

Pterosaur trackways from the Lower Cretaceous Jiaguan Formation (Barremian–Albian) of Qijiang, Southwest China



Lida Xing^{a,*}, Martin G. Lockley^b, Laura Piñuela^c, Jianping Zhang^a, Hendrik Klein^d, Daqing Li^e, Fengping Wang^f

^a School of Earth Sciences Resources, China University of Geosciences, Beijing 100083, China

^b Dinosaur Trackers Research Group, University of Colorado at Denver, CO 80217-3364, USA

^c Museo del Jurásico de Asturias MUJA (Jurassic Museum of Asturias), Colunga E-33328, Spain

^d Saurierwelt Paläontologisches Museum, Alte Richt 7, D-92318 Neumarkt, Germany

^e Geological Museum of Gansu, Lanzhou 730040, China

^f Qijiang District Bureau of Land Resources, Chongqing 401420, China

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ABSTRACT

The Lotus Fortress tracksite in the Qijiang National Geological Park, in Qijiang District, Chongqing Municipality consists of two distinct assemblages associated with different surfaces (Qijiang Layers 1 and 2). The lower of these two assemblages, here labeled as the “*Wupus-Pterainchus* ichnoassemblage” is dominated by multiple, mainly parallel trackways of a small tridactyl and five trackways of pterosaurs (*Pterainchus*). The upper surface assemblage, here labeled as the “*Caririchnium* ichnoassemblage”, is dominated by the tracks of ornithopods (*Caririchnium lotus*). Here we give a detailed description of the *Pterainchus* tracks and evaluate their paleoecological significance together with other reports of pterosaur tracks from East Asia.

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1. Introduction

Almost all Chinese pterosaur body fossils are from the Jehol Biota, which occurs in strata distributed in areas of western Liaoning, northern Hebei and southeastern Inner Mongolia (Wang et al., 2010). As only a few skeletal remains of pterosaurs have been described from outside of the Jehol area, pterosaur tracks help to expand our understanding of the distribution of Chinese pterosaurs.

Before 2008, only one pterosaur tracksite had been recorded from China, which is the Yangouxia site, Gansu Province (Peng et al., 2004; Zhang et al., 2006; Lockley et al., 2008). In recent years, new Early Cretaceous pterosaur tracksites have been added, including the Jimo site (Shandong Province), the Dongyang site (Zhejiang Province), the Zhaojue site (Sichuan Province), and the Wuerhe site (Xinjiang Uyghur Autonomous Region) (Xing et al., 2012a). However, almost all these pterosaur tracksites have yet to be described in detail, except for the Jimo site (Xing et al., 2012b).

We herein report another pterosaur tracksite from Qijiang National Geological Park located in Qijiang District, south of Chongqing Municipality near the southeastern border of the Sichuan Basin. Upper Jurassic and “mid”-Cretaceous rocks crop out within the park. Petrified wood (Coniferopsida), theropod teeth (unpublished data),

and sauropod remains (mamenchisaurid) (Liu et al., 2010) are known from three Upper Jurassic formations and dinosaur tracks from the Cretaceous Jiaguan Formation in the park (Xing et al., 2007).

The “Lotus Fortress” site in the Qijiang National Geological Park is historically famous as a castle dating back to the Mongol invasions of the late 13th century as well as being paleontologically important (Figs. 1–2) (Xing et al., 2011). It is known as the type locality of four vertebrate ichnotaxa: *Caririchnium lotus*, *Wupus agilis*, *Laoyingshanpus torridus* and *Qijiangpus sinensis* (Xing et al., 2007, 2012c) and was revisited and restudied by an international team in November 2012.

Pterosaur tracks were recognized by two of us (DL and FW) in March 2011 while following the initial mapping of Qijiang Layer 1 by Xing et al. (2007). They were briefly mentioned and illustrated by Wang (2012) and Xing et al. (2012a). Here we re-assess and describe this material in detail.

2. Geologic setting

The stratigraphic section in the Qijiang National Geological Park includes three bone bearing Upper Jurassic formations (Shangshaximiao, Suining and Pengliazhen) overlain by the “mid” Cretaceous track-bearing Jiaguan Formation (Xing et al., 2012c). According to Xing et al. (2012c, Fig. 2) the succession at the tracksite is 700 m thick with the Pengliazhen Formation (about 340 m) below and the Jiaguan Formation (about 390 m) above, showing massive sandstones, with thinner

* Corresponding author.

E-mail address: Xinglida@gmail.com (L. Xing).

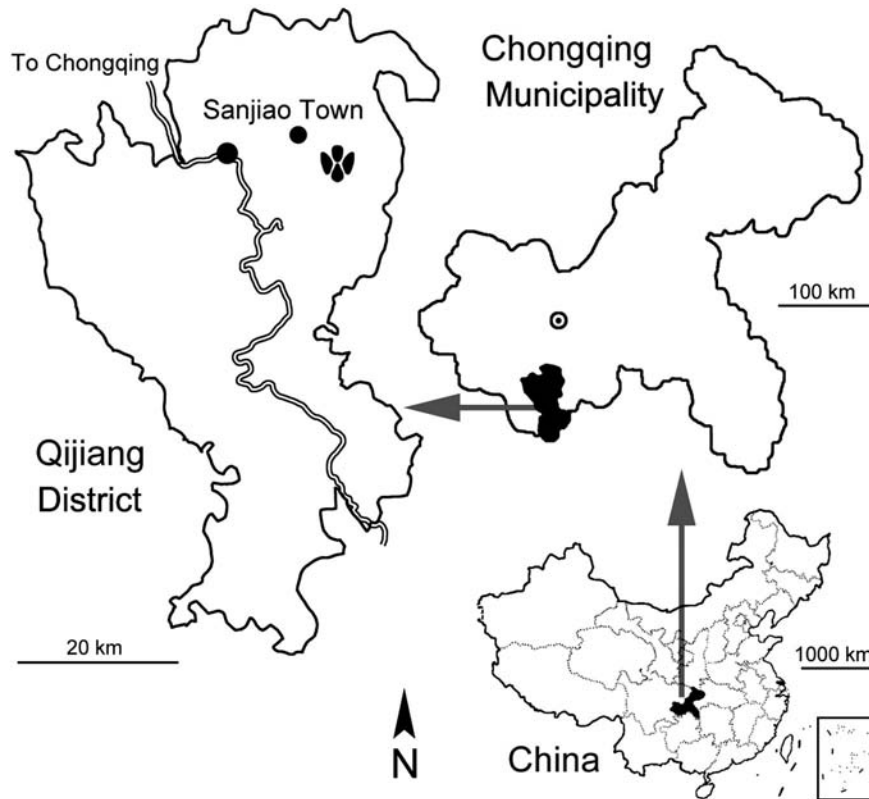


Fig. 1. Geographic map indicating the location (footprint icon) of the Lotus Fortress tracksite locality in Qijiang District, Chongqing Municipality, China.

mudstone intervals. The track bearing Qijiang Layers 1 and 2 (Figs. 2 and 3) occur in the lower part of the Jiaguan Formation about 30–40 m above the base of the unit (Fig. 3). The age of the Jiaguan Formation was differently calculated between 117 Ma and 85 Ma (Aptian–Santonian) by Li (1995) and between 140 and 85 Ma (Berriasian–Santonian) by Gou and Zhao (2001). Recent pollen studies indicate a Barremian–Albian age for the Jiaguan Formation (Chen, 2009). Although the sandstone dominated section of the Jiaguan Formation has not been studied in detail, the stratigraphy of the track-bearing layers clearly indicates a fluvial system. The sedimentary sequences exposed in the notch show an alternation of thin to thick bedded and massive sandstones with fluvial cross bedding and blocky fine-grained siltstones and mudstones. Many of the sandstones are lenticular and contain rip up clasts of the underlying siltstones and mudstones. Some of the sandstone surfaces display

current ripples, and deep desiccation cracks are common in siltstones. Many of the dinosaur tracks penetrate siltstone and mudstone layers or have distinct slide marks (Xing et al., 2007, 2012b).

The initial study of the Lotus Fortress tracksite (Xing et al., 2007) provided a map of an area about 48 m long and averaging about 4 m wide (190–200 m²), showing about 320 tracks. These tracks are distributed on two surfaces, referred to as Qijiang Layers 1 and 2 (Fig. 3). The lower surface (Qijiang Layer 1) is dominated by trackways of the small tridactyl ichnospecies *W. agilis* and the upper layer (Qijiang Layer 2), 10 cm above, by trackways of a large ornithopod that was named *C. lotus* (Xing et al., 2007). In a subsequent study, Xing et al. (2012c) described large ornithopod sandstone casts, which came from a fifth layer about 50 cm above Qijiang Layer 2.

Two other ichnospecies, *Laoyingshanpus torridus* and *Q. sinensis* from this site are nomina dubia (Lockley et al., 2013). They are interpreted as

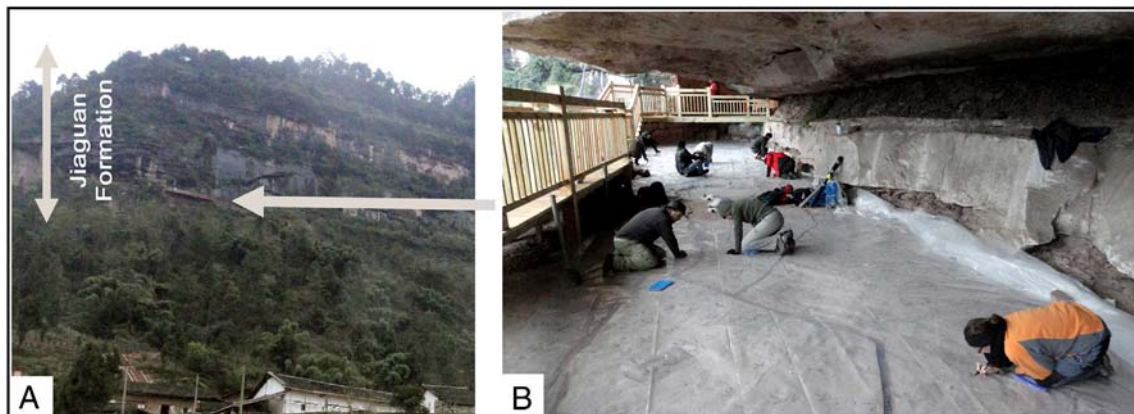


Fig. 2. Photographs of the tracksite location. (A) Steep cliff of Jiaguan Formation sandstone with arrow at right pointing to the location of the 3 meter high notch where the main tracksite is situated. (B) Exposed track bearing layer at the main tracksite.

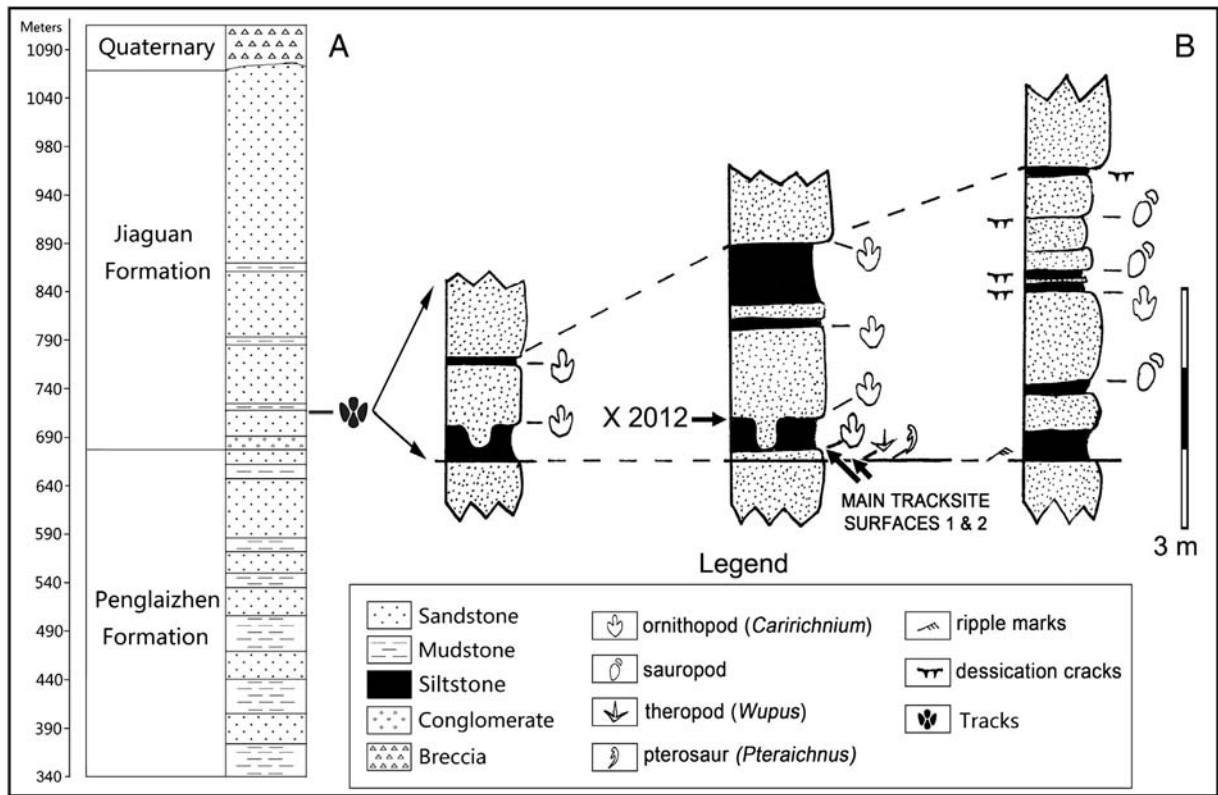


Fig. 3. Stratigraphic sections of the track-bearing units in the Jiaguan Formation. (A) A stratigraphic section after Xing et al. (2012c). (B) Three logs with that of the main tracksite in the middle, showing lateral variation in sandstone and siltstone units. Note that there are five track-bearing layers at the main site including surfaces 1 and 2 described here and in Xing et al. (2007). “X 2012” refers to the layer from which Xing et al. (2012c) described large ornithopod track casts.

poorly preserved ornithopod tracks, presumably *C. lotus*, that were transmitted from Qijiang Layer 3 onto Layer 1 as undertracks.

3. Material and methods

In November 2012, the entire site was mapped on transparent plastic film measuring and photographing the tracks of Qijiang Layers 1 and 2, for 2D and 3D analyses. During this study it was observed that the lower surface yields only tracks of *W. agilis* and *Pteraichnus*, and on the upper surface only the tracks of *C. lotus* and a few invertebrate traces indicating that two different ichnoassemblages are present with only a very thin stratigraphic interval.

A detailed description and analysis of the large samples of *W. agilis* and *C. lotus* will be given elsewhere. In this paper, we focus mainly on the tracks of surface 1 where the co-occurrence of *Pteraichnus* with *W. agilis* has important paleoecological implications.

In order to place the track assemblages in their sedimentary context, two additional sections were measured near the tracksite (Fig. 3). These sections show considerable lateral variation in the thickness of sandstone, siltstone and mudstone beds. The latter have weathered out leaving a deep notch in the cliff. We identified multiple track layers at three different outcrops. With the exception of Qijiang Layer 1 exposed at the main tracksite, all other track levels appear to represent the activity of large dinosaurs including sauropods.

The track length (L), width (W), pace length (PL), pace angulation (PA) stride length (SL), outer trackway width (OTW), and inner trackway width (ITW) were measured for five pterosaur trackways (Figs. 4–8, Table 1). The acetate tracings have been cataloged in the University of Colorado archives as T1591 (trackway 1), T 1592 (trackways 2 and 3) and T 1595 (trackways 4 and 5). The original tracings on plastic film have been repositated at the Qijiang National Geological Park. Replicas were made of several sets. They are housed

in the Qijiang National Geological Park Museum, and in the University of Colorado at Denver, USA.

Institutional and location abbreviations. QJLI: Qijiang Layer I, China. UCM: University of Colorado Museum of Natural History, USA.

4. Description

Trackway 1 is the longest and well-preserved. It was reported with preliminary illustrations by Xing et al. (2012a) and Wang (2012) (Fig. 6). In the present study, four new pterosaur trackways were identified and assigned to trackways 2–5 (Figs. 7–8). A total of 30 pterosaur tracks were recorded from five trackways, which are oriented in different directions.

4.1. Trackway 1

Trackway 1 (Fig. 6), herein designated as QJLI-P1, is nearly straight and consists of 16 tracks (5 pes and 11 manus imprints) preserved as two segments of the same trackway. The segments are separated by a gap of about 3 m where tracks are not preserved.

The first segment begins with a left manus-pes set, referred to as left set 1 (QJLI-P1-LS1). There are no tracks representing right set 1 (QJLI-P1-RS1) but QJLI-P1-LS2 and RS2 are represented by manus tracks. LS3 is a complete manus pes set. Replicas were made of QJLI-P1-LS1 and LS2 (UCM 214, 253 and 214.254 respectively).

Beyond QJLI-P1-LS3, with the exception of an isolated (probably right) pes track, there is no evidence that other manus pes sets were registered until a pes track was inferred to represent QJLI-P1-RS8. Thus, no tracks are preserved between QJLI-P1-RS3 and LS8 along a distance of about 3 m. QJLI-P1-LS9 is represented only by a manus imprint and RS9 is missing. Likewise, in QJLI-P1-LS10, RS10, LS11, RS11 and LS12 only manus tracks are visible. A mold and replica of QJLI-P1-LS11 was

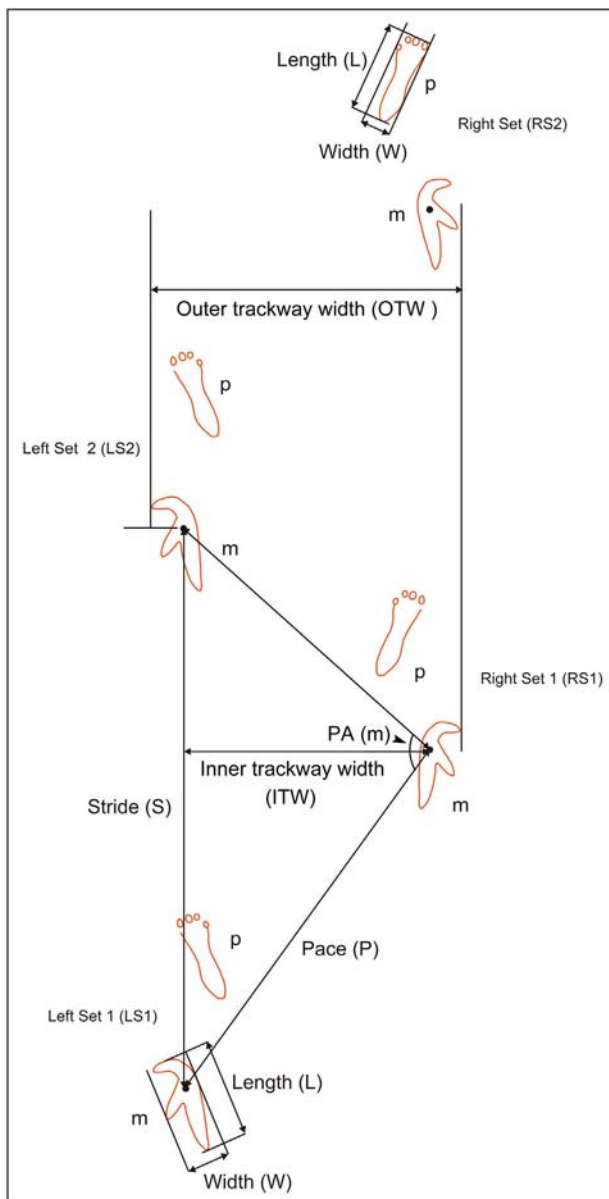


Fig. 4. Pterosaur trackway showing measurements obtained in this study.

made (CU 214.255). QJLI-P1-LS13 is represented by a manus track. The respective mean length and width of the tracks are 9.0 cm and 3.3 cm for the manus and 8.5 and 2.8 cm for the pes. The step and stride averages are 34.1 cm and 52.5 cm respectively with an outer trackway width of 24 cm.

4.2. Trackway 2

Trackway 2 (QJLI-P2) (Fig. 7A) consists of only three consecutive manus tracks. Their mean length and width are 9.8 and 4.6 cm. The pace length averages 31.7 cm and the stride length is 46.3 cm, the trackway width 27 cm.

4.3. Trackway 3

Trackway 3 (QJLI-P3) (Fig. 7B) consists of four tracks including two left pes tracks and a left and right manus track. Their respective mean lengths and widths are 7.0 and 3.1 cm for the manus and 8.3 and

3.1 cm for the pes. The pace length is 32.8 cm and the stride length 45.5 cm, the trackway width between the two manus tracks 22.5 cm.

4.4. Trackway 4

Trackway 4 (QJLI-P4) (Fig. 8A) consists of five footprints, including the first left manus-pes set. A right manus is separated from the former by a gap of ~1.1 m. Another right manus and a left pes occur after two gaps of ~1.3 m and 47 cm, respectively. The average length and width of the tracks are 8.8 and 4.1 cm for the manus and 10.3 and 3.1 cm for the pes.

4.5. Trackway 5

Trackway 5 (QJLI-P5) (Figs. 8B and 9) consists of only two isolated tracks: a right pes and a left manus separated by a gap of 67 cm. The length and width of the tracks are 8.5 and 3.2 cm for the manus and 9.0 and 3.5 cm for the pes.

5. Discussion

All five trackways can be assigned to *Pterainchus*, based on tetradactyl and subtriangular pes tracks with digits II and III being slightly longer than I and IV, and tridactyl and asymmetrical manus tracks with toes increasing in length from I to III, the latter being oriented posteriorly (see also Xing et al., 2012a). The individual tracks are similar in size, but their shapes vary slightly. Trackway 1 shows well-preserved pes digit traces, in two manus-pes sets (QJLI-P1-LS1 and LS3). The pes digit traces also occur in trackway 3 and trackway 5. The differences in manus length result from the variability in the length of digit III. Digit III appears to be longer in the right manus tracks than in the left in trackway 1. Such slight size differences may reflect subtle differences in gait.

The inter-trackway variation in manus and pes size based on all five trackways is less than the intra-trackway variation within trackway 1. The manus track length and width varies between 7.0 cm and 3.1 cm in trackway 3 and 9.0 cm and 3.3 cm in trackway 1, but the values of trackway 1 show a minimum of 7.1 cm and 2.8 cm and a maximum of 10.5 cm and 3.9 cm. Thus, there is no significant size difference between these five trackways. In fact, the track size differences are within the range of variation produced by a single individual. The pace length of trackway 1 is slightly longer than that of trackways 2 and 3.

Manus tracks are often better-preserved and more numerous than pes tracks, due to differences in the weight distribution, which tend to result in a deeper impression of the manus tracks (Lockley et al., 1995). This pattern is reflected in the Qjiang samples which consist of 20 manus tracks and 10 pes tracks.

There is a considerable size range in *Pterainchus*, from 2.0–16.0 cm (Lockley and Harris, in press). As noted above, all trackways from the Lotus Fortress site were made by similar-sized trackmakers, moving with similar gaits. This leads to three possible interpretations: 1) the five trackways were made by five similar-sized track makers, 2) the five trackways were made by less than five, but more than one trackmaker, or 3) the five trackways were made by a single trackmaker. It is impossible to decide which of these interpretations is correct, or to know, how extensive the trackways were, outside the exposed study area.

On surface 1 only two ichnotaxa, *Pterainchus* and *W. agilis* are present. *W. agilis* is a bird-like track (McCrea et al., 2013, comment on the similar morphology of *Limivipes curriei* and *W. agilis*). If *W. agilis* was left by a bird, the lower surface assemblage represents only birds, pterosaurs and several undertracks of *C. lotus* (Fig. 9). This is in contrast to the surface 2 assemblage which comprises only large dinosaur tracks of relatively graviportal trackmakers. An interesting feature of the lower surface assemblage is that while the *Pterainchus* trackways are oriented in very different directions,

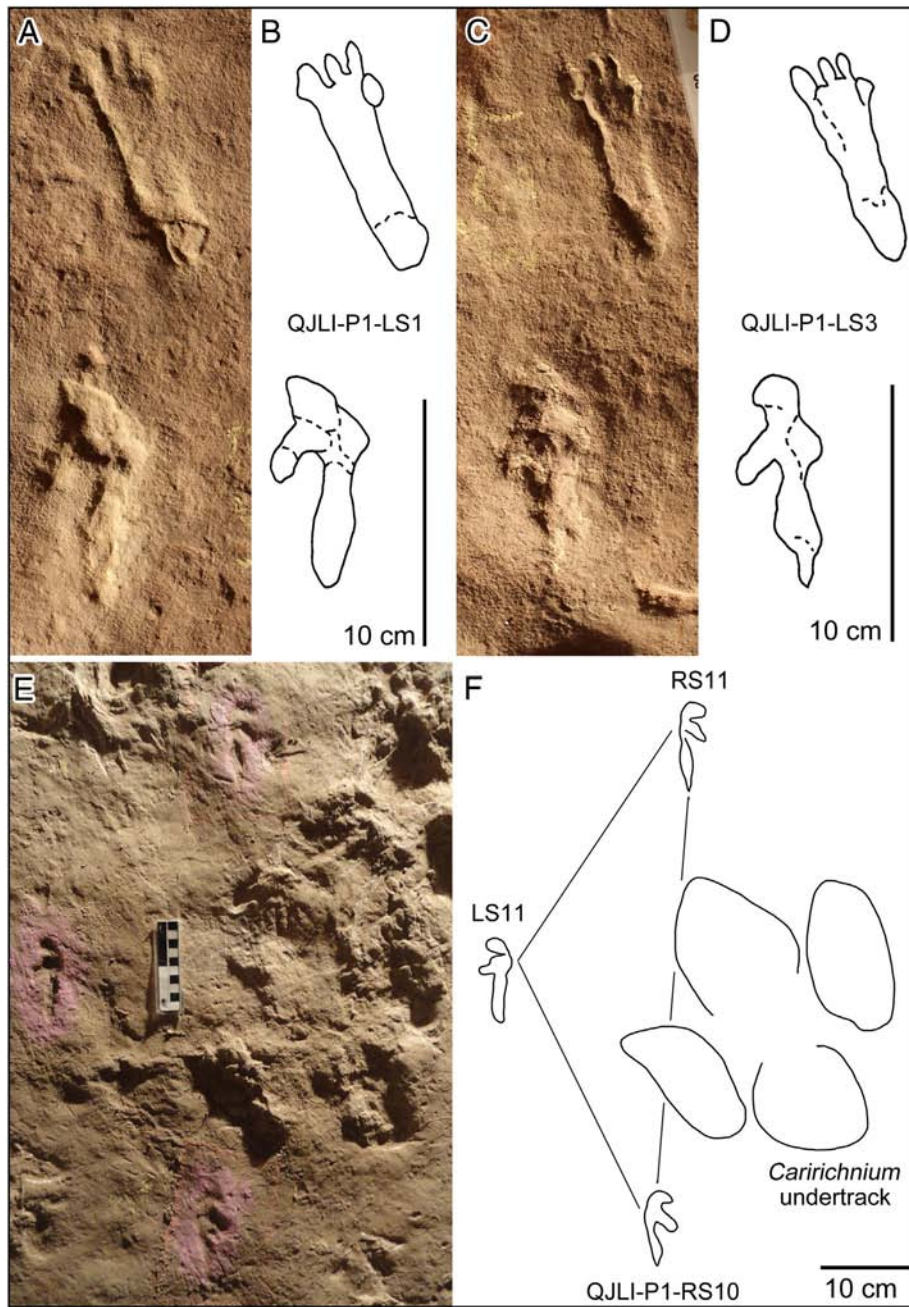


Fig. 5. Photographs and outline drawings of pterosaur tracks from trackway 1 with manus-pes sets LS1 (A–B) and LS3 (C–D) and manus tracks from RS10, LS11 and RS11 (E–F).

almost all *Wupus* trackways are parallel suggesting a herd or a flock (cf. McCrea, 2000). Although a chronological order of trackway formation cannot be determined, it is evident that the two track makers that frequented this area showed a different behavior. While one group was milling around, the other one moved in a preferred direction.

The ichnoassemblage of surface 1 occurs on top of a fine sandstone that lies on a thicker sandstone sequence and probably, like the thin 10 cm bed that covers it, represents the waning stage of a major depositional event that culminated in the deposition of a thick, highly saturated muddy silt (Fig. 3). Evidently, following the deposition of a major sand unit, birds, pterosaurs and ornithopods were attracted to the area, with the latter following another minor depositional event. A further alternation of high energy sand and low energy silt and mud deposition followed, interspersed with several other track horizons and episodes of track making by large dinosaurs. Probably small-sized theropods and pterosaurs preferred a stable sand bed

rather than a highly saturated muddy silt where they would sink in deep and spend much more energy during walking (García-Ramos et al., 2002). Large dinosaurs were present in the area as evidenced by their tracks on the upper layer. Maybe the substrate was still too soft for them, or perhaps this place was one of a few emergent patches of substrate on an otherwise submerged surface that may have acted as a barrier. In any case, the absence of large dinosaurs suggests that these areas were unsuitable (McCrea, 2001, 2003). Nevertheless, we cannot exclude that the preservation of small theropod and pterosaur tracks on one layer and large dinosaur tracks on the other are coincidental events. The discovery of additional tracksites in the future might clear this.

Remarkable is the co-occurrence of pterosaur and small (?avian) theropod tracks with abundant invertebrate traces. This might indicate that birds and pterosaurs were attracted to this area to feed (García-Ramos et al., 2000; He et al., in press). The surface does not show any

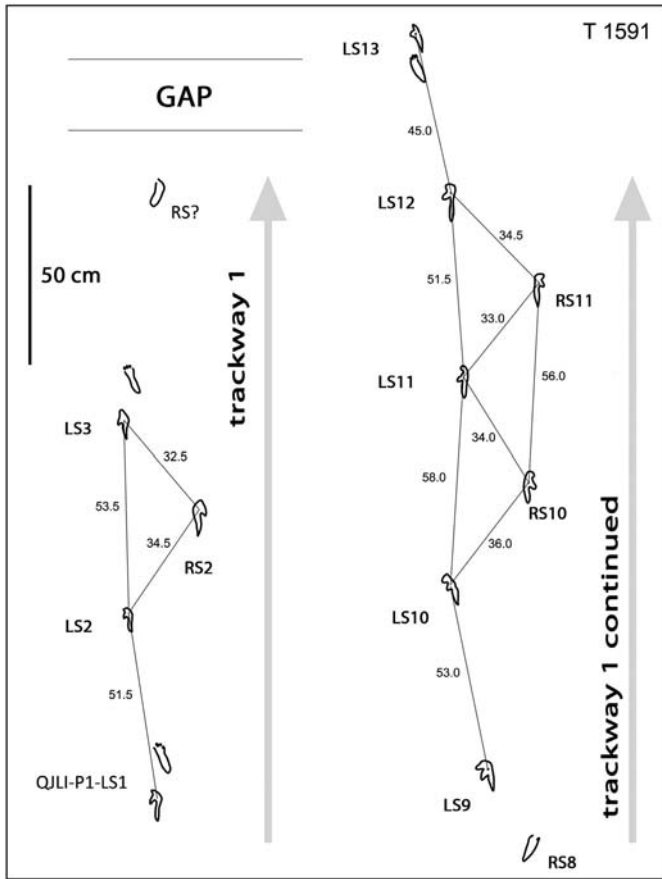


Fig. 6. Sketch map of pterosaur trackway 1.

dessication features, and this along with the preservation of fine details of smallish avian and pterosaur tracks indicates a water-saturated substrate that would have supported an active invertebrate infauna. McCrea and Sarjeant (2001) also comment on the presence of infauna associated with a predominantly avian track surface and speculate on feeding, but acknowledge that no ‘dabbling’ or ‘probing’ features were recognized.

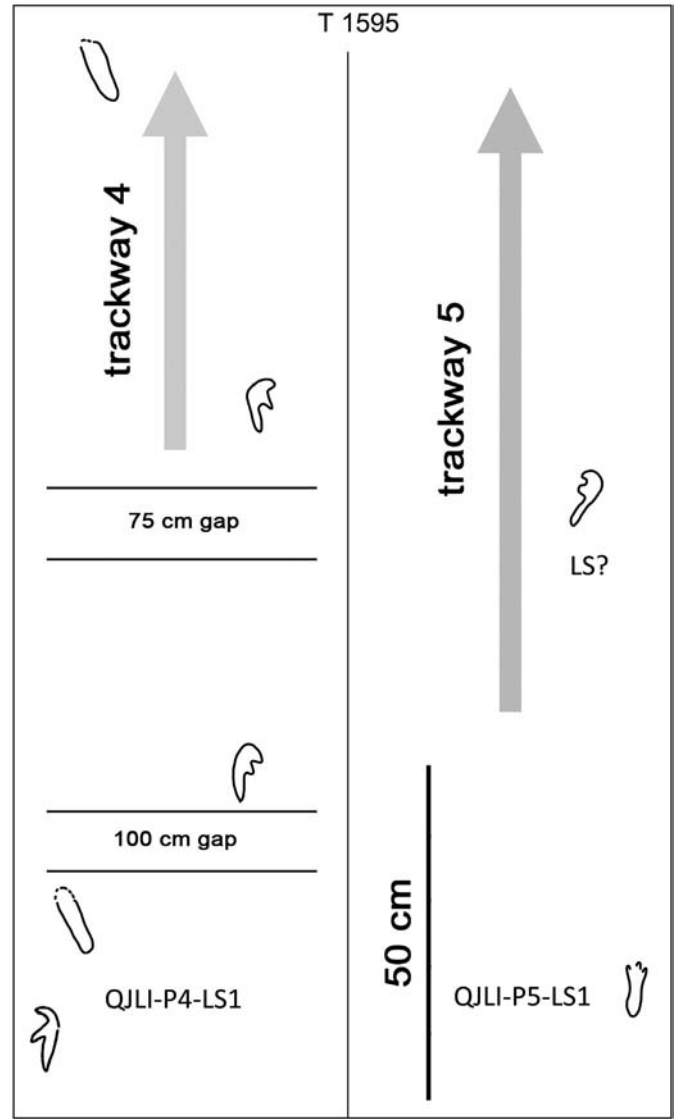


Fig. 8. Sketch map of pterosaur trackways 4 (A) and 5 (B).

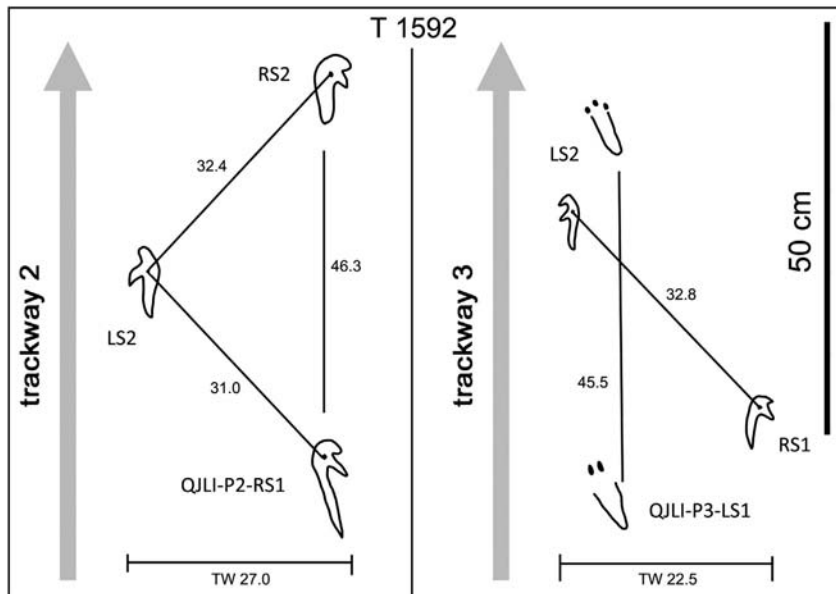


Fig. 7. Sketch map of pterosaur trackways 2 (A) and 3 (B).

Table 1

Measurements for pterosaur trackways 1–5 from the Lotus Fortress tracksite, Qijiang District, Chongqing Municipality, China.

Set R/L	m/p	ML	MW	PL	SL	PA	ITW	OTW
<i>Trackway 1 (QJLL-P1)</i>								
LS1	m	9.0	2.7	–	–	–	–	–
	p	9.3	3.2	–	–	–	–	–
LS2	m	7.1	2.8	–	–	LS1-LS2	51.5	–
	p	–	–	–	–	–	–	–
RS2	m	10.5	3.9	LS2-RS2	34.5	–	106°	20.5
	p	–	–	–	–	–	–	–
LS3	m	8.6	3.4	RS2-LS3	32.5	–	–	–
	p	8.5	2.7	–	–	–	–	–
RS?	m	–	–	–	–	–	–	–
	p	8.0	2.8	–	–	–	–	–
RS8	m	–	–	–	–	–	–	–
	p	8.3	2.8	–	–	–	–	–
LS9	m	9.2	4.3	–	–	–	–	–
	p	–	–	–	–	–	–	–
LS10	m	9.5	3.1	–	–	LS9-LS10	53.0	–
	p	–	–	–	–	–	–	–
RS10	m	9.0	3.5	LS10-RS10	36.0	–	111°	20.1
	p	–	–	–	–	–	–	–
LS11	m	9.0	2.8	RS10-LS11	34.0	LS10-LS11	58.0	109°
	p	–	–	–	–	–	–	–
RS11	m	9.5	3.1	LS11-RS11	33.0	RS10-RS11	56.0	96°
	p	–	–	–	–	–	–	–
LS12	m	10.0	3.8	RS11-LS12	34.5	LS11-LS12	51.5	–
	p	–	–	–	–	–	–	–
LS13	m	7.7	2.8	–	–	LS12-LS13	45.0	–
	p	8.2	2.5	–	–	–	–	–
Average	m	9.0	3.3	–	34.1	–	52.5	106°
	p	8.5	2.8	–	–	–	–	–
<i>Trackway 2 (QJLL-P2)</i>								
RS1	m	12.0	5.7	–	–	–	–	–
LS2	m	8.8	3.7	RS1-LS2	31.0	–	95°	22.0
RS2	m	8.6	4.5	LS2-RS2	32.4	RS1-RS2	46.3	–
Average	m	9.8	4.6	–	31.7	–	95°	22.0
<i>Trackway 3 (QJLL-P3)</i>								
LS1	p	9.0	3.0	–	–	–	–	–
RS1	m	7.0	3.5	–	–	–	–	–
LS2	m	7.0	2.7	RS1-LS2	32.8	–	–	–
	p	7.5	3.1	–	–	LS1-LS2	45.5	–
Average	m	7.0	3.1	–	–	–	–	–
	p	8.3	3.1	–	–	–	–	22.5
<i>Trackway 4 (QJLL-P4)</i>								
LS1	m	9.5	4.0	–	–	–	–	–
	p	10.5	2.8	–	–	–	–	–
	m2	8.8	4.2	–	–	–	–	–
	m3	8.2	4.2	–	–	–	–	–
	p4	10.0	3.3	–	–	–	–	–
Average	m	8.8	4.1	–	–	–	–	–
	p	10.3	3.1	–	–	–	–	–
<i>Trackway 5 (QJLL-P5)</i>								
LS1	p	8.5	3.2	–	–	–	–	–
LS?	m	9.0	3.5	–	–	–	–	–

Abbreviations: ML: maximum length; MW: maximum width; m/p: manus/pes impressions; PA: pace angulation; PL: pace length; SL: stride length; ITW: inner trackway width; OTW: outer trackway width; R/L: right/left.

6. Distribution of *Pterainchus* in East Asia

6.1. China

To date, all pterosaur tracks reported from China come from Cretaceous deposits and have been attributed to the ichnogenus *Pterainchus*.

The first pterosaur tracks were found in the Hekou Group of Yangouxia, Gansu Province, and named *Pterainchus yangouxiaensis* (Peng et al., 2004; Zhang et al., 2006). The original description of *P. yangouxiaensis* lacks a systematic description and informations such as a diagnosis, detailed measurements and comparison to other *Pterainchus* ichnospecies. The material is currently being re-described, and will be published elsewhere. *Pterainchus* isp. from the Qugezhuang

Formation at the Jimo site, Shandong Province was described in detail (Xing et al., 2012b).

Additional pterosaur tracksites are known from China, these are the Dongyang site in the Early Cretaceous Fangyan Formation of Zhejiang Province (Lü et al., 2010), the Zhaojue site in the Lower Cretaceous Feitianshan Formation of Sichuan Province (Liu et al., 2010), and the Wuerhe site in the Lower Cretaceous Tugulu Group of Xinjiang Autonomous region (Xing et al., 2013) (Fig. 10). These reports clearly show that pterosaur tracks are more widespread in China than previously thought.

6.2. Korea and Japan

Pterosaur tracks were first recognized in Korea in 1996 and described in the following year as the first known occurrence in Asia

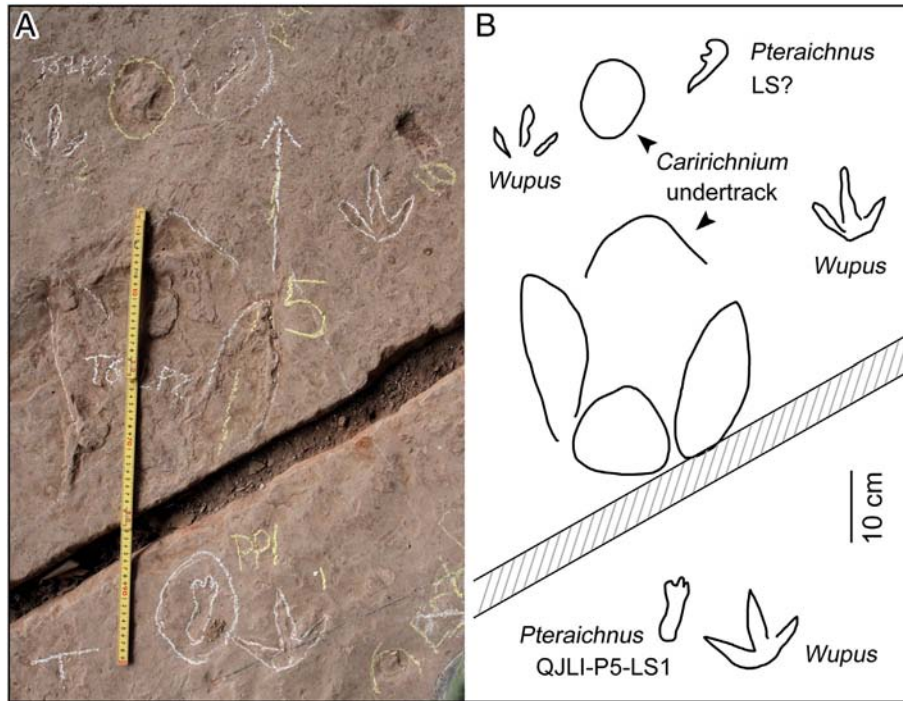


Fig. 9. Photographs and outline drawing of pterosaur tracks from trackway 5 with associated *Wupus* (? bird) track and *Caririchnium* (ornithopod) undertrack.

(Lockley et al., 1997). These tracks were found in the Upper Cretaceous Uhangri Formation and later named *Haenamichnus uhangriensis* (Hwang et al., 2002). Since then, there have been a number of additional reports of pterosaur tracks assigned to the ichnogenus *Pteraichnus*, including *Pteraichnus* isp., (Kim et al., 2006) from the upper Lower to 'Mid' Cretaceous Haman Formation and *Pteraichnus koreanensis* (Lee et al., 2008) from the Lower Cretaceous Hasandong Formation. Recently

Haenamichnus gainensis was reported from the Haman Formation (Kim et al., 2012). In addition to Korean pterosaur tracks Lee et al. (2010) reported small pterosaur tracks named *Pteraichnus nipponensis* from the Lower Cretaceous Kitidani Formation of Japan.

There appears to be a much greater size range in the Korean samples than is currently known from the Chinese assemblages. For example, *P. koreanensis* manus tracks are only about 2.56 cm long,

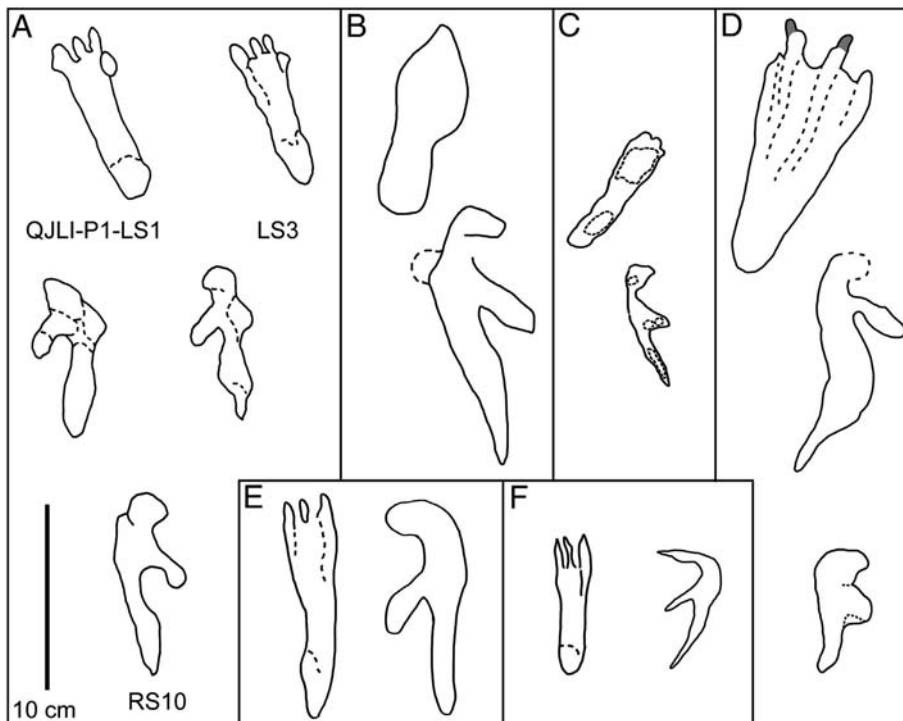


Fig. 10. Pterosaur tracks from China. (A) From Qijiang (Xing et al., 2012a). (B) From Zhaojue (Xing unpublished data). (C) From Jimo (Xing et al., 2012b). (D) From Wuerhe (Xing et al., 2013; unpublished data). (E) From Liujiaxia (Xing unpublished data). (F) From Dongyang (based on Lü et al., 2010: Fig. 2 and a photo taken by Daniel Barta). Scale refers to A–F.

and *P. nipponensis* manus tracks from Japan are even smaller (2.26 cm in length). In contrast *Haenamichnus* tracks are up to 39.0 cm long. Only *Pteraichnus* isp. from the Haman Formation has a size (10–12 cm) similar to many of the Chinese specimens.

The large size range in the Korean samples covers the entire size range known for pterosaur tracks (Lockley et al., 2008). The significance of these size differences is difficult to evaluate, given the relatively small number of documented sites (five in China and five in Korea and Japan). Nevertheless, we infer that the restricted size range of pterosaur tracks from China, Japan or other regions is related to ecological and evolutionary constraints. However, such a speculation is premature until abundant pterosaur tracksites are globally available.

7. Conclusions

- 1) The Lotus Fortress tracksite is one of the most important pterosaur tracksites in the Cretaceous of China due to the large number of imprints and their co-occurrence with possible bird tracks.
- 2) The Lotus Fortress tracksite reveals two distinctive and different (mutually exclusive) ichnoassemblages, the lower *Wupus-Pteraichnus* assemblage and the *Caririchnium* assemblage.
- 3) Thirty tracks from five *Pteraichnus* trackways are described, and interpreted to have been left by the same kind and similar sized pterosaurs.
- 4) The number of known pterosaur tracksite reports from China has increased rapidly in recent years. It compares favorably with the growing record from Korea, and Japan, and adds significantly to the record from East Asia.

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