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A manus dominated pterosaur track assemblage from Gansu, China: implications for behavior

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Abstract The Yangouxia dinosaur tracksites are well known for a diverse assemblage of tetrapod tracks preserved as natural impressions (concave epireliefs) on large bedding planes, representing a locally widespread surface marking the transition from a sand- to a mud-dominated sequence in the Hekou Group. Previous ichnological studies at these large sites have focused on the morphology and ichnotaxonomy of the tracks, including a single trackway representing the first pterosaur tracks reported from China. Here, we report a distinctly different assemblage associated with minor sandstones in the mud-dominated sequence 20 m above the main tracksite level. This assemblage consists of at least 20 pterosaur manus track casts attributed to a single ichnotaxon (*Pteraichnus*). No pes tracks have been identified. These tracks mostly occur in random orientations, although one possible trackway segment is inferred, to represent walking progression. Manus-only pterosaur track assemblages are common and likely reflect differential registration depths of manus and pes and/or sub optimal preservation conditions. The tracks are associated with distinctive invertebrate traces including *Cochlichnus*, *Spongeliomorpha* and *Paleophycus* and suggest the pterosaurs were likely feeding on the invertebrate tracemakers.

Keywords Early Cretaceous · Gansu Province · Yangouxia · Pterosaurs · *Pteraichnus* · Lanzhou-Minhe Basin

1 Introduction

Pterosaurs are the earliest known flying vertebrates. The group flourished worldwide from the Late Triassic until the Late Cretaceous [1] and is represented by thousands of fossil specimens [2]. Most Chinese pterosaur material comes from the Jehol fauna, in western Liaoning, northern Hebei and southeastern Mongolia [3, 4]. A few pterosaur

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specimens have also been founded outside of the Jehol fauna, such as *Dsungaripterus* from Urho, Xinjiang [5] and *Huanhepterus* from Qingyang, Gansu [6].

In recent years, considerable gaps in the fossil record of Chinese pterosaurs have begun to be filled by the discovery of numerous pterosaur tracksites. These sites include: Yanguoxia in Gansu [7, 8], Dongyang in Zhejiang [9, 10], Jimo in Shandong [11], Qijiang in Chongqing [12], Urho in Xinjiang [13, 14], and Zhaojue in Sichuan [15]. Both manus and pes tracks are present at all of the aforementioned tracksites usually in recognizable pairs and often in well-defined trackways. Among these sites, Yanguoxia in Gansu is of historical importance because it was the first site in China from which pterosaur tracks were reported [7, 8]. These tracks occur as part of a single trackway named *Pteraichnus. yanguoxiaensis* by Peng et al. [7].

In 2013, one of us (MGL) discovered a second pterosaur tracksite at Yanguoxia, Gansu (Fig. 1), 300 m north of the original tracksite described by Peng et al. [7] (No. 1), and at a different stratigraphic level 20 m above the main tracksite level from which the original trackway was reported. This is here referred to as the Yangouxia pterosaur tracksite, as to date it has yielded only pterosaur tracks. At this new site, only manus prints are preserved, without associated pes tracks. Similar manus-only pterosaur tracks have been described from the Summerville [16] and Blackhawk Formations of Utah, America [17] and the Rio Limay Formation of Neuquén, Argentina [18]. Such tracks are generally considered as evidence that manus tracks were more deeply impressed than pes tracks.

2 Geological setting

The Lanzhou-Minhe Basin is situated at the border of Gansu and Qinghai provinces and spans 11,300 km^2 (Fig. 1). The Lanzhou-Minhe Basin is a fault basin that developed from the Middle Qilian uplift zone. The red clastic rocks that dominate the basin constitute a single lithological unit, 3,482 m thick and have long been regarded as part of the Hekou Group [19–21]. The Hekou Group is Early Cretaceous in age [22] and is divided into eight informal formation-level units [23].

The whole of the Lanzhou-Minhe area is an inland freshwater lake basin [20]. Within the basin, dinosaur tracks have been discovered at the littoral zone of the border of a former lake basin [24]. The original pterosaur tracksite described by Peng et al. [7] and the pterosaur tracksite described in this paper in the Yanguoxia both occur in the sixth informal formation-level unit defined by Chen [20] and characterized as a shallow-shore lacustrine facies composed of fine gray and gray-green sandstone.

During the course of the present study, two sections were measured, one at the Yangouxia main tracksite area, which includes the new Yangouxia pterosaur tracksite reported here and the other on the west side of Yangouxia

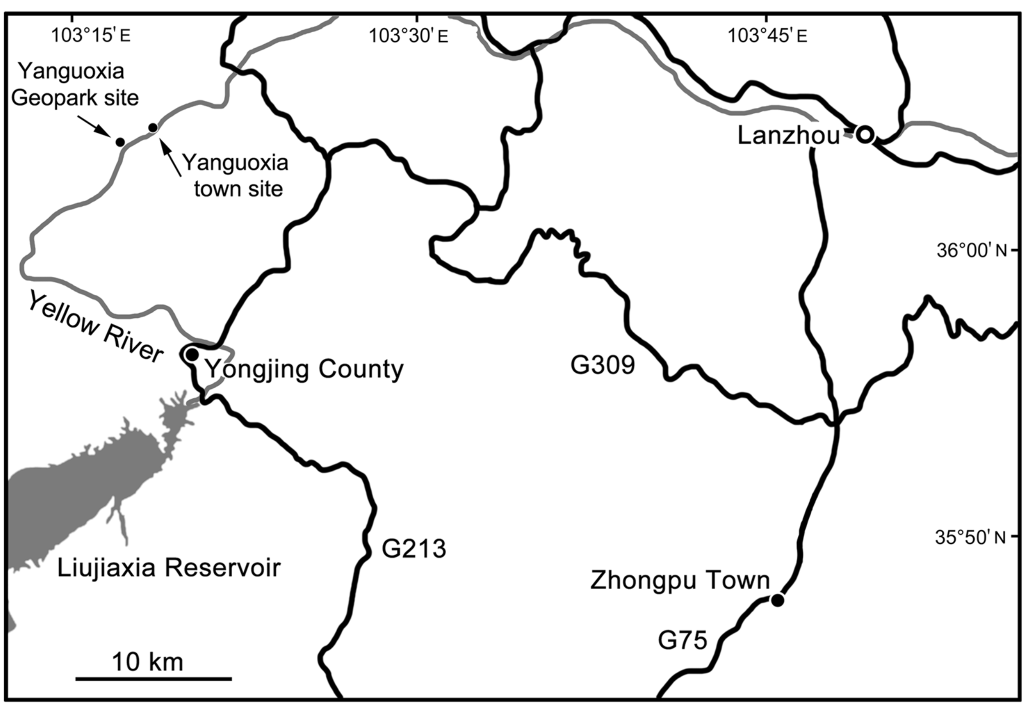

Fig. 1 Map showing the position of the footprint locality, the Yanguoxia pterosaur tracksite, Gansu Province, China

Town (Fig. S1). As shown, the sections consist predominantly of white sandstones alternating with red shale. In places, there are gray shale zones and thin yellow shale intervals. Tetrapod tracks occur at many levels and are particularly abundant at the main tracksite [8]: see Xing et al. [12, 13, 15] and references therein. The pterosaur tracksite occurs about 20 m above the main track level, where a localized sandstone unit is intercalated in a predominantly shale sequence. The tracks are preserved as natural sandstone casts (convex hyporeliefs) on the underside of a compound sandstone unit up to 4 m thick. They occur in association with invertebrate trace fossils.

3 Paleoecology

Invertebrate ichnofossils from the pterosaur tracksite area predominantly comprise *Cochlichnus anguineus* [25] (Fig. 2a), *Spongeliomorpha carlsbergi* [26] (Fig. 2b) and *Palaeophycus tubularis* [27] (Fig. 2c, d).

Cochlichnus anguineus is a snake-like burrow with a sinuous S-shaped morphology. The burrow is about 2 mm in diameter and more than 30 cm in length. The burrow is unbranched and occurs parallel to bedding. *Cochlichnus*, and *Helminthopsis* are similar in general shape but different in detailed characteristics. *Cochlichnus* is characterized by smooth turns, while *Helminthopsis* is less regular and to tends to meander with a less sinusoidal form [28–30].

Spongeliomorpha carlsbergi are straight to sinuous tubular burrows with circular cross sections and knobby and predominantly transverse ridges [31]. The burrows are 3–6 mm in diameter, and the longest burrow is more than 10 cm in length. Burrow fill is structureless and similar to the surroundings matrix. Burrow surfaces are ornamented with thin, tightly spaced and oriented ridges. *S. carlsbergi* resembles *Scoyenia gracilis* [32], but the latter is composed of longitudinally oriented, closely spaced, and paired striations, and the backfill is composed of distinct menisci of contrasting lithologies [33].

Palaeophycus tubularis are straight to slightly curved, smooth cylindrical or sub cylindrical burrows preserved on sole of fine-grained sandstone. The borrows are up to 2 cm long and 1–4 mm in diameter, oriented horizontal to bedding planes, inter-wound, and have parallel annulated surface striae. *Palaeophycus* is similar to *Planolites*, but the infillings of the former are consistent in color and composition with the surrounding rock [34].

Cochlichnus anguineus indicates marine, marginal-marine and continental subaquatic environments, including

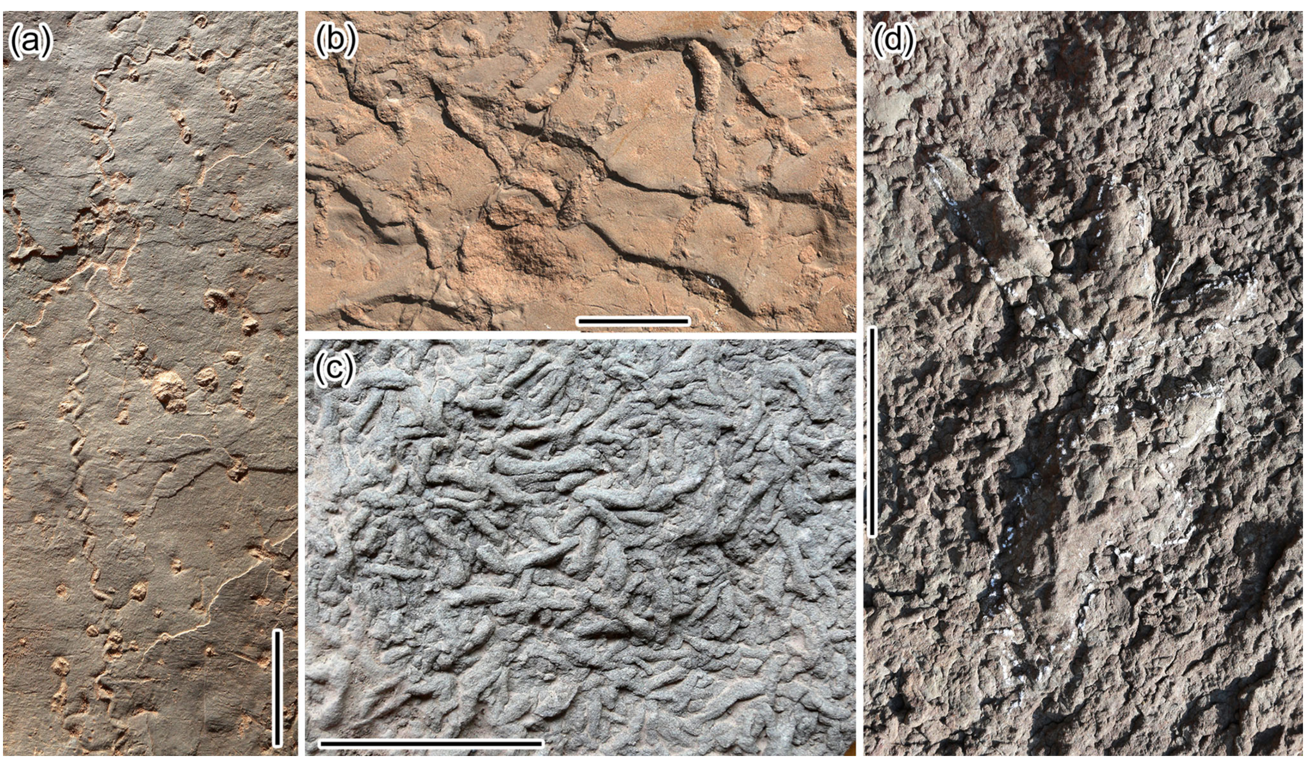

Fig. 2 Invertebrate ichnofossils from Yanguoxia pterosaur tracksite. **a** *Cochlichnus anguineus*; **b** *Spongeliomorpha carlsbergi*; **c** *Palaeophycus tubularis*; **d** *Palaeophycus tubularis* with pterosaur manus prints. Scale bar = 5 cm

lacustrine [25, 27, 35–37], deltaic [38] and fluvial deposits [39], and it also indicates that the trace maker lived in a low energy and probably shallow-water environment [40]. *S. carlsbergi* indicates moderate or less well-drained soil conditions [33]. *P. tubularis* indicates shallow water, usually an intertidal mudflat environment [41]. All these invertebrate ichnofossils indicate that the tracemakers lived in shallow water.

4 Pterosaur tracks

4.1 Material

Twenty-one complete natural casts of manus prints, associated with three samples (surfaces). The samples are designated as Y-PS (Yanguoxia pterosaur tracksite, Gansu, China)1-3, and the individual tracks are cataloged as Y-PS1-1.1–1.9, Y-PS1-2.1–2.5, and Y-PS1-3.1–3.7 (Figs. 3, 4; Fig. S2, Table 1). Original specimen Y-PS2 was collected and preserved as Gansu Dinosaur Museum specimen GDM-P-20130808 and also molded and represented in the University of Colorado collections by replica UCM 214.282 (and tracing T 1620). Original specimens Y-PS1 and YPS3 remain in the field.

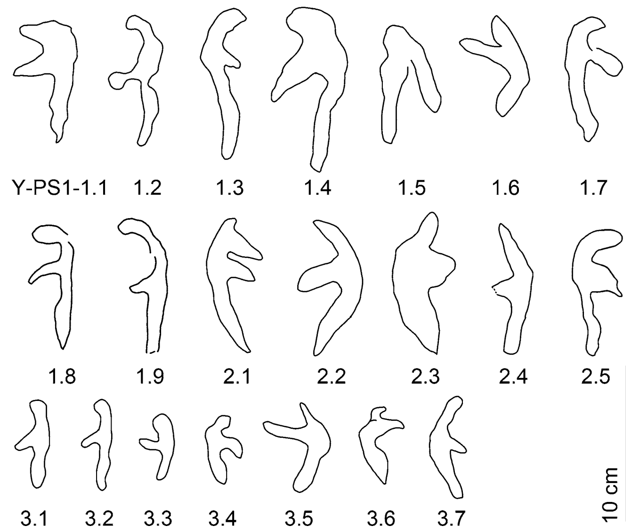

Fig. 4 Sketches of pterosaur manus prints from Yanguoxia pterosaur tracksite

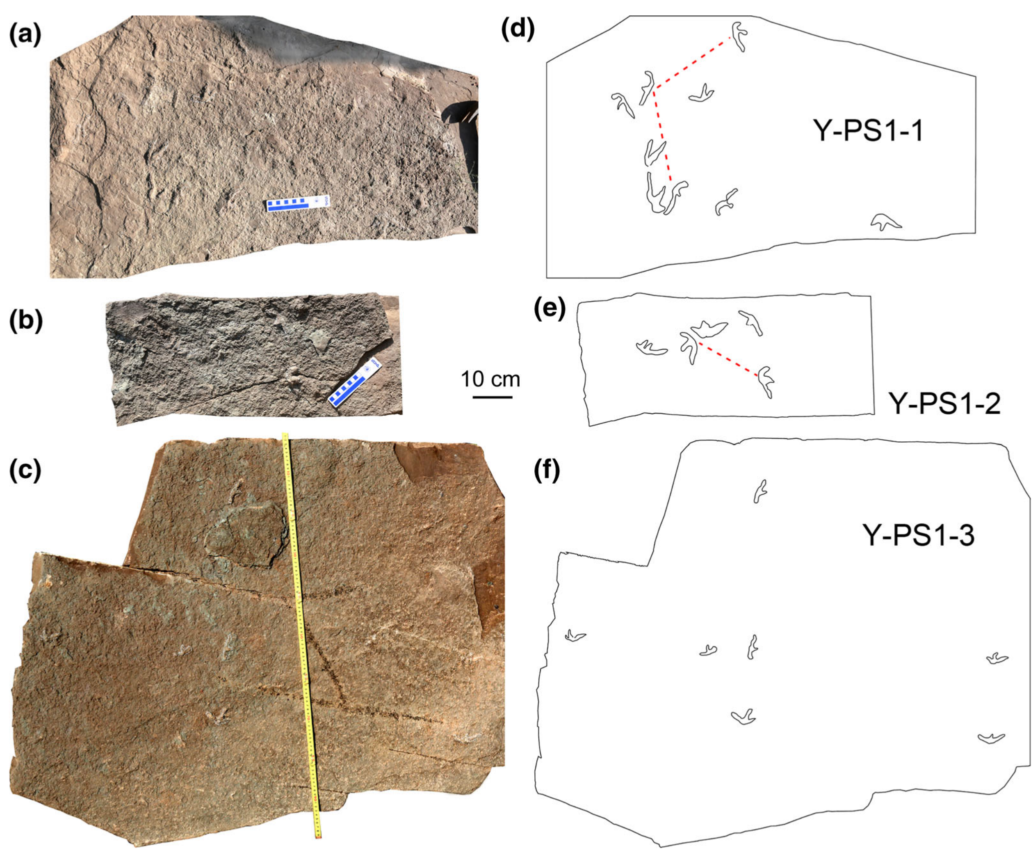

Fig. 3 Photographs (**a–c**) and interpretative outline drawing (**d–f**) of pterosaur manus prints from Yanguoxia pterosaur tracksite. Note that a possible three footprint sequence in Y-PS1-1 shows a probable trackway configuration

Table 1 Measurements (in mm) of pterosaur tracks from the Yanguoxia locality, Gansu Province, China

Specimen	ML	MW*	LDI	LDII	LDIII	I–II	II–III	I–III	l/*w*
Y-PS1-1.1	7.7	4.1	4.2	4.2	5.8	43°	62°	105°	1.9
Y-PS1-1.2	8.2	3.6	2.9	4.1	6.5	75°	40°	115°	2.3
Y-PS1-1.3	9.7	3.1	3.9	2.7	6.6	57°	64°	121°	3.1
Y-PS1-1.4	10.1	4.9	4.4	5.6	7.8	70°	45°	115°	2.1
Y-PS1-1.5	–	–	–	6.3	7.5	–	30°	–	–
Y-PS1-1.6	6.5	4.6	2.6	3.1	4.6	45°	85°	130°	1.4
Y-PS1-1.7	8.0	3.6	2.6	4.1	6.8	50°	50°	100°	2.2
Y-PS1-1.8	8.0	2.9	3.1	3.6	6.3	58°	50°	108°	2.8
Y-PS1-1.9	8.5	3.2	3.4	3.1	6.6	75°	35°	110°	2.7
Mean	8.3	3.8	3.4	4.1	6.5	59°	51°	110°	2.3
Y-PS1-2.1	8.5	3.6	3.4	3.6	7.0	27°	36°	63°	2.4
Y-PS1-2.2	8.7	4.1	3.6	4.3	6.6	68°	38°	106°	2.1
Y-PS1-2.3	9.0	4.1	3.4	3.9	7.0	59°	58°	117°	2.2
Y-PS1-2.4	8.3	2.7	3.9	–	5.4	75°	57°	132°	3.1
Y-PS1-2.5	8.2	3.2	3.6	3.7	6.3	63°	45°	108°	2.6
Mean	8.5	3.5	3.6	3.9	6.5	58°	47°	105°	2.5
Y-PS1-3.1	5.6	2.2	1.7	2.7	4.3	87°	40°	127°	2.6
Y-PS1-3.2	5.8	2.0	1.7	2.4	4.3	93°	42°	135°	2.9
Y-PS1-3.3	4.3	2.4	2.0	2.2	2.4	56°	73°	129°	1.8
Y-PS1-3.4	4.4	2.6	1.9	2.7	3.6	70°	35°	105°	1.7
Y-PS1-3.5	5.8	4.4	3.2	4.4	3.7	37°	73°	110°	1.3
Y-PS1-3.6	5.1	2.9	2.4	3.1	3.7	40°	75°	115°	1.8
Y-PS1-3.7	6.6	2.4	3.1	2.6	4.6	80°	40°	120°	2.8
Mean	5.4	2.7	2.3	2.9	3.8	66°	54°	120°	2.1
YSI-P1-LM2	11.2	4.2	2.9	6.1	9.7	87°	32°	119°	2.7

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, *I–III* angle between digits I and III, *l/w* ML/MW, – measurement not possible or not applicable

* Pterosaur tracks measured using the methods of Xing et al. [12]

4.2 Locality and horizon

Hekou Group, Early Cretaceous. Yanguoxia pterosaur tracksite, Gansu Province, China.

4.3 Description and comparison

Although none of the pterosaur track casts are well preserved, their main morphological features are identifiable. The manus prints are asymmetrical and digitigrade and consist of three digit impression casts. All three digit casts radiate from a central bulge, and the bulge of digit III is the longest. The impressions of manual digits I and II are short and oriented anterio-laterally and posterio-laterally, respectively. Unlike some other well-preserved pterosaur footprints, the Yanguoxia tracks show that the tips of digit I and most of digit II are round and blunt. A weakly curved manual digit III is oriented posteriorly. Digit III casts generally terminate sharply, but all other individual digit morphologies, including pads, are indistinct. The divarication angle between digits I and III is high (ranges between 100° and 132°).

Compared to Y-PS1-3, Y-PS1-1 and Y-PS1-2 are larger. The mean length of Y-PS1-1 and Y-PS1-2 is 8.3 and 8.5 cm, respectively, while the mean length of Y-PS1-3 is 5.4 cm. This suggests that the trackmaker of Y-PS1-3 was smaller than those of Y-PS1-1 and Y-PS1-2. Portions of the various tracks are significantly distorted. Some tracks lack a digit trace (e.g., Y-PS1-1.5), others have enlarged divarication angles (e.g., Y-PS1-1.6, 3.5), others are widened in all general proportions (e.g., Y-PS1-2.3), and others have an unusually small digit I trace (e.g., Y-PS1-3.6). These variations in the tracks are probably caused by the condition of the wet, slippery, and easily deformed substrate [42].

There is one well-preserved pterosaur trackway (YSI-P1) at Yanguoxia No.1. YSI-P1 is composed of natural molds. The manus and pes prints are paired and appear alternately, which is the typical of a *Pteraichnus* trackway (Stokes, 1957). To better identify and compare the tracks, silicon casts of YSI-P1-LM2 and LP2 were scanned with a Non-contact Grating-Type Structured Light 3D Scanning System (JiRui II, supported by Beijing JiRui Xintian Technology Co., Ltd.). The software (JiRui 3D image analysis) generated photogrammetric models of the tracks. The contour intervals equal 0.4 mm. The result suggests that the outline of YSI-P1-LM2 varies from deep to shallow (varying from blue–green–yellow–red on the scan imagery) (Fig. 5). This variation in depth is similar to the well-preserved Y-PS1 tracks, such as Y-PS1-1.4, 2.5. Furthermore, the morphology of P1-LM2, such length/width ratio, and the angle between digits I and II, II and III are close with Y-PS1-1.1–1.9. This suggests that the trackmaker foot morphology from the Yanguoxia main tracksite and new Yanguoxia pterosaur tracksite are similar to each other.

4.4 Discussion

The ichnogenus *Pteraichnus* was initially erected for a pterosaur trackway indicating quadrupedal progression from the Upper Jurassic Morrison Formation of Apache County, Arizona [43]. The ichnogenus proved controversial and was subsequently attributed by some to a crocodilian [44], although since the majority opinion is strongly in favor of a pterosaurian origin: see Xing et al. [15] for review. Subsequently, *Pteraichnus* has become by far the most prevalent and best preserved pterosaur ichnotaxon. In a recent review *Pteraichnus*, Lockley and Harris [45] five valid ichnospecies were recognized: *P. saltwashensis* [43], *P. stokesi* [16], *P. longipodus* [46], *P. parvus* [47], and *P. nipponensis* [48].

The *Pteraichnus* trackway from Yanguoxia No.1 tracksite, representing a single individual, was the first pterosaur trackway reported from China [7, 8, 49]. It was assigned to ichnospecies *Pteraichnus yanguoxiaensis,* so far identified only from this site. The description of *P. yanguoxiaensis* [7] lacks sufficient information, such as detailed measurements and comparison with other *Pteraichnus* ichnospecies [11] to adequately compare it with other ichnospecies. A re-description of this trackway is underway and will be published elsewhere.

Morphologically, the Y-PS1 tracks are extremely similar to other pterosaur tracks in the ichnogenus *Pteraichnus* and are here attributed to that ichnogenus. However, Y-PS1 tracks exhibit deformation, probably caused by variation in substrate consistencies. The small sample size also makes it difficult to discern systematic features across a significant number of tracks, so the material is referred to only as *Pteraichnus* isp.

The lack of pes tracks, predominance of, or greater depth of manus tracks at many pterosaur track sites could reflect the greater proportion of body weight (relative to foot surface area) born by the pterosaur forelimbs. Thus, the high number of relatively deep manus tracks, compared to the total absence of pes traces, on the sandstones containing the Y-PS1 tracks, is quite typical of many pterosaur track assemblages [16, 17]. However, this manus-emphasis trait may also depend on substrate consistency. For example, in specimens of *Pteraichnus* isp. from the Wenxiyuan tracksite, Shandong Province, the pes impressions are as deep or deeper than the manus impressions.

Differing from the manus-only pterosaur trackway described by Lockley et al. [16] and Meijide and Fuentes [47], which consist, respectively, of seven and three regular-distributed manus traces, the direction of the tracks at the Yanguoxia pterosaur tracksite are generally irregularly distributed. Nevertheless, most tracks from samples Y-PS1-2 and Y-PS1-3 are oriented in one or two similar directions, perhaps indicating the remnants of once more regular trackway configurations. Three manus tracks from sample Y-PS1-1.3, 1.9, and 1.7 comprise a possible trackway. The random distribution of the deep tracks could perhaps indicate that the pterosaurs were semi-floating and making irregular contact with bottom of a non-marine shallow-water environment. However, we consider this unlikely, given the remnants of typical walking trackway configurations. The association of the Y-PS1-2 tracks with

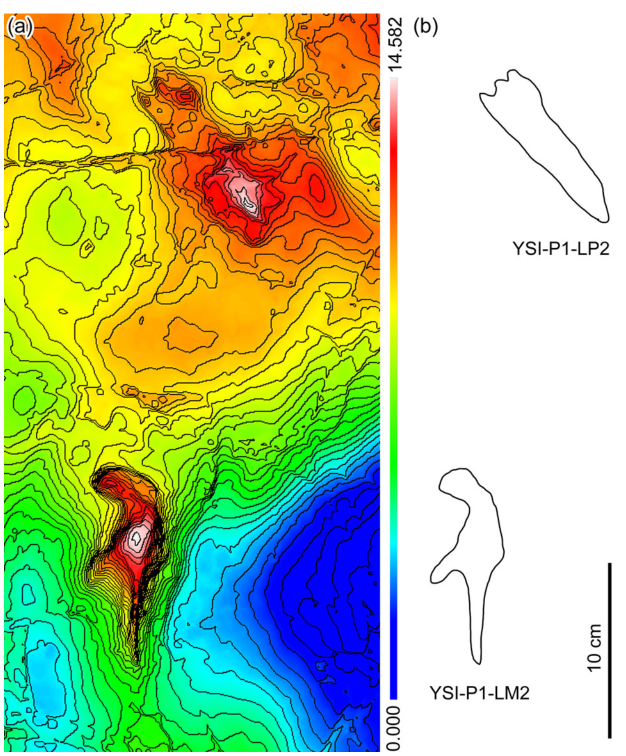

Fig. 5 Computerized photogrammetry (**a**) with 0.4 mm contour lines and the sketches (**b**) of a pterosaur track (YSI-P1-LM2, LP2) from the Hekou Group near Yongjing, Gansu Province. Color banding reflects topography (blue-green = highest, red-white = lowest)

abundant invertebrate ichnofossils (*P. tubularis*) (Fig. 2d) raises the possibility that the pterosaurs were feeding on the invertebrate trackmakers. There are many sites where pterosaur tracks occur with invertebrate traces: e.g., [16, 50] and Lockley and Wright [51] reported such associations in the late Jurassic of the western USA and García-Ramos et al. [52] reported pterosaur footprints associated with *Lockeia* at the Tazones tracksite, in Asturias (northern Spain). However, there is no feeding trace that has been observed on these pterosaur tracks surface, probably due to the preservation or the special feeding way (such as filter-feeding of ctenochasmatids [1]).

The swimming skills of pterosaurs have long been a topic of speculation. The highly pneumatic skeletons [53] of the pterosaurs suggest that they would easily float high in open water. Manus-only tracks associated with partial pes tracks and associated claw marks also suggest that some pterosaurs were capable of paddling with their hindlimbs [51, 52]. Hone and Henderson [54] employed digital models to imitate the swimming strokes of pterosaurs, and their results suggest that many pterosaurs did not regularly rest on the surface of the water and, if immersed, would need to take off rapidly.

It is possible that buoyant or semi-floating pterosaur trackmakers touched the substrate with their forelimbs, while their shorter hindlimbs floated and perhaps paddled in the water above. This would require deliberately lowering the wrist to the substrate, below the level reached by the feet, and thus, as noted below, seems like an improbable interpretation. Much track evidence suggests that the reverse was typically the case: i.e., swim track assemblages usually show only the traces of hind footprints, mostly with associated elongate drag or scratch marks [55]. In such cases, this indicates water depths were roughly equal to the length of the pterosaurs' legs. Given that it is known that pterosaur manus tracks are often deeper, more common and thus more easily preserved than pes tracks, in non-swim track assemblages, it is most parsimonious to infer that the irregular to random distribution of many of the manus tracks at the Yangouxia pterosaur tracksite are most simply explained by variable preservation. Pterosaur tracks are typically associated with shorelines and shallow water and are often represented by quite high-density assemblages with variable combinations of manus and pes tracks. Thus, while we cannot discount the possibility that some manus tracks are associated with swimming trackmakers, this cannot be proven, and it is more parsimonious to infer that the irregular distribution patterns are the result of variable preservation.

4.5 Trackmaker

The Early Cretaceous was the height of pterosaur radiation. Pterodactyloids predominated in the Jehol Biota, but coexisted with anurognathid "rhamphorhynchoids" [56, 57] and "transitional" darwinopterids (wukongopterids) [4, 58]. The Y-PS1 trackmaker was therefore most likely a small to medium-sized pterodactyloid. Pedal digit V is plesiomorphically present in non-pterodactyloids and is absent in all Yanguoxia tracks; however, a non-pterodactyloid track maker cannot be ruled out, because the impression of pedal digit V is rarely impressed clearly and unambiguously [59].

Dsungaripterids were probably widely distributed throughout the Junggar Basin of Xinjiang [5, 60] and western Mongolia [58]. The skull morphology of *Dsungaripterus* indicates a diet of shallow-water hard-shelled animals [58]. The Early Cretaceous *Huanhepterus* [6] was discovered about 400 km east of the Yanguoxia pterosaur tracksite. *Huanhepterus* is assigned to the ctenochasmatids and has a wingspan of approximately 2.5 m. Like other ctenochasmatids, *Huanhepterus* may have used its tightly packed, slender teeth to filter feed for invertebrates and algae in water [1]. Both of these pterosaurs are candidates to have fed on the abundant Yanguoxia invertebrate trackmakers (Fig. 6).

Fig. 6 Life reconstruction of pterosaurs wander and forage through shallow water at the edge of a lake in Cretaceous Gansu, China based on Yanguoxia pterosaur tracks. Illustration by Dr. Mark Witton

5 Conclusions

The Yangouxia pterosaur tracksite yields a non-specific assemblage of pterosaur tracks attributed to the ichnogenus *Pteraichnus*. All tracks represent the manus and are preserved as natural casts associated with local influx of sand into a mud-dominated lacustrine succession. The interpretation of the assemblage is ambiguous because, with the exception of one sequence of three consecutive manus tracks indicating a walking pattern the distribution of tracks is more or less random, indicating either variable, suboptimal preservation or the possibility that some tracks were made by individuals that were swimming or floating. This latter interpretation for some tracks can only be inferred, not proven. The association of the tracks with invertebrate traces suggests that the pterosaurs may have been feeding.

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Conflict of interest The authors declare that they have no conflict of interest.

References

1. Wellnhofer P (1991) The illustrated encyclopedia of Pterosaurs. Salamander Books, London
2. Barrett PM, Butler RJ, Edwards NP et al (2008) Pterosaur distribution in time and space: an atlas. Zittel B 28:61–107
3. Lü JC, Ji S, Yuan C et al (2006) Pterosaurs from China. Geological Publishing House, Beijing
4. Wang XL, Jiang SX, Meng X (2010) Recent progress in the study of pterosaurs from China. Bull Chin Acad Sci 24:86–88
5. Young CC (1964) On a new Pterosaurian from Sinkiang, China. Vertebr Palasiat 8:221–255
6. Dong ZM (1982) On a new Pterosauria (*Huanhepterus quingyangensis* gen.et. sp.nov.) from Ordos, China. Vertebr Palasiat 20:115–121
7. Peng BX, Du YS, Li DQ et al (2004) The first discovery of the Early Cretaceous pterosaur track and its significance in Yanguoxia, Yongjing County, Gansu Province. J Chin Univ Geosci (Earth Sci) 29:21–24
8. Zhang JP, Li DQ, Li M et al (2006) Diverse dinosaur-, pterosaur-, and bird-track assemblages from the Hakou Formation, Lower Cretaceous of Gansu Province, northwest China. Cretac Res 27:44–55
9. Lü JC, Chen RJ, Azuma Y et al (2010) New pterosaur tracks from the early Late Cretaceous of Dongyang City, Zhejiang Province, China. Acta Geosci Sin 31:46–48
10. Chen ZJ, Lü JC, Zhu YX et al (2013) Pterosaur tracks from the early Late Cretaceous of Dongyang City, Zhejiang Province, China. Geol Bull China 32:693–698
11. Xing LD, Harris JD, Gierlinski GD et al (2012) Early Cretaceous pterosaur tracks from a “buried” dinosaur tracksite in Shandong Province, China. Palaeoworld 21:50–58
12. Xing LD, Lockley MG, Piñuela L et al (2013) Pterosaur trackways from the Lower Cretaceous Jiaguan Formation (Barremian-Albian) of Qijiang, Southwest China. Palaeogeogr Palaeoclimatol Palaeoecol 392:177–185
13. Xing LD, Lockley MG, Klein H et al (2013) Dinosaur, bird and pterosaur footprints from the Lower Cretaceous of Wuerhe asphaltite area, Xinjiang, China, with notes on overlapping track relationships. Palaeoworld 22:42–51
14. He Q, Xing LD, Zhang JP et al (2013) New Early Cretaceous pterosaur-bird track assemblage from Xinjiang, China—palaeoethology and palaeoenvironment. Acta Geol Sin-Engl Ed 87:1477–1485
15. Xing LD, Lockley MG, Marty D et al (2015) Re-description of the partially collapsed Early Cretaceous Zhaojue dinosaur tracksite (Sichuan Province, China) by using previously registered video coverage. Cretac Res 52:138–152
16. Lockley MG, Logue TJ, Moratalla JJ et al (1995) The fossil trackway *Pteraichnus* is pterosaurian, not crocodilian: implications for the global distribution of pterosaur tracks. Ichnos 4:7–20
17. Lockley MG, Rainforth EC (2002) The tracks record of Mesozoic birds and pterosaurs. In: Chiappe LM, Witmer LM (eds) Mesozoic birds. Above the heads of dinosaurs. University California Press, California, pp 405–418
18. Calvo JO, Lockley MG (2001) The first pterosaur tracks from Gondwana. Cretec Res 22:585–590
19. Gansu Provincial Bureau of Geology and Mineral Resources (1997) Stratigraphy (Lithostratic) of Gansu Province. China University of Geosciences Press, Wuhan, p 314 (in Chinese)
20. Chen J (2013) Sedimentary characteristics and paleogeography of the Hekou Group in Lanzhou-Minhe Basin in the Early Cretaceous. Master Thesis, China University of Geosciences, Beijing, pp 1–73
21. Chen J, Liu YQ, Kuang HW et al (2013) Sedimentary characteristics and their basin analysis significance of the Lower Cretaceous Hekou Group in Zhongpu area of Lanzhou-Minhe Basin, Gansu Province. J Palaeogeogr 15:155–168
22. Tang YH, Dai S, Huang YB et al (2008) The early Cretaceous tectonic uplift of Qilian Mountains: evidence from the sedimentary facies and susceptibility of rocks of the Hekou group, Lanzhou-Minhe basin. Earth Sci Front 15:261–271
23. Zhang HF, Lin QX, Zhang ZY et al (2003) Study on the sedimentary sequence and sedimentary facies of the Early Cretaceous Hekou Group in Lanzhou-Minhe Basin. Geol Sci Technol Inf 22:21–26
24. Zhou XG, Li DQ, Peng C (2005) Analysis of paleoenvironment and fossil formation based on Yanguoxia dinosaur tracks from Yongjing County, Gansu Province. Gansu Sci Technol 21:114–117
25. Hitchcock E (1858) Ichnology of New England a report on the sandstone of the Connecticut valley especially its footprints. White, Boston
26. Bromley R, Asgaard U (1979) Triassic freshwater ichnocoenoses from Carlsberg Fjord, East Greenland. Palaeogeogr Palaeoclimatol Palaeoecol 28:39–80
27. Hall J (1847) Containing descriptions of the organic remains of the lower division of the New York System. Van Benthuysen, Albany
28. de Gibert JM, Fregenal-Martínez MA, Buatois LA et al (2000) Trace fossils and their palaeoecological significance in Lower Cretaceous lacustrine conservation deposits, El Montsec, Spain. Palaeogeogr Palaeoclimatol Palaeoecol 156:89–101
29. Walter H, Hofmann U (2001) Lebensspuren (Ichnia) ausdem Rotliegend der Döhlen-Senke (Sachsen). Freiberger Forschungshefte C 492:121–158

30. Melchor RN, Bedatou E, de Valais S et al (2006) Lithofacies distribution of invertebrate and vertebrate trace-fossil assemblages in an Early Mesozoic ephemeral fluvio-lacustrine system from Argentina: Implications for the Scoyenia ichnofacies. Palaeogeogr Palaeoclimatol Palaeoecol 239:253–285
31. Ekdale AA, Bromley RG, Pemberton SG (1984) Ichnology: the use of trace fossils in sedimentology and stratigraphy. SEPM Short Course Notes 15:1–317
32. White CD (1929) Flora of the Hermit Shale, Grand Canyon, Arizona. Carnegie Inst Wash Publ 405:1–221
33. Smith JJ, Hasiotis ST, Kraus MJ et al (2008) Relationship of floodplain ichnocoenoses to paleopedology, paleohydrology, and paleoclimate in the Willwood Formation, Wyoming, during the Paleocene-Eocene thermal maximum. Palaios 23:683–699
34. Yang SP, Zhang JP, Yang MF (2004) Trace fossils of China. Science Press, Beijing
35. Buatois LA, Mángano MG (1993) Trace fossils from a Carboniferous turbiditic lake: implications for the recognition of additional nonmarine ichnofacies. Ichnos 2:237–258
36. Buatois LA, Mángano MG (1995) The paleoenvironmental and paleoecological significance of the lacustrine Mermia Ichnofacies: an archetypical subaqueous nonmarine trace fossil assemblage. Ichnos 4:151–161
37. Netto RG, Balistieri PRMN, Lavina ELC et al (2009) Ichnological signatures of shallow freshwater lakes in the glacial Itararé Group (Mafra Formation, Upper Carboniferous–Lower Permian of Paraná Basin, S Brazil). Palaeogeogr Palaeoclimatol Palaeoecol 272:240–255
38. Melchor RN, Bellosi E, Genise JF (2003) Invertebrate and vertebrate trace fossils from a lacustrine delta: the Los Rastros Formation, Ischigualasto Provincial Park, San Juan, Argentina. Publ Esp Asoc Palaeontol Argent 9:17–33
39. Buatois LA, Mángano MG (2007) Invertebrate ichnology of continental freshwater environments. In: Miller W III (ed) Trace fossils concepts, problems, prospects. Elsevier, Amsterdam, pp 285–323
40. Bai ZK, Lü XX, Liu XP et al (2012) Trace fossils from lower Cambrian Wusongger Formation in Xiaoerbulake outcrop, Kalpin Area, Xinjiang. Acta Geol Sin-Engl Ed 86:313–319
41. Jin H, Zhang J, Ma SY (2013) Trace fossils and sedimentary environment of the upper Triassic Xujiahe Formation in Sichuan Basin. Lithol Res 25:24–28
42. Xing LD, Klein H, Lockley MG et al (2014) *Changpeipus* (theropod) tracks from the Middle Jurassic of the Turpan Basin, Xinjiang, Northwest China: new discoveries, ichnotaxonomy, preservation and paleoecology. Vert PalAs 52:233–259
43. Stokes WL (1957) Pterodactyl tracks from the Morrison Formation. J Paleontol 31:952–954
44. Padian K, Olsen PE (1984) The fossil trackway Pteraichnis: not pterosaurian but crocodilian. J Paleoantol 58:178–184
45. Lockley MG, Harris JD (2015) Pterosaur tracks and tracksites: Pteraichnidae. In: Martill D, Unwin D, Loveridge R (eds) The Pterosauria. Cambridge University Press, Cambridge, ISBN: 9780521518956
46. Fuentes VC, Meijide CM, Meijide FF et al (2004) *Pteraichnus longipodus* nov. Ichnosp. In Oncala Mountain (Soria, Spain). Stvdia Geol Salmant 40:103–114
47. Meijide CM, Fuentes VC (2001) Huellas de pterosaurios en el Weald de Soria (España). Actas I Jornadas Internacionales sobre paleontología de dinosaurios y su entorno. Salas de los Infantes, pp 397–406
48. Lee YN, Azuma Y, Lee HJ et al (2010) The first pterosaur trackways from Japan. Cretac Res 31:263–273
49. Li DQ, Azuma Y, Fujita M et al (2006) A preliminary reporto n two new vertebrate tracks sites including dinosaurs from the early Cretaceous Hekou Group, Gansu Province, China. J Paleont Soc Korea 22:29–49
50. Lockley MG, Mitchell L, Odier G (2007) Small theropod track assemblages from Middle Jurassic eolianites of eastern Utah: paleoecological insights from dune facies in a transgressive sequence. Ichnos 14:132–143
51. Lockley MG, Wright JL (2003) Pterosaur swim tracks and other ichnological evidence of behavior and ecology. In: Buffetaut E, Mazin JM, (eds) Evolution and paleobiology of pterosaurs. Geol Soc Lond Spec Publ 217:297–313
52. García-Ramos JC, Pinuela L, Lires J et al (2000) Icnitas de reptiles voladores (pterosaurios) con impressiones de la piel en el Jurassic Superior de Asturias (N. de Espafia). In: Diez JB, Balbino AC (eds) I Congresso Iberico de Paleontologia XVI Jornadas de la Sociedad Española de Paleontologia, Evora (Portugal) 12–14 Outubro, pp 87
53. Claessens LPAM, ÓConnor PM, Unwin DM et al (2009) Respiratory evolution facilitated the origin of Pterosaur flight and aerial gigantism. PLoS One 4:e4497
54. Hone DWE, Henderson DM (2014) The posture of floating pterosaurs: Ecological implications for inhabiting marine and freshwater habitats. Palaeogeogr Palaeoclimatol Palaeoecol 394:89–98
55. Lockley MG, Cart K, Martin J et al (2014) A bonanza of new tetrapod tracksites from the Cretaceous Dakota Group, western Colorado: implications for paleoecology. N M Mus Nat Hist Sci Bull 62:393–409
56. Ji SA, Ji Q (1998) A new fossil pterosaur (Rhamphorhynchoidea) from Liaoning. Jiangsu Geol 22:199–206
57. Hone DWE, Lü J (2010) A new specimen of Dendrorhyncoides (Pterosauria: Anurognathidae) with a long tail and the evolution of the pterosaurian tail. Acta Geosci Sin 31:1082–1089
58. Lü JC, Azuma Y, Dong ZM (2009) New material of dsungaripterid pterosaurs (Pterosauria: Pterodactyloidea) from western Mongolia and its palaeoecological implications. Geol Mag 146:690–700
59. Lockley MG, Harris JD, Mitchell L (2008) A global overview of pterosaur ichnology: tracksite distribution in space and time. Zittel B 28:187–198
60. Young CC (1973) Reports of Paleontological Expedition to Sinkiang (II): Pterosaurian Fauna from Wuerho. Sinkiang, Mem Inst Vertebr Paleontol Paleoanthropol Acad Sin