第52卷　第2期
2014年4月

古 脊 椎 动 物 学 报
VERTEBRATA PALASIATICA

pp. 233–259
figs. 1–14

Changpeipus (theropod) tracks from the Middle Jurassic of the Turpan Basin, Xinjiang, Northwest China: review, new discoveries, ichnotaxonomy, preservation and paleoecology

XING Li-Da[1,2]　Hendrik KLEIN[3]　Martin G. LOCKLEY[4]　Andreas WETZEL[5]
LI Zhong-Dong[6]　LI Jian-Jun[7]　Gerard D. GIERLIŃSKI[8,9]　ZHANG Jian-Ping[1]
Masaki MATSUKAWA[10]　Julien D. DIVAY[11]　ZHOU Long[6]

(1 *School of the Earth Sciences and Resources*, *China University of Geosciences* Beijing 100083, China xinglida@gmail.com)
(2 *Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences* Beijing 100044, China)
(3 *Saurierwelt Paläontologisches Museum* Alte Richt 7, D-92318 Neumarkt, Germany)
(4 *Dinosaur Tracks Museum*, *University of Colorado Denver* PO Box 173364, Denver, CO 80217, USA)
(5 *Geologisch-Paläontologisches Institut der Universität Basel* Bernoullistrasse 32, CH-4056 Basel, Switzerland)
(6 *Geophysical Team of Sichuan Bureau of Geological and Mineral Investigation and Exploration* Chengdu 610072, China)
(7 *Department of Research*, *Beijing Museum of Natural History* Beijing 100050, China)
(8 *JuraPark*, *ul. Sandomierska* 4, 27-400 Ostrowiec Świętokrzyski, Poland)
(9 *Polish Geological Institute* Rakowiecka 4, 00-975 Warszawa, Poland)
(10 *Department of Environmental Sciences*, *Tokyo Gakugei University* Koganei, Tokyo 184-8501, Japan)
(11 *Department of Biological Sciences*, *University of Alberta* 11455 Saskatchewan Drive, Edmonton, Alberta T6G 2E9, Canada)

Abstract　Theropod footprint assemblages from the Sanjianfang Formation (Middle Jurassic) at the Shanshan tracksite, Turpan City, Xinjiang, northwest China are documented and re-described in detail. Together with new discoveries from this locality, they shed light on the different preservation and extramorphological variation of a total of 143 footprints. Ichnotaxonomically, they are assigned to the ichnospecies *Changpeipus carbonicus*, well known from other Jurassic tracksites of China. The presence of two distinct morphotypes, as has been proclaimed in earlier studies, is related to extramorphological variation on surfaces that indicate a soft, wet and slippery substrate. Anatomically based features supporting different ichnospecies are not present. Furthermore, the comparison with similar footprints from other localities suggests a monotypic ichnogenus *Changpeipus* with the type species *C. carbonicus*. Footprint lengths of 12.2 cm (a few isolated examples) to 47 cm at the Shanshan tracksites reflect small to medium-sized trackmakers that can be interpreted either as different age classes or different biological species. Peculiar preservational features include a footprint that documents slipping movement of the pes by three parallel bands obviously reflecting digits II, III and IV. An associated "normally" impressed tridactyl footprint suggests that both constitute a single step. The depositional environment was a gradually expanding and deepening lacustrine setting. This is also supported by the co-occurrence of abundant invertebrate trace fossils. Contrary to earlier interpretations resulting in an assignment to *Lockeia* the invertebrate traces are re-assigned here to the ichnogenus *Fuersichnus* that can be

新疆维吾尔自治区国土资源厅新疆鄯善库木塔格沙漠地质遗迹调查项目(编号：XJYJDC2011-01)和中国科学院脊椎动物演化与人类起源重点实验室开放课题基金(编号：2011LESV008)资助。
收稿日期：2013-05-20

attributed to deposit-feeding insect larvae or other invertebrates. *Fuersichnus* is a characteristic dwelling and/or feeding burrow of muddy floodplains or lake margin settings.

Key words Shanshan, Xinjiang; Middle Jurassic; Sanjianfang Formation; *Changpeipus*, *Fuersichnus*

1 Introduction

The Xinjiang Uyghur Autonomous Region of China is rich in vertebrate fossils, but has few known dinosaur tracksites. At present, the only well preserved dinosaur tracks from the region are the theropod tracks from the Middle Jurassic Sanjianfang Formation, Turpan Basin (Wings et al., 2007), and the dinosaur, pterosaur, and bird footprint assemblages from the Lower Cretaceous Lower Layer of the Tugulu Group, Junggar Basin (Xing et al., 2011, 2013).

The first mention of dinosaur tracks from Xinjiang was by Matsukawa et al. (2006) based on two isolated small theropod track specimens in the collections of the Nanjing Institute of Geology and Paleontology. However these specimens were not illustrated or described in detail. So, the first significant report was by Wings et al. (2007), who investigated the tracksite described here in September and November in 2007 (Fig. 1). In July 2011, Xing Lida was invited by the Resources and Environment Institute of Mineral Exploration Department of the Bureau of Geology and Mineral Resources, Sichuan Province, to participate in the geologic heritage research project re-studying the tracksites in the Kumutage Desert, Shanshan County of Xinjiang. Unfortunately 30% of the middle tracksite (site I B) had collapsed since 2007 (Fig. 2A, B), destroying approximately 35 footprints. Among the excavated footprints, five specimens are stored at the Paleobiology Research Center, Jilin University (serial numbers: CAD07-SS001 to CAD07-SS005); the others remain scattered at the tracksite, and are difficult to prepare.

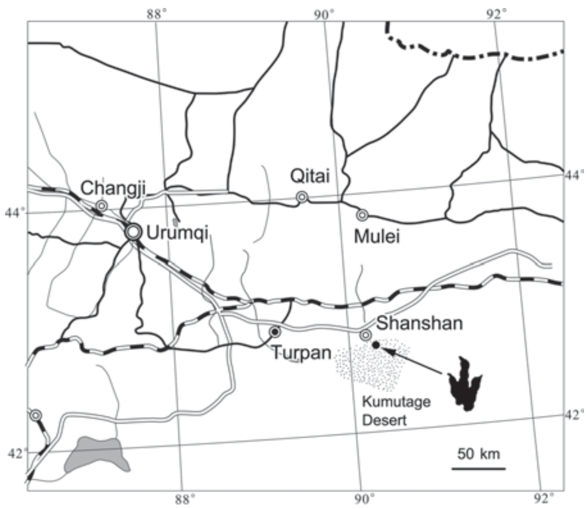

Fig. 1 Map showing the position of the Shanshan tracksites in the Turpan Basin of Xinjiang

Our investigation revealed another tracksite (site II; Fig. 2C) to the northeast, which had not been mentioned by Wings et al. (2007). All footprints at site I A, B, C have been carefully re-investigated and numbered (Fig. 3). 143 footprints have been recognized, including some that had not been described by Wings et al. (2007).

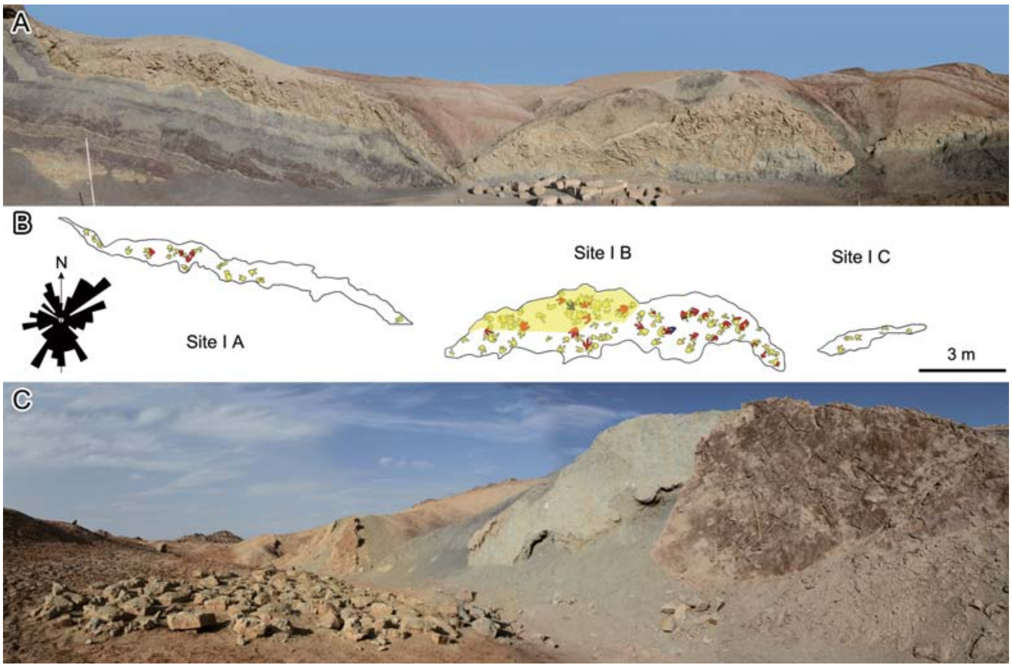

Fig. 2 Photographs and distribution pattern of the Shanshan tracksites
A. site I (composed from three photos); B. distribution pattern and rose diagram of site I, A–C showing the orientations of all footprints (adapted from Wings et al., 2007); the yellow area indicates the collapsed part; C. tracksite II with scattered footprint-bearing blocks at the bottom

Institutional abbreviations AC, Dinosaur Footprint Reservation in Holyoke, Massachusetts, USA; HGM, Henan Geological Museum, Henan, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; MGCM, Moguicheng Dinosaur and Bizarre Stone Museum, Xinjiang, China; MPD, Paleontological Center of the Mongolian Academy of Sciences, Ulan Baatar, Mongolia; SS, Shanshan tracksite, Turpan City, Xinjiang, China; ZLJ, World Dinosaur Valley Park, Yunan, China.

2 Geological setting

Sanjianfang Formation We here describe the theropod tracks from the Shanshan tracksites at the northeastern border of the Kumutage Desert of Kezi Village, Qiketai Township, Shanshan County, Turpan City in the Xinjiang Uyghur Autonomous Region, China (Fig. 1). The Shanshan tracksites are designated as site I (42°55′34.46″N, 90°27′32.04″E) of the lower layer and site II (42°55′36.92″N, 90°27′33.06″E) of the upper layer. Site I is divided into sites 1A, 1B and 1C (Fig. 2A–B). Site II, which is more severely weathered, is positioned approximately 100 m northeast of site I (Fig. 2C).

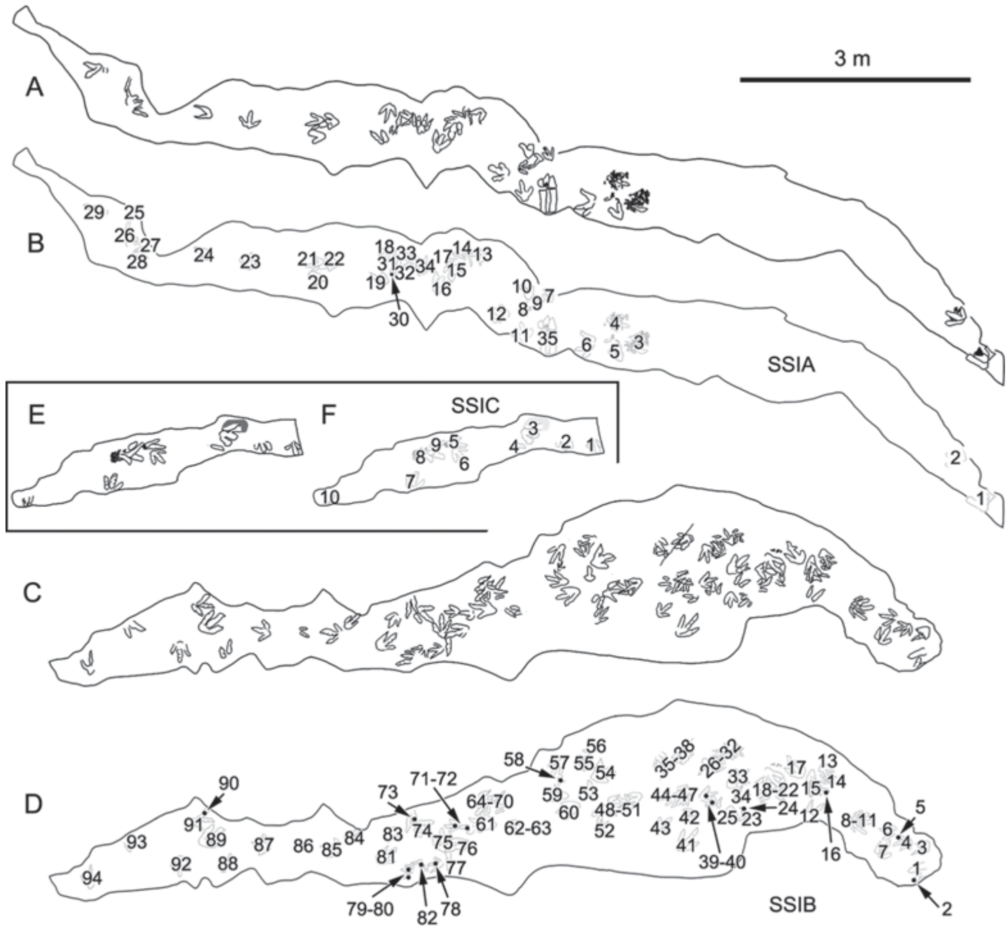

Fig. 3 Re-evaluated distribution pattern and serial numbers of footprints at site I A–C
A, B. site I A; C, D. site I B; E, F. site I C; serial numbers can differ from those in Figs. 5–11, 13

Wings et al. (2007) assigned the Shanshan tracksites to the early-middle Middle Jurassic Sanjianfang Formation. This formation is exposed in the middle and at the northern and western margins of the Turpan Basin (Shao et al., 1999), but no vertebrate body fossils have yet been discovered in this unit (Dong, 2004). Apart from dinosaur tracks (Wings et al., 2007), this formation is dominated by gymnosperm pollen, specifically the *Cyathidites–Classopollis–Piceites* association (Zhang et al., 2002). The sedimentation is characterized by a braided river delta-shore shallow lacustrine facies (Wan et al., 2006) and the depositional environment was probably a muddy floodplain setting (Wings et al., 2007).

Paleoecology The studied interval consists mainly of variegated mudrock in which two, a few tens-of-cm thick sandstone beds are intercalated about 6 m apart (Wings et al., 2007). The lower sandstone interval is about 30 cm thick; it is characterized by abundant and densely packed trace fossils exposed on the lower surface (Figs. 4-5). As this surface is weathered, it cannot be excluded that some surface ornamentation of the burrows is lost (Fig. 4). Because the burrows were only analyzed from photographs, because of their high density and weathering effects, the taxonomic and palecologic evaluation of these traces may be subject to some uncertainty.

The studied trace fossils were found preserved as positive hyporelief. The trace producers penetrated in the sand down to the mud and partially into it. The tubes are all very similar in width (~1 cm) and they do not exhibit a preferred orientation. The studied traces show a varying morphology ranging from simple, curved tubular tunnels over bundles of deviating tubes having a bilobate or a *Phycodes*-like appearance to laterally slightly shifted causative U-tubes and all transitions in between (Fig. 4).

Fig. 4　Densely packed *Fuersichnus* isp. at the surface of track level
Note different morphology of burrows, but their similar diameter and penetration depth

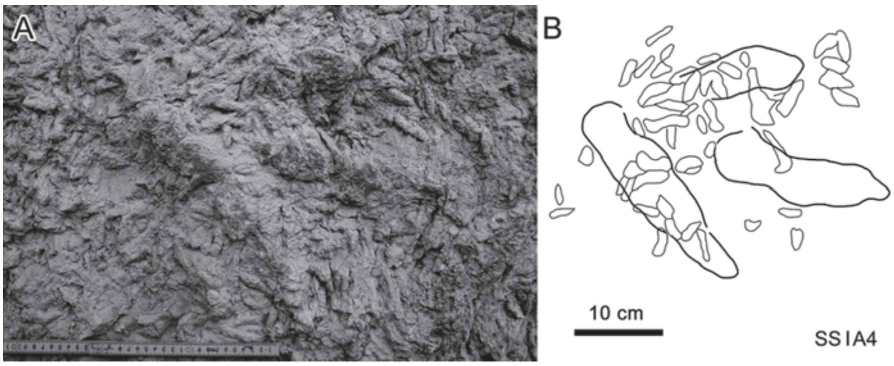

Fig. 5　Photography (A) and outline drawing (B) of *Changpeipus carbonicus* theropod footprint and invertebrate traces *Fuersichnus* isp. from Shanshan tracksite I, SSIA4

In spite of the uncertainties resultant from investigating solely photographs, the studied trace fossils appear to belong to the same ichnogenus, because they are similar in size and penetration depth and as there are transitions between all the different morphologies. The characteristics of the burrows are typical of *Fuersichnus* Bromley & Asgaard, 1979. These authors gave the following diagnosis (p. 59): "Horizontal, retrusive burrow complexes composed of clusters of j-shaped fills, showing varying degrees of organization. Where well organized, an ear- or tongue-shaped spreite-like structure is produced. Passing to reduced grades of organization, the 'spreite' becomes uneven, and resembles a bunch of bananas. It finally disaggregates into a series of loosely clustered, or even isolated, curved burrows." In addition, *Fuersichnus* is described as "shallow vertical to horizontal U-tubes 0.3-1 cm in diameter and 0.1-2 cm in depth. The construction of this burrow type is based on a repetition of a vertical or horizontal tube. Vertical tubes generally follow the same path without increasing its depth, but movement sideways is sometimes visible. Horizontal tubes are added to form a pattern of nested, broad U's from the outside inward. The surficial burrow morphology is typically bulbous, pustulose, to smooth walls. There is no external tube and spreite between them." (Hasiotis, 2002:106).

These burrows are interpreted to have been constructed by deposit-feeding insect larvae that most likely belong to mayflies (Hasiotis, 2002) or by other invertebrates (Bromley and Asgaard, 1979). The traces probably represent dwelling and/or feeding burrows. *Fuersichnus* are commonly found where a standing body of water is present in alluvial plains (MacNaughton and Pickerill, 1995), palustrine, and shallow lacustrine environments (Bromley and Asgaard, 1979). *Fuersichnus* is seen as an indicator of tranquil aquatic environments ranging from ephemeral conditions typical of floodplains or floodplain ponds over palustrine settings where temporary water bodies are common for part of the year, to perennial lakes. Consequently, the studied deposits are ascribed to a muddy floodplain or lake margin setting.

Previously the studied invertebrate trace fossils were tentatively inferred to belong to the ichnogenus *Lockeia siliquaria* (Wings et al., 2007:127; these authors put a '?' to their assignment). However, "*Lockeia* represent small almond-shaped oblong bodies preserved in convex hyporelief; tapering to sharp and obtuse points at both ends; surface commonly smooth, mostly symmetrical" (Häntzschel, 1975:W97). This diagnosis definitely does not match the studied trace fossils. Therefore, the previous taxonomic evaluation is not followed in this study. However, because of the reasons given above also the taxonomic evaluation provided in this paper may be subjected to some uncertainties.

3 Materials and methods

The excavated footprints were preserved *in situ* with acetone-based acrylic lacquer by Wings et al. (2007). All the footprints are natural casts. However, the tracks have suffered constant weathering since. Some covered tracks have likely been exposed since 2007. During the 2011 investigation, all footprints were counted and numbered. All tracks were outlined with chalk, measured (Table 1), and photographically documented. Outlines were also traced. The measurements of Wings et al. (2007) are certainly useful, however, given that new footprints were discovered, new measurements were obtained and have been used here. Future researchers may compare the different data sets if necessary.

Table 1 Measurements of theropod tracks (N=143) from the Shanshan track sites, Xinjiang, China (cm)

Specimen	ML	MW	LD II	LD III	LD IV	LD O	II–III	III–IV	II–IV	III–O	l/w
SSIA1	—	—	—	—	—	34	—	—	—	—	—
SSIA2	29.5	32.4	13.8	24	18	—	51°	34°	85°	—	0.91
SSIA3	—	—	14	>19	20	—	—	—	—	—	—
SSIA4	35.5	25.4	14	20.5	25.2	—	27°	33°	60°	—	1.4
SSIA5	>23.4	—	—	>14.5	—	17.5	—	—	—	39°	—
SSIA6	32	41.9	14.5	24.3	20.5	—	34°	63°	97°	—	0.76
SSIA7	22.7	17.5	8.5	16	13.8	—	21°	33°	54°	—	1.3
SSIA8	>20	19	12.5	>17	13.8	—	36°	45°	81°	—	—
SSIA9	—	—	—	20	—	—	—	—	—	—	—
SSIA10	—	—	—	—	16.5	—	—	—	—	—	—
SSIA11	31.8	24.7	10	19.5	10.5	—	36°	33°	69°	—	1.29
SSIA12	31.5	>26	16.5	24.5	>9	—	38°	>29°	>67°	—	<1.21
SSIA13	—	—	—	20.5	—	16.8	—	—	—	55°	—
SSIA14	—	—	—	20	—	16	—	—	—	27°	—
SSIA15	27	24	18.4	26.3	17	—	30°	46°	78°	—	1.13
SSIA16	28	—	—	19	18.5	—	—	38°	—	—	—
SSIA17	>29.8	28.4	20	>16.8	19.5	—	23°	30°	53°	—	>1.05
SSIA18	30.5	25	13	21	14	—	40°	31°	71°	—	1.22
SSIA19	—	—	19.5	27.5	—	—	35°	—	—	—	—
SSIA20	>25.1	—	—	>14.8	—	10.7	—	—	—	43°	—
SSIA21	29.9	25	13.3	20.6	15.4	—	25°	41°	66°	—	1.2
SSIA22	>29.6	—	—	21	—	13.2	—	—	—	40°	—
SSIA23	26.3	32.5	16.8	19	14	—	47°	50°	97°	—	0.81
SSIA24	31.3	—	—	23.4	—	18.3	—	—	—	30°	—
SSIA25	—	—	—	22.6	—	—	—	—	—	—	—
SSIA26	>20.2	>29.4	14.7	>9.5	>10.6	—	23°	54°	77°	—	—
SSIA27	—	—	—	—	—	13.6	—	—	—	—	—
SSIA28	—	—	—	24.2	—	—	—	—	—	—	—
SSIA29	30.2	—	—	23.1	—	19.8	—	—	—	43°	—
SSIA30	13.7	9.5	8.7	11.7	111.9	—	25°	21°	—	46°	1.44
SSIA31	—	—	—	—	—	21	—	—	—	—	—
SSIA32	21.1	24.3	17.1	19.1	16.3	—	58°	20°	78°	—	0.87
SSIA33	—	—	—	—	—	—	20.8°	—	—	—	—

Contiuned

Specimen	ML	MW	LD II	LD III	LD IV	LD O	II–III	III–IV	II–IV	III–O	l/w
SSIA34	29.7	21	16.4	18.5	19	—	22°	24°	46°	—	1.41
SSIA35	51	14.7	45.3	47.6	43.7	—	9°	10°	19°	—	—
SSIB1	—	—	—	27.4	—	—	—	—	—	—	—
SSIB2	—	—	16.3	17.8	—	—	—	—	—	—	—
SSIB3	32.5	—	—	14.8	—	—	—	—	—	—	—
SSIB4	27	19.3	12.9	19.9	11	—	35.5°	21°	56.5°	—	1.4
SSIB5	28.3	—	—	>16	—	10.9	—	—	—	10.9°	—
SSIB6	>24.2	23.6	12.5	19.8	17	—	39°	40°	79°	—	>1.03
SSIB7	>12.2	24.4	>12	24.8	19.5	—	42°	27°	69°	—	0.5
SSIB8	>24.5	21.7	10.3	20	17.2	—	37°	46°	83°	—	>1.13
SSIB9	—	—	—	—	27.2	—	—	—	—	—	—
SSIB10	—	—	19.7	22	—	—	—	—	—	—	—
SSIB11	—	—	13.8	—	—	—	—	—	—	—	—
SSIB12	—	—	—	23.5	—	19	—	—	—	—	—
SSIB13	30	—	—	18.6	—	11.6	—	—	—	32°	—
SSIB14	>23.8	15.4	13.5	20	17	—	22°	33°	55°	—	>1.55
SSIB15	42.2	25	11.7	22.6	15.7	—	28°	18°	46°	—	1.69
SSIB16	—	—	15	>15	—	—	—	—	—	—	—
SSIB17	40.6	—	19.4	28.3	6.1	—	27°	34°	61°	—	—
SSIB18	42.6	32.6	15.2	30.4	18.3	—	40°	27°	67°	—	1.31
SSIB19	33.5	—	14	17.4	—	—	33°	—	—	—	—
SSIB20	>26.1	18.3	10.9	23.9	9.6	—	60°	26°	86°	—	>1.43
SSIB21	—	—	—	—	—	26.5	—	—	—	—	—
SSIB22	—	—	—	—	—	15.2	—	—	—	—	—
SSIB23	>20.8	14.3	8.8	19	9.1	—	28°	42.5°	70.5°	—	>1.45
SSIB24	—	—	—	—	—	8	—	—	—	—	—
SSIB25	23.9	17.9	13.2	12	8.3	—	22°	33°	55°	—	1.34
SSIB26	—	—	—	—	—	9.6	—	—	—	—	—
SSIB27	—	—	—	—	—	11.3	—	—	—	—	—
SSIB28	29.5	16.6	8.6	18.2	>2.7	—	32°	20°	52°	—	1.78
SSIB29	—	—	—	—	—	11.8	—	—	—	—	—
SSIB30	>25.1	26	11.8	22.5	17.4	—	56°	36°	92°	—	>0.97
SSIB31	—	—	—	—	—	16.6	—	—	—	—	—
SSIB32	29.7	25.2	9.4	18.8	17.1	—	28.5°	32.5°	61°	—	1.18

Contiuned

Specimen	ML	MW	LD II	LD III	LD IV	LD O	II–III	III–IV	II–IV	III–O	l/w
SSIB33	42.1	22.4	26.5	20.3	10.9	—	14.5°	27°	41.5°	—	1.88
SSIB34	—	—	—	20.7	—	18.5	—	—	—	—	—
SSIB35	25.5	—	15.8	20.8	—	—	27°	—	—	—	—
SSIB36	24.2	—	13.7	18.5	—	—	22°	—	—	—	—
SSIB37	—	—	—	—	—	16.1	—	—	—	—	—
SSIB38	—	—	—	—	—	>10	—	—	—	—	—
SSIB39	28.1	23.2	9.9	18.5	13.1	—	32°	37°	69°	—	1.2
SSIB40	>20.3	26	9.8	>16	17	—	54°	40°	94°	—	>0.78
SSIB41	46.2	29	18.6	29	20	—	28°	23°	51°	—	1.6
SSIB42	24.5	—	16.2	>16.6	—	—	31°	—	—	—	—
SSIB43	30.7	24.5	13.8	20	9.2	—	37°	36°	73°	—	1.25
SSIB44	>29.6	26.9	17.5	24.7	18.8	—	30°	33°	63°	—	>1.1
SSIB45	—	—	—	—	—	16.7	—	—	—	—	—
SSIB46	—	—	—	—	—	19	—	—	—	—	—
SSIB47	>17.5	19	8.5	17.5	9.9	—	41°	51°	92°	—	>0.92
SSIB48	>29.1	32.7	20.3	>16.9	14.5	—	31°	39°	70°	—	>0.89
SSIB49	30.8	23.8	15.7	>13.1	15.7	—	—	—	58°	—	1.29
SSIB50	35.8	22.8	14.8	24.3	12	—	27°	26°	53°	—	1.57
SSIB51	—	—	—	21	—	13	—	—	—	—	—
SSIB52	>27.9	20	12.9	20.5	19.2	—	27°	18°	43°	—	>1.39
SSIB53	22	—	—	14.2	—	—	—	—	—	—	—
SSIB54	36	36.8	11	20.8	19.5	—	30°	45°	75°	—	0.98
SSIB55	23.4	20.3	17	18	>12.4	—	32°	30°	62°	—	1.15
SSIB56	26.4	18.2	12.1	13.1	>4	—	35°	26°	61°	—	1.45
SSIB57	34.7	21	12.3	21.6	13.8	—	23°	27°	50°	—	1.65
SSIB58	15.8	11.8	7.3	10.1	5.7	—	22°	40°	62°	—	1.34
SSIB59	35.2	23.5	17.5	23	14.8	—	26°	25°	51°	—	1.5
SSIB60	36.3	24.2	20.8	28.6	22.9	—	22°	29°	51°	—	1.5
SSIB61	41.4	26.7	12	24	10.8	—	36°	21°	57°	—	1.55
SSIB62	—	—	20	—	—	—	—	—	—	—	—
SSIB63	—	—	—	14.1	—	9	—	—	—	—	—
SSIB64	—	—	—	—	—	13.2	—	—	—	—	—
SSIB65	—	—	—	—	—	22	—	—	—	—	—
SSIB66	—	—	—	—	—	15.4	—	—	—	—	—

Contiuned

Specimen	ML	MW	LD II	LD III	LD IV	LD O	II–III	III–IV	II–IV	III–O	l/w
SSIB67	>27.4	24.3	15.9	21.8	12	—	37°	47°	84°	—	1.13
SSIB68	—	—	—	—	—	>15	—	—	—	—	—
SSIB69	—	—	—	—	—	19.2	—	—	—	—	—
SSIB70	—	—	—	—	—	>10	—	—	—	—	—
SSIB71	26	—	7.8	16.2	—	—	—	—	—	—	—
SSIB72	23.7	19.5	11.3	16	11	—	28°	32°	60°	—	1.22
SSIB73	—	—	—	24.3	—	23.7	—	—	—	—	—
SSIB74	>31	28.8	15.5	25.3	14.9	—	33°	47°	80°	—	1.1
SSIB75	35.8	26.7	17.9	23	20.5	—	30°	26°	56°	—	1.34
SSIB76	39.4	—	—	28.8	—	13.8	27°	—	—	—	—
SSIB77	—	—	—	26.4	—	—	—	—	—	—	—
SSIB78	23.4	22.6	11	15.7	15	—	32°	31°	63°	—	1.04
SSIB79	>26.7	—	15	22.3	—	—	35°	—	—	—	—
SSIB80	—	—	—	—	—	15.4	—	—	—	—	—
SSIB81	37	25.8	14	24	14.5	—	35°	18°	53°	—	1.43
SSIB82	>21.9	—	—	—	—	18.5	—	—	—	—	—
SSIB83	24.1	21.8	14.4	18.2	8.3	—	36°	35°	71°	—	1.11
SSIB84	29.5	12.1	12.5	19.1	10	—	20°	15°	35°	—	2.44
SSIB85	>28.9	31	13.6	24.7	18.7	—	59°	40°	99°	—	>0.93
SSIB86	—	—	11.5	14.7	—	—	—	—	—	—	—
SSIB87	30	32	14.5	18	20	—	47°	48.5°	95.5°	—	0.94
SSIB88	—	—	16.6	21.7	—	—	—	—	—	—	—
SSIB89	47	30	22.5	33.8	27.2	—	21.5°	27°	48.5°	—	1.57
SSIB90	—	—	—	—	—	24	—	—	—	—	—
SSIB91	—	—	12	18	—	—	—	—	—	—	—
SSIB92	30.6	26.7	12.9	19.4	16.1	—	34°	34.5°	68.5°	—	1.15
SSIB93	—	—	—	23	—	14.8	—	—	—	—	—
SSIB94	35.9	—	13.1	19.7	—	—	32°	—	—	—	—
SSIC1	21.7	22.7	11	14.4	11.7	—	68°	23.5°	91.5°	—	0.96
SSIC2	>16	23.2	13.5	15	>7.5	—	37°	60°	97°	—	>0.69
SSIC3	>28	34	14	14	18.5	—	42°	25°	67°	—	>0.82
SSIC4	27	19.3	12.9	19.9	11	20.4	—	—	—	—	—
SSIC5	—	—	—	19.4	—	22.5	—	—	—	—	—
SSIC6	26	25	14	19.3	12	—	34°	39°	73°	—	1.04

Contiuned

Specimen	ML	MW	LD II	LD III	LD IV	LD O	II–III	III–IV	II–IV	III–O	l/w
SSIC7	25	27.6	16.8	22.9	19.7	—	38°	42°	80°	—	0.91
SSIC8	—	—	—	—	—	20.5	—	—	—	—	—
SSIC9	33	31.4	17	20	15.5	—	18°	58°	76°	—	1.05
SSIC10	—	—	19.7	22	—	—	—	—	—	—	—
SSIIA1	>18.8	21.4	10.2	>15	13.3	—	40°	42°	82°	—	>0.88
SSIIA2	>31.5	34.1	20.2	>21.5	25.6	—	34°	40°	74°	—	>0.92
SSIIA3	—	—	>10	>12.7	—	—	—	—	—	—	—
SSIIA4	34.1	—	17.7	23.6	—	—	31°	—	—	—	—

Abbreviations: ML. maximum length; MW. maximum width (tracks measured as distance between the tips of digits II and IV); LD II, III and IV. length of digit, II, III and IV, respectively; LD O. length of outer digit; II–III, III–IV and III–O. angle between digits II and III, III and IV, and III and outer digit, respectively; l/w. ML/MW; — measurement impossible or not applicable.

4 Systematic ichnology of Shanshan dinosaur footprints

4.1 Previous studies

The tridactyl theropod tracks from Shanshan (155 imprints reported by Wings et al., 2007; 143 recognized by us in 2011 [139 from site I and 4 from site II]) were assigned to two morphotypes by Wings et al. (2007). The main characteristics of morphotype A include (after Wings et al., 2007): 1) longer than wide and generally of deltoid shape; 2) widths ranging from 17.5–38.2 cm; 3) a more or less well-defined “heel”; 4) digits II and IV approximately 25% shorter than digit III, with digit II tending to be slightly longer than digit IV; 5) phalangeal pad formula of x-2-4-3-x; 6) average angles between digits of II 37° III 40° IV; 7) distinctive V-shaped claw mark at the distal tips of digits II and III, especially.

The main characteristics of morphotype B include (after Wings et al., 2007): 1) elongate footprints of slender and gracile appearance; 2) widths ranging 12.2–33.3 cm; 3) weakly defined “heel”; 4) digits II and IV of subequal lengths and approximately 30% shorter than digit III; 5) phalangeal pad formula of x-2-3/4-3-x; 6) average divarication angle between digits II and IV 73°, with subequal angles between digits II and III and digits III and IV; 7) well defined V-shaped and pointed claw impressions at the tip of the digits.

However, morphological characteristics such as width, divarication angles between digits, and phalangeal pad formulae of morphotypes A and B (2-6) show no obvious differences. V-shaped claw impressions (characteristic 7) are common in theropod tracks. The only obvious difference between these morphotypes is characteristic 1 (elongation and slenderness), but it has not been described in any detail.

4.2 Comments on the previous study

Wings et al. (2007) designated 32 of the identifiable tracks as morphotype A and they also considered them similar to the ichnogenera *Changpeipus* and *Megalosauripus*. However, the phalangeal formula x-2-4-3-x is not typical or even diagnostic of theropod tracks, or either of these ichnogenera, or apparent from the track illustrations. Wings et al. (2007) also identified 17 tracks, with a slightly smaller mean size and size range, as Morphotype B, and compared them with the ichnogenera *Grallator*, *Eubrontes* and *Anchisauripus*, giving the uncertain phalangeal formula of x-2-3/4-3-x. Again this is not typical of theropods where the formula x-2-3-4-x is the norm if discrete pads are discernable, as they are in most reasonably well preserved Jurassic ichnotaxa. 42 additional tracks were measured, but not named or assigned to either category A or B. As has been discussed recently (Lockley et al., 2013) the identification of theropod tracks and their confident assignment to a named ichnotaxon is difficult.

4.3 The present study: description and comparison

Site I can be divided into discrete sections A, B and C. There are 35, 94 and 10 footprints preserved in these individual sections, respectively (Figs. 6–8). Only 4 discernible footprints have been found at site II (Figs. 6, 8). The other footprints from site II are isolated digit traces. Copious quantities of invertebrate traces were discovered in this stratum as well (see above).

In the present study, also two track morphotypes were identified excluding incomplete and seriously deformed tracks. Following the format of the previous study (Wings et al., 2007) the 143 newly analyzed tracks were designated as morphotypes A and B, even though the sample in each category is not the same as that proposed by Wings et al. (2007). It was not impossible to use the same numbering scheme, since an estimated 35 footprints had been lost. Therefore we used prefixes SSIA, SSIB and SSIC respectively for tracks from sites 1A, 1B and 1C.

Morphotype A (e.g. SSIA21; SSIB17, 33, 41, 57, 59–61, 81, 89) Takes the well-preserved SSIB59 as the representative track (Fig. 9A, B). These are medium sized (29.9–47.0 cm length), tridactyl theropod tracks that lack manus and tail traces. The length:width ratio is 1.5. Digit IV is the shortest of the three digits; digit III is the longest. Digit IV is narrower than digits II and III. The divarication angle between digits II and IV is 51° . The divarication angle between digits II and III is nearly equal to that between digits III and IV. Digits II and III have sharp claw impressions. The phalangeal pad formula is x-2-3-?-x (for most footprints, although digit IV lacks distinct pads, a few can be recognized, approximately with 3 or 4 pads). A sub-ovoid metatarsophalangeal pad lies nearly in line with the axis of digit III, close to the proximal end of digit IV.

SSIB33 and SSIB41 constitute a step, 118.9 cm long, which is the most reliable trackway among all preserved tracks (Fig. 10). Supposing that the length of a stride equals that of two

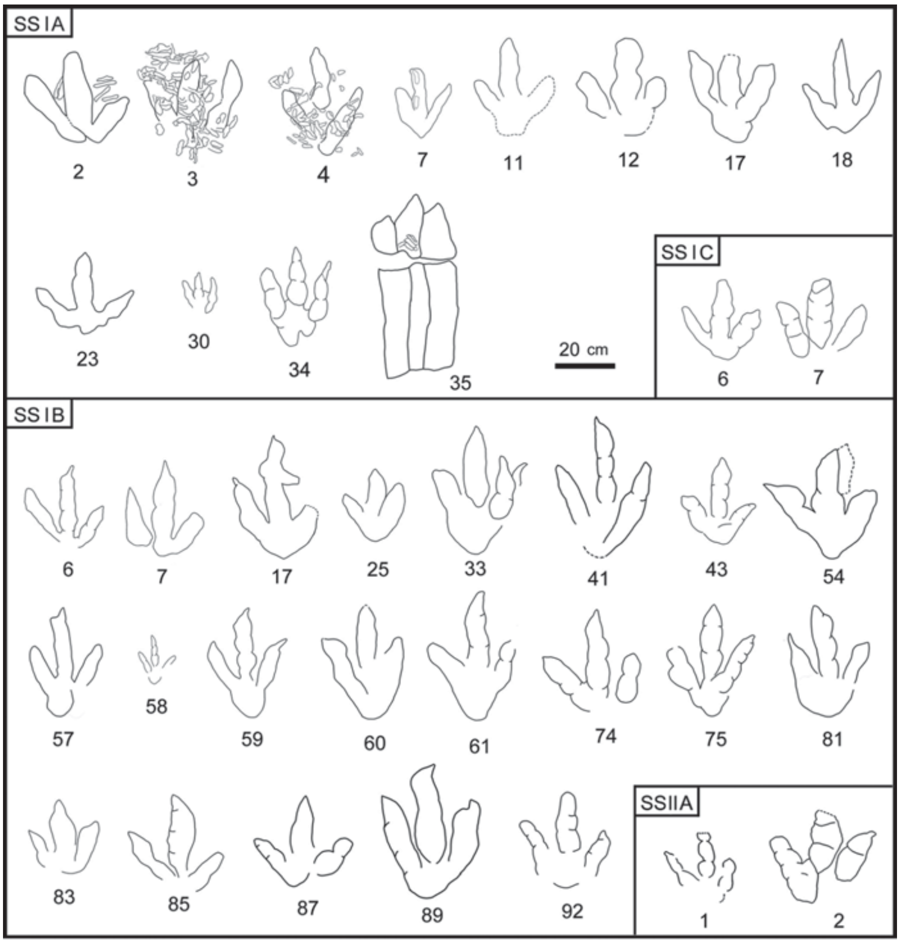

Fig. 6 Sketches with isolated theropod footprints *Changpeipus carbonicus* from Shanshan tracksites I and II Notice extramorphological variation with different digit divarication and presence/absence of a metatarsophalangeal pad IV due to different substrate conditions

steps, we can calculate speed (v) using Alexander's (1976) formula: $v = 0.25g^{0.5} \cdot SL^{1.67} \cdot h^{-1.17}$, where g = gravitational acceleration in m/s; SL = stride length; and h = hip height, estimated as 4.9 times foot length (FL), using the ratio for large theropods proposed by Thulborn (1990). Based on the length of the step, we estimate a speed of ~1.4 m/s or ~5.2 km/hr. The relative stride length (SL/h) is 1.2, implying that the animal was walking, not trotting or running.

Morphotype B (e.g. SSIA18, 23; SSIB7, 43, 74, 87; SSIC6, 7; SSIIA2) Taking the well-preserved SSIA18 as the representative track (Fig. 9C, D), these are small to medium sized (12.2–31.5 cm length) tridactyl theropod tracks that lack manus and tail traces. The length:width ratio is 1.2. The divarication angle between digits II and IV is 71°. The caudal (posterior) margin of the metatarsophalangeal portion is indistinct. Other characteristics are similar to those of Type A.

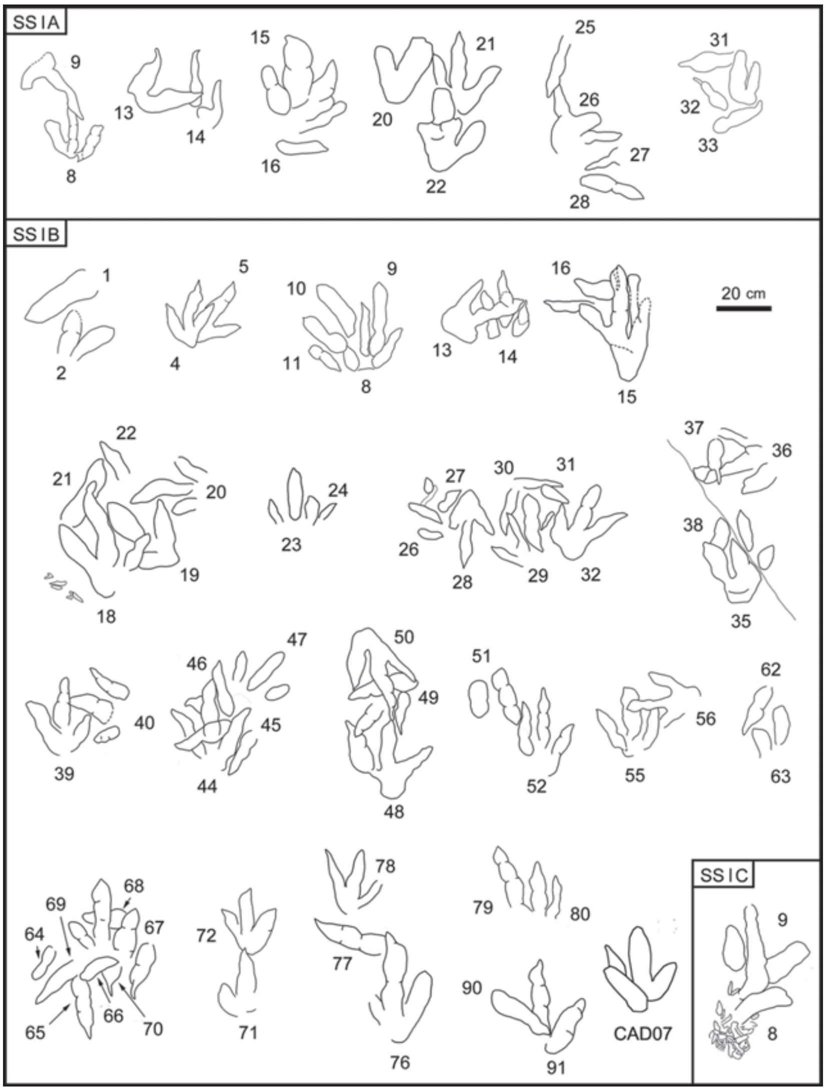

Fig. 7 Sketches with overlapped theropod footprints from Shanshan tracksite I

Types A and B are morphologically different based on length/width ratios, divarication of digits and shape of metatarsophalangeal regions. However, the ratio of length/width and the divarication of digits are linked to the presence/absence of metatarsophalangeal traces. Rescaling SSIB59 and SSIA18 to similar sizes and overlapping them resulted in similar profiles, apart from the metatarsophalangeal portion, present only in SSIB59 (Fig. 11A). Therefore, the two morphotypes at the Shanshan tracksites probably represent a single theropod ichnotaxon. The differences may have been emphasized by the differential consistency of substrate sediments.

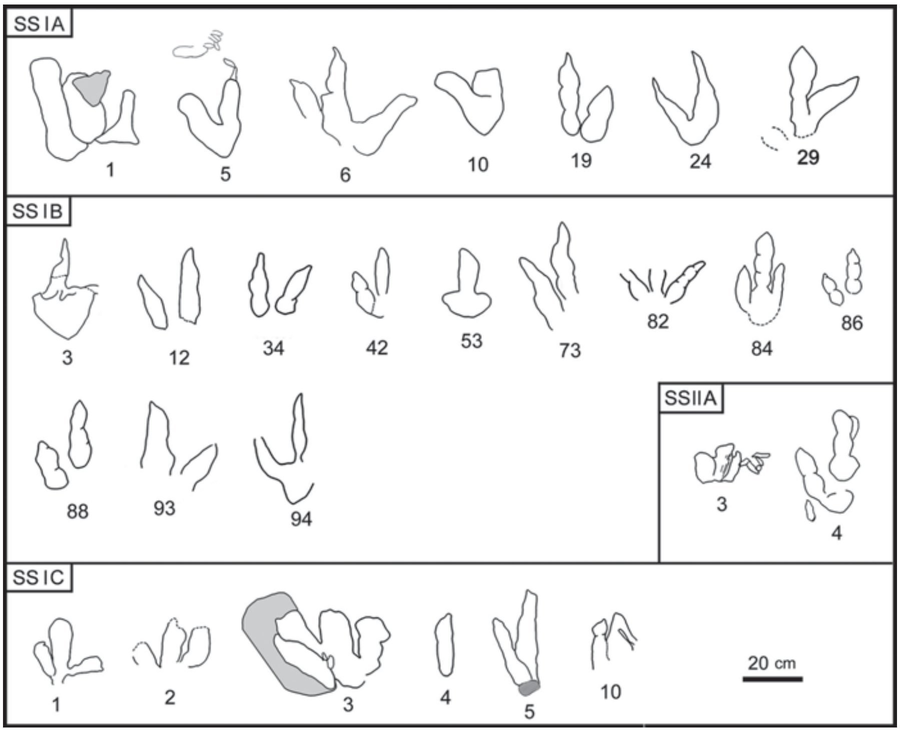

Fig. 8 Sketches with incomplete and isolated theropod footprints from Shanshan tracksites I and II

As shown in Fig 11B, considering SSIB59 to be the most complete track, the different preservations may result in: 1) lack of a metatarsophalangeal pad (SSIA18); 2) incomplete metatarsophalangeal pad (SSIA34); or 3) elongated metatarsophalangeal pad and "heel" (SSIB15). The tracks lacking metatarsophalangeal pads can be divided based on the connection between the digits: 1) two connected digits III and IV with separate digit II (SSIB74); 2) all digits separated (SSIB40); 3) only two digits preserved (II and III)(SSIB88). Furthermore, SSIB58 represents the smallest, probably juvenile individual (see below) and SSIB89 the biggest individual recorded. The size of SSIB59 is the average for all tracks.

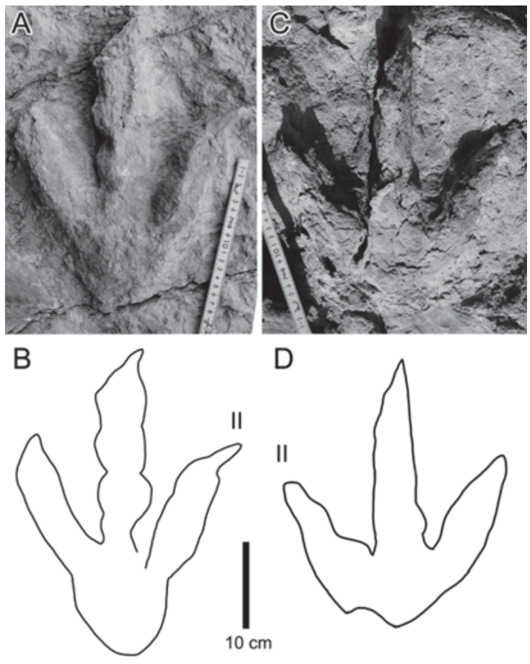

Fig. 9 *Changpeipus carbonicus* from Shanshan tracksite I
A, B. SSIB59; C, D. SSIA18; A, C. photograph; B, D. outline drawing

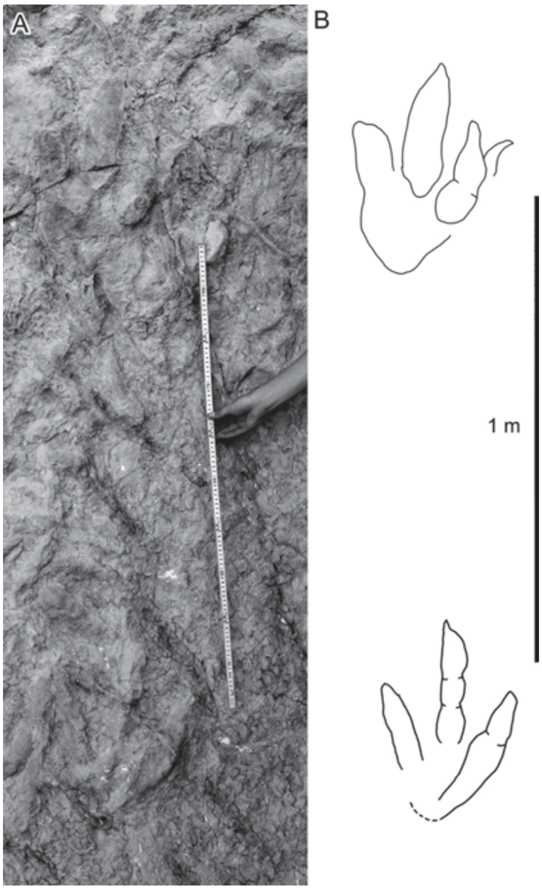

Fig. 10 Photograph and outline drawing of *Changpeipus carbonicus* with two successive imprints SSIB33 (upper) and 41 (lower) from Shanshan tracksite I

Due to the wet and slippery sediment, the footprints have undergone unusual deformation. Most common is the variation of digit divarication and the different enlargement of angles between digits II and III, III and IV, respectively (SSIC1, SSIA23, SSIB84). Other tracks have a completely deformed shape (SSIA2, SSIC3). Again, these observations imply that anatomically based and extramorphological features are often hard to distinguish. As already noted by Wings et al. (2007), a significant number of tracks is not assignable to a distinct ichnotaxon.

5 *Changpeipus* specimens from China

Changpeipus carbonicus (Young, 1960) is a reasonably well-preserved theropod track that exhibits numerous features, such as its digital pad formula, that allies it to the *Grallator–Eubrontes* plexus (sensu Olsen, 1980). Xing et al. (2009) re-described the holotype of *Changpeipus carbonicus* (IVPP V 2472) from the Lower-Middle Jurassic of Jilin Province. *Changpeipus luanpingeris* (Young, 1979) was considered a synonym of *C. carbonicus* by Xing et al. (2009) and a nomen dubium by Lockley et al. (2013). Xing et al. (2009) considered *Changpeipus xuiana* (Lü et al., 2007) similar to *C. carbonicus*, whereas Lockley et al. (2013) proposed the new combination *Eubrontes carbonicus*, implying that *C. xuiana* is allied to *Eubrontes* but not a synonym of *E. carbonicus*. While these studies removed two *Changpeipus* ichnospecies, Xing et al. (2009) introduced *Changpeipus pareschequier* as a new ichnotaxon based on material from the Lower Jurassic Lufeng Basin, Yunnan Province. However, in their review of the Chinese tetrapod track record Lockley et al. (2013) considered *C. carbonicus* valid, but not *C. pareschequier* which they transferred to *Eubrontes* (i.e. *E. pareschequier*). Thus, the combined inferences of Xing et al. (2009) and Lockley et al. (2013) suggest only one valid *Changpeipus* ichnospecies, which is the type ichnospecies *C. carbonicus*. Although many Lower Jurassic theropod tracks have a similar morphology and are in need of revision, Lockley et al. (2013) tentatively concluded that the

Changpeipus type (*C. carbonicus*) is not a junior synonym of *Grallator sensu stricto*, or a senior synonym of *Kayentapus*.

To make comparisons with Shanshan specimens, the leading authors re-studied and traced *Changpeipus carbonicus* (IVPP V 2472, V 2470), *C. luanpingeris* (IVPP TCL), *C. xuiana* (HGM 41HIII-0098), and *Eubrontes pareschequier* (ZLJ-ZQK1, ZLJ-ZQK2)(Fig. 12). As can be seen from the comparative illustrations there is considerable variation and the type material of *C. luanpingeris* (IVPP TCL) and *C. xuiana* (HGM 41HIII-0098) consists of poorly preserved and/or distorted specimens. This justifies suppressing their ill-conceived ichnotaxonomic names, as noted above. Also, we herein follow Lockley et al. (2013) in referring *Changpeipus pareschequier* (ZLJ-ZQK1 and ZLJ-ZQK2) to *Eubrontes pareschequier*.

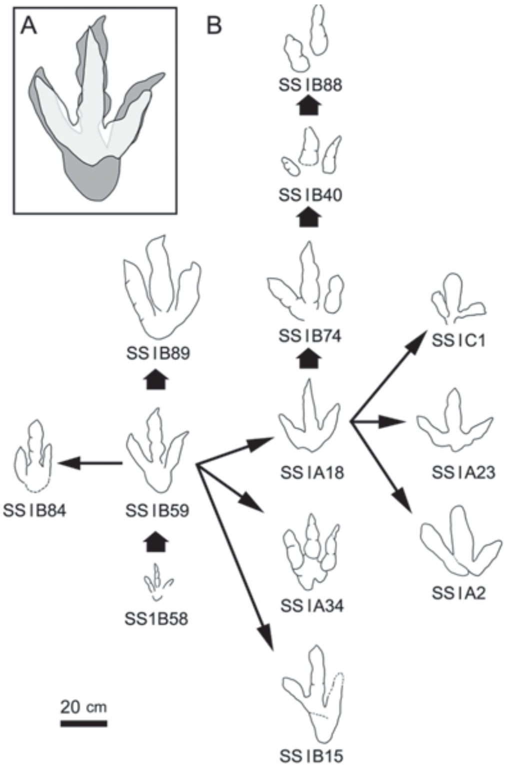

Fig. 11　Comparison of Shanshan theropod tracks
A. SSIB59 and SSIA18 superimposed; B. extramorphological variation of Shanshan theropod tracks; the horizontal axis represents increase in track width (due to divarication) to the right, and the vertical axis represents track elongation, based on completeness of "heel" impressions, decreasing to the top

Changpeipus carbonicus V 2472 (Young, 1960) is from the Middle or the Lower Jurassic of the Songshangang coal mine, Huinan, Jilin Province, and was re-described by Xing et al. (2009). The two large *C. carbonicus* tracks shown in Fig. 12 have quite large divarication angles between digits II and IV (50°–65°). The tracks are generally slender and elongate (L/W ~1.60). The triangular "heel" impression is most pronounced in V 2472.2 which is the best preserved. Since it is impossible to have multiple holotype tracks belonging to different trackways, as implied by Young (1960), when he designated the three tracks shown in Fig. 12, as well as two others from a different locality, as the holotype, we consider V 2472.2 the holotype of *C. carbonicus*. This specimen has been consistently illustrated in many subsequent studies (see also Zhen et al., 1989: fig. 19.3D; Lockley and Matsukawa, 2009: fig. 5C; Lockley et al., 2013: fig. 2c; Xing et al., 2009: fig. 3). A specimen (V 2470) from the Haizhou opencast coal mine near Fuxin in Liaoning Province and referred to *Changpeipus carbonicus* by Young (1960) is poorly-preserved, and of no taxonomic use for improving the description, because *contra* Young (1960) it cannot be considered to belong to the holotype material.

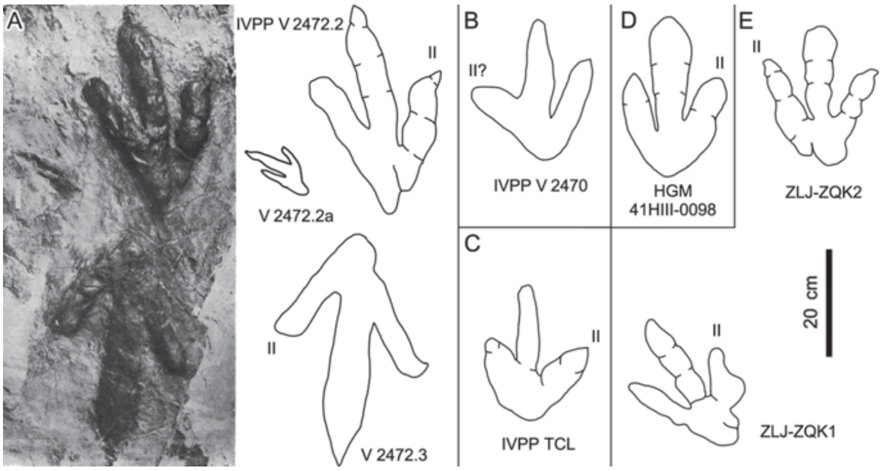

Fig. 12 Jurassic-Cretaceous footprints from China that have been assigned to the ichnogenus *Changpeipus* by different authors

A. photograph (Young, 1960: pl. IV) and outline drawing of *Changpeipus carbonicus* from Huinan, Jilin Province; B. *C. carbonicus* from Fuxin, Liaoning Province; C. *C. luanpingeris* from Luanping, Hebei Province; D. *C. xuiana* from Yima, Henan Province; E. *C. pareschequier* from Yunnan Province; only *C. carbonicus* is considered here as a valid ichnospecies of *Changpeipus*, others belong to different ichnogenera or are *nomina dubia*

Changpeipus luanpingeris (IVPP TCL) from the Lower Cretaceous of Luanping in Hebei Province (Young, 1979) and exhibited at the Paleozoological Museum of China, without a formal specimen number is, as noted above, poorly preserved and likely an extramorphologically overprinted theropod track that cannot be determined with any certainty. Therefore, it is a *nomen dubium*.

Changpeipus xuiana HGM 41HIII-0098 from the Middle Jurassic Yima Formation at the Yima opencast coal mine in Henan Province (Lü et al., 2007), is a poorly-preserved track, probably an undertrack. The divarication angle between digits II and IV is 46°. The metatarsophalangeal portion appears robust, forming a compact “heel”, but lacks a distinct pad impression. The “nail-like metatarsal pad”, mentioned by Lü et al. (2007) is not diagnostic.

Changpeipus pareschequier (*Eubrontes pareschequier*; ZLJ-ZQK1 and ZLJ-ZQK2) from the Lower Jurassic Lufeng Formation, Yunnan Province, China (Xing et al., 2009) is represented by two tracks that are evidently not proven to be part of the same trackway, even if their relative position suggests a single step (right-left). ZLJ-ZQK1 is slightly better preserved than ZLJ-ZQK2 which appears to have the distal pad trace of digit III slightly swollen, probably as a result of preservation rather than pathology. Because of the unclear relationship of these tracks, we designate the better preserved ZLJ-ZQK1 as the holotype and ZLJ-ZQK2 as the paratype.

6 Discussion

The Shanshan tracksites show excellent examples of extramorphological variation and the influence of substrate conditions on the shape of imprints. This allows us to re-interpret some Jurassic theropod tracks from China, such as the Early and Middle Jurassic ichnogenus *Changpeipus*, based on the type ichnospecies *Changpeipus carbonicus* (Young, 1960; Xing et al., 2009; Lockley et al., 2013). At this location, footprints of identical size but different morphology can be observed on the same surfaces. The similar morphology of the *Changpeipus* type specimen IVPP V 2472.2 and the Shanshan specimen SSIA34 suggests that the metatarsophalangeal pad of the former is differently preserved. Digit II of IVPP V 2472.3 is poorly preserved, however its metatarsophalangeal pad is larger than that of V 2472.2, and the metatarsophalangeal pad of SSIB59 even larger than that of V 2472.3. This suggests some variation due to preservation.

A small tridactyl imprint associated with V 2472.2 (V 2472.2a) was first interpreted as a manus print (Young, 1960), but later as a juvenile individual of *Changpeipus carbonicus* (Xing et al., 2009). The differences between V 2472.2 and V 2472.2a resemble those between SSIB58 and SSIB59, and could reflect ontogenetic stages rather than different ichnospecies. As noted above, other specimens of *C. carbonicus* reported by Young (1960: fig.1), are currently difficult to assess, and in any case are quite different from the type specimen V 2472.2 due to incomplete and/or distorted preservation. Nevertheless some (e.g., IVPP V 2470 and IVPP TCL) are similar to tracks such as SSIA2 from the Shanshan tracksite.

Morphologically, the major characteristics of *Changpeipus carbonicus* are: 1) medium-sized tridactyl theropod track, 2) divarication angles between digits II-IV of 50°, 3) a metatarsophalangeal region located more or less directly posterior (or proximal) to digit III, 4) digit IV projecting farther anteriorly (distally) than digit II and exceeding digit II in length (Young, 1960; 1979; Xing et al., 2009). These characteristics are similar to those of the Shanshan tracks. Therefore, we assign the Shanshan tracks to *Changpeipus carbonicus*.

As argued by Gierliński (1994) and reiterated by Lockley et al. (2003), Lockley and Matsukawa (2009), Xing et al. (2009) and Lockley et al. (2013), the larger Early–Middle Jurassic theropod tracks from China cannot be distinguished from *Eubrontes*, or in some cases *Kayentapus*, without resorting to finely delimited, qualitative distinctions, mostly digit divarication angles that may well be attributable to foot-substrate interactions and/or differences in track maker behavior. Although *Changpeipus* is similar to *Eubrontes*, the most significant difference lies in the larger metatarsophalangeal pad and the wider digit divarication angle II–IV, which is 50°–65° for *Changpeipus* (V 2472) and notably larger than 25°–40° observed for *Eubrontes* (Olsen et al., 1998). The metatarsophalangeal pad of V 2472.3 is larger and more V-shaped posteriorly than that of the *Eubrontes* holotype AC 15/3, and a referred specimen AC 45/1, both from Lower Jurassic strata of the Newark Supergroup of North

America (Olsen et al., 1998: fig. 5). In the latter, the metatarsophalangeal pad behind digit II is large enough to give the "heel" of the track a "bilobed" appearance similar to ZLJ-ZQK2 from Yunnan (Xing et al., 2009; Fig. 12E herein). Nevertheless, as several previous reports indicate (Gierliński, 1994; Lockley and Matsukawa, 2009; Lockley et al., 2013), *Changpeipus* and *Eubrontes* are similar ("sister") ichnotaxa.

There are a number of Cretaceous theropod tracks from Asia that should be mentioned briefly for comparative purposes. These are *Asianopodus*, *Jialingpus* and *Chapus*.

Asianopodus pulvinicalyx from the Early Cretaceous Kuwajima Formation of Japan is of interest because it possesses a distinct, bulbous "heel" impression, a length:width ratio ranging from 1.4–1.5, and divarication angles between digits II to IV ranging from 42° to 59° (Matsukawa et al., 2005). These characteristics are similar to *Changpeipus* from Shanshan, especially to SSIB59 which has the most bulbous "heel" trace in the Shanshan sample. However, the "heel" and the digit impressions of *Asianopodus* tend to be separated, and centrally located behind digit III, features not found in the Shanshan specimens. Most *Asianopodus* (*A. pulvinicalyx*) are smaller than *Changpeipus*. But *Asianopodus robustus* (Li et al., 2011) is a larger ichnospecies, again with a distinct, well developed, rounded "heel" pad.

Jialingpus, a small track which is widely distributed in China in the Late Jurassic and Early Cretaceous also shows rounded "heel" impressions, although they are not as pronounced as in *Asianopodus*. In *Jialingpus*, the metatarsophalangeal pad of digit IV is extensive proximally, round and blunt terminally, and connected distally to the first pad of the third digit by a large interpad space (Xing et al., 2011).

Chapus (Li et al., 2006) from the Lower Cretaceous of Nei Mongol is a large theropod track similar in superficial appearance to *Eubrontes* and *Changpeipus*. Based on tracings of the type trackway by one of us (MGL) *Chapus* is less elongate than *Changpeipus* (L/W 1.32) with a lower digit divarication angle (45°–50°). The heel pad of *Chapus* is generally more bulbous than the V-shaped morphology seen in the *Changpeipus* type.

7 Unusual preservation of slipping movement

Particularly distinctive tracks may be left by tetrapods when walking and running, resting (Milner et al., 2009; Xing et al., 2012a), swimming (Milner et al., 2006), taking-off or landing (Mazin et al., 2009). However, when familiar movements encounter soft and wet sediments, the resulting tracks may have a significant variety of morphologies (Gatesy et al., 1999; Xing et al., 2012b).

SSIA35 was preliminarily described (as footprint no. 60) by Wings et al. (2007) as the "slip footprint" (Fig. 13). This previous research considered that "it may represent swimming, or a footprint of a dinosaur slipping either backwards or forwards in the mud". The later discussions by Wings et al. (2007) discounted the swim track version, favoring the possibility of a track documenting slipping movement. We here support the opinion of Wings et al. (2007)

that SSIA35 is not a swim track as it lacks the characteristic morphology of unambiguous swim tracks (such as documented by Milner et al., 2006). However, we recognize distinct scale scratch lines at the lateral side of the distal portion of digit II and, contrary to Wings et al. (2007), we also notice a probable claw impression (Fig. 13D, E).

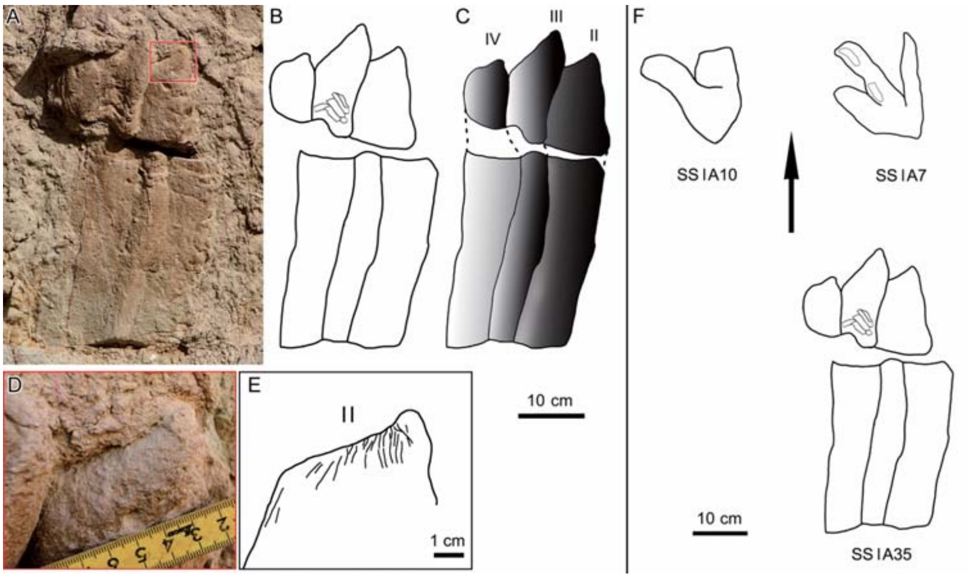

Fig. 13 Footprint from Shanshan tracksite I showing unusual slipping movement of the trackmaker
A. photograph; B. outline drawing; C. eliminating displacement, the color gradient of white to dark indicates the depth of the footprint varying from shallow to deep, respectively; D. scale scratch lines of distal digit II; E. outline drawing of D; F. possible step with SSIA35 and SSIA7 and isolated incomplete imprint SSIA10

SSIA35 is 51 cm long, 14.7 cm wide between the tips of digits II and IV, and 22.6 cm at the widest point. The three digits are approximately parallel. No "heel" print was observed.

It is possible that SSIA35 and SSIA7 constitute a single step (Fig. 13F). This is indicated by the same orientation of the footprints and the similar distance between the tips of digits II and IV. The distance between these two footprints is 38.5 cm. By comparisons with the classic theropod footprint genera *Eubrontes*, *Anchisauripus*, *Kayentapus*, and *Grallator*, we can infer that SSIA7 is probably a left footprint, with digit widths of 5, 4, and 3 cm for digits II, III, and IV, respectively. The 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) has an anterior apex angle of 110°.

The width of the three digit traces of SSIA35 (Fig. 13A–C, from left to right) is 8.8, 7.6, and 10.1 cm, respectively. If SSIA35 represents a step in sequence with SSIA7, these widths correspond to digits IV, III, and II, respectively. The anterior triangle has an anterior angle of 117° similar to that of SSIA7 (110°), and the second digit is the widest in both tracks. The footprints differ in that the widths of the three digits in SSIA35 are almost twice those of SSIA7. SSIA35 also exhibits differences in height (depth), gradually deepening transversely

(Fig. 13A–C, from left to right). This may indicate that the center of gravity of the track maker shifted medially. Gradual shallowing was also observed longitudinally (from the distal to the proximal part of the footprint), but the depth difference is much less than for the transverse deepening. A further interpretation is difficult due to incomplete preservation.

Wings et al. (2007) considered that a potential slippery environment probably contributed to the formation of SSIA35; we here agree with this interpretation. However, almost all tracks at the tracksite were preserved on slippery substrates. The trackmaker's foot may have slipped backward either during acceleration or deceleration. In the former case, the footprint would exhibit deep claw marks, such as reported by Gatesy et al. (1999). If the track had been formed during deceleration, it would exhibit elongated digit traces. The latter feature is rpresent in SSIA35. Although we do not have enough specimens, by comparison with modern bird tracks (see Genise et al., 2009: fig. 7S and T) we suggest that S1A35 was formed during running or following/tracing. Thereby, the trackmaker's foot sank into the slippery substrate and slipped forward and laterally a certain distance, because of inertia.

8 Scale scratch lines

Some Shanshan theropod tracks, such as SSIA35 and SSIB16, preserved scale scratch lines formed when individual pedal scales dragged through the sediment. In SSIB16, the scale scratch lines of ?digit II average 0.5 mm in width, showing a density of 8–14 lines per centimeter (Fig. 14). The scratch lines of SSIA35 (Fig. 13D–E) average 0.6 mm in width, showing a density of 8 lines per centimeter. Their direction conforms to entry striations of the digits that have slid forward after contact with the substrate (Gatesy, 2001). The similar scale scratch lines of SSIA35 and SSIB16 suggest a similar origin. In small-sized (18.4 cm in length) theropod tracks of cf. *Jialingpus* isp. (MGCM H8) from the Lower Cretaceous Huangyangquan tracksite of Xinjiang, the scale scratch lines average 1.3 mm in width, showing a density of 6–7 lines per centimeter (Xing et al., 2011). A large-sized (68.9 cm in length) theropod track (MPD 100F/12) from the Late Cretaceous of the Gobi region in Mongolia, has 5–6 scratch lines per centimeter (Currie et al., 2003). Conversely, scale scratch lines of the Shanshan theropod tracks are thinner.

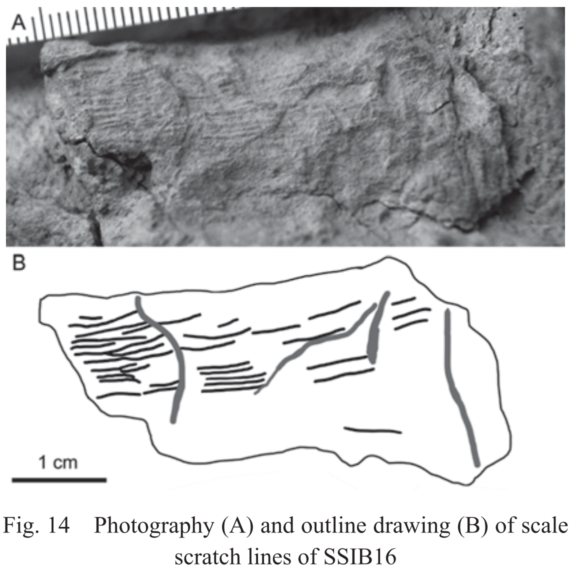

Fig. 14 Photography (A) and outline drawing (B) of scale scratch lines of SSIB16

9 Paleobiological implications

The Shanshan tracks suggest no preferred direction of movement besides their predominant northeast orientation (Fig. 2B). SSIB58 and SSIA30 are significantly smaller than other tracks at the Shanshan tracksites. The general morphology of SSIB58 (15.8 cm long) is similar to SSIB59, but it is only 45% as large as the latter. The divarication angle between digits II and IV is 62°, slightly larger than in SSIB59. SSIB58 possibly represents a juvenile individual of the same taxon as the SSIB59's trackmaker. SSIA30 (13.7 cm in length) is the smallest track at the Shanshan tracksites and of similar morphology, except for the metatarsophalangeal portion which is incomplete. The co-occurrence of tracks of similar morphology but significantly different size was also observed at some theropod tracksites from Liaoning Province. Isolated small-sized tracks like SSIB58 and SSIA30 suggest either the presence of cohabiting groups composed of members of the same trackmaker species with different age classes (juvenile, adult), ethologically similar to some extant lizards and *Alligator* (Olsen et al., 1998; Xing et al., 2011) or different biological species. The similarity with SSIB59 in morphology just indicates that these two footprints were made by different-sized theropods with similar foot morphology. With regard to theropod tracks Lockley and Hunt (1995) (contrary to Olsen et al., 1998) argued that, because *Grallator* and *Eubrontes* occur as discrete size classes (at least in the North American west), they represent different species, not age groups. However, contrary to the Shanshan specimens, these tracks from North America can be distinguished by different morphologies. Lockley and Hunt (1995) stress, that small tracks of juvenile dinosaurs are generally more scarce because of the reduced potential for preservation and the relatively short ontogenetic period, assuming fairly rapid growth rates, during which they could have been left. The assemblage from Shanshan has not produced discrete morphological or size related clusters to support the inference that multiple trackmaking species existed. The Shanshan tracksites contain a few small tracks but otherwise offer no possibilities to test these hypotheses.

10 Conclusions

1) Theropod footprints from the Shanshan tracksites are assigned to the ichnogenus *Changpeipus* based on diagnostic features that are different from those of the classical theropod ichnogenera *Grallator* and *Eubrontes* such as the large metatarsophalangeal pad positioned nearly in line with digit III, the digit proportions with IV>II and the relatively large divarication angle between digits II and IV.

2) The re-assessment and comparison of the Shanshan tracks and different *Changpeipus* ichnospecies described from other localities support a single ichnotaxon and type ichnospecies *C. carbonicus* as has been suggested in earlier studies; i.e., claims of multiple ichnospecies of

the ichnogenus *Changpeipus* are not based on convincing morphological evidence.

3) Previous interpretations of Wings et al. (2007), who distinguished two different morphotypes of the Shanshan tracks, are re-evaluated. Differences fall within the "normal" variability related to substrate conditions and/or pes posture. Wide extramorphological variation is demonstrated by a sample of 143 footprints and trackways on surfaces that indicate a depositional environment with soft, wet and slippery substrates. This is a case study suggesting a cautious ichnotaxonomic evaluation of tracksites in general.

4) Similar-shaped footprints of different size can be interpreted either as having been left by individuals of different age (ontogenetic stage) or by different biological species with identical pes morphology. However, convincing evidence of size-independent track morphology or discrete morphological clusters, suggestive of different species of trackmaker, were not observed.

5) Peculiar preservational features include a footprint that documents slipping movement of the pes by three parallel bands obviously reflecting digits II, III and IV, and gradually deepening transversely from the lateral to the medial margin. It lacks a "heel" imprint.

6) The depositional environment is interpreted as a gradually expanding and deepening lacustrine setting. Mass occurrences of invertebrate burrows that can be assigned to the ichnogenus *Fuersichnus* on some surfaces support this view.

Acknowledgements We thank the Shanshan County Bureau of Land and Resources, which provided logistical support; Sun Ge (Shenyang Normal University, China) for his critical comments on this paper; Peter L. Falkingham (Royal Veterinary College, UK) and Li Rihui (Qingdao Institute of Marine Geology, China) for their helpful reviews of the manuscript; He Qing, Hu Jian and Mao Lei (China University of Geosciences, China) provided measured data. Alfred Uchman and Dirk Knaust are thanked for comments on the invertebrate traces in an earlier version of the manuscript. This research was supported by the Department of Land and Resources of Xinjiang Uygur Autonomous Region (Geologic Relic Resources Investigation and Evaluation Project at the Kumutage Desert, Shanshan County, Xinjiang (XJYJDC2011-01), and the Key Laboratory of Vertebrate Evolution and Human Origins of CAS (2011LESV008).

新疆吐鲁番盆地中侏罗统张北足迹(***Changpeipus***, 兽脚类)的重新研究

邢立达[1,2] Hendrik KLEIN[3] Martin G. LOCKLEY[4] Andreas WETZEL[5] 李忠东[6]
李建军[7] Gerard D. GIERLIŃSKI[8,9] 张建平[1] 松川正树[10] Julien D. DIVAY[11] 周 隆[6]

(1 中国地质大学(北京)地球科学与资源学院 北京 100083)

(2 中国科学院脊椎动物演化与人类起源重点实验室 北京 100044)

(3 德国古爬行及两栖动物博物馆 诺伊马克特 D-92318)

(4 美国科罗拉多大学丹佛分校恐龙足迹博物馆　丹佛　80217)
(5 瑞士巴塞尔大学地质古生物研究所　巴塞尔　CH-4056)
(6 四川省地矿局物探队资源与环境研究所　成都　610072)
(7 北京自然博物馆研究部　北京　100050)
(8 波兰侏罗纪公园　奥斯特罗维茨　4, 27-400)
(9 波兰地质研究所　华沙　4, 00-975)
(10 日本东京学艺大学环境科学系　东京　184-8501)
(11 加拿大阿尔伯塔大学生物科学系　埃德蒙顿　T6G 2E9)

摘要：详细描述了中国西北部新疆吐鲁番市鄯善足迹点、中侏罗统三间房组的兽脚类足迹组合。连同新发现在内，共描述了143个足迹，并阐明其不同的保存状况与额外形态变化。在足迹分类学上，这批足迹被归入石炭张北足迹(*Changpeipus carbonicus*), 该足迹种常见于中国其他侏罗纪足迹点。前人的研究认为此地有两种不同的足迹形态，但研究表明这是由软且湿滑的基底造成的额外形态变化。足迹的结构特征亦不支持此地存在不同的足迹种。此外，对比了其他化石点类似的足迹，认为张北足迹为单型属，即模式种石炭张北足迹。鄯善足迹点的足迹长度从12.2 cm (几个孤立的样本)到47 cm, 足迹应由不同年龄段的、小型至中型的同类造迹者或不同类的造迹者所留。奇异的足迹状态包括了一个滑动造成的足迹，足迹由三道平行条带构成，条带应为第II, III和IV趾所留。一个与其关联的“正常”足迹可能与该滑动足迹构成一个单步。与足迹共生的、丰富的无脊椎动物遗迹化石支持该化石点的沉积环境是一个逐步扩大和深化的湖泊。前人的研究将此地的无脊椎动物遗迹化石归入洛克迹(*Lockeia*), 新的研究将其归入福尔斯斯迹(*Fuersichnus*), 这类遗迹被归于泥食性昆虫幼虫或其他无脊椎动物所留。福尔斯斯迹指示的环境特征是在泥泞的河漫滩或湖泊边缘居住与/或觅食。

关键词：新疆鄯善，中侏罗世，三间房组，张北足迹，福尔斯斯迹
中图法分类号：Q915.2　**文献标识码：**A　**文章编号：**1000-3118(2014)02-0233-27

References

Alexander R M, 1976. Estimates of speeds of dinosaurs. Nature, 261: 129–130

Bromley R G, Asgaard U, 1979. Triassic freshwater ichnocoenoses from Carlsberg Fjord, East Greenland. Palaeogeogr, Palaeoclimatol, Palaeoecol, 28: 39–80

Currie P J, Badamgarav D, Koppelhus E B, 2003. The first Late Cretaceous footprints from the Nemegt locality in the Gobi of Mongolia. Ichnos, 10: 1–13

Dong Z M, 2004. Mesozoic fossil vertebrates from the Junggar Basin and Turpan Basin, Xinjiang, China. In: Sun G, Mosbrugger V, Ashraf A R eds. Proceedings of the Sino-German Cooperation Symposium on Paleontology. Urumqi: Geological Evolution and Environmental Changes of Xinjiang, China. 95–103

Gatesy S M, 2001. Skin impressions of Triassic theropods as records of foot movement. Bull Mus Comp Zool, 156(1): 137–149

Gatesy S M, Middleton K M, Jenkins F A et al., 1999. Three-dimensional preservation of foot movements in Triassic theropod dinosaurs. Nature, 339: 141–144

Genise J F, Melchor R N, Archangelsky M et al., 2009. Application of neoichnological studies to behavioural and taphonomic interpretation of fossil bird-like tracks from lacustrine settings: the Late Triassic–Early Jurassic? Santo Domingo Formation, Argentina. Palaeogeogr, Palaeoclimatol, Palaeoecol, 272: 143–161

Gierliński G, 1994. Early Jurassic theropod tracks with the metatarsal impressions. Przegl Geol, 42: 280–284

Häntzschel W, 1975. Trace Fossils and Problematica: Treatise on Invertebrate Paleontology, v. Part W, Miscellanea, Supplement I. New York: Geological Society of America and University of Kansas. 1–269

Hasiotis S T, 2002. Continental trace fossils. SEPM Short Course Notes, 51: 1–132

Li J J, Bater, Zhang W H et al., 2006. A new type of dinosaur tracks from Lower Cretaceous of Chabu, Otog Qi, Inner Mongolia. Acta Paleont Sin, 45: 221–234

Li J J, Bai Z Q, Wei Q Y, 2011. On the Dinosaur Tracks from the Lower Cretaceous of Otog Qi, Nei Mongol. Beijing: Geological Publishing House. 1–109

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

Lockley M G, Hunt A P, 1995. Dinosaur Tracks and Other Fossil Footprints of the Western United States. New York: Columbia University Press. 1–338

Lockley M G, Li J J, Li R H et al., 2013. A review of the tetrapod track record in China, with special reference to type ichnospecies: implications for ichnotaxonomy and paleobiology. Acta Geol Sin-Engl, 87(1): 1–20

Lockley M G, Matsukawa M, 2009. A review of vertebrate track distributions in East and Southeast Asia. J Paleontol Soc Korea, 25: 17–42

Lockley M G, Matsukawa M, Li J J, 2003. Crouching theropods in taxonomic jungles: ichnological and ichnotaxonomic investigations of footprints with metatarsal and ischial impressions. Ichnos, 10: 169–177

Lü J C, Zhang X L, Jia S H et al., 2007. The discovery of theropod dinosaur footprints from the Middle Jurassic Yima Formation of Yima County, Henan Province. Acta Geol Sin-Chinese Ed, 81: 439–444

MacNaughton R B, Pickerill R K, 1995. Invertebrate ichnology of the nonmarine Lepreau Formation (Triassic), southern New Brunswick, eastern Canada. J Paleont, 69: 160–171

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 Res, 27: 3–21

Matsukawa M, Shibata K, Kukihara R et al., 2005. Review of Japanese dinosaur track localities: implications for ichnotaxonomy, paleogeography and stratigraphic correlation. Ichnos, 12: 201–222

Mazin J M, Billon-Bruyat J P, Padian K, 2009. First record of a pterosaur landing trackway. Proc R Soc, B276: 3881–3886

Milner A R C, Harris J D, Lockley M G et al., 2009. Bird-like anatomy, posture, and behavior revealed by an Early Jurassic theropod dinosaur resting trace. PLoS ONE, 4(3): e4591 1–14

Milner A R C, Lockley M G, Johnson S B et al., 2006. The story of the St. George Dinosaur Discovery Site at Johnson Farm: an important new Lower Jurassic dinosaur tracksite from the Moenave Formation of southwestern Utah. The Triassic-Jurassic Terrestrial Transition. N M Mus Nat Hist Sci Bull, 37: 329–345

Olsen P E, 1980. Fossil great lakes of the Newark Supergroup in New Jersey. In: Manspeizer W ed. Field Studies of New Jersey Geology and Guide to Field Trips. 52nd Annual Meeting of the New York State Geological Association. Newark: Rutgers University. 352–398

Olsen P E, Smith J B, McDonald N G, 1998. Type material of the type species of the classic theropod footprint genera

Eubrontes, *Anchisauripus*, and *Grallator* (Early Jurassic, Hartford and Deerfield basins, Connecticut and Massachusetts, U.S.A.). J Vert Paleont, 18: 586–601

Shao L, Stattegger K, Li W et al., 1999. Depositional style and subsidence history of the Turpan Basin (NW China). Sediment Geol, 128: 155–169

Thulborn R A, 1990. Dinosaur Tracks. London: Chapman and Hall. 1–410

Wan Y R, Yang Z L, Wei L H et al., 2006. Sedimentary facies features of Sanjianfang and Qiketai Formation of Middle Jurassic in north of Taibei, Tuha Basin. Nat Gas Geosci, 17(5): 693–697

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, Virgina. Virg Div Min Res Publ, 119: 113–127

Wings O, Schellhorn R, Mallison H et al., 2007. The first dinosaur tracksite from Xinjiang, NW China (Middle Jurassic Sanjianfang Formation, Turpan Basin) – a preliminary report. Global Geol, 10(2): 113–129

Xing L D, Harris J D, Toru S et al., 2009. Discovery of dinosaur footprints from the Lower Jurassic Lufeng Formation of Yunnan Province, China and new observations on *Changpeipus*. Geol Bull China, 28(1): 16–29

Xing L D, Harris J D, Jia C K, 2011. Early Cretaceous bird-dominated and dinosaur footprint assemblages from the northwestern margin of the Junggar Basin, Xinjiang, China. Palaeoworld, 20: 308–321

Xing L D, Gierliński G D, Harris J D et al., 2012a. A probable crouching theropod dinosaur trace from the Jurassic-Cretaceous boundary in Hebei, China. Geol Bull China, 31(1): 20–25

Xing L D, Bell P R, Harris J D et al., 2012b. An unusual, three-dimensionally preserved, large hadrosauriform pes track from "mid"-Cretaceous Jiaguan Formation of Chongqing, China. Acta Geol Sin-Engl, 86: 304–312

Xing L D, Lockley M G, McCrea R T et al., 2013. First record of *Deltapodus* tracks from the Lower Cretaceous of China. Cretaceous Res, 42: 55–65

Young C C, 1960. Fossil footprints from China. Vert PalAsiat, 4(2): 53–66

Young C C, 1979. Footprints from Luanping, Hebei. Vert PalAsiat, 17(2): 116–117

Zhang D S, Fu G B, Qing E P et al., 2002. Jurassic palaeoclimate, palaeovegetation and palaeoenvironment in the Tuha Basin in Xinjiang. Geoscience, 16(2): 147–152

Zhen S N, Li J J, Rao C G et al., 1989. A review of dinosaur footprints in China. In: Gillette D D, Lockley M G eds. Dinosaurs Past and Present. Cambridge: Cambridge University Press. 187–197