

## Research paper

## Early Cretaceous pterosaur tracks from a “buried” dinosaur tracksite in Shandong Province, China

Li-Da Xing<sup>a,b,\*</sup>, Jerald D. Harris<sup>c</sup>, Gerard D. Gierliński<sup>d,e</sup>, Murray K. Gingras<sup>f</sup>,  
Julien D. Divay<sup>a</sup>, Yong-Gang Tang<sup>g</sup>, Philip J. Currie<sup>a</sup><sup>a</sup> Department of Biological Sciences, University of Alberta, 11455 Saskatchewan Drive, Edmonton, Alberta T6G 2E9, Canada<sup>b</sup> Key Laboratory of Evolutionary Systematics of Vertebrates, Chinese Academy of Sciences, PO Box 643, Beijing 100044, China<sup>c</sup> Physical Sciences Department, Dixie State College, 225 South 700 East, St. George, UT 84770, USA<sup>d</sup> JuraPark, ul. Sandomierska 4, 27-400 Ostrowiec Świętokrzyski, Poland<sup>e</sup> Polish Geological Institute, Rakowiecka 4, 00-975 Warszawa, Poland<sup>f</sup> Department of Earth and Atmospheric Sciences, University of Alberta, Edmonton, Alberta, Canada<sup>g</sup> Institute of Geology and Palaeontology, Linyi University, Linyi 276000, China

Received 27 September 2011; received in revised form 13 January 2012; accepted 9 February 2012

Available online 16 February 2012

## Abstract

Here we describe the pterosaur and tridactyl dinosaur footprint assemblage from a new tracksite in the Early Cretaceous Qugezhuang Formation near the Wenxiyuan Community in Jimo County-level City, Qingdao City, Shandong Province, East China. The construction of a community building has, since the discovery, covered the majority of tracks, but a few specimens on abandoned building stones constitute the first pterosaur track record in eastern China. The pterosaur tracks are assigned to *Pteraichnus* isp. and were probably made by a small to medium-sized pterodactyloid. The new pterosaur trackway contributes to the growing database of pterosaurian ichnites in Asia. The Wenxiyuan tridactyl dinosaur tracks are morphologically similar to those of theropods, but they are too poorly preserved to be referred to any particular ichnotaxon.

© 2012 Elsevier B.V. and Nanjing Institute of Geology and Palaeontology, CAS. All rights reserved.

**Keywords:** Qugezhuang Formation; Early Cretaceous; Pterosaur track; *Pteraichnus*; Tridactyl dinosaur track

## 1. Introduction

The Early Cretaceous Laiyang Group (120–130 Ma) in the Laiyang region of Shandong Province, China, consists of lacustrine deposits that produce fossils, most famously fishes, insects, plants, and dinosaur tracks (Li and Zhang, 2001; Wang et al., 2010a). The similarity of fossil faunas indicates that the Laiyang Group corresponds in age to the Jehol Group of northeastern China. This fauna is considered part of the Jehol Biota (Zhang, 1992; Lucas, 2001; Wang et al., 2010a; Zhang et al., 2010). Young (1958) and Chao (1962) reported remains of the basal ceratopsian dinosaur *Psittacosaurus* from Laiyang, and Young

(1958, 1964) reported pterodactyloid pterosaur fossils from the region.

In April 2009, construction in the Wenxiyuan Community, Jimo City, 80 km northeast of Laiyang City, uncovered many tridactyl dinosaur tracks 5 m below the surface. The Jimo Municipal Museum was aware of the existence of the tracks but took neither photographs nor measurements. Initial reports estimated that hundreds of tridactyl tracks were found (Jiao, 2009). In 2011, Xing L.-D. and Tang Y.-G. obtained photographs that had been taken for journalistic purposes from Mr. Jiao, as well as a few track-bearing slabs from the building contractor. Later, the dinosaur tracksite was covered by the buildings of the Wenxiyuan Community. In May 2011, Tang Y.-G. discovered and collected pterosaur tracks on a single slab (Specimen No. LUGP3-001) at a neighboring building site in the Wenxiyuan Community. These tracks constitute the first pterosaur track record in eastern China. The new pterosaur trackway contributes

\* Corresponding author at: Department of Biological Sciences, University of Alberta, 11455 Saskatchewan Drive, Edmonton, Alberta T6G 2E9, Canada.  
E-mail address: [xinglida@gmail.com](mailto:xinglida@gmail.com) (L.-D. Xing).



Fig. 1. Location of the Wenxiyuan track locality (indicated by the pterosaur track icon) in Shandong Province, China.

to the growing database of pterosaurian ichnites in Asia. Here we describe the Wenxiyuan pterosaur and tridactyl dinosaur footprint assemblage.

## 2. Geological setting

### 2.1. Qugezhuang Formation

The Wenxiyuan Community, Jimo County-level City, Qingdao City, Shandong Province, is located at the junction of Wenhua Road and Gaoshan Er Road (Fig. 1), and is surrounded by domestic architecture. The nearby outcrops are lithologically and stratigraphically comparable to those of the Mashan National Nature Reserve, which provides a stratigraphic basis for the tracks. The outcrop at the Mashan National Nature Reserve exposes the uppermost Qugezhuang Formation, the uppermost unit in the Early Cretaceous Laiyang Group (Qiao, 2001).

In eastern Shandong Province, the Laiyang Group has been divided into six formations (in stratigraphic order): the Wawukuang, Linsishan, Zhifengzhuang, Shuinan, Longwangzhuang, and Qugezhuang formations (Zhang and Liu, 1996). The Qugezhuang Formation comprises magenta and yellow-green, medium-fine sandstone, gravelly sandstone with interbedded sandy conglomerates and calcareous siltstone. The Qugezhuang Formation in this area was deposited in an anastomosing river paleoenvironment (Regional Geological Survey Team of the Bureau of Geology and Mining of Shandong Province, 1990).

The Wenxiyuan tridactyl tracks are preserved on top of 2–3 closely spaced layers of yellow-green, medium-fine sandstone (Fig. 2). No desiccation cracks or ripple marks were observed in any of the track-bearing horizons, but the tridactyl tracks and the more poorly preserved tridactyl tracks (probably representing undertracks) were observed in the same layers of

sandstone. The tracks discussed herein are the first reported from the Qugezhuang Formation, although dinosaur tracks have already been found in both the underlying Yangjiazhuang and Longwangzhuang formations (Li et al., 2010; Xing et al., 2010).

### 2.2. Paleoecology

Common wood clasts and invertebrate traces occur 4–5 m above the track-bearing layers (Fig. 3). Wood clasts lie parallel to the bedding planes, but seem to be unoriented. The wood fragments are preserved predominantly as imprints, although some permineralized body fossils occur locally. Invertebrate ichnofossils predominantly comprise *Naktodemasis boweni* (Smith et al., 2008) and *Scoyenia gracilis* (White, 1929). *Naktodemasis boweni* is a meniscate, backfilled tunnel that may have been made by beetle larvae and/or adults (Smith et al., 2008). Also, several large



Fig. 2. Track-bearing outcrop of the Qugezhuang Formation strata at the Wenxiyuan Community as exposed during construction. A man was pointing to a tridactyl footprint (photograph by Gong-Shen Jiao).

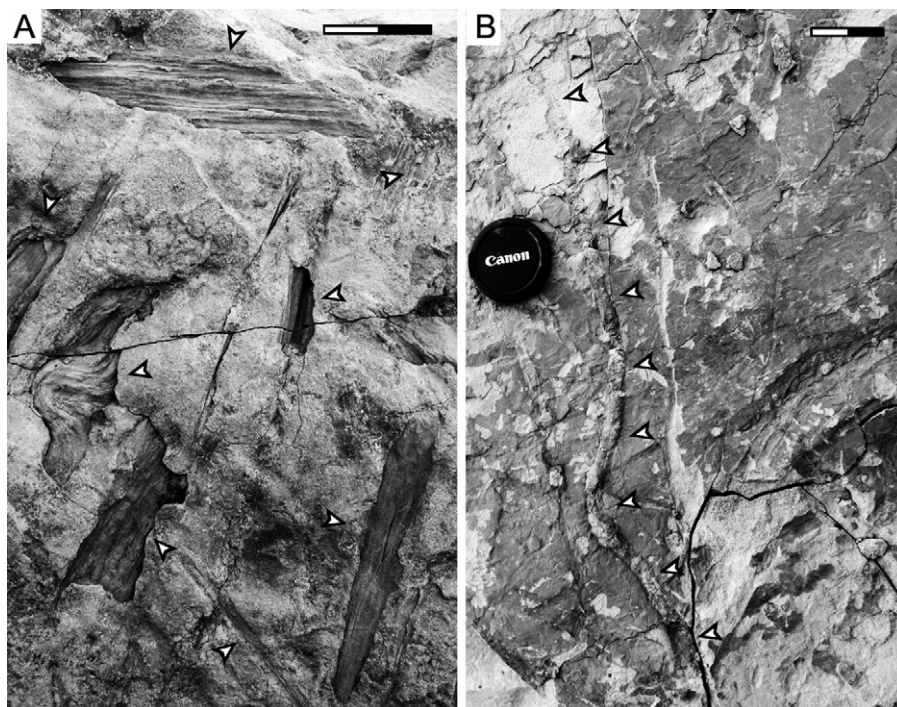


Fig. 3. Plant remains and invertebrate ichnofossils from the Wenxiyuan tracksite. Wood clasts (A) and the invertebrate trace *Naktodemasis boweni* (B) on two single slabs. Scale bar = 50 mm.

desiccation cracks (in strata other than the track-bearing layers) are cross cut by vertical and horizontal traces assigned to *Scoyenia gracilis*. These traces are unlined and locally display scratch marks, indicating burrowing in firm sediment (White, 1929; Frey et al., 1984), likely by insects and/or annelids (Stanley and Fagerstrom, 1974; Bromley and Asgaard, 1979). *Scoyenia* is commonly found in the mudstone and muddy siltstone layers of the Qugezhuang Formation, and is most frequently observed in association with desiccation cracks, suggesting that the trace makers might have inhabited occasionally exposed, low-lying floodplains (Li and Zhang, 2001).

### 3. Systematic ichnology

#### 3.1. Pterosaur tracks

*Pteraichnus* Stokes, 1957

*Pteraichnus* isp.

**Materials.** Five complete natural molds of pes and manus prints cataloged as LUGP3-001.1p (p=pes) and LUGP3-001.2m (m=manus) (LUGP=Institute of Geology and Palaeontology, Linyi University, Linyi City, Shandong, China), LUGP3-001.2p, and LUGP3-001.3m and LUGP3-001.3p (Figs. 3 and 4) from the Wenxiyuan tracksite (36°23′0.12″N, 120°25′41.05″E). Artificial molds of the tracks are stored at the Huaxia Dinosaur Tracks Research and Development Center, where they are cataloged as HDT.217–221 (Huaxia Dinosaur Tracks Research and Development Center, Gansu, China).

**Methods.** To better identify the pterosaur tracks, the casts were scanned with a Non-contact Grating-Type Structured Light 3D Scanning System (JiRui II, supported by Beijing JiRui Xintian

Technology Co., Ltd.) to obtain the 3D data; the software (JiRui 3D image analysis software) generated photogrammetric models of the tracks. All topographic images were obtained from silastic casts. The contour intervals equal 0.12 mm.

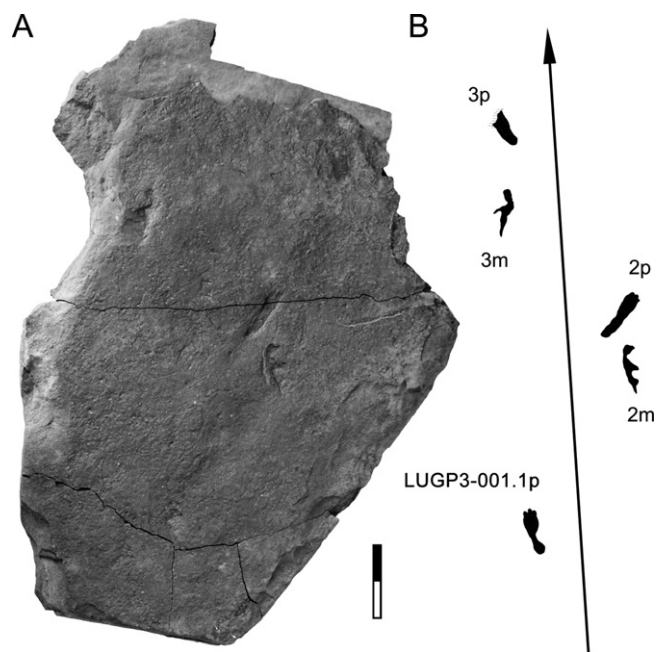


Fig. 4. Wenxiyuan pterosaur trackway. (A) Photograph and (B) outline drawings; black arrow indicates the direction of track maker progression and the trackway midline. Manus track 1m was probably out of this slab, and was not preserved. Scale bar = 10 cm. All specimen numbers begin with the prefix LUGP3-001. For clarity, tracks are only labeled with their suffixes except LUGP3-001.1p.



**Locality and horizon.** Qugezhuang Formation, Laiyang Group, Early Cretaceous. Wenxiyuan tracksite, Jimo City, Shandong Province, China.

**Description.** Although none of the pterosaur tracks are well preserved, their main morphological features remain identifiable. The five tracks comprise a single quadrupedal trackway consisting of alternating manus and pes prints. The asymmetrical and digitigrade manus prints (LUGP3-001.2m and LUGP3-001.3m) consist of three digit impressions, and are rotated outward. All three digits radiate from a central depression, and digit III is the deepest. The clawed impressions of manual digits I and II are short and oriented cranio-laterally and caudolaterally, respectively. A weakly curved manual digit III is oriented caudally. Digital pad impressions are indistinct; digit II of LUGP3-001.2m seems to possess two pads and digit III one long, narrow pad, leaving a deeper impression towards its distal end. The best-preserved medial margin of LUGP3-001.2m bears one longitudinal, concave impression; the caudomedial margin of digit II of LUGP3-001.3m (Fig. 5C, I) bears one rounded, cranio-laterally oriented concavity that may be part of an impression of the metacarpophalangeal joint of digit IV (Billon-Bruyat and Mazin, 2003; Mazin et al., 2003; Lockley and Harris, in press). However, the possibility that these features are extramorphological effects cannot be excluded. Digit III possesses a sharp ungual imprint. The divarication angle between digits I and III is very high (average  $115.8^\circ$ ). Frey et al. (2003) suggested that there are at least two different manus types (long-clawed and short-clawed) among pterosaurs depending on whether or not the claws were hyperextended while walking. The presence of claw impressions in the Wenxiyuan pterosaur tracks suggests that they were made by a short-clawed pterosaur.

The plantigrade pes prints are narrow and have U-shaped heels as well as indistinct digit traces. Three indentations at the distal ends of LUGP3-001.1p and LUGP3-001.2p may be the proximal ends of digits I–III; in no tracks are any traces of digit IV visible. LUGP3-001.3p lacks its distal end. The tracks gradually deepen anteriorly and posteriorly from a shallow center; the distal ends are typically the deepest.

In the trackway, the pes prints lie cranial to the manus prints; the latter are located farther from the midline than the former. Both manus prints are inwardly rotated ( $8^\circ$  and  $13^\circ$ , respectively); the manual step length is 26.3 cm, and the distance between tracks is 12.1 cm. The pes prints are, in contrast, outwardly rotated ( $13^\circ$ ,  $42^\circ$ , and  $31^\circ$ , respectively); the pedal stride length is 54.5 cm and the average pace length is 28.9 cm; the pace angulation is  $127^\circ$  and the distance between tracks is 9.8 cm. The widths between the Wenxiyuan pterosaur manus prints are wider than the widths between their associated pes prints (Lockley and Harris, in press).

In general, the manus imprints are more deeply impressed than the pes imprints, as has been noted for other pterosaur trackways (Lockley et al., 1995; Billon-Bruyat and Mazin, 2003). However, the depths of the Wenxiyuan manus and pes prints vary (Fig. 5A–C), probably as a function of substrate consistency.

**Discussion.** Worldwide, at least 50 pterosaur tracksites have been reported from Middle–early Late Jurassic through latest

Cretaceous localities (Lockley et al., 2008; Lockley and Harris, in press). The newest discoveries have been concentrated in China, South Korea, and Japan (Lee et al., 2008, 2010; Lü et al., 2010). Pterosaur tracks are not abundant in China: only four pterosaur tracksites have been discovered thus far, all from Cretaceous rock units. The first tracks described, from the Early Cretaceous Hekou Group in Yanguoxia, Gansu Province (Peng et al., 2004; Li et al., 2006; Zhang et al., 2006), were assigned to a unique ichnospecies, *Pteraichnus yanguoxiaensis*. The description of *P. yanguoxiaensis* (Peng et al., 2004) lacks sufficient information, such as detailed measurements and comparison to other *Pteraichnus* ichnospecies (Lockley and Harris, in press). They are being redescribed, and will be published elsewhere. Other Chinese *Pteraichnus* tracks have been described from Zhejiang Province (Lü et al., 2010), and additional tracks (from Qijiang County, Chongqing City) have yet to be described in detail.

Morphologically, the Wenxiyuan tracks are extremely similar to other pterosaur tracks in the ichnogenus *Pteraichnus* and are here attributed to that ichnotaxon. *Pteraichnus* was initially erected for a quadrupedal pterosaur trackway from the Upper Jurassic Morrison Formation of Apache County, Arizona (Stokes, 1957). Subsequently, *Pteraichnus* has become by far the most prevalent and best preserved pterosaur ichnotaxon. In a recent review of the ichnotaxon, Lockley and Harris (in press) recognized five valid ichnospecies: *P. saltwashensis* (Stokes, 1957), *P. stokesi* (Lockley et al., 1995), *P. longipodus* (Fuentes Vidarte et al., 2004), *P. parvus* (Meijide Calvo and Fuentes Vidarte, 2001), and *P. nipponensis* (Lee et al., 2010).

Since *Pteraichnus* was first named by Stokes (1957), its diagnosis has been emended twice (Lockley et al., 1995; Billon-Bruyat and Mazin, 2003). Although the Wenxiyuan pterosaur tracks meet the updated diagnosis of *Pteraichnus* (Lockley and Harris, in press), they differ in some respects from currently known ichnospecies. One of these differences, the absence of distinct digit I–IV impressions and claw impressions in the pes prints, is more similar to *Haenamichnus uhangriensis* (Lockley et al., 1997; Hwang et al., 2002) than to *Pteraichnus*, though this is probably the effect of substrate conditions rather than morphology. Other differences, however, have less clear etiologies. First, the Wenxiyuan pes prints are ovoid rather than subtriangular like in the other ichnospecies. Second, the manual digit I impressions of the Wenxiyuan tracks are relatively short and thick, similar to *P. stokesi* and *Purbeckopus pentadactylus* (Wright et al., 1997) but unlike the slim digits I of *P. saltwashensis*, *P. koreanensis*, and *P. nipponensis*. It is unclear whether or not these differences can also be attributed to deformation caused by substrate consistencies or actual morphological characteristics on the part of the track-making taxon. The small sample size makes it difficult to discern systematic features across a significant number of tracks, so the material is referred to only as *Pteraichnus* isp.

Compared with other *Pteraichnus* trackways (e.g., Mazin et al., 2003; Lee et al., 2008), the Wenxiyuan pterosaur trackway exhibits a clear “narrow gauge”. Mazin et al. (2003) considered that a relatively short stride and narrow width between manus tracks imply that the body of the track maker was held

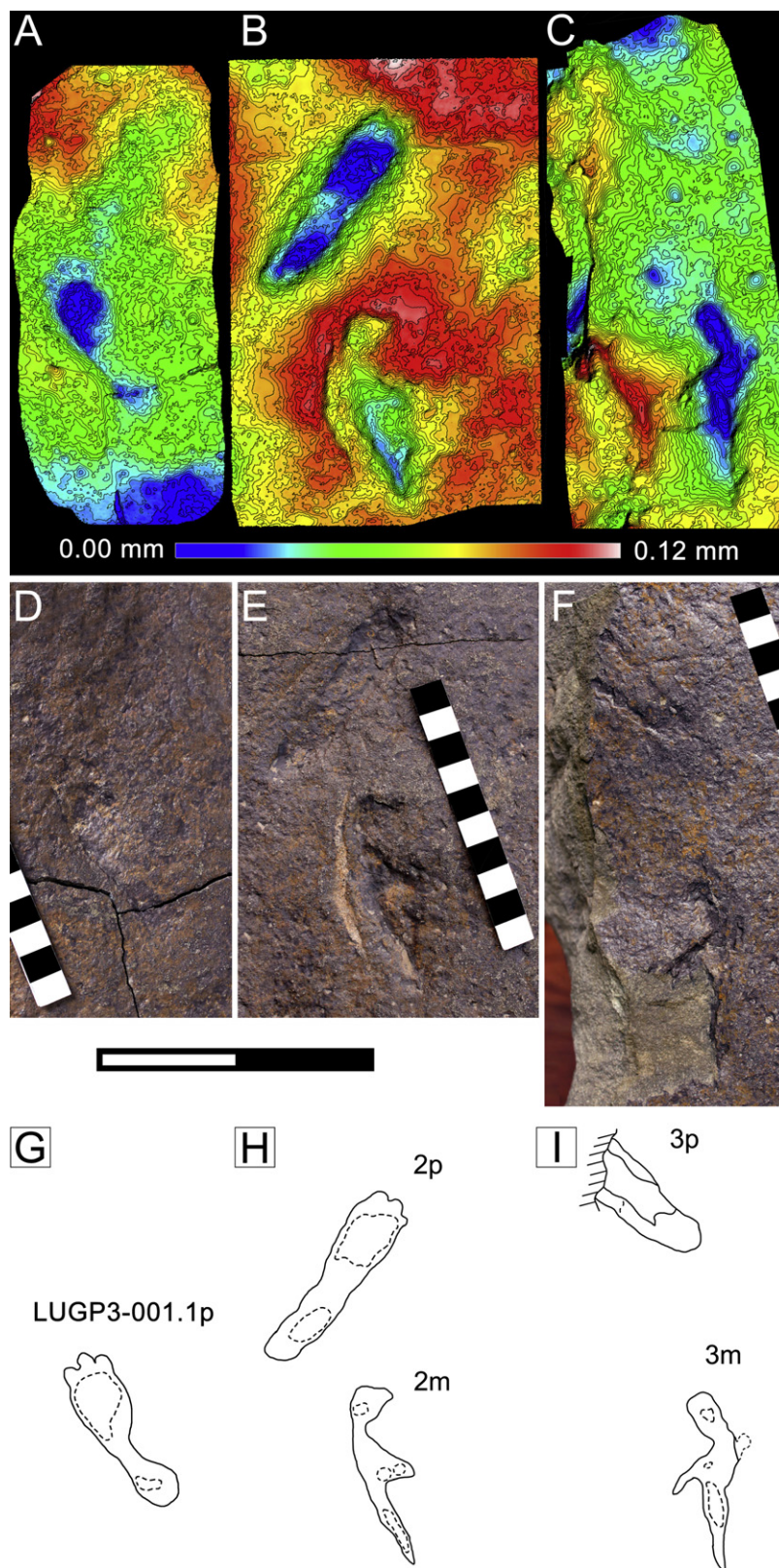


Fig. 5. Wenxiyuan pterosaur tracks. (A–C) Photogrammetric 3D model of artificial casts of pterosaur tracks LUGP3-001.1–3. Color banding reflects topography (blue-green = highest, red-white = deepest). (D–F) Photographs of original tracks. (G–I) Outline drawings made from the photogrammetric maps. Scale bar = 10 cm. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)



semi-erect during low-velocity walking. The distance between paired manus-pes print sets increases from 6.8 cm between LUGP3-001.2p–LUGP3-001.2m to 11.9 cm between LUGP3-001.3p–LUGP3-001.3m, probably suggesting an increase in velocity.

**Track maker identification.** The Jehol Biota includes a diverse pterosaurian fauna (Wang et al., 2005; Lü and Ji, 2006; Lü et al., 2006), including both basal and derived taxa (Lü et al., 2006; Lü, 2010). Jehol pterosaurs span a considerable size range, from a wingspan less than 25 cm in *Nemicolopterus* (Wang et al., 2008) to a wingspan of approximately 5 m in *Liaoningopterus* (Wang and Zhou, 2003). The Wenxiyuan tracks could have been made by a Jehol pterosaur, or a morphologically similar close relative. Pterodactyls predominate in the Jehol Biota, though some anurognathid “rhamphorhynchoids” (Ji and Ji, 1998; Hone and Lü, 2010) and “transitional” darwinopterids (wukongopterids) (Lü et al., 2009; Wang et al., 2010b) were also present. The Wenxiyuan track maker was therefore most likely a small to medium-sized pterodactyl. However, a non-pterodactyl track maker cannot be ruled out because the impression of pedal digit V, which is plesiomorphically present in non-pterodactyls, is rarely impressed clearly and unambiguously (Lockley et al., 2008).

### 3.2. Tridactyl dinosaur tracks

**Materials.** Based on the initial, albeit informal, survey of Jiao (2009), there were at least 100 tridactyl dinosaur tracks at the Wenxiyuan site. However, today, only one photograph, and six tracks are preserved (Figs. 6 and 7). These six uncataloged tracks belong to the Jin-Hong-Yuan Real Estate Co., Ltd., and were displayed by this company in Qingdao City, Shandong Province. Artificial molds of these six tracks are stored at the Huaxia Dinosaur Tracks Research and Development Center, Geological

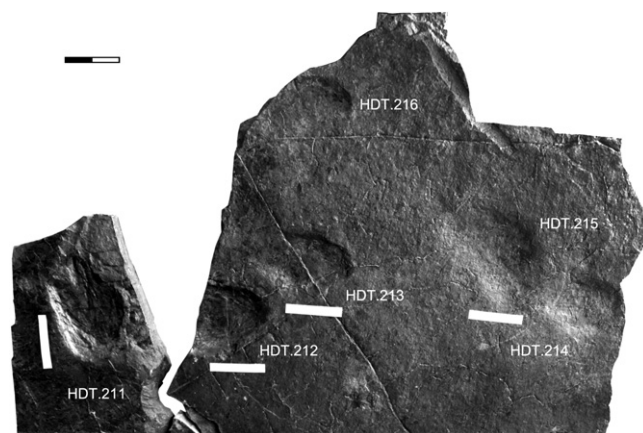


Fig. 6. Photograph of Wenxiyuan tridactyl dinosaur track slab. Scale bar = 10 cm.

Museum of Gansu, where they are cataloged as HDT.211–216. The photograph of the site is cataloged as HDT.210P.

**Locality and horizon.** Qugezhuang Formation, Early Cretaceous. Wenxiyuan tracksite, Jimo City, Shandong Province, China.

**Description.** HDT.210P and HDT.211–212 are medium-sized, asymmetric, tridactyl dinosaur tracks (measurements are given in Table 1). No trackways can be identified.

HDT.210P, which is the most complete track in the sample, has a length:width ratio of 1.99. Digit III is directed cranially, and digit IV is longer than digit II, the divarication angle between digits II and IV is 37°, the phalangeal pad formula is  $x-2-3-?-x$ , the impression of pad III of digit III is the largest, and pad II is larger than pad I. A sub-ovoid metatarsophalangeal region lies nearly in line with the axis of digit III, close to the proximal end of digit IV. The phalangeal pad formula of HDT.211 is unclear. Its divarication angle between digits II and IV (47.6°)

Table 1  
Measurements (in mm) of pterosaur and tridactyl dinosaur tracks from the Wenxiyuan locality, Shandong Province, China.

Specimen number	ML	MW <sup>a</sup>	LD I	LD II	LD III	LD IV	I–II	II–III	III–IV	l/w
<b>Pterosaur</b>										
LUGP3-001.1p	6.28	1.98	–	–	–	–	–	–	–	3.17
LUGP3-001.2m	6.73	1.31	1.91	2.71	5.34	–	85.9°	30.2°	–	3.70
LUGP3-001.2p	7.32	1.92	–	–	–	–	–	–	–	3.81
LUGP3-001.3m	6.40	1.51	2.56	3.36	4.76	–	72.0°	43.4°	–	1.94
LUGP3-001.3p	>4.77	1.93	–	–	–	–	–	–	–	–
<b>Dinosaur</b>										
HDT.210P	19.93	10.03	–	9.75	15.53	14.02	–	22.0°	15.0°	1.99
HDT.211	19.34	11.90	–	7.74	14.04	11.36	–	21.0°	26.6°	1.62
HDT.212	–	–	–	–	–	–	–	–	–	–
HDT.213	17.43	11.08	–	–	–	–	–	–	–	1.57
HDT.214	15.00	11.84	–	–	–	–	–	–	–	1.27
HDT.215	16.33	9.79	–	–	–	–	–	–	–	1.67
HDT.216	13.78	9.02	–	–	–	–	–	–	–	1.53

**Abbreviations:** ML: maximum length; MW: maximum width; LD I: length of digit I; LD II: length of digit II; LD III: length of digit III; LD IV: length of digit IV; I–II: angle between digits I and II; II–III: angle between digits II and III; III–IV: angle between digits III and IV; l/w: ML/MW; –: measurement not possible or not applicable.

<sup>a</sup> Pterosaur tracks measured using the methods of Sánchez-Hernández et al. (2009, fig. 4); tridactyl dinosaur track width measured as distance between the tips of digits II and IV, length measured as distance between the tips of digits III and metatarsophalangeal region.

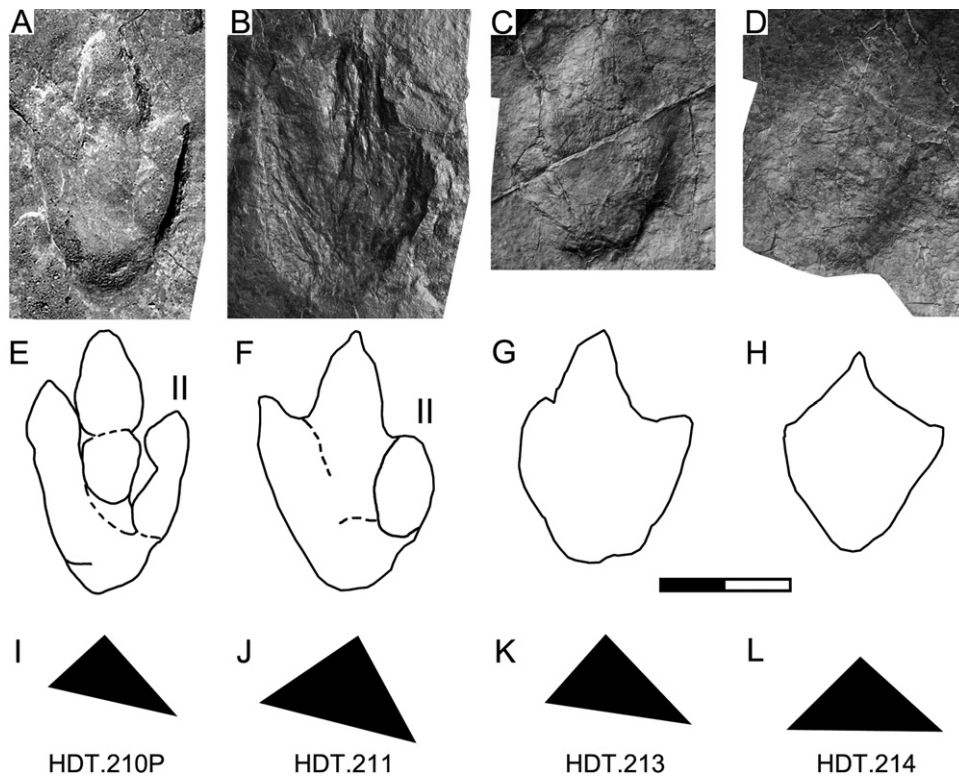


Fig. 7. Wenxiyuan tridactyl dinosaur tracks HDT.210P, 211, 213, and 214. (A–D) Photographs; (E–H) outline drawings; (I–L) anterior triangles, drawn between the tips of the distal ends of digits II, III, and IV (sensu Weems, 1992; Lockley, 2009), indicating the degree of mesaxony. Scale bar = 10 cm.

slightly exceeds that of HDT.210P. Except for having an unusually short digit II impression, the track is otherwise similar to HDT.210P in morphology. The distal end of HDT.212 is damaged, but its metatarsophalangeal region appears similar to those of HDT.210P and 211. HDT.213–216 are faint undertracks with no clearly discernible detail.

**Discussion.** Morphologically, the Wenxiyuan tridactyl tracks are too poorly preserved to be referred to any particular ichnotaxon. According to Olsen (1980), Weems (1992), and Lockley (2009), tridactyl theropod tracks can be differentiated in part by the degree of mesaxony. The anterior triangle of the best-preserved Wenxiyuan tridactyl track HDT.210P (Fig. 7I), with a height close to one-half of its baseline width and a length:width ratio of 0.48, indicates moderate mesaxony, unlike the moderate to strong mesaxony typical of the ichnofamilies Eubrontidae and Grallatoridae, respectively (Li et al., 2010). The unusually short digit II of HDT.211 gives its anterior triangle a length:width ratio of 0.54. Although HDT.213 and 214 are very poorly preserved, the tips of their digits can still be distinguished. The length:width ratios of the anterior triangles of HDT.213 and 214 are 0.51 and 0.47, respectively. This range of values is small, indicating that, although tracks constitute a small sample size, all the Wenxiyuan tridactyl tracks should pertain to one type of track. Occasionally, poorly preserved, tridactyl dinosaur tracks may lack the distal parts of digit II and become “didactyl” variants (Gaston et al., 2003). The unusually short digit II of HDT.211 may be such a track, though it could also be a pathological effect (injury or congenital deformation) on the foot of the track maker or even

an extramorphological variant created by a particular behavior of the track maker, substrate interactions, or both.

### Acknowledgements

We thank Daniel Marty (Section d’archéologie et paléontologie – Paléontologie A16, Switzerland) and Matteo Belvedere (Università degli Studi di Padova, Padova, Italy) for their critical comments and suggestions on this paper. Thanks to Mrs. Shen-Na Wang and Mr. Gong-Shen Jiao for assistance and logistical support during the field expedition to study the tracks. Thanks to Jin-Hong-Yuan Real Estate Co., Ltd. of Qingdao City for access to the specimens. This research project was supported by the Key Laboratory of Evolutionary Systematics of Vertebrates, CAS (2011LESV008).

### References

- Billon-Bruyat, J.P., Mazin, J.M., 2003. The systematic problem of tetrapod ichnotaxa: the case study of *Pteraichnus* Stokes, 1957 (Pterosauria, Pterodactyloidea). In: Buffetaut, E., Mazin, J.M. (Eds.), *Evolution and Palaeobiology of Pterosaurs*, 217. Geological Society, London, pp. 315–324.
- Bromley, R.G., Asgaard, U., 1979. Triassic freshwater ichnocoenoses from Carlsberg Fjord, East Greenland. *Palaeogeography, Palaeoclimatology, Palaeoecology* 28, 39–80.
- Chao, S.T., 1962. On a new species of *Psittacosaurus* from Laiyang, Shantung. *Vertebrata Palasiatica* 6, 349–360.
- Frey, R.W., Pemberton, S.G., Fagerstrom, J.A., 1984. Morphological, ethological, and environmental significance of the ichnogenera *Scoyenia* and *Ancorichnus*. *Journal of Paleontology* 58, 511–528.

- Frey, E., Tischlinger, H., Buchy, M.C., Martill, D.M., 2003. New specimens of Pterosauria (Reptilia) with soft parts with implications for pterosaurian anatomy and locomotion. In: Buffetaut, E., Mazin, J.M. (Eds.), *Evolution and Palaeobiology of Pterosaurs*, 217. Geological Society, London, pp. 233–266.
- Fuentes Vidarte, C., Meijide Calvo, M., Meijide Fuentes, F., Meijide Fuentes, M., 2004. *Pteraichnus longipodus* nov. icnosp. en la Sierra de Oncala (Soria, España). *Studia Geologica Salmanticensia* 40, 103–114.
- Gaston, R., Lockley, M.G., Lucas, S.G., Hunt, A.P., 2003. Grallator-dominated fossil footprint assemblages and associated enigmatic footprints from the Chinle Group (Upper Triassic), Gateway area, Colorado. *Ichnos* 10, 153–163.
- Hone, D.W.E., Lü, J.C., 2010. A new specimen of *Dendrorhynchoides* (Pterosauria: Anurognathidae) with a long tail and the evolution of the pterosaurian tail. In: Lü, J.C., Unwin, D., Ji, S.A., Ji, Q. (Eds.), *Proceedings of the Third International Symposium on Pterosaurs “Flugsaurier 2010”*. *Acta Geoscientia Sinica* 31, 29–30.
- Hwang, K.G., Huh, M., Lockley, M.G., Unwin, D.M., Wright, J.L., 2002. New pterosaur tracks (Pteraichnidae) from the Late Cretaceous Uhangri Formation, southwestern Korea. *Geological Magazine* 139, 421–435.
- Ji, S.A., Ji, Q., 1998. A new fossil pterosaur (Rhamphorhynchoidea) from Liaoning. *Jiangsu Geology* 22, 199–206.
- Jiao, G.S., 2009. The suspected dinosaur tracks were discovered in Jimo City, Shandong Province. *Peninsula City Daily*, April 27, A12 (in Chinese).
- Lee, Y.N., Lee, H.J., Lü, J.C., Kobayashi, Y., 2008. New pterosaur tracks from the Hasandong Formation (Lower Cretaceous) of Hadong County, South Korea. *Cretaceous Research* 29, 345–353.
- Lee, Y.N., Azuma, Y., Lee, H.J., Shibata, M., Lü, J.C., 2010. The first pterosaur trackways from Japan. *Cretaceous Research* 31, 263–267.
- Li, R.H., Zhang, G.W., 2001. A preliminary study of nonmarine trace fossils from the Laiyang group (Early Cretaceous), Laiyang Basin, Eastern China. *Acta Palaeontologica Sinica* 40, 252–261.
- Li, D.Q., Azuma, Y., Fugita, M., Lee, Y.N., Arakawa, Y., 2006. A preliminary report on two new vertebrate track sites including dinosaurs from the Early Cretaceous Hekou Group, Gansu Province, China. In: Lee, Y.N. (Ed.), *Proceedings of the 2006 Goseong International Dinosaur Symposium*. *Journal of the Paleontological Society of Korea* 22, 29–49.
- Li, R.H., Lockley, M.G., Matsukawa, M., Wang, K., Liu, M., 2010. An unusual theropod track assemblage from the Cretaceous of the Zhucheng area, Shandong Province, China. *Cretaceous Research* 32, 422–432.
- Lockley, M.G., 2009. New perspectives on morphological variation in tridactyl footprints: clues to widespread convergence in developmental dynamics. *Geological Quarterly* 53, 415–432.
- Lockley, M.G., Harris, J.D., 2009. Pterosaur tracks and tracksites: Pteraichnidae. In: Martill, D., Unwin, D., Loveridge, R. (Eds.), *The Pterosauria*. Cambridge University Press, Cambridge, ISBN: 9780521518956, in press.
- Lockley, M.G., Logue, T.J., Moratalla, J.J., Hunt, A.P., Schultz, R.J., Robinson, J.W., 1995. The fossil trackway *Pteraichnus* is pterosaurian, not crocodilian: implications for the global distribution of pterosaur tracks. *Ichnos* 4, 7–20.
- Lockley, M.G., Huh, M., Lim, S.K., Yang, S.Y., Chun, S.S., Unwin, D.M., 1997. First report of pterosaur tracks from Asia, Chulnam Province, Korea. In: Yang, S.Y., Huh, M., Lee, Y.N., Lockley, M.G. (Eds.), *International Dinosaur Symposium for Uhangri Dinosaur Center and Theme Park in Korea*. *Journal of Paleontological Society of Korea* 2, 17–32.
- Lockley, M.G., Harris, J.D., Mitchell, L., 2008. A global overview of pterosaur ichnology: tracksite distribution in space and time. *Zitteliana B* 28, 185–198.
- Lü, J.C., 2010. An overview of the pterosaur fossil record in China. *Acta Geoscientia Sinica* 31 (Suppl. 1), 49–51.
- Lü, J.C., Ji, Q., 2006. Preliminary results of a phylogenetic analysis of the pterosaurs from western Liaoning and surrounding areas. *Journal of Paleontological Society of Korea* 22, 239–261.
- Lü, J.C., Ji, S., Yuan, C., Ji, Q., 2006. Pterosaurs from China. *Geological Publishing House*, Beijing, 147 pp.
- Lü, J.C., Unwin, D.M., Jin, X., Liu, Y., Ji, Q., 2009. Evidence for modular evolution in a long-tailed pterosaur with a pterodactyloid skull. *Proceedings of the Royal Society B: Biological Sciences* 277, 383–438.
- Lü, J.C., Chen, R.J., Azuma, Y., Zheng, W.J., Tanaka, I., Jin, X.S., 2010. New pterosaur tracks from the early Late Cretaceous of Dongyang City, Zhejiang Province, China. *Acta Geoscientia Sinica* 31 (Suppl. 1), 46–48.
- Lucas, S.G., 2001. *Chinese Fossil Vertebrates*. Columbia University Press, New York, 375 pp.
- Mazin, J.M., Billon-Bruyat, J.P., Hantzpergue, P., Lafaunie, G., 2003. Ichnological evidence for quadrupedal locomotion in pterodactyloid pterosaurs: trackways from the Late Jurassic of Crayssac (southwestern France). In: Buffetaut, E., Mazin, J.M. (Eds.), *Evolution and Palaeobiology of Pterosaurs*, 217. Geological Society, London, pp. 283–296.
- Meijide Calvo, M., Fuentes Vidarte, C., 2001. Huellas de pterosaurios en el Weald de Soria (España). In: *Colectivo Arqueológico-Paleontológico de Salas* (Ed.), *Actas de las I Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno*. *Colectivo Arqueológico-Paleontológico de Salas*, Burgos, pp. 397–406.
- 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. New York State Geological Association, Rutgers University, pp. 352–398.
- Peng, B.X., Du, Y.S., Li, D.Q., Bai, Z.C., 2004. The first discovery of the Early Cretaceous pterosaur track and its significance in Yanguoxia, Yongjing County, Gansu Province. *Earth Science—Journal of China University of Geosciences* 29, 21–24.
- Qiao, Z.X., 2001. Mashan: “World Geological Park”. *Teaching Reference of Middle School Geography* 11, 55 (in Chinese).
- Regional Geological Survey Team of the Bureau of Geology and Mining of the Shandong Province, 1990. *The Stratigraphical Paleontology of Laiyang Basin, Shandong Province*. Geological Publishing House, Beijing, 292 pp.
- Sánchez-Hernández, B., Przewieslik, A.G., Benton, M.J., 2009. A reassessment of the *Pteraichnus* ichnospecies from the Early Cretaceous of Soria Province, Spain. *Journal of Vertebrate Paleontology* 29, 487–497.
- Smith, J.J., Hasiotis, S.T., Kraus, M.J., Woody, D.T., 2008. *Naktodemas bowni*: new ichnogenus and ichnospecies for adhesive meniscate burrows (AMB), and palaeoenvironmental implications, Palaeogene Willwood Formation, Bighorn Basin, Wyoming. *Journal of Paleontology* 82, 267–278.
- Stanley, K.O., Fagerstrom, J.A., 1974. Miocene invertebrate trace fossils from a braided river environment, western Nebraska, U.S.A. *Palaeogeography, Palaeoclimatology, Palaeoecology* 15, 63–82.
- Stokes, W.L., 1957. Pterodactyl tracks from the Morrison Formation. *Journal of Paleontology* 31, 952–954.
- Wang, X.L., Zhou, Z.H., 2003. Two new pterodactyloid pterosaurs from the Early Cretaceous Jiufotang Formation of western Liaoning, China. *Vertebrata Palasiatica* 41 (1), 34–41.
- Wang, X.L., Kellner, A.W., Zhou, Z.H., Campos, D., 2005. Pterosaur diversity and faunal turnover in Cretaceous terrestrial ecosystems in China. *Nature* 437, 875–879.
- Wang, X.L., Kellner, A.W.A., Zhou, Z.H., Campos, D., 2008. Discovery of a rare arboreal forest-dwelling flying reptile (Pterosauria, Pterodactyloidea) from China. *Proceedings of the National Academy of Sciences* 105, 1983–1987.
- Wang, X.L., Wang, Q., Wang, J.H., Zhang, J.L., Cheng, X., Jiang, S.X., Pan, R., 2010a. An overview on the Cretaceous dinosaurs and their eggs from Laiyang, Shandong Province, China. In: Dong, W. (Ed.), *Proceedings of the Twelfth Annual Meeting of the Chinese Society of Vertebrate Paleontology*. Ocean Press, Beijing, pp. 293–306.
- Wang, X.L., Kellner, A.W.A., Jiang, S., Chang, X., Meng, X., Rodrigues, T., 2010b. New long-tailed pterosaurs (Wukongopteridae) from western Liaoning, China. *Anais da Academia Brasileira de Ciências* 82, 1045–1062.
- Weems, R.E., 1992. A re-evaluation of the taxonomy of Newark Supergroup saurischian dinosaur tracks, using extensive statistical data from a recently exposed tracksite near Culpeper Virginia. In: Sweet, P.C. (Ed.), *Proceedings of the 26th Forum on the Geology of Industrial Minerals*. Division of Mineral Resources, Virginia, pp. 113–127.
- White, C.D., 1929. *Flora of the Hermit Shale, Grand Canyon, Arizona*. Carnegie Institute of Washington Publication, 405, 221.



- Wright, J.L., Unwin, D.M., Lockley, M.G., Rainforth, E.C., 1997. Pterosaur tracks from the Purbeck Limestone Formation of Dorset, England. *Proceedings of the Geologists' Association* 108, 39–44.
- Xing, L.D., Harris, J.D., Wang, K.B., Li, R.H., 2010. An Early Cretaceous non-avian dinosaur and bird footprint assemblage from the Laiyang Group in the Zhucheng Basin, Shandong Province, China. *Geological Bulletin of China* 29 (8), 1–8.
- Young, C.C., 1958. The dinosaurian remains of Laiyang, Shantung. *Palaeontologica Sinica, New Series C* 12, 1–138.
- Young, C.C., 1964. On a new pterosaurian from Sinkiang, China. *Vertebrata Palasiatica* 8, 221–256.
- Zhang, J., 1992. Late Mesozoic entomofauna from Laiyang, Shandong Province, China, with discussion of its palaeoecological and stratigraphical significance. *Cretaceous Research* 13, 133–145.
- Zhang, Z.Q., Liu, M.W., 1996. *Lithostratigraphy of Shandong Province*. China University of Geosciences Press, Wuhan, 328 pp.
- Zhang, J., Li, D., Li, M., Lockley, M.G., Bai, Z., 2006. Diverse dinosaur-, pterosaur-, and bird-track assemblages from the Hakou Formation, Lower Cretaceous of Gansu Province, northwest China. *Cretaceous Research* 27, 44–55.
- Zhang, H., Wang, B., Fang, Y., 2010. Evolution of insect diversity in the Jehol Biota. *Science China: Earth Sciences* 53, 1908–1917.