



Theropod tracks from the Lower Jurassic of Gulin area, Sichuan Province, China

Li-Da Xing^a, Martin G. Lockley^b, Jian-Ping Zhang^a, Hendrik Klein^c, Susanna B. Kümmell^d, W. Scott Persons IV^e, Hong-Wei Kuang^{f,*}

^a School of the Earth Sciences and Resources, China University of Geosciences, Beijing 100083, China

^b Dinosaur Trackers Research Group, CB 172, University of Colorado Denver, PO Box 173364, Denver, CO 80217-3364, USA

^c Saurierwelt Paläontologisches Museum, Neumarkt D-92318, Germany

^d Department of Biological Sciences, University of Alberta, 11455 Saskatchewan Drive, Edmonton, Alberta T6G 2E9, Canada

^e Institute of Evolutionary Biology, University Witten/Herdecke, Stockumerstr. 10-12, 58454 Witten, Germany

^f Institute of Geology, Chinese Academy of Geological Sciences, No.26 Baiwanzhuang Road, Beijing 100037, China

Received 17 September 2014; received in revised form 10 October 2015; accepted 5 November 2015

Available online 17 November 2015

Abstract

The Jiaoyuan tracksite in the Gulin area of Sichuan Province, China represents a typical saurischian-dominated assemblage with trackways of theropods and sauropods. They occur in the Lower Jurassic Da'anzhai Member of the Ziliujing Formation, a sandstone-siltstone succession of fluvial origin and deposited in the southern Sichuan Basin. Four trackways as well as isolated tracks of theropods are documented and analyzed in this first part a study of sauropod tracks will follow elsewhere. Two morphotypes and size-classes, respectively, can be observed. The larger one is 25–34 cm in length and shows weak to moderate mesaxony. The smaller is 7–15 cm in length and moderately mesaxonic. Despite a few similarities with the ichnogenus *Kayentapus*, the former is assigned here to *Eubrontes*, well known from Lower Jurassic assemblages, in North America, Europe, and southern Africa. The smaller morphotype resembles typical *Grallator* tracks except in its wider digit divarication and the metatarsophalangeal pad IV being positioned in line with the long-axis of digit III, similar to *Jialingpus* described, for example, from Upper Jurassic deposits of Sichuan. A relatively wide digit divarication in *Grallator*-type tracks is apparently common in Jurassic assemblages of China and may represent a distinct feature related to provinciality of theropod faunas in this region.

© 2015 Elsevier B.V. and Nanjing Institute of Geology and Palaeontology, CAS. All rights reserved.

Keywords: Sichuan Basin; Lower Jurassic; Ziliujing Formation; Theropod tracks; *Eubrontes*; *Grallator*

1. Introduction

Fossil tracks from the Early Jurassic of China, much like skeletal material, are rare. The Early Jurassic track record includes those from Jining (Yunnan Province) (Zhen et al., 1986; Lockley et al., 2013), Zigong (Xing et al., 2014a), Weiyuan (Xing et al., 2014b), Lufeng (Yunnan Province) (Xing et al., 2009a), and Wusu (Xinjiang Province) (Xing et al., 2014c). Zhen et al. (1986) named four ichnogenera

from the Lower Jurassic Fengjiahe Formation of Jining, Yunnan Province: *Paracoelurosaurichnus monax*, *Schizograllator xiaohebaensis*, *Youngichnus xiyangensis*, and *Zhenichnus jinningsensis*. In addition, Zhen et al. (1986) recognized the new ichnospecies *Grallator limnosus*, and the previously known ichnospecies *Eubrontes platypus* (Lull, 1904). Lockley et al. (2013) reviewed these ichnogenera, and referred them to the *Grallator-Eubrontes-Kayentapus* plexus: i.e., to well-known and ubiquitous ichnogenera. Early Jurassic tracks from the Zizhong sites were assigned to a *Grallator-Eubrontes/Changpeipus-Kayentapus* plexus (Lockley et al., 2013; Xing et al., 2014d). These ichnofaunal assemblages are consistent with what appears to have been the near global

* Corresponding author. Tel.: +86 10 68998618.

E-mail address: kuanghw@126.com (H.W. Kuang).

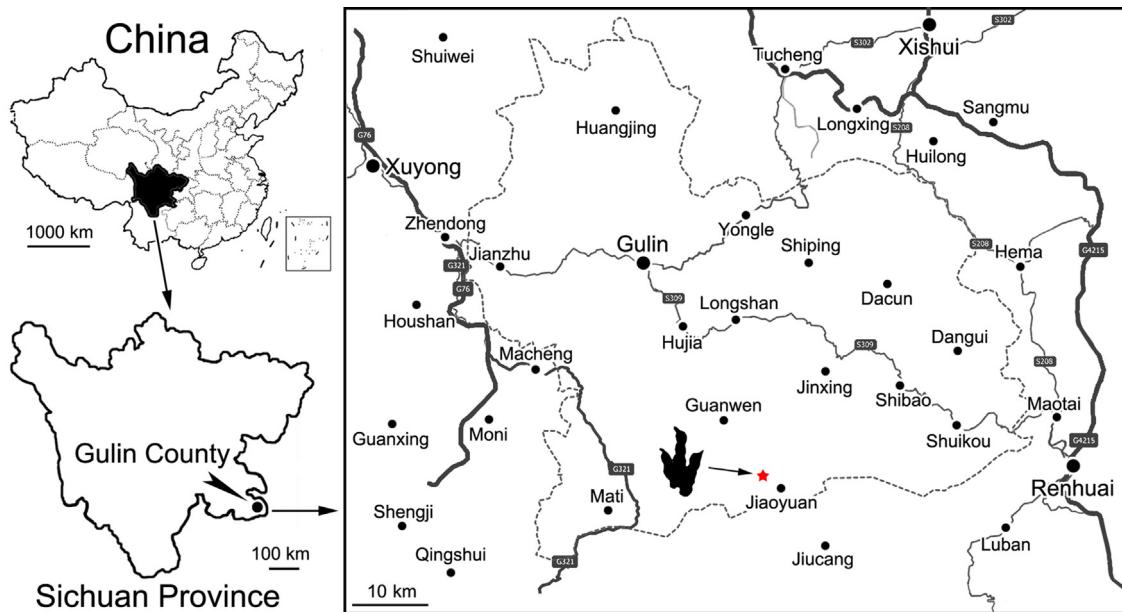


Fig. 1. Geographical setting showing the location (footprint icon) of the Jiaoyuan dinosaur tracksite in Gulin County, Sichuan Province, China.

distribution of *Grallator*- and *Eubrontes*-dominated Early Jurassic ichnofaunas (Olsen and Galton, 1984; Lucas, 2007; Lockley et al., 2011).

In May, 2009, Yi-Guang Chen and Jian-Ming Tang, engineers of the No. 113 Geological Team, Sichuan Bureau of Geology and Mineral Resources, discovered Early Jurassic sauropodomorph trackways at Heping brickfield, Jiaoyuan Township, Gulin County (Fig. 1). Unfortunately, due to the steep cliff (~70° dip), the ensuing expedition was unable to reach the fossils. During 2010–2014, the senior author of this paper worked at the site on six occasions. Other authors (MGL and SBK) also participated in field work. Two experienced climbers from the Sichuan Mountaineering Association were employed to set ropes and assist with gaining access to the site. This paper elaborates on a very preliminary note on the site by Xing (2010). Theropod and sauropodomorph tracks (*Liujianpus shunan*, Xing et al., in press) were discovered, including at least 10 parallel sauropodomorph trackways with bimodal distribution. Here we describe the theropod tracks, whereas the sauropodomorph trackways will be described in detail elsewhere.

Institutional and other abbreviations

JY = Jiaoyuan tracksite, Gulin County, Sichuan, China; T = theropod; L/R = left/right; I = isolated; UCM = University of Colorado Museum.

2. Geological setting

The Gulin County is situated at the southern border of the Sichuan Basin, in the northern portion of the Yunnan-Guizhou Plateau. The Jiaoyuan tracksite (24°02'32.78"N, 105°48'53.05"E) is part of the Lower Jurassic Da'anzhai Member of the Ziliujing Formation. From base to top, the Ziliujing Formation is divided into the Dongyuemiao, Ma'anshan and

Da'anzhai members (Gu et al., 1997). The Ziliujing Formation lies on top of the Lower Jurassic Zhenzhuchong Formation and is overlain by the Middle Jurassic Xintiangou Formation. The Da'anzhai Member and the lower part of the Xintiangou Formation meet at a conformable contact.

The Early Jurassic age of the Da'anzhai Member is based on the presence of characteristic invertebrate and vertebrate body fossils including bivalves and the sauropodomorph dinosaur *Lufengosaurus* (Cai and Liu, 1978; Dong et al., 1983; Dong, 1984).

Lithologically the Da'anzhai Member comprises carbonatic and siliciclastic successions. The main Jiaoyuan tracksite occurs as part of a sequence dominated by friable siltstones with a few resistant sandstones (Figs. 2, 3), in which a minimum of eight track-bearing levels have been identified. Each of these layers also bears developed ripple marks and desiccation cracks.

The depositional environment can be characterized as lacustrine freshwater with fluctuating water levels and occasional drying up along the margin as indicated by the mud cracks. A detailed sequence stratigraphic succession of the Da'anzhai Member of the Ziliujing Formation was documented by Zheng (1998).

3. Methods and materials

Four theropod trackways (JYT1–JYT4) are present. These include 7, 4, 3 and 3 continuous footprints, respectively (Figs. 4–8). Furthermore four separate isolated tracks (JYT1–4) occur on the main surface. A replica of the best preserved one is housed in the UCM collections and catalogued as UCM 178.20.

Maximum length (ML), maximum width (MW), divarication angle (II–IV), pace length (PL), stride length (SL), and pace angulation (PA) were measured according to the standard procedures of Leonardi (1987) and Lockley and Hunt (1995).

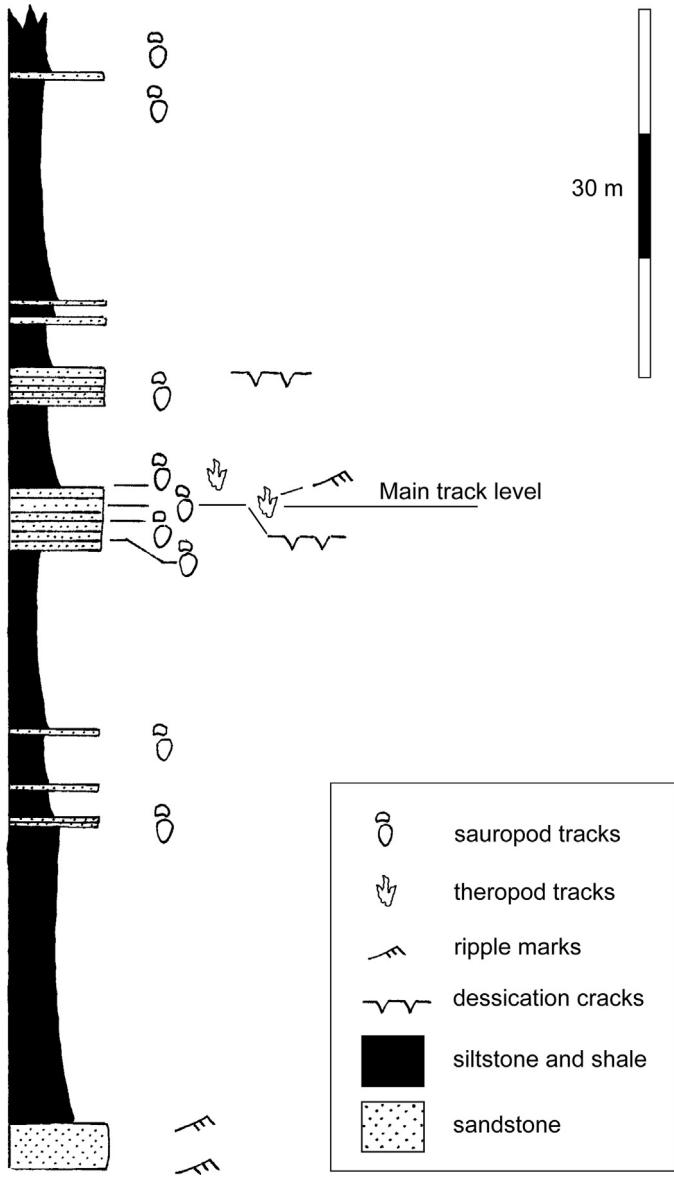


Fig. 2. Stratigraphic section of Lower Jurassic Da'anzhai Member of Ziliujing Formation as logged at the Jiaoyuan tracksite with the position of the track-bearing levels.

According to Olsen (1980), Weems (1992), and Lockley (2009), theropod tracks can be differentiated on the basis of mesaxony: i.e., the degree to which the central digit (III) protrudes anteriorly beyond the medial (II) and lateral (IV) digits, making an anterior triangle with variable (acute to obtuse) anterior or apical angles and length/width (L/W) ratios (Lockley, 2009).

4. Theropod tracks

4.1. Description

Based on size, the theropod tracks can be divided into two general types.

Type A: Natural mold tridactyl theropod tracks JYT1–JYT2 (Figs. 4–6, Table 1), and JYTI-4 (Fig. 7, Table 1). These range from 25 to 34 cm in length. The average L/W ratio of the imprints is 1.0–1.4. The pace angulation of JYT1 and JYT2 are both 173°. JYT2-R1 is the better preserved. The digits of JYT2-R1 are isolated from each other. The average davarication angle between digits II and IV is 58°. Digit III is the shortest, slightly shorter than digit II, and digit IV is the longest. The outline of digit pads is unclear. Claw marks are all sharp. The metatarsophalangeal pad of digit IV is displaced laterally with respect to the axis of digit III. One step is about 2.6–3.3 times footprint length.

The shape of JYT1 (Fig. 5) is basically similar to that of JYT2-R1; however, the heel impression of JYT1-R4 is poorly preserved. This may give an imprecise estimate of track length resulting in falsely low values of L/W ratio, compared with JYTI-L4 and R5.

A separate isolated right footprint, JYTI-4 (Fig. 7) was molded and replicated as UCM 178.20. There are well developed mud cracks at this track level. JYTI-4 is about 26.5 cm long and 28.6 cm wide ($l/w = \sim 1.0$). Although the heel is rather shallow and, as in JYT1-R4, may give an imprecise estimate of track length.

The moisture of the substrate appears to have had great impact on the morphology of some of the footprints. For example, digit II of JYT1-R2 (Fig. 5) has a displacement rim, whereas all three digits of JYT2-L1 (Fig. 6) are almost parallel. These phenomena also occur at the Shanshan tracksite (Xing et al., 2014d). Furthermore, only part of the posterior area of JYT1-R2 was preserved; the anterior area was overlapped by a sauropodomorph track.

Type B: Natural mold tridactyl theropod tracks JYT3–JYT4, and JYTI-1–3 (Fig. 8, Table 1). These range from 7 to 15 cm in length. The average L/W ratio of the imprints is 1.1–1.6. The pace angulation of JYT3 and JYT4 are 169° and 176°, respectively. Of JYT3–JYT4, JYT3-L1 is the best-preserved. The digits of JYT4-R1 are isolated from each other. The average davarication angle between digits II and IV is 64°. Digit III is the longest and digit II is the shortest. The pad formula of digits II–IV is 2–3–4. All claw marks are sharp. The metatarsophalangeal pad of digit IV is displaced in line with the long axis of digit III. One step is about 2.9–4.1 times footprint length.

4.2. Comparison and discussion

Taken as a whole, Jiaoyuan type A (large-sized) theropod tracks are all rather poorly-preserved and lack sufficient morphological features to be assigned to a particular ichnospecies.

Type A is characterized by weak to moderate mesaxony (average L/W ratio for the anterior triangle: 0.39, range 0.32–0.59, $N=7$), which is close to the value typical for footprints of the ichno- or morphofamily Eubrontidae (Lull, 1904) (0.37–0.58, *Eubrontes* type, Lockley, 2009).

The relatively large digit davarication of Type A resembles known *Kayentapus* and *Kayentapus*-like tracks (Lockley et al., 2011), but the davarication angle of *Kayentapus* type tracks is generally larger. Based on four North American *Kayentapus* tracks from the holotype trackway figured by Lockley et al. (2011), the angles between digit II and IV are 68°, 68°, 68°, and



Fig. 3. Photograph of the Jiaoyuan dinosaur tracksite. The box A corresponding to the JYT1 trackway (Figs. 4, 5); B: JYT1-4 track (Fig. 6); C: JYT3 and 4 trackways (Fig. 7); D: JYT2 trackway (Fig. 8), respectively.

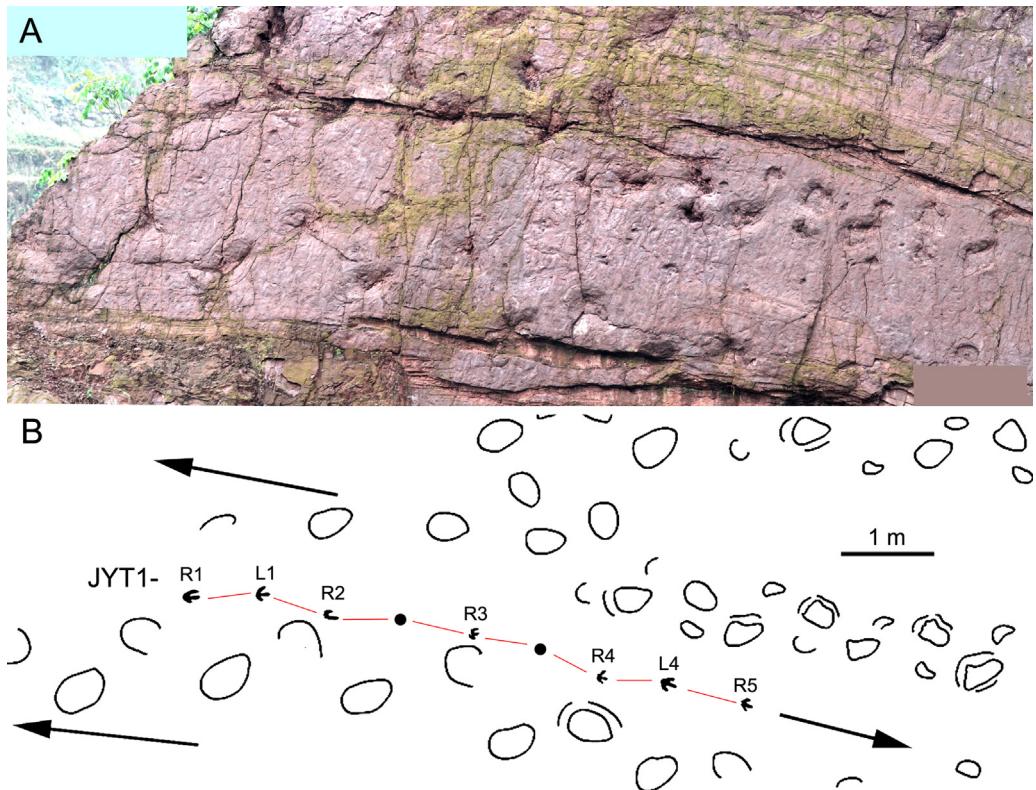


Fig. 4. Photograph (A) and interpretative outline drawing (B) of Jiaoyuan theropod trackway JYT1 associated with different sauropod trackways described in a further study.

59° respectively. The digit divarication of a *Kayentapus xiaohuangensis* specimen from the Lower Jurassic Fengjiahe Formation of Yunnan Province is 73° (Lockley et al., 2013, fig. 2f). If the poorly-preserved JYT1-R4 and JYT1-4 and the distorted JYT2-L1 are omitted, the Type A tracks have an angle between 54° and 58° . This is less than that of the *Kayentapus*-like tracks from USA and China. Due to a lack of a developed metatarsophalangeal area, the Type A tracks can be excluded from *Changpeipus* (Xing et al., 2014d). *Eubrontes zigongensis* (Xing

et al., 2014b) from the Lower Jurassic Zhenzhuchong Formation at the Shaba tracksite in Weiyuan County, Sichuan Province, shares many features with the Jiaoyuan type A tracks; for example, the L/W ratio is 1.4, the angle between digit II and IV is 55° , and the step length is three times of that of footprint in the latter. However, the length of *E. zigongensis* (42 cm) is obviously larger than that of Jiaoyuan type A tracks. A key feature of *E. zigongensis* is the short antero-medially directed hallux trace (Xing et al., 2014b) lacking in the Jiaoyuan specimens.

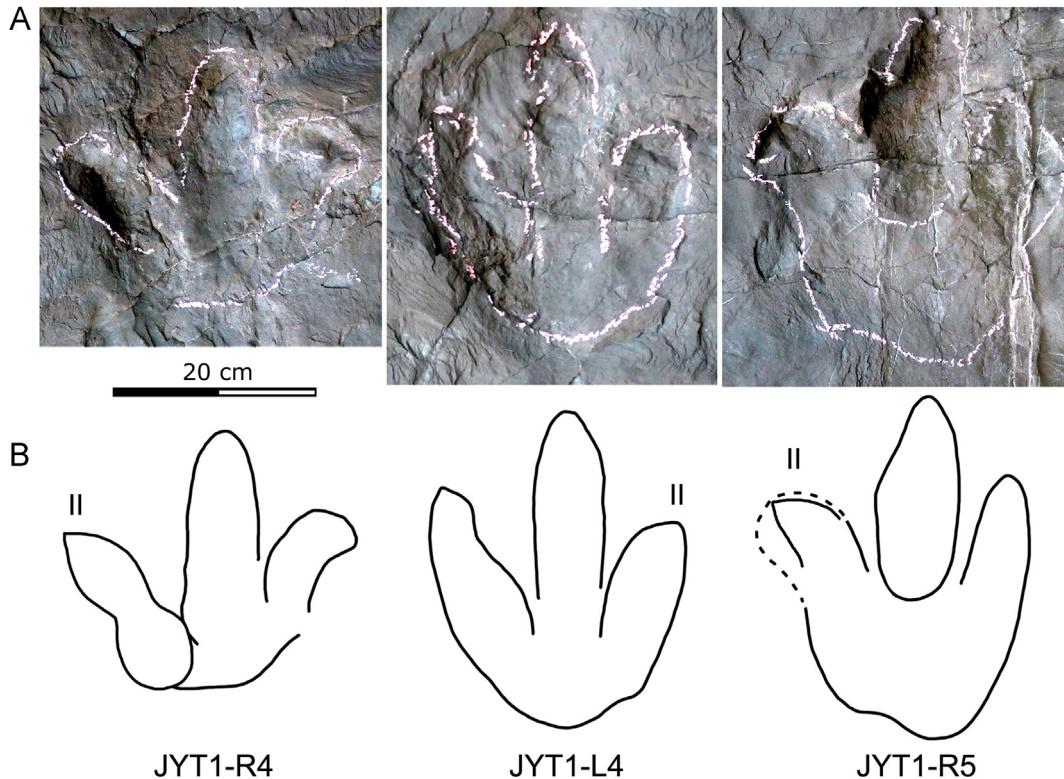


Fig. 5. Photograph (A) and interpretative outline drawings (B) of well-preserved Jiaoyuan theropod tracks JYT1.

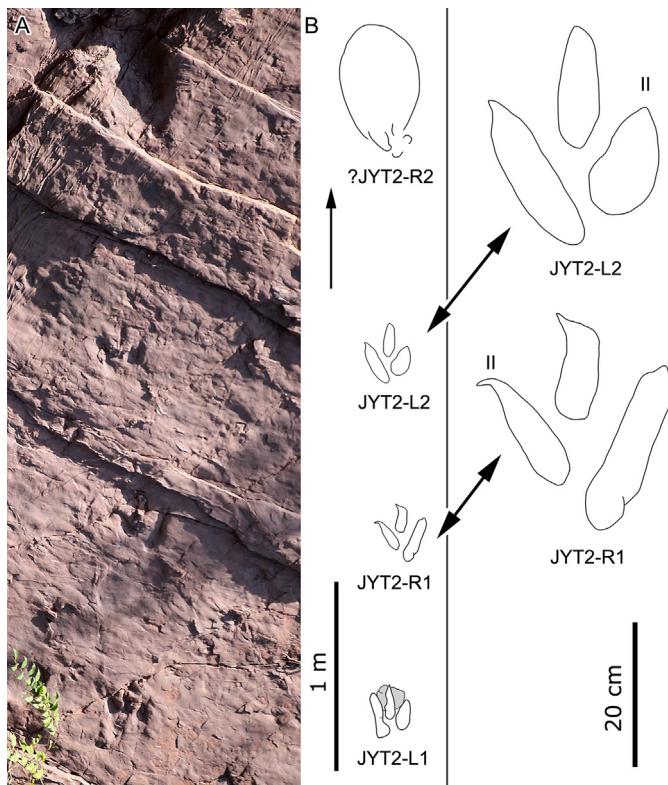


Fig. 6. Photograph (A) and interpretative outline drawing (B) of Jiaoyuan theropod trackway JYT2.

The Jiaoyuan type A tracks are morphologically similar to the type specimens of *Eubrontes* (AC 151). Among their shared features are: large size (>25 cm long), functionally tridactyl ichnrite with a relatively short digit III, and a broad pes, divarication of outer digits averaging 25°–40° (Olsen et al., 1998). Based on these similarities, the Jiaoyuan type A tracks are here classified as *Eubrontes* type tracks.

Type B is characterized by moderate mesaxony (average 0.61, range 0.54–0.67, N=5), which is close to that in the typical *Grallator* from Zigong (average 0.63, range 0.51–0.81, N=5, Xing et al., 2014a, fig. 4A). Moreover, Type B has relatively wide divarication angles (62° between digits II and IV vs 51° from Hejie *Grallator*). However, the metatarsophalangeal pad of digit IV of Type B is positioned in line with the long axis of digit III, this feature is much closer to that of *Jialingpus* from the Late Jurassic of Sichuan (Zhen et al., 1983; Xing et al., 2014e). The metatarsophalangeal pad of digit IV of the Hejie *Grallator* also lies nearly in line with the long axis of digit III.

Grallator is a common, small (<15 cm long), narrow, tridactyl track type made by bipedal theropods (Hitchcock, 1858). In terms of the number of both specimens and named ichnospecies, *Grallator* is an ichnogenus that encompasses many small, predominantly Late Triassic and Early Jurassic theropod tracks (Lockley, 1991; Olsen et al., 1998). However, the *Grallator* morphotypes from the Early Jurassic of China are not completely consistent with those from North America. The Early–Middle Jurassic *Grallator* type tracks currently known from China (Fig. 9) are:

Table 1

Measurements (in cm) of the theropod tracks from Jiaoyuan tracksite, Gulin, Sichuan Province.

Number	ML	MW	II–III	III–IV	II–IV	PL	SL	PA	M	L/W
JYT1-R4	25.6	27.6	46°	40°	86°	73.0	177.0	173°	0.36	1.0
JYT1-L4	31.5	23.8	29°	28°	57°	84.0	—	—	0.42	1.3
JYT1-R5	34.0	25.0	36°	18°	54°	—	—	—	0.39	1.4
Mean	30.4	25.5	37°	29°	66°	78.5	177.0	173°	0.39	1.2
JYT2-L1	26.7	18.0	25°	22°	47°	96.0	190.0	173°	0.32	1.5
JYT2-R1	30.4	24.0	29°	29°	58°	97.0	—	—	0.32	1.3
JYT2-L2	30.5	21.7	27°	31°	58°	—	—	—	0.59	1.4
Mean	29.2	21.2	27°	27°	54°	96.5	190.0	173°	0.41	1.4
JYT3-L1	13.2	9.0	37°	29°	66°	50.5	82.0	176°	0.60	1.5
JYT3-R1	14.0	8.5	33°	23°	56°	32.0	—	—	0.55	1.6
JYT3-L2	15.0	—	—	—	—	—	—	—	—	—
Mean	14.1	8.8	35°	26°	61°	41.3	82.0	176°	0.58	1.6
JYT4-R1	11.0	10.0	54°	57°	111°	58.0	100.0	169°	—	1.1
JYT4-L1	15.0	10.7	33°	31°	64°	48.0	—	—	0.67	1.4
Mean	13.0	10.35	44°	44°	88°	53.0	100.0	169°	0.67	1.3
JYTI-1	15.2	10.3	26°	41°	67°	—	—	—	—	1.5
JYTI-2	7.5	7.0	43°	64°	107°	—	—	—	0.54	1.1
JYTI-3	12.0	9.0	41°	15°	56°	—	—	—	—	1.3
JYTI-4	29.0	28.6	37°	45°	82°	—	—	—	0.36	1.0

Abbreviations: ML: maximum length; MW: maximum width; II–III: angle between digits II and III; III–IV: angle between digits III 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); L/W: maximum length/maximum width.

- 1) *Grallator wuhuangensis* (~11 cm in length) (Fig. 9A) and *Grallator microscus* (~13 cm in length) (Fig. 9B) are known from the Middle Jurassic Xintiangou Formation near Zizhong County, Sichuan. The L/W ratios (and anterior triangle L/W ratio) are 2.0 (0.92) and 2.0 (0.71), respectively (Yang and Yang, 1987; Lockley et al., 2013; Xing et al., 2013). The divarication angle between digits II and IV are 48° and 39°, respectively.
- 2) *Grallator yemaoxiensis* (17.8 cm in length) (Fig. 9C) is known from the Middle Jurassic middle Shangshaximiao Formation in Nan'an tracksite of Chongqing City. The L/W ratio is 1.7 (0.78) (Yang and Yang, 1987; Lockley et al., 2013; Xing et al., 2013). The divarication angle between digits II and IV is 50°.
- 3) *Grallator limnosus* (27–28 cm in length) (Fig. 9D) is known from the Lower Jurassic Fengjiahe Formation of Jinning, Yunnan. The L/W ratio is 1.7 (0.66) (Zhen et al., 1986; Lockley et al., 2013). The divarication angle between digits II and IV is 55°. It is important to note that the size of this footprint is obviously larger than morphotype A, and similar to that of *Grallator maximus* from the lower Lias of Vendée, France (Lapparent and Montenat, 1967).
- 4) Small *Grallator* (11–15 cm in length) (Fig. 9E–G) is known from the Lower Jurassic Ziliujing Formation at the Hejie tracksite of Zigong City, Sichuan. The L/W ratio is 1.7 (0.63). The divarication angle between digits II and IV is 51° (Xing et al., 2014a).

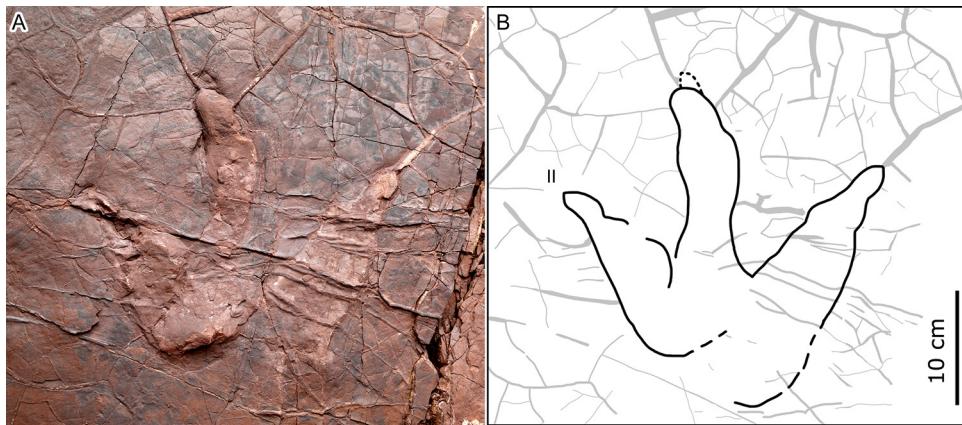


Fig. 7. Interpretative outline drawing (A) of Jiaoyuan theropod trackways JYT3 and 4, and photographs and interpretative outline drawings (B) of well-preserved tracks in JYT3 and 4.

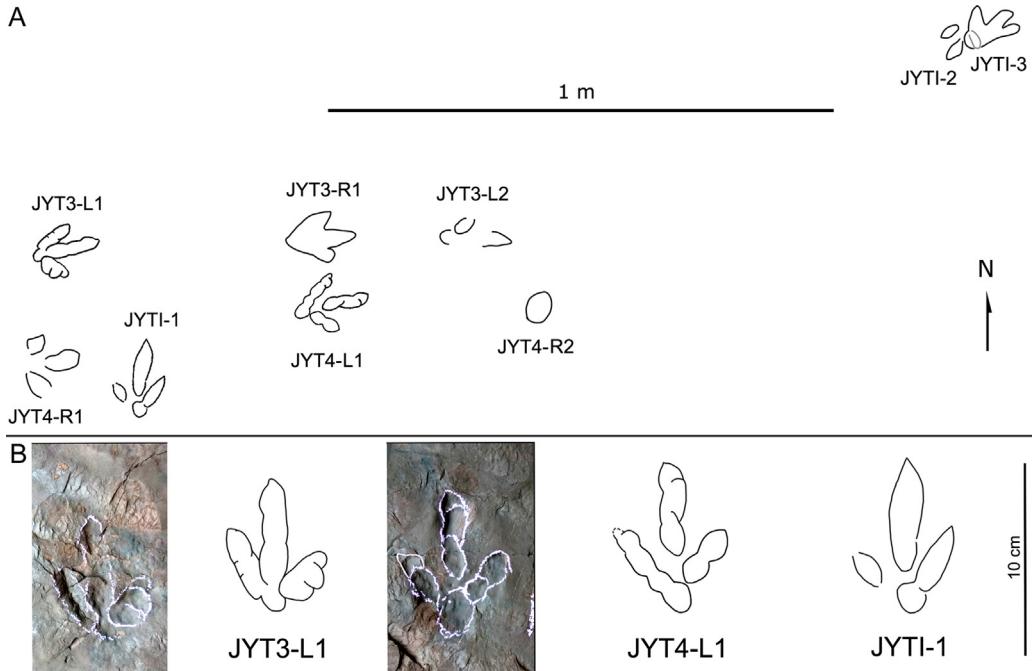


Fig. 8. Photograph (A) and interpretative outline drawing (B) of Jiaoyuan theropod track JYTI-4, represented in UCM collections by replica UCM 178.20.

The L/W ratio (and anterior triangle L/W ratio) of typical North American *Grallator* type footprints (Hitchcock, 1858) is 2.1 (1.0) (Lockley, 2009). In North American *Grallator* type footprints, digit III typically projects relatively farther anteriorly than the other digits, the foot is narrower than in *Eubrontes* and *Anchisauripus* (L/W ratio ≥ 2), and the divarication of the outer digits ranges from 10° to 30° (Hitchcock, 1858; Lull, 1953; Olsen et al., 1998).

The L/W ratio and the anterior triangle L/W ratio of most *Grallator*-type tracks from the Early to Middle Jurassic, such as *G. yemiaoxiensis*, *G. microiscus*, *G. limnosus*, and Hejie *Grallator*, are less than that of the typical North American *Grallator*-type tracks, suggesting that they are generally less elongate. In addition, the divarication angle between digits II and IV (39° – 55°) is larger than that of North American specimens. This could help contribute to the lower L/W ratios, although, in

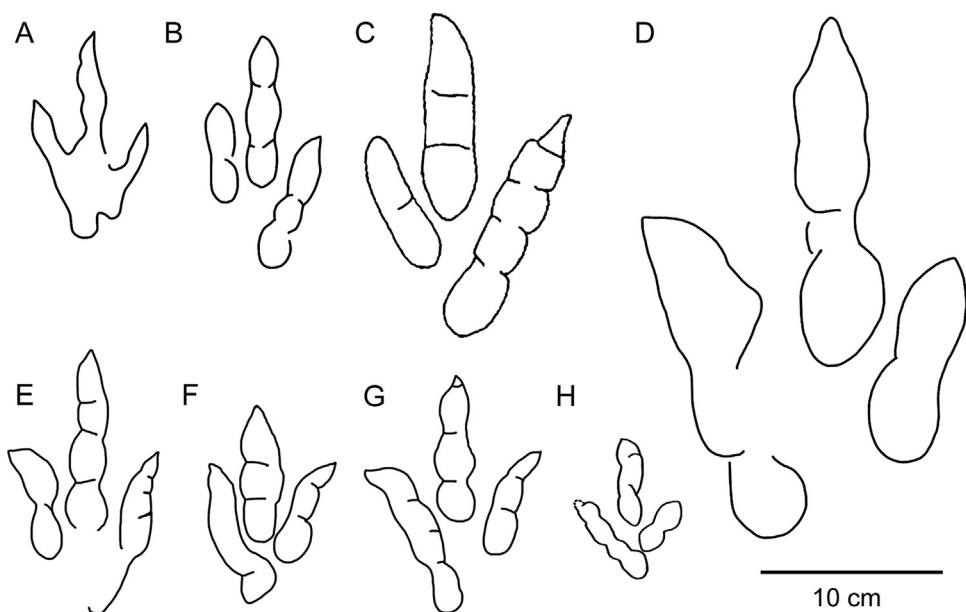


Fig. 9. Interpretative outline drawings of *Grallator* ichnotaxa drawn to the same scale. (A) *Grallator wuhuangensis* (from Lockley et al., 2013); (B) *Grallator microiscus* (from Lockley et al., 2013); (C) *Grallator yemiaoxiensis* (from Yang and Yang, 1987); (D) *Grallator limnosus* (from Lockley et al., 2013); (E–G) Hejie *Grallator* (from Xing et al., 2014a); (H) Jiaoyuan *Grallator* (this text).

comparison with relative digit length, divarication angles have relatively slight influence on this ratio (Lockley, 2009). These features (low L/W ratios, wide divarication angle) are retained in Chinese *Grallator* type tracks, including *Jialingpus*, until at least the Early Cretaceous (Xing et al., 2014e).

Using the average hip height to body length ratio of 1:2.63 (Xing et al., 2009b), the trackmaker of the type A trackways are estimated to have been 3.20 and 3.07 m in length, and the track maker of the type B trackways are estimated to have been 1.48 and 1.37 m in length. Using the stride length equation of Alexander (1976) ($SL/h = 2.15$) and the hip height equation of Henderson (2003) (hip height $\approx 4 \times$ footprint length), the trackmakers of the Jiaoyuan theropod type A trackways (JYT1, JYT2) are estimated to have been trotting at 1.62 and 1.91 m/s, and the trackmakers of the Jiaoyuan theropod type B trackways (JYT3, JYT4) are estimated to have been traveling at 1.10 and 1.68 m/s.

5. Conclusions

By the beginning of the Early Jurassic, theropods were thriving in the Sichuan Basin as indicated by trackways and tracks of different size (Xing et al., 2014a). Large-sized tracks indicate the presence of medium-sized theropod dinosaurs with a body length of at least three meters. Furthermore, the track record documents small-sized individuals extending the geographic distribution of typical Lower Jurassic associations to China. The Jiaoyuan track assemblage is consistent with those found in Lower Jurassic deposits of other regions, such as North America (Hitchcock, 1858; Lull, 1953; Lockley and Hunt, 1995; Olsen et al., 1998), North Africa (Ishigaki, 1988), South Africa (Ellenberger, 1972, 1974) and Europe (Lapparent and Montenat, 1967; Lockley and Meyer, 2000; Avanzini et al., 2006), where significant size range, morphological variability, and inferred diversity have been observed as well. This matches the Early Jurassic age of the track-bearing Da'anhai Member determined by body fossils. Early Jurassic saurischian dominated ichnofaunas represent one of the first globally widespread dinosaurian ichnofaunas (sensu Lucas, 2007).

The theropod tracks described here are part of an exclusive theropod-sauropodomorph assemblage: i.e., an ichnofauna representing saurischians only.

Acknowledgments

The authors thank Jian Liu and Bing Xiao (Sichuan Mountaineering Association, China) for their participation in field research; Lisa G. Buckley, Spencer G. Lucas, Da-Qing Li, and anonymous reviewers for their critical comments and suggestions on this paper. This research project was supported by the special projects grants of Gulin County People's Government, Sichuan Province, special projects grants of Yanqing Geopark, Yanqing County, Beijing, and the 2013 support fund for graduate student's science and technology innovation from China University of Geosciences (Beijing), China.

References

- Alexander, R.M., 1976. Estimates of speeds of dinosaurs. *Nature* 261, 129–130.
- Avanzini, M., Piubelli, D., Mietto, P., Roghi, G., Romano, R., Masetti, D., 2006. Lower Jurassic (Hettangian–Sinemurian) dinosaur track megasites, southern Alps, Northern Italy. *New Mexico Museum of Natural History and Science Bulletin* 37, 207–216.
- Cai, S.Y., Liu, X.Z., 1978. *Lamellibranchia* (non-marine section). In: Southwest Institute of Geological Sciences (Ed.), *The Paleontological Atlas in Southwest Sichuan (II)*. Geological Publishing House, Beijing, pp. 365–403 (in Chinese).
- Dong, Z.M., 1984. A new prosauropod from Ziliujing Formation of Sichuan Basin. *Vertebrata Palasiatica* 22, 310–313 (in Chinese).
- Dong, Z.M., Zhou, S., Zhang, Y., 1983. *Dinosaurs from the Jurassic of Sichuan*. Science Press, Beijing, 136 pp. (in Chinese).
- Ellenberger, P., 1972. Contribution à la classification des pistes de vertébrés du Trias: Les types du Stromberg d'Afrique du Sud (I). *Palaeovertebrata, Mémoire Extraordinaire*, 1–152.
- Ellenberger, P., 1974. Contribution à la classification des pistes de vertébrés du Trias: Les types du Stromberg d'Afrique du Sud (II partie: Le Stromberg supérieur – I. Le biome de la zone B/I ou niveau de Moyeni: ses biocénoses). *Palaeovertebrata, Mémoire Extraordinaire*, 1–142.
- Gu, X., Liu, X., Li, Z., 1997. *Stratigraphy (Lithostratigraphic) of Sichuan Province*. China University of Geosciences Press, Wuhan, 417 pp. (in Chinese).
- Henderson, D.M., 2003. Footprints, trackways, and hip heights of bipedal dinosaurs testing hip height predictions with computer models. Alberta Palaeontological Society, Seventh Annual Symposium, “Fossils in Motion” Abstracts, pp. 33–37.
- Hitchcock, E., 1858. *Ichnology of New England: A Report on the Sandstone of the Connecticut Valley, Especially Its Fossil Footmarks*. William White, Boston, 220 pp. (reprinted 1974 by Arno Press, New York).
- Ishigaki, S., 1988. Les empreintes de dinosaures du Jurassique inférieur du Haut Atlas central marocain. *Notes Service Géologique Maroc* 44, 79–86.
- Lapparent, A.F.d., Montenat, C., 1967. Reptile footprints from the lower Lias of Veillon (Vendée). *Mémoires de la Société géologique de France, Nouvelle Série* 107, 1–44.
- Leonardi, G., 1987. *Glossary and Manual of Tetrapod Footprint Palaeoichnology*. Departamento Nacional de Produção Mineral, Brazil, 75 pp.
- Lockley, M.G., 1991. *Tracking Dinosaurs*. Cambridge University Press, Cambridge, 238 pp.
- Lockley, M.G., 2009. New perspectives on morphological variation in tridactyl footprints: clues to widespread convergence in developmental dynamics. *Geological Quarterly* 53, 415–432.
- Lockley, M.G., Hunt, A.P., 1995. *Dinosaur Tracks and Other Fossil Footprints of the Western United States*. Columbia University Press, New York, 360 pp.
- Lockley, M.G., Meyer, C.A., 2000. *Dinosaur Tracks and Other Fossil Footprints of Europe*. Columbia University Press, Berkeley, 323 pp.
- Lockley, M.G., Gierlinski, G.D., Lucas, S.G., 2011. *Kayentapus* revisited: notes on the type material and the importance of this theropod footprint ichnogenus. *New Mexico Museum of Natural History and Science Bulletin* 53, 330–336.
- Lockley, M.G., Li, 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 Geologica Sinica* 87, 1–20.
- Lucas, S.G., 2007. Tetrapod footprint biostratigraphy and biochronology. *Ichnos* 14, 5–38.
- Lull, R.S., 1904. Fossil footprints of the Jura-Trias of North America. *Memoirs of the Boston Society of Natural History* 5 (11), 461–557.
- Lull, R.S., 1953. Triassic life of the Connecticut Valley (revised edition). State of Connecticut State Geological and Natural History Survey 81, 1–336.
- Olsen, P.E., 1980. A comparison of the vertebrate assemblages from the Newark and Hartford Basins (Early Mesozoic, Newark Supergroup) of Eastern North America. In: Jacobs, L.L. (Ed.), *Aspects of Vertebrate History, Essays In Honor of Edwin Harris Colbert*. Museum of Northern Arizona Press, Flagstaff, pp. 35–53.

- Olsen, P.E., Galton, P.M., 1984. A review of the reptile and amphibian assemblages from the Stormberg of southern Africa, with special emphasis on the footprints and the age of the Stormberg. *Palaeontologia Africana* 25, 87–110.
- Olsen, P.E., Smith, J.B., McDonald, N.G., 1998. The material of the species of the classic theropod footprint genera *Eubrontes*, *Anchisauripus* and *Grallator* (Early Jurassic, Hartford and Deerfield basins, Connecticut and Massachusetts, U.S.A.). *Journal of Vertebrate Paleontology* 18, 586–601.
- Weems, R.E., 1992. A re-evaluation of the taxonomy of Newark Supergroup saurischian dinosaur tracks, using extensive statistical data from a recently exposed tracksite near Culpeper, Virginia. In: Sweet, P.C. (Ed.), *Proceedings of the 26th Forum on the Geology of Industrial Minerals*, May 14–18. Virginia Division of Mineral Resources Publication 119. Commonwealth of Virginia Department of Mines, Minerals and Energy, Charlottesville, pp. 113–127.
- Xing, L.D., 2010. Report on dinosaur trackways from Early Jurassic Ziliujing Formation of Gulin, Sichuan Province, China. *Geological Bulletin of China* 29 (11), 1730–1732 (in Chinese).
- Xing, L.D., Harris, J.D., Toru, S., Masato, F., Dong, Z.M., 2009a. Discovery of dinosaur footprints from the Lower Jurassic Lufeng Formation of Yunnan Province, China and new observations on *Changpeipus*. *Geological Bulletin of China* 28 (1), 16–29.
- 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. *Geological Bulletin of China* 28 (6), 705–712.
- Xing, L.D., Lockley, M.G., Chen, W., Gierliński, G.D., Li, J.J., Persons IV, W.S., Matsukawa, M., Ye, Y., Gingras, M.K., Wang, C.W., 2013. Two theropod track assemblages from the Jurassic of Chongqing, China, and the Jurassic stratigraphy of Sichuan Basin. *Vertebrata Palasiatica* 51 (2), 107–130.
- Xing, L.D., Peng, G.Z., Ye, Y., Lockley, M.G., Klein, H., Persons IV, W.S., Zhang, J.P., Shu, C.K., Hao, B.Q., 2014a. Sauropod and small theropod tracks from the Lower Jurassic Ziliujing Formation of Zigong City, Sichuan, China with an overview of Triassic–Jurassic dinosaur fossils and footprints of the Sichuan Basin. *Ichnos* 21, 119–130.
- Xing, L.D., Peng, G.Z., Ye, Y., Lockley, M.G., McCrea, R.T., Currie, P.J., Zhang, J.P., Burns, M.B., 2014b. Large theropod trackway from the Zhenzhuchong Formation, Lower Jurassic of Weiyuan County, Sichuan Province, China: review, new observations, and special preservation. *Palaeoworld* 23, 285–293.
- Xing, L.D., Lockley, M.G., Wang, Q.F., Li, Z.D., Klein, H., Persons IV, W.S., Ye, Y., Matsukawa, M., 2014c. Earliest records of dinosaur footprints in Xinjiang, China. *Vertebrata Palasiatica* 52 (3), 340–348.
- Xing, L.D., Klein, H., Lockley, M.G., Wetzel, A., Li, Z.D., Li, J.J., Gierliński, G.D., Zhang, J.P., Matsukawa, M., Divay, J.D., Zhou, L., 2014d. *Changpeipus* (theropod) tracks from the Middle Jurassic of the Turpan Basin, Xinjiang, Northwest China: review, new discoveries, ichnotaxonomy, preservation and paleoecology. *Vertebrata Palasiatica* 52 (2), 233–259.
- 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., 2014e. 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., Zhang, J.P., Klein, H., Li, D.Q., Miyashita, T., Li, Z.D., Kümmell, S.B., in press. A new sauropodomorph ichno-genus from the Lower Jurassic of Sichuan, China fills a gap in the track record. *Historical Biology: An International Journal of Paleobiology*, <http://dx.doi.org/10.1080/08912963.2015.1052427>.
- Yang, X., Yang, D., 1987. Dinosaur Footprints from Mesozoic of Sichuan Basin. Sichuan Science and Technology Publications, Chengdu, 30 pp. (in Chinese).
- Zhen, S.N., Li, J., Zhen, B., 1983. Dinosaur footprints of Yuechi, Sichuan. *Memoirs of the Beijing Natural History Museum* 25, 1–19 (in Chinese).
- Zhen, S.N., Li, J., Rao, C., 1986. Dinosaur footprints of Jinning, Yunnan. *Memoirs of the Beijing Natural History Museum* 33, 1–19 (in Chinese).
- Zheng, R.C., 1998. High-resolution sequence stratigraphy of the Da'anzhai Formation, Lower Jurassic, Sichuan Basin, China. *Acta Sedimentologica Sinica* 16 (2), 42–49 (in Chinese).