Available online at www.sciencedirect.com
ScienceDirect
Palaeoworld
Palaeoworld xxx (2013) xxx–xxx
www.elsevier.com/locate/palwor

Theropod and possible ornithopod track assemblages from the Jurassic–Cretaceous boundary Houcheng Formation, Shangyi, northern Hebei, China

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Received 11 July 2013; received in revised form 19 September 2013; accepted 11 October 2013

Abstract

Dinosaur track assemblages from the Houcheng Formation in the small continental Shangyi Basin of northern Hebei Province, China bridge a gap in the record of vertebrates from this unit and enrich our knowledge of ichnofaunas from the Jurassic–Cretaceous boundary. Their stratigraphic position between the Middle Jurassic Yan-Liao Biota and the Lower Cretaceous Jehol Biota gives them a special importance. New discoveries allow a re-assessment of theropod and possible ornithopod tracks that are present with several trackways. Seventy-three footprints were examined and documented. Despite their smaller size, the tridactyl mesaxonic theropod tracks show morphological similarities with the ichnogenus *Therangospodus* known from the Upper Jurassic deposits of North America, Europe, and Central Asia. The possible ornithopod tracks lack an associated manus imprint, suggesting a bipedal trackmaker. These possible ornithopod tracks from the Houcheng Formation provide evidence for the presence of small basal ornithopods or basal Cerapoda in the Upper Jurassic–Lower Cretaceous in this region. The depositional environment was the margin of an extensive shallow lake with fluctuating water levels under seasonally dry climate.

Keywords: Theropod tracks; Possible ornithopod tracks; Jurassic–Cretaceous boundary; Houcheng Formation; Shangyi

1. Introduction

Vertebrate fossils from the Upper Jurassic–Lower Cretaceous Houcheng Formation (= Tuchengzi Formation) are rare; therefore, the dinosaur tracks from these strata are important (Zhang et al., 2012) specifically because of their stratigraphic position between the Middle Jurassic Yan-Liao Biota (comprising the Jiulongshan and Tiaojishan formations) and the Lower Cretaceous Jehol Biota (comprising the Zhangjiakou, Dabeigou, Yixian, and Jiufotang formations). Both biotas are famous for their feathered dinosaurs, primitive birds, mammals, pterosaurs, fishes, and insects.

To date at least ten tracksites have been discovered in Houcheng/Tuchengzi Formation strata (Houcheng Formation from Hebei Province = Tuchengzi Formation from Liaoning Province). Abundant dinosaur tracks have been described, including those of theropods such as *Anchisauripus* isp. (Sullivan et al., 2009), *Grallator* type (Yabe et al., 1940; Shikama, 1942; Young, 1960; Zhang Y.Z. et al., 2004; Matsukawa et al., 2006; Fujita et al., 2007; Xing et al., 2011; Zhang J.P. et al., 2012), *Megalosauripus* isp. (Xing et al., 2011), *Menglongipus* (Xing et al., 2009), and *Therangospodus* isp. (Xing et al., 2011). Other known ichnofossils are rare theropod swim tracks (Xing et al., 2011) and a crouching trace (Xing et al., 2012), as well as the avian ichnite *Pullornipes* (Lockley et al., 2006). In 2012, hundreds of thyreophoran (cf. *Deltapodus* isp.), theropod, ornithopod, and sauropod tracks were discovered in Yanqing, Beijing (Zhang et al., 2012) (The present study shows that these thyreophorans can be interpreted as poorly-preserved

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http://dx.doi.org/10.1016/j.palwor.2013.10.002

sauropod tracks; these specimens will be published elsewhere). Other theropod and questionable sauropod (possible ornithopod, too; see section 4.2. in this paper) track assemblages were described from Shangyi, Hebei Province (Liu et al., 2012). These abundant dinosaur and bird track assemblages have bridged the gap in the vertebrate fossil record of the Houcheng/Tuchengzi Formation. In 2013, the first author and Liu Y.Q.'s team investigated the Shangyi tracksite again. Here we redescribe these tracks based on the newly collected data.

2. Institutional abbreviations

IVPP = Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, China. SY = Shangyi tracksite, Zhangjiakou City, Hebei Province, China. YQS = Yanqing tracksite, Beijing City, China.

3. Geological setting

The Shangyi tracksite (GPS: 40°56′36″N, 114°15′44″E) lies 7 km north of Xiaosuangou Town in Shangyi Country, Zhangjiakou City, northwestern Hebei Province (Fig. 1). The Shangyi Basin has been a small continental basin since the late Mesozoic and includes the Archean–Proterozoic, Mesozoic and Cenozoic strata.

Historically, the Upper Jurassic to Lower Cretaceous stratal sequences in the Western Hills of Beijing and in Hebei Province have been assigned to the Houcheng Formation, whereas those in Liaoning Province have been referred to as the Tuchengzi Formation. The term Houcheng is preferred in the present paper. The age of the aeolian sand bed mixed with tuff of the third member (dinosaur track layer) of the Tuchengzi Formation in Beipiao and Chaoyang, in the northern Liaoning Province, is 137 Ma based on SHRIMP zircon U-Pb (Xu et al., 2012). Swisher et al. (1999) have dated the plagioclase Ar-Ar from the tuffs under the dinosaur track layer from Beipiao in the northwestern Liaoning Province at 139 Ma. The dinosaur tracks were found in the rhythmically deposited siltstone and fine sandstone from the upper member of the Houcheng Formation. Its age is probably early Early Cretaceous (Liu et al., 2012).

Irregularly and cresentic ripples are also developed within the footprint layer (Fig. 2E) along with different sized mud cracks, raindrop imprints, and invertebrate burrowing traces and burrows. The sedimentary facies indicate that they were formed near the edge of an extensive, shallow lake within a seasonal, drought environment (Liu et al., 2012).

4. Ichnology

4.1. Theropod tracks

Material. At least 54 complete natural molds cataloged as SYT1-54 (Figs. 2C, D, 3A–C, 4–6; Table 1). These original tracks were not collected and are still in situ.

Locality and horizon. Houcheng Formation, Lower Cretaceous. Shangyi tracksite, Zhangjiakou City, Hebei Province, China.

Description

Originally upon discovery, there were 71 theropod tracks at the tracksite (Liu et al., 2012). However, with more than one year of weathering, some tracks are now indistinct and broken. Furthermore, new tracks were discovered in April 2013 on which the descriptions herein are based. Except for four specimens (SYT43–46), the theropod tracks at Shangyi tracksite are generally of the same size and morphology.

SYT53 (Fig. 4) is the best-preserved imprint. The digit III trace is directed anteriorly and the longest, whereas that of digit II is shorter than digit IV. Digit II possesses two phalangeal pad traces, and digits III and IV, three phalangeal pad traces. Claw marks are distinct. The metatarsophalangeal region lies nearly in line with the long axis of digit III. SYT53 has two distinct circular metatarsophalangeal pad traces, a smaller one corresponding to digit II and the other, larger one corresponding to digit IV. The metatarsophalangeal pad trace of digit II is connected to the trace of the first pad of digit II via an inter-pad space and also in contact with the metatarsophalangeal pad of digit IV. The divarication angle between digits II and III is almost equal to that of digits III and IV. SYT51–53 constitute one distinct trackway (Fig. 3C). The mean pace length is 108 cm and the pace angulation 166°.

The specimens SYT7, 14, 20, 30, 34, 40, 50, and 52 (Fig. 5) are well-preserved, similar to SYT53. The metatarsophalangeal pad of digit IV is nearly in line with the axis of digit III, such as in T14, 34, 40, but in others it is slightly displaced. The borders between the metatarsophalangeal pad traces of digits II and IV are shallow.

The mean divarication angle between the traces of digits II and IV of the Shangyi theropod tracks is 54°, ranging from 43° to 61°, and the divarication angles between digits II and III are on average larger than those between digits III and IV. The imprints have a mean length width (L/W) ratio of 1.66 (N = 38), and the mean L/W ratio of the anterior triangle is 0.69 (N = 36) (Fig. 4), indicating moderate mesaxony, unlike the strong mesaxony typical of the *Grallator* type (Lockley, 2009).

SYT43–46 (Figs. 3B, 6) are tracks that were likely revealed by recent weathering because Liu et al. (2012) did not report them. The average length of SYT43–46 is 4.9 cm. The four footprints constitute one trackway. SYT45 (Fig. 6) is the best-preserved and similar in morphology to the large-sized theropod tracks represented by SYT53. The border between the metatarsophalangeal region and digits II and IV is indistinct. Distinct claw marks are preserved. The L/W ratio of the anterior triangle is 0.62, the mean pace length 30 cm, and the pace angulations range 173°.

Comparison and discussion

Tridactyl tracks such as those from Shangyi were typically left by bipedal theropods.

In size, the Shangyi theropod tracks (mean length 16 cm) are similar to *Anchisauripus* isp. (Sullivan et al., 2009), *Grallator* morphotype type B and C (Fujita et al., 2007), and *Therangospodus* isp. (Xing et al., 2011) from the Tuchengzi Formation. However, the materials of *Anchisauripus* isp. from the Nanshuangmiao tracksite described by Sullivan et al. (2009) are insufficient (eight tracks) for confident identification. For example, digit III of IVPP VC 15815 G is wider than in B and F

Table 1
Measurements (in cm) of theropod and possible ornithopod tracks from Shangyi tracksite, China.

Specimen	ML	MW	LD II	LD III	LD IV	II–III	III–IV	II–IV	PL	SL	PA	L/W
SYT1[*]	17.5	9.6	8.4	11.3	9.4	22°	21°	43°	—	—	—	1.8
SYT2	15.1	—	—	—	—	—	—	—	—	—	—	—
SYT3	16.4	9.0	7.9	11.4	8.5	27°	20°	47°	—	—	—	1.8
SYT4	18.4	11.7	—	—	—	—	—	54°	—	—	—	1.6
SYT5	16.5	9.1	7.9	11.6	8.2	24°	25°	49°	—	—	—	1.8
SYT6	16.6	11.0	7.5	10.9	9.2	29°	32°	61°	—	—	—	1.5
SYT7	16.2	9.6	7.9	12.0	7.7	25°	27°	52°	—	—	—	1.7
SYT8	15.4	10.4	7.3	10.5	7.8	30°	26°	56°	—	—	—	1.5
SYT9	17.7	—	—	—	—	—	—	—	—	—	—	—
SYT10	16.6	—	—	—	—	—	—	—	—	—	—	—
SYT11	16.9	10.6	9.1	10.7	9.3	25°	26°	51°	—	—	—	1.6
SYT12	17.9	9.7	—	11.1	—	—	—	51°	—	—	—	1.8
SYT13	15.1	9.8	6.6	8.3	—	28°	27°	55°	—	—	—	1.5
SYT14	17.0	9.8	8.5	11.6	7.0	26°	22°	48°	—	—	—	1.7
SYT15	14.6	10.1	6.8	10.6	8.0	27°	28°	55°	—	—	—	1.4
SYT16	15.5	8.5	—	10.3	—	25°	22°	47°	—	—	—	1.8
SYT17	15.5	9.3	—	—	—	30°	20°	50°	—	—	—	1.7
SYT18	15.9	—	—	—	—	—	—	—	—	—	—	—
SYT19	17.0	10.6	—	—	—	—	—	52°	—	—	—	1.6
SYT20	16.8	11.4	7.8	12.2	9.0	30°	27°	57°	—	—	—	1.5
SYT21	15.9	8.9	8.1	11.4	7.2	27°	23°	50°	—	—	—	1.8
SYT22	15.1	8.2	—	9.0	—	30°	21°	51°	—	—	—	1.8
SYT23	15.2	9.1	7.7	10.7	7.5	26°	24°	50°	—	—	—	1.7
SYT24	15.8	—	—	—	—	—	—	—	—	—	—	—
SYT25	15.1	8.3	6.7	10.5	—	26°	27°	53°	—	—	—	1.8
SYT26	15.0	—	—	—	—	—	—	—	—	—	—	—
SYT27	17.7	—	—	—	—	—	—	—	—	—	—	—
SYT28	16.0	9.3	7.1	10.9	8.8	27°	23°	50°	—	—	—	1.7
SYT29	—	10.3	8.4	—	—	—	—	—	—	—	—	—
SYT30	16.0	10.8	8.8	12.1	8.3	—	25°	57°	—	—	—	1.5
SYT31	—	8.9	6.6	—	—	—	—	53°	—	—	—	—
SYT32	14.9	9.5	6.4	10.6	7.2	26°	23°	49°	—	—	—	1.6
SYT33	15.7	8.8	7.0	10.4	8.2	—	—	—	—	—	—	1.8
SYT34	15.7	9.2	7.8	11.2	7.7	31°	22°	53°	—	—	—	1.7
SYT35	—	8.7	—	—	—	—	—	—	—	—	—	—
SYT36	15.0	8.4	7.8	11.4	—	—	—	—	—	—	—	1.8
SYT37	14.5	8.4	6.8	10.7	6.2	25°	29°	54°	—	—	—	1.7
SYT38	—	8.6	—	11.7	—	30°	28°	58°	—	—	—	—
SYT39	14.9	—	7.4	—	—	—	—	—	—	—	—	—
SYT40	16.0	8.3	7.3	11.4	7.2	29°	21°	50°	—	—	—	1.9
SYT41	—	—	6.5	—	—	—	—	—	—	—	—	—
SYT42	15.0	—	—	—	—	—	—	—	—	—	—	—
SYT43	4.3	—	2.5	—	—	—	—	—	29.0	59.5	165	—
SYT44	5.5	3.0	—	—	—	33°	16°	49°	31.0	60.0	180	1.8
SYT45	4.9	2.9	2.3	3.3	2.6	32°	20°	52°	29.0	—	—	1.6
SYT46	4.8	3.0	—	—	—	—	—	—	—	—	—	1.6
SYT47	15.6	9.8	6.8	9.3	—	26°	34°	60°	—	—	—	1.6
SYT48	15.6	10.2	8.5	10.7	9.1	26°	28°	54°	—	—	—	1.5
SYT49	14.3	9.6	7.6	9.9	7.8	31°	20°	51°	—	—	—	1.5
SYT50	15.7	9.6	8.1	11.3	7.0	29°	20°	49°	—	—	—	1.6
SYT51	—	—	—	—	—	—	—	—	106.0	213.5	166	—
SYT52	17.9	11.1	7.8	11.1	8.5	30°	23°	53°	109.0	—	—	1.6
SYT53	17.3	11.6	8.0	12.0	8.3	30°	28°	58°	—	—	—	1.5
SYT54	14.5	8.5	—	—	—	—	—	52°	—	—	—	1.7
SYS1-1L[#]	13.5	15.0	—	—	—	—	—	—	51.5	99.5	150	0.9
SYS1-2R	15.5	15.1	—	—	—	—	—	—	51.4	98.2	147	1.0
SYS1-3L	14.8	16.5	—	—	—	—	—	—	51.0	99.0	153	0.9
SYS1-4R	14.8	15.5	—	—	—	—	—	—	50.8	96.0	148	1.0
SYS1-5L	16.0	16.0	—	—	—	—	—	—	49.0	95.5	154	1.0
SYS1-6R	16.0	15.8	—	—	—	—	—	—	49.0	91.0	147	1.0
SYS1-7L	16.5	15.3	—	—	—	—	—	—	45.8	88.4	152	1.1
SYS1-8R	14.2	15.5	—	—	—	—	—	—	45.4	93.0	150	0.9
SYS1-9L	15.5	14.0	—	—	—	—	—	—	50.8	98.0	165	1.1

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Table 1 (*Continued*)

Specimen	ML	MW	LD II	LD III	LD IV	II–III	III–IV	II–IV	PL	SL	PA	L/W
SYS1-10R	13.5	13.2	—	—	—	—	—	—	48.0	89.0	143	1.0
SYS1-11L	15.0	14.0	—	—	—	30°	37°	67°	45.8	85.5	139	1.1
SYS1-12R	15.5	17.0	—	—	—	32°	30°	62°	45.5	90.5	163	0.9
SYS1-13L	16.0	15.5	—	—	—	—	—	—	46.0	90.0	156	1.0
SYS1-14R	15.0	14.0	—	—	—	—	—	—	46.0	—	—	1.1
SYS1-15L	14.3	14.6	—	—	—	—	—	—	—	—	—	1.0
SYS2-1R	11.6	11.8	—	—	—	—	—	—	53.5	—	—	1.0
SYS2-2L	12.5	12.0	—	—	—	—	—	—	—	—	—	1.0
SYS2-10L	11.6	12.0	—	—	—	—	—	—	51.0	—	—	1.0
SYS2-11R	12.5	12.1	6.5	9.1	7.1	37°	27°	64°	—	—	—	1.0

Abbreviations: ML: maximum length; MW: maximum width; 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; PL: pace length; SL: stride length; PA: pace angulation; L/W: ML/MW.

* Measured as the distance between the tips of digits II and IV.

\# Measured as the distance between the maximum width of the footprint.

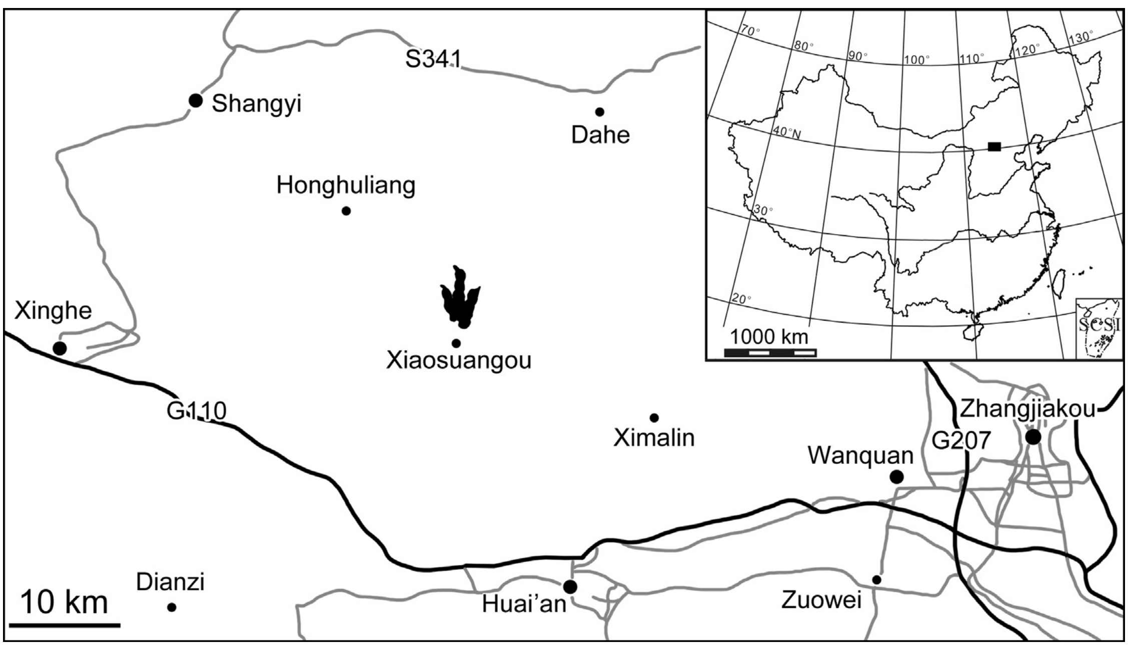

Fig. 1. Geographic position of the Shangyi dinosaur footprint locality (footprint icon).

Fig. 2. Photograph and distribution pattern of the Shangyi tracksite. A and B are ornithopod trackways, C and D are theropod trackways, and E is a surface with ripple marks.

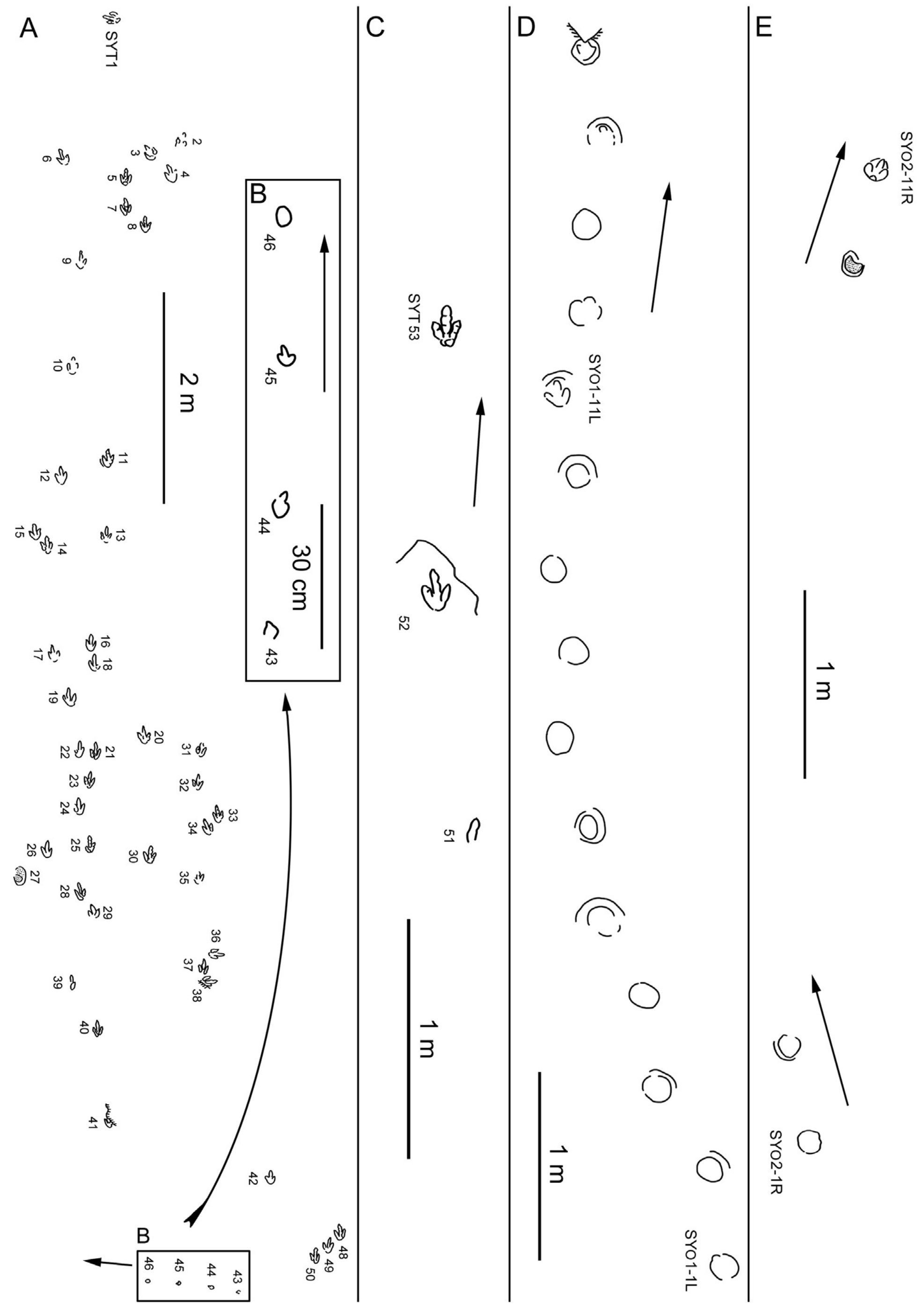

Fig. 3. Distribution pattern of the Shangyi tracksite. A–C are theropod trackways, and D and E are ornithopod trackways.

(Sullivan et al., 2009, fig. 4) and the anterior triangles are 1.00 (G) and 0.63 (B and F), respectively. They likely represent two different ichnospecies. The Shangyi theropod tracks are most similar to IVPP VC 15815 B and F (Fig. 5).

For B1 and C14 (Fujita et al., 2007, fig. 6), which are well-preserved specimens of *Grallator*, the length width (L/W) ratio ranges from 1.7 to 1.8, and the L/W ratio of the anterior triangle ranges from 0.5 to 0.55. However, both B1 and C14 have a distinctive, relatively swollen metatarsophalangeal region, positioned in line with the long axis of digit III, which makes B1 and C14 more similar to *Jialingpus* than *Grallator*. The Shangyi theropod tracks lack such a developed metatarsophalangeal region.

The Shangyi theropod tracks are similar to *Therangospodus* isp. from the Luofenggou tracksite (Xing et al., 2011); especially the best-preserved LF 1 that has a length width (L/W) ratio of 1.3 and a L/W ratio of the anterior triangle of 0.54. Lockley et al. (1998) originally described the theropod ichnotaxon *Therangospodus* from the Upper Jurassic of North America, Europe, and central Asia for medium sized (averaging 28 cm long),

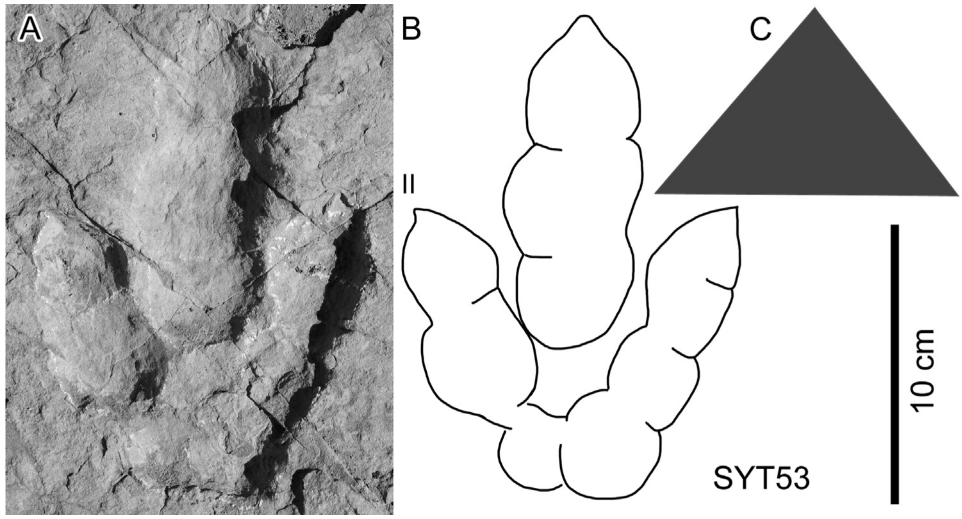

Fig. 4. SYT53, theropod footprint from the Shangyi tracksite. (A) Photography; (B) Outline drawing; (C) Anterior triangle, drawn between the tips of the distal ends of digits II, III and IV (sensu Weems, 1992; Lockley, 2009), indicating the degree of mesaxony.

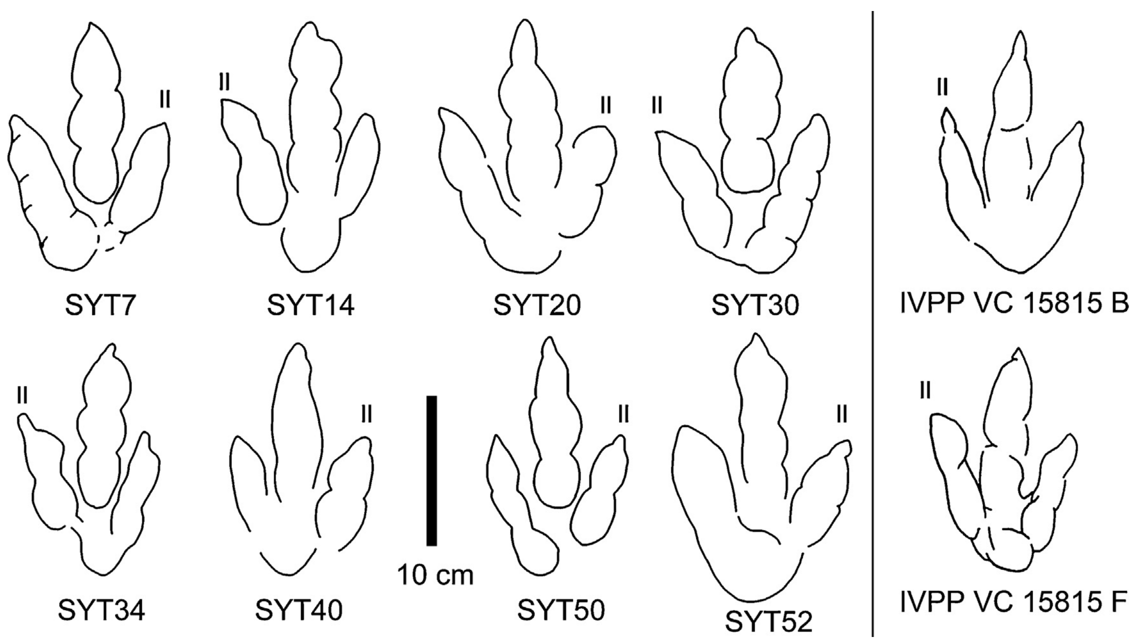

Fig. 5. Well-preserved theropod footprints from the Shangyi tracksite (SYT specimens), and theropod footprints from the Nanshuangmiao tracksite (IVPP specimens) (Sullivan et al., 2009).

elongate, asymmetric theropod tracks with coalesced, elongate, oval digital pads that are not subdivided into discrete phalangeal pads, and with a mean L/W ratio of the anterior triangle of 0.55 (ranging 0.47 to 0.61, based on Lockley et al., 1998, fig. 6A–G). The size of the Shangyi theropod tracks is smaller than that of *Therangospodus* (Lockley et al., 1998), and the claw marks are sharper. According to these morphological differences, the Shangyi specimens are therefore referred here tentatively to cf. *Therangospodus*.

In China, assemblages with the typical Lower Jurassic forms (*Grallator*, *Kayentapus* and *Anomoepus*) evidently persist through the Middle and Upper Jurassic formations, and these theropod tracks show a continuous range of morphological and preservational variation that is difficult to differentiate in space and time (Lockley et al., 2013; Xing et al., 2013).

Abundant theropod tracks yielded from the Houcheng/Tuchengzi Formation will need further comparison and discussion.

4.2. Possible ornithopod tracks

Material. Fifteen complete natural molds, cataloged as SYO1-1–15, constitute one trackway (Figs. 2A, 3D, 7A, B); four complete natural molds, cataloged as SYO2-1–2, 10–11, constitute one incomplete trackway (Figs. 2B, 3E, 7C, D).

Locality and horizon. Same as 4.1.

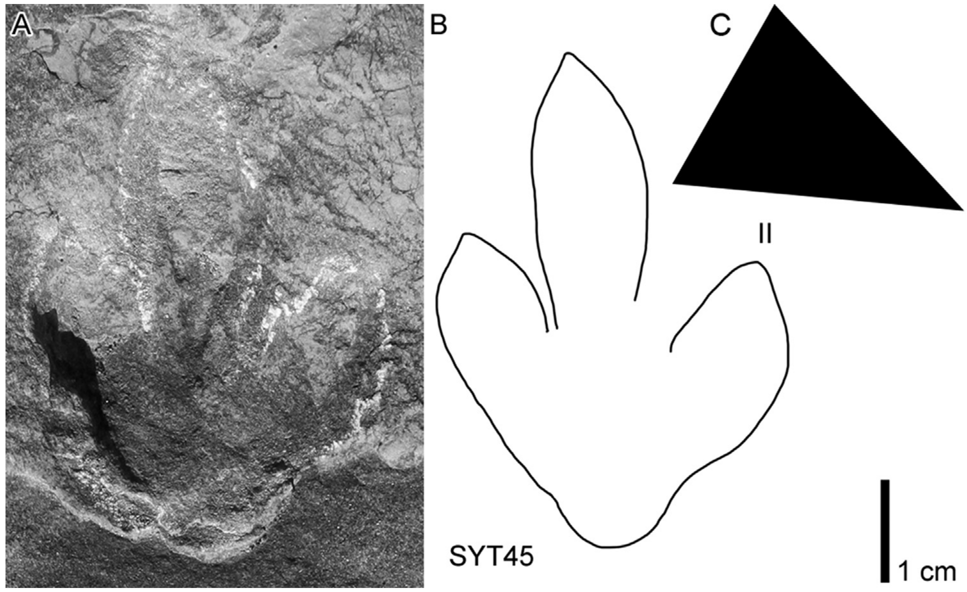

Fig. 6. SYT45, theropod footprint from the Shangyi tracksite. (A) Photography; (B) Outline drawing; (C) Anterior triangle.

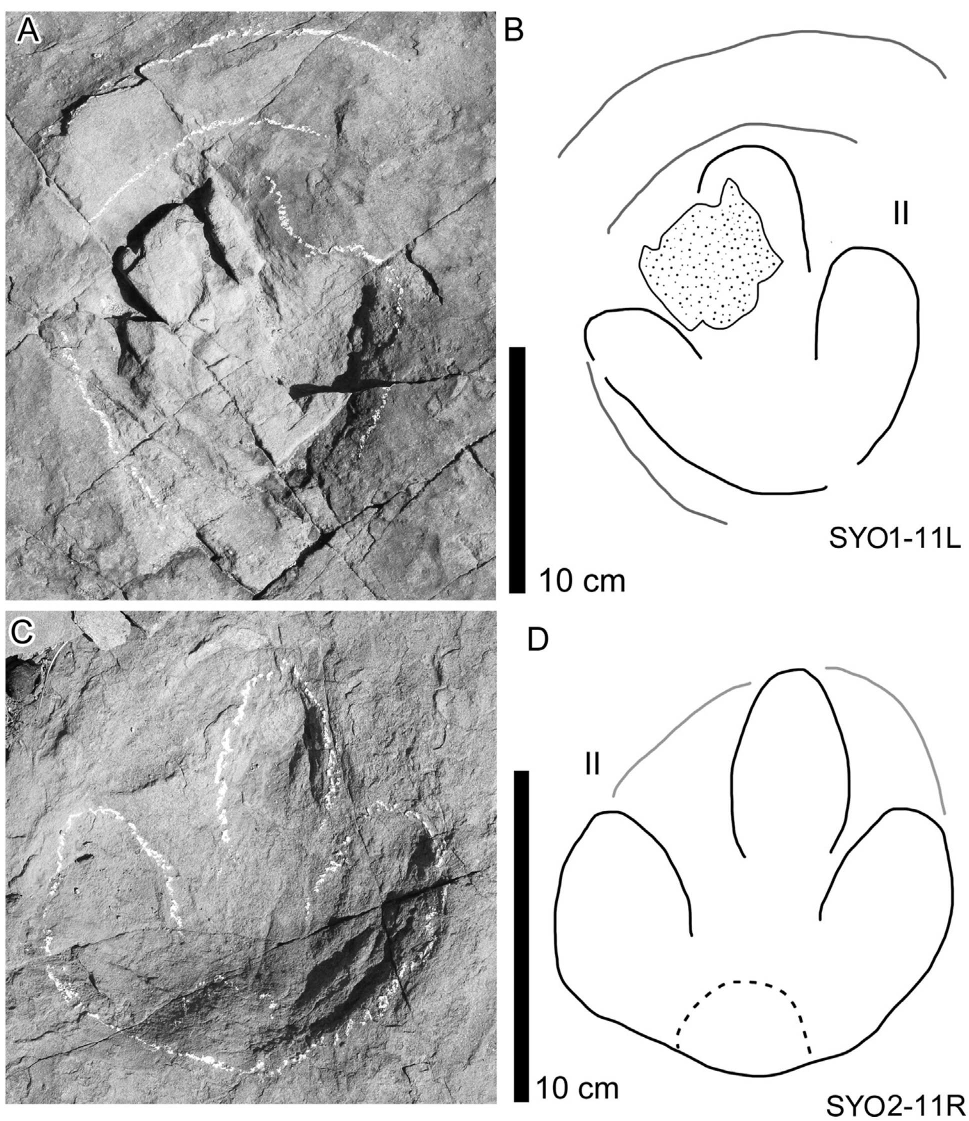

Fig. 7. Ornithopod footprints SYO1-11L and SYO2-11R from the Shangyi tracksite. (A and C) Photography; (B and D) Outline drawing.

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Description

The Shangyi SYO1 trackways are poorly-preserved, mostly as round impressions, and were identified as sauropod tracks (Liu et al., 2012). Shangyi SYO2 is a newly-discovered track. The average length of Shangyi SYO1 is 15.1 cm (N = 15). Shangyi SYO2 is shorter than SYO1 with an average length of 12.1 cm (N = 4). The mean pace length of Shangyi SYO1 and SYO2 is 48.2 and 52.3 cm, respectively, and the mean pace angulation 151° for SYO1.

The well-preserved SYO2-11R (Fig. 7C, D) is tridactyl, with digit II being the shortest and widest; digit III is longer than other two lateral digits. The metatarsophalangeal pad is large and semi-circular in shape with an indistinct border to the three digits.

Most tracks of Shangyi SYO1 and SYO2 are round impressions with no distinct digital traces. The maximum length/maximum width ratio is 1.00 (Table 1), with the width measured along the maximum distance between the inner and outer margins of the footprint. If measured as the distance between the tips of digits II and IV, the widths of SYO1-11L, 12R, and SYO2-11R are 12, 13, and 9.8 cm and the L/W ratio is 1.3, 1.2, and 1.3, respectively.

Comparison and discussion

Ornithopod tracks are rare in the Tuchengzi Formation. Zhang et al. (2012) reported three imprints, but all are poorly-preserved. The newly-discovered Shangyi SYO1 and SYO2 tracks lack distinct claw marks and their widths are subequal to their lengths. All show the characteristic shape of common ornithopod tracks (Lockley and Hunt, 1995).

In morphology, the Shangyi SYO1 and SYO2 tracks are similar to *Dinehichnus* (Lockley et al., 1998, 2009; Gierliński et al., 2009) from the Upper Jurassic Morrison Formation of the United States and from the Lower Cretaceous of Spain. *Dinehichnus* was attributed to a mid-sized ornithopod (Lockley et al., 1998). Its size (length 10–19 cm) and trackway narrow with pace angulation of about 155° are similar to that of the Shangyi specimens. However, the divarication angles between digits II–IV are 90°, which is larger than in the Shangyi specimens (64°). In addition, in *Dinehichnus* digit III is sharp anteriorly, whereas in the Shangyi specimen it is round and blunt. SYO1 and SYO2 are similar to the Yanqing ornithopod tracks (Zhang et al., 2012). For YQS1D-D1 the length is 14 cm, the L/W ratio is 1.3, and the divarication angle between digits II and IV is 61°.

The Late Jurassic fossil record of basal ornithopods or basal Cerapoda in China is scarce. The former includes *Gongbusaurus wucaiwanensis* from the Shishugou Formation of Xinjiang Autonomous Region (Dong, 1989), *Yandusaurus hongheensis* from the Shangshaximiao Formation of Sichuan Province (He, 1979), and the latter includes *Hexinlusaurus multidens*, also from the Shangshaximiao Formation of Sichuan Province (He and Cai, 1983; Barrett et al., 2005). The Early Cretaceous basal ornithopods represented by Jeholosauridae (Han et al., 2012) and include *Jeholosaurus shangyuanensis* from the Yixian Formation of Liaoning Province (Xu et al., 2000; Han et al., 2012) and *Changchunsaurus parvus* from the Quantou Formation of Jilin Province (Zan et al., 2005). The discovery of small ornithopod tracks at Shangyi and Yangqing indicates that small-size basal ornithopods or basal cerapods exist near the Jurassic–Cretaceous boundary when the Houcheng/Tuchengzi Formation sediments were deposited.

The Shangyi SYO1 and SYO2 tracks lack manus imprints. This implies that the trackmaker was bipedal, which coincides with the skeleton morphology of small-sized ornithopods such as dryosaurids (Heinrich et al., 1993). In addition, it is possible that the manus imprints were too shallow to have been preserved (Castanera et al., 2013).

The Shangyi SYO1 and SYO2 trackways of the same morphotype might suggest that the trackmakers exhibited a gregarious behavior, but this is a mere speculation, not strongly supported by any other evidence. Alternatively this could indicate that a similar pathway necessitated by the local topography was taken independently by different individuals.

5. Conclusions

Small theropods and possible ornithopods frequented the margin of a shallow lake in today's northern Hebei Province during deposition of the Houcheng Formation. This is evidenced by preserved trackways that enrich our knowledge of dinosaur faunas near the Jurassic–Cretaceous boundary. The new discoveries allow a re-assessment of the ichno-assemblage and a comparison with similar forms from other localities. The theropod tracks show some similarities with the ichnogenus *Therangospodus* from the Upper Jurassic, whereas the possible ornithopod tracks cannot be assigned more closely.

Acknowledgements

We thank Martin G. Lockley (Dinosaur Tracks Museum, University of Colorado Denver, USA) for his suggestions on an earlier version of the manuscript; Richard T. McCrea (Peace Region Palaeontology Research Centre, Canada) and Lisa G. Buckley (University of Alberta, Canada) for their helpful reviews of the manuscript. Thanks to Mr. Tong Wang for assistance and logistical support during the field expedition to study the tracks.

References

Barrett, P.M., Butler, R.J., Knoll, F., 2005. Small-bodied ornithischian dinosaurs from the Middle Jurassic of Sichuan, China. Journal of Vertebrate Paleontology 25, 823–834.

Castanera, D., Vila, B., Razzolini, N.L., Falkingham, P.L., Canudo, J.I., Manning, P.L., Galobart, À., 2013. Manus track preservation bias as a key factor for assessing trackmaker identity and quadrupedalism in basal ornithopods. PLoS ONE 8 (1), e54177, http://dx.doi.org/10.1371/journal.pone.0054177.

Dong, Z.M., 1989. On a small ornithopod (*Gongbusaurus wucaiwanensis* sp. nov.) from Kelamaili, Junggar Basin, Xinjiang, China. Vertebrata PalAsiatica 27 (2), 140–146 (in Chinese, with English abstract).

Fujita, M., Azuma, Y., Lee, Y.N., Lü, J.C., Dong, Z.M., Noda, Y., Urano, K., 2007. New theropod track site from the Upper Jurassic Tuchengzi Formation of Liaoning Province, northeastern China. Memoir of the Fukui Prefectural Dinosaur Museum 6, 17–25.

Gierliński, G., Niedźwiedzki, G., Nowacki, P., 2009. Small theropod and ornithopod foot prints in the Late Jurassic of Poland. Acta Geologica Polonica 59, 221–234.

Han, F.L., Barrett, P.M., Butler, R.J., Xu, X., 2012. Postcranial anatomy of *Jeholosaurus shangyuanensis* (Dinosauria, Ornithischia) from the Lower Cretaceous Yixian Formation of China. Journal of Vertebrate Paleontology 32 (6), 1370–1395.

He, X.L., 1979. A newly discovered ornithopod dinosaur *Yandusaurus* from Zigong, Sichuan. In: Contributions to International Exchange of Geology. Part 2. Stratigraphy and Paleontology, Geological Publishing House, Beijing, pp. 116–123 (in Chinese, with English abstract).

He, X.L., Cai, K.J., 1983. A new species of *Yandusaurus* (hypsilophodont dinosaur) from the Middle Jurassic of Dashanpu, Zigong, Sichuan. Journal of Chengdu College of Geology, Supplement 1, 5–14 (in Chinese).

Heinrich, R.E., Ruff, C.B., Weishampel, D.B., 1993. Femoral ontogeny and locomotor biomechanics of *Dryosaurus lettowvorbecki* (Dinosauria, Iguanodontia). Zoological Journal of the Linnean Society 108, 179–196.

Liu, Y.Q., Kuang, H.W., Peng, N., Xu, H., Chen, J., Xu, J.L., Liu, H., Zhang, P., 2012. New discovery of dinosaur footprints in the Upper Jurassic–Lower Cretaceous Houcheng Formation at Shangyi, northwestern Hebei Province and its biogeographical implications. Journal of Palaeogeography 14 (5), 617–627.

Lockley, M.G., 2009. New perspectives on morphological variation in tridactyl footprints: clues to widespread convergence in developmental dynamics. Geological Quarterly 53, 415–432.

Lockley, M.G., Hunt, A.P., 1995. Dinosaur Tracks and Other Fossil Footprints of the Western United States. Columbia University Press, New York, 360 pp.

Lockley, M.G., dos Santos, V.F., Meyer, C.A., Hunt, A., 1998. A new dinosaur tracksite in the Morrison Formation, Boundary Butte, southeastern Utah. Modern Geology 23, 317–330.

Lockley, M.G., Matsukawa, M., Ohira, H., Li, J.J., Wright, J., White, D., Chen, P.J., 2006. Bird tracks from Liaoning Province, China: new insights into avian evolution during the Jurassic–Cretaceous transition. Cretaceous Research 27, 33–43.

Lockley, M.G., McCrea, R.T., Matsukawa, M., 2009. Ichnological evidence for small quadrupedal ornithischians from the basal Cretaceous of SE Asia and North America: implications for a global radiation. In: Buffetaut, E., Cuny, G., Le Loeuff, J., Suteethorn, V. (Eds.), Late Palaeozoic and Mesozoic Ecosystems in SE Asia. Special Publications of the Geological Society of London 315, pp. 255–269.

Lockley, M.G., Li, J.J., Li, R.H., Matsukawa, M., Harris, J.D., Xing, L.D., 2013. A review of the tetrapod track record in China, with special reference to type ichnospecies: implications for ichnotaxonomy and paleobiology. Acta Geologica Sinica (English Edition) 87 (1), 1–20.

Matsukawa, M., Lockley, M.G., Li, J.J., 2006. Cretaceous terrestrial biotas of East Asia, with special reference to dinosaur-dominated ichnofaunas: towards a synthesis. Cretaceous Research 27, 3–21.

Shikama, T., 1942. Footprints from Chinchou, Manchoukuo, of *Jeholosauripus*, the Eo-Mesozoic dinosaur. Bulletin of the Central National Museum of Manchoukuo 3, 21–31.

Swisher, C.C., Wang, Y.Q., Wang, X.L., Xu, X., Wang, Y., 1999. Cretaceous age for the feathered dinosaurs of Liaoning, China. Nature 400, 58–61.

Sullivan, C., Hone, D.W.E., Cope, T.D., Liu, Y., Liu, J., 2009. A new occurrence of small theropod tracks in the Tuchengzi Formation of Hebei Province, China. Vertebrata PalAsiatica 47, 35–52.

Weems, R.E., 1992. A re-evaluation of the taxonomy of Newark Supergroup saurischian dinosaur tracks, using extensive statistical data from a recently exposed tracksite near Culpeper Virginia. In: Sweet, P.C. (Ed.), Proceedings of the 26th Forum on the Geology of Industrial Minerals. Division of Mineral Resources, Virginia, pp. 113–127.

Xing, L.D., Harris, J.D., Sun, D.H., Zhao, H.Q., 2009. The earliest known deinonychosaur tracks from the Jurassic–Cretaceous boundary in Hebei, China. Acta Palaeontologica Sinica 48, 662–671.

Xing, L.D., Harris, J.D., Gierliński, G.D., 2011. *Therangospodus* and *Megalosauripus* track assemblage from the Upper Jurassic–Lower Cretaceous Tuchengzi Formation of Chicheng County, Hebei Province, China and their paleoecological implications. Vertebrata PalAsiatica 49, 423–434.

Xing, L.D., Gierliński, G.D., Harris, J.D., Divay, J.D., 2012. A probable crouching theropod dinosaur trace from the Jurassic–Cretaceous boundary in Hebei, China. Geological Bulletin of China 31, 21–26.

Xing, L.D., Lockley, M.G., Chen, W., Gierliński, G.D., Li, J.J., Persons, W.S., IV, Matsukawa, M., Ye, Y., Gingras, M.K., Wang, C.W., 2013. Two theropod track assemblages from the Jurassic of Chongqing, China, and the Jurassic stratigraphy of Sichuan Basin. Vertebrata PalasiAtica 51 (2), 107–130.

Xu, H., Liu, Y.Q., Kuang, H.W., Jiang, X.J., Peng, N., 2012. U-Pb SHRIMP age for the Tuchengzi Formation, northern China, and its implications for biotic evolution during the Jurassic–Cretaceous transition. Palaeoworld 21, 222–234.

Xu, X., Wang, X.L., You, H.L., 2000. A primitive ornithopod from the Early Cretaceous Yixian Formation of Liaoning. Vertebrata PalAsiatica 38 (4), 318–325 (in Chinese, with English abstract).

Yabe, H., Inai, Y., Shikama, T., 1940. Discovery of dinosaurian footprints from the Cretaceous of Yangshan, Chinchou: preliminary note. Proceedings of the Imperial Academy of Japan 16, 560–563.

Young, C.C., 1960. Fossil footprints in China. Vertebrata PalAsiatica 4, 53–66.

Zan, S.Q., Chen, J., Jin, L.Y., Li, T., 2005. A primitive ornithopod from the Early Cretaceous Quantou Formation of Central Jilin, China. Vertebrata PalAsiatica 43 (3), 182–193 (in Chinese, with English abstract).

Zhang, J.P., Xing, L.D., Gierliński, G.D., Wu, F.D., Tian, M.Z., Currie, P.J., 2012. First record of dinosaur trackways in Beijing, China. Chinese Science Bulletin (Chinese Edition) 57, 144–152 (in Chinese, with English abstract).

Zhang, Y.Z., Zhang, J.P., Wu, P., Zhang, X.B., Bai, S., 2004. Discovery of dinosaur tracks from the Middle–Late Jurassic Tuchengzi Formation in the Chaoyang area, Liaoning Province. Geological Review 50, 561–566 (in Chinese, with English abstract).