New Early Cretaceous Pterosaur-Bird Track Assemblage from Xinjiang, China: Palaeoethology and Palaeoenvironment

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Abstract: A pterosaur-bird track assemblage from a sandstone-siltstone-mudstone sequence of the Lower Cretaceous Tugulu Group of Xinjiang comprises the first pterosaur track record from this province and the largest specimen thus far known from China. The pterosaur tracks are assigned to the ichnogenus *Pteraichnus* based on the triangular overall-shape, the four elongate digit traces and the robust manual digit trace III. Supposed trackmakers were dsungaripterid pterodactyloids whose skeletal remains are well known from the Tugulu Group. The bird tracks that occur on the same surface, are those of typical shorebirds, known from different other localities in southeast Asia. The congruence with *Koreanaornis dodsoni* described from the same stratigraphic level justifies an assignment to this ichnospecies. This is a further evidence of the co-occurrence of pterosaurs and birds in a typical lakeshore environment with possible seasonal alteration of water supply and aerial exposure indicated by wave ripples, mudcracks and repeated cycles of coarse to fine sediment. Pterosaurs and birds frequented the shoreline and may have fed also on the numerous invertebrates such as the *Scoyenia* tracemaker that left abundant burrows.

Key words: *Pteraichnus*, *Koreanaornis*, Early Cretaceous, Tugulu Group, Xinjiang

1 Introduction

Mesozoic and Cenozoic strata of the Junggar Basin of Xinjiang Uyghur Autonomous Region are well-developed and extensively exposed. Previous studies of the vertebrate paleofauna, such as the China-Canada Dinosaur Project (CCDP) (Currie and Zhao, 1993), and the recent discovery of an assemblage from the Shishugou Formation (He et al., 2013), have focused on the southern and eastern portions of the basin, while the northwestern margin has remained relatively unexplored. Vertebrate fossils are concentrated in the Upper and Grey-green layers of the Tugulu Group and include remains of pterosaurs, stegosaurs, theropods, sauropods etc. (Dong, 2001). They are sparse in the Lower Layer and comprise remains of pterosaurs, stegosaurs, and theropods (Xing et al., 2011; Xing et al., 2013). Beginning in 2002, several vertebrate tracksites (including the Huangyangquan tracksites and the Asphaltite tracksites) have been reported from the Lower Layer of the Tugulu Group in the Wuerhe (Urho) District (Xing et al., 2011) (Fig. 1). In July of 2009, AN Jianfu and XING Lida discovered the first pterosaur tracks in this unit in the northwestern border of the Junggar Basin, Xinjiang.

Institutional and location abbreviations: MGCM= Moguicheng Dinosaur and Bizarre Stone Museum, Xinjiang, China; H= Huangyangquan tracksite, Wuerhe District, Karamay City, Xinjiang, China.

2 Geological Setting

The tracksite lies on the margin of the Huangyangquan

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Fig. 1. Map of the Huangyangquan track locality (track icon), Wuerhe District, Xinjiang Uyghur Autonomous Region, China.

Reservoir, Wuerhe District, Karamay City, Xinjiang (N 46°03′06.29″, E 85°36′22.87″) (Fig. 1) in Lower Cretaceous strata of the Tugulu Group. According to the regional geological survey (Academy of Prospecting and Developing, Xinjiang Bureau of Petroleum, 1977, 1996, 1997) and the former studies (Xing et al., 2011), the Early Cretaceous age here is reliable. The Tugulu Group around Wuerhe District crops out on the northwestern margin of the Junggar basin. These are fluvial-lacustrine mudstone, shale, and fine-sandstone interlayers (Brinkman et al., 2001; Pol et al., 2004). Jiang et al. (2008) divide the Tugulu Group into four subgroups, while others (Academy of Prospecting and Developing, Xinjiang Bureau of Petroleum, 1977, 1996, 1997; Eberth et al., 2001; Li et al., 2009) divide it into three subgroups: Upper, Grey-green, and Lower Layers. The southern margin of the Junggar Basin is divided into four formations: Qingshuihe, Hutubihe, Shengjinkou, and Lianmuqin (in ascending order) (Eberth et al., 2001; Jia et al., 2009).

A stratigraphic succession measured at the seventh layer of the Lower Layers (Fig. 2) is approximately 7.12 m thick and consists of horizontal gray or reddish-gray mudstone and sandstone deposits that are each 0.37 m to 1.8m thick. These are interpreted as the results of hyperpycnal flows or seasonal changes (Houck and Lockley, 2006). The measured sequence contains at least four upward-fining sedimentary cycles from 2.9 m to 0.92 m in thickness. Each cycle consists of a lower sandstone and an upper mudstone deposit, the pattern reflecting a cyclical change from bed load deposits (sandstone) to suspension deposits (mudstone). The fine-grained red mudstone indicates periods of low sedimentation rates in a subaqueous setting, while the coarser grained and thicker gray-white sandstones reflect increased sedimentation rates in a lake environment fed by higher energy flows. Horizontal bedding and oblique bedding are visible in the deformed sandstone and mudstone interlayer. The red color of the mudstone implies long subaerial exposure and a more arid climate. The overall section shows a fining-upward trend and an increase in the extent of the lake.

The tracks reported here are preserved on the fourth sandstone deposit. This deposit contains a laminated gypsum layer approximately 3–10 mm thick. Gypsum usually occurs in isolated and closed water systems, such as seasonal lakes or lagoons, where rates of evaporation exceed precipitation. The track surface contains footprints of a pterosaur and numerous birds and non-avian dinosaur footprints, as well as exposure structures (mud cracks).

3 Systematic Ichnology

3.1 Pterosaur tracks

Pteraichnus isp.

Materials: One set of well-preserved manus and pes natural casts on a sandstone slab cataloged as MGCM H30a.m and p. The tracks are now stored at Moguicheng Dinosaur and Bizarre Stone Museum, Xinjiang, China (Figs. 3, 4, 5a and Table 1).

Locality and Horizon: Lower Layer of the Tugulu Group, Early Cretaceous. Huangyangquan tracksite, Wuerhe District, Karamay City, Xinjiang, China.

Table 1 Measurements (in cm and degrees) of pterosaur tracks from Huangyangquan tracksites

MGCM.	R/L	ML	MW	LD I	LD II	LD III	LD IV	L/W
H30a.m	L	12.3	5.2	3.3	5.2	9.7	—	2.37
H30a.p	L	14.0	6.0	4.1	7.7	8.8	3.6	2.33

Abbreviations: R/L: Right/Left; LD I: length of digit I; LD II: length of digit II; LD III: length of digit III; LD IV: length of digit IV; ML: maximum length; MW: maximum width*; L/W: Maximum length/ Maximum width (measured as distance between the tips of digits II and IV).

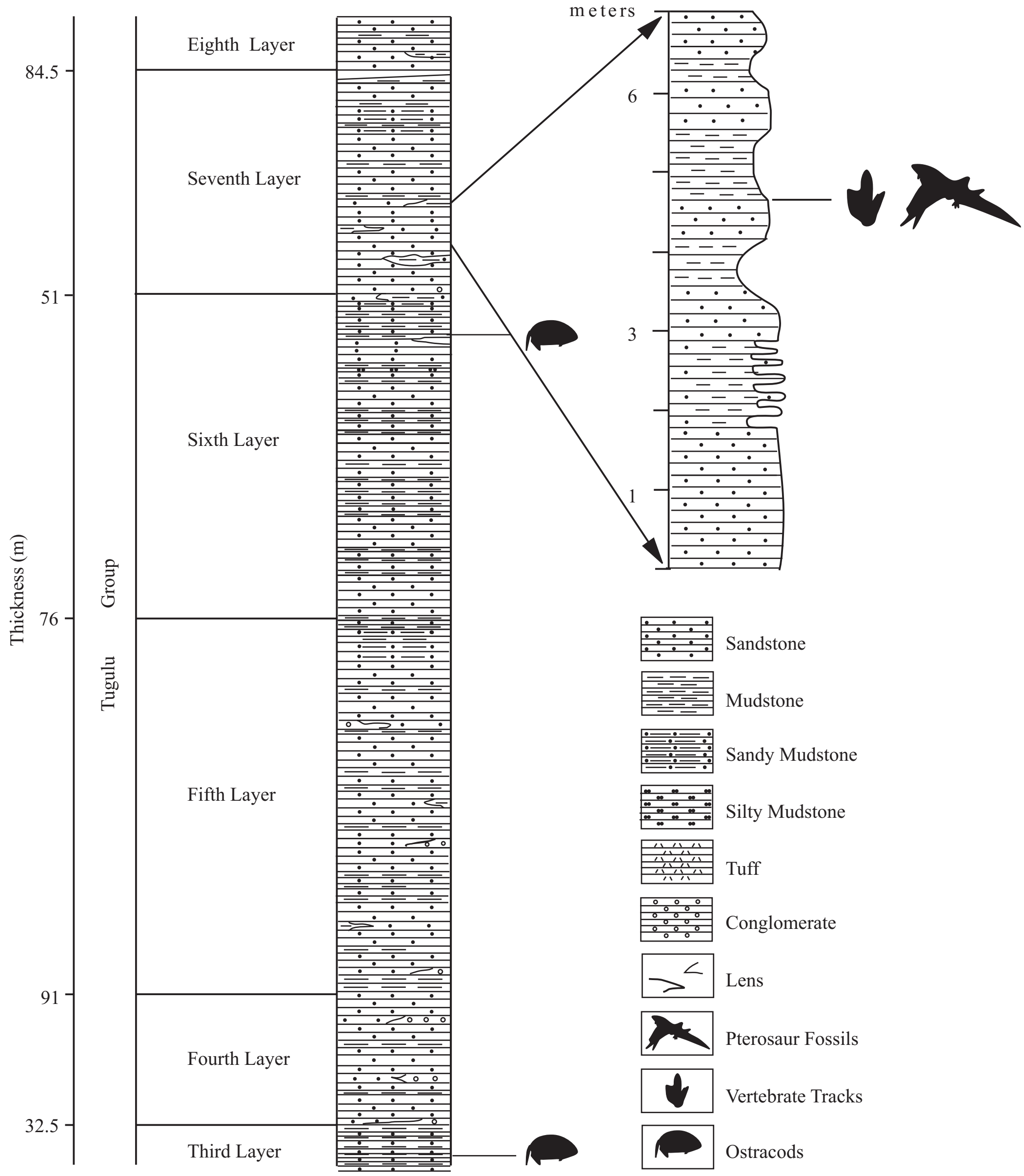

Fig. 2. Stratigraphic section of the Lower layer of the Tugulu Group at the Huangyangquan tracksite with the position of the tracks described herein (emended from Qi et al., 1995; Xing et al., 2011).

Description: The tracks consist of one left manus-pes set. The pes impression is positioned anterior to the manus impression. The strongly asymmetrical manus print (MGCM H30a.m) has three digit impressions but lacks pad impressions. Digit I is shortest, laterally oriented, and curved. Digit II is nearly straight and posterolaterally oriented. The crescent-shaped digit III is the widest and longest and oriented posterolaterally with a distal curvature toward the medial side. The distal end of digit III preserves a possible claw impression, which is absent in digit I and digit II. A few drag marks are running outward from the midline of digit III. The divarication angle of digit I and digit II is 58°, which is lower than that between digit II and digit III (70°). The total divarication in the specimen is large (128°). There is no impression of digit IV.

The pes imprint (MGCM H30p) is plantigrade with four slender digit impressions and indistinct digital pads. It is sub-triangular in overall shape. Digits are straight, II and IV slightly curved inward. Digits II and III are longest and subequal in length, I and IV are short. Claws on the distal ends of digits are distinct in digits II and III, that of digit III (9 mm) is slightly longer than that of digit II (8 mm). The divarication angle between digits I and IV is 25°. The metatarsal area is elongate showing a sub-triangular outline.

Discussion: More than 50 pterosaur tracksites have been reported from East Asia, North America, South America, Europe, and North Africa (Lockley et al., 2008). In recent years, 10 pterosaur tracksites have been reported

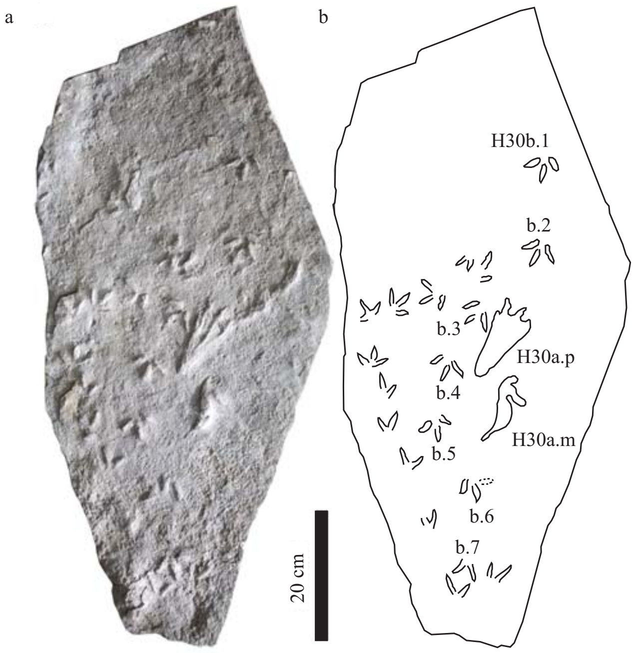

Fig. 3. Photograph (a) and outline drawing (b) of the slab with pterosaur and bird tracks from the Huangyangquan tracksite.

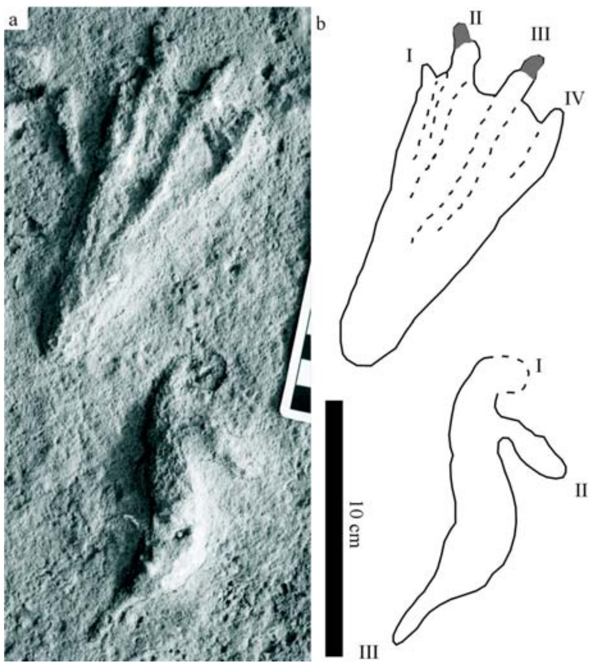

Fig. 4. Photograph (a) and outline drawing (b) of *Pteraichnus* isp. pterosaur tracks MGCM H30a.m and H30a.p from the Huangyangquan tracksite.

from various Cretaceous exposures throughout Asia (Hwang et al., 2002, Kim et al., 2006, Lee et al., 2010). We recognize three valid pterosaur ichnogenera: *Pteraichnus, Purbeckopus* and *Haenamichnus*, and we consider the ichnogenus *Agadirichnus* a *nomen nudum* (Lockley and Harris, in press). Five pterosaur tracksites are known from China: *Pteraichnus* is known from the Lower Cretaceous Hekou Formation of Gansu Province (Li et al., 2006; Zhang et al., 2006) and from the Jimo site in Shandong Province (Xing et al., 2012a); various other pterosaur tracks with limited published details are known from the Dongyang site in Zhejiang Province (Lü et al., 2010), the Qijiang District in Chongqing city (Xing et al., 2012b) and the Zhaojue site in Sichuan Province (Liu et al., 2010).

The morphology of the Wuerhe tracks is extremely similar to that of *Pteraichnus*. Stokes (1957) reported the first credible pterosaur ichnogenus *Pteraichnus* from the Upper Jurassic. *Pteraichnus* remains the most prevalent and well-represented pterosaur ichnotaxon (Lockley et al., 2008). At present, only five *Pteraichnus* ichnospecies are valid: *P. saltwashensis*, *P. stokesi*, *P. longipodus*, *P. parvus*, and *P. nipponensis* (Lockley and Harris, in press).

Morphologically, the Wuerhe pterosaur tracks are consistent with the initial diagnosis of *Pteraichnus* (Stokes, 1957) and have several traits in common with the type ichnospecies *P. saltwashensis*, from the Morrison Formation in Arizona, including slim digits, a triangle-shaped pes, and the gradually curved orientation of the manus digit prints. However, the Wuerhe tracks also show some characteristics that distinguish them from *P. saltwashensis*. The biggest difference is the size of the Wuerhe manus print, which is shorter than the pes print, whereas the opposite is true in *P. saltwashensis* (~8.2 cm and 7.6 cm length of the manus and the pes, respectively). The manual digit III of the Wuerhe tracks is robust relative to the other digits, whereas manual digit III in *P. saltwashensis* is slender. Finally, the four digits of the Wuerhe pes impression are more straight compared with the tracks from Arizona. The Wuerhe tracks differ from *P. longipodus*, *P. parvus*, and *P. nipponensis* in having long pedal digit impressions. The wider manual digit III of the Wuerhe specimen is similar to that of *P. stokesi* but longer. The lack of multiple manus-pes sets makes it difficult to assign the Wuerhe tracks to a particular ichnospecies. Herein, we prefer an open nomenclature assigning the Wuerhe pterosaur tracks to *Pteraichnus* isp.

Five other Chinese pterosaur tracks, with similar morphologies, belong to *Pteraichnus* isp. (Xing et al., 2012b). The first Chinese pterosaur tracks were described from the Lower Cretaceous Hekou Formation of Liujiaxia, Gansu Province (Zhang et al., 2006; Li et al., 2006) (Fig. 5b). Compared to the Liujiaxia tracks, the specimen from Wuerhe has more distinct pes digit impressions, a metatarsal impression that is subtriangular with a round heel imprint (rather than rectangular with a pointed heel imprint), and a manus digit III that is oriented caudolaterally.

The second reported pterosaur tracksite in China is the

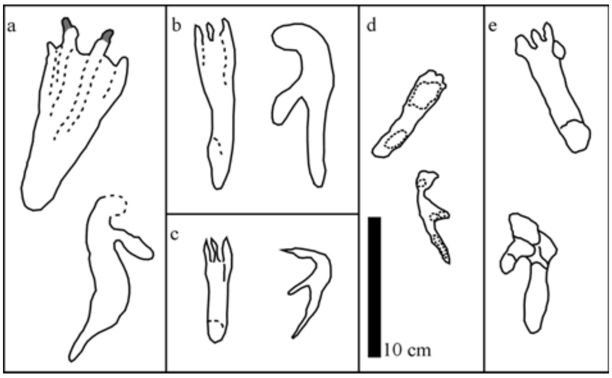

Fig. 5. Comparison of pterosaur tracks from different Lower Cretaceous localities in China. a, Huangyangquan locality; b, Liujiaxia locality (Xing unpublished data); c, Dongyang locality (based on Lü et al., 2010, fig. 2 and a photo taken by Daniel Barta); d, Jimo locality (Xing et al., 2012a), e, Qijiang locality (Xing et al., 2012b). Scale refers to a–e.

Dongyang site, in Zhejiang Province which is in the Fangyan Formation of the late Lower Cretaceous (Lü et al., 2010) (Fig. 5c). The material from this location also differs from the Wuerhe pterosaur tracks in both morphology and size. The Wuerhe pterosaur tracks are roughly 6 times wider than the Dongyang tracks, which are only 1.5 cm wide and have a larger divarication between manual digits I and III (128° vs. 81°). The pes imprint of the Dongyang specimen is rectangular with relatively longer metatarsal impressions (Lü et al., 2010).

A third well-studied *Pteraichnus* tracksite was described from the Jimo site, in the Lower Cretaceous Qugezhuang Formation, Shandong Province (Xing et al., 2012a) (Fig. 5d). Although similar in overall size, the Jimo tracks and the Wuerhe tracks are quite different in morphology. The Jimo pedal prints are rectangular with indistinct digit traces, and only three digits (I- III) are recognizable, being shorter than in the Wuerhe print. The Jimo manus prints occasionally have digit pad impressions, which are entirely absent in the Wuerhe material. Compared with the Jimo tracks, the manus digit I impression of the Wuerhe pterosaur track is thinner and the digit III impression is more curved (Xing et al., 2012a).

At least one pterosaur trackway has been previously found in the Early Cretaceous Jiaguan Formation in Qijiang District, Chongqing City (Xing et al., 2012b) (Fig. 5e). One obvious difference between the Qijiang and Wuerhe pterosaur tracks is the occasional preservation of a partial metacarpophalangeal joint impression of manual digit IV in the Qijiang specimens. The manual digits I and II in the Qijiang pterosaur prints are thicker and the pedal digits are shorter and wider. The pes of the Qijiang pterosaur tracks also differs by its more rectangular shape (Xing et al., 2012b). The lack of a detailed research on the Zhaojue pterosaur tracks in the Sichuan Province presently hinders a detailed comparison with the Wuerhe tracks.

In brief, the Wuerhe tracks differ from other Chinese pterosaur tracks in three major features:

(1) The Wuerhe pes impression is subtriangular rather than rectangular.

(2) The four digits in the Wuerhe pes print are more slender and longer.

(3)The overall size of the Wuerhe tracks exceeds that of all other Chinese pterosaur tracks.

Comparison with known skeletons: Pterosaurs are traditionally divided into the Rhamphorhynchoidea (a primitive Late Triassic- Early Cretaceous grade) and the Pterodactyloidea (an advanced Late Jurassic-Late Cretaceous clade) (Wellnhofer, 1991). The Wuerhe pterosaur trackmaker was most likely a small to medium-sized pterodactyloid based on the lack of a pedal digit V impression. Pedal digit V is plesiomorphically present in rhamphorhynchoids and absent or strongly reduced in pterodactyloids. However, rarely a pedal digit V impression is preserved among rhamphorhynchoid tracks (Lockley et al., 2008). Therefore, a rhamphorhynchoid trackmaker cannot be excluded. The early Cretaceous pterosaur osteological record in the Junggar basin is exclusively composed of dsungaripterid pterodactyloids (Maisch et al., 2004). Dsungaripteridae comprise five genera: *Dsungaripterus* (Young, 1964), *Noripterus* (Young, 1973), *Lonchognathosaurus* (Young, 1964), *Domeykodactylus* (Martill et al., 2000), and "*Phobetor*" (which is only known from the Lower Cretaceous of East and Central Asia, South America and possibly eastern Europe [Maisch et al., 2004]). *Dsungaripterus, Noripterus*, and *Lonchognathosaurus* are present in the Junggar basin. *Dsungaripterus weii* is the first pterodactyloid collected in China, but the known material includes no autopodia (Young, 1964). The *Dsungaripterus weii* locality and the Wuerhe pterosaur tracksite are tantalizingly close to each other (less than one hundred meters apart, and from the same level of the Tugulu Group). At present, the Wuerhe *Pteraichnus* isp. cannot be confidently assigned to the body fossil record of any particular pterosaur genus. However, the Wuerhe pterosaur tracks are most probably referable to the Dsungaripteridae.

3.2 Bird tracks

Koreanaornis dodsoni Xing et al., 2011.

Materials: Twenty distinct tracks on the same sandstone slab as the pterosaur tracks, cataloged as MGCM H30b1-20. Tracks are now stored at Moguicheng Dinosaur and Bizarre Stone Museum, Xinjiang, China (Figs. 3, 6).

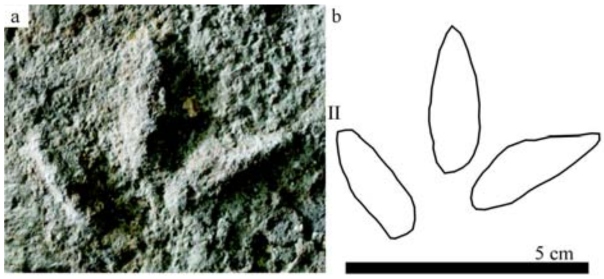

Fig. 6. Photograph (a) and outline drawing (b) of *Koreanaornis dodsoni* bird track MGCM H30b1 from the Huangyangquan tracksite.

Locality and Horizon: Lower Layer of the Tugulu Group, Early Cretaceous. Huangyangquan tracksite, Wuerhe District, Karamay City, Xinjiang, China.

Description: Medium size, tridactyl bird tracks, lacking hallux impressions. Digit impressions are often separate, and not connected proximally. MGCM H30b1 (Fig. 6) is well-preserved, and measures 4.5 cm in length and 5.4 cm in width. Digit II is the shortest. Digit III is almost equal to digit IV in length. The divarication angles between digit II and III (51°) are slightly smaller than between digits III and IV (59°). The divarication angle between II and IV is 110°. Digital pads are absent. The average length/width ratio is 0.83. MGCM H30b1-7 (Fig. 3) comprises a trackway with 7 consecutive tracks.

Discussion: The Wuerhe bird tracks, MGCM H30b1-20, are referred here to the ichnogenus *Koreanaornis*, which is characterized by small, wide (range 2.5–3 m), sub-symmetric, and functionally tridactyl tracks with a small digit I occasionally present and divarication between digits II and IV about 90°–115° (Kim, 1969; Lockley et al., 2006). Proximally unconnected digit traces are also present in *Koreanaornis* (Lockley et al., 2006). As described in Xing et al. (2011), the Wuerhe bird tracks are slightly larger than the type ichnospecies of *Koreanaornis*, but the size may be exaggerated slightly by subtle dissolution of the tracks soon after they were made (Lockley et al., 2011). The Wuerhe bird tracks match those of *Koreanaornis dodsoni* (Xing et al., 2011) in being medium to large and wide tridactyl tracks with slender digits, divarication angles between digits II and IV reaching 110° and lacking distinct digital pad and hallux impressions. Therefore, the Wuerhe tracks are assigned to *Koreanaonis dodsoni*.

4 Palaeoethology: Relationship between Bird and Pterosaur Tracks

The Huangyangquan tracksite is one of many localities where pterosaurs tracks have been found alongside bird tracks (e.g., the Uhangri Formation of South Korea, the Hekou Formation of Gansu province, and the Jiaguan Formation of Chongqing Municipality in China) (Hwang et al., 2002; Li et al., 2006; Zhang et al., 2006; Xing et al., 2012a). Track assemblages can provide important clues for reconstructing paleoenvironments and faunas. At the Huangyangquan tracksite, twenty individual bird tracks MGCM H30b1-20 comprise at least one trackway, the other two or three indistinct trackways. The bird tracks show no single preferred orientation and distinct walking direction. However, there is a suggestion of a bimodal distribution of directions parallel to the long axis of the slab. The pterosaur tracks are also more or less parallel to this axis. The pes length of the pterosaur tracks is 14 cm, approximately four times longer than the length of the bird tracks (average about 4 cm). The coexistence of a larger pterosaur trackmaker with a small bird trackmaker has also been reported form the Cretaceous of South Korea. By contrast, the North Horn assemblage of Utah (Late Cretaceous, Maastrichtian) records the tracks of a small bird and a similarly sized pterosaur (Lockley, 1999). The Wuerhe tracks document another instance of pterosaur and bird co-occurrence, and further affirm that cohabitation between these two diverse groups of flying vertebrates was not unusual throughout the Cretaceous world.

On the basis of skeletal anatomy, Bakurina and Unwin (1995) suggested that Cretaceous pterosaurs began to favor more terrestrial environments. Cretaceous pterosaur tracks most frequently occur in non-marine facies, usually fluvio-lacustrine environments (Lockley et al., 1995), while Jurassic pterosaur tracks are mostly found in regionally-extensive coastal plain sedimentary facies (Lockley et al., 2008). The Wuerhe pterosaur tracks are preserved on a lake shoreline, adding further support to such a conclusion.

Although the Wuerhe pterosaur tracks appear with those of birds, dinosaur tracks, and invertebrate traces, non-avian theropod (Xing et al., 2011) and stegosaur (Xing et al., 2013) tracks occur separately, at a distinct distance from the pterosaur and bird tracks. This difference probably reflects the difference in substrate properties, and local paleoenvironments. Soft sediments more easily register small pterosaur and bird tracks, but heavier dinosaurs (stegosaurs) may have registered tracks on firmer ground (Hwang et al., 2002).

The robust digit III of the Wuerhe pterosaur tracks may be related to a morphological abnormality or simply to substrate deformation. Osteoarthritis of metacarpophalangeal joints are known from at least four pterosaur skeletons (Kellner and Tomida, 2000, Bennett, 2003; Lü and Ji, 2005).

5 Palaeoenvironmental Analysis and Interpretation

In the Cretaceous, influenced by the Yanshan movement, the tectonics of northern Xinjiang were dominated by lifting movement. But, in general, the sedimentary environment was relative stable and is characterized as a fluvial and lacustrine setting with a moist and hot climate (Zhou et al., 2008). The Junggar district primarily consists of developed lacustrine deposits. The sediments of the northern and eastern regions are fluvial-lacustrine, while those of the south are dominated by coarse clastic fluvial deposits of piedmont (Wu and liu, 1988).

In the study area, the absence of plant fossils suggests sparse vegetation, which is supported by the rarity of herbivorous dinosaur bones and tracks. All mudstone facies are full of invertebrate traces and bioturbation, indicating that the shallow lacustrine sediments were well-oxygenated (Houck and Lockley, 2006). The presence of small-scale symmetrical wave ripple marks (Xing et al., 2011: Fig. 5) attests to a lake expansion (Paik et al., 2001). The occurrence of invertebrate traces and vertebrate tracks (bird-dinosaur tracks) in the middle part of the sequence (track-bearing horizon) indicates that the water was fairly shallow (Xing et al., 2011: Fig. 4 and 5). The presence of mud cracks, indicates periodically sustained subaerial exposure, with occasional emergence on the same horizons (Plummer and Gostin, 1981). It suggests that the environment of the Huangyangquan tracksite was the shoreland zone of a shallow lake. Birds and non-avian dinosaurs are known to have co-occurred in shoreline environments frequently in the early Cretaceous (Lockley, 1992).

Climate conditions play an important part in lake deposition (Wu et al., 2012). The paleoclimate reconstruction of the Early Cretaceous in China is a typically seasonal “semiarid” climate (Houck and Lockley, 2006). Abundant sediments carried by summer rainstorms in upland areas were transported into stream valleys. Because of rapid aggradation, the channels became shallower and wider on the alluvial belt (Smith, 1991; Houck and Lockley, 2006), and an ephemeral lake was formed. Ripples are the best evidence for receiving sediments from a surrounding river valley. Furthermore, bedded gypsum and few plant fossils indicate an arid season and seasonal precipitation. Such a non-perennial lake would periodically provide a water source to pterosaurs and dinosaurs which may have lived outside of the study area (Paik et al., 2001; Li et al., 2011).

Near the Huangyangquan tracksite, some animals may have suffered from the arid climate conditions that increased death rates. There are lots of dinosaur and turtle bone remains preserved with calcareous concretions (Retallack, 1997; Paik et al., 2001).

The Huangyangquan tracksite is a bird-dominated ichnofauna. Of 16 bird ichnogenera reported from the Cretaceous, many represent shorebird-like species including *Koreanaornis*, *Aquatilavipes*, and *Moguiornipes* (Kim et al., 2012; Lockley et al., 2013). Modern shorebirds have different substrate preferences. Redshanks, Dunlins, Lapwings, and Snipes choose muddy habitats along the coast of the Orkney Islands. Only Dunlins have a preference for sandy habitats (Summers et al., 2002). According to Xing et al. (2011), *Goseongornipes* isp. from the Huangyangquan tracksite represents a tactile-searching shorebird-like form that usually foraged in groups. These trackmakers may be members of a Scolipacidae-like clade, which inserted elongated bills into coastal sand and mudflats in search of invertebrates (Cunningham et al., 2007). In addition, *Goseongornipes* isp. trackways are parallel to ripple crests, which can be explained by environmental factors, such as penetrability, physical sediment variability, sorting and organic content. The modern species *Limnodromus griseus* left more impressions on the crests which have higher penetrability and finer sediments than troughs in tidally formed sand ripples (Grant, 1984).

Bird tracks indicate palaeobathymetry and habitats along the shoreline (Lockley et al., 1992). The different shorebirds may have been adapted to different ecological niches and food resources. Often they co-occur with invertebrate traces. The invertebrate ichnogenus *Scoyenia* is common, the tracemaker representing the possible prey of *Koreanaornis dodsoni*. Generally, *Koreanaornis dodsoni* and *Moguiornipes* show a high imprint density with a few distinct trackways (Xing et al., 2011).

6 Conclusions

A manus-pes set from the Tugulu Group is attributed to a pterodactyloid, and herein assigned to *Pteraichnus* isp. based on characteristic features such as the triangular outline of the pes imprint, the four elongate digits impressions, and a robust manual digit trace III. The Wuerhe tracks represent the first pterosaur record from Xinjiang and the largest pterosaur tracks currently known from China.

The preserved bird tracks are those of typical shorebirds and are assigned to *Koreanaornis dodsoni*, an ichnotaxon known from other Lower Cretaceous strata in Southeast Asia.

All tracks in the Huangyangquan site are preserved on mudstones, which were deposited in a lakeshore environment. Many sedimentary characteristics indicate that the climate in the early Cretaceous was arid. We infer that it was a seasonal lake that provided a regular source of water.

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