Palaeogeography, Palaeoclimatology, Palaeoecology 452 (2016) 28–39

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

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

A new *Minisauripus* site from the Lower Cretaceous of China: Tracks of small adults or juveniles?

Lida Xing [a,*], Martin G. Lockley [b], Geng Yang [c], Jun Cao [c], Michael Benton [d], Xing Xu [e], Jianping Zhang [a], Hendrik Klein [f], W. Scott Persons IV [g], Jeong Yul Kim [h], Guangzhao Peng [i], Yong Ye [i], Hao Ran [j]

[a] *School of the Earth Sciences and Resources, China University of Geosciences, Beijing, China*
[b] *Dinosaur Trackers Research Group, University of Colorado, Denver, CO, USA*
[c] *Regional Geological Survey Team, Sichuan Bureau of Geological Exploration and Development of Mineral Resources, Chengdu 610213, China*
[d] *School of Earth Sciences, University of Bristol, Bristol BS8 1RJ, UK*
[e] *Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China*
[f] *Saurierwelt Paläontologisches Museum, Neumarkt, Germany*
[g] *Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada*
[h] *Department of Earth Science Education, Korea National University of Education, Cheongwon, Chungbuk 363-791, South Korea*
[i] *Zigong Dinosaur Museum, Zigong, Sichuan, China*
[j] *Key Laboratory of Ecology of Rare and Endangered Species and Environmental Protection, Ministry of Education, Guilin 541004, China*

ARTICLE INFO

Article history:
Received 6 January 2016
Received in revised form 3 April 2016
Accepted 4 April 2016
Available online 11 April 2016

Keywords:
Minisauripus
Jialingpus
Small theropod tracks
Feitianshan Formation
Yangmozu tracksite

ABSTRACT

Because skeletal remains of very small theropods are delicate and rare, diminutive tracks provide valuable, additional evidence of body size. The distinctive Asian ichnogenus *Minisauripus* has assumed importance in this debate and has played a role in the challenging question about whether it represents a small trackmaker species or juveniles of a larger species. New discoveries of *Minisauripus* footprints from the Lower Cretaceous Feitianshan Formation at Yangmozu in Sichuan Province, China, support the conclusion that all known examples of this ichnotaxon are small. The main Yangmozu site reveals 65 theropod tracks (~20 trackways) of different-sized trackmakers. Three trackways, comprising 10 pes imprints of 2.5–2.6 cm length, are assigned to *Minisauripus*. The remaining 17 trackways represent small–medium-sized theropods (track lengths 9.9–19.6 cm), including one assigned to cf. *Jialingpus*. All unequivocally identified *Minisauripus* tracks from Korea (five sites) and China (three sites) fall in the size range of ~1.0–6.1 cm. Assuming a small adult trackmaker, and based on standard foot length, leg length and body length ratios, all *Minisauripus* tracks indicate trackmakers with hip heights of <~5.0 and ~28.0 cm and body lengths in the range of ~12.0–72.0 cm. Based on lack of large tracks (longer than 6.1 cm) at any known sites, and various precedents in the ichnological literature we infer that *Minisauripus* represents a small theropod species. However, we cannot completely exclude the possibility that such tracks represent juveniles of larger trackmaking species.

1. Introduction

Body size is an important parameter for understanding theropod biology, and a key factor in bird evolution. While skeletal remains are an obvious source of data on theropod size, very small species and juveniles are rare in most deposits, due to bias against the preservation of delicate bones. Tracks, therefore, are useful in indicating the size and frequency of small trackmakers. Although comparatively rare, well preserved assemblages of small or "diminutive" theropod tracks (length <~5.0 cm) include dune assemblages from the Jurassic of the western USA (Rainforth and Lockley 1996; Lockley, 2011), and several *Minisauripus* assemblages from the Cretaceous of China and Korea (Zhen et al., 1994; Lockley et al., 2008; Kim et al., 2012). Although small tracks might also be rare due to preservational bias (Leonardi, 1981), this explanation is weakened by the abundance of small bird tracks, particularly in the Cretaceous of China and Korea, in some cases at the same sites as *Minisauripus*.

Various Jurassic assemblages have been interpreted as evidence that desert faunas were characterized by diminutive species (Rainforth and Lockley, 1996). In the case of *Minisauripus* the debate has not been about palaeoenvironmental influences, but rather about whether the tracks represent a small species or juveniles of larger species (Kim et al., 2012). As new evidence accumulates, such as that from the Yangmozu site described here, it becomes easier to discuss this question. As noted below, both tracks and pes skeletons of small individuals are known and can be compared. Ideally it should be possible to identify likely trackmakers for known tracks, or tracks for known trackmakers, if not at the species level, then perhaps at the genus or family level.

* Corresponding author.
E-mail address: xinglida@gmail.com (L. Xing).

http://dx.doi.org/10.1016/j.palaeo.2016.04.006

At present, the smallest known skeleton of an adult non-avialian theropod is *Anchiornis*, with a total skeletal length of between 34 and 40 cm (Xu et al., 2009; Hu et al., 2009). Others are *Epidexipteryx*, a non-avialian in some phylogenetic analyses, the dromaeosaurid *Microraptor*, the troodontid *Mei*, and several alvarezsauroids such as *Xixianykus* and *Parvicursor* (Karhu and Rautian, 1996; Xu et al., 2000, 2010; Xu and Norell, 2004; Zhang et al., 2008).This is not to imply any demonstrated correlation of these potential trackmakers with *Minisauripus*. For any such correlations to be convincing, in addition to correlation between foot and footprint morphology, feasible geographical and stratigraphic distribution of tracks and potential trackmakers should also be demonstrated.

Minisauripus, originally classified as an ornithopod track (Zhen et al., 1994), but later unequivocally recognized as a theropod track (Lockley et al., 2008) is the smallest known non-avialian theropod track ichnogenus. The smallest *Minisauripus* specimen is 1.05 cm long (CUE 08 1003, Kim et al., 2012). Small theropod hip height is generally estimated as 4.5 times foot length (Thulborn, 1990), and body length can be estimated at 2.63 times hip height (Xing et al., 2009). Based on this method, and assuming an adult trackmaker for the smallest *Minisauripus*, a hip height of 4.7 cm and a body length of just over 12 cm can be calculated. Assuming a juvenile trackmaker, values might be overestimates because of the relative larger pes length compared with the leg length that occurs in some juveniles and paedomorphic forms (Lockley, 2007). Even the largest (presumably adult) *Minisauripus* (foot length 6.0 cm) implies an estimated hip height and body length of ~27.0 and ~71.0 cm, respectively.

Unlike tracks of the *Grallator* type, which are widely distributed and variable in size (Lockley et al., 2013), *Minisauripus* has a unique morphology and is presently regarded as an Early Cretaceous ichnogenus endemic to East Asia (Kim et al., 2012; Lockley et al., 2013). Prior to this study ~82 *Minisauripus* tracks, representing at least 52 trackways, had been documented from two Chinese (Emei and Houzuoshan) and five Korean (Gain, Sinsu, Godu, Buyun, and Gae Je) localities (Kim et al., 2012). With the addition of the present report, a total of ~92 *Minisauripus* tracks, representing at least 55 trackways, are now recorded from a total of eight localities.

Investigations of Cretaceous tracksites in Zhaojue County, Sichuan Basin by L.X. and M.G.L. in 2013 and 2014 revealed three new tracksites with hundreds of footprints of sauropods, ornithopods, theropods, and pterosaurs (Xing et al., 2013, 2014a, 2015). Meanwhile, in June 2013, the Regional Geological Survey Team from the Sichuan Bureau of Geological Exploration and Development of Mineral Resources, reported middle-sized tridactyl tracks found during geological mapping along the western outskirts of Luowuyiti Village, Yangmozu Township, Zhaojue County (Fig. 1). Subsequently, L.X and M.G.L. investigated the tracksite and identified it as the third *Minisauripus* site known from China. In the following sections, we describe this assemblage in detail and discuss arguments supporting either small adult or juvenile trackmaking groups.

1.1. Institutional and location abbreviations

CU = University of Colorado, Denver, USA; IVPP = Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; NIGP = Nanjing Institute of Geology and Palaeontology, Nanjing, China; UCM = University of Colorado Museum of Natural History, Boulder, USA.

1.2. Ichnological abbreviations

L/W = length/width; M = mesaxony; ML = maximum track length; MW = maximum track width; ML/MW = maximum length/ maximum width; PL = step length; SL = stride length; PA = pace angulation.

2. Geological setting

The southwestern area of Sichuan Province, consisting of Liangshan autonomous prefecture and Panzhihua city, is commonly known as the Panxi (Panzhihua–Xichang) region. Here, Cretaceous formations are widely exposed, and the largest accumulations are in the Mishi (Xichang)–Jiangzhou Basin (Luo, 1999). Based on ostracods and charophytes, the Cretaceous sediments in the Mishi–Jiangzhou Basin can be divided into the Lower Cretaceous Feitianshan and Xiaoba formations, and the Upper Cretaceous–Palaeogene Leidashu Formation (Gu and Liu, 1997).

Rhythmic bedding in the Lower Cretaceous Feitianshan Formation consists of purplish red and brick-red medium-grained feldspathic quartzose sandstone, siltstone, and shale overlying silty mudstones of the Guanggou Formation, which is considered to be Jurassic in age. The Feitianshan Formation is Berriasian–Barremian in age (Tamai et al., 2004). The Lower Member of the Feitianshan Formation, 517 m thick, comprises fluvial and lacustrine delta facies. The Upper Member, 604 m thick, belongs to lacustrine delta facies (Xu et al., 1997). Dinosaur tracks from the Lower Member of the Feitianshan Formation are preserved in purplish red, medium-grained quartzose sandstone (Fig. 2). Diverse invertebrate trace fossils, ripple marks, mud cracks and raindrop imprints indicate a lakeshore environment (Lim et al., 2002).

3. Methods

Ladders, scaffolding and the help of a professional mountaineering team were used to gain access to most of the track-bearing portion of the surfaces. This permitted examination of the tracks at close quarters, and allowed us to make a chalk grid over the main body of the track-preserving surface. The grid was divided into 50 cm squares, which were photographed separately using a digital Canon 5D MKIII camera. The photographs were merged using Adobe Photoshop CS6, and the distribution pattern was mapped from the composite image. As a back-up, the surface was also mapped on graph paper using traditional methods. This allowed the map to be used to record information on individual tracks and plot the location of those tracks that were traced, moulded and replicated.

Individual tracks were also photographed and outlined with chalk prior to being traced on transparent acetate (CU tracing T 1653) and other plastic sheets. Once all the tracks in the uppermost sector of the outcrop had been outlined, a large sheet of transparent plastic was used to trace most of the trackway segments in this sector. Well-preserved tracks, which were moulded with latex, have been converted into plaster of Paris hard copies and are deposited at the CU and UCM in the series 214.286–214.293.

4. The Yangmozu tracksite

Almost all the tracks identified here are from the Yangmozu site I (YMZI) where they are preserved as natural casts on steeply inclined bare rock surfaces, which form a steep overhang dipping west at 45° (Fig. 1). This overhang represents a bedding surface about 5 m above the base of the thick sandstone-dominated sequence making up the Feitianshan Formation, in which there are only a few fine siltstone and mudstone intercalations. This contrasts with the underlying silty mudstones of the Guanggou Formation, which contain few sandy units. Poorly preserved tracks occur at the base of the Feitianshan sequence close to the interface with the underlying silty mudstone of the Guanggou Formation. The main track-bearing units described here are associated with the first, silty mudstone intercalation and the thin sandy units that immediately overly it. Other track-bearing surfaces occur higher in the section (Fig. 1), include the site here referred to as YMXII (Yangmozu II) which occurs a little more than 100 m above the main site (YMZI; Fig. 2).

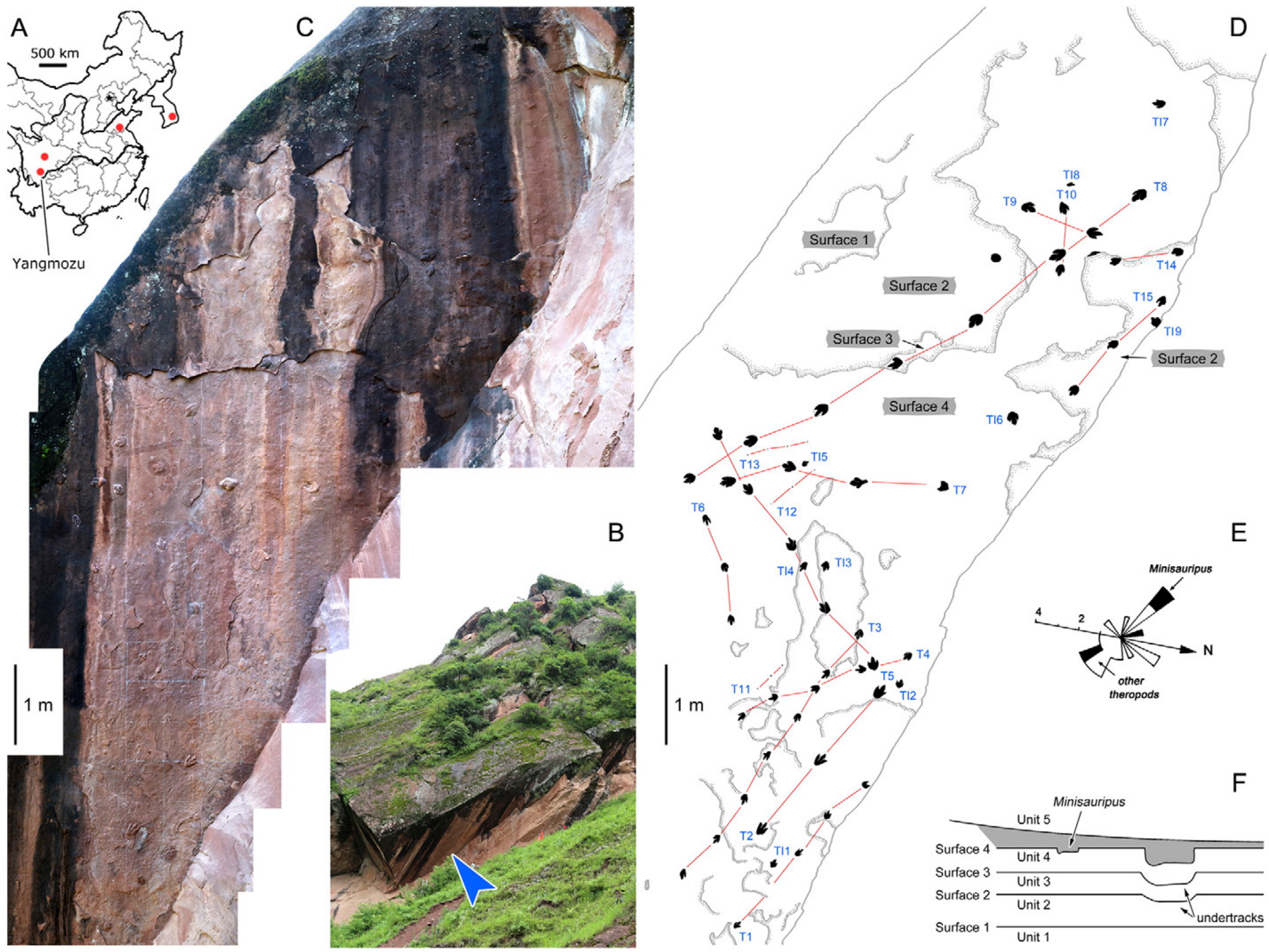

Fig. 1. Locality map (A) showing position of tracksites in China and South Korea yielding *Minisauripus*; photograph (B) of the main Yangmozu tracksite (YMZI), Zhaojue County, Liangshan, China (arrow indicates the track surface); overview (C) of track surface; map (D) of the main tracksite and rose diagram (E) showing orientation of trackways; (F) scheme showing four different track-bearing surfaces and their relationship to true tracks of *Minisauripus* and undertracks representing larger morphotypes.

There are at least three track-bearing surfaces associated with the main tracksite interval (YMZI). However, these are all associated with thin layers only a few centimetres apart, which vary slightly in thickness across the outcrop. As shown in Fig. 1, the stratigraphically lowest surface (surface 1) appears to be best exposed in the upper, topographically highest parts of the exposure. However, it is only a few centimetres thick and does not appear to reveal any recognizable tracks. It is also mostly covered with a black stain and a greenish algal film. The overlying layers are better exposed lower in the outcrop where the underlying layers have been stripped off by erosion, leaving lighter coloured surfaces (surfaces 2–4) exposed. These layers are also no more than 1–2 cm thick. The longest trackway (T8), representing a medium-sized theropod, exposed on the upper part of the outcrop, can be seen on surfaces 2, 3 and 4, with surface 4 being stratigraphically highest. Clearly the tracks on surfaces 2 and 3 are underprints, and the deeper underprint, on surface 2, is the least visible, having the least relief. Since we cannot see whether or not surface 4 represents the underside of a thin bed, it is possible that some of its tracks are also undertracks. However, as small *Minisauripus* tracks (length 2–3 cm), with a depth of no more than 1–2 mm, occur on surface 4 (Fig. 3), it is probable that these are true tracks. Impressions of such small *Minisauripus* indicate lightweight trackmakers leaving true tracks or near-surface tracks but not deeper undertracks. An alternative explanation is that the larger imprints registered as undertracks after the small tracks were covered by another sediment layer.

5. Ichnotaxonomy

At least three distinct track morphotypes have been identified at the Yangmozu site. We use the broad term “morphotype” to refer to both named ichnotaxa, and unnamed morphotypes. The most distinctive is *Minisauripus* (Morphotype A; Figs. 3, 4), which is identified unequivocally and is represented only by small tracks (length 2.5–2.6 cm), here assigned to the existing ichnospecies *Minisauripus zhenshuonani* Lockley et al., 2008. The remaining morphotypes (B and C; Figs. 5, 6) are considerably larger (track length 9.9–19.6 cm) and fall into two categories: medium-sized tridactyl tracks with typical theropod morphology (morphotype B), including a 2–3–4 phalangeal pad formula corresponding to digits II, III and IV; and medium-sized tridactyl tracks with wide digit impressions (morphotype C) that lack digital pad traces.

5.1. Morphotype A

Ichnogenus *Minisauripus* Zhen et al., 1995.

5.1.1. Type ichnospecies

Minisauripus chuanzhuensis Zhen et al., 1995.

5.1.2. Diagnosis

Small tridactyl track with sub-parallel, elongate, well-padded digits with blunt distal terminations connected to narrow distal claw traces.

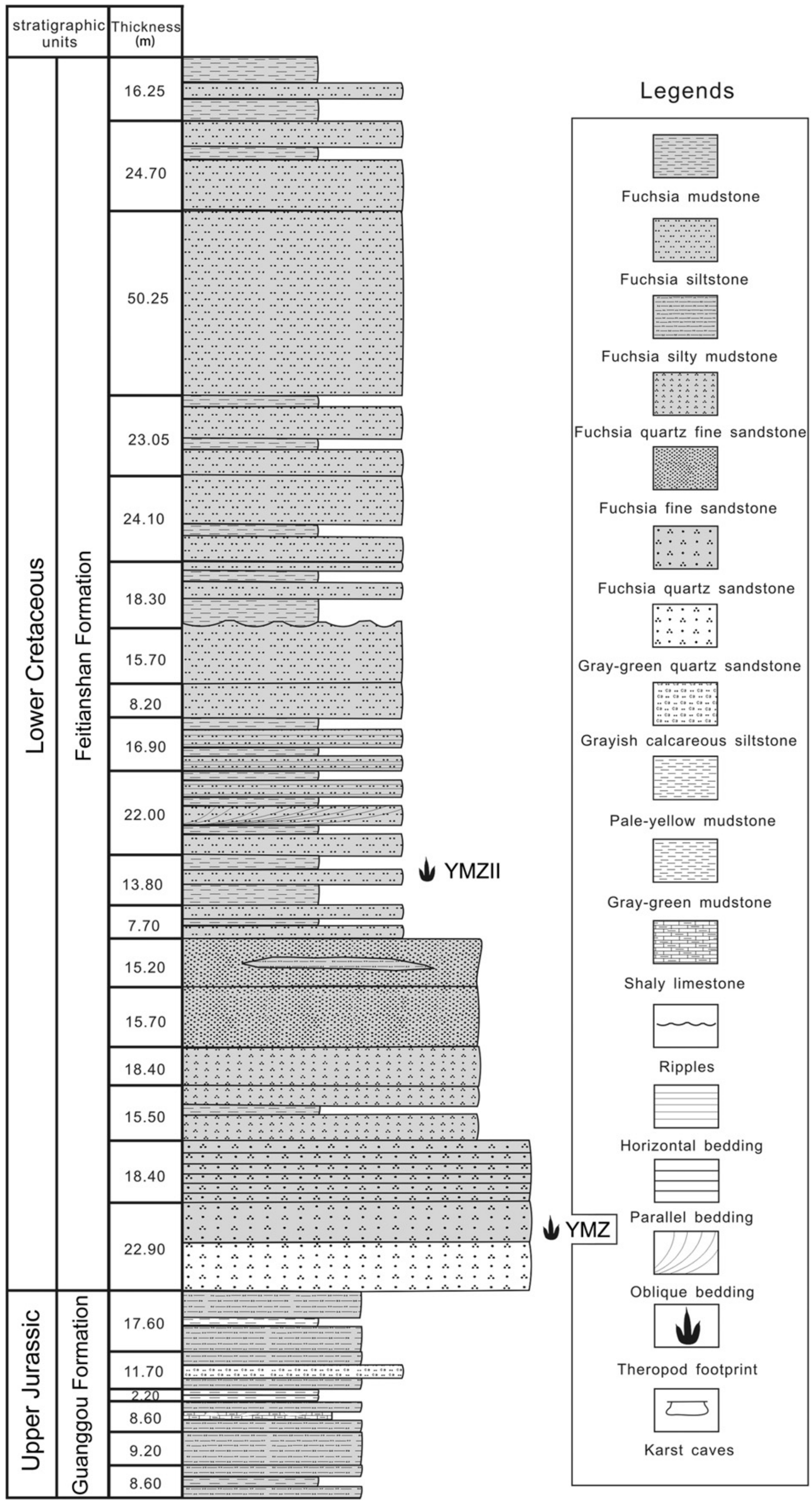

Fig. 2. Stratigraphic section of Upper Jurassic–Lower Cretaceous strata as logged at the Yangmozu tracksite with the position of the track-bearing levels. Note that upper track level is referred to as YMZII to distinguish from main tracksite (YMZ).

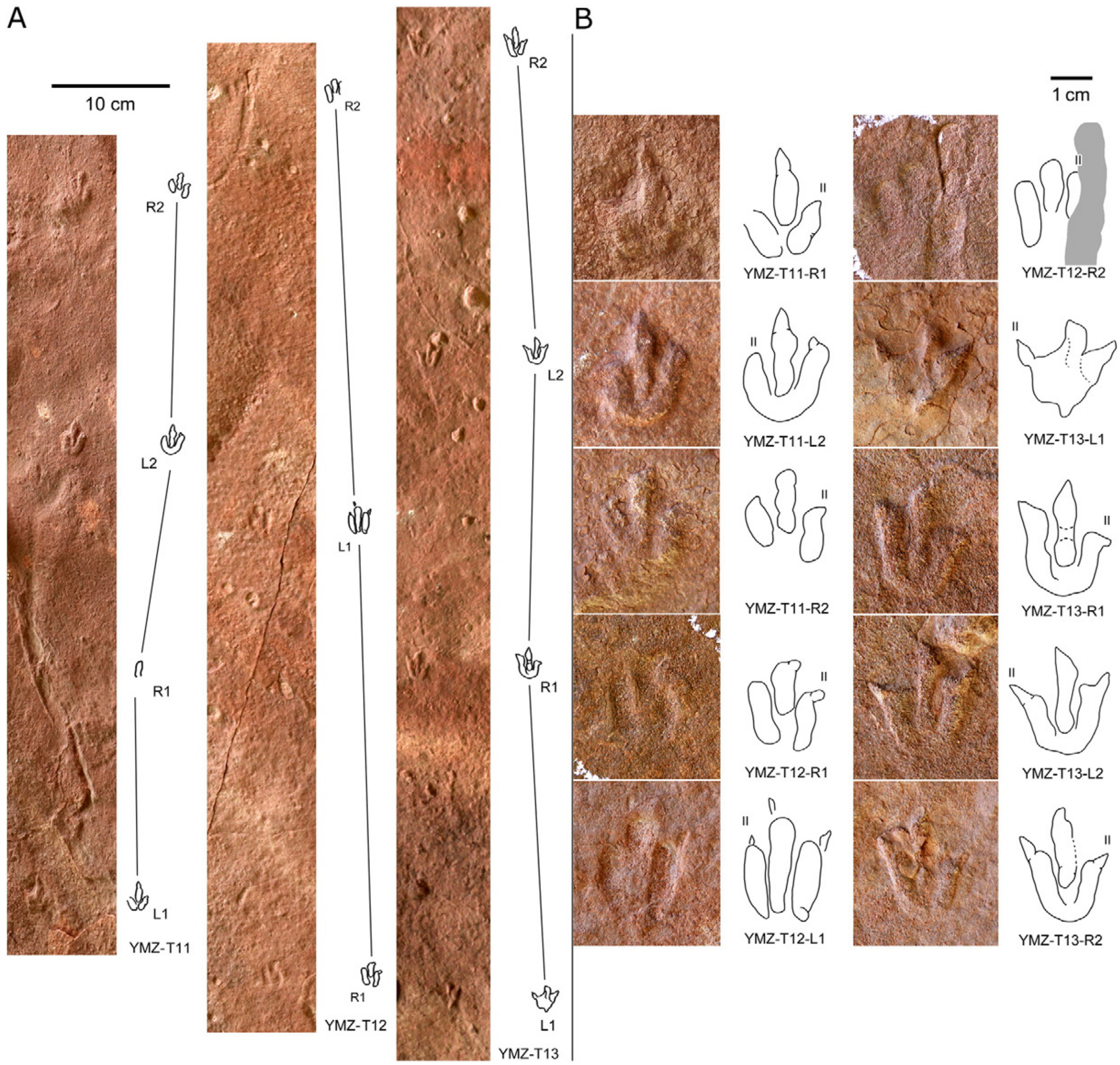

Fig. 3. Photograph and interpretative outline drawings of Yangmozu *Minisauripus* trackways (A), and well-preserved Yangmozu *Minisauripus* tracks (B).

Digit III only slightly longer than IV, which is slightly longer than digit II. Phalangeal formula of 2–3–?4 for digits II, III and IV, respectively, discernible in well preserved examples. Trackway narrow. (Emended after Zhen et al. (1994) and Lockley et al. (2008).)

5.1.3. Ichnospecies

M. zhenshuonani Lockley et al., 2008.

5.1.4. Diagnosis

Small, elongate, tridactyl track with parallel digits with conspicuous claw traces. Track narrower than in *M. chuanzhuensis* with digits less divergent, and digit II relatively shorter. Pace and stride about 10 times footprint length and typically longer than in *M. chuanzhuensis*. Trackway very narrow (Lockley et al., 2008).

5.1.5. Material

Three trackways (Figs. 3, 4; Table 1). Trackways YMZ-T11–T13, have 4, 3, and 4 imprints, respectively, that remain in situ. CU/UCM 214.291 and 214.292, respectively, are latex moulds and replicas of the best preserved tracks in trackways T11 and T12 and UCD/UCM 214.293 represents a mould and replica of all four visible tracks in trackway T13.

5.1.6. Locality and horizon

Lower Member of the Feitianshan Formation, Early Cretaceous. Yangmozu tracksite, Zhaojue County, Sichuan Province, China.

5.1.7. Description

Small, elongate, tridactyl tracks, 68–88% as wide as 1.7–2.3 cm and as long as 2.5–2.6 cm. The YMZ-T11 and T12 imprints have a mean ML/MW ratio of 1.4–1.5; this value is a little lower in YMZ-T13 about 1.1 (about 1.4 without claw marks) (Figs. 3, 4). The mean L/W ratio of the anterior triangle is 0.40–0.53.

L2 (Fig. 3) is the best preserved of the YMZ-T11 tracks. The distal part of digit II may be slightly damaged and, therefore, lacks a claw mark; however, distinct claw marks are present in digits III and IV. Digit III is only slightly longer than digit IV, which is in turn significantly longer (more anteriorly projected) than II. The proximal ends of digits II and IV do not show well-defined boundaries. These two digits, together with the metatarso-phalangeal pad IV, form a distinct U or horseshoe-like shape. Phalangeal pads are indistinct, although they are slightly visible in some of the tracks in T11 and T12. The metatarso-phalangeal region is smoothly curved.

In three tracks of the YMZ-T12 trackway (Figs. 3, 4E), digits II–IV are strictly separated and oriented parallel to each other. There is no distal

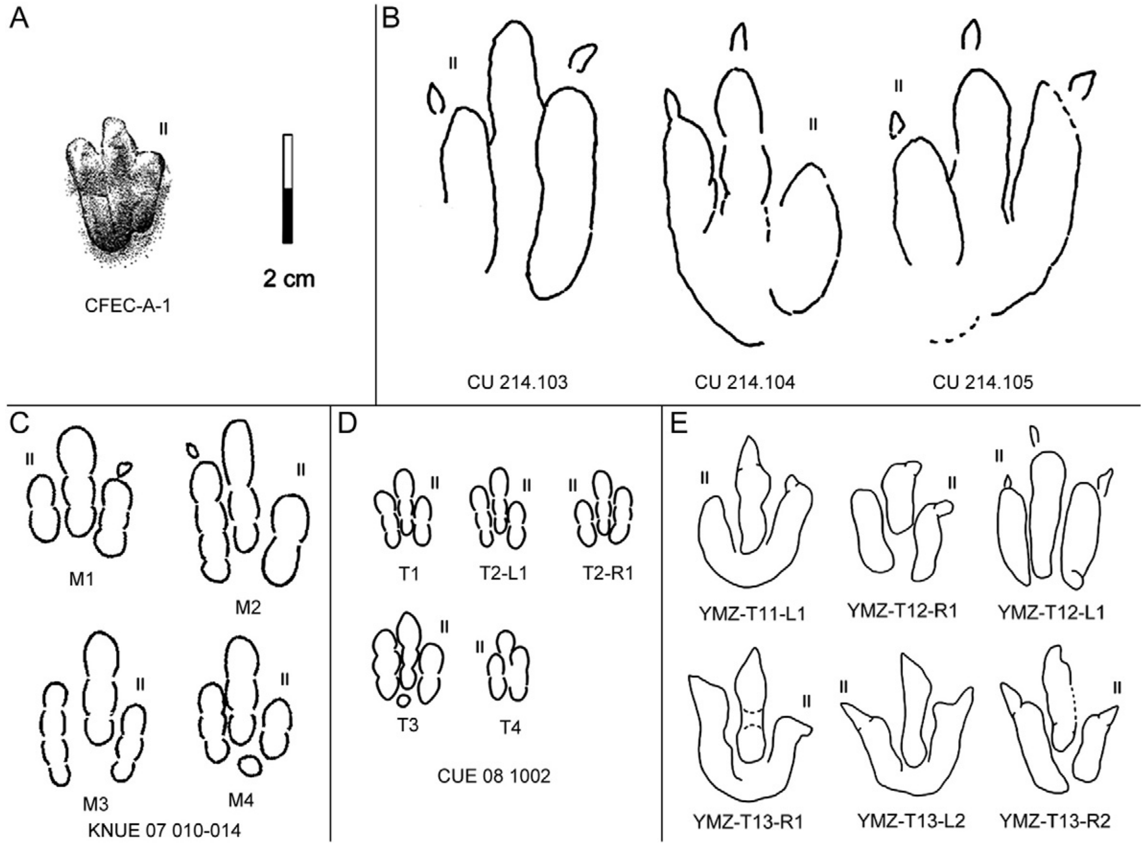

Fig. 4. *Minisauripus* from different localities in South Korea and China. A: *Minisauripus chuanzhuensis*, China (Zhen et al., 1994; Lockley et al., 2008); B: *Minisauripus zhenshuonani*, China (Lockley et al., 2008); C: *Minisauripus*, South Korea (Kim et al., 2012); D: *Minisauripus*, South Korea (Kim et al., 2012); E: this paper. Scale refers to all specimens.

tapering, especially in digit III traces. The claw of digit II is strongly developed. Digit IV is wider than digit II and equal to or slightly wider than digit III. Digit II of R2 is covered by an invertebrate trace. The pace is long, up to 15 times footprint length.

YMZ-T13 is the best-preserved trackway. R1, L2 and R2 are quite similar to the T11–L2 morphologically (Fig. 3). Digit III of R1 has three phalangeal pad traces while those of other digits are indistinct. Digit IV is slightly wider than digits II and III. The claw marks of all digits are highly developed, with the claw mark of digit II being slightly more distinct. L1 is an extramorphological (substrate-related) variation. The interdigital divarication of digits II–IV is relatively large (67°) compared with the other tracks (Table 1) and the ML/MW ratio is smaller (1.1) vs YMZ-T11 and T12.

5.1.8. Comparison

Zhaojue YMZ-T11–T13 theropod tracks clearly show all diagnostic characteristics of *Minisauripus* (Lockley et al., 2008): i.e. they are 1) small tridactyl tracks with sub-parallel and elongate digits with blunt distal terminations connected to narrow distal claw traces; 2) have a phalangeal formula of 2–3–?4 for digits II–IV, respectively, discernible in well-preserved examples; 3) have a long pace that is 8–15 times footprint length; and 4) form narrow trackways with pace angulation of 174°–179°.

The most obvious difference between the two described ichnospecies of *Minisauripus* is that *M. zhenshuonani* has a larger size range, reaching a larger maximum size (2.5–6.1 cm vs. 2.5–3.0 cm for *M. chuanzhuensis* Zhen et al., 1994), and is proportionately narrower, with less divergent digits, and conspicuous slender claw traces. Additionally, digit II of *M. zhenshuonani* is relatively shorter and, in the trackway, pace length is up to 10 times footprint length, which is longer than in *M. chuanzhuensis* (Lockley et al., 2008). The lengths of the Zhaojue YMZ-T11–T1 range from 2.5 to 2.6 cm. The ratio of track length to pace length is 1:8–1:15, similar to *M. zhenshuonani* (1:10). For example, track length in trackway TW4 from Changseon Island, Korea is 1.3 cm, and the single pace length is 23.4 cm, giving a ratio of 1:18. Therefore, YMZ-T11–T13 is more similar to *M. zhenshuonani* in trackway configuration.

5.2. Morphotype B

Ichnogenus *Jialingpus* Zhen et al., 1983.
Cf. *Jialingpus* isp.

5.2.1. Material

A single trackway (Figs. 5, 6; Table 1) designated as trackway YMZ-T2, with three consecutive tracks, is tentatively assigned to cf., *Jialingpus*. Other trackways that might be attributed to this morphotype are insufficiently well preserved to be assigned with confidence to this or any other ichnotaxon (trackways T1, 3–10 and 14–20). They are discussed below under Morphotype C.

5.2.2. Locality and horizon

Lower Member of the Feitianshan Formation, Early Cretaceous. Yangmozu tracksite, Zhaojue County, Sichuan Province, China.

5.2.3. Description

Trackway YMZ-T2 is represented by a right–left–right sequence of natural casts with the first two tracks represented by the replicas CU/UCM 214.286 and CU/UCM 214.287. The mean track length and width values are 19.4 and 12.0 cm (Table 1), the mean pace length is 114.5 cm and the stride is 228.1 cm. YMZ-T2-R1 and L1 are the best-preserved imprints. Digit III is the longest and is directed anteriorly. Digit II is shorter than digit IV. Digit II possesses two digit pad traces. Digit III has three phalangeal pad traces, and the impression of distal

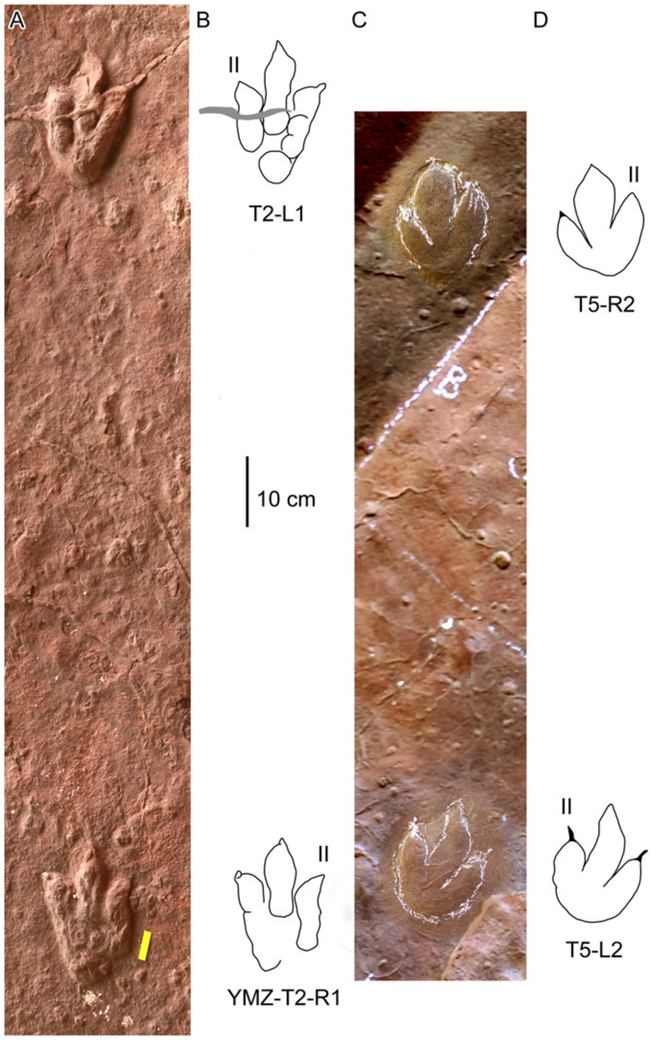

Fig. 5. A and B: photograph and interpretative outline drawing of Yangmozu theropod trackways cf. *Jialingpus* (morphotype B). C and D: composite photograph (based on two close-up photos and their corresponding background region) and interpretative outline drawing of Yangmozu theropod trackways designated as morphotype B. Compare with Xing et al. (2014b).

pad 3 and part of pad 2 are shallower due to weathering. Digit IV has three phalangeal pad traces, best preserved in T2-L1. Although the margins of the third (distal) pad are distinct, the creases separating the more proximal pad impressions are indistinct in YMZ-T2-R1. The proximal metatarsophalangeal pad of digit IV is positioned in line with the long axis of digit III. Claw marks are sharp, especially those of digit IV. The third track in the sequence (YMZ-T2-R2) exhibits an unusual style of preservation in comparison with YMZ-T2-R1 and YMZ-T2-L1: it shows sandstone remnants of the casts of digits III and IV adhering to a relatively smooth surface that represents a layer above the surface on which the tracks were originally impressed. This suggests that the track was originally filled only to the level of the surface on which it was made, and may have been draped by fine mud before the next layer was deposited.

5.2.4. Comparison

Morphotype B tracks represented by the YMZ-T2 trackway morphologically resemble Lower Cretaceous *Jialingpus* from China (Xing et al., 2014b), which is reflected in some characteristic values: the ML/MW ratio is 1.6, the L/W ratio of the anterior triangle is 0.49, and the divarication angle between digits II and IV is 46°. However, an important character of *Jialingpus* is absent in YMZ-T2: *Jialingpus* has two distinct metatarsophalangeal pad traces — a smaller one behind digit II and another larger one continuous with digit IV, whereas YMZ-T2 has only one larger metatarsophalangeal pad trace in digit IV. Therefore, the tracks are tentatively referred here to cf. *Jialingpus* isp.

5.3. Morphotype C

Ichnogenus uncertain.

5.3.1. Material

Trackways T1, 3–10, 14–15, and isolated tracks TI1–9 (Figs. 5, 6; Table 1) are assigned to Morphotype C. Trackways T1, T3–10, 14–15 account for 37 tracks (T1: 4, T3: 4, T4: 3, T5: 4, T6: 3, T7: 4, T8: 6, T9: 2, T10: 2, T14: 2, T15: 3) and tracks TI1–9 are each represented by a single track. Trackway T1 is documented by replica CU 214.290, trackway T3 by replica CU 214.289, and T7 by replica CU 214.288.

As noted above, trackway morphotype C is used as a general category to include all tracks that lack well preserved morphological details such as pad impressions. This constitutes all trackways except T2 and T11–T13. Almost all these tracks have very wide digit traces that give the tracks a fleshy appearance (Figs. 5, 6). As discussed below, these tracks probably all display extramorphological features to various degrees (Haubold, 1986). However, such tracks may still provide useful general information on size and step. Better preserved tracks, such as T5 and T7, have mean ML/MW ratios of 1.6 and 1.4 and mean L/W ratios of the anterior triangle of 0.50 and 0.43, respectively. Other characteristics like divarication angles between digits II and IV and the pace angulation resemble those of T2. T7-R1 has poorly preserved metatarsal or heel drag traces, and the heel of T7-R2 preserves about eight striation marks, probably reflecting the angles at which the foot entered the sediment. Tracks from trackways T1, T4, T5 and T9 show distinct claw marks, indicating theropod affinity.

Tracks from most of the trackways assigned to this morphotype have very wide digit traces, giving them a fleshy appearance somewhat reminiscent of ornithopod tracks. However, the long step and high pace angulation values (163°–179° in all examples except T7) are typical of theropods. Thus, we infer that the wide digit traces, and lack of discrete pad traces are probably extramorphological features caused by flattening of the track by post-burial overburden pressures, which often produces a characteristic widening of the distal part of the trace of digit III. This flattening phenomenon has been described in detail elsewhere (Lockley and Xing, 2015).

5.3.2. Locality and horizon

Lower Member of the Feitianshan Formation, Early Cretaceous. Yangmozu tracksite, Zhaojue County, Sichuan Province, China.

5.3.3. Description and comparison

Given that Morphotype C tracks may owe their morphologies to extramorphological factors (Lockley et al., 2013), it is not appropriate to assign them ichnotaxonomic names. The largest tracks (T7 and T8) are very similar in size, mesaxony and pace angulation to morphotype B (T2), although the step is somewhat shorter. Thus it is possible that some Morphotype C tracks are simply poorly preserved examples of Morphotype B: i.e. cf. *Jialingpus*. This could be explained by extramorphological variation due to changes in substrate consistency, especially if the trackmakers left their footprints at different times. The other Morphotype C tracks are smaller: for example tracks TI3, TI5 and TI8 have foot lengths in the range of 9.9–11.7 cm. Thus, the smallest track is about half the length of the largest.

6. Juvenile or adult theropod tracks?

If we hope to suggest likely trackmakers of *Minisauripus*, it is important to determine whether the trackmakers were juveniles or adults. As their name implies *Minisauripus* tracks are consistently reported as

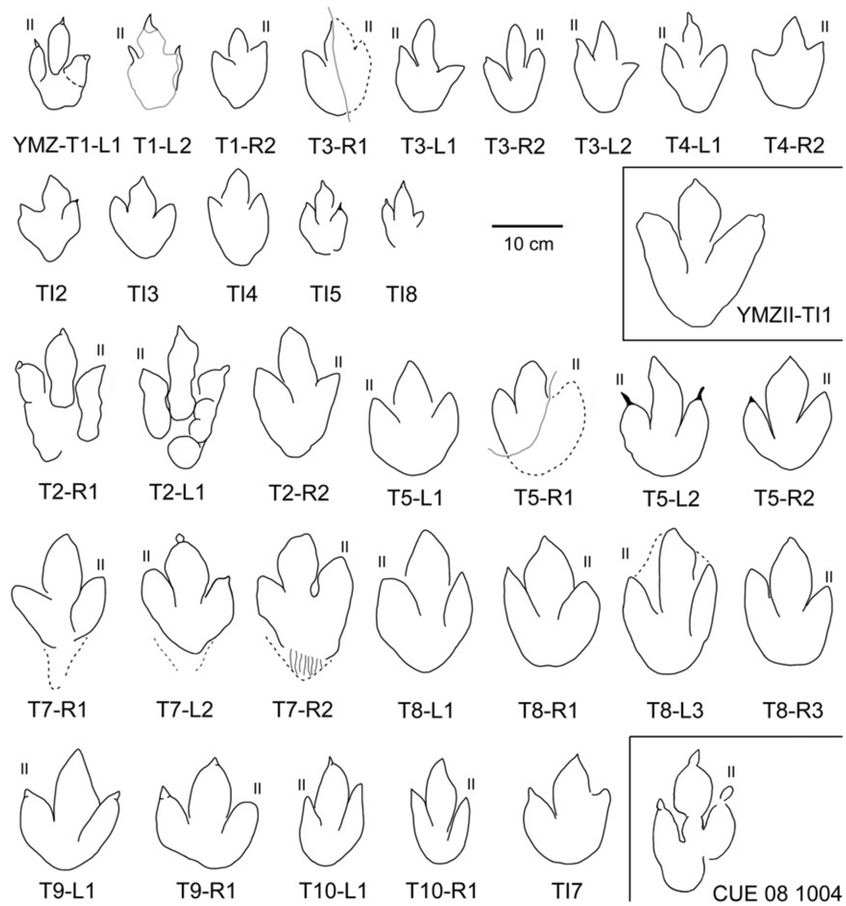

Fig. 6. Interpretative outline drawings of Yangmozu theropod trackways. T2 series represent morphotype B (cf. *Jialingpus*). Bottom right inset: cf. *Minisauripus* from South Korea, Kim et al., 2012). Others represent YMZI morphotype B. All are preserved as natural casts except for YMZII (inset near top right) from the upper level, preserved as a natural impression.

small (1.0–6.1 cm in length) (Lockley et al., 2008). However, two large (16.1 and 20.0 cm in length) theropod tracks from The Changseon site in Korea (Kim et al., 2012) were "provisionally inferred to represent adults" and have been described under cf. *Minisauripus* (Kim et al., 2012). The weakness of this argument is: 1) that medium-sized *Minisauripus* tracks (6.3–16.1 cm in length) are absent at all (seven) previously known sites from China and Korea, and 2) that the large tracks cannot clearly be shown to be morphologically close to *Minisauripus*. The Yangmozu data supports this trend adding another site (no. 8) with only small tracks (length 2.5–2.6 cm).

If *Minisauripus* represents juvenile dinosaurs, they would seem to have lived segregated from adults, at all known sites, leaving only abundant small footprints on surfaces that otherwise lack those of larger individuals. This is plausible, but hard to prove. Leonardi (1981) argued that the lack of small tracks, was in fact an indication of the rarity of juveniles. But this lack of small tracks could be also attributed to a general preservational bias in favour of large tracks rather than a biological signal: in other words it could equally well be used as an argument for the rarity of small species. But the rarity argument cannot be used convincingly in the case of the eight Minisauripus sites which yield small tracks.

Tridactyl theropod tracks found with YMZ *Minisauripus* have lengths ranging from 9.9 to 19.6 cm, suggesting that they could possibly reflect "adult" *Minisauripus* trackmakers. However, although ostensibly revealing well-padded or "fleshy" digit traces, as is the case with *Minisauripus*, it has been argued that this appearance is the result of extramorphological factors pertaining to preservation which causes flattening of tracks and erasing of diagnostic inter-pad creases (Lockley and Xing, 2015). Typical theropod track Morphotype B, provisionally compared with *Jialingpus*, is considered to be a true, undistorted, reflection of foot morphology, whereas track Morphology C appears distorted by flattening, and therefore has not been named. Thus, it cannot be considered to have any ichnotaxonomic relationship with *Minisauripus*.

We compared the YMZ tracks with those assigned to morphotypes B and C by plotting three scatter diagrams (ML vs. MW ratio, ML/MW vs. M, and PL/ML vs. ML). The former two ratios indicate no obvious allometric difference between *Minisauripus* and the larger tracks (Fig. 7). However, the scatter diagram showing the ratio of track length to step length clearly distinguishes YMZ *Minisauripus* from other morphotypes (B and C) indicating a very long step and differences in gait and speed. Nevertheless, we note that we cannot exclude a change of these parameters during ontogenetic growth, which could imply that the trackmakers were juveniles rather than a small adult species.

Further differences between *Minisauripus* and the larger tracks can be identified. Digit II of YMZI *Minisauripus* is much shorter than other digits, and the proximal margins of the traces of digits II and IV do not have consistent well-defined boundaries. In some cases the posterior margins of digits II and IV form a distinctive U-shaped configuration. However, this is not observed consistently in all tracks. In evaluating whether diagnostic features of small *Minisauripus* and the larger tracks are related to ontogenetic growth (age) or different biotaxonomic affinity, we note that morphotype B is clearly morphologically, and by implication, biotaxonomically distinct, and morphotype C is extramorphologically compromised. This simply means that *Minisauripus* and morphotype B would not represent the same trackmaker, but again it is not conclusive evidence of the former being the track of an adult of a small species. Unfortunately, studies of ontogenetic growth in the theropod limb are based on the relative lengths of autopodia and proximal parts only (Foster and Chure, 2006). Data on possible allometric growth within pes and digits

Table 1
Measurements (in cm) of the theropod tracks from Yangmozu tracksite, Sichuan Province, China.

Number	ML	MW	II-IV	PL	SL	PA	M	ML/MW
YMZ-T1-L1	13.3	7.9	48°	–	119.5	–	0.56	1.7
YMZ-T1-R1	–	–	–	–	–	–	0.85	–
YMZ-T1-L2	13.6	7.3	45°	59.3	120.5	167°	–	1.9
YMZ-T1-R2	11.5	7.5	45°	62.6	–	–	0.49	1.5
Mean	12.8	7.6	46°	61.0	120.0	167°	0.63	1.7
YMZ-T2-R1	19.2	12.2	48°	113.9	228.1	179°	0.42	1.6
YMZ-T2-L1	20.5	12.2	45°	115.1	–	–	0.50	1.7
YMZ-T2-R2	18.6	11.7	51°	–	–	–	0.55	1.6
Mean	19.4	12.0	48°	114.5	228.1	179°	0.49	1.6
YMZ-T3-R1	13.9	8.5	46°	67.0	129.4	170°	0.49	1.6
YMZ-T3-L1	13.4	9.6	63°	63.8	125.8	168°	0.55	1.4
YMZ-T3-R2	12.7	7.6	47°	61.4	124.1	165°	0.59	1.7
YMZ-T3-L2	13.1	9.7	55°	63.8	–	–	0.49	1.4
Mean	13.3	8.9	53°	64.0	126.4	168°	0.53	1.5
YMZ-T4-R1	–	–	–	62.4	123.4	166°	–	–
YMZ-T4-L1	14.4	8.4	45°	61.2	115.6	165°	0.43	1.7
YMZ-T4-R2	13.2	10.0	57°	55.1	–	–	0.45	1.3
Mean	13.8	9.2	51°	59.6	119.5	166°	0.44	1.5
YMZ-T5-L1	16.4	11.0	51°	94.1	181.5	160°	0.47	1.5
YMZ-T5-R1	16.3	11.0	47°	91.3	178.6	164°	0.34	1.5
YMZ-T5-L2	17.2	10.2	50°	88.3	–	165°	0.65	1.7
YMZ-T5-R2	16.2	10.7	53°	–	–	–	0.55	1.5
Mean	16.5	10.7	50°	91.2	180.1	163°	0.50	1.6
YMZ-T7-L1	–	–	–	–	–	–	–	–
YMZ-T7-R1	17.5	13.0	70°	85.5	163.2	170°	0.50	1.3
YMZ-T7-L2	17.3	11.5	54°	76.2	–	150°	0.42	1.5
YMZ-T7-R2	18.0	12.1	50°	–	–	–	0.36	1.5
Mean	17.6	12.2	58°	80.9	163.2	160°	0.43	1.4
YMZ-T8-L1	20.4	11.4	45°	127.3	259.5	174°	0.59	1.8
YMZ-T8-R1	18.7	11.1	45°	132.1	242.4	166°	0.42	1.7
YMZ-T8-L2	–	–	–	114.8	223.5	171°	–	–
YMZ-T8-R2	–	–	–	110.1	–	168°	–	–
YMZ-T8-L3	20.9	11.4	44°	–	–	–	0.51	1.8
YMZ-T8-R3	18.3	11.3	47°	–	–	–	0.47	1.6
Mean	19.6	11.3	45°	121.1	241.8	170°	0.50	1.7
YMZ-T9-L1	17.4	13.1	61°	90.3	–	–	0.55	1.3
YMZ-T9-R1	15.9	13.1	63°	–	–	–	0.41	1.2
Mean	16.7	13.1	62°	90.3	–	–	0.48	1.3
YMZ-T10-L1	15.7	7.9	39°	78.4	–	–	0.47	2.0
YMZ-T10-R1	15.0	7.9	43°	–	–	–	0.63	1.9
Mean	15.4	7.9	41°	78.4	–	–	0.55	2.0
YMZ-T11-L1	2.7	2.0	–	18.3	38.9	173°	0.60	1.3
YMZ-T11-R1	–	–	–	20.7	41.8	175°	–	–
YMZ-T11-L2	2.8	1.6	47°	21.2	–	–	0.42	1.7
YMZ-T11-R2	2.3	1.7	–	–	–	–	0.57	1.3
Mean	2.6	1.8	47°	20.1	40.4	174°	0.53	1.4
YMZ-T12-R1	2.2	1.7	57°	38.9	75.0	179°	0.45	1.3
YMZ-T12-L1	3.1	1.9	48°	36.0	–	–	0.43	1.6
YMZ-T12-R2	2.1	1.5	–	–	–	–	0.31	1.5
Mean	2.5	1.7	53°	37.5	75.0	179°	0.40	1.5
YMZ-T13-L1	2.4	2.3	67°	28.2	54.5	176°	0.49	1.0
YMZ-T13-R1	2.8	2.4	63°	26.4	53.0	175°	0.40	1.2
YMZ-T13-L2	2.6	2.4	66°	26.5	–	–	0.52	1.1
YMZ-T13-R2	2.7	2.2	61°	–	–	–	0.62	1.3
Mean	2.6	2.3	64°	27.0	53.8	176°	0.51	1.1
YMZ-TI2	12.4	8.1	51°	–	–	–	0.54	1.5
YMZ-TI3	11.7	8.4	52°	–	–	–	0.33	1.4
YMZ-TI4	13.9	7.4	41°	–	–	–	0.51	1.9
YMZ-TI5	10.6	4.9	38°	–	–	–	0.62	2.2
YMZ-TI7	15.7	11.0	54°	–	–	–	0.48	1.4
YMZ-TI8	9.9	5.3	47°	–	–	–	0.55	1.9
YMZII-TI1	20.7	16.7	55°	–	–	–	0.30	1.2

Abbreviations: ML: maximum length; MW: maximum (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; M: mesaxony (length/width ratio for the anterior triangle); ML/MW is dimensionless.

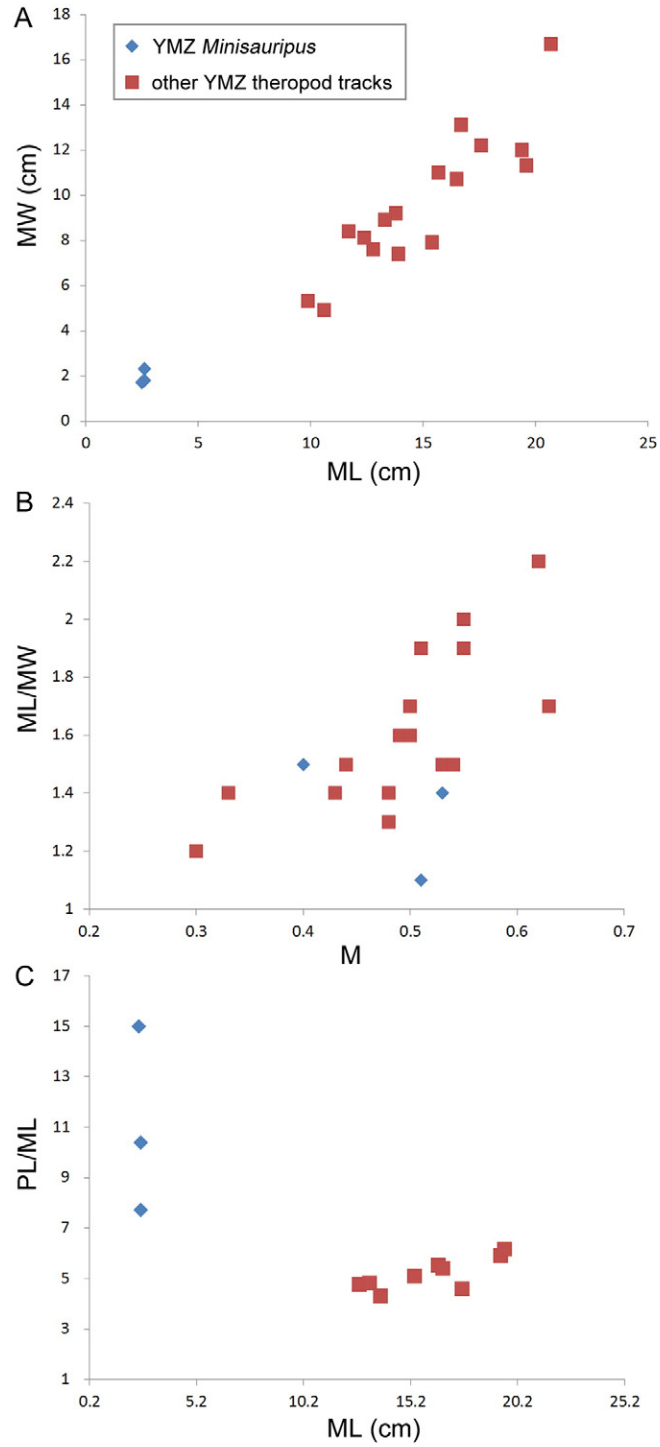

Fig. 7. Scatter diagrams plotting track length (ML) against track width (MW) (A), mesaxony (M) against ML/MW (B) and track length (ML) against step length (PL)/track length (ML) (C) in YMZ theropod tracks.

are lacking for fossil species. Given this uncertainty, the most parsimonious conclusion is that our concept of *Minisauripus* should be restricted only to tracks with the diagnostic ichnogenus morphology: i.e., small tracks.

The gap in YMZI track size between *Minisauripus* (maximum length 2.6 cm) and the next smallest track (9.9 cm) theoretically fills part of the aforementioned size gap (6.1–16.1 cm) based on the *Minisauripus* samples from Korea and other Chinese sites (Kim et al., 2012). However, this conjecture is tenuous, given the preservational contrast between the well-defined small *Minisauripus* and the extramorphological nature of the larger tracks.

Thus, as admitted in the original study, interpretation of large tracks like CUE 08 1004, 1005 and 1006 from Buyun-ri, Changseon Island (Lockley et al., 2008; Kim et al., 2012), as cf. *Minisauripus* is tenuous at best, and inconsistent with the evidence from seven other *Minisauripus* sites. The Korean samples are overwhelmingly represented by small tracks (length ~1.0–5.0 cm). Likewise all the positively identified Chinese *Minisauripus* fall in the length size range of 2.1–6.1 cm. The possibility that larger tracks from YMZ or other sites might represent adults of the *Minisauripus* track maker is unproven, and in the final analysis there is no convincing evidence that any tracks larger than 6.1 cm show a diagnostic *Minisauripus* morphology. A good argument for small adult trackmaker hypothesis is the occurrence of *Minisauripus* during multiple track making episodes and over a wide geographical area. Such reasoning is also consistent with previous ichnological conventions, discussed below (Haubold, 1986; Lockley and Eisenberg, 2006), that attribute large assemblages of small tracks to small species rather than juveniles, a position ostensibly supported by Leonardi (1981). However, this could also be an effect of a preservational bias, with juveniles of some theropod species being segregated from adults, or perhaps preferring distinct habitats with good potential for footprint preservation.

7. Discussion

In dealing with fossil footprints it is difficult to differentiate between tracks of juveniles and small adults, especially when we must concede that likely trackmakers are unknown, or represented by skeletal remains that lack feet. However, there are marked differences between assemblages that consist only of tracks of a single, small size class, and assemblages where tracks of a particular type fall into different size classes. In the case of all the *Minisauripus* assemblages we are dealing with the former category (only small theropod tracks), and there is no convincing evidence that other larger co-occurring tracks belong to the same ichnotaxon. There are ichnological precedents for interpreting such assemblages of small tracks. For example, Haubold (1986) defined a latest Triassic "small *Grallator* assemblage" identified in both Europe and North America (Lockley and Eisenberg, 2006). Based on the known existence of small theropods at this time, there is no suggestion that these tracks represent juveniles: i.e. has been assumed, without debate, that they represent a small species or possibly several small species. On the other hand, the ichnogenus *Grallator* has been also considered as part of a continuum with larger *Eubrontes* by some authors (Olsen, 1980; Rainforth, 2007), at least in the Lower Jurassic, possibly representing different ontogenetic stages of the same trackmaker. In this case however, the continuum is inferred by pooling data on tracks of different sizes and ichnogenus designations from many sites: i.e., the ontogenetic or allometric inferences are not based on samples comparable to those containing *Minisauripus* which lack large morphologically similar tracks.

As suggested previously, numerous bird (avian theropod) track assemblages from the Cretaceous and Cenozoic have been documented (Lockley and Harris, 2010). However, here ichnologists have the advantage of knowing that similar modern track assemblages represent small, rapidly growing adults.

Grallator-type tracks (<15 cm long) with strong mesaxony (Olsen et al., 1998) occur not only in the Jurassic of North America and Europe, but also in China from the Jurassic–Cretaceous boundary and the Early Cretaceous (Olsen et al., 1998; Lockley et al., 2013), in some cases in huge assemblages consisting of a single size class, as at the Yangshan site in Liaoning (Matsukawa et al., 2006). They are generally considered here as the tracks of a relatively small species, even if a juvenile origin cannot be excluded.

A juvenile track interpretation is likely in the case of very diminutive ichnospecies such as *Grallator emeiensis* (2.7 cm) (Olsen et al., 1998; Lockley et al., 2013), which occur in isolation: i.e., not as part of a large assemblages of small tracks. For two reasons, such isolated examples might represent juveniles. First they share the same morphology as larger tracks. Second they do not require postulating a large assemblage of juveniles and the absence of adults.

Considering the first hypothesis and starting from the premise that *Minisauripus* is the track of a small adult theropod, it could be compared with known skeletons of small theropod species from the Lower Cretaceous. At present, the smallest skeleton of an adult non-avialian theropod is *Anchiornis*, which like the small taxa *Epidexipteryx*, *Microraptor* and *Parvicursor*, had a body length greater than 20 cm (Karhu and Rautian, 1996; Xu et al., 2000; Xu and Norell, 2004; Zhang et al., 2008; Xu et al., 2000). Comparison of the foot skeletons of the small Jehol dinosaurs *Caudipteryx* sp. (IVPP V 12430) (Zhou et al., 2000) and *Sinosauropteryx prima* (NIGP 127587) (Currie and Chen, 2001) with *Grallator* isp. (NGMC V2115B) shows (Xing et al., 2009) that it is more similar to the former. Strong mesaxony, the typical feature of *Grallator*-like tracks (including *Jialingpus*, e.g. DJP-4 from the Lower Cretaceous of Shaanxi, China), is a feature seen in the foot bones of IVPP V 12430. Though these comparisons cannot determine whether or not the NGMC V2115 trackmaker was oviraptorosaurian, the trackmaker may have more affinity to oviraptorosaurs than to compsognathids. Chinese oviraptorosaurians (e.g. *Caudipteryx* and *Incisivosaurus*) were diverse from the Jurassic–Cretaceous boundary to the Early Cretaceous, especially during the Early Cretaceous, and include some exceptionally small genera, such as *Similicaudipteryx* (Xu et al., 2010).

Compared to *Grallator*-type tracks, *Minisauripus* has smaller size and lower mesaxony (0.40–0.53). It has been argued (Lü et al., 2013) that the hindlimb proportions of oviraptorids do not essentially change during growth, indicating a more sedentary lifestyle and thus probably herbivory. Though changes in toe length of oviraptorids during growth (ontogeny) are unclear, such a feature is most likely to be conservative. *Minisauripus* from the Emei tracksite of Sichuan Province co-occurs with didactyl *Velociraptorichnus* tracks on the same slab (Zhen et al., 1994), *Minisauripus* from the Junan tracksite of Shandong Province co-occurs with *Velociraptorichnus* and *Dromaeopodus* (Li et al., 2007), and *Minisauripus* from the Godu tracksite of Korea co-occurs with didactyl *Dromaeosauripus* tracks (Kim et al., 2012). The relatively consistent association of *Minisauripus* and dromaeopodid tracks suggests (Xing et al., 2013) a close ecological association between the makers of these two track types. However, no dromaeopodid tracks have been found together with *Minisauripus* at the YMZ tracksite.

All eight *Minisauripus* track sites are in East Asia, and from the Lower Cretaceous. They consistently reveal track assemblages composed of small tracks. Such evidence, including the new SMG assemblage would suggest a single extremely small theropod species of trackmaker, with a minimum body length of only about 12 cm. This is smaller than any theropod body lengths known from skeletal remains.

If the *Minisauripus* trackmaker is indeed a small adult theropod, these ichnofossils could contribute to our knowledge of theropod palaeobiology and fill a gap in the body fossil record. Besides the smallest non-avialian theropod *Anchiornis* (troodontid), some juveniles or subadults such *Epidendrosaurus* (Naish and Sweetman, 2011) and *Epidexipteryx* (Zhang et al., 2008) have total skeletal lengths of only about 16 cm and 25 cm, respectively. The Ashdown maniraptoran, from England, is thought to have had a body length between only 16 and 40 cm (Naish and Sweetman, 2011). Many other non-avialian theropods are known from specimens shorter than 100 cm, such as *Parvicursor* (39 cm) (Karhu and Rautian, 1996), *Sinosauropteryx* (68 cm) (Chen et al., 1998), *Mei* (53 cm) (Xu and Norell, 2004), *Mahakala* (70 cm) (Turner et al., 2007), and the oviraptorosaur *Yulong* ("chicken-sized", ~70 cm) (Lü et al., 2013). Thus small non-avialian theropods cover a number of clades, that would have left small tracks. Troodontids and dromaeosaurids can be ruled out as *Minisauripus* track makers because they would have registered didactyl, not tridactyl, tracks, as proven by ichnology (Zhen et al., 1994; Li et al., 2007). Early Cretaceous alvarezsaurids have not yet been found in China, although *Haplocheirus* is known from the Upper Jurassic Shishugou Formation in northwestern China (Choiniere et al., 2010). Scansoriopterygids are thought to have been largely arboreal (Naish and Sweetman, 2011) and, besides being rare, most occur in Middle Jurassic deposits. Among them *Epidendrosaurus* (IVPP V12653) (Zhang et al., 2002) has poorly preserved feet, and the feet of *Epidexipteryx* (IVPP V15471) (Zhang et al., 2008) are not known. This is a common problem when it comes to matching feet and footprints, leading ichnologists to point out that they cannot be expected to identify trackmakers in such circumstances. Ornithomimosaurians are also possible trackmakers, though, in China, most, such as *Sinornithomimus* (Kobayashi and Lü, 2003), are known from the late stages of the Cretaceous. Early Cretaceous Ornithomimosauria are only represented by *Shenzhousaurus* (Ji et al., 2003), also preserved without foot bones! Compsognathids and oviraptorosaurians are known from abundant specimens from the same age and location, and would make these two groups the most likely candidates for the trackmakers.

The best preserved YMZ-T13-L2 shows consistency with *Sinosauropteryx prima* (NIGP 127587) pedal morphology (Fig. 8). *Sinosauropteryx* and *Compsognathus* are similar (Currie and Chen, 2001) and based on computer simulations, *Compsognathus* appears to have been able to run very fast reaching maximum speeds up to nearly 64 km/h (=17.8 m/s) (Sellers and Manning, 2007). The high running speed estimated at up to 22.5 km/h (=6.2 m/s) for the *Minisauripus* trackmaker from the YMZ sample is at least consistent with rapid movement by these small theropod trackmakers (Table 2). Previously no estimates of speed of the *Minisauripus* trackmaker had been published. Here, therefore, we tentatively suggest that *Minisauripus* tracks could indicate compsognathids with good cursorial ability. However, we stress, that presently any proposed affinity of *Minisauripus* to small adult theropods cannot be proved with certainty, and that a juvenile origin cannot be ruled out.

8. Conclusions

A new assemblage with trackways from the Lower Cretaceous Yangmozu tracksite of Sichuan Province are interpreted as those of theropods and assigned to the ichnogenera *Minisauripus* and cf. *Jialingpus*. Others are indeterminate.

Minisauripus is considered to most likely represent a small theropod species. Support for this hypothesis is consistent with most previous interpretations in the literature (ichnological precedent) and the repeated occurrence in the Lower Cretaceous of Asia of small *Minisauripus*, on surfaces lacking the tracks of larger, but morphologically similar, specimens.

The alternative interpretation of *Minisauripus* as representing juvenile trackmakers cannot entirely be ruled out. However, we consider this a dubious interpretation because it would suggest the less-parsimonious interpretation that juvenile age classes were segregated from adults, with ecological preferences for different environments favouring the preservation of their tracks.

Table 2
Estimated data of the speed of Yangmozu theropod trackmakers.

No.	SL/h	Motion	S (m/s)	S (km/h)
YMZ-T1	2.08	Trotting	2.02	7.27
YMZ-T2	2.61	Trotting	3.64	13.10
YMZ-T3	2.11	Trotting	2.11	7.60
YMZ-T4	1.92	Walking	1.84	6.62
YMZ-T5	2.43	Trotting	2.96	10.66
YMZ-T7	2.06	Trotting	2.33	8.390
YMZ-T8	2.74	Trotting	3.96	14.26
YMZ-T11	3.45	Running	2.12	7.63
YMZ-T12	6.67	Running	6.24	22.46
YMZ-T13	4.60	Running	3.42	12.31

Abbreviations: SL/h, relative stride length; S = absolute speed.

We recognize the track preservational biases that might result in small tracks being less easily preserved or observed than large tracks. However, especially in the Cretaceous of Asia, small *Minisauripus*-sized avian tracks are quite commonly preserved, suggesting no strong bias against the preservation of small tracks.

Trackmakers were possibly cursorial compsognathids, but this interpretation is tentative, and we caution that matching tracks with trackmakers at low taxonomic levels (genus or species) is difficult, especially so in cases where potential trackmakers lack foot skeletons.

Acknowledgements

The authors thank Spencer G. Lucas, Michael D'Emic and an anonymous reviewer for their critical comments and suggestions on this paper. This work was supported by the special projects grants of Zhaojue County People's Government, China (No. 20140703), and the 2013, 2015 support fund for graduate student's science and technology innovation from China University of Geosciences (Beijing), China (No. 51223229).

References

Chen, P., Dong, Z., Zhen, S., 1998. An exceptionally well-preserved theropod dinosaur from the Yixian Formation of China. Nature 391, 147–152.
Choiniere, J.N., Xu, X., Clark, J.M., Forster, C.A., Guo, Y., Han, F.L., 2010. A basal alvarezsauroid theropod from the Early Late Jurassic of Xinjiang, China. Science 327, 571–574.
Currie, P.J., Chen, P.J., 2001. Anatomy of *Sinosauropteryx prima* from Liaoning, northeastern China. Can. J. Earth Sci. 38, 705–727.
Foster, J.R., Chure, D.J., 2006. Hindlimb allometry in the Late Jurassic theropod dinosaur *Allosaurus*, with comments on its abundance and distribution. N. M. Mus. Nat. Hist. Sci. Bull. 36, 119–122.

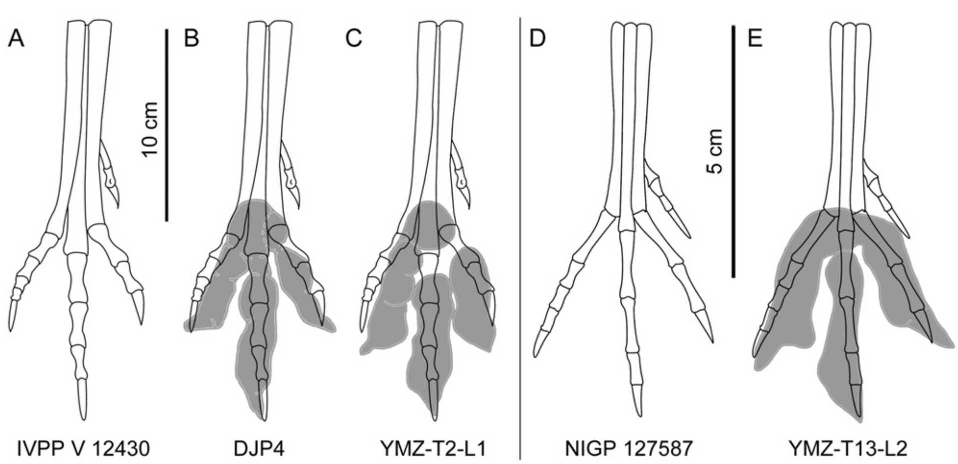

Fig. 8. Comparison between Yangmozu theropod tracks and foot skeletons of selected theropod dinosaurs. A, *Caudipteryx* sp. (IVPP V 12430); B, *Caudipteryx* pes skeleton superimposed on *Jialingpus* DJP4 (Xing et al., 2014b); C, *Caudipteryx* pes skeleton superimposed on YMZ-T2-L1; D, *Sinosauropteryx prima* (NIGP 127587); E, *Sinosauropteryx* pes skeleton superimposed on YMZ-T13-L2.

Gu, X.D., Liu, X.H., 1997. Stratigraphy (Lithostratic) of Sichuan Province. China University of Geosciences Press, Wuhan.
Haubold, H., 1986. Archosaur footprints at the terrestrial Triassic–Jurassic transition. In: Padian, K. (Ed.), The Beginning of the Age of Dinosaurs: Faunal Change Across the Triassic–Jurassic Boundary. Cambridge University Press, Cambridge, pp. 189–201.
Hu, D., Hou, L., Zhang, L., Xu, X., 2009. A pre-*Archaeopteryx* troodontid theropod from China with long feathers on the metatarsus. Nature 461, 640–643.
Ji, Q., Norell, M.A., Makovick, P.J., Gao, K.Q., Ji, S.A., Yuan, C.X., 2003. An early ostrich dinosaur and implications for ornithomimosaur phylogeny. Am. Mus. Novit. 3420, 1–19.
Karhu, A.A., Rautian, A.S., 1996. A new family of Maniraptora (Dinosauria: Saurischia) from the Late Cretaceous of Mongolia. Paleontol. J. Russ. Acad. Sci. 30, 583–592.
Kim, K.S., Lockley, M.G., Kim, J.Y., Seo, S.J., 2012. The smallest dinosaur tracks in the world: occurrences and significance of *Minisauripus* from East Asia. Ichnos 19, 66–74.
Kobayashi, Y., Lü, J.C., 2003. A new ornithomimid dinosaur with gregarious habits from the Late Cretaceous of China. Acta Palaeontol. Pol. 48, 235–259.
Leonardi, G., 1981. Ichnological rarity of young in Northeast Brazil dinosaur populations. Ann. Acad. Bras. Cienc. 53, 345–346.
Li, R.H., Lockley, M.G., Makovicky, P.J., Matsukawa, M., Norell, M.A., Harris, J.D., Liu, M.W., 2007. Behavioral and faunal implications of Early Cretaceous deinonychosaur trackways from China. Naturwissenschaften 95, 185–191.
Lim, J.D., Martin, L.D., Zhou, Z., Baek, K.S., Yang, S.Y., 2002. The significance of Early Cretaceous bird tracks. In: Zhou, Z., Zhang, F. (Eds.), Proceeding of the 5th Symposium of the Society of Avian Paleontology and Evolution. Science Press, Beijing, pp. 157–163.
Lockley, M.G., 2007. The morphodynamics of dinosaurs, other archosaurs and their trackways: holistic insights into relationships between feet, limbs and the whole body. In: Bromley, R., Melchor, R. (Eds.), Ichnology at the Crossroads: A Multidimensional Approach to the Science of Organism — Substrate Interactions. Society of Economic Paleontologists and Mineralogists Special Publication Vol. 88, pp. 27–51.
Lockley, M.G., 2011. Putting the best foot forward: a single case of 'toe extension' has implications for the broader concept of 'toe extension' in theropod dinosaur feet and footprints. N. M. Mus. Nat. Hist. Sci. Bull. 53, 301–305.
Lockley, M.G., Eisenberg, L., 2006. A preliminary report on a spectacular dinosaur tracksite in the Chinle Group, Dirty Devil river valley, Wayne County, Utah. N. M. Mus. Nat. Hist. Sci. Bull. 37, 263–268.
Lockley, M.G., Harris, J., 2010. On the Trail of Early Birds: A Review of the Fossil Footprint Record of Avian Morphological Evolution and Behavior. Trends in Ornithological ResearchNovapublishers, pp. 1–63.
Lockley, M.G., Xing, L.D., 2015. Flattened fossil footprints: implications for paleobiology. Palaeogeogr. Palaeoclimatol. Palaeoecol. 426, 85–94.
Lockley, M.G., Kim, J.Y., Kim, K.S., Kim, S.H., Matsukawac, M., Li, R.H., Li, J.J., Yang, S.Y., 2008. *Minisauripus*—the track of a diminutive dinosaur from the Cretaceous of China and Korea: implications for stratigraphic correlation and theropod foot morphodynamics. Cretac. Res. 29, 115–130.
Lockley, M.G., Li, J.J., Li, R.H., Matsukawa, M., Harris, J.D., Xing, L.D., 2013. A review of the tetrapod track record in China, with special reference to type ichnospecies: implications for ichnotaxonomy and paleobiology. Acta Geol. Sin. 87, 1–20.
Lü, J., Currie, P.J., Xu, L., Zhang, X.L., Pu, H.Y., Jia, S.H., 2013. Chicken-sized oviraptorid dinosaurs from central China and their ontogenetic implications. Naturwissenschaften 100, 165–175.
Luo, C.D., 1999. The Danxia landforms in southwest Sichuan. Econ. Geol. 19, 65–70.
Matsukawa, M., Lockley, M.G., Li, J., 2006. Cretaceous terrestrial biotas of east and Southeast Asia, with special reference to dinosaur dominated ichnofaunas: towards a synthesis. Cretac. Res. 27, 3–21.
Naish, D., Sweetman, S.C., 2011. A tiny maniraptoran dinosaur in the Lower Cretaceous Hastings Group: evidence from a new vertebrate-bearing locality in south-east England. Cretac. Res. 32, 464–471.
Olsen, P.E., 1980. Fossil great lakes of the Newark Supergroup in New Jersey. In: Manspeizer, W. (Ed.), Field studies in New Jersey geology and guide to field trips 52nd Ann. Meeting. New York State Geological Association, Newark College of Arts and Sciences. Newark, Rutgers University, pp. 2–39.
Olsen, P.E., Smith, J.B., McDonald, N.G., 1998. Type material of the type species of the classic theropod footprint genera *Eubrontes*, *Anchisauripus*, and *Grallator* (Early Jurassic, Hartford and Deerfield basins, Connecticut and Massachusetts, U.S.A.). J. Vertebr. Paleontol. 18, 586–601.
Rainforth, E.C., 2007. Ichnotaxonomic updates from the Newark Supergroup. Contributions to the paleontology of New Jersey (II). Geological Association of New Jersey, XXIV Annual Conference and Field Trip, pp. 49–59.
Rainforth, E.C., Lockley, M.G., 1996. Tracks of diminutive dinosaurs and hopping mammals from the Jurassic of North and South America. In: Morales, M. (Ed.), The Continental Jurassic. Museum of Northern Arizona Bulletin Vol. 60, pp. 265–269.
Sellers, W.I., Manning, P.L., 2007. Estimating dinosaur maximum running speeds using evolutionary robotics. Proc. R. Soc. Lond. B Biol. Sci. 274, 2711–2716.
Tamai, M., Liu, Y.Y., Lu, L.Z., Yokoyama, M., Halim, N., Zaman, H., Otofuji, Y.I., 2004. Palaeomagnetic evidence for southward displacement of the Chuan Dian fragment of the Yangtze Block. Geophys. J. Int. 158, 297–309.
Thulborn, T., 1990. Dinosaur Tracks. Chapman & Hall, London.
Turner, A.H., Pol, D., Clarke, J.A., Erickson, G.M., Norell, M.A., 2007. A basal dromaeosaurid and size evolution preceding avian flight. Science 317, 1378–1381.
Xing, L.D., Harris, J.D., Feng, X.Y., Zhang, Z.J., 2009. Theropod (Dinosauria: Saurischia) tracks from Lower Cretaceous Yixian Formation at Sihetun, Liaoning Province, China and possible track makers. Geol. Bull. Chin. 28, 705–712.
Xing, L.D., Lockley, M.G., Zhang, J.P., Milner, A.R.C., Klein, H., Li, D.Q., Persons IV, W.S., Ebi, J.F., 2013. A new Early Cretaceous dinosaur track assemblage and the first definite non-avian theropod swim trackway from China. Chin. Sci. Bull. (Eng. Ver.) 58, 2370–2378.
Xing, L.D., Lockley, M.G., Zhang, J.P., Klein, H., Persons IV, W.S., Dai, H., 2014a. 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., Lockley, M.G., Klein, H., Gierliński, G.D., Divay, J.D., Hu, S.M., Zhang, J.P., Ye, Y., He, Y.P., 2014b. The non-avian theropod track *Jialingpus* from the Cretaceous of the Ordos Basin, China, with a revision of the type material: implications for ichnotaxonomy and trackmaker morphology. Palaeoworld 23, 187–199.
Xing, L.D., Lockley, M.G., Marty, D., Piñuelad, L., Kleine, H., Zhang, J.P., Persons IV, W.S., 2015. Re-description of the partially collapsed Early Cretaceous Zhaojue dinosaur tracksite (Sichuan Province, China) by using previously registered video coverage. Cretac. Res. 52, 138–152.
Xu, X., Norell, M.A., 2004. A new troodontid dinosaur from China with avian-like sleeping posture. Nature 431, 838–841.
Xu, X.S., Liu, B.J., Xu, Q., 1997. Analysis of the Large Scale Basins in Western China and Geodynamics. Geological Publishing House, Beijing.
Xu, X., Zhou, Z.H., Wang, X.L., 2000. The smallest known non-avian theropod dinosaur. Nature 408, 705–708.
Xu, X., Zhao, Q., Norell, M., Sullivan, C., Hone, D., Erickson, G., Wang, X.L., Han, F.L., Guo, Y., 2009. A new feathered maniraptoran dinosaur fossil that fills a morphological gap in avian origin. Chin. Sci. Bull. 54, 430–435.
Xu, X., Wang, D.Y., Sullivan, C., Hone, D.W.E., Han, F., Yan, R.H., Du, F.M., 2010. A basal parvicursorine (Theropoda: Alvarezsauridae) from the Upper Cretaceous of China. Zootaxa 2413, 1–19.
Zhang, F., Zhou, Z., Xu, X., Wang, X., 2002. A juvenile coelurosaurian theropod from China indicates arboreal habits. Naturwissenschaften 89, 394–398.
Zhang, F., Zhou, Z., Xu, X., Wang, X., Sullivan, C., 2008. A bizarre Jurassic maniraptoran from China with elongate ribbon-like feathers. Nature 455, 1105–1108.
Zhen, S., Li, J., Zhang, B., Chen, W., Zhu, S., 1994. Dinosaur and bird footprints from the Lower Cretaceous of Emi County, Sichuan, China. Mem. Beijing Nat. Hist. Mus. 54, 105–124.
Zhou, Z.H., Wang, X.L., Zhang, F.C., Xu, X., 2000. Important features of *Caudipteryx* — evidence from two nearly complete new specimens. Vert. Palas. 38, 241–254.