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The first record of *Anomoepus* tracks from the Middle Jurassic of Henan Province, Central China

Lida Xing[a], Nasrollah Abbassi[b], Martin G. Lockley[c], Hendrik Klein[d], Songhai Jia[e], Richard T. McCrea[f] and W. Scott PersonsIV[g]

[a]School of the Earth Sciences and Resources, China University of Geosciences, Beijing, China; [b]Faculty of Sciences, Department of Geology, University of Zanjan, Zanjan, Iran; [c]Dinosaur Tracks Museum, University of Colorado Denver, Denver, CO, USA; [d]Saurierwelt Paläontologisches Museum, Neumarkt, Germany; [e]Henan Geological Museum, Henan Province, China; [f]Peace Region Palaeontology Research Centre, British Columbia, Canada; [g]Department of Biological Sciences, University of Alberta, Edmonton, Canada

ABSTRACT
Small, gracile mostly tridactyl tracks from the Middle Jurassic of Henan Province represent the first example of the ichnogenus *Anomoepus* from this region. They represent a growing number of reports (at least eight) of this ichnogenus from the Jurassic of China. In conjunction with *Changpeipus* and *Eubrontes,* they appear characteristic of known global footprint biochrons. *Anomoepus* indicates the presence of ornithischian dinosaurs that are often scarce or unknown from skeletal remains in coeval deposits. When first discovered, these tracks were informally referred to as bird tracks. This interpretation reflects convergence between small Jurassic *Anomoepus* and avian theropod tracks that are hitherto known only from the Cretaceous and the Cenozoic. However, most *Anomoepus* are larger and more robust than any hitherto known Mesozoic avian tracks.

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Anomoepus; ornithischian; Jurassic; Henan; China

Introduction

In China, the known Jurassic skeletal dinosaur record consists of three major faunas: the Early–Jurassic *Lufengosaurus* (basal sauropodomorph) Fauna, the Middle–Jurassic *Shunosaurus* (sauropod) Fauna and the Late–Jurassic *Mamenchisaurus* (sauropod) Fauna (Dong, 1992; Peng et al. 2005). All three are best known from the Yunnan, Sichuan and Xinjiang areas (Dong 1992). In the last 15 years, a fourth fauna has come to be well documented and sampled: the late Middle Jurassic–early Late Jurassic Daohugou Biota of Northeast China, which also includes a substantial pterosaur and synapsid record (Liu et al. 2006; Xu et al. 2015). In all these Jurassic faunas, skeletal fossils of ornithischia are rare, although small neornithischians (e.g. *Xiaosaurus* Dong & Tang 1983; *Agilisaurus* Peng 1990) are known from the Middle Jurassic of Sichuan Basin and heterodontosaurids (*Tianyulong*, Zheng et al. 2009) are known from the Daohugou Biota.

For this reason, the occurrences of the small ornithischian track type *Anomoepus* are important supplements to the scarce ornithischian skeletal record. Currently, *Anomoepus* is mainly known from Sichuan, Chongqing and Yunnan in Southwest China as well as from Inner Mongolia and Shaanxi, in North China. Most specimens were Lower–Middle Jurassic in age, while one example was found in Upper–Jurassic deposits (Xing et al. in press).

In western Henan Province of Central China, Jurassic strata are sporadically distributed in the Mianchi and Yima areas. Exposures in the Yima Basin are typically the result of coal mine exploration. In August 2006, the Henan Geological Museum found two dinosaur tracks in Yima Northern Open-pit Coal Mine. Lü et al. (2007) described these specimens and named a new ichnotaxon: *Changpeipus xuiana*. Subsequently, Xing et al. (2009, 2014) referred *C. xuiana* to *Changpeipus carbonicus*. Recently, Mr. Xuelei Duan, an employee of Northern Open-pit Coal Mine, found dinosaur tracks on a mechanically exposed coal bed, and this discovery led to additional findings by the Henan Geological Museum and Beijing Natural History Museum, including large and small-sized tridactyl tracks. However, none of these tracks have been appropriately described. We here offer a detailed description of the ornithischian tracks found by Mr. Xuelei Duan. Furthermore, we discuss and re-evaluate the ichnotaxonomy of the Yima tracks based on the new findings, comparing them with similar tracks from other localities of China and the global record. Another aspect considered is their biostratigraphic importance.

Institutional abbreviations

HGM = Henan Geological Museum, Henan Province, China; YNM = Yima Northern Open-pit Coal Mine, Yima City, Henan Province, China

Geological setting

The dinosaur tracks described here were located at the north side of Yima Northern Open-pit Coal Mine, 1.5 km south-east

CONTACT Lida Xing xinglida@gmail.com

of Yima City (Figures 1 and 2), and are preserved in an argillaceous siltstone layer of the Yima Formation (Lü et al. 2007). The bottom of the Yima Formation consists of a sandy conglomerate layer with a lower part comprised of grey siltstone interbedded with fine- to medium-grained feldspathic quartzose sandstone, and an upper part comprised of gray black claystone interbedded with siltstone and thin coal beds (Xi & Pei 2008) (Figure 3). The Yima Formation is a typical inland intermountain basin deposit, progressively transitioning from coarse-grained deltaic fan facies to muddy fine-grained lacustrine facies (Chen 2013).

The Yima Formation was considered an Early–Jurassic deposit when first named (No. 104 geological team of Henan Coal Geology Bureau 1960), however, the Henan Bureau of Geology and Mineral Resources (1989) referred it to the Early–Middle Jurassic. The Yima flora (*Coniopteris–Phoenicopsis*), as documented by specimens from the open pit mine, is similar to typical Middle–Jurassic flora from around the world (Zhou & Zhang 1989; Yao et al. 1998), and the Yima Formation has, therefore, been deemed Early–Middle Jurassic (Zhou & Zhang 1989; Zeng et al. 1995; Yao et al. 1998; Chen 2013).

Gingko dominates the Yima flora (34.5%), followed by filicinae (24.1%), sphenopsida (13.8%), cycad (11.6%), conifers (11.6%), and bryophytes (2.3%) (Zeng et al. 1995). The Yima floral assemblage is similar to that of modern flora in warm temperate zones, reflecting a warm and damp climate (Chen 2013).

Materials and methods

Mr. Xuelei Duan collected three specimens from the Yima Northern Open-pit Coal Mine, which were stored in the planned Yima Dinosaur and Bizarre Stone Museum, catalogued as YNM-1-3. YNM-1 and 2 have been photographed, measured and converted into 3D models. The casts are stored at China University of Geosciences (Beijing) catalogued as CUGB-YNM-1-2. YNM-3 was badly damaged during collecting and is broken into several pieces permitting no repair. Research on YNM-3 is entirely based on photos taken before damage.

The 3D-1 model was compiled from 11 photographs taken from an average height of 0.988 m with a Canon EOS5D Mark III camera (5760 × 3840 resolution – pixel size = 6.43599um). 3D-2 model was compiled from 28 photographs taken from an average height of 1.59 m with a Canon EOS5D Mark III camera (5760 × 3840 resolution – pixel size = 6.43599 μm). Both photogrammetric models were generated with Agisoft Photoscan Professional (v 1.0.4) and colour topographic profiles were built with Cloud Compare (v 2.5.3). The error for the 3D-1 model was 0.143pix and the error for the 3D-2 model was 0.129 pix. Tracings were taken from the topographic profile models. The measurements comprise standard parameters such as maximum length of footprint (ML), maximum width of footprint (MW), ML/MW ratio, divarication angle between digit traces II–IV and

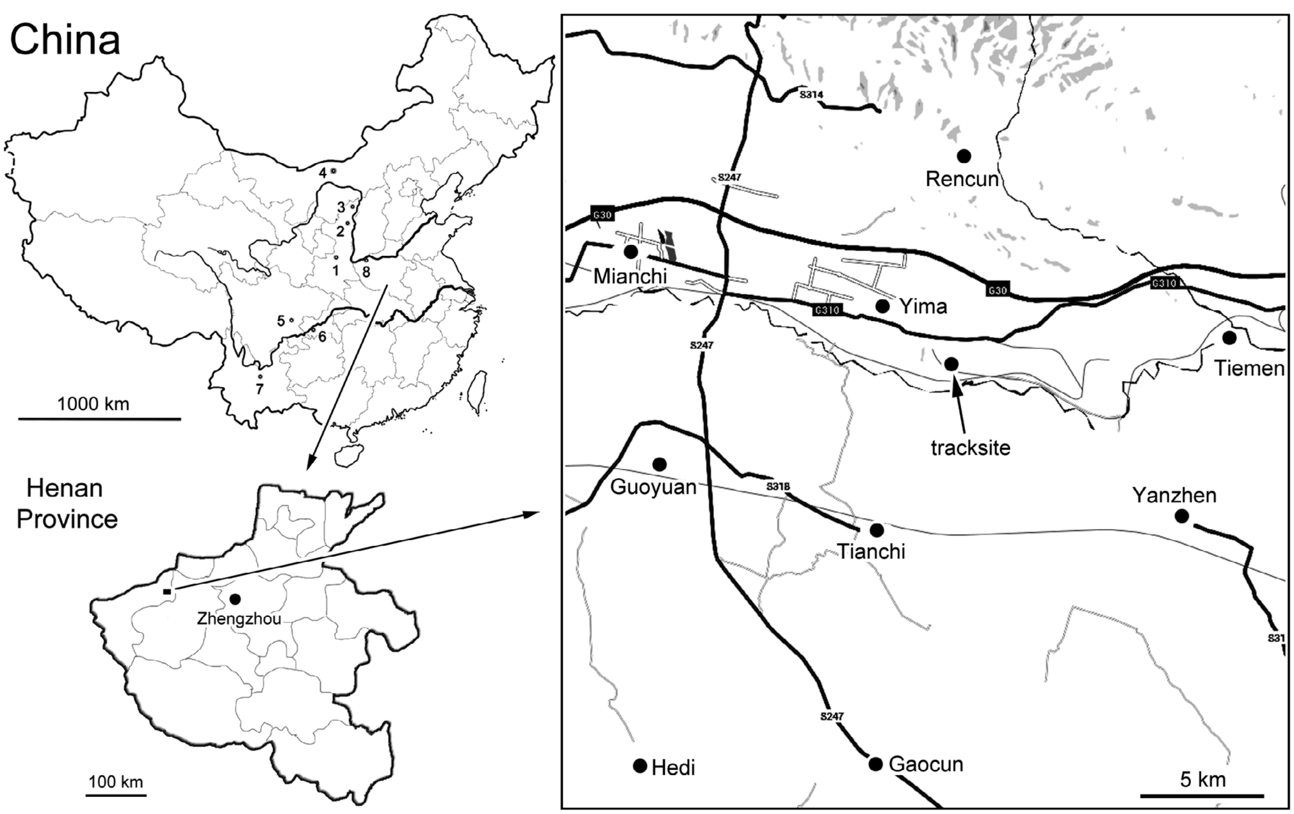

Figure 1. Geographic map indicating the location of the dinosaur footprint localities in Henan Province, China and the distribution of *Anomoepusm* tracks from China: 1, Middle–Jurassic Jiaoping Coal Mine site, Shaanxi Province (Xing et al. 2015); 2, Middle–Jurassic Huo and Wang sites from Shaanxi Province (Xing et al. 2015); 3, Lower–Jurassic Lijiananwa site from Shaanxi Province (Li et al. 2012); 4, Lower–Jurassic Wulatezhongqi site from Inner Mongolia (Li et al. 2010); 5, Middle–Jurassic Jinlijing site, Sichuan Province (Lockley & Matsukawa 2009); 6, Upper–Jurassic Nan'an site from Chongqing municipality (Xing et al. 2013); 7, Lower–Jurassic Dalishu tracksite III from Yunnan Province (Xing et al. in press); 8, this text.

Figure 2. Photograph of the outcrop of Yima Northern Open-pit Coal Mine tracksite.

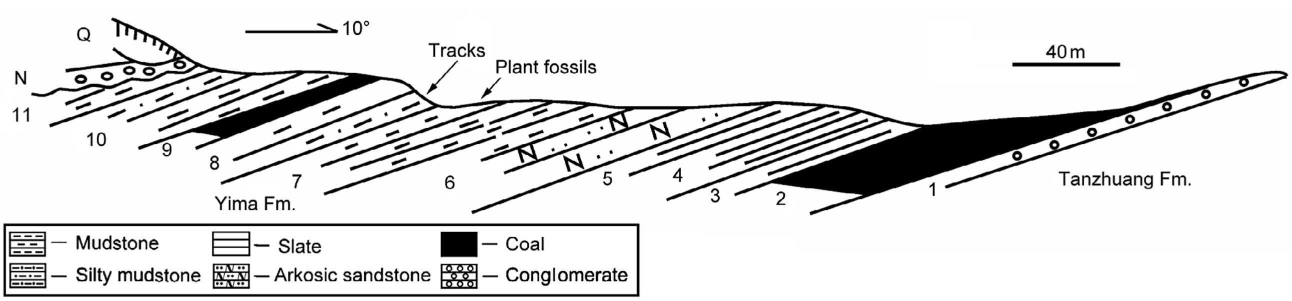

Figure 3. Lithological section of the Yima Formation and its related strata (modified from Lü et al. 2007).

mesaxony value based on length/width of anterior triangle (AT) using the method of Weems (1992) (Table 1)

Ichnotaxonomy

Ornithischia Seeley 1887
Thyreophora Nopcsa 1923
Ichnofamily Anomoepodidae Lull 1904
Anomoepus Hitchcock 1848

Type ichnospecies: *Anomoepus scambus* Hitchcock 1848

Anomoepus isp.

Description and comparisons

YNM-1-1 (Figure 4) is the smallest of the YNM specimens (4.5 cm long). YNM-1-1 is tridactyl with width being distinctly larger than length (length/width ratio is 0.6). Digit II has two digital pads while the pads of other two digits are indistinctly impressed. The claw marks of digits II and IV are sharper than

Table 1. Measurements (in cm and degrees) of tridactyl tracks from Yima Northern Open-pit Coal Mine, Yima City, Henan Province, China.

Number	ML	MW	II–IV	AT	ML/MW
YNM-1-1	4.5	7.0	128°	0.38	0.6
YNM-2-1	6.4	9.0	110°	0.33	0.7
YNM-2-2	8.2	9.3	107°	0.53	0.9
YNM-2-3	10.9	–	–	–	–
YNM-3-1	7.5	9.6	114°	0.42	0.8
YNM-3-1*	8.8	–	93°	–	0.9
YNM-3-2	10.6	13.0	98°	0.37	0.8
YNM-3-3	5.9	8.7	125°	0.37	0.7
YNM-3-4	8.5	7.7	110°	0.58	1.1
YNM-3-5	6.8	9.1	127°	0.46	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; AT: anterior triangle length-width ratio; ML/MW is dimensionless.
*These measurements include the digit I.

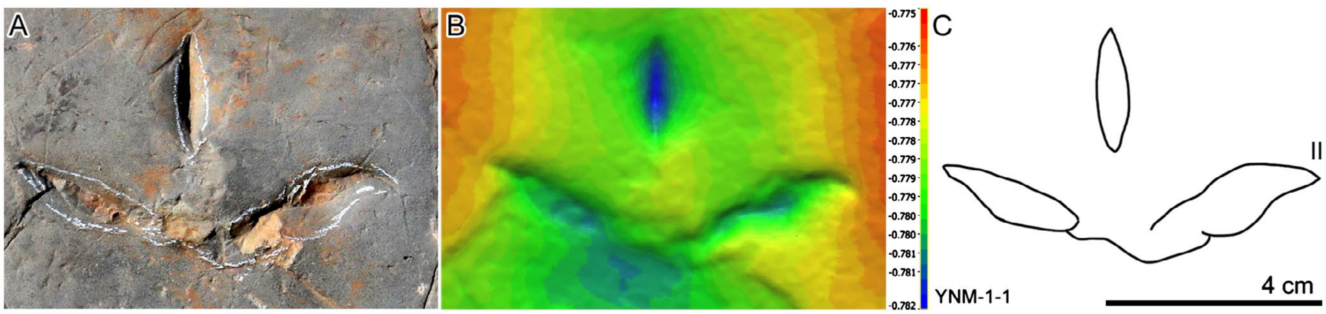

Figure 4. (Colour online) Photograph (A), 3D height map (lowest parts = blue, highest parts = orange), (B) and interpretative outline drawing (C) of Yima *Anomoepus* track YNM-1-1.

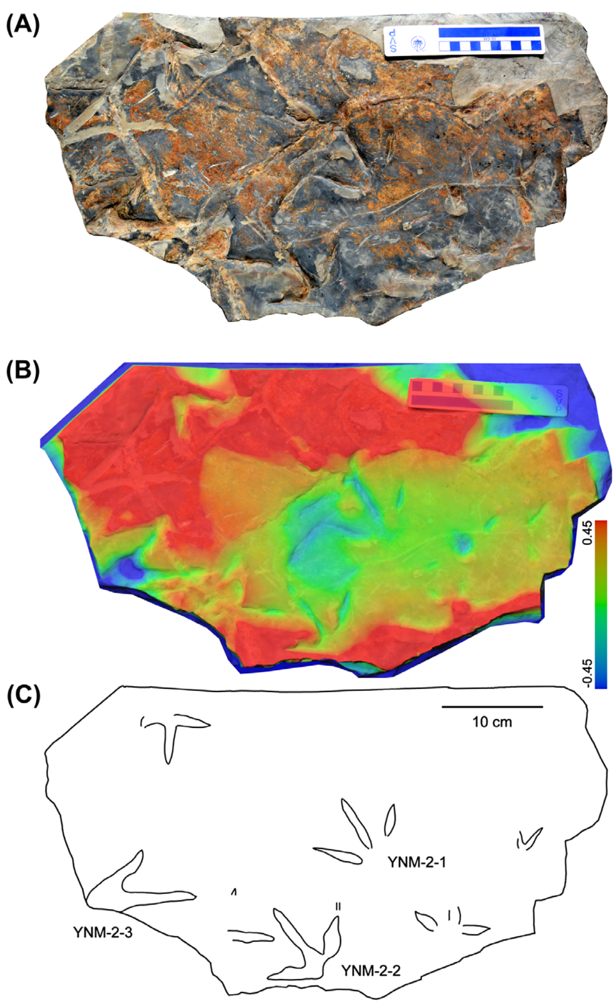

Figure 5. (Colour online) Photograph (A), 3D height map (lowest parts = blue, highest parts = red), (B) and interpretative outline drawing, (C) of slab with Yima *Anomoepus* tracks YNM-2.

that of digit III. The proximal region of digits II and IV form a U-shaped metatarsophalangeal region that lies in line with the axis of digit III. YNM-1-1 shows an exceptionally wide digit divarication angle (II–IV = 128°) and weak mesaxony, with an AT length/width ratio of 0.38. Of note, digit III of YNM-1-1 is especially deep and narrow along its middle axis, while the edges are relatively steep, however this feature may imply damp or highly fluid sediment: i.e. the track suggests some degree of extramorphological preservation.

YNM-2 (Figure 5) preserves at least seven tracks, among which YNM-2-1-3 are well preserved and have basically the same morphology as YNM-1-1, except that YNM-2-1 lacks traces of the metatarsophalangeal region.YNM-2-2 has a strong indentation behind digit II, its length/width ratio is 0.9, and its AT length/width ratio is 0.53. YNM-2-3 is the largest specimen from YNM, with a length of 10.9 cm although the track is incomplete lacking an outer digit due to breakage of the block.

YNM-3 (Figure 6) preserves at least 19 tracks, but no clear trackways are visible. NM-3-1 is tetradactyl, its length/width ratio is 0.8, and its AT length/width ratio is 0.42. The digit I (hallux) trace is relatively long and clearly oriented medially. The angle between the midline of the hallux and the track axis along digit III subtends an angle of about 70°. YNM-3-6 and 3-8 have possible hallux traces or, alternatively, this could be affected by overlapping other tracks. Most tracks from YNM-3 show similar morphological features like YNM-1-1. Hallux traces left by some trackmakers might be facilitated by soft and damp sediments.

The morphology of the small tridactyl/tetradactyl tracks from YNM strongly resembles that of the ichnogenus *Anomoepus*, being similar in size and having wide divarication angles, and weak mesaxony. *Anomoepus* is well known from Lower–Jurassic strata of North America (Olsen & Rainforth 2003). Interestingly, in the trackways from North America, the hallux trace occurs mostly in 'sitting tracks' in combination with a trace of the metatarsal, whereas normal walking tracks are tridactyl and lack a digit I. Thus, here the YNM tracks are tentatively assigned to *Anomoepus* isp. The preservation does not allow a diagnostic ichnospecies to be determined.

Discussion

Comparing YNM tracks with other Anomoepus from China

In China, most *Anomoepus* tracks are found in Lower–Middle Jurassic formations. Main localities that yielded specimens assigned to this ichnogenus are:

(1) Lower–Jurassic Wulatezhongqi site from Inner Mongolia (Li et al. 2010).
(2) Lower–Jurassic Lijiananwa site from Shaanxi Province (Li et al. 2012).
(3) Lower–Jurassic Dalishu site III from Yunnan Province (Xing et al. in press).

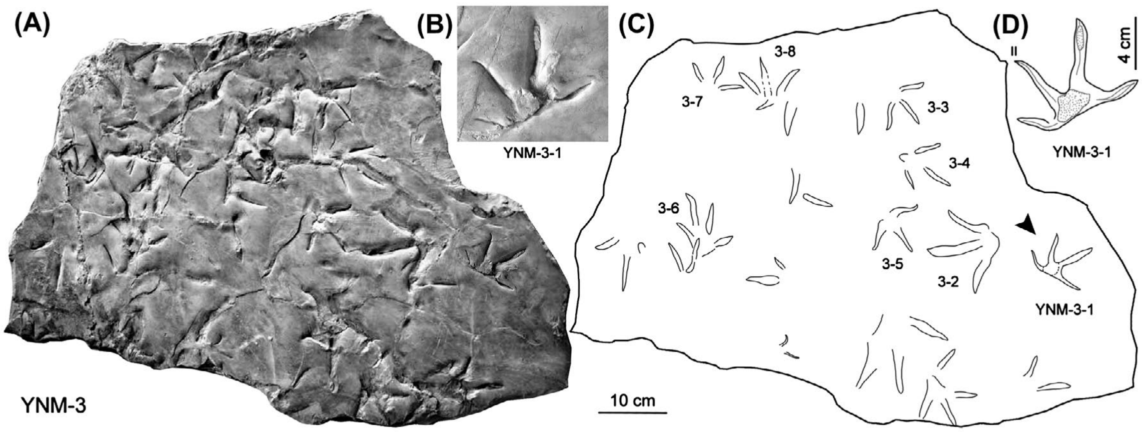

Figure 6. Photographs (A, B), and interpretative outline drawings (C, D) of slab with Yima *Anomoepus* tracks YNM-3. B, D with close-up of YNM-3–1.

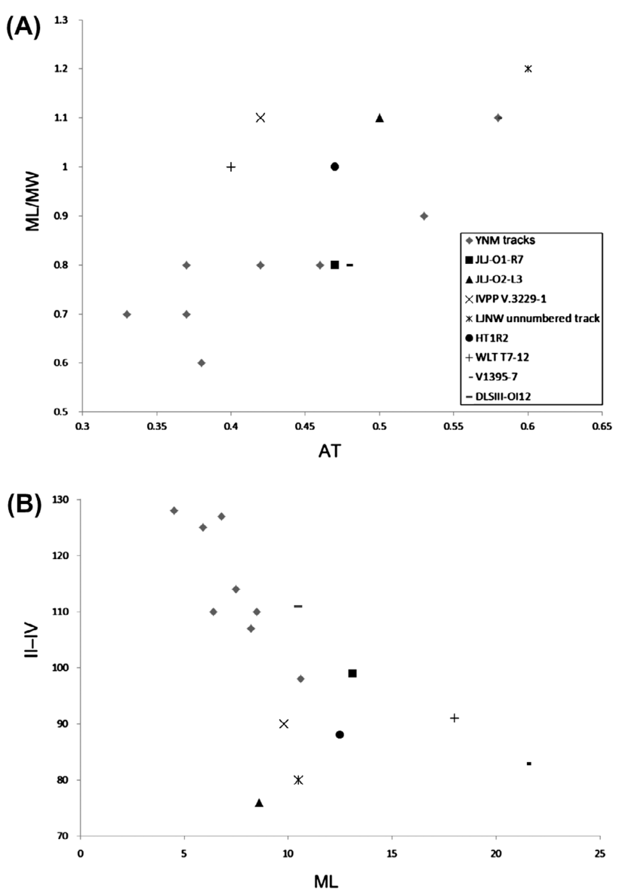

Figure 7. Scatter diagrams plotting track mesaxony (AT) against ML/MW (A) and track length (ML) against angle between digits II and IV (II–IV), (B) in *Anomoepus* tracks from Yima and other localities in China.

Notes: DLSIII = Dalishu site III; HT = Huo and Wang sites; IVPP = Jiaoping Coal Mine site, Institute of Vertebrate Paleontology and Paleoanthropology; JLJ = Jinlijing site; LJNW = Lijiananwa site; V = Nan'an site; WLT = Wulatezhongqi site.

(4) Middle–Jurassic Jinlijing site, Sichuan Province (Lockley & Matsukawa 2009; Xing et al. in press).
(5) Middle–Jurassic Jiaoping Coal Mine site from Shaanxi Province (Xing et al. 2015).
(6) Middle–Jurassic Huo and Wang sites from Shaanxi Province (Xing et al. 2015).
(7) Upper–Jurassic Nan'an site from Chongqing municipality (Xing et al. 2013).

Compared with other ichnogenera, *Anomoepus* has only been known for a short time from localities in China. The first discovery was made by Lockley and Matsukawa (2009) in the Middle–Jurassic Jinlijing site in Sichuan Province. These authors also recognised examples from Chonqing municipality (Xing et al. 2013). Researchers then came to realise that this ichnogenus had been frequently confused with small-sized theropod tracks such as *Grallator*. In general, all these tracks, except specimens from the Lijiananwa site, which are yet to be described in detail, have characteristics of *Anomoepus*, such as the wide digit divarication angles (80°–111°), weak mesaxony (0.40–0.60), and in some cases, inconspicuous traces of digit I, and/or characteristic trackway configurations with diagnostic inward rotation of the pes. As yet, no *Anomoepus* with diagnostic manus traces have been reported from China. Nevertheless, recognition of the occurrences cited above proves that *Anomoepus* is not as rare as previously supposed in China. This shows the benefits of an improved 'search image' among ichnologists working in China, and also helps demonstrate that these Jurassic ichnofaunas from China are more typical of the Jurassic biochrons defined by Lucas (2007).

We have plotted mesaxony value (AT) against ML/MW and ML against the divarication angle between digit traces II–IV of *Anomoepus* from the Yima site and other localities in China (Figure 7). The scatter diagram reveals their congruence but also some peculiarities of the Yima tracks. The YNM *Anomoepus* isp., shows digit divarication angles and mesaxony values similar to most *Anomoepus* from China. There are, however, some differences: (1) the L/W ratios range 0.6–1.1 with a median of 0.8, which are lower than those of other *Anomoepus*; (2) the mesaxony value ranges 0.33–0.58 with a median of 0.4, which is significantly lower than values of other *Anomoepus*; (3) the divarication angles between digits II–IV range from 98° to 128° with a median of 112°, which is larger than in those of other *Anomoepus*. In addition, specimens from YNM are not as long as other *Anomoepus*, although, this discrepancy may reflect a preservation artifact or regional divergence in trackmaker types.

Only *Anomoepus* specimens from Wulatezhongqi site (Li et al. 2010) and Dalishu site III (Xing et al. in press) show hallux traces. Hallux traces of YNM specimens resemble the former in position and orientation, but do not have metatarso-phalangeal pads. Unlike the YNM specimens, hallux traces of Dalishu specimens points backward (Xing et al. in press).

To estimate the size of the trackmakers, 4.8 × the ML of the pes trace is used as the hip height conversion factor (Thulborn 1990) and the average ratio of hip height to body length is assumed to be 1:2.63 (Xing et al. 2009). The trackmakers of YNM *Anomoepus* isp. are thereby estimated to have been 0.57–1.38 m long, similar to those of trackmakers from Dalishu site III (~1.3 m, Xing et al. in press). The calculated body length also corresponds with ornithischian skeletons from the Sichuan Basin, e.g. *Xiaosaurus* Dong & Tang 1983; *Agilisaurus* Peng 1990 and *Hexinlusaurus* Barrett et al., 2005 that have been calculated with 1.4–2 m body length by Peng et al. 2005). This indicates that the Early–Middle Jurassic dinosaur fauna in Yima Basin has something in common with that in Southwest China (Sichuan and Yunnan).

Comparing YNM tracks with bird – and other footprints

It is noteworthy that some YNM specimens have strong affinities with bird tracks, especially by the large digit divarication. In fact, when the authors first became aware of specimen YNM-3 through seeing photographs, they suggested that these were bird tracks. This is a perennial problem when dealing with small, gracile widely divaricated tridactyl tracks. For example, with the exception of size, YNM-1-1 is quite similar to Koreanaornipodidae (Kim 1969; Lockley et al. 2006) in many aspects such as its small size, wide splay, sub-symmetric form, functionally tridactyl stance, slender digit impressions and wide divarication angles between digits II and IV as are YNM-2-1, YNM-3-3, and YNM-3-7. Similar '*Anomoepus*-like' tracks occur in Middle–Jurassic strata of Msemrir (Morocco), Northern Gondwana (Belvedere et al. 2011). Except in size, YNM-1-1 is also remarkably similar to an isolated, widely divaricated, but larger, track from the Upper Jurassic of Asturias, Spain, illustrated by García-Ramos et al. (2002)

Though Middle–Jurassic avian theropods are yet to be found, the differences and similarities between contemporaneous avian theropod tracks and *Anomoepus* type tracks need to be noted and understood. Clearly some *Anomoepus* and avian tracks are convergent in certain features such as trackway configuration and gracile appearance; however they generally differ in size with most *Anomoepus* by being larger, and in some cases much larger and more robust (Lockley & Gierliński 2006). The position of the *Anomoepus* hallux, when preserved, is also generally different, being more anteromedially situated.

Other ichnogenera that show some similarity with the YNM tracks and those of birds are *Trisauropodiscus* and *Carmelopodus*. *Trisauropodiscus* was originally based on material from Upper Triassic strata of the Stormberg Group of southern Africa (Ellenberger 1970). It has a very bird-like shape. However, in well-preserved specimens, the hallux is backward oriented, mostly in line with digit III. This cannot be observed in the YNM tracks. *Carmelopodus* from the Middle Jurassic of North America is more similar to the ichnogenus *Grallator* with stronger mesaxony compared with the YNM tracks (Lockley et al. 1998). There are some Cretaceous bird tracks such as *Magnoavipes* that are also similar (Lockley & Rainforth 2002). Obviously, bird-like feet developed independently in different groups along the dinosaur-bird line. *Anomoepus*, probably the track of an ornithischian, can show a very bird-like shape with wide digit divarication, especially if preserved with incomplete, tridactyl variations.

Changpeipus–Anomoepus track assemblages

In addition to *Anomoepus* tracks, the YNM site also reveals *Changpeipus* tracks. Lü et al. (2007) named *Changpeipus xuiana* based on HGM 41HIII-0098. However, HGM 41HIII-0098 is a poorly preserved track, probably an undertrack. The metatarsophalangeal portion appears robust, forming a compact 'heel', but lacks a distinct pad impression. The digit divarication angle is relatively narrow (~46° between digits II and IV). Xing et al. (2014) reviewed *Changpeipus* specimens from China, and considered this ichnogenus to be a monotypic ichnogenus with the type species *C. carbonicus*, and similar to *Eubrontes*.

The *Changpeipus–Anomoepus* track assemblages from the YNM site resemble *Eubrontes* and *Anomoepus* track assemblages from the Middle–Jurassic Xiashaximiao Formation of Zizhong County, Sichuan, indicating that Sichuan Basin and Yima Basin were home to similar faunas during Middle–Jurassic time.

Conclusions

(1) Reports of *Anomopeus* from the Middle Jurassic of Yima in Henan Province represent at least the eighth report of the ichnogenus from China.
(2) The increased frequency of reports of this ichnogenus from China represent an improved 'search image' among ichnologists and the ability to distinguish these tracks from those of small tridactyl footprints attributable to theropods.
(3) *Anomoepus–Changpeipus* and *Anomoepus–Eubrontes* type assemblages are typical of the globally widespread Jurassic track biochron.
(4) Initial reports that the Yima tracks were those of birds indicated that small, gracile *Anomoepus* are superficially similar to Mesozoic avian theropod tracks. However, the latter groups are almost always smaller, more gracile and are currently known only from the Cretaceous.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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