of some well-preserved specimens, including the holotype, which were formally in the University of Colorado Denver collection, are now kept at the University of Colorado Museum of Natural History (UCM), USA.

All in all 41 tracks and a possible tail trace were discovered in July 1982 by Ming Zhao (Science and Technology Committee, Yuechi County). After Zhao's report, the technicians from the IVPP selected and collected three of the best-preserved ones. DT (= dinosaur track, IVPP) 1 and 2 were extracted on the same slab, while DT 3 was collected on a different one. Later, researchers

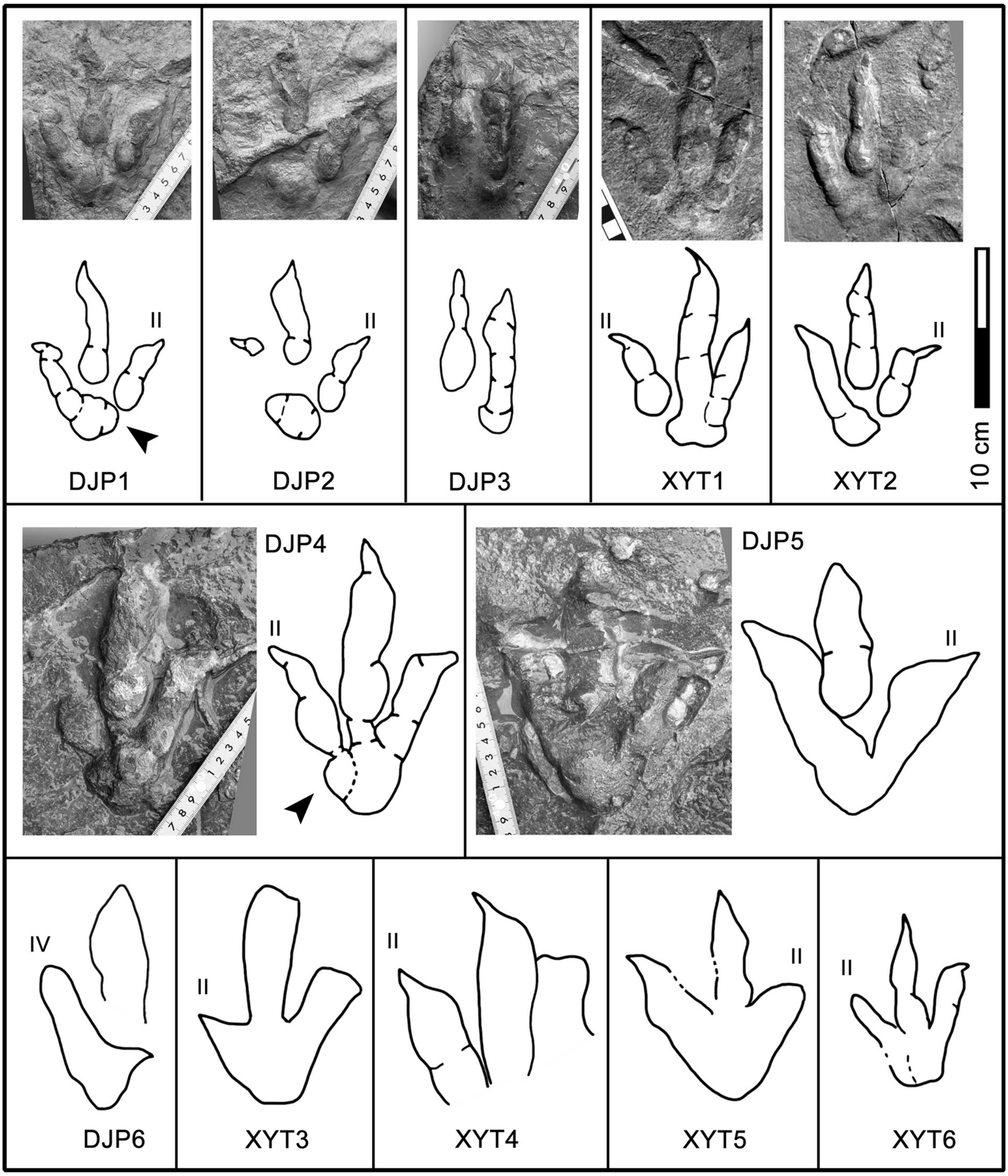

Fig. 5. Photographs and outline drawings of Dijiaping specimens DJP1–6 and Bawangzhuang specimens XYT1–6.

and technicians from the BNHM collected the remaining 38 tracks and the possible tail trace; the track-bearing slabs are numbered as BNHM-SCFP 1–25. Arguably, the IVPP specimens are better preserved than the BNHM specimens; however, the only available description of the IVPP specimens is a brief account by Xing et al. (2011). The lead authors (Li-Da Xing and Martin G. Lockley) have studied the specimens and casts curated in the IVPP and CU, as well as the better-preserved specimens from the BNHM.

The holotype of *Jialingpus yuechiensis* is BNHM-SCFP 24 (cast: CU 199-34). It is a unique specimen, with an elongated metatarsal impression (14.8 cm in length) and a well-preserved digit I. Digit I is represented by two digital pad traces, of which the first (proximal) one is longer than the second. Digital pad formulas are 2-3-3-4-x and x-3-3-4-x respectively, if a hallux trace is absent. We emphasize, that throughout this paper and contrary to the practise in other studies, we included the trace of the metatarsophalangeal pad II which is very small but mostly

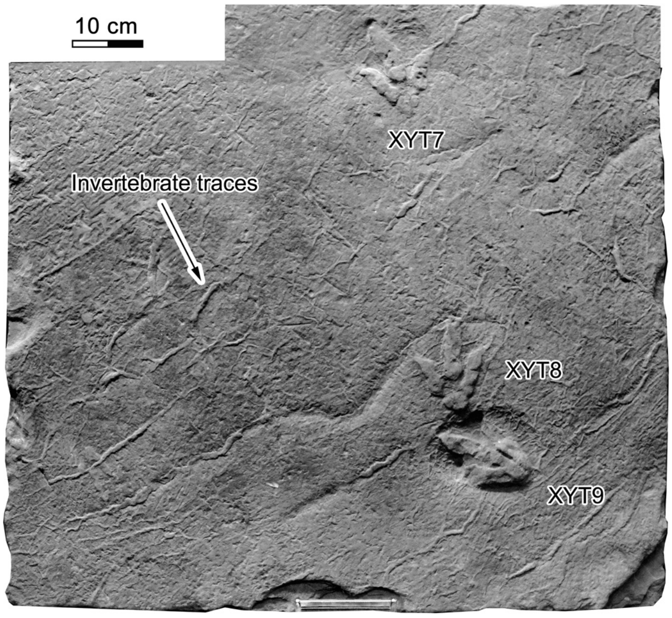

Fig. 6. Photograph of slab with Bawangzhuang specimens XYT7–9.

visible in *Jialingpus*. Digit IV is elongated, proximally running into the impression of the metatarsus. The attachment of digit I is positioned slightly posterior to the metatarsophalangeal area. Digit III preserves a sharp claw mark, and scale scratch lines were observed in digits I and II, and in the elongate metatarsal impression. The scratch lines of digit I average 1 mm in width, with a density of about 6 lines per centimeter. The scale scratch lines of digit II are 0.8 mm wide on average, with a density of 9 to 10 lines per centimeter. The scratch lines of the metatarsal impression are indiscernible.

The imprints seen in BNHM-SCFP 21 probably include digit I and a partial metatarsal impression. As in BNHM-SCFP 24, the supposed digit I imprint is located proximal to, or behind, digit II close to the medial side of the metatarsophalangeal pad II, a position that indicates a narrow configuration of digits along their base. In the imprint this might occasionally cause the fusion of pad traces in this region. Thus, in the tridactyl variants lacking a distinct digit I, the small pad behind digit II could also represent small coalesced portions of the metatarsophalangeal pad II and the proximal hallux.

IVPP DT 2, the best-preserved topotype of *Jialingpus yuechiensis*, lacks an elongated metatarsal impression. Digit III is longest, and digit IV shortest in this tridactyl track. Digits II–IV respectively have 3, 3, and 4 digital pads, among which the first digital pad of digit II is larger in comparison with the first digital pad of digit III. IVPP DT 2 has two distinct metatarsophalangeal pad traces; the smaller, behind digit II likely belongs to digit II and the larger to digit IV. In fact the holotype is morphologically different from the other paratypes in the sample. In any event, the smaller pad proximal to digit II is situated close to or just anterior to the point where the trace of digit I is located in the afore-described specimens (BMNH-SCFP 21 and 24). The metatarsophalangeal pad trace of digit IV is located in line with the long axis of digit III. The metatarsophalangeal pad trace behind digit II (representing digit II) is slightly damaged, but it is generally oval in shape, and connected to the trace of

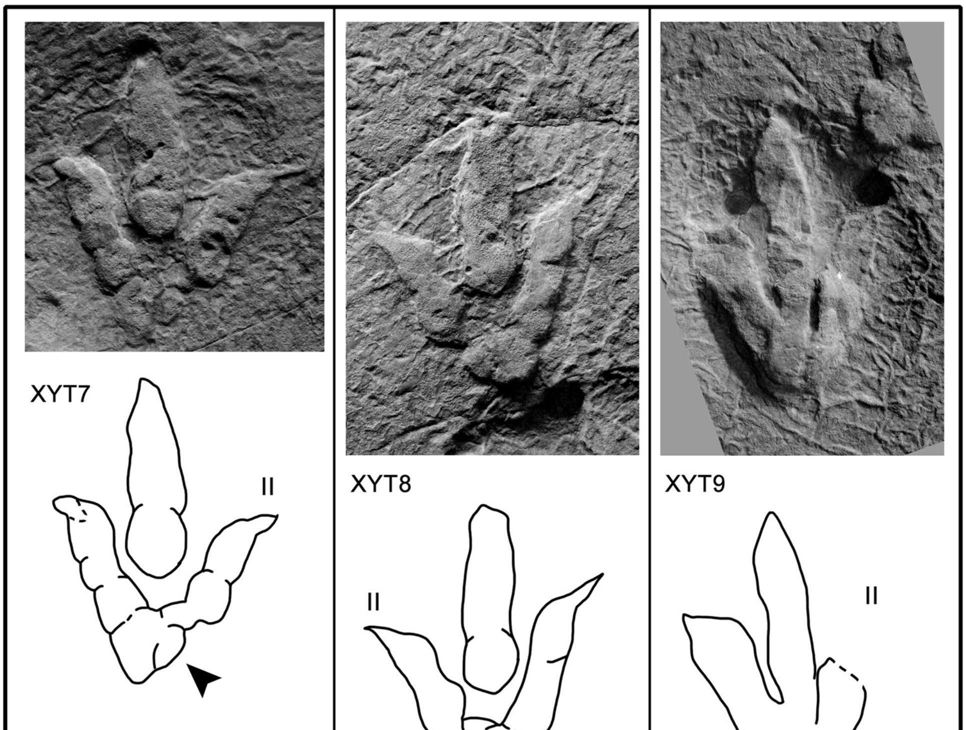

Fig. 7. Photographs and outline drawings of Bawangzhuang specimens XYT7–9.

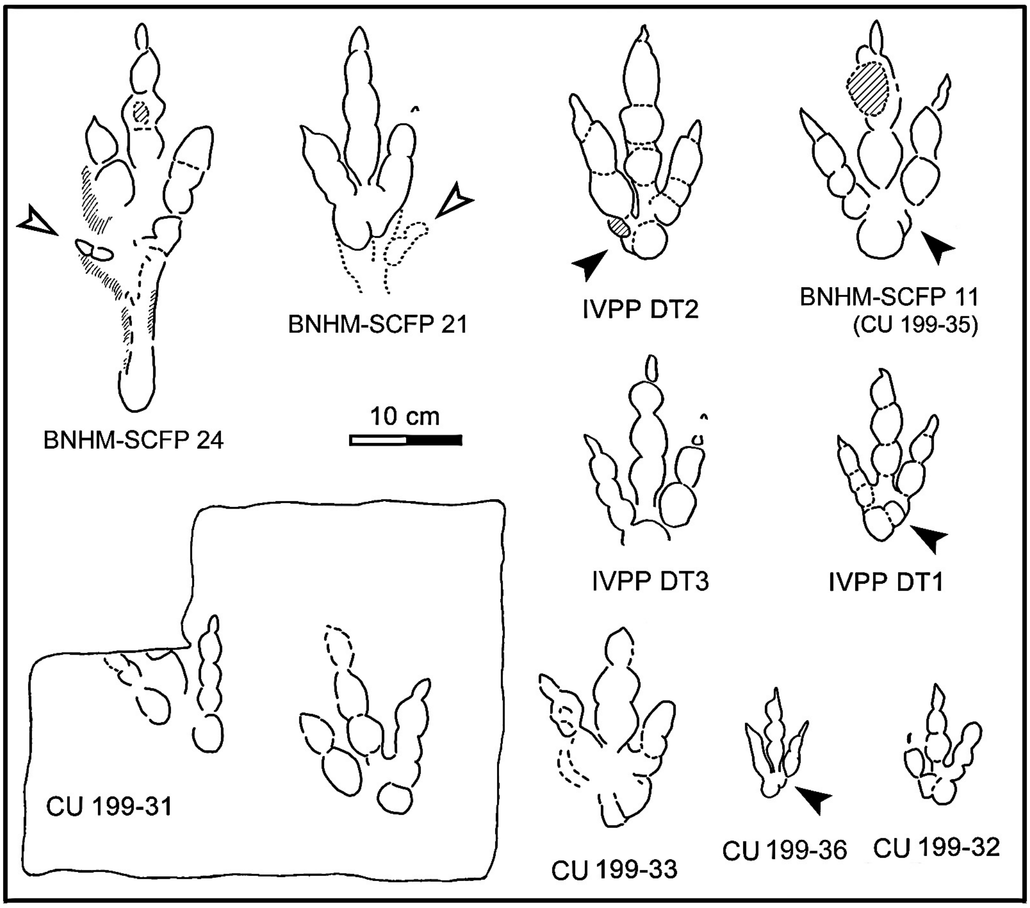

Fig. 8. *Jialingpus* tracks from Sichuan Province. White arrows indicate digit I trace; black arrows indicate small semicircular metatarsophalangeal pad on the medial side of the metatarsal phalangeal area.

the first pad of digit II via a short inter-pad space. A distinct space was observed between the metatarsophalangeal pad and the first digital pad of digit IV. Digit II preserves the largest claw mark (3.6 cm long), whereas that of digit IV is smaller (2.4 cm long), and the claw mark of digit III is the smallest (0.9 cm long).

BMNH-SCFP 11 (CU 199-35) is similar to IVPP DT 2, and also well-preserved. It also shows two distinct metatarsophalangeal pad traces. IVPP DT 1 is smaller, but otherwise morphologically identical to DT 2, aside from a relatively more pronounced metatarsophalangeal pad of digit II. The crease separating the two metatarsophalangeal pads is located along the long axis of digit III. CU 199-36 is the smallest track, but the divarication angles of its digits and its anterior triangle are similar to those of other tracks, especially those of IVPP DT 1. The other specimens such as IVPP DT 3, CU 199-31, 32, and 33 are less well-preserved, although their morphological characteristics are consistent with those of the above-mentioned tracks.

The mean divarication angle between digits II and IV of the *Jialingpus yuechiensis* tracks is 48°, ranging between 44° and 56°, and the divarication angles between digits III and IV are generally larger than those between digits II and III. The imprints have a mean L/W ratio of 1.7 ($N = 9$), and the mean L/W ratio of the anterior triangle is 0.78 ($N = 7$), indicating moderate mesaxony, unlike the somewhat stronger mesaxony typical of *Grallator* type tracks (Lockley, 2009).

The track orientations in the type sample of *Jialingpus yuechiensis* are irregular (Zhen et al., 1983, fig. 4). Only two pairs of footprints represent possible steps, for one of which the average length of the two footprints is 19 cm for a step length of 68 cm, while the corresponding measurements for the other pair of tracks are 10 cm and 54 cm, respectively (Zhen et al., 1983).

3.4. *Comparison and discussion of* Jialingpus yuechiensis

Jialingpus tracks have well-defined digital pad impressions, and are the most distinctive Late Jurassic tracks reported from China, as well as representing the largest and best preserved sample available for analysis. Because of the presence of hallux and metatarsal traces, Zhen et al. (1983, 1989) compared *Jialingpus* to *Anomoepus*, an ichnotaxon essentially known from the Lower Jurassic deposits of North America, Europe, and southern Africa and placed it in the ichnofamily Anomoepodidae. However, *Jialingpus* rather resembles the Early Jurassic *Grallator* than *Anomoepus*, given the projection of the middle toe and mesaxony which is slightly stronger in *Grallator* but much weaker in *Anomoepus*. Gierliński (1994) treated *Jialingpus* as a junior synonym of *Grallator*. Lockley et al. (2003) also interpreted *Jialingpus* as a theropod track based on narrow divarication angles. Thus, the consensus is that in general morphology, *Jialingpus* tracks are of the *Grallator* morphotype and are similar to both *Grallator* and *Anchisauripus*. Lockley et al. (2013) considered *Jialingpus* as a valid ichnotaxon, based on the distinctively well-preserved pad, hallux, and metatarsal traces. These characters indicate that *Jialingpus* is similar to *Grallator* in some features but different from this ichnotaxon in others. The ichnotaxon is in need of detailed comparison with other ichnotaxa.

All *Jialingpus* specimens exhibit a strongly projecting middle digit III, but in contrast to the *Eubrontes–Grallator–Anchisauripus* plexus tracks, the metatarsophalangeal area is complex, large, elongate and located more centrally, behind digit III. Such a distinctive, centrally placed, swollen metatarsophalangeal area is a diagnostic feature of *Jialingpus*. It consists of a larger metatarsophalangeal pad behind digit IV and a smaller metatarsophalangeal pad behind digit II, which appears to be related to the location of digit I. Along with the hallux trace, this is a feature seen in *Jialingpus* but absent from *Grallator*. The metatarsophalangeal area is larger than any digit pad of the track. In the best-preserved specimens, a crease separates the small metatarsophalangeal pad region behind digit II and the larger region behind digit IV.

The metatarsophalangeal area is located behind the middle toe, possibly indicating a narrow arctometatarsalian arrangement of the metatarsals. A number of Cretaceous derived theropod groups have a 'pinched' metatarsal III resulting in the arctometatarsalian condition (Holtz, 1995), which probably increased their agility. This homoplasy suggests multiple adaptive pathways and adaptive advantages for predation and predator evasion (Snively et al., 2004).

The presence of a metatarsal impression and of a hallux imprint in the *Jialingpus* type specimen BNHM-SCFP 24 and in another track, interpreted as an anomoepodid-like manual print with 4–5 digits, led Zhen et al. (1983, 1989) to the conclusion that the tracks were similar to the Early Jurassic ornithischian tracks of *Anomoepus* Hitchcock, 1848. The alleged manual print BNHM-SCFP 2 is not convincingly associated with any pedal print of *Jialingpus*, and it does not look like a manus to us. The presence of a metapodium impression and the occurrence of the hallux imprint in a plantigrade footprint like BNHM-SCFP 24 cannot prove its ornithischian origin, nor can it justify an assignment to *Anomoepus*. Evidently, several other theropod ichnites have also been misinterpreted as ornithischian on the basis of the presence of a metapodium trace (see Gierliński, 1994, 1996). In fact, theropods possessed metapodia that could be registered while sitting, traveling across soft substrates or otherwise crouching. The idea that only *Anomoepus* displays elongate metatarsal traces has persisted for historical reasons, owing to the original descriptions (Hitchcock, 1848). However, it is now clear that theropod tracks with metatarsal traces are as common as *Anomoepus*, if not more so (Kuban, 1989; Lockley et al., 2003; Gierliński et al., 2009b).

In their general morphology, *Jialingpus* footprints, with their highly projecting middle toe and tulip-like shape, strongly resemble the Early Jurassic ichnogenus *Grallator*. The digit length ratios of IVPP DT 2 are 1.58 (III/II) and 1.09 (III/IV). These ratios are1.31 and 0.93, respectively, for BMNH-SCFP 11. Similar digit length ratios are observed among the Early Jurassic grallatorids (*Anchisauripus sillimani*: 1.45, 0.94; *Grallator parallelus*: 1.78, 1.14; Olsen et al., 1998). However, the morphology of *Jialingpus* differs from most other Jurassic–Cretaceous theropod tracks in its relatively widely divaricated digits and the larger, compound metatarsophalangeal region, as well as in the presence of a hallux, in some specimens. In comparison, *Grallator* does not have widely divaricated digits (10°–30°, Olsen et al., 1998), and *Kayentapus* has similar widely divaricated digits but lacks a large, compound metatarsophalangeal region (Lockley et al., 2011).

Among Jurassic and Cretaceous theropod tracks, the association of widely divaricated digits and a large, metatarsophalangeal region seen in *Jialingpus* is similar to the Early Cretaceous ichnites known from Asia (Matsukawa et al., 2005) and North America (unpublished data), which Matsukawa et al. (2005) named *Asianopodus*. However, *Asianopodus* comprises medium-sized footprints, 27–30 cm in length according to Matsukawa et al. (2005), which are clearly larger than those of *Jialingpus* that are approximately 10–20 cm in length. In addition, the robust "heel" pad is more developed in *Asianopodus* than in *Jialingpus*, in which the small metatarsophalangeal portion behind digit II does not constitute a separate pad.

3.5. *Comparisons among the Chinese examples of* Jialingpus

Jialingpus tracks are also found in northeastern China. Fujita et al. (2007) described three different sizes of theropod tracks from the Tuchengzi Formation (Upper Jurassic), Sijiaban, Beipiao City, Liaoning Province, China. For the well-preserved tracks B1 and C14, the L/W ratios are similar at 1.7 and 1.8, and the L/W ratios of the anterior triangle are 0.5 and 0.55. However, both B1 and C14 have a distinctively swollen metatarsophalangeal area, positioned in line with the long axis of digit III, which makes B1 and C14 more similar to *Jialingpus* than to *Grallator*. These tracks are different from *Jialingpus* in their lack of a small metatarsophalangeal pad behind digit II, but this can be an extramorphological feature related to substrate conditions and imprint depth.

Apart from *Jialingpus* from the Jurassic strata of the Sichuan Basin and Liaoning Province, Xing et al. (2011) reported cf. *Jialingpus* isp. from the Lower Cretaceous (Lower Layer of the Tugulu Group) Huangyangquan tracksites in Wuerhe District, Xinjiang. Among these, the well-preserved MGCM.H7 (Fig. 9) is consistent with the characteristics of *Jialingpus*: 14.9 cm long, a divarication angle between digits II and IV of 44°, and a phalangeal pad formula of x-3-3-4-x. The sub-ovoid metatarsophalangeal pad of digit IV lies nearly in line with the long axis of digit III, close to the proximal end of digit IV. The track also has a metatarsophalangeal area consisting of metatarsophalangeal pads IV and II. The latter is somewhat indistinct in these specimens, a feature that may reflect substrate consistency or the shallowness of the imprints. Thus, we here assign the Huangyangquan tracks to *Jialingpus*. Additionally, *Jialingpus* tracks were discovered at the Asphaltite tracksite in Wuerhe

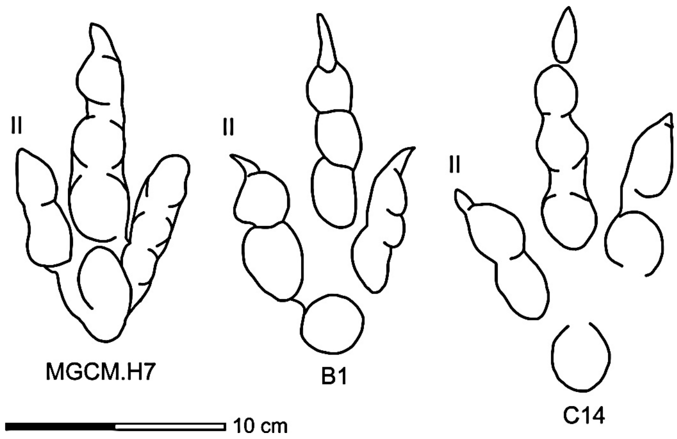

Fig. 9. *Jialingpus* tracks from Xinjiang Region (MGCM.H7; based on Xing et al., 2011) and from Liaoning Province (B1 and C14; based on Fujita et al., 2007).

District, near the Huangyangquan tracksite but in the Upper Layer of the Tugulu Group, among which were probable juvenile *Jialingpus* tracks (Xing et al., 2013a).

Interestingly, there is one significant difference between *Jialingpus* from the Late Jurassic and *Jialingpus* from the Early Cretaceous, which is that the divarication of digits of the former is generally less than that of the latter.

3.6. Comparison and discussion of the Xunyi specimens

The morphological characteristics of the tracks from the Dijiaping site are consistent with those of the Bawangzhuang site. Both are small tridactyl theropod tracks with a relatively large and slightly elongated metatarsophalangeal area located centrally behind the middle toe. This feature is also seen in the type material of *Jialingpus*.

The Dijiaping and Bawangzhuang tracks are here assigned to *Jialingpus* isp. based on: (1) a phalangeal pad formula of x-3-3-4-x, (2) a distinctive, swollen metatarsophalangeal area located behind digit III that includes a large metatarsophalangeal pad of digit IV and a smaller metatarsophalangeal pad behind digit II. These characteristics are consistent with those of *Jialingpus* (Zhen et al., 1983; Gierliński et al., 2009a, b; Xing et al., 2011, 2013a). Furthermore, the digit length ratios of specimen XYT7 are 1.65 (III/II) and 1.02 (III/IV). The corresponding ratios of track DJP4 are, respectively, 1.68 and 0.97. Such digit length ratios are also consistent with those of *Jialingpus yuechiensis*. The imprints have a mean L/W ratio of 1.3 ($N = 10$), and the mean L/W ratio of the anterior triangle is 0.61 ($N = 7$), indicating moderate mesaxony, similar to, although slightly less than, that in *Jialingpus yuechiensis*.

The tracks reported here differ slightly from the *Jialingpus* type material in having wider digit divarication angles, similar to those of *Asianopodus* (Matsukawa et al., 2005). In *Jialingpus*, the angles between the traces of digits II and IV range between 44° and 52°, which contrasts with the divarication angles ranging between 59.5° and 69.8° in the Dijiaping and Bawangzhuang tracks. The small sample size and the lack of trackways make it difficult to discern systematic features across a significant number of tracks, but the Dijiaping and Bawangzhuang tracks may represent a *Jialingpus* ichnospecies different from the Jurassic forms. On the other hand, *Asianopodus* represents medium-sized footprints (20–30 cm long), which are clearly larger than the material from Dijiaping and Bawangzhuang site.

The lengths of DJP1, DJP2, XYT1 and XYT2 range between 11.1 cm and 12.6 cm, XYT7 and XYT8 are 14.1 and 15.4 cm long, and DJP4 is 17.1 cm in length. In spite of this, their morphologies are consistent, which suggests that in different developmental stages, *Jialingpus* isp. did not significantly change its pes shape; allometry was not pronounced.

So far, at least six deinonychosaurian tracksites have been discovered in the Lower Cretaceous of Asia (Lockley et al., in press; Xing et al., 2013b). The most remarkable characteristic of deinonychosaurian tracks is their didactyly. The two parallel digits of DJP3 are typical of didactyl theropod tracks, such as *Dromaeopodus* from Shandong Province (Li et al., 2007) or *Dromaeosauripus* from Korea (Kim et al., 2008, 2012). DJP3 lacks an impression corresponding to the proximal portion of digit II, but is otherwise similar to *Dromaeosauripus*. However, Gaston et al. (2003) suggested that some poorly-preserved tridactyl tracks may lack the distal parts of digit II and become a "didactyl" variant. If this were the case for DPJ3, its morphology would still be unusual in that the two preserved digit impressions are nearly parallel. As DJP3 is morphologically unique among the discovered tracks, it is difficult to determine whether it represents an actual didactyl track, or an extramorphological variant created by a particular behavior of the track maker, by the influence of the substrate, or by a combination of both. Given the isolated occurrence of DJP3 among many tridactyl tracks, the latter interpretation is most parsimonious.

4. Conclusions

Jialingpus isp. from the Dijiaping and Bawangzhuang tracksites are the first record of this ichnogenus from central China. These footprints also enrich the Early Cretaceous dinosaur track record from the Ordos Basin. The discoveries extend the distribution of *Jialingpus* in China from Sichuan (Zhen et al., 1983) and Wuerhe, Xinjiang (Xing et al., 2011, 2013a) to the Shaanxi Province. Furthermore, it is the second record of *Jialingpus* in the Chinese Cretaceous strata after the reports from the Huangyangquan tracksites in Xinjiang, China. This suggests that the track-making taxon or taxa, small- to medium-sized, functionally-tridactyl theropods of similar foot structures, were widely distributed across China in space and time. The review given here suggests that *Jialingpus* is distinct from *Grallator* not only in the presence of a hallux (digit I) which, fortuitously, is characteristic of the holotype, but also in the presence of a large metatarsophalangeal area consisting of metatarsophalangeal pads II and IV separated only by a crease. The hallux in the holotype suggests the trackmaker possessed a relatively long digit I in comparison with the *Grallator* trackmaker. A review of the Sichuan *Jialingpus* and its relationships to forms such as *Asianopodus* will be the subject of future study. The "trackmaker" of *Jialingpus* might actually represent a large number of species, a possibility consistent with the wide geographic and temporal range of this ichnotaxon.

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