Palaeogeography, Palaeoclimatology, Palaeoecology 466 (2017) 303–313

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Late Cretaceous ornithopod-dominated, theropod, and pterosaur track assemblages from the Nanxiong Basin, China: New discoveries, ichnotaxonomy, and paleoecology

Lida Xing [a,b,*], Martin G. Lockley [c], Daliang Li [b], Hendrik Klein [d], Yong Ye [e], W. Scott Persons IV [f], Hao Ran [g]

[a] State Key Laboratory of Biogeology and Environmental Geology, China University of Geosciences, Beijing 100083, China
[b] School of the Earth Sciences and Resources, China University of Geosciences, Beijing 100083, China
[c] Dinosaur Trackers Research Group, University of Colorado Denver, PO Box 173364, Denver, CO 80217, USA
[d] Saurierwelt Paläontologisches Museum, Alte Richt 7, D-92318 Neumarkt, Germany
[e] Zigong Dinosaur Museum, Zigong, Sichuan, China
[f] Department of Biological Sciences, University of Alberta, 11455 Saskatchewan Drive, Edmonton, Alberta T6G 2E9, Canada
[g] Key Laboratory of Ecology of Rare and Endangered Species and Environmental Protection, Ministry of Education, Guilin 541004, China

ARTICLE INFO

Article history:
Received 23 February 2016
Received in revised form 20 November 2016
Accepted 21 November 2016
Available online 22 November 2016

Keywords:
Zhutian Formation
Hadrosauropodus
Wupus
Pteraichnus
Yangmeikeng site

ABSTRACT

Re-examination of the Late Cretaceous Yangmeikeng tracksite, in the Zhutian Formation (Nanxiong Group) near Nanxiong, Guangdong Province, China, has led to the documentation of over 30 vertebrate tracks. The track assemblage is dominated by large and small ornithopod tracks. The larger ornithopod tracks have been assigned to *Hadrosauropodus nanxiongensis* and *Hadrosauropodus* isp. indet. The smaller ornithopod tracks are consistently incomplete, showing only three pes digit traces, without heel or manus impressions. For this reason the smaller tracks probably represent pes tracks penetrating from a higher layer, and therefore have not been assigned to any particular ichnotaxon. Previous photography at Yangmeikeng site confirms the presence of at least one small *Wupus*-like theropod track and a *Pteraichnus*-like pterosaur pes track. Large enigmatic didactyl tracks could be of deinonychosaurian affinity, but are more likely the poorly preserved prints of a tridactyl theropod trackmaker. The Nanxiong dinosaur tracks and skeleton records represent the most important and diverse ichnofauna from Upper Cretaceous strata of South China, and can be compared with the Shandong and Heilongjiang Late Cretaceous faunas. The composition of the ichnofauna, is significant because it reflects a diverse tetrapod community with hadrosaurs, avian theropods, non-avian theropods and pterosaurs, a co-occurrence not evident from the skeletal record of this region. From a global perspective this assemblage permits a unique insight into archosaur communities and interaction of animals in a typical Late Cretaceous lakeshore environment. Non-avian theropods may have been attracted by the other groups that were considered as a potential prey.

1. Introduction

China's known Late Cretaceous dinosaur fauna is predominantly a hadrosaur–titanosaur dominated assemblage (Dong, 1992) and was slightly less diverse than that known from the Early Cretaceous. Late Cretaceous skeletal fossil assemblages are widely distributed in the Yuliangze Formation of northern Heilongjiang Province (e.g., *Mandschurosaurus* Riabinin, 1925), the Wangshi Group (e.g., *Tanius* Wiman, 1929; *Shantungosaurus* Hu, 1973) and the Jingangkou Formation (e.g., *Tsintaosaurus* Young, 1958) of eastern Shandong Province, and in the Wulansuhai Formation of Bayan Mandahu, northern Inner Mongolia (e.g., *Linheraptor* Xu et al., 2010a). In addition, a sparser record of specimens is now known from Heyuan and Nanxiong (former Nanhsiung) in northern Guangdong Province, and neighboring Ganzhou (formerly Kanchou) in southern Jiangxi Province.

The coexistence of skeletal fossils, egg shells, and tracks in the same basin is quite rare, but the Nanxiong Basin contains all three in abundance. The Nanxiong Basin is located across the northern portion of Guangdong Province (Fig. 1) and extends into Jiangxi Province, covering an area of about 1800 km^2 (1240 km^2 of which is within Guangdong Province).

The first record of dinosaurs in the Nanxiong Basin, a number of phalanges identified as belonging to a coelurosaur, was discovered in 1961 by the Guangdong Bureau of Geology (Young and Chow, 1962). The current record of dinosaurs and other Mesozoic vertebrates in the Nanxiong region is relatively rich, although most specimens are largely incomplete, and includes the hadrosaurid *Microhadrosaurus* (*nomen dubium*) (Dong, 1979), the therizinosaurid *Nanshiungosaurus* (Dong,

* Corresponding author at: State Key Laboratory of Biogeology and Environmental Geology, China University of Geosciences, Beijing 100083, China.
E-mail address: xinglida@gmail.com (L. Xing).

http://dx.doi.org/10.1016/j.palaeo.2016.11.035
0031-0182/

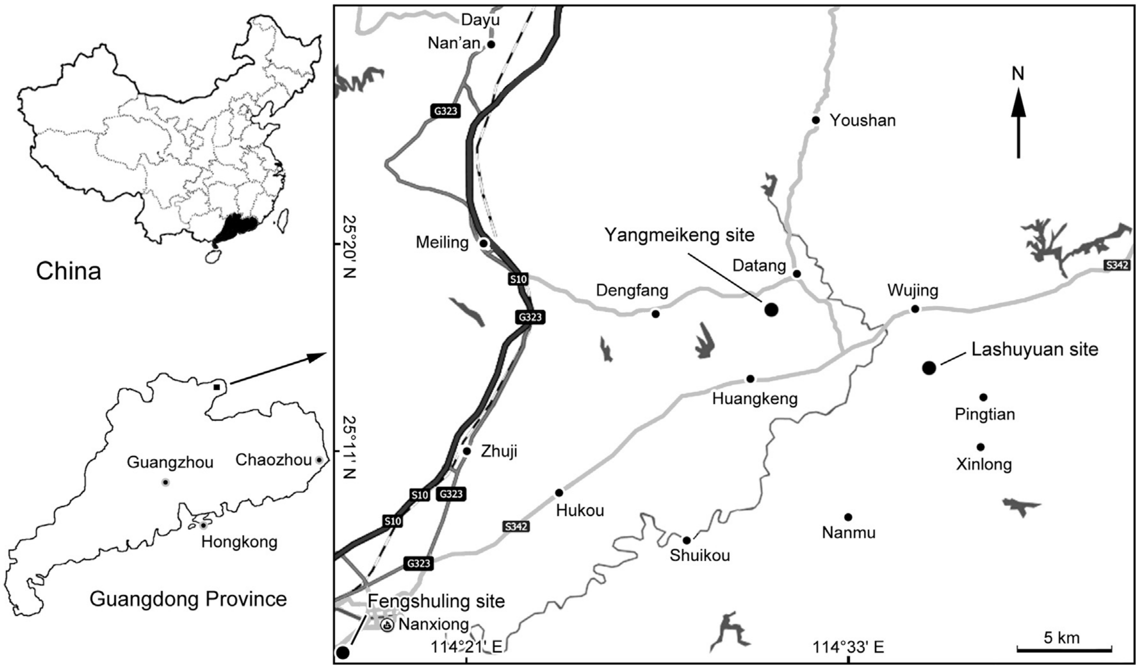

Fig. 1. Geographical location of the tracksites.

1979), and the oviraptorid *Shixinggia* (Lü and Zhang, 2005). Other Nanxiong findings include tyrannosaurid teeth (Dong, 1980), fragments of other coelurosaur teeth (Young, 1965a), sauropod teeth (Young, 1965a), a 1.7 m long broken sauropod rib, nodosaur osteoderms (Young, 1965a), numerous remains from large turtles (Yeh, 1966), and fragmentary mammal elements (Chow et al., 1977). The neighboring Ganzhou region boasts the sauropod *Gannansaurus* (Lü et al., 2013), the tyrannosaurid *Qianzhousaurus* (Lü et al., 2014) and the oviraptorids *Banji* (Xu and Han, 2010) and *Jiangxisaurus* (Wei et al., 2013). The Nanxiong Basin is especially rich in dinosaur eggs, in terms of both quantity and diversity (Fang et al., 2009). However, herein, we focus on the track record of the Nanxiong Basin, offering a unique perspective on the composition of tetrapod communities of the region (Xing et al., 2009a).

The aim of this study is the detailed documentation of an ichnofauna that besides the dominance of ornithopod dinosaurs appears to be different from other Late Cretaceous skeletal faunas from the region by the additional track record of birds or birdlike theropods and pterosaurs. Previous studies of Cretaceous ichnofaunas from China have shown that Upper Cretaceous tracksites are rare, comprising only 6 of the 106 reported (Lockley et al., 2014). Similarly the majority of track-rich deposits from Korea are Early Cretaceous in age, with the dating of Late Cretaceous tracks being problematic (Houck and Lockley et al., 2006). In Europe there are also few Late Cretaceous tracksites (Lockley and Meyer (2000), and in North America a recent review shows that Early and "mid" Cretaceous sites outnumber Late Cretaceous sites by 15 to 5 (Lockley and Lucas, 2014). Thus, the Nanxiong site adds significantly to the sparse ichnological record from this epoch, both in China and elsewhere in the Northern Hemisphere.

2. History of discovery

In the early 1980s, local geologists discovered non-avian theropod tracks in the Nanxiong Basin (Chen et al., 2006), but no formal descriptions or photographs were ever published. In 1983–1985, a series of Sino-German scientific expeditions (operated jointly by the Chinese Academy of Sciences and the University of Bonn) reported the discovery of more than 20 dinosaur footprints, including two possible sauropod tracks, at the Yangmeikeng tracksite near Youshan Town (formerly Datang) (Erben, 1995). Later, in 1993, another international joint expedition (operated by the University of Notre Dame, China University of Geosciences [Beijing], and by the Beijing Museum of Natural History) discovered more than 50 dinosaur footprints, also at the Yangmeikeng tracksite. The largest of these tracks was roughly 70 cm long and the smallest only 7–8 cm long. Unfortunately, these tracks were never formerly described and have now been lost to weathering.

In 2004, Xiaosi Fang (Geological Museum of China) and Xianqiu Zhang (Sinopec Star Petroleum., Ltd.) discovered 14 dinosaur footprints at the Fengshuling tracksite (GPS: 25°2′51.37″ N, 114°14′48.51″E), near Tianziyin Village, south of Gushi Town. Xing et al. (2009a) described these weathered tracks and referred them to *Hadrosauropodus* isp.

In 2008, at the invitation of the Nanxiong County Bureau of Land and Resources, the senior author (L.X.) examined these dinosaur footprints. Xing et al. (2009a) described the Yangmeikeng site tracks, reviewed similar tracks attributable to large ornithopods from across China, and ultimately named a new ichnospecies *Hadrosauropodus nanxiongensis*. As the former are completely weathered, the research was based on photographs taken in 1983 and 1993 and molds of the two best-preserved footprints housed in the Nanxiong Dinosaur Museum.

In summer of 2015, Lu Li, from the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, found the trackway of a biped on a ridge in the south of Lashuyuan Village, 9 km southeast of Yangmeikeng site (GPS: 25°13′35.91″ N, 114°36′ 1.31″ E). In 2012–2015, at the invitation of the Nanxiong County Bureau of Land and Resources, Nanxiong Dinosaur Provincial Nature Reserve Administration, the senior authors (L.X., D.L., M.L. and Y.Y.) explored Nanxiong for dinosaur footprints. New tracks were found at the Yangmeikeng tracksite (GPS: 25°15′25.02″ N, 114°30′58.86″ E), and an excavation was organized. This paper focuses on new information revealed by these tracks and by archived photographs. In 1993, one of the authors, Daliang Li, at the time a member of the joint China-US investigation, photographed some of the discovered tracks. These included common hadrosaur tracks and unusual theropod and pterosaur tracks (see below), which have now been rediscovered.

3. Geological setting, stratigraphy and environment

3.1. Nanxiong Basin

The Nanxiong Basin is a faulted basin controlled by a fault zone that stretches from northeast to southwest. Fang et al. (2009) measured a complete Cretaceous section in the Nanxiong Basin and proposed a nomenclature for the various strata. The basin's Cretaceous-Paleogene succession consists of continental red beds (Fig. 2) formed by successive sedimentation and includes, from bottom to top: the Lower Cretaceous Changba Formation, the Upper Cretaceous Nanxiong Group (Yuanfu, Zhutian and Zhenshui formations) and the Paleogene Luofozhai Group (Shanghu, Nongshan and Guchengcun formations). Innumerable fossils of reptiles, mammals, eggs, ostracoda, conchostraca and brackish-water foraminifera have be found in these strata (e.g., Young and Chow, 1963; Young, 1965a,b; Zhang and Tong, 1963; Lü and Zhang, 2005; Xing et al., 2009a).

Abundant microfossils occur in the Nanxiong Group, among them the *Talicypridea-Mongolocypris-Candona* ostracod assemblage. In this assemblage, most species are known to be Late Cretaceous, and *Talicypridea* is the most typical Late Cretaceous ostracod genus in East Asia. Also present is the *Porochara anluensis-Charites tenuis* charophyte assemblage (Chen, 1996, 2003, 2006), which indicates a Maastrichtian age (Xing et al., 2009a).

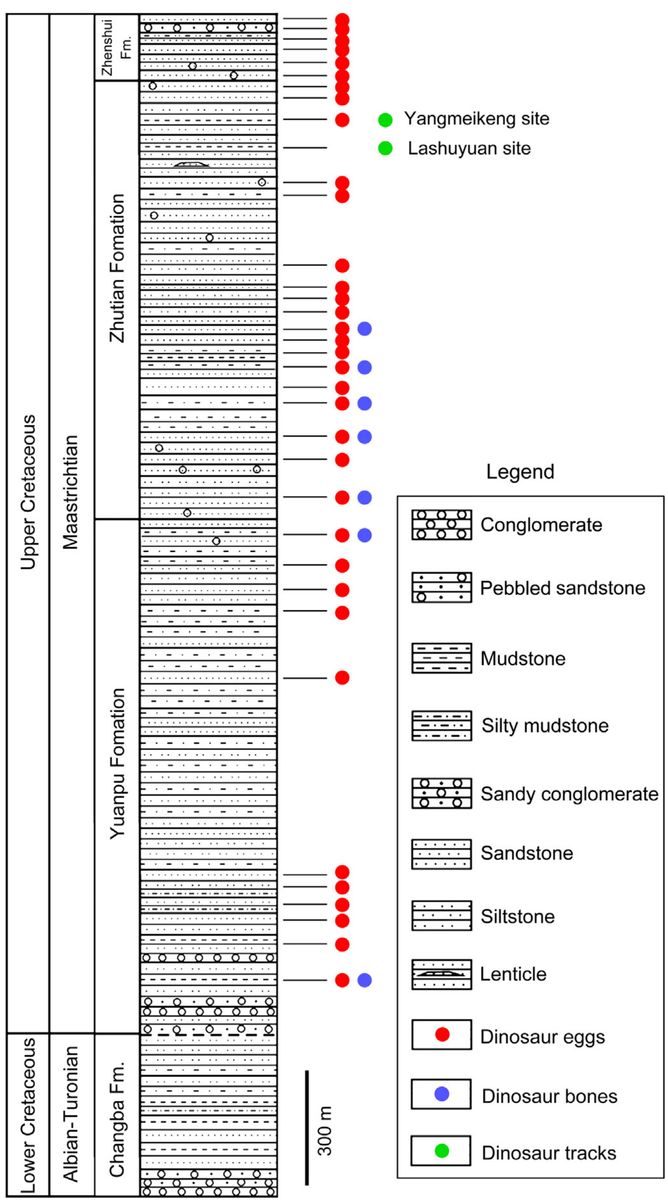

Fig. 2. Stratigraphic section of the Cretaceous in the study area with the position of dinosaur eggs, footprints and body fossil remains.

The track-bearing Zhutian Formation occurs in the vicinity of the Zhenshuihe River, in the central Nanxiong Basin, and primarily consists of brownish red siltstone and mudstone (Xing et al., 2009a; Fang et al., 2009) deposited in a fluvio-lacustrine environment.

Tracks at the Yangmeikeng site are preserved in greyish green medium-thick fine sandstone layers and are covered by purple red siltstone. These layers yield numerous invertebrate traces. Mud cracks are ubiquitous, indicating intermittent desiccation. The Lashuyuan site track layer is slightly lower than the Yangmeikeng site layer and consists of weathered tracks on greyish green siltstone.

3.2. Invertebrate traces

Invertebrate traces from the Yangmeikeng site include *Scoyenia gracilis* White, 1929 and *Skolithos linearis* Haldemann, 1840 (Fig. 3). *Scoyenia* is typical of the *Scoyenia* ichnofacies (Yang et al., 2004) and is interpreted as a browsing trace. *Skolithos linearis* specimens are unbranched burrows perpendicular to the rock surface with diameters of 1.5–2 mm. They are hollow and manifest as round or sub-rounded sections. *Skolithos*, which also occurs in shallow marine facies, are thought to have been made by annelids and phoronids (Alpert, 1974). *Scoyenia gracilis* traces are also oriented perpendicular to surfaces, unbranched, and approximately 1.7–4 cm in length with diameters of about 6–12 mm. Backfill layering within the burrows is evidence of a bilaterally symmetrical animal (Retallack, 2001). The *Scoyenia* trace makers may be arthropods (Graham and Pollard, 1982; Frey et al., 1984). Usually, *Scoyenia* ichnofacies suggest a low-energy depositional environment with periodic surface exposure and flooding, which typically developed near lake edges, intermittently exposed fluvial channel margins and floodplain surfaces (Yang et al., 2004).

3.3. Dinosaur eggs

Siltstone localities at the Yangmeikeng site have yielded the dinosaur ootaxa *Macroolithus yaotunensis* and *Elongatoolithus elongates*. Cheng et al. (2008) suggested that *M. yaotunensis* is probably the egg of an oviraptorosaurian, such as *Heyuania*. *Elongatoolithus* has also been regarded as a theropod egg (Mikhaillov, 2000; Weishampel et al., 2008).

4. Ichnology of the Yangmeikeng tracksite

4.1. Theropod tracks

Only one isolated tridactyl pes trace, numbered YMK-PT1 (YMK = Yangmeikeng tracksite, Guangdong, China.) is interpreted as theropodian. YMK-PT1 is 8.3 in length, with a length/width ratio of 1.0 (Fig. 4A-B; Table 1). All digits are slender. Digit III is the longest, and digit II is the shortest. The metatarsophalangeal pad of digit IV is located lateral to the long axis of digit III. Distal claw traces are also clearly visible. The phalangeal pads of all three digits are undifferentiated and indistinct. The divarication angle between digits II-IV is large (76°).

The length:width ratio of the anterior triangle is 0.39, which suggests a weak to medium mesaxonic track (Lockley, 2009). Among other Cretaceous theropod tracks in China, YMK-PT1 is similar to *Wupus*, from the Jiaguan Formation (Aptian-Albian), Chongqing (Xing et al., 2007, 2015a) and cf. *Wupus* isp., from the Shenhuangshan Formation (Albian), Hunan (Xing et al., 2016a). All *Wupus* specimens have a footprint width greater than length and three, moderately thick, functional pedal digits. In *Wupus* and cf. *Wupus* isp., the length/width ratio and the length/width ratio of the anterior triangle are 0.9 and 0.46, 0.8

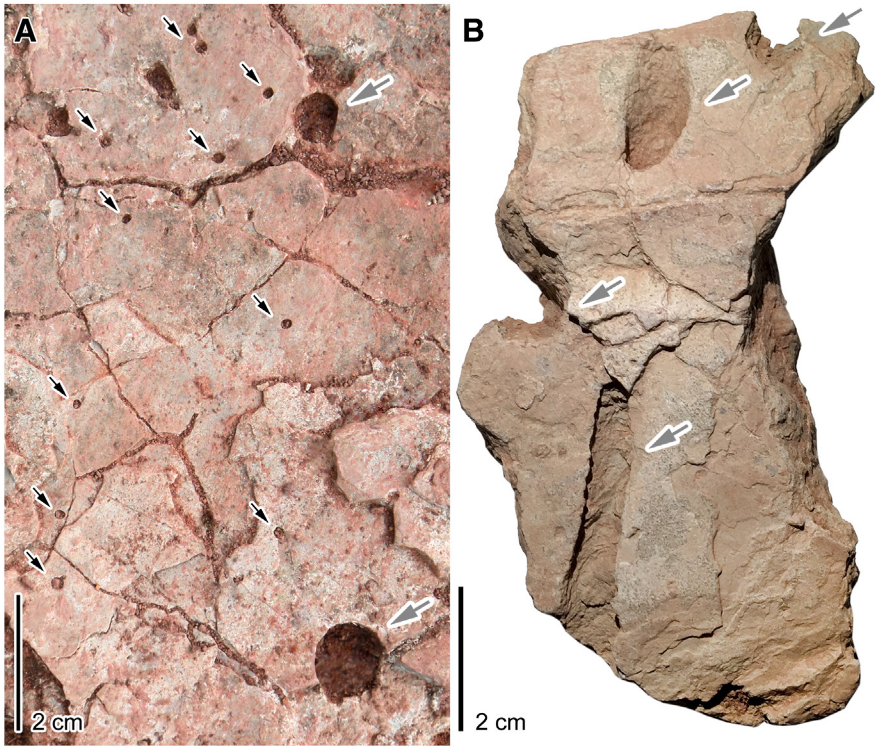

Fig. 3. Photographs with details of invertebrate traces from the Yangmeikeng tracksite. Big gray arrows indicate *Scoyenia* traces; small black arrows indicate *Skolithos* traces.

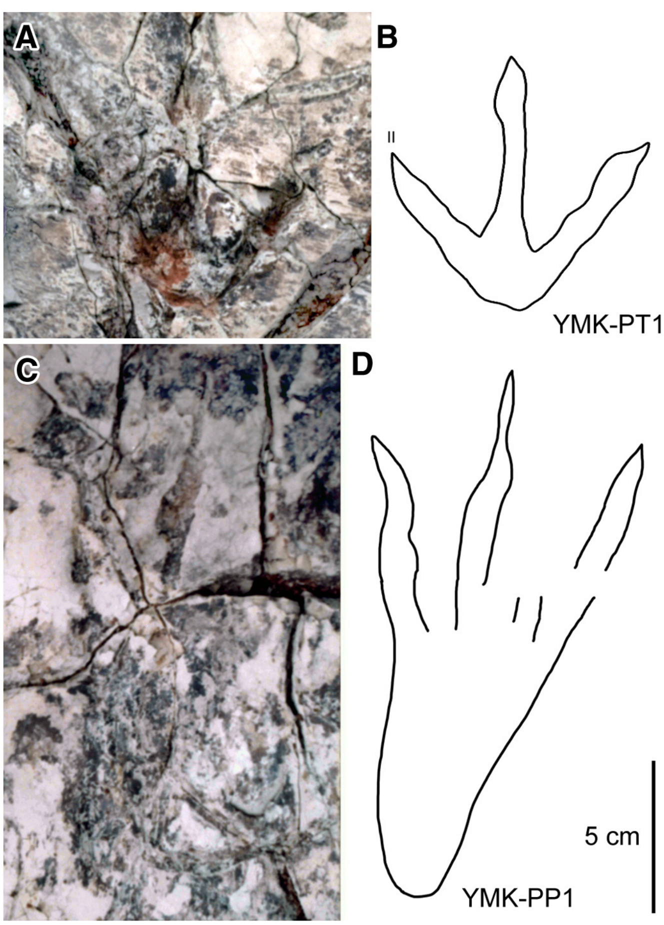

Fig. 4. Photographs taken prior to the present study show a *Wupus*-like theropod track (A and B) and a *Pteraichnus*-like pterosaur track (C and D).

and 0.51, respectively. According to the personal observations of Daliang Li, when the excavation was conducted in 1993, tracks with morphology like YMK-PT1 were present in dense concentrations. In this regard, the tracks would also be similar to *Wupus* (Xing et al., 2007). Due to the small sample size, it is difficult to discern systematic features, and thus the material is here tentatively referred to cf. *Wupus*

Table 1
Measurements (in cm) of ornithopod and theropod tracks from Yangmeikeng (YMK) and Lashuyuan (LSY) sites, Guangdong Province, China.

Number	ML	MW	II-IV	PL	SL	PA	M	L/W
YMK-PT1	8.3	8.6	76°	–	–	–	0.39	1.0
YMK-PT2	17.7	9.0	–	–	–	–	–	2.0
YMK-O1R1	60.0	59.0	51°	126.0	235.0	160°	0.24	1.0
YMK-O1L1	63.0	72.5	63°	109.0	–	–	0.22	0.9
YMK-O1R2	56.0	56.0	65°	–	–	–	0.37	1.0
Mean	59.7	62.5	60°	117.5	235.0	160°	0.28	1.0
YMK-O2R1	–	–	–	–	–	–	0.24	–
YMK-O2R2	39.0	37.5	65°	–	–	–	–	1.0
YMK-O3R1	13.5	18.0	78°	59.0	–	–	0.50	0.8
YMK-O3L1	15.0	20.0	92°	–	–	–	0.60	0.8
YMK-O4L1	10.0	21.0	91°	52.0	–	–	0.20	0.5
YMK-O5	50.0	52.0	–	–	–	–	–	1.0
YMK-O7L1	15.0	19.5	80°	69.0	–	–	0.45	0.8
YMK-O7R1	21.0	21.0	60°	–	–	–	0.34	1.0
YMK-O8	27.5	28.0	–	–	–	–	0.21	1.0
YMK-O9	28.5	23.0	40°	–	–	–	0.45	1.2
YMK-O10	59.0	56.0	65°	–	–	–	–	1.1
YMK-O11	52.0	51.0	75°	–	–	–	0.28	1.0
YMK-O12	15.0	21.0	93°	–	–	–	0.34	0.7
YMK-T1	39.0	19.0	31°	–	–	–	–	2.1
YMK-T2	28.0	14.5	32°	–	–	–	–	1.9
LSY-O1L1	34.0	41.0	–	102.0	214.0	146°	–	0.8
LSY-O1R1	34.0	40.6	–	112.0	–	–	–	0.8
LSY-O1L2	35.0	41.0	–	–	–	–	–	0.9
Mean	34.3	40.9	–	107.0	214.0	146°	–	0.8

Abbreviations: ML: Maximum length; MW: Maximum width (measured as the distance between the tips of digits II and IV); II-IV: angle between digits II and IV; PL: Pace length; SL: Stride length; PA: Pace angulation; ML/MW is dimensionless.

isp. Xing et al. (2015a) proposed that the trackmakers of *Wupus* were large wading birds.

4.2. Pterosaur tracks

All pterosaur tracks discovered in China are from Cretaceous strata and have been referred to *Pteraichnus* (Xing et al., 2013). The first described Chinese *Pteraichnus* track is from the Yanguoxia site, Gansu Province (Peng et al., 2004; Zhang et al., 2006). The number of known pterosaur tracksites in China has greatly increased since 2008. New sites include the Jimo site in Shandong Province (Xing et al., 2012), the Huangyangquan site in Xinjiang Province (Xing et al., 2013; He et al., 2013), and the Lotus site in Chongqing (Xing et al., 2013).

Only one isolated tetradactyl pes trace, numbered YMK-PP1, is interpreted as pterosaurian (Fig. 4C-D; Table 1). Although the track is partially disturbed by mudcracks, the main morphological features remain identifiable. The plantigrade pes print YMK-PP1 (17.7 cm in length, L/W ratio is 2) is narrow and has a U-shaped heel. The distal ends of YMK-PP1 have three complete digits and one digit with only the proximal portion preserved. These four digits represent digits I-IV respectively. All the digits are slender and have sharp ends and obscure digit pads.

YMK-PP1 is similar to MGCM.H30a.p, from the Lower Cretaceous Huangyangquan site, in Xinjiang. The latter is slightly smaller, 14 cm in length with an L/W ratio of 2.3, and has been identified as *Pteraichnus* (He et al., 2013). *Pteraichnus* was initially erected for a pterosaur trackway representing a quadruped, from the Upper Jurassic Morrison Formation of Apache County, Arizona (Stokes, 1957). *Pteraichnus* is widely known from the Late Jurassic and Cretaceous (Lockley et al., 2008). YMK-PP1 can be referred to a *Pteraichnus* type pes track based on being elongate, subtriangular, plantigrade, and tetradactyl (Lockley et al., 1995; Billon-Bruyat and Mazin, 2003). Large pterosaur pes tracks are known from Late Cretaceous Korean sites, such as *Haenamichnus* from the Uhangri Formation (Hwang et al., 2002). One pes track of *Haenamichnus* is 35 cm long (Kim et al., 2012), making it the largest known pterosaur track. A postero-lateral impression of digit V distinguishes it from YMK-PP1. YMK-PP1 is the largest and youngest pterosaur track known from China.

4.3. Ornithopod tracks

The Yangmeikeng ornithopod tracks fall into several size categories (Fig. 5; Table 1). Large pes prints are about 42–63 cm in length, including YMK-O1 (trackway) and YMK-O5, O10, O11 (isolated tracks). Medium-sized pes prints are about 29 cm in length, including YMK-O2, O8,

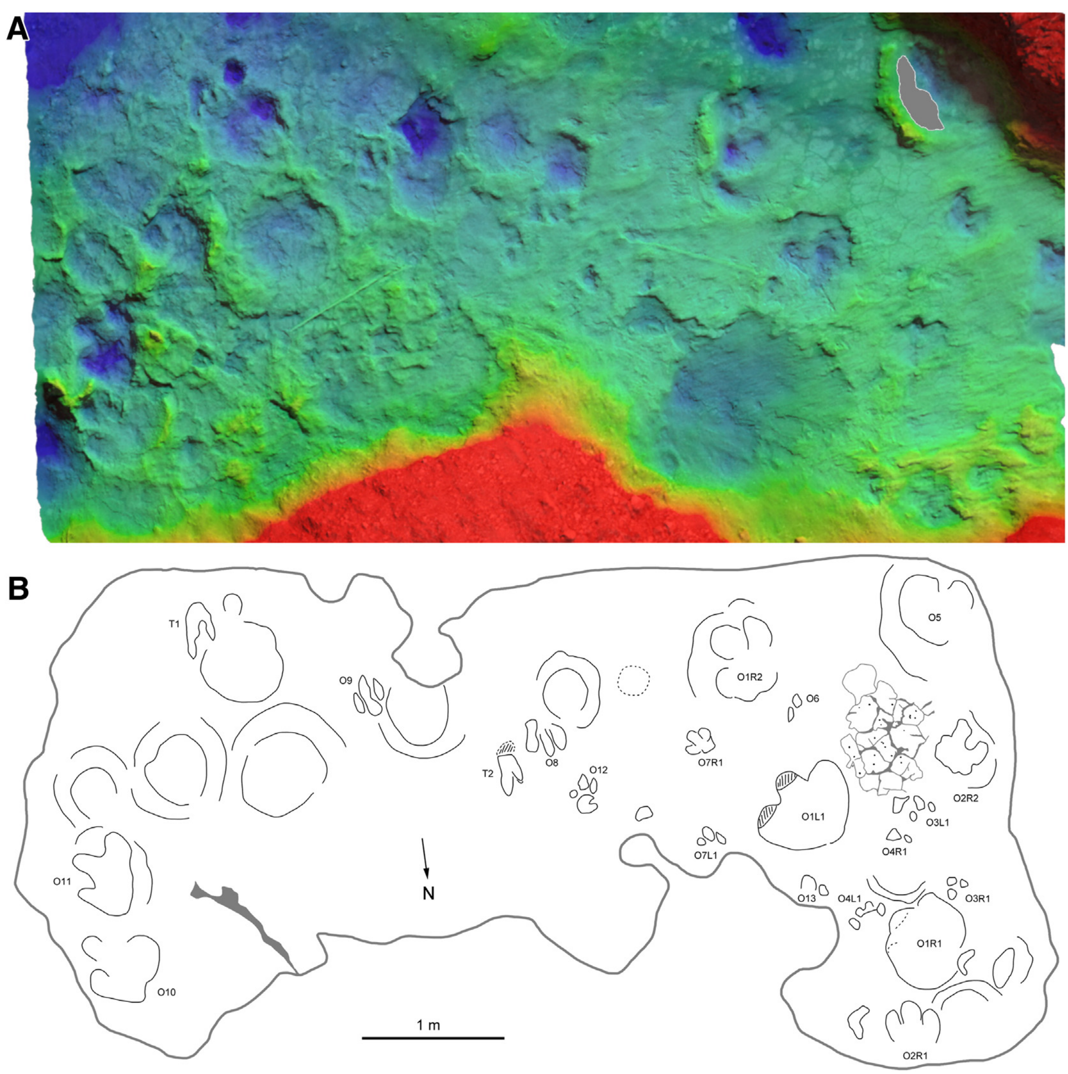

Fig. 5. Photogrammetric map (A) of track-bearing surface with corresponding outline map (B) based on original full size tracing of surface. B shows north arrow and designations of individual tracks referred to in text. Note that a well-preserved and representative section of the surface with desiccation cracks and invertebrate traces is shown between tracks O1L1 and O5.

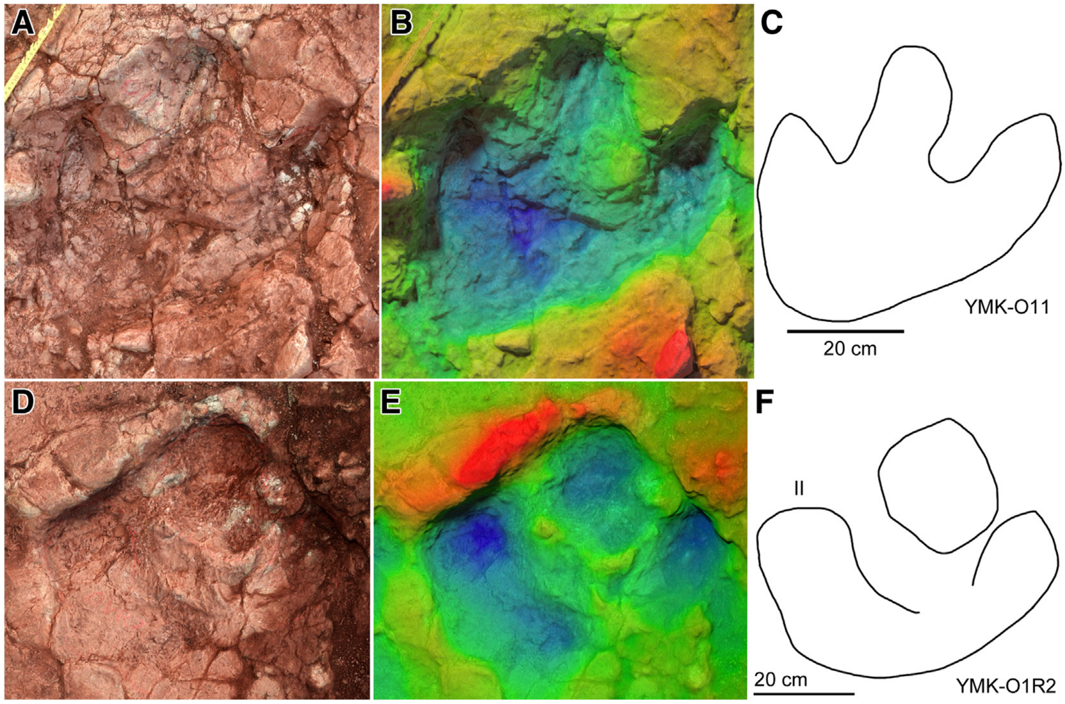

Fig. 6. Large tridactyl ornithopod tracks O11 (A-C) and O1R2 (D-F). Each shows photograph (A, D) 3D image (B, E) and outline drawing (D, F). Compare with Fig. 5.

and O9. Several slightly smaller digit-only tracks are 13–19 cm in length, including YMK-O3, O4, O6, O7, O12 and O13. None have manus prints or tail traces.

Among the large ornithopod tracks, YMK-O11 and YMK-O1R2 are the best preserved (Fig. 6). YMK-O11 is a natural mold of a tridactyl ornithopod pes track. The length:width ratio is ~1.0. Digit III is the longest, and its distal toe (ungual) trace is broadly parabolic. The divarication angle between digits II and IV is 75°. The L/W ratio of the anterior triangle is 0.28.

YMK-O1R2 is morphologically similar to YMK-O11. The step length of YMK-O1 is short, roughly twice the length of the foot. The axes of the YMK tracks are rotated inward, relative to the trackway midline.

Most medium and smaller ornithopod tracks are preserved only with digit traces. YMK-O3R1, O3L1, O7L1, O7R1 and O12 are reasonably well preserved and morphologically similar, showing three separate toe traces without heel impressions. Thus track lengths are partial measurements, and track widths more reliable as a measure of trackmaker size. The two tracks in the pair YMK-O3L1 and O3R1 have lengths of ~13.5 and ~15.0 cm and widths of ~18.0 and ~20.0 cm, respectively, and are separated by a step length of 59 cm (Fig. 7). YMK-O7L1 and O7R1 have lengths of ~15 and ~21.0 cm and widths of ~19.5 and ~21.0 cm, respectively, and are separated by a step length of 69 cm. YMK-O7L1 is the better preserved track. Digit III is the most developed. The ungual trace of digit II is the sharpest, while the other two digits are round. Digit III has a raised lingulate sand mound at its posterior portion, likely caused by pushing back a layer of surface sediment. The L/W ratio of the anterior triangle is 0.45. YMK-O7R1 shows a faint heel trace allowing estimate of the L/W ratio at 1.0. O12 is also 21.0 cm wide and 15.0 cm long. When including YMK-O4R1, which is also 21.0 cm wide, there is notable consistency in the range of widths of tracks in the O3, O4, O7 and O12 series (19.0–21.0 cm).

Similar digit-only tracks have been interpreted as swimming traces (Fujita et al., 2012). However, recent research interprets such prints as the result of animals walking on a soft mud-silt substrate, projecting their claws deeply to register their traces on an underlying sand layer, where they gained more grip during progression (Xing et al., 2016b). The Yangmeikeng specimens appear to represent this scenario, as the few step lengths recorded for tracks O3 and O7 indicate a normal walking progression.

The Yangmeikeng site also displays a nearly complete medium-sized track resembling *Hadrosauropodus* (YMK-O9). Despite partial weathering, the heel of O9 is well-preserved. The digits show the same morphology as the digit-only tracks. O9 is 28.5 cm long and 23.0 cm wide, with an L/W ratio of 1.2. The divarication angle between digits II and IV is wide (40°). The L/W ratio of the anterior triangle is 0.45. Xing et al. (2009a) described the hadrosaur ichnotaxa *Hadrosauropodus nanxiongensis* from the Yangmeikeng site, and *Hadrosauropodus* isp. from the Fengshuling site. The former is 38–40 cm in length and the latter is slightly shorter (36 cm). The Fengshuling *Hadrosauropodus* tracks comprise four almost parallel trackways, suggesting a gregarious behavior similar to that inferred for other ornithopods (e.g., Zhaojue *Caririchnium*, Xing et al., 2014). In the *Hadrosauropodus nanxiongensis* tracks NDM.F1 and F2, (NDM = Nanxiong Dinosaur Museum, Guangdong, China.) the L/W ratios are 0.8, the L/W ratios of the anterior triangles are 0.29–0.32. In the *Hadrosauropodus nanxiongensis* track NCBLR.F.M1 (NCBLR = Nanxiong County Bureau of Land and Resources, Guangdong, China.), from the Fengshuling site, the L/W ratio is 1.1 and the L/W ratio of the anterior triangle is 0.22. Thus YMK-O9 is more elongate than the tracks reported from the Fengshuling site.

The large ornithopod tracks at Yangmeikeng are very similar to *Hadrosauropodus nanxiongensis* described by Xing et al.(2009a), being large tridactyl tracks with wide pes digit traces and no manus or tail traces, and having angles between digits II and IV ranging from 51° to 95° and maximum width of digit II roughly twice that of digit IV. Note that, due to the poor preservation of the tracks, Xing et al. (2009a) confused medial with lateral digits of NDM.F1 and F2.

By the L/W ratio of the anterior triangle, large and medium-sized ornithopod tracks from the Yangmeikeng tracksite can be differentiated. The former show weak mesaxony (0.28) while the latter have stronger mesaxony (~0.45–0.60) (Lockley, 2009). Large and small *Caririchnium* tracks from the Lotus tracksite of Chongqing also differ in terms of mesaxony, which is thought to reflect the different foot morphologies of ornithopods at different ages (Xing et al., 2015b). Because of the

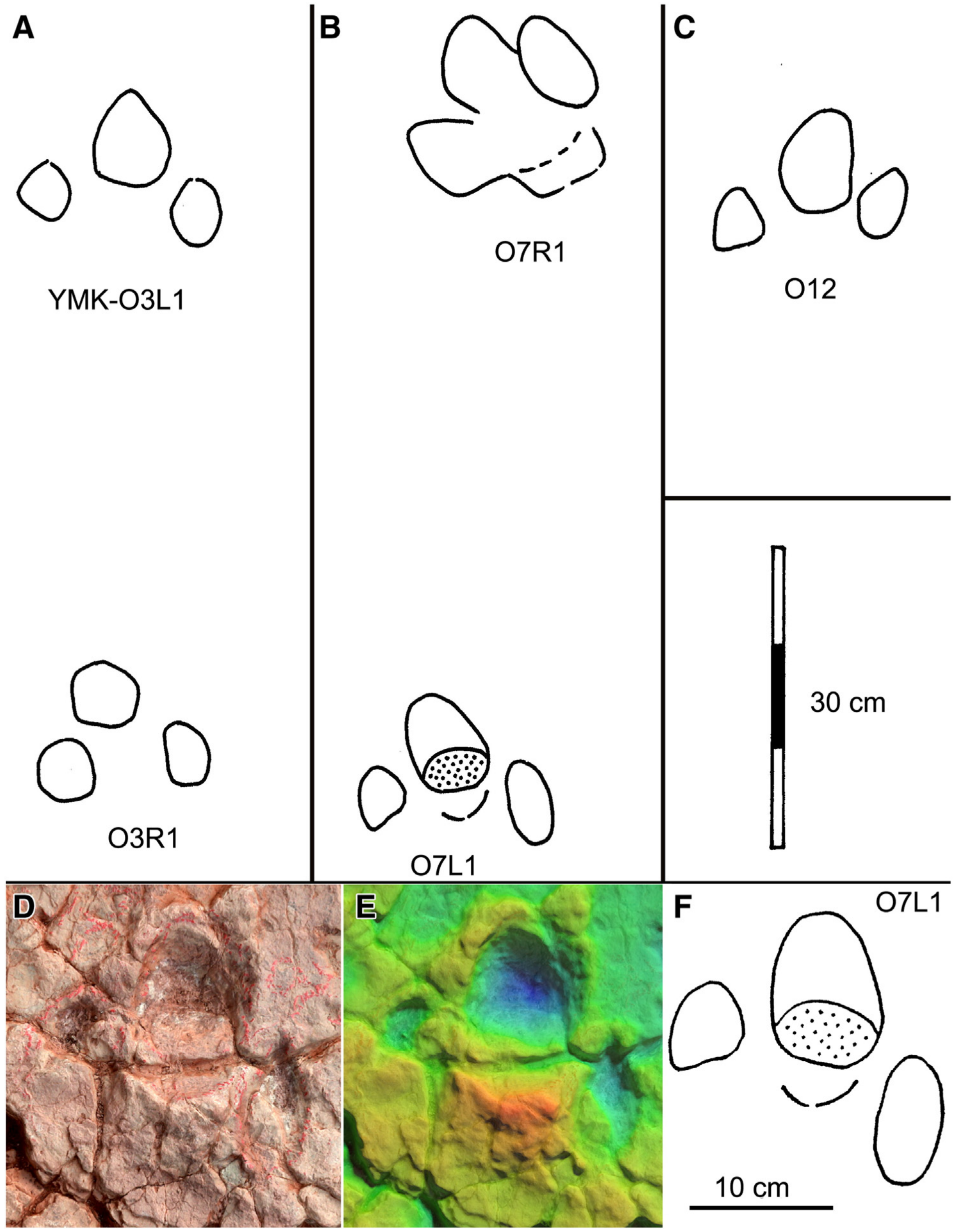

Fig. 7. Outline drawings of small ornithopod tracks. A: Inferred single step sequence between O3R1 and O3L1. B: s Inferred single step sequence between O7L1 and O7R1. C: Specimen O12. Other images are photograph (D), 3D depth model (E) and outline drawing (F) of the small ornithopod track O7L1.

absence of better preserved medium sized Yangmeikeng ornithopod tracks, we tentatively refer the tracks to *Hadrosauropodus* isp.

4.4. Enigmatic didactyl tracks

Two isolated didactyl tracks, YMK-T1 and T2, have been found at Yangmeikeng site (Fig. 8). Neither is well preserved, but the elongate digit traces suggest a theropod affinity. T1 is better preserved and is 39 cm in length with an L/W ratio of 2.1. It has relatively narrow, elongated digit traces inferred to be digits III and ?IV and a well-developed rounded metatarsophalangeal area. These digit traces (III and ?IV) are almost parallel, but digit III is significantly longer. Digit III has three faint digit pads, while digit ?IV has no identifiable pad traces. T2 is smaller and is poorly preserved. It is 28 cm in length and generally resembles YMK-T1.

Such occurrences of apparently didactyl tracks raises at least three possibilities: 1) they could be poorly preserved tridactyl tracks, 2) they could be of deinonychosaurian affinity, or 3) they could be examples of tracks reflecting a pathological pes or injury. We have arranged these three possibilities, in order of decreasing probability. First, we recognize that tracks at the Yangmeikeng site are not very well preserved. However, most tridactyl tracks are identifiable as ornithopods, and the elongate nature of these didactyl tracks is strongly suggestive of a theropod affinity. Therefore, rather than dismiss them as extramorphological and not worth describing, we should consider the second and third possibilities, which assume the tracks reflect either an original didactyl pes anatomy or their shape is pathological.

Regarding the second possibility, we recognize the danger of over interpreting these large didactyl tracks as deinonychosaurian, because they are much larger than any currently known, and moreover they

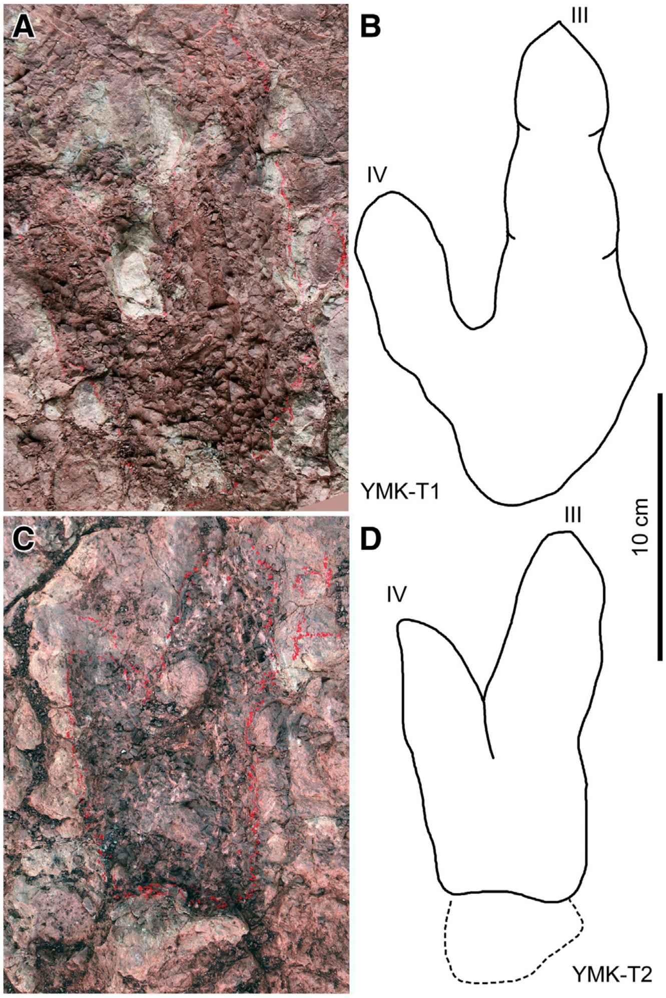

Fig. 8. Photographs (A, C) and outline drawings (B, D) of the large apparently didactyl tracks of theropod affinity, tentatively considered of possible deinonychosaurian affinity or alternatively as incomplete tridactyl tracks.

would also be the first Late Cretaceous reports from China and the second globally. It is also worth noting that the relative lengths of digits III and ?IV suggest that if the tracks are those of deinonychosaurians they are more likely of troodontid than dromaeosaurid affinity (Lockley et al., 2016a, 2016b). Large theropod hip-height is estimated as 4× (Alexander, 1976) or 4.9× (Thulborn, 1990) the track length, and body length is estimated to be 2.63× the hip height (Xing et al., 2009b). The YMK-T1 and T2 trackmakers had body lengths of ~4.1–5.0 m and ~2.9–3.6 m respectively, regardless of whether they were tridactyl or didactyl. The largest troodontid, *Troodon* (Leidy, 1856), in North America, was only about 2.5 m long (Paul, 2010). The largest Asian troodontid *Saurornithoides* (Osborn, 1924; Norell et al., 2009) from Mongolia was only about 2.3 m long (Paul, 2010). Nevertheless, we cannot completely rule out the possibility that large deinonychosaurians lived in South China during the Maastrichtian.

The third alternative explanation is that these are incomplete tracks of relatively large tridactyl theropods with an injured or deformed foot. As noted by Abel (1935) and reviewed by Lockley (1991) and McCrea et al. (2015), a trackway of a relatively large tridactyl theropod showed an injury, or pathology, which resulted in the loss of digit II of the right foot. Such a trackway would easily be mistaken for a deinonychosaurian trackway if only the right footprints were found. However, in this case the unmolested left footprint was also preserved and indicated a normal tridactyl foot.

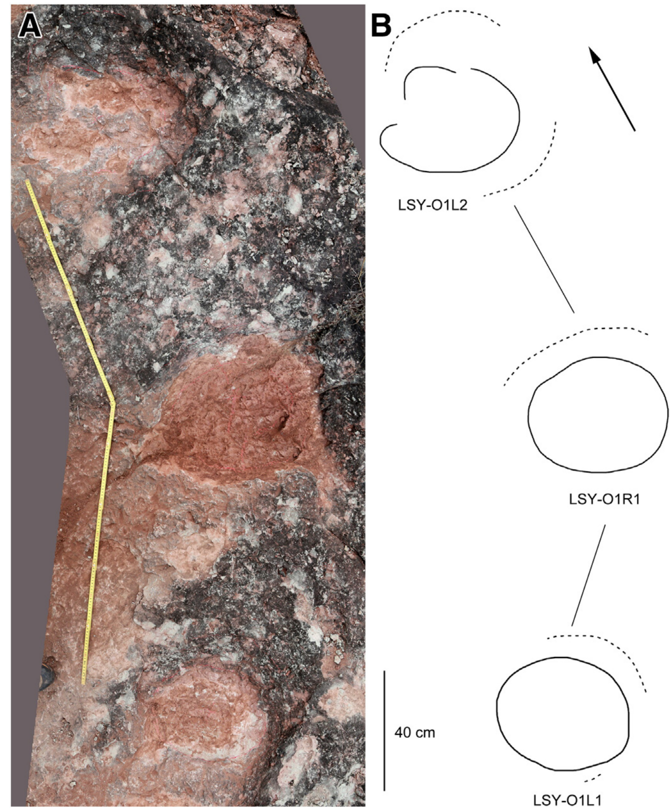

Fig. 9. Photographs (A) and outline drawings (B) of an ornithopod trackway from the Lashuyuan site.

5. Ichnology of the Lashuyuan tracksite

There are at least six Lashuyuan tracks, with a mean length of 34.3 cm. They comprise the trackway LSY-O1, which is severely weathered (Fig. 9), likely due to long exposure and suboptimal substrate conditions at the time of registration. The first three tracks in the trackway are better preserved, but only a few morphological features can be observed. Only LSY-O1L2 has a possible outer digit and part of the digit III trace. The sequence (LSY-O1L1-L2) lacks any traces of the manus, and the inferred pes tracks are transverse with a mean L/W ratio of 0.8, and a pace angulation of 146°. Both have widths greater than lengths and pace angulations similar to YMK-O1, indicating that LSY-O1 may have an affinity to the widely distributed *Hadrosauropodus*.

6. Comparison with other Late Cretaceous dinosaur faunas from China and paleoenvironmental implications

The Nanxiong Basin has yielded the greatest diversity of Upper Cretaceous dinosaurs from red beds in South China (Fang et al., 2009), and Yangmeikeng has enhanced the known diversity of Late Cretaceous dinosaur faunas in the area (Table 2). *Microhadrosaurus* is the only named hadrosaur from the Nanxiong Basin (Dong, 1979). However, the specimen is only an incomplete juvenile whose body was about 2.6 m long (Dong, 1987). Brett-Surman (1989) suspected that it is a *nomen dubium*. *Microhadrosaurus* may correspond to the small and medium-sized trackmakers of *Hadrosauropodus* isp. The discovery of *Hadrosauropodus* is the first evidence of larger hadrosaur individuals in the Nanxiong Basin, while the skeletal record has yielded only small juveniles thus far. Similarly, deinonychosaurs, birds, and pterosaurs are also absent in the skeletal record. Bones of these small lightweight animals are particularly difficult to preserve. Fortunately, track assemblages help mitigate this preservation bias.

Table 2
Comparison of skeleton and track records of Late Cretaceous Nanxiong dinosaur fauna.

		Bone records	Tracks
Ornithopod	Hadrosaurid	*Microhadrosaurus* (Dong, 1979)	*Hadrosauropodus*
Ankylosaur	Nodosauria	Osteoderms (Young, 1965a)	–
Non-avian	Therizinosaurid	*Nanshiungosaurus* (Dong, 1979)	–
theropod	Tyrannosaurid	*Qianzhousaurus* (Lü et al., 2014)	–
	Oviraptorids	*Shixinggia* (Lü and Zhang, 2005)	–
		Banji (Xu and Han, 2010)	–
		Jiangxisaurus (Wei et al., 2013)	–
	Coelurosauria	Fragments (Young, 1965a)	–
	Deinonychosaurian	–	? troodontid tracks
Bird	–	–	cf. *Wupus* isp.
Sauropod	Titanosauriformes	*Gannansaurus* (Lü et al., 2013)	–
Pterosaur	–	–	*Pteraichnus*
Turtle	–	*Nanhsiungchelys* (Yeh,1966)	–

The Wangshi Group, from Shandong Province, records a dinosaur fauna dominated by hadrosaurs (Hu, 1973), with representatives of the Coronosauria (Xu et al., 2010b) and also tyrannosaurids (Hone et al., 2011). The Yuliangze Formation, of Heilongjiang Province, was also dominated by hadrosaurs (Godefroit et al., 2008a), and bone fragments document indeterminate tyrannosaurids and ornithomimosaurs from this unit (Wang et al., 2015). The Nanxiong dinosaur fauna is similar to the Shandong and Heilongjiang Late Cretaceous faunas.

Perhaps the best sampled, geographically proximate, and nearly contemporaneous dinosaur fauna is that from the Wulansuhai Formation of Bayan Mandahu in northern Inner Mongolia. The Bayan Mandahu dinosaur fauna is also similar in composition to the nearby Djadochta Formation, Mongolia (Xu et al., 2010a). These faunas are dominated by the protoceratopsid *Protoceratops* (Lambert et al., 2001) and the dromaeosaurid *Velociraptor* (Godefroit et al., 2008b). Also abundant are Oviraptoridae (Nicholas et al., 2010), Hadrosauridae indet. Sauropoda indet., Tyrannosauridae indet. (Nicholas et al., 2010), Crocodylomorpha (Mook, 1924), and lizards (Gilmore, 1943). However, the Bayan Mandahu dinosaur fauna has relatively few hadrosaurs, while the Nanxiong Region lacks ceratopsians. This may reflect differences in the paleoenvironment. The paleoenvironment of Bayan Mandahu was semi-arid and characterized by alluvial (stream-deposited) and eolian (wind-deposited) sediments. The Nanxiong Region represents a lacustrine depositional environment (Yang et al., 2004). This matches with the co-occurrence of pterosaur and bird footprints, in the Cretaceous mostly found in lakeshore and fluvio-lacustrine deposits (He et al., 2013; Kim et al., 2006; Xing et al., 2013, 2015a, b). Bakhurina and Unwin (1995) suggested a shift of pterosaur habitats from marginal marine to terrestrial environments such as lakes between the Jurassic and the Cretaceous, which is supported by the track record (Lockley et al., 1995, 2008). Late Cretaceous pterosaur-bird assemblages are well-known for example from North America and South Korea (Lockley and Gillette, 1999; Hwang et al., 2002). The Upper Cretaceous Nanxiong ichnofauna is characterized by a high diversity and co-occurrence of the footprints of large pterosaurs, large birds, large (hadrosaur) and small ornithopods as well as medium-sized to large theropods. This gives insight into typical lakeshore environments in the Late Cretaceous. Based on the ichnofauna, a hypothetical scenario can be reconstructed: While pterosaurs and birds were hunting small arthropods, annelids and fishes along the lakeshore, groups of ornithopods used this place for water supply and plant food resources, an animal community attracting theropods that were roaming around looking for potential pray. The small number of theropods versus abundant other archosaur groups reflects a typical predator-pray relationship seen in many vertebrate assemblages up to the present.

7. Conclusions

The Late Cretaceous Zhutian Formation at the Yangmeikeng tracksite was excavated and restudied. It revealed an ornithopod dominated track assemblage, which was documented by creating a complete map of the site using both photogrammetry and traditional mapping techniques. The assemblage consists of about 30 large and small ornithopod tracks with sparse evidence of theropods and pterosaurs. The large ornithopod tracks are assigned to *Hadrosauropodus nanxiongensis* and *Hadrosauropodus* isp. indet. The small ornithopod tracks show only three pes digit traces, without heel or manus impressions, and probably represent pes tracks penetrating from a higher level. A small *Wupus*-like theropod track and a *Pteraichnus*-like pes track are confirmed on the basis of photographs taken at the site, prior to the present study. Large enigmatic didactyl tracks could be of deinonychosaurian affinity, but are more likely the result of poor preservation of a tridactyl track. The Nanxiong dinosaur fauna is reminiscent of the Shandong and Heilongjiang Late Cretaceous faunas and is consistent with the Nanxiong region track record. However, the importance of the Nanxiong ichnofauna lies in its composition and co-occurrence of the tracks of hadrosaurs, avian theropods and non-avian theropods and pterosaurs not documented from the Late Cretaceous of this region by the skeletal record. From a global perspective this assemblage documents a complex animal community in a Late Cretaceous lakeshore environment. The ichnofauna gives a direct insight into paleoecology, behavior and interaction among tracemakers in this habitat. Moreover, Late Cretaceous tracksites are generally rare, both in China and elsewhere in well-studied regions of the Northern Hemisphere. Sites previously described from the Nanxiong region as well as the site described here deal with material that has suffered previous loss from erosion, as well as ongoing deterioration due to lithologies that are not strongly resistant to the humid subtropical climate. For these reasons the detailed documentation of these sites is important.

Acknowledgments

The authors thank to the Nanxiong Dinosaur Provincial Nature Reserve Administration, which provided logistical support. We also thank Peter Falkingham for the contribution on the 3D height map of tracks. Detailed revisions by Xu Xing, Spencer G. Lucas and the editor Thomas Algeo greatly improved the final version and we are appreciative of their efforts. This research was supported by the 2013 and 2015 support fund for graduate student's science China University of Geosciences (Beijing) (No. 51223229), China.

References

Abel, O., 1935. Vorzeitliche Lebensspuren. Gustav Fischer, Jena.
Alexander, R.M., 1976. Estimates of speeds of dinosaurs. Nature 26, 129–130.
Alpert, S.P., 1974. Systematic review of the genus *Skolithos*. J. Pal. 48, 661–669.
Bakhurina, N.N., Unwin, D.M., 1995. A survey of pterosaurs from the Jurassic and Cretaceous of the former Soviet Union and Mongolia. Hist. Biol. 10, 197–245.
Billon-Bruyat, J.P., Mazin, J.M., 2003. The systematic problem of tetrapod ichnotaxa: the case study of *Pteraichnus* Stokes, 1957 (Pterosauria, Pterodactyloidea). In: Buffetaut, E., Mazin, J.M. (Eds.), Evolution and Palaeobiology of Pterosaurs, 217. Geological Society, London, pp. 315–324.

Brett-Surman, M.K., 1989. A Revision of the Hadrosauridae (Reptilia:Ornithischia) and Their Evolution During the Campanian and Maastrichtian. Ph.D. Dissertation. Graduate School of Arts and Sciences of The George Washington University, Washington, D.C.
Chen, P.J., 1996. Freshwater biota, stratigraphic correlation of Late Cretaceous of China. Geol. Soc. India Mem. 37, 35–62.
Chen, P.J., 2003. Jurassic and Cretaceous biostratigraphy of China. In: Zhang, W.T., et al. (Eds.), Biostratigraphy of China. Science Press, Beijing, pp. 423–546.
Chen, P.J., Li, J., Matsukawa, M., Zhang, H., Wang, Q., Lockley, M.G., 2006. Geological ages of dinosaur-track-bearing formations in China. Cretac. Res. 27, 22–32.
Cheng, Y.N., Qiang, J.I., Wu, X.C., Shan, H.Y., 2008. Oviraptorosaurian eggs (Dinosauria) with embryonic skeletons discovered for the first time in China. Acta Geol. Sin. 82, 1089–1094.
Chow, M.Z., Zhang, Y.P., Wang, B.Y., Ding, S.Y., 1977. Mammalian fauna from the Paleocene of Nanxiong Basin, Guangdong. Acta Palaeontol. Sin. 20, 1–100.
Dong, Z.M., 1979o. The Cretaceous dinosaur fossils in southern China. In: Institute of Vertebrate Paleontology and Paleoanthropology and Nanjing Institute of Paleontology (Ed.), Mesozoic and Cenozoic Red Beds of South China. Science Press, Nanxiong, China, pp. 342–350.
Dong, Z.M., 1980. On the dinosaurian faunas and their stratigraphic distribution in China. J. Stratigr. 4, 256–263.
Dong, Z.M., 1987. Dinosaurs from China. China Ocean Press, Beijing.
Dong, Z.M., 1992. Dinosaurian Faunas of China. Springer Verlag, Berlin.
Erben, H.K., 1995. The Cretaceous/Tertiary Boundary in the Nanxiong-Basin Continental Facies, SE-China. 32. Erdwissenschaftliche Forschung, Wiesbaden, Germany, pp. 1–245.
Fang, X., Li, P., Zhang, Z., Zhang, X., Lin, Y., Guo, S., Cheng, Y., Li, Z., Zhang, X., Cheng, Z., 2009. Cretaceous strata in Nanxiong Basin of Guangdong and the evolution from the dinosaur egg to the bird egg. Acta Geol. Sin. 30, 167–186.
Fujita, M., Lee, Y.N., Azuma, Y., Li, D., 2012. Unusual tridactyl trackways with tail traces from the Lower Cretaceous Hekou Group, Gansu Province, China. PALAIOS 27, 560–570.
Frey, R.W., Pemberton, S.G., Fagerstrom, J.A., 1984. Morphological, ethological and environmental significance of the ichnogenera *Scoyenia* and *Anchorichnus*. J. Paleontol. 58, 511–528.
Gilmore, C.W., 1943. Fossil lizards of Mongolia. Bull. Am. Mus. Nat. Hist. 81, 361–384.
Godefroit, P., Hai, S.L., Yu, T.X., Lauters, P., 2008a. New hadrosaurid dinosaurs from the uppermost Cretaceous of north–eastern China. Acta Palaeontol. Pol. 53, 47–74.
Godefroit, P., Currie, P.J., Li, H., Shang, C.Y., Dong, Z.M., 2008b. A new species of *Velociraptor* (Dinosauria: Dromaeosauridae) from the Upper Cretaceous of northern China. J. Vertebr. Paleontol. 28, 432–438.
Graham, J.R., Pollard, J.E., 1982. Occurrence of the trace fossil Beaconites antarcticus in the Lower carboniferous fluviatile rocks of County Mayo, Ireland. Palaeogeogr. Palaeoclimatol. Palaeoecol. 38, 257–268.
Haldemann, S.S., 1840. Supplement to number one of a monograph of the Limniades and other freshwater bivalves shells of the apparently new animals in different classes, and names and characters of the subgenera in *Paludina* and *Anculosa*. Philadelphia 1–3.
He, Q., Xing, L.D., Zhang, J.P., Lockley, M.G., Klein, H., Persons, W.S.I.V., Qi, L.Q., Jia, C.K., 2013. New Early Cretaceous pterosaur–bird track assemblage from Xinjiang, China – palaeoethology and palaeoenvironment. Acta Geol. Sin. 87, 1477–1485.
Hone, D.W.E., Wang, K.B., Sullivan, C., Zhao, X.J., Chen, S.Q., Li, D.J., Ji, S.A., Ji, Q., Xu, X., 2011. A new, large tyrannosaurine theropod from the Upper Cretaceous of China. Cretac. Res. 32, 495–503.
Houck, K., Lockley, M.G., 2006. Life in an active volcanic arc: petrology and sedimentology of the dinosaur track beds of the Jindong Formation (Cretaceous), Gyeongsang basin, South Korea. Cretac. Res. 27, 102–122.
Hu, C.C., 1973. A new hadrosaur from the Cretaceous of Chucheng, Shantung. Acta Geol. Sin. 2, 179–206.
Hwang, K.G., Huh, M., Lockley, M.G., Unwin, D.M., Wright, J.L., 2002. New pterosaur tracks (Pteraichnidae) from the Late Cretaceous Uhangri Formation, southwestern Korea. Geol. Mag. 139, 421–435.
Kim, J.Y., Kim, S.H., Kim, K.S., Lockley, M.G., 2006. The oldest record of webbed bird and pterosaur tracks from South Korea (Cretaceous Haman Formation, Changseon and Sinsu islands): more evidence of high avian diversity in East Asia. Cretac. Res. 27, 56–69.
Kim, J.Y., Lockley, M.G., Kim, K.S., Seo, S.J., Lim, J.D., 2012. Enigmatic giant pterosaur tracks and associated ichnofauna from the Cretaceous of Korea: implication for the bipedal locomotion of pterosaurs. Ichnos 19, 50–65.
Lambert, O., Godefroit, P., Li, H., Shang, C.Y., Dong, Z.M., 2001. A new species of *Protoceratops* (Dinosauria, Neoceratopsia) from the Late Cretaceous of Inner Mongolia (P. R. China). Bull. Inst. R. Sci. Nat. Belg. Sci. Terre 5–28.
Leidy, J., 1856. Notices of remains of extinct reptiles and fishes, discovered by Dr. F. V. Hayden in the bad lands of Judith River, Nebraska Territory. Proc. Acad. Natl. Sci. Phila. 8, 72–73.
Lockley, M.G., 1991. Tracking Dinosaurs: A New Look at an Ancient World. Cambridge University Press.
Lockley, M.G., Gillette, D.D., 1999. Pterosaur and bird tracks from a new Late Cretaceous locality in Utah. Vertebrate Paleontology in Utah: Utah Geol. Surv. Misc. Publ. 99. 1, pp. 355–360.
Lockley, M.G., 2009. New perspectives on morphological variation in tridactyl footprints: clues to widespread convergence in developmental dynamics. Mar. Geol. Quat. Geol. 53, 415–432.
Lockley, M.G., Logue, T.J., Moratalla, J.J., Hunt, A.P., Schultz, R.J., Robinson, J.W., 1995. The fossil trackway *Pteraichnus* is pterosaurian, not crocodilian: implications for the global distribution of pterosaur tracks. Ichnos 4, 7–20.
Lockley, M.G., Harris, J.D., Mitchell, L., 2008. A global overview of pterosaur ichnology: tracksite distribution in space and time. Zitteliana B 28, 185–198.
Lockley, M.G., Lucas, S.G., 2014. Tracking dinosaurs and other tetrapods in the wild west of North America. N. M. Mus. Nat. Hist. Sci. Bull. 62, 1–4.
Lockley, M.G., Meyer, C.A., 2000. Dinosaur Tracks and Other Fossil Footprints of Europe. Columbia University Press (323p).
Lockley, M.G., Xing, L., Kim, J.-Y., Matsukawa, M., 2014. Tracking Early Cretaceous dinosaurs in China: a new database for comparison with ichnofaunal data from Korea, the Americas and Europe. Biol. J. Linn. Soc. 113, 770–789.
Lockley, M.G., Xing, L., Matthews, N.A., Breithaupt, B., 2016a. Didactyl raptor tracks from the Cretaceous, plainview sandstone at Dinosaur Ridge, Colorado. Cretac. Res. 61, 161–168.
Lockley, M.G., Harris, J.D., Li, R., Xing, L.D., Lubbe, T.v.d., 2016b. Two-toed tracks through time: on the trail of "raptors" and their allies. In: Falkingham, P.L., Marty, D., Richter, A. (Eds.), Dinosaur Tracks, The Next Steps. Indiana University Press, Bloomington, pp. 183–200.
Lü, J.C., Zhang, B.K., 2005. A new oviraptorid (Theropoda: Oviraptorosauria) from the Upper Cretaceous of the Nanxiong Basin, Guangdong Province of southern China. Acta Palaeontol. Sin. 44, 412–422.
Lü, J.C., Yi, L., Zhong, H., Wei, X., 2013. A new somphospondylan sauropod (Dinosauria, Titanosauriformes) from the Late Cretaceous of Ganzhou, Jiangxi Province of southern China. Acta Geol. Sin. 87, 678–685.
Lü, J.C., Yi, L., Brusatte, S.L., Yang, L., Li, H., Chen, L., 2014. A new clade of Asian Late Cretaceous long-snouted tyrannosaurids. Nat. Commun. 5, 3788.
McCrea, R.T., Tanke, D.H., Buckley, L.G., Lockley, M.G., Farlow, J.O., Xing, L.D., Matthews, N.A., Helm, C.W., Pemberton, S.G., Breithaupt, B.H., 2015. Vertebrate ichnopathology: pathologies inferred from dinosaur tracks and trackways from the Mesozoic. Ichnos 22 (3–4), 235–260.
Mikhaillov, K.E., 2000. Eggs and eggshells of dinosaurs and birds from the Cretaceous of Mongolia. In: Benton, M.J., Shishkin, M.A., Unwin, D.M., Kurochkin, E.N. (Eds.), The Age of Dinosaurs in Russia and Mongolia. Cambridge University Press, Cambridge, pp. 561–572.
Mook, C.C., 1924. A new crocodilian from Mongolia. Am. Mus. Novit. 117, 1–5.
Nicholas, R.L., Currie, P.J., Dong, Z.M., 2010. A new oviraptorid (Dinosauria: Theropoda) from the Upper Cretaceous of Bayan Mandahu, Inner Mongolia. Palaeontology 53, 945–960.
Norell, M.A., Makovicky, P.J., Bever, G.S., Balanoff, A.M., Clark, J.M., Barsbold, R., Rowe, T., 2009. A review of the Mongolian Cretaceous dinosaur Saurornithoides (Troodontidae: Theropoda). Am. Mus. Novit. 3654, 1–63.
Osborn, H.F., 1924. The discovery of an unknown continent. Nat. Hist. 24, 133–149.
Paul, G.S., 2010. The Princeton Field Guide to Dinosaurs. Princeton University Press, Princeton.
Peng, B.X., Du, Y.S., Li, D.Q., Bai, Z.C., 2004. The first discovery of the Early Cretaceous pterosaur track and its significance in Yanguoxia, Yongjing County, Gansu Province. Earth Sci. J. China Univ. Geosci. 29, 21–24.
Riabinin, A.N., 1925. A Mounted Skeleton of the Giant Reptile *Trachodon amurense* nov. sp: Izvest. Geol. Kon. (USSR). 44 pp. 1–12.
Retallack, G.J., 2001. *Scoyenia* burrows from Ordovician palaeosols of the Juniata Formation in Pennsylvania. Palaeontology 44, 209–235.
Stokes, W.L., 1957. Pterodactyl tracks from the Morrison Formation. J. Paleontol. 31, 952–954.
Thulborn, R.A., 1990. Dinosaur Tracks. Chapman and Hall, London.
Wang, N., Kuang, H., Liu, Y., Peng, N., Xu, H., Zhang, P., Wang, M., Wang, B., 2015. An Wei1Taphonomic characteristics of the Late Cretaceous cluster dinosaur fossils in eastern China and comparison between domestic and abroad. J. Palaeogeogr. 17, 593–610.
Wei, X., Pu, H., Xu, L., Liu, D., Lü, J.C., 2013. A new oviraptorid dinosaur (Theropoda: Oviraptorosauria) from the Late Cretaceous of Jiangxi Province, Southern China. Acta Geol. Sin. (Engl. Ed.) 87, 899–904.
Weishampel, D.B., Fastovsky, D.E., Watabe, M., Varricchio, D., Jackson, D., Tsogtbaatar, K., Barsbold, R., 2008. New oviraptorid embryos from Bugin-tsav, Nemegt Formation (Upper Cretaceous), Mongolia, with insights into their habit and growth. J. Vertebr. Paleontol. 28, 1110–1119.
White, C.D., 1929. Flora of the Hermit Shale, Grand Canyon. Carnegie Institute of Washington Publication, Arizona.
Wiman, C., 1929. Die Kreide-Dinosaurier aus Shantung. Acta Palaeontol. Sin. 6, 1–67.
Xing, L.D., Wang, F.P., Pan, S.G., Chen, W., 2007. The discovery of dinosaur footprints from the Middle Cretaceous Jiaguan Formation of Qijiang County, Chongqing City. Acta Palaeontol. Sin. 81, 1591–1602.
Xing, L.D., Harris, J.D., Dong, Z.M., Lin, Y.L., Chen, W., Guo, S.B., Ji, Q., 2009a. Ornithopod (Dinosauria: Ornithischia) tracks from the Upper Cretaceous Zhutian Formation in Nanxiong Basin, China and general observations on large Chinese ornithopod footprints. Geol. Bull. China 28, 829–843.
Xing, L.D., Harris, J.D., Feng, X.Y., Zhang, Z.J., 2009b. Theropod (Dinosauria: Saurischia) tracks from Lower Cretaceous Yixian Formation at Sihetun, Liaoning Province, China and possible track makers. Geol. Bull. China 28, 705–712.
Xing, L.D., Harris, J.D., Gierliński, G.D., Gingras, M.K., Divay, J.D., Tang, Y.G., Currie, P.J., 2012. Early Cretaceous pterosaur tracks from a "buried" dinosaur tracksite in Shandong Province, China. Palaeoworld 21, 50–58.
Xing, L.D., Lockley, M.G., Piñuela, L., Zhang, J.P., Klein, H., Li, D.Q., Wang, F.P., 2013. Pterosaur trackways from the Lower Cretaceous Jiaguan Formation (Barremian–Albian) of Qijiang, Southwest China. Palaeogeogr. Palaeoclimatol. Palaeoecol. 392, 177–185.
Xing, L.D., Lockley, M.G., Zhang, J.P., Klein, H., Persons, W.S.I.V., Dai, H., 2014. Diverse sauropod–, theropod–, and ornithopod–track assemblages and a new ichnotaxon *Siamopodus xui* ichnosp. nov. from the Feitianshan Formation, Lower Cretaceous of

Sichuan Province, southwest China. Palaeogeogr. Palaeoclimatol. Palaeoecol. 414, 79–97.

Xing, L.D., Buckley, L.G., McCrea, R.T., Lockley, M.G., Zhang, J.P., Piñuela, L., Klein, H., Wang, F.P., 2015a. Reanalysis of *Wupus agilis* (Early Cretaceous) of Chongqing, China as a large avian trace: differentiating between large bird and small non-avian theropod tracks. PLoS One 10, e0124039.

Xing, L.D., Lockley, M.G., Marty, D., Zhang, J.P., Wang, Y., Klein, H., McCrea, R.T., Buckley, L.G., Belvedere, M., Mateus, O., Gierliński, G.D., Piñuela, L., Persons, W.S.I.V., Wang, F.P., Ran, H., Dai, H., Xie, X.M., 2015b. An ornithopod-dominated tracksite from the Lower Cretaceous Jiaguan Formation (Barremian–Albian) of Qijiang, South-Central China: new discoveries, ichnotaxonomy, preservation and palaeoecology. PLoS One 10, e0141059.

Xing, L.D., Lockley, M.G., Hu, N.Y., Li, G., Tong, F.H., Matsukawa, M., Klein, H., Ye, Y., Zhang, J.P., Persons, W.S.I.V., 2016a. Saurischian track assemblages from the cretaceous Shenhuangshan Formation in the Yuanma Basin, Southern China. Cretac. Res. 65, 1–9.

Xing, L.D., Li, D.Q., Falkingham, P.L., Lockley, M.G., Benton, M.J., Klein, H., Zhang, J.P., Ran, H., Persons, W.S.I.V., Dai, H., 2016b. Digit-only sauropod pes trackways from China – evidence of swimming or a preservational phenomenon? Sci. Report. 6, 21138.

Xu, X., Han, F.L., 2010. A new oviraptorid dinosaur (Theropoda: Oviraptorosauria) from the Upper Cretaceous of China. Vert. PalAsiat. 48, 11–18.

Xu, X., Choinere, J.N., Pittman, M., Tan, Q.W., Xiao, D., Li, Z.Q., Tan, L., Clark, J.M., Norell, M.A., Hone, D.W.E., Sullivan, C., 2010a. A new dromaeosaurid (Dinosauria: Theropoda) from the Upper Cretaceous Wulansuhai Formation of Inner Mongolia, China. Zootaxa 2403, 1–9.

Xu, X., Wang, K.B., Zhao, X.J., Sullivan, C., Chen, S.Q., 2010b. A new leptoceratopsid (Ornithischia: Ceratopsia) from the Upper Cretaceous of Shandong, China and its implications for neoceratopsian evolution. PLoS One 5, e13835.

Yang, S., Zhang, J., Yang, M., 2004. Trace Fossils of China. Science Press, Beijing.

Young, C.C., 1958. The dinosaurian remains of Laiyang, Shantung. Pal. Sin. N. Ser. C 16, 1–138.

Yeh, H.K., 1966. A new Cretaceous turtle of Nanhsiung, northern Kwangtung. Vert. PalAsiat. 10, 191–200.

Young, C.C., 1965a. Fossil reptiles from Nanxiong, Guangdong. Vert. PalAsiat. 9, 292–297.

Young, C.C., 1965b. Fossil eggs from Nanhsiung, Kwangtung and Kanchou, Kiangsi. Vert. PalAsiat. 9, 141–189.

Young, C.C., Chow, M.M., 1962. Some reptilian fossils from the “red beds” of Kwangtung and Chekiang. Vert. PalAsiat. 6, 130–135.

Young, C.C., Chow, M.C., 1963. Cretaceous and Paleocene vertebrate horizons of North Kwangtung. SCIENCE CHINA Math. 6, 1411.

Zhang, Y.P., Tong, Y.S., 1963. Subdivision of the Nanxiong Basin “red beds” in Guangdong Province. Vert. PalAsiat. 7, 249–260.

Zhang, J., Li, D., Li, M., Lockley, M.G., Bai, Z., 2006. Diverse dinosaur-, pterosaur-, and bird-track assemblages from the Hakou Formation, Lower Cretaceous of Gansu Province, northwest China. Cretac. Res. 27, 44–55.