A new pterosaur tracksite from the Lower Cretaceous of Wuerho, Junggar Basin, China: inferring the first putative pterosaur trackmaker

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ABSTRACT

We report the discovery of 114 small pterosaur footprints preserved in a greyish-green fine sandstone slab comprising 57 manus imprints and 57 pes imprints. Due to the chaotic distribution of footprints, the trackways are difficult to recognize. The pes imprints are sub-triangular and enlongate, the metatarsal part is roughly subequal to the digital part. The manus imprints are asymmetrical, longer than wide, and the lengths of digits I–III gradually increase. According to the diagnostic features of the Wuerho small pterosaur tracks, the present set was classified as *Pteraichnus* and is different from the nine reported valid ichnospecies of *Pteraichnus*. We therefore propose a new ichnospecies, *Pteraichnus wuerhoensis* isp. nov. The description is based on the anatomical characteristics (lengths of digits I–IV, length of digital part, length of metatarsal part) extracted from the pes imprints and comparisons with the pes bone fossils of *Noripterus complicidens*. We infer that the footprints were probably left by *N. complicidens* and the total width of the wings was presumably 2–2.3 m. In addition, the high density (365 per square meter) and varied sizes of the Wuerho small pterosaur tracks suggest that many pterosaurs of different ages lived in Huangyangquan Reservoir tracksite 1 area. Thus the trackmakers may have had gregarious behavior.

Subjects Animal Behavior, Biodiversity, Evolutionary Studies, Paleontology, Zoology
Keywords Pterosaur tracks, *Pteraichnus wuerhoensis* isp. nov., Lower Cretaceous, Junggar Basin, Wuerho, Xinjiang

INTRODUCTION

The study of purported pterosaur footprints began in the 1860s, when Oppel (1862) reported simple straight locomotion traces from the Late Jurassic Solenhofen Limestone in Germany and argued that the tracks were attributable to the pterosaur *Rhamphorhynchus*. However, these traces were later convincingly demonstrated to be the tracks of limulids (Caster, 1941; Malz, 1964). Stokes (1957) reported pterosaur tracks and trackway from the Upper Jurassic Morrison Formation in Apache, Arizona, USA, and named them

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Pteraichnus saltwashensis. However, Padian (1983a, 1983b), and Padian & Olsen (1984) argued that *Pteraichnus* had been made by a small crocodilian. They showed some similarities between the footprints of small crocodilian and *Pteraichnus* trackways. Due to the scarcity of specimens at that time, their reinterpretation was widely accepted. However, with the discovery of a large number of new obvious *Pteraichnus* or *Pteraichnus*-like tracksites in the mid-1990s (Logue, 1994; Lockley et al., 1995; Lockley & Hunt, 1995; Mazin et al., 1995), manus imprints only include the traces of digits I–III (Mazin et al., 1995), and most studies acknowledge that *Pteraichnus* and *Pteraichnus*-like tracks were pterosaurian (Lockley et al., 1995; Unwin, 1996; Mazin et al., 2003). The first convincing non-pterodactyloid pterosaur footprints were reported from the Upper Jurassic Cazals Formation in the pterosaur Beach, Crayssac, France; these were characterized by being pentadactyl (with a well-preserved digit V), with plantigrade to digitigrade pes imprints and tridactyl digitigrade manus imprints with digits anteriorly oriented (Mazin & Pouech, 2020). To date, three pterosaur ichnofamilies, five pterosaur ichnogenera, 15 pterosaur ichnospecies and more than 19 *Pteraichnus* isp., cf. *Pteraichnus*, *Pteraichnus*-like tracks have been reported from at least 77 pterosaur tracksites in 13 countries (Lockley, Harris & Mitchell, 2008; Fiorillo et al., 2009, 2015; Mazin & Padian, 2009; Lee et al., 2010; Hornung & Reich, 2013; Li, 2015; Xing et al., 2016a, 2016b; Ha et al., 2018; Elgh, Pieńkowski & Niedźwiedzki, 2019). The first pterosaur footprints from China were reported by Peng et al. (2004), who named them *P. yanguoxiaensis*. Additional tracksites of pterosaur footprints in China have been discovered, but the preservation conditions have been poor, and the quantities relatively small. There are eight pterosaur tracksites that have been reported in China and all the pterosaur footprints belong to the genus *Pteraichnus* (Li, 2015; Xing et al., 2016a, 2016b). The age of the pterosaur footprints in China is concentrated in the Early Cretaceous and only the pterosaur footprints discovered in Zhejiang and Guangdong provinces are from the Late Cretaceous (Li, 2015; Xing et al., 2016a, 2016b).

The paleontological research in Wuerho region began in the 1960s. In 1963, Jingming Wei of the paleontological Division, Institute of Science, Bureau of Petroleum of Xinjiang, collected a batch of vertebrate fossils in Wuerho in the northwestern Junggar Basin and sent the fossils to the IVPP. Subsequently, Young (1964) identified the fossils as a kind of pterosaur fossils and named them as *Dsungaripterus weii*, which is the earliest named pterosaur fossil in China. Subsequently, a Xinjiang paleontology expedition team was organized by the IVPP in 1964 to conduct further investigations and fossil excavations in the Wuerho region. In addition to collecting abundant pterosaur fossils, turtle, crocodyliform, plesiosaur, and a variety of dinosaur fossils were also discovered, demonstrating that the Wuerho region was a new location abundant in Early Cretaceous vertebrate fossils. This vertebrate group was named the Wuerho Pterosaur Fauna (Young, 1973). Later, when some researchers studied the sedimentary characteristics of the Tugulu group in the Wuerho region, they found fossils of *Psittacosaurus xinjiangensis* (Brinkman et al., 2001), and this enriched the abundance and diversity of the Wuerho Pterosaur Fauna. Due to the relative fragmentation of the fossils, the subsequent research on the Wuerho Pterosaur Fauna mainly focused on the re-study and complemental characters of pterosaurs, dinosaurs and turtles (Norman, Dodson & Osmólska, 1990;

Dong, 1992; *Sun et al., 1992*; *Sues, 1997*; *Lucas, 2002*; *Rauhut & Xu, 2005*; *Danilov & Parham, 2007*; *Lü et al., 2009*; *Li & Ji, 2010*; *Hone, Jiang & Xu, 2018*; *Xu et al., 2018*; *Chen et al., 2020*).

The second large-scale investigation of the Wuerho area began in 2006. In order to compare the Mesozoic vertebrate faunas between the Turpan-Hami Basin and the Junggar Basin, the Hami scientific expedition team (IVPP) has conducted scientific investigations for more than ten years in the Hami and Wuerho regions. In addition to the discovery of a large number of pterosaur and dinosaur fossils in the Wuerho region, a high diversity of vertebrate footprints has also been found (*Li, Jiang & Wang, 2020*). These include pterosaur, dinosaur, bird and turtle tracks. *Li, Jiang & Wang (2020)* reported theropod footprints in Huangyangquan Reservoir tracksite that are the largest footprints of *Asianopodus*. During this period, some researchers also reported footprints in Moguicheng Dinosaur and Bizarre Stone Museum specimens, including pterosaur, bird, and dinosaur footprints (*He et al., 2013*; *Xing et al., 2013a*, *2013b*, *2014*). Among the reported three pterosaur footprints were described by *Xing et al. (2013a)* and *He et al. (2013)* as belonging to medium to large pterosaur footprints; they were classified as *Pteraichus* isp. *He et al. (2013)* reported a manus-pes set found in the southeastern margin of Huangyangquan Reservoir. The imprints were dated to the Early Cretaceous, but the specific horizon is unknown. *Xing et al. (2013a)* reported a single manus imprint in the Wuerho asphaltite tracksite located about 15 km to the east of Huangyangquan Reservoir. Although the specific horizon is also unknown, it is stratigraphically higher than tracksite reported by *He et al. (2013)* (*Xing et al., 2013a*). The newly-discovered Wuerho small pterosaur tracks described in this paper were located in the valley on the northwestern side of Huangyangquan Reservoir, a new tracksite that we named Huangyangquan Reservoir tracksite 1. We have no evidence with which to judge whether the newly-discovered footprint layer is the same layer described by *He et al. (2013)* (because there is no field section photo in the latter paper), but it is not the same layer reported by *Xing et al. (2013a)* (lower than the asphaltite footprint layer).

The Wuerho region has abundant pterosaur footprints, and this article focuses on the newly- discovered small pterosaur tracks. We conducted specific research on the detailed morphological features, the forward orientations of each pterosaur footprint, and the features of local pterosaur pes bone fossils to infer the probable trackmaker and its possible behavior.

MATERIALS AND METHODS

IVPP V 26281.2, which is a greyish green sandstone block (125 cm × 25 cm) with 114 natural casts (convex hyporelief) of small pterosaur tracks was collected from Huangyangquan Reservoir tracksite 1, Wuerho region, northwestern Junggar Basin, Xinjiang, China. The photographs of the overall block and parts of the block were taken, and we then use the CorelDRAW to draw the outlines of the footprints. According to the recent standard protocol for documenting fossil ichnological data proposed by *Falkingham et al. (2018)*, we used photogrammetry and Agisoft PhotoScan Professional to establish three-dimensional models. The 3D Photographic-model and associated data have been uploaded to the MorphoSource (ark:/87602/m4/346640). Length of pes imprint (Lp), width of pes imprint (Wp), length of manus imprint (Lm), width of manus imprint (Wm), length/width (L/W), length of digits I–III or I–IV (LD), divarication angles between digits (DA), length of digital part in pes imprint (D), length of metatarsal part in pes imprint (Me), and forward orientation of each footprint (FO) were measured according to the standards of *Pascual-Arribas & Hernández-Medrano (2012)* and *Hernández-Medrano, Pascual-Arribas & Pérez-Lorente (2017)*. Statistical analysis was performed using Grapher 12 and IBM SPSS Statistics 24.

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RESULTS

Geological setting and stratigraphic sequence

The Wuerho region is located in the northwestern Junggar Basin that belongs to Karamay City, Xinjiang Uygur Autonomous Region, China and is about 100 km away from the urban area of Karamay city. The exposed beds in the Wuerho region are mainly Cretaceous lacustrine sediments (*Dong, 1973*) that belong to the Tugulu Group (Lower Cretaceous). The Tugulu Group is divided into three Formations from the bottom to top, the Hutubihe Formation, the Shengjinkou Formation, and the Lianmuqin Formation (*Zhao, 1980*). The Wuerho region lacks the Qingshuihe Formation. The lithology of the Hutubihe Formation is thick or medium-thick greyish-green fine sandstone interbedded with red-brown, light-red mudstone or mudstone lenses and the bottom is medium-thick chartreuse breccia. The fine sandstone also has pillow calcic nodules (*Dong, 1973*; *Zhao, 1980*). The lithology of the Shengjinkou Formation is thin or thick greyish-green sandstone interbedded with greyish-yellow, greyish-green mudstone or mudstone lenses. In the middle and upper parts, a large number of calcic nodules (varying in size) are developed. At the top, the main signing bed of white tuffaceous sandstone (approximately 1.5 m) is well developed (*Dong, 1973*; *Zhao, 1980*). The lithology of Lianmuqin Formation is thin or thick greyish-green sandstone interbedded with thin red-brown or light-red mudstone. At the top, a large number of ferruginous nodules are developed in the sandstone (*Dong, 1973*; *Zhao, 1980*).

The site of Wuerho small pterosaur tracks is located at the west of Wuerho region. The stratigraphic section of the tracksite is divided into five beds and is 28.5 m thick (Fig.1). The stratigraphic sequence is as follows (from top to bottom).

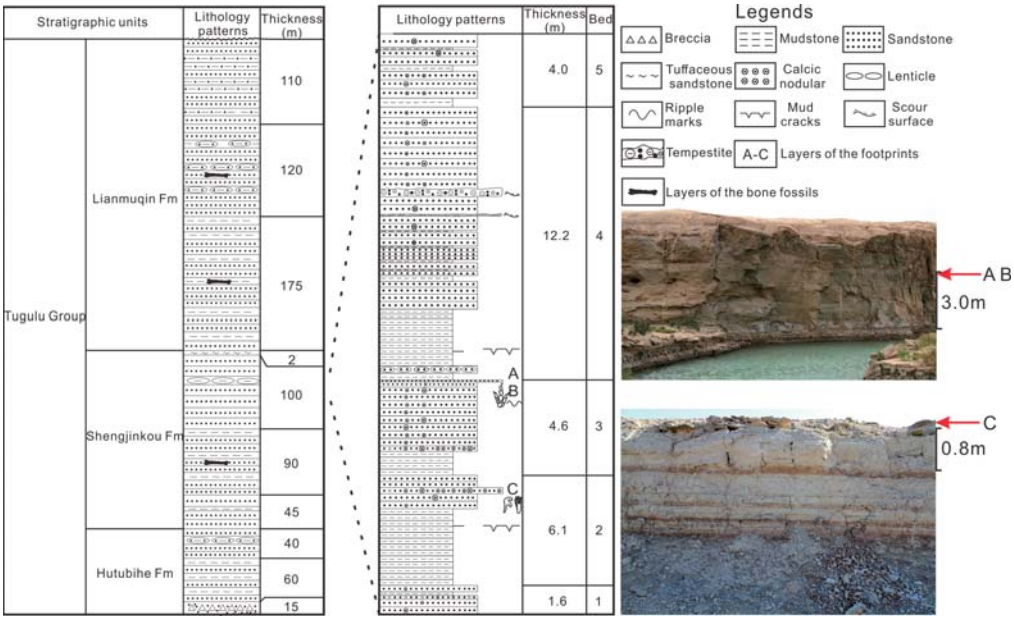

Figure 1 The comprehensive column of Huangyangquan Reservoir tracksite 1 in the Wuerho region. (A–C) represent the layers of the footprints. Full-size DOI: 10.7717/peerj.11361/fig-1

The fifth bed, which is composed of the lower red mudstone and the upper variegated fine sandstone (interbedded with red mudstone, gray mudstone and fine sandstone) has a thickness of 4.0 m and the sandstone is rich in calcic nodules.

The fourth bed, which is composed of lower mudstone and upper greyish fine sandstone, has a thickness of 12.2 m. The mudstone is composed of lower red mudstone and upper greyish mudstone. The red mudstone develops mud cracks structure and the sandstone is interbedded by two layers of tempestite and multiple layers of variegated mudstone. The sandstone also contains abundant spherical and beading calcic nodules varying in size.

The third bed, which consists of greyish mudstone (with red mudstone) in the lower part and greyish-white fine sandstone in the upper part, has a thickness of 4.6 m. The bottom of the sandstone is a greyish-white calcareous fine sandstone layer (parts of the region are coarse sandstone) with a thickness of about 40 cm rich in variously shaped calcic nodules (spherical, dendritic and beading nodules). The top of the sandstone is greyish-green fine sandstone with a thickness of about 6 cm that is rich in *Asianopodus* footprints, invertebrate traces and symmetrical ripples (Fig. 1, footprint layers of A and B) (*Li, Jiang & Wang, 2020*).

The second bed, which is composed of lower mudstone and upper greyish fine sandstone, has a thickness of 6.1 m. The mudstone consists of lower greyish mudstone and upper variegated mudstone (mainly red, but also mixed with gray mudstone or sandstone). The sandstone is rich in calcic nodules of different sizes. The middle part of the sandstone contains a greyish-white calcareous fine sandstone layer (parts of the region are gravel-bearing sandstone) with a thickness of 40 cm that is abundant with calcic nodules of various sizes (mainly spherical and beading nodules) and small pterosaur footprints (Fig.1, footprint layer C).

The first bed, which is composed of greyish fine sandstone, has a thickness of 1.6 m. The sandstone is rich in calcic nodules of different sizes and the middle part is interbedded with a calcareous gravel-bearing sandstone (roughly 20 cm).

According to the petrological characteristics of the stratigraphic section in Huangyangquan Reservoir tracksite 1 and detailed field surveys, all of the footprint layers are located below the main signing layer of white tuffaceous sandstone. The overall lithology of the section is greyish-green fine sandstone interbedded with greyish mudstone or variegated mudstone and the sandstone is rich in calcic nodules of different sizes. These features are consistent with the lithological characteristics of the sixth bed described by *Dong (1973)* and *Zhao (1980)*. Therefore, the horizon of the footprint layers belongs to the Shengjinkou Formation (Fig. 1).

Systematic Ichnology

Order: Pterosauria *Kaup, 1834*

Suborder: Pterodactyloidea *Plieninger, 1901*

Ichnofamily: Pteraichnidea *Lockley et al., 1995*

Ichonogenus: *Pteraichnus* *Stokes, 1957*

Quadruped, elongate, asymmetrical, digitigrade, tridactyl manus imprint; digit I anterior or anterolateral (generally with a claw mark); digit II anterolateral to posterolateral; digit III posterior, digits increasing respectively in length, rounded impression in the medial margin of the well-preserved manus imprint (impression of the fourth metacarpo-phalangeal joint); elongate, subtriangular, plantigrade, tetradactyl pes imprint; middle two digits are longer than the lateral digits; manus imprints on the same axis or more laterally to the pes imprints and the pes imprints anterior to the manus imprints; manus imprints generally as or more deeply impressed than pes imprints.

Type ichnospecies: *Pteraichnus wuerhoensis* isp. nov.

Derivation of the name: from the locality where the small pterosaur tracks were discovered. The Wuerho region is also the fossil site of Wuerho Pterosaur Fauna.

Materials: One slab with 114 natural casts (Fig. 2) on a greyish fine sandstone cataloged as IVPP V 26281.2. The tracks are now stored at IVPP, Beijing, China.

Holotype: manus imprint of 45MR, pes imprint of 58PR. The footprints are now stored at IVPP, Beijing, China.

Paratype: well preserved manus imprints of 49ML, 104 ML and pes imprints of 7PR and 29PR. The footprints are now stored at IVPP, Beijing, China.

Referred specimens: all other footprints (98 footprints, 1ML-6MR, 8P-28P, 30PR-44ML, 46MR-57ML, 59P-103P,105ML-114P) except the holotype and paratype.

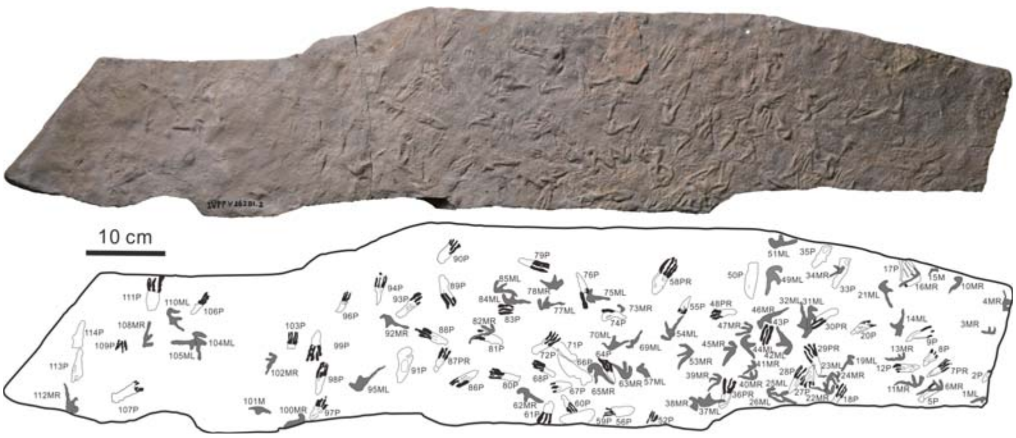

Figure 2 **The photograph and outline drawings of *Pteraichnus wuerhoensis* isp. nov. (Photo credit: Wei Gao).** Abbreviations: M = Manus imprint; P = Pes imprint; ML = Left imprint of manus; MR = Right imprint of manus; PR = Right imprint of pes. Full-size DOI: 10.7717/peerj.11361/fig-2

Locality and Horizon: Shengjinkou Formation (Fig. 1), Tugulu Group, Lower Cretaceous. Huangyangquan Reservoir tracksite 1, Wuerho District, Karamay City, Xinjiang, China.

Diagnosis: Quadrupedal tracks, no tail trace; manus imprints are strongly asymmetrical, small-sized, roughly 3.40 cm in length, and 1.59 cm in width, tridactyl, longer than wide, with an average Lm/Wm ratio of 2.14. Digit I is the shortest (roughly 1.31 cm), generally laterally or posterolaterally oriented straight; digit II is intermediate in length (roughly 1.90 cm), posterolaterally oriented, The crescent-shaped digit III is the longest (roughly 3.15 cm), posteriorly oriented with a distal curvature toward the medial side. The average divarication of digit II and digit III is approximately 1.74 times the average divarication between digit I and digit II (33.5°). The pes imprints are elongate and fully plantigrade, tetradactyl, sub-triangular shaped, small-sized (roughly 4.02 cm in length, 1.46 cm in width), with an average Lp/Wp ratio of 2.75. The digit I imprint is the shortest and the other three digits are roughly subequal in length (average length of digits I–IV are 1.66–2.16–2.06–1.97 cm). The metatarsal part is narrow and elongate, roughly subequal to the digital part. The interdigital angle between digits I and IV is about 14.6°.

Description:

The footprints (57 manus imprints and 57 pes imprints) are located on one slab (125 cm × 25 cm), with symmetric, functionally tetradactyl, fully plantigrade pes impressions and asymmetric, tridactyl, digitigrade manus impressions (Fig. 2).

The distribution of the tracks is disordered. In order to find the trackways as far as possible, we computed statistics on the forward orientations of the 114 tracks (Fig. 3, assuming that the orientation perpendicular to the long axis of the slab is 0°) We found that some of the tracks that may have been on the same trackway were uncertain (Fig. 3). For example, according to the forward orientations and sizes of the Wuerho small pterosaur tracks, the following footprints may well be on the same trackway (the same sizes and forward orientations). The tracks of 94P, 98P, and 103P may be on the same trackway (Fig. 3A).

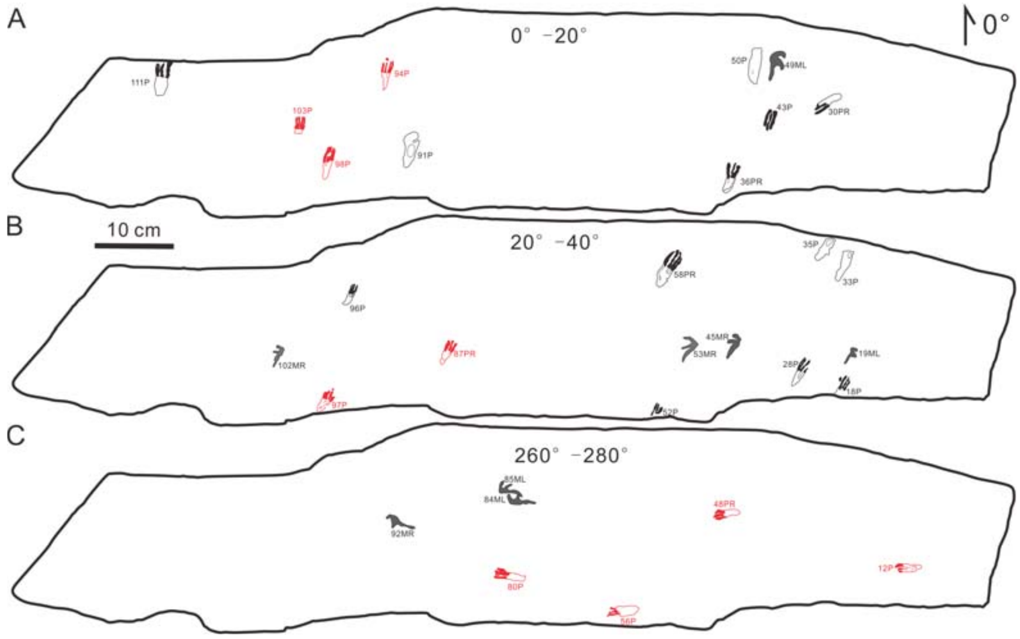

Figure 3 Some possible but uncertain trackways of the same size and forward orientation footprints (the red color possibly represents the same trackway). (A) The tracks in forward orientations of 0°–20°, (B) the tracks in forward orientations of 20°–40°, (C) The tracks in forward orientations of 260°–280°. Abbreviations: P = Pes imprint; ML = Left imprint of manus; MR = Right imprint of manus; PR = Right imprint of pes. Full-size DOI: 10.7717/peerj.11361/fig-3

Similarly, the 97P and 87PR could also be potentially on the same trackway (Fig. 3B). The tracks 12P, 48PR, 56P and 80P may also belong to the same trackway (the same sizes and orientations). However, there are no manus imprints or other tracks that may form a consecutive trackway, so it is impossible to identify whether they are on the same trackway (Figs. 3A–3C). The footprints are very close to each other, and there are many overlapping footprints (Fig. 2). All tracks are similar in shape (Figs. 2, 4A–4H).

The pes footprints are elongate and fully plantigrade, small-sized (roughly 4.02 cm in length, 1.46 cm in width), with an average Lp/Wp ratio of 2.75 (Table 1). Most footprints are sub-triangular shaped (Figs. 4D–4F), while some are rectangular (possibly related to different preservation conditions, Fig. 2). The tracks show four functional digits and indistinct digital pads. The digit I imprint is the shortest, and the other three digits are roughly subequal in length (the medial two digits are slightly longer than digit IV; average lengths of digits I–IV are 1.66, 2.16, 2.06, and 1.97 cm, respectively). Only one footprint (7PR) retains a clear claw mark on the anterior part of digit III. The claw mark is curved laterally and gradually distended toward the distal end. The metatarsal area is narrow and elongate and is roughly subequal to the digital area (Table 1, average D/Me = 1.00). Most heel imprints are very poorly marked and slightly lighter than the digital prints. The interdigital angle between digits I and IV is about 5.4°–35.7° (Table 1, average 14.6°). There is no preservation of impressions formed by the fifth metatarsal and digit V.

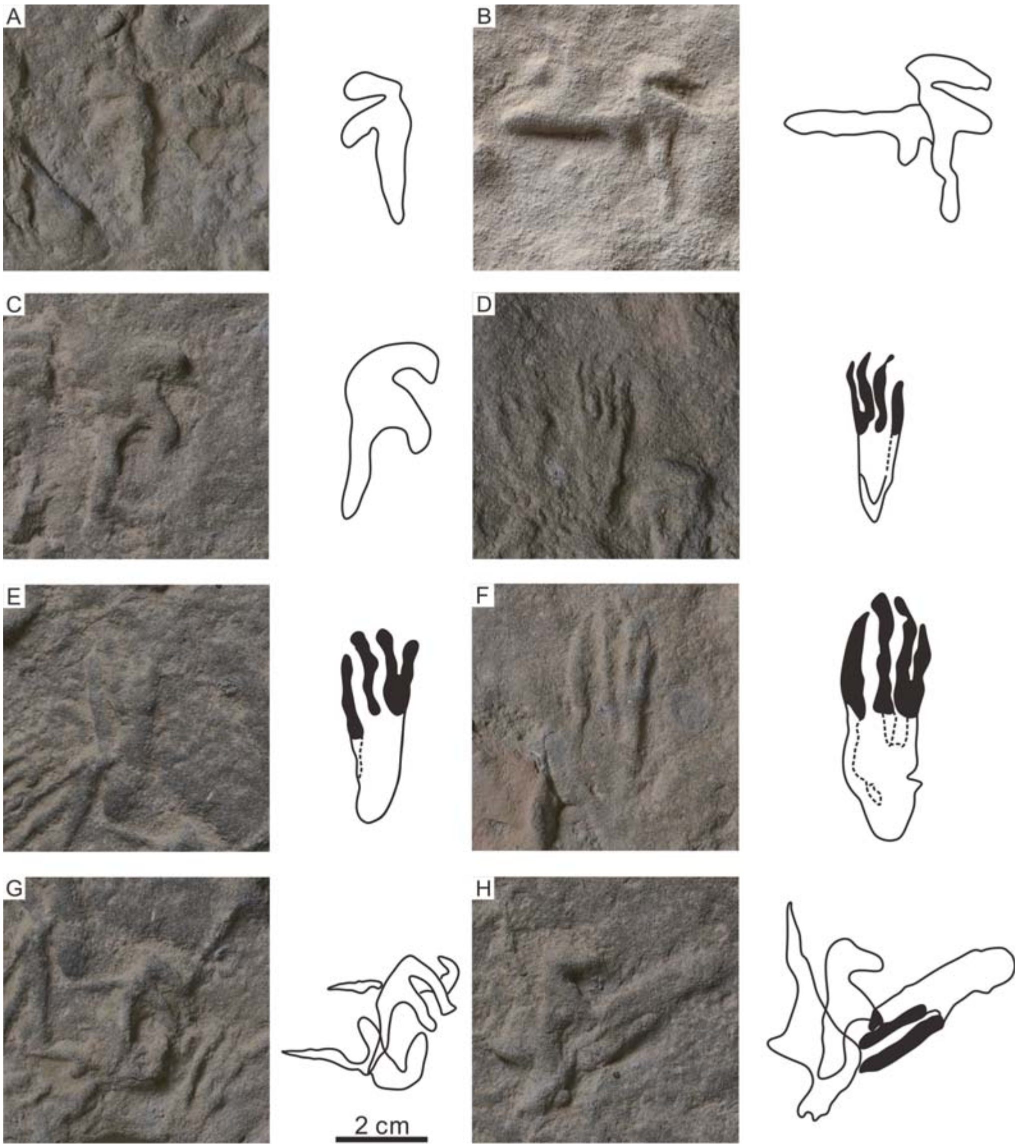

Figure 4 The photographs and outline drawings of the holotype, paratype, and overlapping pterosaur footprints of *Pteraichnus wuerhoensis* isp. nov. in Huangyangquan Reservoir tracksite 1. (A) 45MR, holotype, digit I points to lateral orientation; (B) 104ML, paratype, digit I points to posterolateral orientation; (C) 49ML, paratype, with a little curved digit I; (D)–(E) 7PR, 29PR, paratype, with the shortest digit I and subequal length of other digits; (F) 58PR, holotype, with the shortest digit I and subequal length of other digits; (G) 22MR, 23ML, 24MR, overstepping imprints of three manus imprints; (H) 30PR, 31ML, 32ML, overstepping imprints of two manus imprints and one pes imprint. Abbreviations: P = Pes imprint; ML = Left imprint of manus; MR = Right imprint of manus; PR = Right imprint of pes.
Full-size DOI: 10.7717/peerj.11361/fig-4

The strongly asymmetrical manus imprints (Figs. 2, 4A–4C) are also small-sized (Table 1, roughly 3.40 cm in length, 1.59 cm in width), tridactyl, longer than wide, with an average Lm/Wm ratio of 2.14 (Table 1). The manus imprints have three digital impressions but lack digit pad impressions and claw marks. In general, digit I is the shortest (roughly 1.31 cm), generally laterally or posterolaterally oriented (of 42 well-preserved manus imprints, 38 are lateral or posterolateral, Table 1) and nearly straight, while some digit I impressions of the manus imprints are slightly curved (Fig. 4C). Digit II is intermediate in length (roughly 1.90 cm), 1.45 times the size of digit I, posterolaterally oriented and nearly straight. The crescent-shaped digit III is the longest (roughly 3.15 cm), 2.4 times the size of digit I, posteriorly oriented with a distal curvature toward the medial side. The total divarication of digit I–III impressions ranges from 38.1° to 138.8° (Table 1, average 91.8°). Average divarication of digit II and digit III is 58.3°, which is approximately 1.74 times the average divarication between digit I and digit II (33.5°). There are no metacarpophalangeal joint or digit IV impressions.

DISCUSSION

Comparison with the pterosaur footprints

More than 77 pterosaur tracksites have been reported from East Asia, North America, South America, Europe and North Africa (13 countries) (*Lockley, Harris & Mitchell, 2008*; *Fiorillo et al., 2009*, *2015*; *Lee et al., 2010*; *Hornung & Reich, 2013*; *Li, 2015*; *Xing et al., 2016a*, *2016b*; *Ha et al., 2018*). Since the first confirmed pterosaur footprints were discovered along the southwestern coastline of South Korea (*Lockley et al., 1997*), more than 30 pterosaur tracksites have been reported from the Early Cretaceous to the Late Cretaceous throughout Asia (Korea, China and Japan) (*Lockley, Harris & Mitchell, 2008*; *Lee et al., 2010*; *Li, 2015*; *Xing et al., 2016a*, *2016b*; *Ha et al., 2018*). To date, we recognize three pterosaur ichnofamilies, five pterosaur ichnogenera and 15 pterosaur ichnospecies as valid (*Lockley et al., 1995*; *Li, 2015*; *Lockley, Harris & Mitchell, 2008*; *Sánchez-Hernández, Przewieslik & Benton, 2009*; *Masrour et al., 2018*; *Mazin & Pouech, 2020*). These are Ramphichnidae (*Ramphichnus crayssacensis*, *R. pereiraensis*, and *R. lafaurii*) (*Mazin & Pouech, 2020*), Agadirichnidae (*Agadirichnus Elegans and Haenamichnus uhangriensis*) (*Hwang et al., 2002*; *Masrour et al., 2018*), and Pteraichnidae (*Purbeckopus pentadactylus*, *Pteraichnus stokesi*, *P. saltwashensis*, *P. parvus*, *P. longipodus*, *P. koreanensis*, *P. palacieisaenzi*, *P. dongyangensis*, *P. yanguoxiaensis*, and *P. nipponensis*) (*Stokes, 1957*; *Lockley et al., 1995*; *Wright et al., 1997*; *Peng et al., 2004*; *Sánchez-Hernández, Przewieslik & Benton, 2009*; *Lee et al., 2010*; *Chen et al., 2013*; *Pascual-Arribas et al., 2014*).

The Ichnofamily Rhamphichnidae (*Mazin & Pouech, 2020*) comprising non-pterodactyloid pterosaur trackway reported from the Upper Jurassic (Cazals Formation) in the Pterosaur Beach, Crayssac, France, is characterized by pentadactyl (with well-preserved digit V) plantigrade to digitigrade pes imprints and tridactyl digitigrade manus imprints with digits anteriorly orientated (Figs. 5A–5C). The manus trackway is wider than, or equal to the pes trackway. There is no tail trail. Several features of Rhamphichnidae are unparalleled and are quite different from the Wuerho small pterosaur tracks and almost all of the reported pterosaur footprints (i.e., elongate and fully plantigrade pes imprints, strongly asymmetrical manus imprints, and the manus trackway being wider than the pes trackway).

Ichnofamily Agadirichnidae (*Masrour et al., 2018*), was defined by large-sized footprints (pes imprints ranging from 77 to 170 mm for *Agadirichnus* and reaching 340 mm for

Table 1 The measurement parameters of *Pteraichnus wuerhoensis* isp. nov. and pes bone fossils of *N. complicidens*. Abbreviations: M = Manus imprint; P = Pes imprint; ML = Left imprint of manus; MR = Right imprint of manus; PR = Right imprint of pes; FL = Footprint length; FW = Footprint width; L/W = Length/Width; LD = Lengths of digits I–III or I–IV; DA = Divarication angels between digits; D = Length of digital part in pes imprint; Me = Length of metatarsal part in pes imprint; FO = Forward orientation of each footprint.

Footprints	FL	FW	L/W	LD	DA			D(cm)	Me(cm)	D/Me	FO	M
				I–II–III/I–II–III–IV	I–II	II–III	I–III/I–IV					Digit I position
1ML	2.30	0.85	2.71	0.45?–0.90–2.00	48.6°	65.0°	113.6°				69.1°	laterally
2P	2.0?										42.0°	
3MR	1.90	1.00	1.90	1.10–1.40–1.80	24.3°	79.8°	104.1°				96.7°	laterally
4MR	2.85	1.24	2.30	1.04–1.71–2.80	6.5°	80.8°	87.3°				174.8°	laterally
5P	3.06?	1.34?	2.28?				19.5°	0.88?	2.18?	0.40?	40.8°	
6MR	3.83	1.66	2.31	1.30–1.74–3.68	27.2°	58.5°	85.7°				73.5°	laterally
7PR	3.87	1.28	3.02	1.22–1.74–1.58–1.60			17.6°	1.90	1.97	0.96	64.5°	
8P	2.62?	1.35	1.94?				22.2°	0.56?	2.06	0.27?	42.9°	
9P	4.03?	1.43	2.82?				15.4°	1.74?	2.29	0.76?	72.0°	
10MR	2.72?	1.15?	2.66?			47.7°					47.9°	
11MR	3.77	1.86	2.03	1.33–1.81–3.32	42.0°	56.6°	98.6°				102.8°	anterolaterally
12P	3.56?	1.61	2.21?				11.8°	1.04?	2.52	0.41?	266.5°	
13MR	2.68	1.07	2.50	0.87–1.01–2.56	31.7°	56.7°	88.4°				85.7°	laterally
14ML		1.86?				69.1°					193.4°	
15M												
16MR	3.30	1.30?	2.54?	1.17–1.19?–3.28	23.3°	60.1°	83.4°				58.1°	laterally
17P		2.71?					37.0°?				155.1°	
18P	3.12?	0.99	3.15?				2.7°?	2.07			33.1°	
19ML	2.58	1.21	2.13	0.83–1.39–2.44	23.1°	81.7°	104.8°				31.3°	laterally
20P	3.49	1.22	2.86				19.9°	1.75?	1.74?	1.01?	59.6°	
21ML	3.66	1.53	2.39	1.38–1.95–3.41	50.5°	45.6°	96.1°				338.5°	laterally
22MR	3.19	1.41	2.26	1.17–1.91–3.12	44.6°	41.5°	86.1°				106.4°	laterally
23ML	2.87	1.75	1.64	1.62–1.78–2.83	5.7°	50.0°	55.7°				19.2°?	posterolaterally
24MR	2.95	0.90?	3.28?	0.87–?–2.75			102.9°				90.6°	laterally
25ML						47.2°					289.7°	
26ML	2.95	1.41	2.09	1.21–1.95–2.89	18.8°	33.8°	52.6°				298.1°?	posterolaterally
27P	3.35	1.89	1.77				35.7°	0.99?	2.36	0.42?	198.7°	
28P	4.31	1.25	3.45				16.2°	2.12	2.19	0.97	31.3°	
29PR	4.39	1.58	2.78	1.67–2.00–1.91–1.95			16.7°	2.25	2.14	1.05	334.8°	
30PR	4.28	1.27	3.37	?–?–?–2.19			5.4°	2.18	2.10	1.04	240.4°	
31ML	3.24	1.29	2.51	1.17–1.97–3.17	19.9°	59.9°	79.8°				9.2°	posterolaterally
32ML	5.00	2.04	2.45	1.61–2.08–4.09	73.7°	65.1°	138.8°				164.9°	anterolaterally
33P	4.49	1.38	3.25				14.4°				24.9°	
34MR	2.44?	1.43?	1.71?		123.7°?	29.2°	152.9°?				61.0°	
35P	3.74	1.52	2.46				6.6°				38.4°	
36PR	4.25	1.82	2.34	?–?–?–1.94			8.3°	2.14	2.11	1.01	14.9°	
37ML	3.71	1.79	2.07	1.24–2.19–3.45	45.9°	68.3°	114.2°				263.4°	
38MR				1.17–?–?								

(Continued)

Table 1 (continued)

Footprints	FL	FW	L/W	LD	DA			D(cm)	Me(cm)	D/Me	FO	M
				I–II–III/I–II–III–IV	I–II	II–III	I–III/I–IV					Digit I position
39MR	2.75	1.55	1.77	1.27–1.72–2.70	13.9°	47.1°	61.0°				42.3°?	laterally
40MR	2.59	1.48	1.75	1.26–1.18–2.40	21.1°	66.3°	87.4°				102.9°	laterally
41MR	2.31	1.12	2.06	1.07–1.13–2.02	48.8°	66.5°	115.3°				58.5°	laterally
42ML	4.00	1.90	2.11	1.46–2.18–3.40	53.4°	65.2°	118.6°				151.9°	laterally
43P											18.0°	
44ML	3.26	1.79	1.82	1.64–2.06–2.93	27.7°	59.3°	87.0°				320.6°	laterally
45MR	3.51	1.60	2.19	1.30–1.88–3.19	42.5°	53.2°	95.7°				31.1°	laterally
46MR	4.71	1.40	3.36	1.12–1.88–4.54	36.4°	77.1°	113.5°				244.6°	laterally
47MR	2.50	1.67	1.50	1.30–1.54–2.49	12.6°	25.5°	38.1°				75.0°?	laterally
48PR	3.64	1.41	2.58	?–?–1.31–1.40			13.9°	1.79	1.85	0.97	261.5°	
49ML	4.25	2.17	1.96	1.55–2.26–3.82	39.6°	44.6°	84.2°				10.6°	laterally
50P	4.88	1.60	3.05				9.4°				7.9°	
51ML	3.82	1.84	2.08	1.54–2.00–3.24	39.5°	74.7°	114.2°				255.8°	anterolaterally
52P											28.0°	
53MR	3.35	2.01	1.67	1.98–2.29–3.17	53.6°	34.2°	87.8°				39.2°	laterally
54ML	4.26	2.06	2.07	1.40–2.55–3.68	49.6°	49.2°	98.8°				215.5°	laterally
55P	2.68	1.15	2.33				14.7°	0.92?	1.76	0.52?	209.9°	
56P	4.30	1.41	3.05				7.8°	1.74?	2.56	0.68?	261.6°	
57ML												laterally
58PR	5.66	1.93	2.93	2.10–2.73–2.70–2.37			9.4°	2.82	2.84	0.99	32.0°	
59P	4.77	1.87	2.55				13.2°				76.5°	
60P	3.59	1.61	2.23				19.1°	1.81	1.78	1.02	144.8°	
61P	3.31	1.86	1.78				17.3°	1.62?	1.69	0.96?	199.0°	
62MR	3.71	1.68	2.21	1.02–1.92–3.40	38.7°	62.3°	101.0°				300.1°	laterally
63MR	3.20	1.79	1.79	1.74–2.40–3.11	9.8°	44.9°	54.7°				126.8°?	posterolaterally
64P	3.90	1.32	2.95				13.7°	2.40?	1.50	1.60?	336.9°	
65MR	4.09	2.03	2.01	1.50–2.76–3.89	37.9°	49.5°	87.4°				309.5°	laterally
66P	5.71	1.79	3.19				21.8°				128.1°	
67P	2.73?	1.50	1.82?				24.3°	0.98?	1.78	0.55?	257.5°	
68P	3.46	1.12	3.09				11.1°	1.71	1.75	0.98	297.0°	
69ML	3.00	0.79?	3.80?	0.67?–0.98?–2.73			131.8°				214.7°	
70ML	3.48	1.63	2.13	1.39–2.07–2.92	53.6°	63.5°	117.1°				242.7°	
71P	3.52?	1.39	2.53?				13.2°				308.4°	
72P	4.19	1.61	2.60				10.1°	2.10	2.09	1.00	52.3°	
73MR												
74P	3.32	1.59	2.09				20.4°	1.66?	1.66	1.00?	278.0°?	
75ML						78.5°					277.2°?	
76P	4.97	1.41	3.52				17.4°	2.31?	2.66	1.15?	158.3°	
77ML	3.62	1.56	2.32	1.52–2.12–3.35	31.0°	57.0°	88.0°				259.5°	laterally
78MR	2.87?	1.93?	1.49?	1.58?–2.06–2.56?	47.1°	65.2°	112.3°				117.1°	

Table 1 (continued)

Footprints	FL	FW	L/W	LD	DA			D(cm)	Me(cm)	D/Me	FO	M
				I–II–III/I–II–III–IV	I–II	II–III	I–III/I–IV					Digit I position
79P	4.23	1.32	3.20				17.1°	2.38?	1.85	1.29?	107.9°	
80P	4.06	1.43	2.84				11.1°	2.01	2.05	0.98	279.8°	
81P	3.59?	1.33	2.70?				14.3°	1.33?	2.26	0.59?	291.9°	
82MR	3.78	1.89	2.00	1.05–1.93–3.64	42.4°	48.4°	90.8°				68.9°	laterally
83P											90°	
84ML	3.83	1.32?	2.90?	1.29–1.50?–3.33	36.0°	79.3°	115.3°				268.6°	anterolaterally
85ML	3.19	1.67	1.91	1.60–1.97–3.00	32.6°	48.4°	81.0°				269.6°	laterally
86P	3.95	1.35	2.93				14.9°	2.10?	1.85	1.14?	232.3°	
87PR	3.62	1.41	2.57	?–?–?–1.50			14.2°	1.67?	1.95	0.86?	26.7°	
88P	4.05	1.30	3.12				11.3°	2.05?	2.00	1.03?	291.3°	
89P	4.15	1.55	2.68				10.5°	2.00?	2.15	0.93?	156.5°?	
90P	3.85	1.40	2.75				9.4°	1.94	1.91	1.02	42.4°	
91P	4.70	2.05	2.29				18.2°				14.0°	
92MR	4.00	1.70	2.35	0.80–1.75–3.70	31.1°	85.2°	116.3°				279°	laterally
93P	4.05	1.30	3.12				8.9°	1.50?	2.55	0.59?	52.1°	
94P	4.35	1.40	3.11				18.0°	2.20	2.15	1.02	7.2°	
95ML	5.15	1.90?	2.71?		67.6°	65.9°	133.5°				229.3°	
96P	3.00	1.20	2.50				6.2°	1.40?	1.60	0.88?	27.2°	
97P	3.40	1.40	2.43				19.4°	1.70?	1.70	1.00?	35.1°	
98P	4.15	1.30	3.19				12.9°	2.10	2.05	1.02	10.8°	
99P	3.95	1.65	2.39				22.9°	1.95	2.00	0.98	190.8°	
100MR				1.10?–?–?								laterally
101M												
102MR	2.75	1.30	2.12	1.00–1.60–2.60	10.3°	78.4°	88.7°				29.2°	laterally
103P								1.65			8.5°	
104ML	3.50	1.45	2.41	1.30–1.95–3.30	2.8°	66.2°	69.0°				355.7°	posterolaterally
105ML						87.1°					90.3°	
106P	3.30	0.95	3.47				6.5°	1.80?	1.50	1.20?	41.3°	
107P	4.00?	1.55	2.58?				8.0°				63.2°	
108MR	3.40	1.30	2.62	1.15–2.10–3.20	43.7°	34.8°	78.5°				193.0°	posterolaterally
109P											184°	
110ML	3.60	1.80	2.00	1.80–2.30–3.30	3.0°	38.1°	41.1°				315.2°	posterolaterally
111P	4.40?	2.15	2.05?				12.6°	1.90?	2.50	0.76	7.8°	
112MR	3.75	1.40	2.68	1.0–1.85–3.30	27.6°	55.4°	83.0°				165.0°	posterolaterally
113P	3.95	1.30	3.04				16.2°				188.9°	
114P	3.30	1.25	2.64				17.3°				191.9°	
Average M	3.40	1.59	2.14	1.31–1.90–3.15	33.5°	58.3°	91.8°					
P	4.02	1.46	2.75	1.66–2.16–2.06–1.97			14.6°	2.07	2.07	1.00		
Data of pes bone	5.98			1.90–2.45–2.55–2.40				2.98	3.00	0.99		

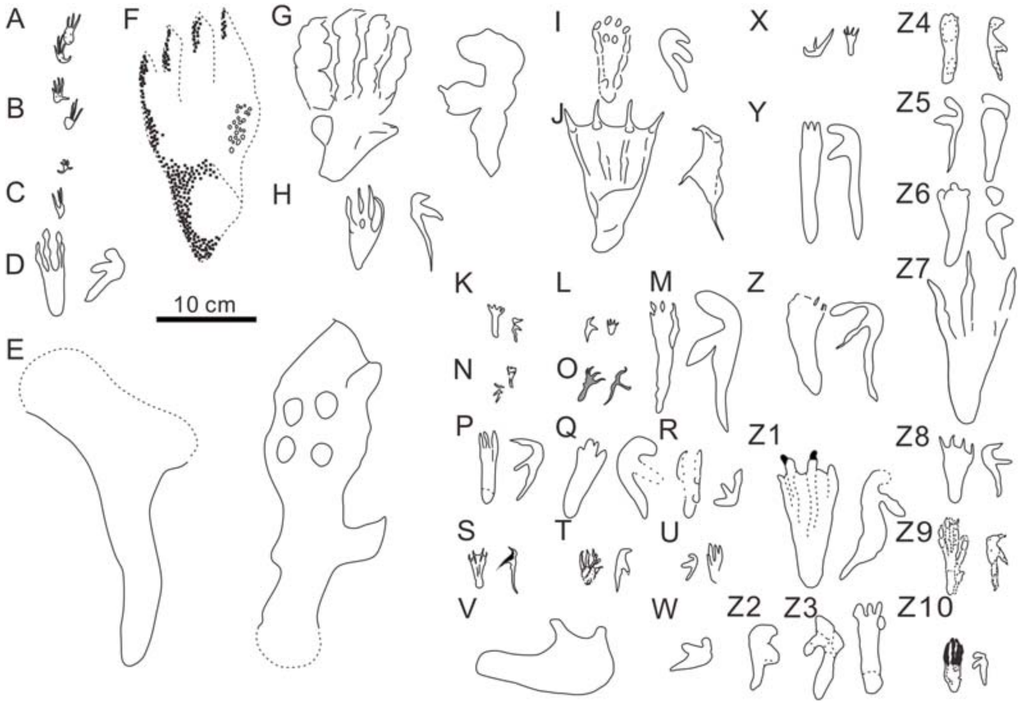

Figure 5 Comparison of reported pterosaur footprints found worldwide. (A) *Ramphichnus crayssacensis*, holotype, Lower Tithonian, Upper Jurassic, Crayssac, France (Mazin & Pouech, 2020); (B) *Ramphichnus pereiraensis*, holotype, Lower Tithonian, Upper Jurassic, Crayssac, France (Mazin & Pouech, 2020); (C) *Ramphichnus lafaurii*, holotype, Lower Tithonian, Upper Jurassic, Crayssac, France (Mazin & Pouech, 2020); (D) *Agadirichnus elegans*, holotype, Maastrichtian, Upper Cretaceous, Agadir, Morocco (Masrour et al., 2018); (E) *Haenamichnus uhangriensis*, holotype, Uhangri Formation, Upper Cretaceous, Jeollanam Province, Korea (Hwang et al., 2002); (F) *Haenamichnus gainensis*, holotype, Aptian-Albian, Upper Lower Cretaceous, Gyeongsang Province, Korea (Kim et al., 2012); (G) *Purbeckopus pentadactylus*, holotype, Lower Cretaceous, Dorset, England (Delair, 1963); (H) *Pteraichnus saltwashensis*, holotype, Morrison Formation, Late Jurassic, Arizona, America (Stokes, 1957); (I) *Pteraichnus stokesi*, holotype, Sundance Formation, Upper Jurassic, Wyoming, America (Lockley et al., 1995); (J) *Pteraichnus palacieisaenzi*, pes from the holotype, manus from the paratype, Middle Berriasian, Lower Cretaceous, Soria, Spain (Pascual-Arribas et al., 2014); (K) *Pteraichnus longipodus*, holotype, Berriasian, Lower Cretaceous, Soria Province, Spain (Fuentes-Vidarte et al., 2004); (L) *Pteraichnus parvus*, holotype, Berriasian, Lower Cretaceous, Soria Province, Spain (Meijide-Calvo, 2001); (M) *Pteraichnus yanguoxiaensis*, holotype, Lower Cretaceous, Gansu, China (Peng et al., 2004); (N) *Pteraichnus koreanensis*, holotype, Lower Cretaceous, Hadong County, South Korea (Lee et al., 2009); (O) *Pteraichnus nipponensis*, holotype, Lower Cretaceous, Fukui Prefecture, Japan (Lee et al., 2010); (P) *Pteraichnus dongyangensis*, holotype, Lower Cretaceous, Zhejiang, China (Chen et al., 2013); (Q) cf. *Pteraichnus*, Lower or Later Cretaceous, Neuquén State, Argentina (Calvo & Lockley, 2001); (R) *Pteraichnus*-like, Maastrichtian, Upper Cretaceous, Utah, America (Lockley, 1999); (S) *Pteraichnus* isp., Lower Tithonian, Upper Jurassic, Crayssac tracksite, France (Mazin et al., 2003); (T) *Pteraichnus* isp., Early Kimmeridgian, Upper Jurassic, Wierzbica, Poland (Pieńkowski & Niedźwiedzki, 2005); (U) cf. *Pteraichnus*; Upper Jurassic, Utah, America (Mickelson et al., 2004); (V) *Pteraichnus* isp., Lower Cantwell Formation, Upper Cretaceous, Alaska, America (Fiorillo et al., 2009); (W) *Pteraichnus* isp., Lower Cantwell Formation, Upper Cretaceous, Alaska, America (Fiorillo et al., 2015); (X) cf. *Pteraichnus*, Maastrichtian, Upper Cretaceous, Agadir, Morocco (Masrour et al., 2017); (Y) *Pteraichnus* isp., Aptian-Albian, Lower Cretaceous, southern coast of Korea (Kim et al., 2006); (Z) *Pteraichnus* isp., Lower Cretaceous, Ulsan, Korea (Ha et al., 2018); (Z1) *Pteraichnus* isp., Lower Cretaceous, Huangyangquan tracksite, Wuerho, Xinjiang, China (He et al., 2013); (Z2) *Pteraichnus* isp., Lower Cretaceous, Wuerho, Xinjiang, China (Xing et al., 2013a); (Z3) *Pteraichnus* isp., Lower Cretaceous, Chongqing, China (Xing et al., 2013c); (Z4) *Pteraichnus* isp., Lower Cretaceous, Jimo city, Shandong

Figure 5 (continued)
Province, China (*Xing et al., 2012*); (Z5) *Pteraichnus* isp., Lower Cretaceous, Zhaojue County, Sichuan Province, China (*Xing et al., 2015*); (Z6) *Pteraichnus* isp., Lower Cretaceous, Gulin County, Sichuan, China (*Xing et al., 2016b*); (Z7) *Pteraichnus* isp., Upper Cretaceous, Nanxiong, Guangdong, China (*Xing et al., 2016a*); (Z8) pterosaur landing tracks, Upper Jurassic, Crayssac, France (*Mazin & Padian, 2009*); (Z9) *Pteraichnus* isp., Upper Jurassic, Radom, Poland (*Elgh, Pieńkowski & Niedźwiedzki, 2019*); (Z10) *Pteraichnus wuerhoensis* isp. nov., Lower Cretaceous, Wuerho, China.
Full-size DOI: 10.7717/peerj.11361/fig-5

Haenamichnus), longer and slender tetradactyl, plantigrade pes imprints, generally with narrow and rounded pes heels and rather massive tridactyl manus imprints (*Masrour et al., 2018*; *Mazin & Pouech, 2020*). To date, there are two ichnogenera and two ichnospecies are attributed to this family: *Agadirichnus* (*Ambroggi & De Lapparent, 1954*), with the ichnospecies *A. elegans* (*Ambroggi & De Lapparent, 1954*), and *Haenamichnus* (*Hwang et al., 2002*), with the single ichnospecies *H. uhangriensis* (*Hwang et al., 2002*). *A. elegans*, was first described from Upper Cretaceous (Maastrichtian, Tagragra Formation) by *Ambroggi & De Lapparent (1954)*, but the original specimens are assumed to be lost, and this is assessed as an invalid ichnotaxon (*Sánchez-Hernández, Przewieslik & Benton, 2009*; Lockley MG, Harris JD, in press). However, *Masrour et al. (2018)* rediscovered *A. elegans* at the same tracksite, and the tracks are quite different from the small-sized pterosaur tracks in the Wuerho region in size and morphology. The pterosaur tracks from the Wuerho region are approximately half size of *A. elegans* (Table 2). The pes imprint of *A. elegans* has rounded heels and subparallel edges that are quite different from the small pterosaur tracks in the Wuerho region (Fig. 5D) (pes imprints are sub-triangular). The manus imprint of *A. elegans* has a short and rounded digit I (Fig. 5D) that is different from the well-preserved manus imprints from the Wuerho region. The digit I imprints of Wuerho small pterosaur tracks are often oriented laterally or posterolaterally so that the divarication between digits I and II is much smaller than in *A. elegans*. *H. uhangriensis* was reported from the Upper Cretaceous (Uhangri Formation) and is also quite different from the Wuerho small pterosaur footprints in morphology and size. The greatest difference between the *H. uhangriensis* and Wuerho pterosaur footprints is in size; the former is approximately nine times the size of the latter (Table 2). The length/width of *H. uhangriensis* pes imprints is 3.33, larger than the Wuerho small pterosaur tracks (2.75). The pes imprint of *H. uhangriensis* has a narrow, rounded heel and digit V impression (Fig. 5E), also different from the Wuerho small pterosaur tracks (the shape of the pes imprints is sub-triangular, and there are no digit V imprints). There is another fossil of *H. gainensis* from the Lower Cretaceous (Haman Formation) that was considered to be pterosaur footprints (Fig. 5F) (*Kim et al., 2012*), but more recent studies attributed it to bipedal crocodylomorph tracks (*Kim et al., 2020*).

Ichnofamily Pteraichnidae (*Lockley et al., 1995*) was described from a wide trackway of a quadrupedal animal with elongate, symmetrical, functional tetradactyl, plantigrade pes impressions, and an asymmetric tridactyl manus impressions. The impression of manus digit III was elongate, curved, and posteriorly directed, parallel to the trackway axis. Manus impressions often were more deeply impressed than pes impressions. The characteristics of

the Wuerho small pterosaur tracks are consistent with the main features of the Pteraichnidae. To date, there are two described ichnogenera, 10 ichnospecies and more than 19 *Pteraichnus* isp., cf. *Pteraichnus*, *Pteraichnus*-like and *Purbeckopus* cf. *pentadactylus* are attributed to this family: *Pteraichnus* (*Stokes, 1957*), with the ichnospecies *P. saltwashensis* (*Stokes, 1957*); *P. stokesi* (*Lockley et al., 1995*); *P. parvus* (*Calvo & Lockley, 2001*); *P. longipodus* (*Fuentes-Vidarte, et al., 2004*); *P. koreanensis* (*Lee et al., 2009*); *P. palacieisaenzi* (*Pascual-Arribas & Sanz-Pérez, 2000*); *P. dongyangensis* (*Chen et al., 2013*); *P. yanguoxiaensis* (*Peng et al., 2004*); *P. nipponensis* (*Lee et al., 2010*); and the ichnogenera *Purbeckopus* (*Delair, 1963*), with one ichnospecies *Purbeckopus pentadactylus* (*Delair, 1963*). *Purbeckopus* was first established by *Delair (1963)* and then was amended by *Wright et al. (1997)* and was maded by a quadrupedal animal with elongate (approximately twice as long as wide), subtriangular, symmetrical, functionally tetradactyl, plantigrade pes impressions; elongate, asymmetrical tridactyl manus impressions may also be present. The digits of the pes are sub-equal in length and are curved slightly inwards, the curvature being most pronounced in the outermost toe (digit IV). Digits II and III of the pes imprints are slightly longer than the outer digits I and IV. Manus impressions, if present, lie outside the pes impressions (Fig. 5G).
The Wuerho small pterosaur tracks differ significantly from the *Purbeckopus* tracks in size and morphology; the latter are roughly 4.65 times the size of the former (Table 2).
In addition, the pterosaur footprints from Wuerho are much more slender than those of *Purbeckopus*, and D/Me is 1.72 times as much as the Wuerho small pterosaur tracks (Table 2, Figs. 6 and 7). Ichnogenus *Pteraichnus* was first reported by *Stokes (1957)* and subsequently amended by *Lockley et al. (1995)* and *Billon-Bruyat & Mazin (2003)*.
The fossil is described as quadruped tracks with an elongate, asymmetrical, digitigrade, and tridactyl manus imprint; digit I imprint anterior or anterolateral (generally with claw mark); digit II imprint anterolateral to posterolateral (rarely with claw mark); digit III imprint posterior (exceptionally with claw mark), digital imprints increasing in length; digit IV is rarely marked and limited to the impression of the proximal part of the fourth manus digit (oriented posteromedially); a rounded impression in the medial margin of the manus imprint (impression of the fourth metacarpo-phalangeal joint); elongate, subtriangular, plantigrade, and tetradactyl pes imprint; toe II and III imprints are slightly longer than I and IV; toe I–IV imprints are clawed; manus imprints on the same axis or more laterally to the pes imprints; pes imprint anterior to the ipsilateral manus imprint; manus imprint as or more deeply impressed than pes imprint. The Wuerho small pterosaur footprints feature strongly asymmetrical, tridactyl, elongate manus imprints; digit I is the shortest and is laterally or posterolaterally oriented,; digit II is intermediate in length, longer than digit I and posterolaterally oriented; the crescent-shaped digit III is the longest and is posterolaterally oriented with a distal curvature toward the medial side and elongate, fully plantigrade, sub-triangular, tetradactyl pes imprints, with toe II and III prints longer than I and IV. Therefore, the small-sized Wuerho pterosaur tracks have similar characteristics to the features of *Pteraichnus*.

P. saltwashensis, which was the first reported pterosaur trackway, was described from the Upper Jurassic (Morrison) in Apache, Arizona, USA. The imprints are quite different

Table 2 Comparative data for the 15 reported ichnospecies and *Pteraichnus* isp. reported from Wuerho region. Abbreviations: Lp = Length of pes imprint; Wp = Width of pes imprint; Lm = Length of manus imprint; Wm = Width of manus imprint; D = Length of digital part in pes imprint; Me = Length of metatarsal part in pes imprint.

Ichnospecies	Horizon	Lp × Wp (cm)	Lm × Wm (cm)	Divarication angles (manus)		D × Me (cm)	Lp/Wp	D/Me
				I–II	II–III			
Ramphichnus crayssacensis	Cazals Fm Upper Jurassic	2.91 × 0.52	3.13 × 0.55	14.80°	22.50°	2.47 × 0.44	5.60	5.61
R. pereiraensis	Cazals Fm Upper Jurassic	2.40 × 1.73	2.40 × 0.96	6.40°	17.20°	1.71 × 0.69	1.39	2.48
R. lafaurii	Cazals Fm Upper Jurassic	1.68 × 1.45	2.17 × 0.74	7.00°	12.00°		1.16	
Purbeckopus pentadactylus	Purbeck Limestone Fm Lower Cretaceous	18.70 × 9.80	14.00 × 8.50	22.90°	79.00°	11.82 × 6.88	1.91	1.72
Agadirichnus elegans	Tagragra Formation Upper Cretaceous	9.16 × 3.13	6.21 × 3.09	64.60°	34.40°	4.67 × 4.49	2.93	1.04
Haenamichnus uhangriensis	Uhangri Formation Upper Cretaceous	35.0 × 10.50	33.00 × 11.00				3.33	
Pteraichnus saltwashensis	Morrison Fm Upper Jurassic	8.76 × 4.33	8.20 × 3.15	43.40°	48.10°	3.71 × 5.05	2.02	0.73
Pteraichnus stokesi	Sundance Fm Upper Jurassic	9.00 × 4.10	7.00 × 3.40	13.70°	31.00°	4.48 × 4.52	2.20	0.99
Pteraichnus parvus	Huérteles Allo Fm Lower Cretaceous	1.53 × 1.14	2.46 × 1.20	64.00°	58.00°	0.44 × 1.09	1.34	0.40
Pteraichnus longipodus	Huérteles Allo Fm Lower Cretaceous	3.40 × 1.74	2.45 × 1.67	47.00°	49.00°		1.95	0.22
Pteraichnus koreanensis	Hasandong Fm Lower Cretaceous	2.57 × 1.28	2.56 × 1.23	68.50°	47.60°	0.81 × 1.76	2.01	0.46
Pteraichnus palacieisaenzi	Huérteles Allo Fm Lower Cretaceous	15.34 × 11.9	13.02 × 4.85	75.90°	56.20°	8.67 × 6.67	1.29	1.30
Pteraichnus dongyangensis	Jinhua Fm Lower Cretaceous	9.00 × 3.00	6.50 × 4.00	52.00°	29.00°		3.00	
Pteraichnus nipponensis	Kitadani Fm Lower Cretaceous	1.94 × 1.05	2.01 × 0.88	83.18°	81.70°	0.47 × 1.23	1.85	0.38
Pteraichnus yanguoxiaensis	Hekou Fm Lower Cretaceous	12.30 × 3.60	12.20 × 4.80	60.70°	53.90°		3.42	
Pteraichnus isp.	Tugulu Group Lower Cretaceous		6.70 × 2.90	62.70°	56.00°			
Pteraichnus isp.	Tugulu Group Lower Cretaceous	14.00 × 6.00	12.30 × 5.20	58.00°	70.00°	6.07 × 7.93	2.33	0.77

Note:
The values obtained directly from the original papers or the outline drawings in the papers.

from the Wuerho small pterosaur tracks in size and morphology. First, *P. saltwashensis* tracks are approximately 2.18 times the size of the Wuerho pterosaur tracks, where the pes length is 87.6 mm (Fig. 5H, Table 2). Second, *P. saltwashensis* (D/Me = 0.73) has a more elongate metatarsal impression than the Wuerho small pterosaur tracks (D/Me = 1.00) (Table 2, Fig. 7). Third, the Wuerho small pterosaur pes footprints (Lp/Wp = 2.75) are much more slender than those of *P. saltwashensis* (Lp/Wp = 2.02) (Fig. 6). Fourth, the