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Cretaceous saurischian tracksites from southwest Sichuan Province and overview of Late Cretaceous dinosaur track assemblages of China

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ABSTRACT

Dinosaur tracks from Upper Cretaceous deposits of Sichuan Province, China have proved of great significance for two reasons: they (1) provide unambiguous evidence of dinosaurs from this epoch in this region, and (2) demonstrate that the track bearing units of the Leidashu Formation are not Paleocene-Eocene in age as previously claimed by some authors. We herein describe five small sites, from the Zhaojue area and the nearby Xide areas. Two sites are dominated by theropod tracks, including one with small tracks of *Eubrontes*-like morphology, and another with deep tracks revealing long metatarsal impressions, probably indicating a soft substrate. Three sites yield only sauropod tracks. Combined data from these five tracksites document a typical saurischian dominated ichnofauna, and based on present evidence these assemblages are less diverse than those from Lower Cretaceous sites in the region. However a larger sample is necessary to test this suggestion.

1. Introduction

Early Cretaceous vertebrate skeletal fossils from the Sichuan area (including Sichuan Basin and Panxi region) are limited to very scarce theropod and sauropod fragments (Wang et al., 2008), which currently lack scientific description. By comparison, the Early Cretaceous vertebrate track record of the Sichuan area is rich and diverse, comprising at least 15 mostly-documented sites. Since 2007, the main authors of this paper have found and documented a growing number of Early Cretaceous vertebrate tracksites in the Sichuan area including non-avian theropod, bird, sauropod, ornithopod and pterosaur tracks (Xing et al., 2007, 2013a, 2014a, 2015; Xing and Lockley, 2014). Therefore, the reconstruction of the Early Cretaceous dinosaur fauna of the Sichuan area is largely based on the track record. In contrast, the composition of the Late Cretaceous dinosaur fauna of Sichuan is almost obscure. Both the Late Cretaceous skeletal and track records have been sparse in the Sichuan area and were limited to the Zhengyang Basin at the eastern margin. The Upper Cretaceous Zhengyang Formation has yielded teeth of theropods, titanosaurs and hadrosaurs (Wang et al., 2008), but these have never been formally described.

In 2014, a regional geological survey team from the Sichuan Bureau of Geological Exploration and Development of Mineral Resources discovered two groups of new tracksites in the Zhaojue area and the nearby Xide area, in Sichuan Province (Fig. 1). Both localities include tracksites in Lower and Upper Cretaceous strata. The Late Cretaceous tracks provide the first solid dinosaur record from this time interval in the Sichuan area.

1.1. Institutional abbreviations

CGCMS = Compiling Group of Continental Mesozoic Stratigraphy and Palaeontology in Sichuan Basin of China; JBSI = Jierboshi I tracksite, Zhaojue County, Liangshan, China; JBSII = Jierboshi II tracksite, Zhaojue County, Liangshan, China; SBGED = Sichuan

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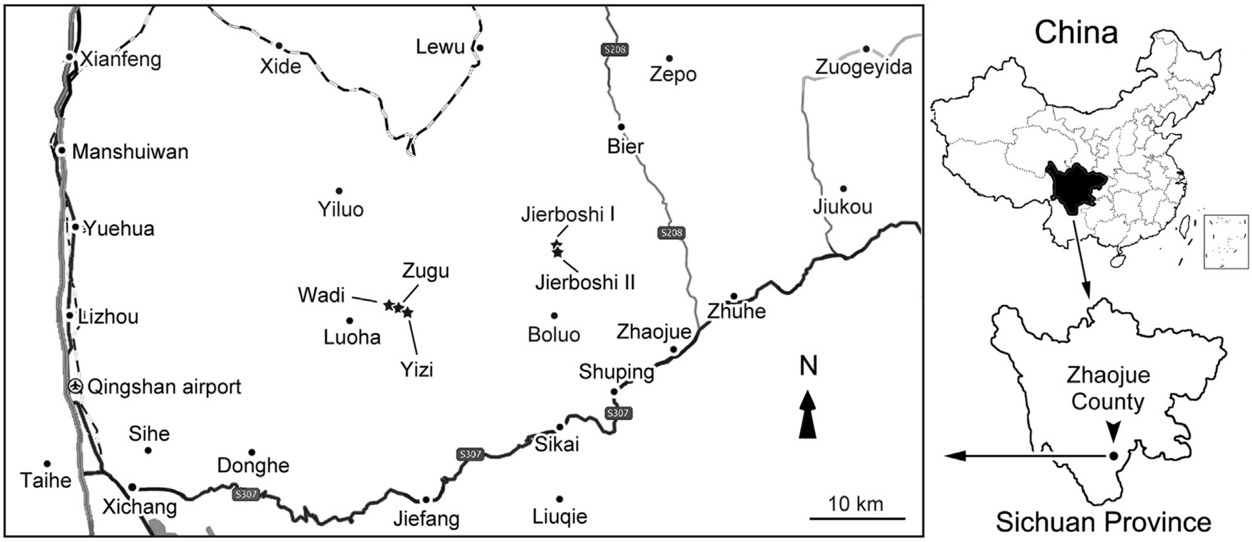

Fig. 1. Geographic map showing the location (star icon) of the dinosaur tracksites in the Zhaojue-Xide area, Sichuan Province, China.

Bureau of Geological Exploration and Development of Mineral Resources; SBGMR = Sichuan Bureau of Geology and Mineral Resources; WD = Wadi tracksite, Xide County, Liangshan, China; YZ = Yizi tracksite, Xide County, Liangshan, China; ZG = Zugu tracksite, Xide County, Liangshan, China.

2. Geological setting

The Southwestern area of Sichuan Province, consisting of the Liangshan autonomous prefecture and Panzhihua city, is commonly known as the Panxi (Panzhihua–Xichang) region. Within the Panxi region, the Cretaceous strata are widely distributed. The largest basin in this area is the Mishi (Xichang)–Jiangzhou Basin (Luo, 1999). Based on biostratigraphic indices (ostracod, and plants/stoneworts), the Cretaceous strata in the Mishi-Jiangzhou Basin have been divided into the Lower Cretaceous Feitianshan and Xiaoba formations, and the Upper Cretaceous-Paleogene Leidashu Formation (Gu and Liu, 1997; SBGED, 2014; but see re-evaluation below). The Xiaoba Formation is in conformable contact with the Feitianshan Formation below and the Leidashu Formation above.

In the Zhaojue-Xide region, the Xiaoba Formation is divided into three members (Fig. 2). The First Member is 1315 m thick. The lower layers mainly consist of medium and fine purplish red sandstone that is occasionally interbedded with mudstone and argillaceous siltstone; upper layers mainly consist of purplish red thin and medium bedded siltstone and silty mudstone. Planar bedding is typical. The Second Member is 573.7 m thick. Its lower layers are formed by dark purple mudstone, argillaceous siltstone and mudstone interbedded with greyish-green marlstone. Convolute bedding and planar bedding, respectively, are developed within the siltstone and argillaceous siltstone units. The middle layers consist of mudstone, argillaceous siltstone, silty mudstone interbedded with argillaceous siltstone and fine sandstone interbedded with thin siltstone layers. The upper layers mainly consist of dark purple mudstone, purplish red thick bedded-massive fine sandstone and pebbly sandstone. The Third Member is 545.8 m thick. Its lower layers are comprised of purplish red thick-bedded fine sandstone and medium-bedded fine sandstone interbedded with mudstone in unequal thickness. The middle layers are mainly formed by mudstone and argillaceous siltstone interbedded with mudstone in unequal thickness. The upper layers are comprised of purplish red medium-thick bedded coarse sandstone interbedded with mudstone, medium-thick bedded siltstone interbedded with mudstone, and gravel developed along the surface. The gravel is mainly formed by mudstone.

Based on its lithostratigraphic zone, the Xiaoba Formation has been referred to the "mid-" or Upper Cretaceous (SBGMR, 1991). The sedimentary depositional environments were alluvial-fan, fluvial river and lacustrine systems (Chang et al., 1990). The First Member of the Xiaoba Formation matches the Jiaguan Formation from the Sichuan Basin based on the lithostratigraphic correlation (CG CMS, 1982).

In the Zhaojue-Xide region, the Upper Cretaceous-Paleogene Leidashu Formation is divided into two Members. The First Member is 643.5 m thick, with a set of purplish red pebbly sandstone at the bottom; lower layers that are purplish red medium-thick bedded feldspathic quartzose sandstone with parallel beddings developed inside; and upper layers with smaller granularity consists of thin-medium bedded sandstone and siltstone interbedded with mudstone. The Second Member is 285.8 m thick and lithologically characterized by purplish red thin-medium siltstone and mudstone with cross bedding and argillaceous siltstone with parallel bedding.

The sedimentary depositional environment of the Leidashu Formation was a lacustrine system (Yao et al., 2002). Some authors have referred the Leidashu Formation to the Paleocene-Eocene based on its lithostratigraphic zone (SBGMR, 1991; Zhang, 2009). However, this conclusion is clearly erroneous based on the presence of a dinosaur fossil track record (see below).

3. Distribution of dinosaur tracks

(1). The Jierboshi I tracksite (GPS: 28° 6′55.13″N, 102°42′38.52″E) (WGS84 Datum) of Jierboshi Village, Zhaojue County, Liangshan, China, is an exposed calcareous siltstone surface from the First Member of the Xiaoba Formation. Highly developed ripple marks are readily observed. Tracks include those of theropods and possibly sauropods.

(2). Jierboshi II tracksite (GPS: 28° 6′51.04″N, 102°42′38.90″E) of Jierboshi Village, Zhaojue County, Liangshan, China, is an exposed purplish red sandstone surface from the First

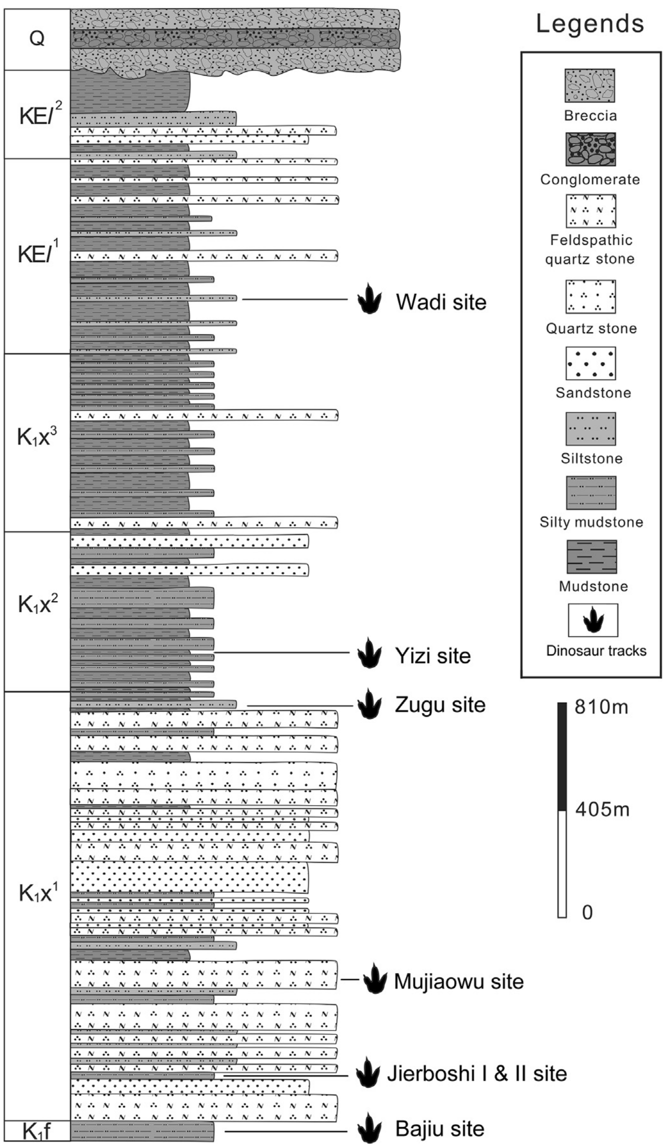

Fig. 2. Stratigraphic section of the Cretaceous sedimentary sequences in the Zhaojue-Xide area. K_1f, Feitianshan Formation (Lower Cretaceous); K_1x^{1-3}, First/Second/Third Member of the Xiaoba Formation (Lower Cretaceous); KEl^{1-2}, First/Second Member of the Leidashu Formation (Upper Cretaceous); Q, Quaternary. The Mujiaowu and Bajiu site will be published elsewhere.

Member of the Xiaba Formation. This site has yielded theropod tracks, most of them exhibiting metatarsal pad impressions.

(3). The Zugu tracksite (GPS: 28° 2′47.00″N, 102°32′39.00″E) of Zugu Village, Luoha Town, Xide County, Liangshan, China, is an exposed bright red siltstone surface from the top of First Member of theXiaoba Formation. Four sauropod tracks have been found thus far.

(4). Yizi tracksite (GPS: 28° 1′55.00″N, 102°32′54.00″E) of Yizi Village, Luoha Town, Xide County, Liangshan, China, is an exposed dark purplish-red silty mudstone surface from the Second Member of the Xiaoba Formation. This site exhibits developed mud cracks and twelve sauropod tracks.

(5). Wadi tracksite (GPS: 28° 3′5.50″N, 102°31′7.15″E) of Wadi Village, Luoha Town, Xide County, Liangshan, China, is an exposed grayish-purple silty mudstone from the First Member of the Leidashu Formation. This site yielded a rich sauropod ichnofauna.

4. Tracks and trackways

4.1. Theropod and possible sauropod tracks from Jierboshi I tracksite

4.1.1. Description

The Jierboshi I tracksite shows thirty isolated footprints catalogued as JBSI-TI1–30; and one trackway comprised of three tracks, catalogued as JBSI-T1 (Figs. 3 and 4; Table 1). A natural cast of JBSI-TI29 was collected and is stored in Zigong Dinosaur Museum catalogued as ZDM201501. All other tracks remain in situ.

The JBSI trackmakers mostly obliterated local ripple marks when leaving their tracks. The sediments that preserved the tracks were often relatively wet and soft, and most tracks, therefore, lack identifiable digit pads. Several tracks have wide outlines formed in soft surface sediments. Others have narrow outlines (as shown in Fig. 4 by dotted lines) formed in contact with firmer underlying sediment. These narrower outlines probably offer a better representation of the actual morphology of the trackmakers' feet. Similar tracks (*Therangospodus* isp.) have been found in the Upper Jurassic–Lower Cretaceous Luofenggou site, in the Tuchengzi Formation of Chicheng County, Hebei Province, China (e.g. LF1, Xing et al., 2011).

The best preserved of the JBSI tracks is JBSI-T1-R1 (Fig. 4A, B). In this specimen, digit pads are partially visible; it is 15.4 cm long with a length/width ratio of 1.2. Digit III projects the farthest anteriorly, followed by digits II and IV. Two metatarsophalangeal pad traces can be seen: a smaller one posterior to digit II and another larger one posterior to digit IV. The former is close to the trace of the first pad of digit II and separated from this by a distinct crease. The latter is round and blunt and positioned near the axis of digit III, but closer to digit IV. Digits show sharp claw marks. The divarication angles between digits II and IV are relatively wide (64°). The pace angulation in JBSI-T1 is 163°. The overall morphology of JBSI-T1-R1 resembles *Gypsichnites pascensis* an ichnotaxon first described from Lower Cretaceous strata of Canada (Sternberg, 1932) that was originally considered to be an ornithopod track, but later reinterpreted and assigned to a theropod trackmaker (McCrea, 2000; Gangloff et al., 2004; Díaz-Martínez et al., 2015). Interestingly, theropod tracks and trackways are sometimes confused with those of ornithopods and vise versa, if they are less well preserved (see Castanera et al., 2013). However, JBSI-T1-R1 is clearly a theropod trackway based on the pad configuration, the degree of mesaxony and the outward rotation of the imprints relative to the midline. In JBSI-TI27 (Fig. 4C, D), another well preserved track, digit III shows three digit pad traces. Other theropod tracks are similar to T1-R1 in general morphology.

An isolated sub-round impression with a diameter of about 40 cm was catalogued as JBSI-SI1p (Fig. 3). Similar large round impressions from other Lower Cretaceous tracksites are generally identified as sauropod tracks (cf., Lockley, 1999).

The orientation of the theropod tracks from the Jierboshi I tracksite is largely consistent with that of the current flow as inferred from the ripple traces.

4.1.2. Comparison and discussion

According to Olsen (1980), Weems (1992), and Lockley (2009), tridactyl tracks can be differentiated on the basis of various features, but particularly mesaxony: i.e., the degree to which the central digit (III) protrudes anteriorly beyond the medial (II) and lateral (IV) digits. Most studies of mesaxony pertain to differentiating theropod tracks. The mesaxony of the Jierboshi I theropod tracks is weak to moderate (range 0.41–0.65), which is typical for footprints of the ichno- or morphofamily Eubrontidae Lull, 1904. A characteristic feature of JBSI-T1-R1 is the presence of a distinct

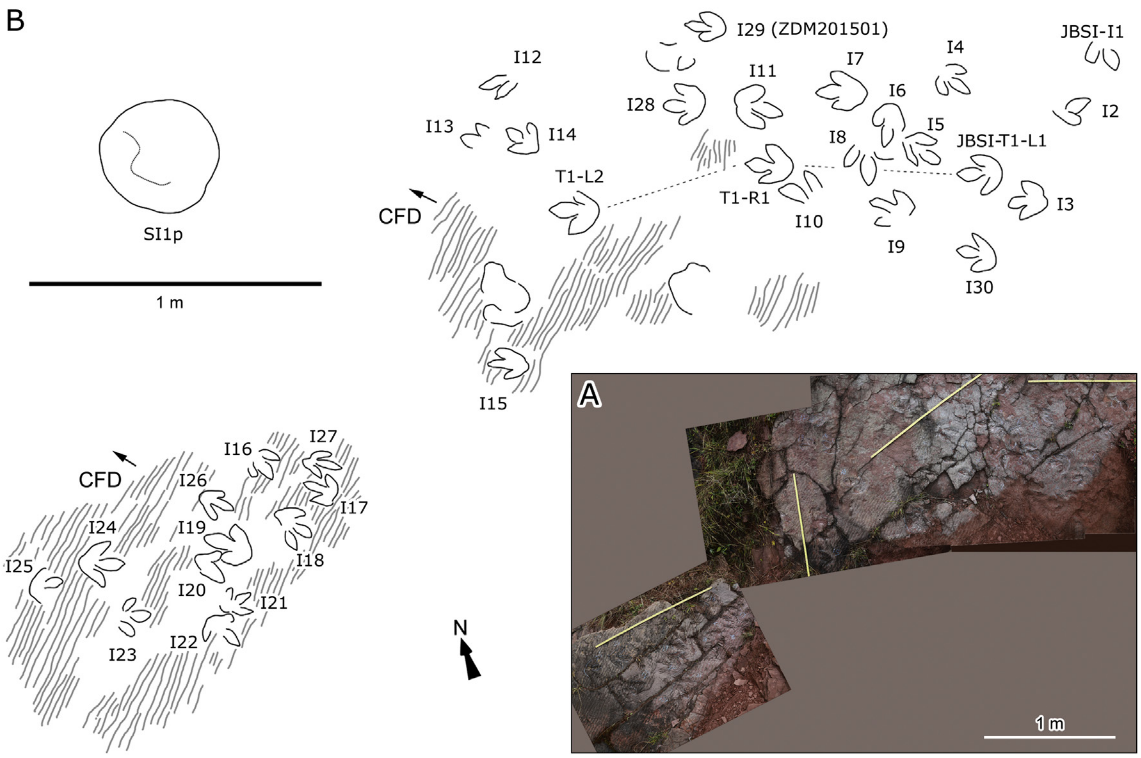

Fig. 3. Photograph (A) and interpretative outline drawing (B) of theropod and sauropod tracks from the Jieboshi I site, Sichuan Province, China. CFD = current flow direction.

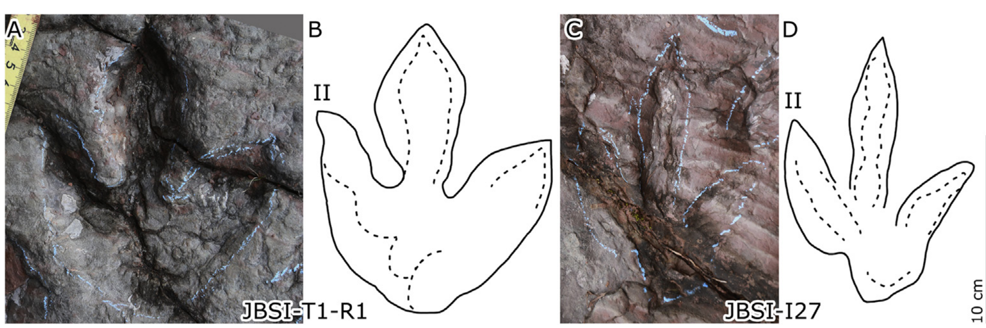

Fig. 4. Photograph (A, C) and interpretative outline drawings (B, D) of well-preserved theropod tracks from the Jieboshi I site, Sichuan Province, China.

metatarsophalangeal pad trace posterior to digit II. This character is common in *Eubrontes* tracks, for example in the type specimen AC 151 (Olsen et al., 1998). However, the Jierboshi I tracks are smaller than most assigned to this ichnogenus, which is traditionally regarded as a large theropod morphotype with a footprint length of at least 25 cm (cf., Thulborn, 1990). According to Xing et al. (2014b) some Early Cretaceous theropod tracks that are similar to *Eubrontes* in their overall-shape appear to have larger divarication angles than typical Early Jurassic *Eubrontes*. *Eubrontes*-like tracks are especially common in Lower Cretaceous deposits of China (Lockley et al., 2013; Xing et al., 2015). As mentioned above, the First Member of the Xiaoba Formation can be correlated with the Jiaguan Formation from the Sichuan Basin (CGCMS, 1982). Most *Eubrontes*-like tracks from the Jiaguan Formation have been found at the Hanxi tracksite (Xing et al., submitted for publication) and the Xinyang tracksite (Lockley and Xing, 2015; Xing et al., 2015b), indicating that theropod tracks of Barremian-Albian age (Chen, 2009) from the Sichuan Basin and the Panxi region are morphologically similar.

JBSI-T1 constitutes a single trackway. We calculated the track-maker's speed (v) using Alexander's (1976) formula: $v = 0.25\, g^{0.5}\, SL^{1.67}\, h^{-1.17}$, where g = gravitational acceleration in m/sec; SL = stride length; and h = hip height, estimated as 4.5 times foot length (FL), using the ratio for large theropods proposed by Thulborn (1990). Based on the length of the step, speed is estimated at ~1.9 m/s or ~7.0 km/h. The relative stride length (SL/h) is 1.9, implying that the animal was walking, not trotting or running.

4.2. *Theropod tracks from Jierboshi II tracksite*

4.2.1. *Description and comparison*

Jierboshi II tracksite is about 130 m away from Jierboshi I tracksite and has yielded two tridactyl trackways catalogued as JBSII-T1 and T2, which preserve five and four tracks, respectively (Fig. 5). There is also an isolated footprint catalogued as JBSII-TI1. All tracks remain in situ. However their mode of preservation is quite different from that observed at the Jierboshi I tracksite. Due to large extramorphological variation, the JBSII tracks cannot be confidently referred to any ichnogenus.

The trackway and the tracks from JBSII-T1 and TI1 have typical theropod features, such as the strongly forward projecting digit III,

Table 1
Measurements (in cm and degrees) of theropod tracks from the Zhaojue-Xide tracksites, Sichuan Province, China.

Number	ML	MW	II–IV	PL	SL	PA	M	ML/MW
JBSI-T1-R1	15.4	12.5	64°	70.0	135.0	163°	0.44	1.2
JBSI-T1-L2	17.1	13.5	71°	67.0	–	–	0.58	1.3
JBSI-T1-L1	14.9	12.2	69°	–	–	–	0.51	1.2
Mean	**15.8**	**12.7**	**68°**	**69.0**	**135.0**	**163°**	**0.51**	**1.2**
JBSI-TI3	14.9	12.9	67°	–	–	–	0.41	1.2
JBSI-TI5	13.9	11.2	64°	–	–	–	0.45	1.2
JBSI-TI6	16.2	10.4	60°	–	–	–	0.65	1.6
JBSI-TI11	16.5	13.8	76°	–	–	–	0.44	1.2
JBSI-TI24	18.7	17.1	72°	–	–	–	0.42	1.1
JBSI-TI27	14.1	9.9	61°	–	–	–	0.56	1.4
JBSI-TI29	16.6	10.1	52°	–	–	–	0.62	1.6
JBSII-T1-L1	35.7	21.6	–	–	–	–	0.41	1.7
JBSII-T1-R1	35.8	22.0	–	71.9	158.4	162°	–	1.6
JBSII-T1-L2	35.8	–	–	88.6	–	–	–	–
Mean	**35.8**	**21.8**	–	**80.3**	**158.4**	**162°**	**0.41**	**1.6**
JBSII-T2-R1	23.3	27.6	–	80.6	167.0	163°	–	0.8
JBSII-T2-L1	–	24.0	–	–	–	–	–	–
Mean	**23.3**	**25.8**	–	**80.6**	**167.0**	**163°**	–	**0.8**

Abbreviations: ML: Maximum length; MW: Maximum width (measured as the distance between the tips of digits II and IV); II–IV: angle between digits II and IV; PL: Pace length; SL: Stride length; PA: Pace angulation; M: Mesaxony; ML/MW is dimensionless.

high pace angulation (162°), and a relatively high length/width ratio (1.6 on average). However both tracks of JBSII-T1 and TI1 preserve an elongated, club-shaped "heel" or trace of the metatarsals. Generally, the metatarsal pad region of all these tracks shows relatively indistinct borders, evidently due to an originally soft and wet substrate (see also McCrea et al. (2014). Although it is not clearly understood how such well-developed metatarsal pad traces were formed (Kuban, 1986, 1989), it seems certain that they are associated with soft wet substrates at the time of registration (Lockley et al., 2006). Abundant theropod tracks with metatarsal pad traces found in the Jiaguan Formation at the Hanxi tracksite suggest that the trackmakers had been walking with a distinctive gait on extremely soft sediment, and it seems that this gait did not strongly diminish its walking speed (Xing et al., submitted for publication). Such tracks may reflect a specific variety of theropod trackmaker.

4.3. Sauropod tracks from Zugu and Yizi tracksite

4.3.1. Description and comparison

Most of the tracks at the Zugu tracksite are poorly preserved. A single moderately well preserved sauropod pes imprint is catalogued as ZG-SI1p (Fig. 6, Table 2). Individual tracks at the Yizi tracksite are well-preserved, but there are no trackways. Two sets of well-preserved tracks are catalogued asYZ-SI1 and SI2 (Fig. 7, Table 2). These tracks are roughly the same size, the pes prints are about 48.8–53.3 cm in length with an L/W ratio 1.1–1.2. This ratio is similar to that of typical sauropod tracks, such as *Brontopodus* (Farlow et al., 1989).

The ZG-SI1p track interior is partially filled by sediment and relatively featureless in internal morphology. The metatarsophalangeal pad impression is complete with smoothly curved margins. Highly developed mud cracks have destroyed the shapes of YZ-SI1 and SI2 and obliterate any identifiable digit traces. The ratio of manus to pes size is 1:1.9, in this regard the tracks differ from *Brontopodus birdi* tracks from Texas, which have a high heteropody of 1:3 (Farlow et al., 1989; Lockley et al., 1994) but otherwise resemble Early Cretaceous *Brontopodus* tracks from China, such as those from the Jishan tracksite. The latter, however, show a high heteropody (1.5) (Xing et al., 2013b). The sauropod tracks from the Zugu and Yizi sites suggest that the dinosaur fauna continued in the Second Member of the Xiaba Formation in the Panxi region.

4.4. Sauropod tracks from the Wadi tracksite

4.4.1. Description

Weathered tracks are preserved on the surface of a silty mudstone exposure (Figs. 8–10, Table 2). However, some of the tracks still retain some clear features. The Wadi tracksite yielded a large number of tracks, but in random patterns. There are three well-preserved trackways catalogued as WD-S1–S3 (Figs. 8–10). S1 has two right sets of manus and pes prints, S2 has five pes prints and two manus prints, and S3 has three pes-manus couples. Three sets of isolated manus and pes prints and an isolate pes print are also seen at the Wadi tracksite.

WD-S1 is well-preserved, with mean manus and pes lengths of 30.3 and 41.5 cm, respectively. The average length/width ratios of the manus and pes impressions are 1.1 and 1.2, respectively. Taking the best-preserved manus-pes association: RP2 and RM2, the round manus imprint shows distinct impressions of digits I–V and a trace of the metatarsophalangeal region. The pes impression is oval, digits I–IV have distinct claw marks (the traces of digits I–III are the best developed), and the metatarsophalangeal region is smoothly curved. The manus impression is rotated approximately outward from the trackway axis. This rotation (approximately 77°) is greater than the outward rotation of the pes impressions (32°). The isolated left I4m–I4p prints may belong to the WD-S1 trackway, but absolute proof is lacking. However the similarity in the preservation of well-developed digit I–III claw marks suggest the tracks were made at the same time and belong to the same trackway. Assuming this to be the case the trackway is very wide gauge, as clearly shown in Fig. 8.

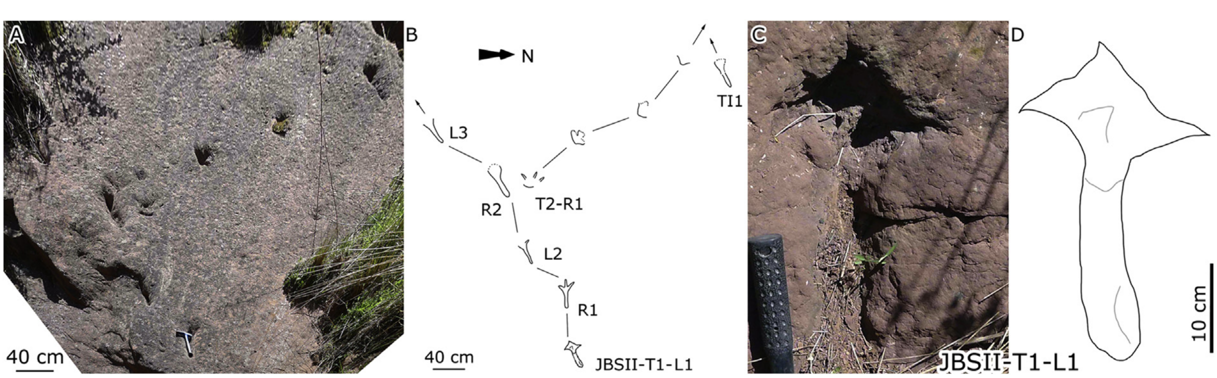

Fig. 5. Photograph (A, C) and interpretative outline drawings (B, D) of theropod tracks from the Jieboshi II site, Sichuan Province, China.

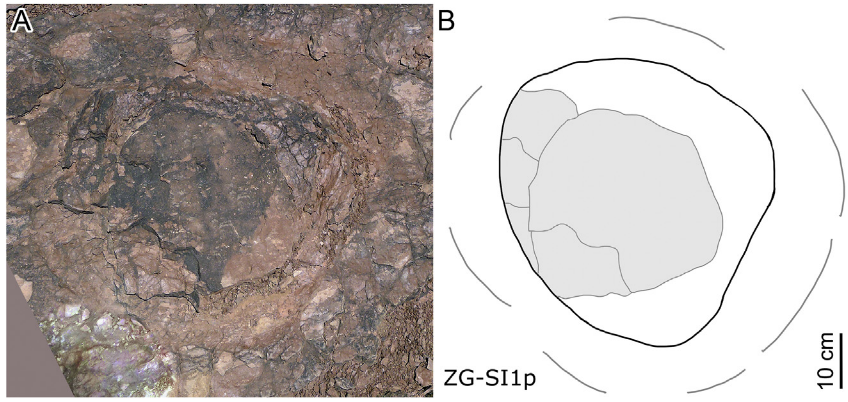

Fig. 6. Photograph (A) and interpretative outline drawing (B) of sauropod track from the Zugu site, Sichuan Province, China.

WD-S2 is a middle-sized sauropod trackway in which the mean lengths of the manus and pes impressions are 24.0 and 32.6 cm, respectively. The average length/width ratios of the manus and pes impressions are 1.1 and 1.2 respectively. Neither manus print nor pes print preserves distinct digit traces/claw marks. The manus impressions of WD-S2 lie slightly anteromedially to the pes impressions. The pes impression is rotated approximately 23° outward from the trackway axis. The average PA from the manus and pes is 96°. Some isolated footprints, like I1, I2 and I3, may belong to the WD-S2 trackway, but the varied ranges of their pace and stride length exceed the average values of WD-S2.

The mean lengths of manus and pes impressions in WD-S3 are 16.3 and 38 cm, respectively. The average length/width ratios of the manus and pes impressions are 0.8 and 1.3, respectively. As in WD-S2, weathering makes it impossible to recognize distinct digit traces.

4.4.2. Comparison and discussion

Gauge (trackway width) of the quadruped trackways was determined for pes and manus tracks using the ratios WAP/P'ML

Table 2
Measurements (in cm and degrees) of the sauropod trackways from the Zhaojue-Xide tracksites, Sichuan Province, China.

Number	ML	MW	R	PL	SL	PA	ML/MW	WAP	WAP/P'ML	WAM	WAM/M'MW
WD-S1-RP1	46.0	41.0	77°	–	186.0	–	1.1	–	–	–	–
WD-S1-RM1	36.0	30.5	32°	–	186.0	–	1.2	–	–	–	–
WD-S1-RP2	37.0	31.0	–	–	–	–	1.2	–	–	–	–
WD-S1-RM2	24.5	24.0	–	–	–	–	1.0	–	–	–	–
Mean(P)	**41.5**	**36.0**	**77°**	–	**186.0**	–	**1.2**	–	–	–	–
Mean(M)	**30.3**	**27.3**	**32°**	–	**186.0**	–	**1.1**	–	–	–	–
WD-S2-LP1	32.5	24.0	26°	59.0	77.5	80°	1.4	48.7	1.5	–	–
WD-S2-LM1	23.0	21.0	–	62.6	–	–	1.1	–	–	–	–
WD-S2-RP1	33.0	27.0	27°	55.0	85.5	100°	1.2	43.8	1.3	–	–
WD-S2-RM1	25.0	21.0	–	–	–	–	1.2	–	–	–	–
WD-S2-LP2	30.5	27.0	15°	61.0	94.0	107°	1.1	37.6	1.2	–	–
WD-S2-LM2	–	–	–	–	–	–	–	–	–	–	–
WD-S2-RP2	32.0	27.0	–	59.0	–	–	1.2	–	–	–	–
WD-S2-RM2	–	–	–	–	–	–	–	–	–	–	–
WD-S2-LP3	35.0	27.5	–	–	–	–	1.3	–	–	–	–
WD-S2-LM3	–	–	–	–	–	–	–	–	–	–	–
Mean(P)	**32.6**	**26.5**	**23°**	**58.5**	**85.7**	**96°**	**1.2**	**43.4**	**1.3**	–	–
Mean(M)	**24.0**	**21.0**	–	**62.6**	–	–	**1.1**	–	–	–	–
WD-S3-LP1	>33.0	29.0	–	150.0	205.0	91°	–	95.6	–	–	–
WD-S3-LM1	14.0	14.5	–	141.4	191.0	85°	1.0	–	–	103.0	7.1
WD-S3-RP1	43.0	30.5	–	155.0	–	–	1.4	–	–	–	–
WD-S3-RM1	21.0	24.0	–	151.0	–	–	0.9	–	–	–	–
WD-S3-LP2	33.0	30.0	–	–	–	–	1.1	–	–	–	–
WD-S3-LM2	14.0	22.0	–	–	–	–	0.6	–	–	–	–
Mean(P)	**38.0**	**29.8**	–	**152.5**	**205.0**	**91°**	**1.3**	**95.6**	**2.5**	–	–
Mean(M)	**16.3**	**20.2**	–	**146.2**	**191.0**	**85°**	**0.8**	–	–	**103.0**	**7.1**
WD-SI1p	35.0	36.0	–	–	–	–	1.0	–	–	–	–
WD-SI1m	20.5	28.0	–	–	–	–	0.7	–	–	–	–
WD-SI2p	28.0	24.0	–	–	–	–	1.2	–	–	–	–
WD-SI3p	34.0	26.0	–	–	–	–	1.3	–	–	–	–
WD-SI4p	39.0	33.5	–	–	–	–	1.2	–	–	–	–
WD-SI4m	23.0	25.5	–	–	–	–	0.9	–	–	–	–
ZG-SI1p	53.3	48.8	–	–	–	–	1.1	–	–	–	–
YZ-SI1p	51.2	41.6	–	–	–	–	1.2	–	–	–	–
YZ-SI1m	35.2	34.5	–	–	–	–	1.0	–	–	–	–
YZ-SI2p	48.8	39.7	–	–	–	–	1.2	–	–	–	–
YZ-SI2m	30.1	30.7	–	–	–	–	1.0	–	–	–	–

Abbreviations: ML: Maximum length; MW: Maximum; R: Rotation; PL: Pace length; SL: Stride length; PA: Pace angulation; WAP: Width of the angulation pattern of the pes (calculated value); WAM: Width of the angulation pattern of the manus (calculated value); ML/MW, WAP/P'ML and WAM/M'MW are dimensionless.

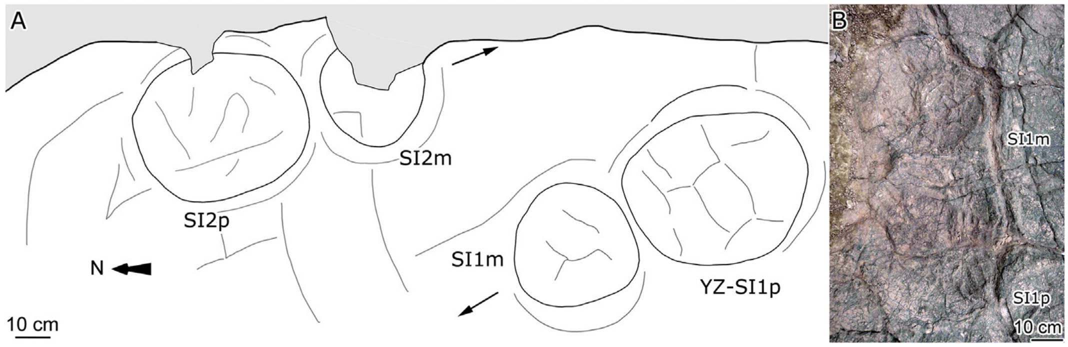

Fig. 7. Photograph (A) and interpretative outline drawing (B) of sauropod tracks from the Yizi site, Sichuan Province, China.

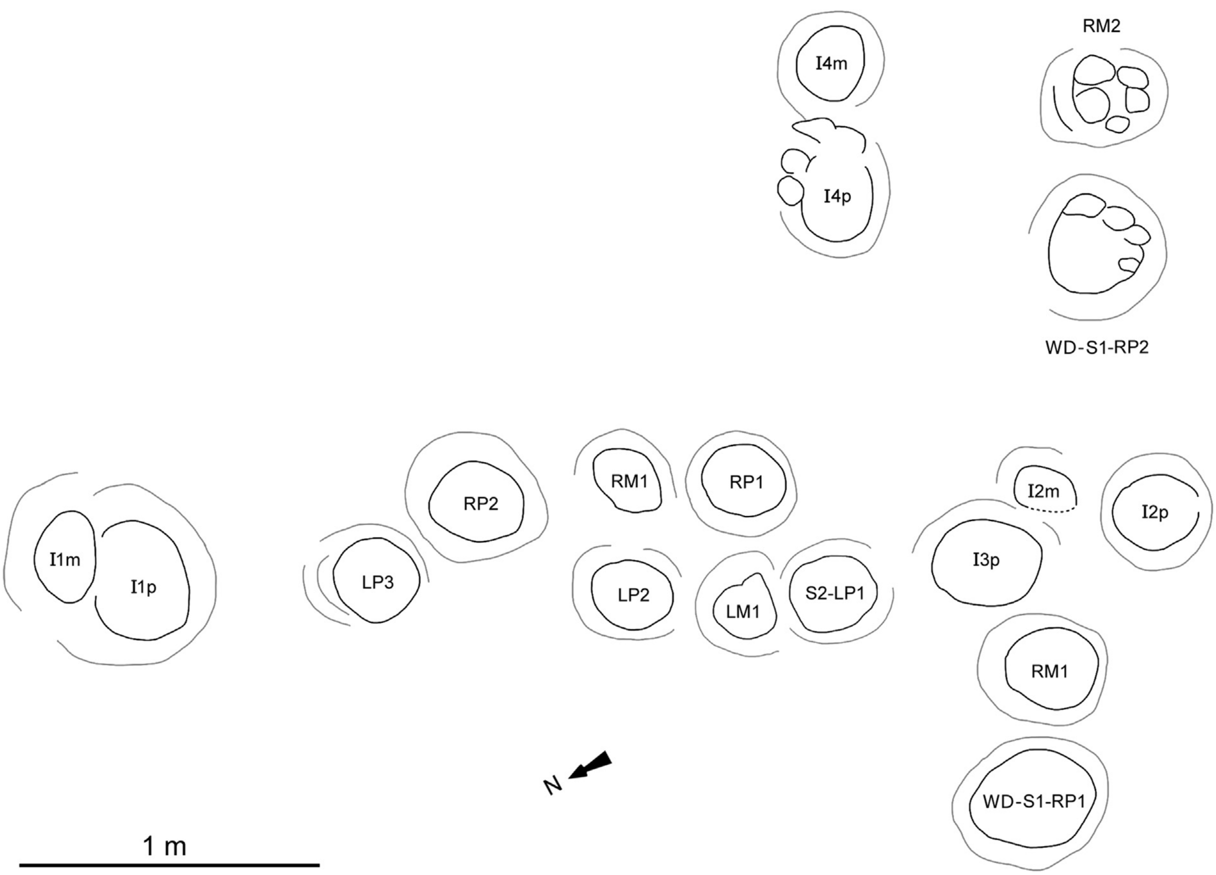

Fig. 8. Interpretative outline drawing of sauropod tracks from the Wadi site, Sichuan Province, China.

and WAM/M'ML (see Marty, 2008 and Marty et al., 2010). This calculation is based on pace and stride length and on the assumption that the width of the angulation pattern crosses the stride at a right angle and at the approximate midpoint of the stride (Marty, 2008). If the (WAP/P'ML)-ratio is 1.0, the pes tracks possibly touch the trackway midline. If the ratio is below 1.0, the tracks intersect the trackway midline and are considered narrow-gauge (see Farlow, 1992; Lockley et al., 1994). A value of 1.0 distinguishes narrow-gauge from medium-gauge trackways, while the value 1.2 is a definitive divide of medium-gauge and wide-gauge trackways, and a value above than 2.0 presents a very wide-gauge (Marty, 2008). As noted above WD-S1 appears to be a very wide gauge trackway, but the lack of three consecutive manus-pes sets makes exact quantitative estimates of gauge a little imprecise. WAP/P'ML of WD-S2 and S3 are 1.3 and 2.5, respectively, indicating wide-gauge trackways (Marty, 2008). This is also consistent with skeletal features of known Late Cretaceous Chinese sauropods, such as Titanosauriformes (Wilson and Carrano, 1999; Day et al., 2002). The WAP/P'ML of the Wadi sauropod tracks is also higher than that of the sauropod trackways from the Lower Cretaceous Feitianshan Formation (1.0–1.3, Xing et al., 2014a).

Most sauropod trackways in China are wide- (or medium-) gauge and are therefore referred to the ichnogenus *Brontopodus* (Lockley et al., 2002). Morphologically, the Wudu sauropod trackway configurations are also consistent with the characteristics of *Brontopodus* type tracks from the Lower Cretaceous of the USA (Farlow et al., 1989; Lockley et al., 1994). These features include wide-gauge; L/W ratio of pes larger than 1, large size, outward orientation; U-shaped/rounded manus prints; and a high degree of heteropody (ratio of manus to pes size). The mean heteropody of

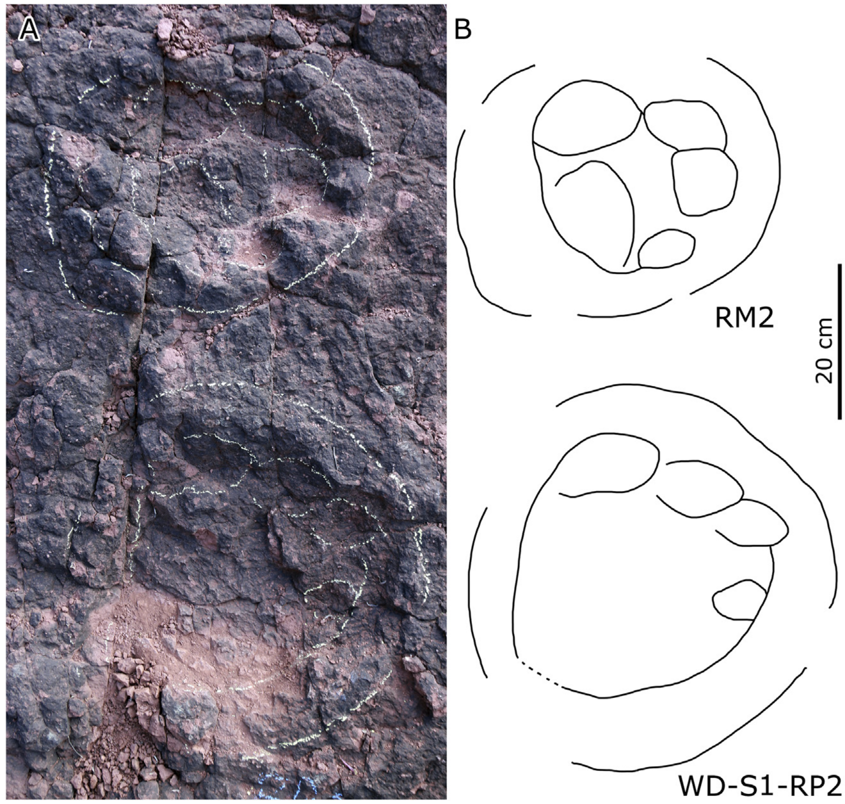

Fig. 9. Photograph (A) and interpretative outline drawing (B) of well-preserved sauropod tracks from the Wadi site, Sichuan Province, China.

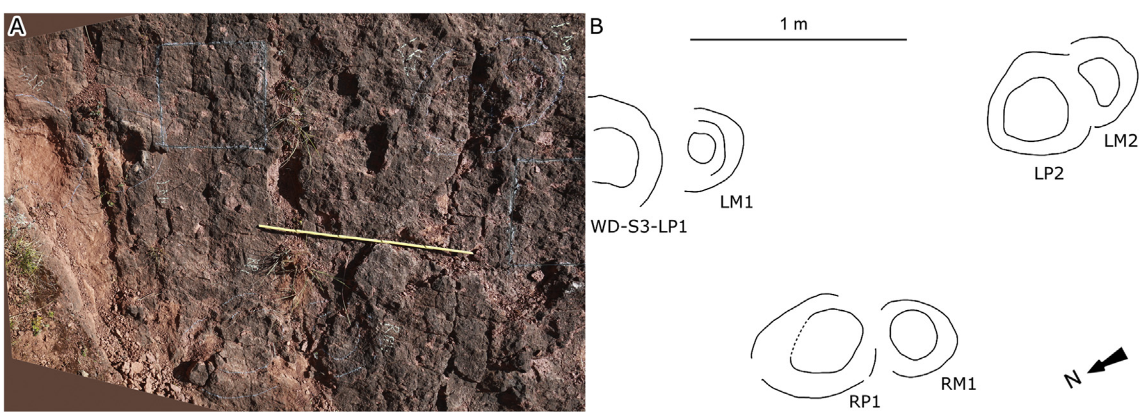

Fig. 10. Photograph (A) and interpretative outline drawing (B) of sauropod trackway from the Wadi site, Sichuan Province, China.

the WD-S1-3 sauropod tracks are 1.7, 1.7, and 2.8, respectively. The heteropody of WD-S3 (1: 2.8) is very close to that of *B. birdi* (1:3, Lockley et al., 1994), while WD-S1–2 resembles Early Cretaceous *Brontopodus* tracks from China (see. 4.3). Records of Wudu sauropod trackways confirm that typical Cretaceous sauropod faunas from China persisted until the end of the Mesozoic.

5. Discussion

5.1. Late Cretaceous dinosaur track assemblages from China

There are few Late Cretaceous dinosaur tracks known from China (Fig. 11). Current tracksites include:

(1) Cangling sites, which consist of sauropod tracks originally named *Chuxiongpus changlingens* and *Conassiminea zheni* and theropod tracks assigned to *Yunnanpus* from the Upper Cretaceous Luozuomei Member in the lower part of the Jiangdihe Formation (probably Turonian or Turonian-?Coniacian in age, Lockley et al., 2002), Chuxiong, Yunnan Province, southwest China (Chen and Huang, 1993, 1994). Lockley et al. (2002) redescribed this tracksite and referred the tracks to *Brontopodus changlingensis*. The geological age of this tracksite was controversial. Varricchio et al. (2006) considered the locality to be within the Chuanjie Formation and to be early Middle Jurassic in age. Preliminary rare earth element analyses also indicate that the tracksite belongs to the Jurassic (Huang et al., 2009). However, according to

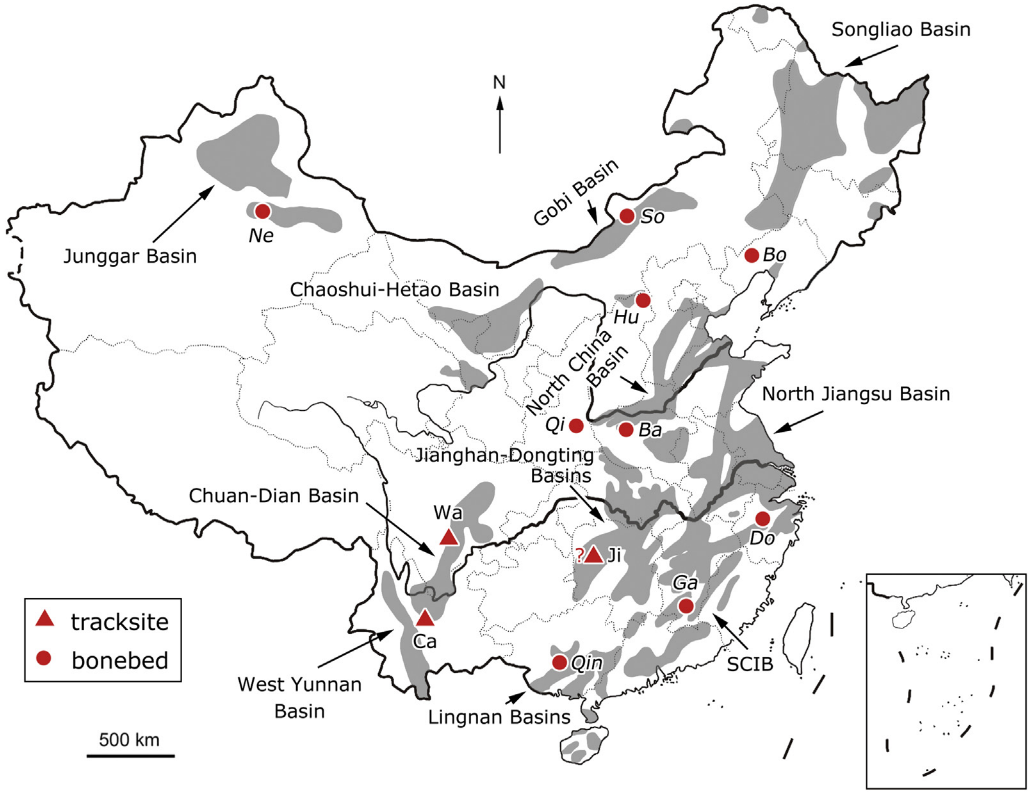

Fig. 11. Distribution of Upper Cretaceous sedimentary basins and sauropod bonebeds and tracksites of China. Ba = *Baotianmansaurus*, Bo = *Borealosaurus*, Do = *Dongyangosaurus*, Ga = *Gannansaurus*, Hu = *Huabeisaurus*, Ne = *Nemegtosaurus*, Qi = *Qinlingosaurus*, Qin = *Qingxiusaurus*, So = *Sonidosaurus*; Ca = Cangling site, Ji = Jiuquwan site, Wa = Wadi site; SCIB = Southeast China intermontane Basins.

1:2,500,000 Geologic Map of Yunnan Province (Compilation Committee of Geological Atlas of China (2002)), spore and pollen grain analysis and ostracods indicate a Late Cretaceous age (Lockley et al., 2002; Chen et al., 2006). Additionally, all sauropod tracks at the Cangling sites are slightly wide gauge (Lockley et al., 2002), not narrow gauge as proclaimed by Varricchio et al. (2006). The gauge pattern is a general feature for distinguishing typical Jurassic (narrow gauge) and Cretaceous (wide gauge) sauropod trackways (Lockley et al., 1994), even if some wide gauge trackways are known from the Jurassic as well (Santos et al., 2009). The *Yunnanpus* tracks are poorly preserved, and represent an undiagnostic biped, probably of theropodan origin. Matsukawa et al. (2006) considered *Yunnanpus* a nomen dubium (Lockley et al., 2013).

(2) The Yongancun site, which consists of ornithopod tracks assigned to the ichnogenus *Jiayinosauripus* from the lower Upper Cretaceous Yong'ancun Formation (Coniacian-Santonian; Quan, 2005; Terada et al., 2011) of Heilongjiang Province, north China (Dong et al., 2003; Xing et al., 2009). The holotype of *Jiayinosauripus* is based on an isolated natural cast (convex hyporelief) and partial paratype (Xing et al., 2009). Lockley et al. (2014a) reviewed large Cretaceous ornithopod tracks and suggested that this ichnogenus was valid and reflected the latest (Maastrichtian) large ornithopod tracks, together with *Hadrosauropodus* (Lockley et al., 2004).

(3) Yanmeikeng site, which consist of tracks from the ornithopod *Hadrosauropodus nanxiongensis*, from the Upper Cretaceous Zhutian Formation (Maastrichtian) from Guangdong Province, southeast China (Xing et al., 2009; Lockley et al., 2014b). These tracks were found initially in the 1980s. Decades of weathering has greatly obscured the tracks and their description is mainly based on two specimens collected by the Nanxiong Dinosaur Museum. In 2013, one of the authors (XL) found about ten new large and small sized ornithopod tracks roughly 50 m from the original site, most likely belonging to adults and subadult or juvenile *H. nanxiongensis* trackmakers. Moreover, investigation during 1990s yielded pterosaur and theropod pes tracks (Dr. Daliang Li, personal communications, May 2013) which are not yet described. Further field investigation is ongoing.

(4) Shangshangen site, which consist of non-avian theropod and bird track assemblages, from the Upper Cretaceous Xiaoyan Formation (early Maastrichtian, Sullivan, 2006) Xiaohutian site and Huizhou Formation (?Aptian–?Albian, Wang et al., 2012) Shangshangen site from Anhui Province, east China (Matsukawa et al., 2006; Xing et al., 2014c). The Xiaohutian site has three different morphotypes of non-avian theropod tracks, including the new ichnotaxon *Paracorpulentapus zhangsanfengi* with wide digit divarication and weak mesaxony, and *Eubrontes*-like or *Therangospodus*-type tracks. The Shangshangen site has yielded small bird tracks (cf. *Koreanaornis*) in association with small tracks of non-avian theropods.

(5) Jiuquwan site, which consists of theropod and isolated sauropod tracks from the Upper Cretaceous Xiaodong Formation (upper Lower Cretaceous Shenhuangshan Formation), Hunan Province, middle China (Zeng, 1982a and b; Matsukawa et al., 2006). Zeng (1982a) described *Xiangxipus chenxiensis*, *Xiangxipus youngi*, and *Hunanpus jiuquwanensis* from the Hongwei site. *Xiangxipus*, is distinctive in having very widely splayed toes. It may represent a coelurosaurian

dinosaur such as an ornithomimid (Matsukawa et al., 2006; Lockley et al., 2013). Matsukawa et al. (2006) reported isolated sauropod tracks from the same site, which were morphologically similar to typical *Brontopodus*, but it is unclear if they are narrow or wide gauge.

For many reasons, there has been controversy over the division of Cretaceous continental strata in China. The Xiaodong Formation was originally considered Upper Cretaceous (Bureau of Geology and Mineral Resources of Hunan Province (1988)). Then, it was classified among the Shenhuangshan Formation by a stratum division and comparison program for Hunan Province between 1992 and 1994 (Li, 1997). Based on ostracod, stonewort, plant and bivalve fossils, the Shenhuangshan Formation is classified as a late stage of the Lower Cretaceous (Albian) (Li, 1997). However, evidence from conchostracan fossils appears to favor an early stage of the Upper Cretaceous (Chen, 1989, 2003). Based on magnetostratigraphy in the Hengyang Basin, the age of the Shenhuangshan Formation is Early–Late Cretaceous (Ge et al., 1994).

(6) *Brontopodus* sauropod tracks from the Upper Cretaceous–Paleogene Leidashu Formation are know from the Wadi site (described in this text).

In conclusion, Late Cretaceous dinosaur tracks from China (including those from the Jiuquwan site) comprise non-avian theropod tracks such as *Xiangxipus*, *Hunanpus* and *Paracorpulentapus* as well as *Eubrontes*-like, *Therangospodus*-type tracks and an unnamed theropod morphotype from Nanxiong. These are distributed at four tracksites co-occurring with 1) bird tracks cf. *Koreanaornis* at one locality, 2) sauropod tracks (*Brontopodus*) at three localities and 3) ornithopod tracks (*Jiayinosauropus*, *Hadrosauropodus*) at two tracksites. Theropod and sauropod tracks are prominent in these track records while ornithopod tracks are relatively uncommon. This differs from records of skeletal fossils, which are dominated by both theropods and hadrosaurs (Dong, 2003). We take three typical Upper Cretaceous localities with bonebeds in China as examples:

(1) Laiyang of Shandong Province: tyrannosaurs (*Chingkankousaurus* Young, 1958), hadrosaurs (*Taninus* Wiman, 1929; Zhen, 1976; *Tsintaosaurus* Young, 1958) and pachycephalosaurs (*Micropachycephalosaurus* Dong, 1978).
(2) Zhucheng of Shandong Province: tyrannosaurs (*Zhuchengtyrannus* Hone et al., 2011), hadrosaurs (*Shantungosaurus* Hu, 1973; Zhao et al., 2007) and ceratopsians (*Zhuchengceratops* Xu et al., 2010a; *Sinoceratops* Xu et al., 2010b).
(3) Erlianhaote (Erenhot in ancient language) of Inner Mongolia: ornithomimosaurs (*Archaeornithomimus* Russell, 1972), therizinosaurs (*Neimongosaurus* Zhang et al., 2001; *Erliansaurus* Xu et al., 2002), oviraptorosaurs (*Gigantoraptor* Xu et al., 2007), titanosaurs (*Sonidosaurus* Xu et al., 2006) and hadrosaurs (*Bactrosaurus* Gilmore, 1933; *Gilmoreosaurus* Brett-Surman, 1979)

5.2. Late Cretaceous sauropod skeletal records from China

Titanosauriformes were relatively diverse in the Early Cretaceous of China (Li et al., 2014). However, compared to the Jurassic, sauropods are rare throughout Asia during the Cretaceous, especially during the Late Cretaceous. At present, only twelve Late Cretaceous sauropod genera have been reported from Asia (Lü et al., 2013). Late Cretaceous sauropods are recorded in nine provinces and regions of China and belong to nine genera, all are from the early Late Cretaceous (Cenomanian) to the late Late Cretaceous (Maastrichtian) (Table 3). *Nemegtosaurus* "*pachi*" (Dong, 1977) was named based on only four teeth, and thus Wilson (2005) considered it as a nomen dubium. Most of the species belong to titanosauriformes or titanosaurs, mainly advanced titanosaurian and somphospondylian groups. The geographical distributions of Late Cretaceous sauropod bonebeds and tracksites do not overlap, however, the tracksites evidence a wider distribution of Late Cretaceous sauropods. Slightly wide gauge trackways from the Yunnan (Lockley et al., 2002) and Wadi sites, and typical wide gauge trackways from the Wadi site imply different trackmaker taxa, suggesting that the diversity of sauropods in southeast China even remained high in middle-late stages of the Late Cretaceous.

Skeletal fossils of Late Cretaceous sauropods from China are mainly distributed in the Junggar Basin (e.g. *Nemegtosaurus* "pachi"), the Gobi Basin (e.g. *Sonidosaurus*), the Chaoshui-Hetao Basin (e.g. *Huabeisaurus*), the northern Jiangsu Basin (e.g. *Dongyangosaurus*), some intermontane basins of Southeast China (e.g. *Gannansaurus*), the North China Basin (e.g. *Baotianmansaurus*), and the Lingnan Basins (e.g. *Qingxiusaurus*). The Chuan-Dian Basin only yielded track fossils. The sedimentary environment there is a combination of red inland basin fluvio-lacustrine sandy and muddy rocks. Uplift of the Qinghai-Tibet Plateau kept shrinking the basin, and intensive evaporation, due to drought, formed massive salt deposits. The Sichuan Basin comprises plaster-containing red sand and shale (Wang, 1985). Such an inland basin under drought conditions corresponds to the environment in which sauropod tracks are most commonly preserved (Lockley et al., 1994, 2002).

6. Conclusions

The tracksites described here are all saurischian dominated having yielded only theropod and sauropod tracks. This ichnofaunal composition is fairly typical of Cretaceous red beds in China. However, to date, while some Early Cretaceous ichnofaunas are also exclusively saurischian dominated, others are more diverse and have yielded bird (non-avian theropod), ornithischian and pterosaur tracks. However, at present the Lower Cretaceous sites of China are significantly more numerous than the Upper Cretaceous ones.

Table 3
The Upper Cretaceous sauropod records from China.

Taxon		Location	Stage	References
Nemegtosaurus "pachi"	nomen dubium	Xinjiang	Lower Maastrichtian	Dong, 1977; Wilson, 2005
Qinlingosaurus luonanensis	?Neosauropoda	Shannxi Province	?Maastrichtian	Xue et al., 1996
Huabeisaurus allocotus	Euhelopodidae	Shanxi Province	?Cenomanian–?Campanian	Pang and Cheng, 2000; D'Emic et al., 2013
Borealosaurus wimeni	titanosaurian	Liaoning Province	Lower Cenomanian	You et al., 2004
Sonidosaurus saihangaobiensis	titanosaurian	Inner Mongolia	Middle–upper Campanian	Xu et al., 2006
Dongyangosaurus sinensis	Saltasaurid	Zhejiang Province	Cenomanian–Santonian	Lü et al., 2008
Qingxiusaurus youjiangensis	titanosaurian	Guangxi Province	Cenomanian–Maastrichtian	Mo et al., 2008
Baotianmansaurus henanensis	Titanosauriformes	Henan Province	Coniacian–Campanian	Zhang et al., 2009; Cao and Wang, 2011
Gannansaurus sinensis	Somphospondyli	Jiangxi Province	Maastrichtian	Lü et al., 2013

Moreover, many of the Lower Cretaceous sites are much larger. Thus, the apparent lower diversity at Upper Cretaceous sites may be an artifact of small sample size. Compounding this problem is the fact that the dating of Cretaceous red bed sites in China is difficult. Nevertheless, regardless of our ability to date some of these sites precisely within the Cretaceous of China, it is clear that the rapidly-growing Cretaceous tracksite database (Lockley et al., 2014b) is becoming important in improving our understanding of Cretaceous dinosaur-dominated, tetrapod faunas. Further work may help us evaluate the relative importance of the tracks and bone records and how they may be mutually complimentary in characterizing tetrapod life in the Cretaceous of the region.

At present the track evidence suggests that the Sichuan region was heavily saurischian dominated in the Late Cretaceous. There is no skeletal evidence to change this picture, for this region. Track evidence from elsewhere in the Upper Cretaceous of China also indicates the presence of hadrosaurs, which are well-known from body fossils. Important bone beds from Shandong and Nei Mongol provinces add to the known diversity of skeletal remains in these regions, but add no direct evidence to enhance our understanding of the Sichuan region in the Late Cretaceous.

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