


ORIGINAL ARTICLE

Open Access



The new ichnotaxon *Eubrontes nobitai* ichnosp. nov. and other saurischian tracks from the Lower Cretaceous of Sichuan Province and a review of Chinese *Eubrontes*-type tracks

Li-Da Xing^{1,2*} , Martin G. Lockley³, Hendrik Klein⁴, Li-Jun Zhang⁵, Anthony Romilio⁶, W. Scott Persons IV⁷, Guang-Zhao Peng⁸, Yong Ye⁸ and Miao-Yan Wang²

Abstract

The Jiaguan Formation and the underlying Feitianshan Formation (Lower Cretaceous) in Sichuan Province yield multiple saurischian (theropod–sauropod) dominated ichnofaunas. To date, a moderate diversity of six theropod ichnogenera has been reported, but none of these have been identified at the ichnospecies level. Thus, many morphotypes have common “generic” labels such as *Grallator*, *Eubrontes*, cf. *Eubrontes* or even “*Eubrontes-Megalosauripus*” morphotype. These morphotypes are generally more typical of the Jurassic, whereas other more distinctive theropod tracks (*Minisauripus* and *Velociraptorichnus*) are restricted to the Cretaceous. The new ichnospecies *Eubrontes nobitai* ichnosp. nov. is distinguished from Jurassic morphotypes based on a very well-preserved trackway and represents the first-named *Eubrontes* ichnospecies from the Cretaceous of Asia.

Keywords: Ichnofossils, Dinosaur footprints, Theropod, Myths

1 Introduction

With over 17 track sites documented so far, the Jiaguan Formation and the underlying Feitianshan Formation hold among the richest records of dinosaur tracks in China (Young 1960; Xing and Lockley 2016; Xing et al. 2007, 2014a, 2016a, 2018a, 2018b). Most Jiaguan track sites are saurischian-dominated (Xing and Lockley 2016; Xing et al. 2016a), with exceptions of the Lotus (Xing et al. 2015a) and Huibu (Xing et al. 2018b) track sites, where ornithopod tracks are equally or nearly equally abundant. Among these saurischian tracks, sauropods

are represented by *Brontopodus*-type tracks. The non-avian theropod tracks consist of *Eubrontes*-type, grallatorid, *Yangtzeopus*, *Velociraptorichnus*, cf. *Dromaeopodus*, *Minisauripus*, cf. *Irenesauripus*, and *Gigandipus*, while the bird tracks include *Koreanaornis* and *Wupus* (Xing and Lockley 2016). A few dinosaur bone fragments are known from the Jiaguan Formation, making it a Type 2 track-dominated deposit (Lockley 1991).

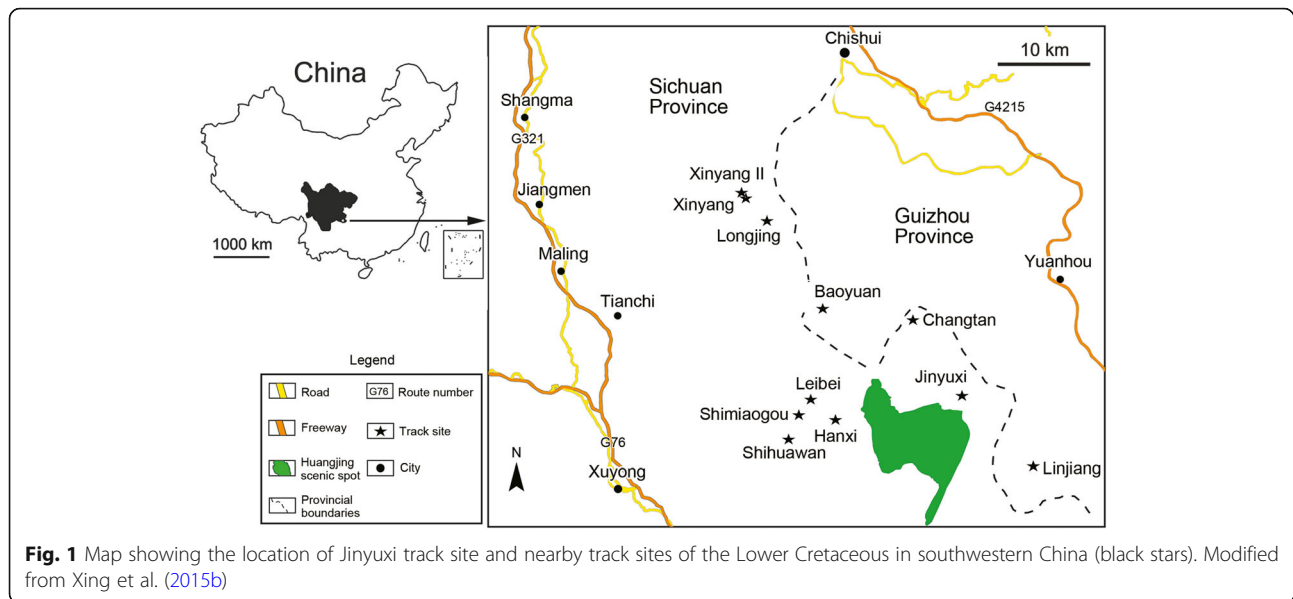
Starting in 2017, the Dinosaur Lab of China University of Geosciences (Beijing) conducted a new exploration along the border between Sichuan and Guizhou provinces. Several new track sites were documented. On July 10, 2020, Yong-Ping Lin, a resident of Yuanlin Village, Huangjing Town, salvaged a stone with strange marks in the Jinyuxi creek (meaning goldfish creek) and displayed it on the roadside (Fig. 1). Ting Xu, the director of Huangjing Integrated Cultural Station, discovered the

* Correspondence: xinglida@gmail.com

¹State Key Laboratory of Biogeology and Environmental Geology, China University of Geosciences, Beijing 100083, China

²School of the Earth Sciences and Resources, China University of Geosciences, Beijing 100083, China

Full list of author information is available at the end of the article



stone and reported it to the Dinosaur Lab. On August 25, the author team examined the track site to confirm the original horizon and discovered additional tracks.

2 Historical background

Local residents have traditionally interpreted the tracks on stone slabs from the Jinyuxi site as resembling bubble eye fish (a small variety of fancy goldfish with upward-protruding eyes). It may be from this interpretation that the name Jinyuxi is derived. Steering Group of Placenames in Gulin County Sichuan Province (1983) mentioned one folktale recorded in the local chronicle of Renhuai Zhiliting about how a man surnamed Xu saw a pair of goldfishes while digging foundations besides the stream in the Qing Dynasty. There are at least three possibilities for the so-called “Jinyu” of Jinyuxi: (1) the colorful goldfish *Carassius auratus* was considered lucky (Chen 1841) and Mr. Xu’s sighting of these fish in the river could have been regarded as a highly auspicious sign; (2) Mr. Xu’s sighting might be fictional or irrelevant, and the name could instead be derived from the golden-colored fish, which was rare, tasty, and considered a local specialty (Chen 1841); and (3) goldfish-shaped theropod tracks were uncovered by Mr. Xu during his excavation for the building foundation. If the latter is true, this situation is reminiscent of many other place names and folklore throughout China (Xing et al. 2011). The “goldfish’s eyes” and “heads” are the heel impressions and the “flowing fishtails” are the three toe impressions.

3 Methods

All tracks were photographed, outlined with chalk, and traced on large sheets of transparent plastic. The whole surface was photographically recorded using a remote-

controlled four-axis quadcopter (DJI Inspire 1) (Xing et al. 2018c). Detailed tracings of selected tracks were made on transparent acetate film. All traces, latex molds, plaster replicas, and digital track records were repositioned at the Zigong Dinosaur Museum.

For the trackways of quadrupeds, gauge (trackway width) is quantified for pes tracks using the ratios WAP/P’ML, where WAP is the width of the angulation pattern of the pes, and P’ML is the maximum length of the pes (see Marty et al. 2010). For the calculation of sauropod hip height and speed derived from the trackways, controversial methods of Alexander (1976), Thulborn (1990), and González Riga (2011) were adopted. The different values resulting from these methods are juxtaposed, but the differences are left undiscussed.

A virtual 3D model of the ex situ track JYX-T1-L1 (JYX = Jinyuxi site) was created following standard photogrammetry methods (Xing et al. 2018d; Lallensack et al. 2020). Here, 10 digital photographs were added to Agisoft Metashape Professional (v.1.6.3). The models were repositioned to the centre of the Cartesian coordinate system using Meshlab (Cignoni et al. 2008), and then the surface topography was visualized using Paraview (v. 2020.06; Ahrens et al. 2005) CloudCompare (v. 2.10.2; <http://www.cloudcompare.org/>) filters.

4 Results

4.1 Materials

The Jinyuxi track site is a weathered siltstone surface located on the bed of a stream running through Yuanlin Village. Currently, there are at least three sauropod trackways on the original horizons, catalogued as JYX-S1–S3 and consisting of 8, 10, and 8 tracks, respectively (Table 1; Figs. 2 and 3). Six tracks in JYX-S3 are covered

by river water. The tracks in situ were heavily weathered due to long-time exposure. There are also well-developed mud cracks, some shorter trackways, and isolated tracks on a slab that was newly stripped during the summer flood of 2020. Among these, the theropod trackway JYX-T1, which consists of four consecutive tracks, the theropod trackway JYX-T2, which consists of one continuous single step, isolated tracks JYX-TI1–TI4, and the sauropod trackway JYX-S4 which consists of five consecutive tracks, are identified.

4.2 Geological setting

4.2.1 Jiaguan Formation

The Jinyuxi track site is located at the southern edge of the Sichuan Basin (28°14′13.80″N, 105°49′35.92″E). Based on the regional geological survey report, the Cretaceous strata in the Jinyuxi area belong to the late Lower Cretaceous Jiaguan Formation (Fig. 4) (Sichuan Provincial Bureau of Geology Aviation Regional Geological Survey Team 1976; Xing et al. 2015b). The Jiaguan Formation comprises thick, brick-red, feldspathic, quartz-sandstone, and it shows conformable contact with the sandy conglomerate and mudstone of the overlying Upper Cretaceous Guankou Formation (Sichuan Provincial Bureau of Geology Aviation Regional Geological Survey Team 1976). The Lower Cretaceous Jiaguan Formation was deposited unconformably above the red mudstone of the Lower Cretaceous Tianmashan Formation and/or the Upper Jurassic Penglaizhen Formation (Gu and Liu 1997).

Numerous Early Cretaceous dinosaur tracks have been discovered in this area, and relevant geological information has been described in detail by the author team (Xing et al. 2015a, 2016a). Moreover, according to investigations by the Sichuan Provincial Bureau of Geology Aviation Regional Geological Survey Team (1976), the Jiaguan Formation consists of two members. The Lower Member of the Jiaguan Formation is 211–405 m thick and has a lithology of feldspathic quartz sandstone interbedded with multiple layers of mudstone, with a less than 10 m thick conglomerate layer at the bottom and a 2–10 m thick mudstone layer at the top. The Upper Member is 345–1000 m thick and is composed of feldspathic quartz sandstone interbedded with thin layers of lenticular mudstone and siltstone. The surface of the sandstone displays current ripples, and mud cracks are common in the siltstones. The sediments of the Jiaguan Formation are alluvial fan, river and desert deposits (Geng 2011). Chen (2009) argued that the Upper Member represents a meandering fluvial deposit interbedded with deposits from small braided rivers.

The Jinyuxi track site is associated with the feldspathic quartz sandstone of the Upper Member of the Jiaguan Formation.

4.2.2 Invertebrate traces

Taenidium isp. (Fig. 5) mainly appears as unlined, cylindrical, straight to sinuous tubes with meniscate backfill (Ekdale et al. 2007). *Taenidium* tubes do not cross-cut one another. *Arenicolites* isp. (Fig. 5) co-occurs with *Taenidium* isp. and consists of two parallel U-shaped vertical tubes without spreiten (Hauck et al. 2009). The *Arenicolites* tubes are cylindrical and smoothly walled. These trace fossil assemblages occur alongside mud cracks, confirming a floodplain of braided river (Hu and Wu 1993; Chen et al. 2019).

Arenicolites and *Taenidium* also occur in direct association with the dinosaur tracks. Based on their cross-cutting relationships, the dinosaur tracks were formed first, in the wet mud substrate of the floodplain. Then *Arenicolites* and *Taenidium* were left by the invertebrate burrowing (both dwelling and feeding). During the dry season, the mud cracks were formed and cross-cut both the trackways and burrows. Subsequently, silty sediments covered this area, forming track casts. During the late weathering, argillaceous sediments and molds were denuded, and the silty casts were preserved and exposed.

4.3 Eubrontid tracks from China

More than 100 track sites in China have yielded various tridactyl theropod tracks. A considerable number of these specimens are simply classified as eubrontid tracks or *Eubrontes*-type tracks (e.g. Xing and Lockley 2016, Table 2) (see Fig. 6). In the case of small and poorly preserved samples, this situation is predictable and acceptable: i.e., precise and confident identifications may be difficult to make. Since the 1980s, ichnologists from China named some new ichnospecies of *Eubrontes* or new ichnogenera of *Eubrontes*-type tracks. Some of their validity has been discussed and verified (such as Lockley et al. 2013), and some have not been discussed in detail.

4.3.1 *Eubrontes pareschequier* (Xing et al. 2009b) Lockley et al. 2013

Changepeipus pareschequier ZLJ-ZQK1 and ZLJ-ZQK2 from the Lower Jurassic Lufeng Formation, Yunnan Province (Xing et al. 2009a) are represented by two tracks. Lockley et al. (2013) reassigned *C. pareschequier* to *Eubrontes pareschequier*. Xing et al. (2014b) designated the better preserved ZLJ-ZQK1 as the holotype and ZLJ-ZQK2 as the paratype (see Fig. 6h). However, the validity of *E. pareschequier* is questionable. The morphological characteristics of ZLJ-ZQK1 are similar to *E. giganteus*. The most distinct difference between these

Table 1 Measurements (in cm and degree^o) of sauropod and theropod tracks from the Jiaguan Formation, Lower Cretaceous of Sichuan Province, China

	ML	MW	R	L/W	II–IV	PL	SL	PA	WAP	WAP/P/ML
JYX-T1-L1	31.5	23.0	4	1.37	47°	81.0	164.8	161	–	–
JYX-T1-R1	31.5	22.8	10	1.38	50°	86.0	164.0	158	–	–
JYX-T1-L2	30.7	21.8	–	1.41	48°	81.0	–	–	–	–
JYX-T1-R2	31.8	–	–	–	43°	–	–	–	–	–
Mean	31.4	22.5	7	1.40	47°	82.7	164.4	160	–	–
JYX-T2-L1	13.3	7.40	–	1.80	–	61.4	–	–	–	–
JYX-T2-R1	11.8	8.80	–	1.34	–	–	–	–	–	–
Mean	12.6	8.10	–	1.56	–	61.4	–	–	–	–
JYX-TI1	12.0	9.00	–	1.33	47°	–	–	–	–	–
JYX-TI2	11.3	8.20	–	1.38	50°	–	–	–	–	–
JYX-TI3	12.4	7.50	–	1.65	–	–	–	–	–	–
JYX-TI4	19.7	16.1	–	1.22	61°	–	–	–	–	–
JYX-S1-RP1	42.2	38.4	45	1.10	–	68.2	108.8	97	48.0	1.1
JYX-S1-RM1	–	–	–	–	–	–	–	–	–	–
JYX-S1-LP1	39.5	34.8	6	1.14	–	77.0	114.4	95	51.0	1.3
JYX-S1-LM1	23.9	31.8	17	0.75	–	85.2	108.2	78	–	–
JYX-S1-RP2	38.7	33.8	46	1.14	–	78.6	122.1	105	46.8	1.2
JYX-S1-RM2	23.0	29.0	–	0.80	–	86.5	–	–	–	–
JYX-S1-LP2	42.6	36.3	–	1.17	–	75.4	–	–	–	–
JYX-S1-LM2	44.2	38.2	–	1.16	–	–	–	–	–	–
JYX-S1-RP3	23.9	28.1	–	0.85	–	–	–	–	–	–
Mean-M	30.3	33.0	17	0.92	–	85.9	108.2	78	–	–
Mean-P	37.4	34.3	32	1.09	–	74.8	115.1	99	48.6	1.2
JYX-S2-LP1	30.9	24.4	65	1.27	–	57.8	93.8	115	29.9	1.0
JYX-S2-LM1	18.1	17.2	–	1.05	–	–	–	–	–	–
JYX-S2-RP1	28.2	23.0	2	1.23	–	53.3	100.7	114	32.5	1.2
JYX-S2-LP2	31.5	25.0	62	1.26	–	66.8	113.3	112	38.1	1.2
JYX-S2-RP2	33.0	26.4	9	1.25	–	70.2	99.6	95	45.9	1.4
JYX-S2-RM2	19.7	23.5	–	0.84	–	79.7	–	–	–	–
JYX-S2-LP3	30.1	29.2	12	1.03	–	65.3	93.5	95	41.8	1.4
JYX-S2-LM3	22.3	21.3	–	1.05	–	–	–	–	–	–
JYX-S2-RP3	33.5	26.1	–	1.28	–	61.4	–	–	–	–
JYX-S2-LP4	31.1	27.1	–	1.15	–	–	–	–	–	–
Mean-M	20.0	20.6	–	0.97	–	79.7	–	–	–	–
Mean-P	31.2	25.9	30	1.20	–	62.5	100.2	106	37.6	1.2
JYX-S3-LP1	43.8	41.1	31	1.07	–	90.1	156.8	114	51.7	1.2
JYX-S3-RP1	56.4	47.0	40	1.20	–	97.3	145.4	111	49.4	0.9
JYX-S3-LP2	56.4	41.4	55	1.36	–	78.5	153.4	113	49.8	0.9
JYX-S3-RP2	42.2	44.1	17	0.96	–	104.9	153.0	101	62.5	1.5
JYX-S3-LP3	49.6	45.3	45	1.09	–	92.9	141.2	106	53.5	1.1
JYX-S3-RP3	50.7	43.5	29	1.17	–	84.1	141.5	110	49.8	1.0
JYX-S3-LP4	49.4	46.8	–	1.06	–	88.3	–	–	–	–
JYX-S3-RP4	43.5	40.2	–	1.08	–	–	–	–	–	–

Table 1 Measurements (in cm and degree/°) of sauropod and theropod tracks from the Jiaguan Formation, Lower Cretaceous of Sichuan Province, China (*Continued*)

	ML	MW	R	L/W	II–IV	PL	SL	PA	WAP	WAP/P/ML
Mean-P	49.0	43.7	36	1.12	–	90.8	148.6	109	52.8	1.1
JYX-S4-LP1	43.0	35.5	–	1.21	–	91.5	–	–	–	–
JYX-S4-LM1	28.0	34.5	–	0.81	–	94.0	–	–	–	–
JYX-S4-RP2	47.0	36.5	–	1.29	–	–	–	–	–	–
JYX-S4-LM2	28.5	31.5	–	0.90	–	–	–	–	–	–
Mean-M	28.3	33.0	–	0.86	–	94.0	–	–	–	–
Mean-P	45.0	36.0	–	1.25	–	91.5	–	–	–	–

Abbreviations: ML Maximum length, MW Maximum width, R Rotation, II–IV The divarication angle between digit II and digit IV, PL Pace length, SL Stride length, PA Pace angulation, WAP Width of the angulation pattern of the pes (calculated value), P/ML Maximum length of pes, L/W and WAP/P/ML are dimensionless, Mean-M An average of the data of manus, Mean-P An average of the data of pes

two ichnospecies is that ZLJ-ZQK1 has a comparatively low length/width ratio (1.3 vs. 1.7).

4.3.2 *Eubrontes zigongensis* (Gao 2007) Lockley et al. 2013

Gao (2007) preliminarily described one large theropod trackway from the Lower Jurassic Zhenzhuchong Formation of Weiyuan County, Sichuan Province, and named it *Weiyuanpus zigongensis*. Lockley et al. (2013) assigned *W. zigongensis* to *Eubrontes zigongensis* n. comb. Xing et al. (2014c) described *E. zigongensis* in detail and defined new diagnostic features (Fig. 6i). The most prominent diagnostic feature of *E. zigongensis* is the thin, anteromedially directed hallux trace.

4.3.3 *Eubrontes platypus* Hitchcock 1858 (Zhen et al. 1986)

Zhen et al. (1986) described a series of theropod tracks from Lower Jurassic Fengjiahe Formation of Jinning County, Yunnan Province, and classified it as *E. platypus* = *E. giganteus*. Lockley et al. (2013) retained this category. The author team of this article visited track sites and museum collections in 2015 and planned to publish detailed morphological features. According to the interpretive outline drawing provided by Zhen et al. (1986), the metatarsophalangeal pad of the Xiyang specimen was incomplete and had insufficient features to be assigned to a recognizable ichnospecies (Fig. 6j).

4.3.4 *Eubrontes monax* (Zhen et al. 1986) Lockley et al. 2013

Zhen et al. (1986) described *Paracoelurosaurichnus monax* from the Lower Jurassic Fengjiahe Formation of Jinning County, Yunnan Province. Lockley et al. (2013) assigned *P. monax* to *Eubrontes monax* n. comb., and provided a new interpretive outline drawing (Fig. 6k). According to this morphological evaluation, *E. monax* was registered three separated (non-connected) digit traces. It is possible that *E. xiyangensis*, *E. monax* and *E. platypus* are all extramorphological variants of *Eubrontes*-type tracks on a soft, wet and slippery substrate, such as

Changpeipus carbonicus from the Middle Jurassic of the Turpan Basin, Xinjiang (Xing et al. 2014c) (Fig. 6m).

4.3.5 *Eubrontes xiyangensis* (Zhen et al. 1986) Lockley et al. 2013

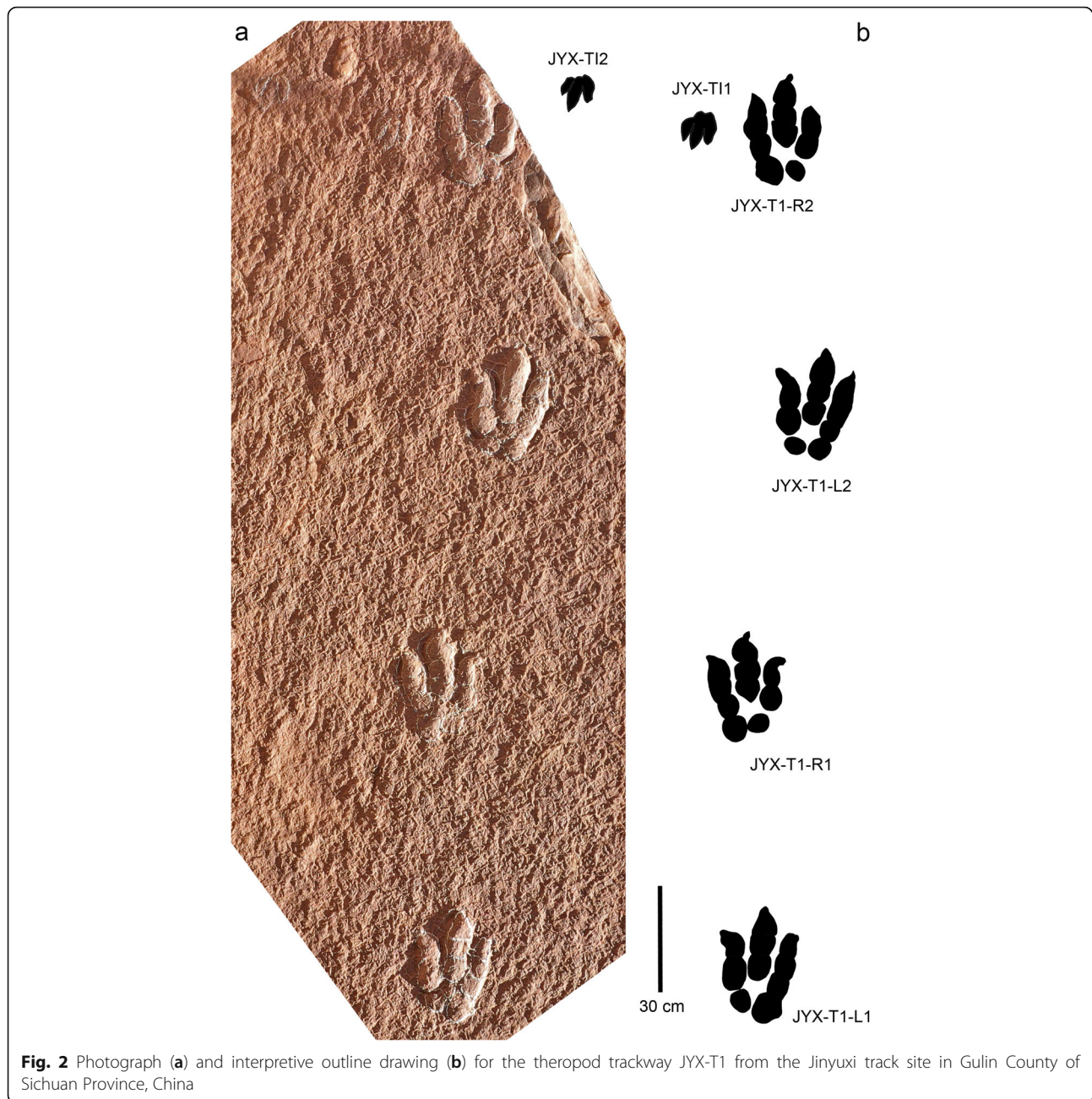
Zhen et al. (1986) described *Youngichnus xiyangensis* from the Lower Jurassic Fengjiahe Formation of Jinning County, Yunnan Province. Lockley et al. (2013) assigned *Y. xiyangensis* to *Eubrontes xiyangensis* n. comb. and provided a new interpretive outline drawing (Fig. 6l). However, according to the new interpretive outline drawing, the metatarsophalangeal pad of *E. xiyangensis* was incomplete and had insufficient features to be classified at the ichnospecies level.

4.3.6 *Changpeipus carbonicus* Young 1960 (Xing et al. 2014c)

Changpeipus carbonicus from the Lower–Middle Jurassic of Jilin Province is a reasonably well-preserved theropod track and exhibits a digital pad formula that allies it to the *Grallator–Eubrontes* plexus (sensu Olsen 1980). Xing et al. (2014c) reviewed all the *Changpeipus* specimens of China, and proposed that *Changpeipus* is a monotypic ichnogenus, furthermore, *Changpeipus* and *Eubrontes* are similar (“sister”) ichnotaxa. The most prominent diagnostic feature of *C. carbonicus* is the inner hypex between digits II and III, which is situated distinctly posterior to the outer hypex between digits III and IV. Xing et al. 2009b, Xing et al. 2014c) also considered *C. xuiiana* from the Middle Jurassic Yima Formation at the Yima opencast coal mine in Henan Province (Lü et al. 2007) a *nomen dubium*.

4.3.7 *Eubrontes nianpanshanensis* (Yang and Yang 1987) Lockley et al. 2013

Yang and Yang (1987) described one theropod trackway from the Middle Jurassic Xintiangou Formation of Sichuan Province, and named it *Jinlijingpus nianpanshanensis*. Lockley et al. (2013) re-assigned the ichnotaxon



to *Eubrontes nianpanshanensis* n. comb. Xing et al. (2016c) described *E. zigongensis* in detail and provided new diagnostic features (Fig. 6n). The prominent diagnostic feature of *E. nianpanshanensis* is the low length/width ratio and wide divarication angle.

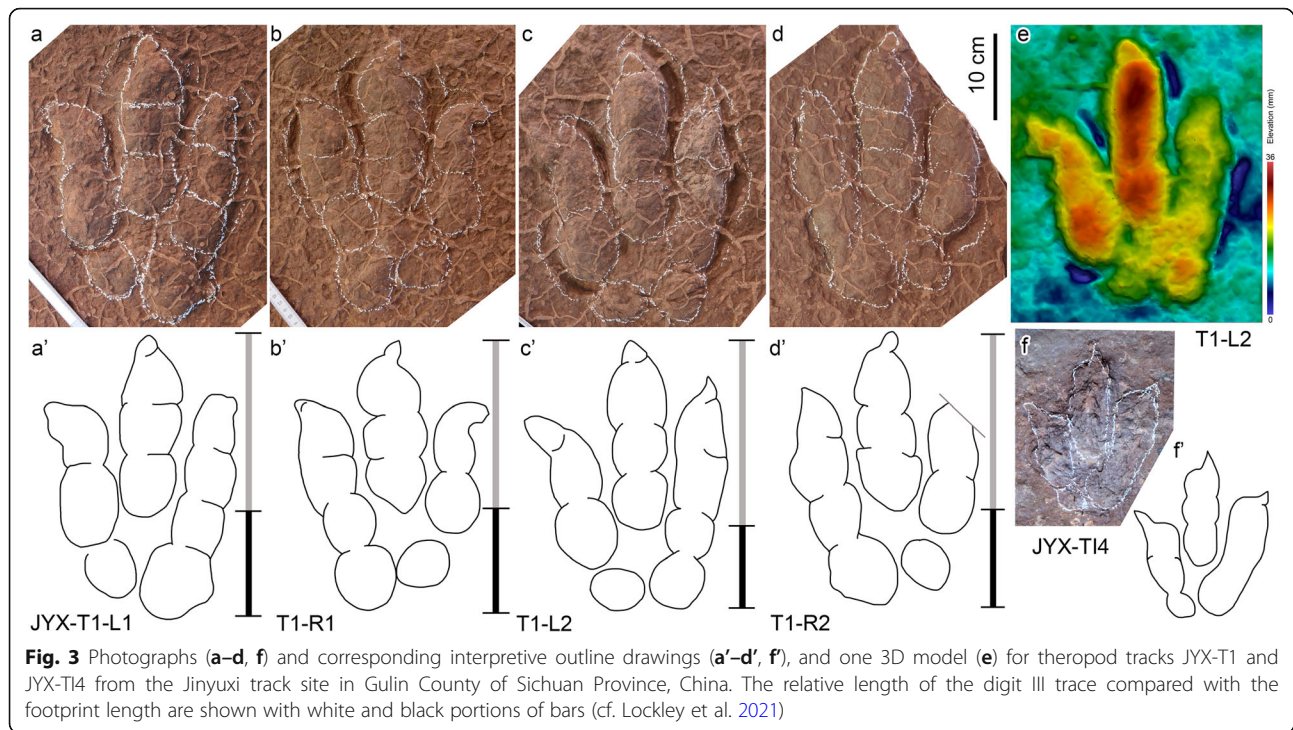
4.3.8 *Lufengopus dongi* Lü et al. 2006

Lü et al. (2006) described the first dinosaur footprint, an imperfectly preserved isolated large (37.8 cm in length) theropod track, from the Middle Jurassic Chuanjie Formation of the Lufeng Basin in Yunnan Province, and named it as *Lufengopus dongi* (Fig. 6o). Xing et al.

(2014e) re-described this specimen, and referred it to *Eubrontes* isp.

4.3.9 *Eubrontes* (?) *glenrosensis* Shuler 1935; Farlow et al. 2012 (Li et al. 2010)

Langston (1974) had previously assigned *Eubrontes* (?) *glenrosensis* to the ichnogenus *Irenesauripus*. Li et al. (2010) assigned one theropod trackway from the Middle Jurassic Zhaogou Formation at the Hailitu site in Inner Mongolia, China, and classified it as *Eubrontes* (?) *glenrosensis*. Xing et al. (2021) reviewed all the tracks from this site, and considered the length/width ratio and



mesaxony of *Eubrontes* (?) *glenrosensis* Hailiutu specimen are more similar to *Kayentapus*, and then rejected the identification of the dubious ichnospecies *Eubrontes* (?) *glenrosensis* among any of the Hailiutu theropod tracks (Fig. 6p).

4.3.10 *Lockleypus luanpingeris* (Young 1979) Xing et al. 2018b

Changpeipus luanpingeris was discovered from the Lower Cretaceous of Luanping coal mine in Hebei Province by Young (1979). Xing et al. (2014c) considered it a *nomen dubium*. With further research reviewing the track specimens from the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) of the Chinese Academy of Sciences, Xing et al. (2018b) considered *C. luanpingeris* as a new ichnogenus — *Lockleypus*, based on the free length of digit IV which is twice as long as the free length of digit II (Fig. 6q).

4.3.11 *Chapus lockleyi* Li et al. 2006

Li et al. (2006) described the large (42 cm in length) theropod track *Chapus lockleyi* (Fig. 6r) from the Lower Cretaceous Jingchuan Formation in Inner Mongolia, with relatively low anterior triangles (0.48) and low length of digit III/footprint length (0.60).

4.3.12 *Asianopodus pulvinicalyx* Matsukawa et al. 2005

Matsukawa et al. (2005) described *Asianopodus pulvinicalyx* from the Lower Cretaceous Kuwajima Formation of Japan, based on a somewhat gracile track of 29 cm

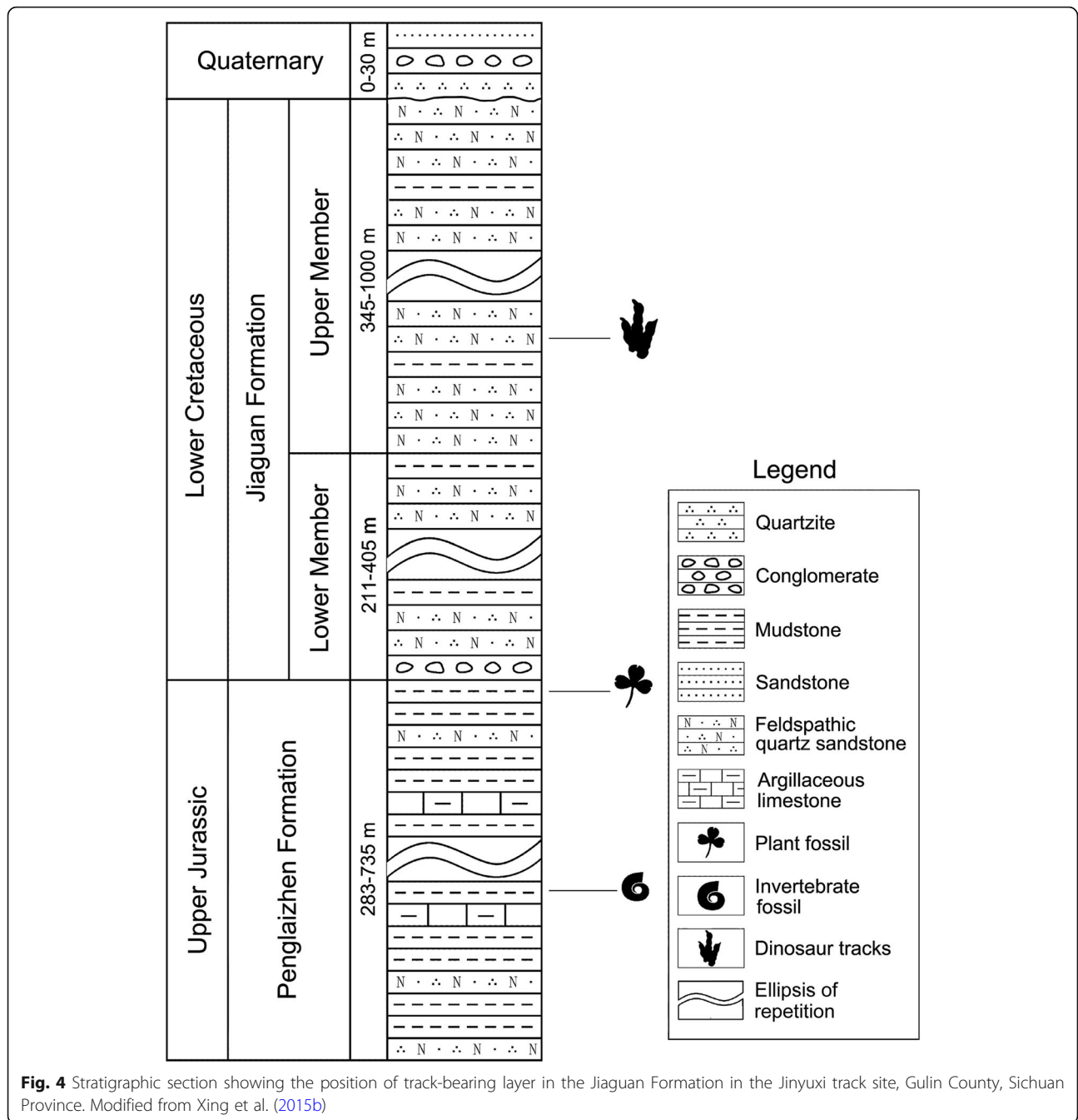
long and 21 cm wide (length/width ratio = 1.38) from an incomplete trackway. The ichnotaxon is distinctive in possessing a distinct, bulbous “heel” impression (see Fig. 6s).

4.3.13 *Asianopodus robustus* Li et al. 2011

Li et al. (2011) described *Asianopodus robustus* as a larger, more “robust” and slightly wider ichnospecies (length, width and length/width ratio are respectively 33 cm, 23 cm and 1.43) than *A. pulvinicalyx*. *A. robustus* also has a distinct, well-developed, rounded “heel” pad (see Fig. 6t). The choice of the holotype was based on an illustration by Lockley et al. 2002, Fig. 4) for a track that is not a part of a trackway. Thus, trackway parameters are not known for this ichnospecies.

4.3.14 *Asianopodus niui* Li et al. 2020

Recently, Li et al. (2020) described a new ichnospecies of *Asianopodus* (*A. niui*) from the Upper Cretaceous Shenjinkou Formation in the Xinjiang Uygur Autonomous Region. The material they described was based on a large track with length of 56 cm and width of 42 cm (length/width ratio of 1.33) which more closely resemble *Chapus* than either of the previously described *Asianopodus* ichnospecies. However, the type material was poorly illustrated, and we consider it a *nomen dubium*. The senior authors have re-evaluated the status of this ichnotaxon elsewhere (Xing et al. 2021; Xing et al. in press), so it is not illustrated or further analyzed here.



4.4 Taxonomy of Jinyuxi site

Eubrontidae Lull 1904

Theropoda Marsh 1881

Eubrontidae Lull 1904

Eubrontes Hitchcock 1845, Olsen et al. 1998

Type ichnospecies *E. giganteus* Hitchcock 1836, Hitchcock 1845, Olsen et al. 1998

***Eubrontes nobitai* ichnospp. nov.**

Etymology: The specific name honors Mr. Nobita (known as Noby in the English versions). He is

the protagonist of the Doraemon series. Japanese animated films *Doraemon: Nobita's Dinosaur* in 1980 and *Doraemon: Nobita's New Dinosaur* in 2020 are unforgettable dinosaur films. In the film, Mr. Nobita's dream is to have a dinosaur named after him.

Holotype: A complete natural cast of a pes track represented by four footprint trackways was catalogued as JYX-T1-L1 from the Jinyuxi track site (Table 1; Figs. 2 and 3). The plaster mold is stored in the Zigong Dinosaur Museum.

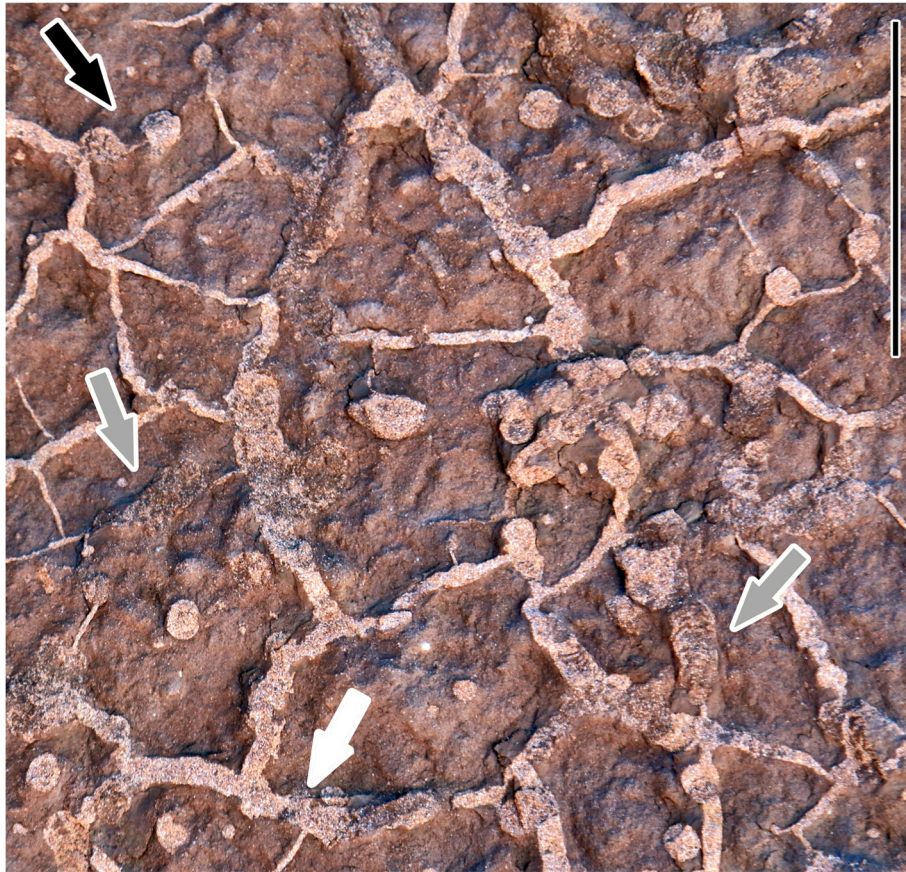


Fig. 5 Photograph of invertebrate traces similar to *Taenidium* isp. (gray arrows), and *Arenicolites* isp. (black arrow) on a mud cracked (white arrow) surface at the Jinyuxi track site, Gulin County, Sichuan Province. Scale bar = 5 cm

Type horizon and locality: Lower Cretaceous, Jiaguan Formation, Jinyuxi track site, Gulin County, Sichuan Province, China.

Diagnosis: A relatively large-sized tridactyl footprint with pes length/width ratio of 1.4, weak mesaxony of 0.37, and relatively small divarication angle (about 47°) between digit II and IV. Digit III is 65% of the total pes length. Digit II is 85% of the length of digit III. The metatarsophalangeal pads of digit II are fairly well developed, with a size almost as large as the phalangeal pad of digit IV. The metatarsophalangeal pads lie sub-symmetrically on either side of the midline of the track. This is a feature that differentiates the tracks from many less symmetrical theropod tracks including some *Eubrontes*, *Asianopodus* and *Chapus*. Step length is about 2.6× footprint length, and the mean pace angulation is high (about 160°). *E. nobitai* is different from the type ichnospecies *E. giganteus* by (1) wider digit II–IV divarication, (2) weaker mesaxony, and (3) lower length/width ratio; and, different from *E. zigongensis*, *E. veillonensis* and *E. nianpashensis* by (1) smaller digit II–IV divarication and (2) weaker mesaxony.

Description:

All tracks in the trackway are equally well preserved, on the scale of Belvedere and Farlow (2016), so each track is equally representative of the individual footprint morphology. The mean length and width of all four tracks (JYX-T1-L1–R2) are 31.4 cm and 22.5 cm, respectively, and the mean length/width ratio is 1.4. JYX-T1-L1 exemplifies the morphology, and was selected for replication as the holotype for the Zigong Dinosaur Museum. Digit III projects the farthest anteriorly, followed by digits IV and II. The mean ratio between the length of digit III and foot length is 0.65 with a range of 0.63–0.69. Two distinct metatarsophalangeal pad traces, a smaller one posterior to digit II and a larger one posterior to digit IV, can be seen. Both metatarsophalangeal pad traces are round and blunt and positioned on either side of the axis of digit III. The deep, concave digit impressions retain pad impressions that have a formula of x-3-3-4-x, including metatarsophalangeal pads II and IV. Each digit has a sharp claw trace, and digit II has the clearest and longest trace. The divarication angle between digits II and IV is 47°. The divarication angle

Table 2 Measurement element comparison of *Eubrontes* from China, Europe and America

Specimens	Age	L/W	M	II–IV	II/III	III/L	Reference	Interpretive outline drawing
America								
<i>Eubrontes giganteus</i> (type)	J1	1.7	0.58	48°	0.76	0.67	Lockley 2009	Fig. 6a
<i>Eubrontes giganteus</i>	J1	1.6	0.53	46°	0.80	0.63	Olsen et al. 1998	Fig. 6b
Utah <i>Eubrontes</i> 1	J1	1.5	0.48	53°	0.73	0.71	Lockley et al. 1998	Fig. 6c
Utah <i>Eubrontes</i> 2 (T3)	J1	1.3	0.44	46°	0.81	0.60	Lockley et al. 2021	Fig. 6d
Connecticut <i>Eubrontes</i>	J1	1.3	0.44	56°	—	0.64	Ishigaki and Fujisaki 1989	Fig. 6e
<i>Eubrontes</i> (?) <i>glenrosensis</i>	K1	1.3	0.36	56°	—	0.54	Adams et al. 2010	Fig. 6f
Europe								
<i>Eubrontes veillonensis</i>	J1	1.5	0.50	49°	0.57	0.62	de Lapparent and Montenat 1967	Fig. 6g
China								
<i>Eubrontes pareschequier</i>	J1	1.3	0.51	58°	0.68	0.66	Xing et al. 2009a, 2014b	Fig. 6h
<i>Eubrontes zigongensis</i>	J1	1.4	0.49	55°	0.74	0.66	Xing et al. 2014c	Fig. 6i
<i>Eubrontes platypus</i> Xiyang specimen	J1	1.3	0.43	57°	—	0.71	Hitchcock 1858; Yang and Yang 1987	Fig. 6j
<i>Eubrontes monax</i>	J1	1.2	0.49	65°	—	0.74	Zhen et al. 1986; Lockley et al. 2013	Fig. 6k
<i>Eubrontes xiyangensis</i>	J1	1.8	0.68	46°	—	0.74	Zhen et al. 1986; Lockley et al. 2013	Fig. 6l
<i>Changpeipus carbonicus</i>	J1-2	1.6	0.46	50°	0.66	0.63	Xing et al. 2014b	Fig. 6m
<i>Eubrontes nianpanshanensis</i>	J2	1.1	0.37	64°	0.81	0.62	Xing et al. 2016b	Fig. 6n
<i>Lufengopus dongji</i>	J2	1.1	0.29	63°	0.96	0.61	Lü et al. 2006; Xing et al. 2014d	Fig. 6o
<i>Eubrontes</i> (?) <i>glenrosensis</i> Hailiutu specimen	J2	1.0	0.47	80°	0.70	—	Li et al. 2010; Xing et al. 2021	Fig. 6p
<i>Lockleypus luanpingeris</i>	K1	1.3	0.56	66°	0.73	0.61	Xing et al. 2018e	Fig. 6q
<i>Chapus lockleyi</i>	K1	1.3	0.48	53°	0.68	0.60	Li et al. 2006	Fig. 6r
<i>Asianopodus pulvinicalyx</i>	K1	1.4	0.45	55°	0.91	0.57	Matsukawa et al. 2005	Fig. 6s
<i>Asianopodus robustus</i>	K1	1.2	0.40	58°	0.87	0.56	Li et al. 2011; Lockley et al. 2018	Fig. 6t
<i>Eubrontes nobitai</i>	K1	1.4	0.37	47°	0.85	0.65	This study	Fig. 6u
<i>Eubrontes</i> HX-T3	K1	1.4	0.37	56°	0.69	0.68	Xing et al. 2015b	Fig. 6v
<i>Eubrontes</i> BJA-T4	K1	1.4	0.46	51°	0.75	0.69	Xing et al. 2016c	Fig. 6w

Abbreviation: L/W The length/width ratio, M Mesaxony, II–IV The divarication angle between digit II and digit IV, II/III The digit II/digit III length ratio, III/L The digit III/footprint length ratio

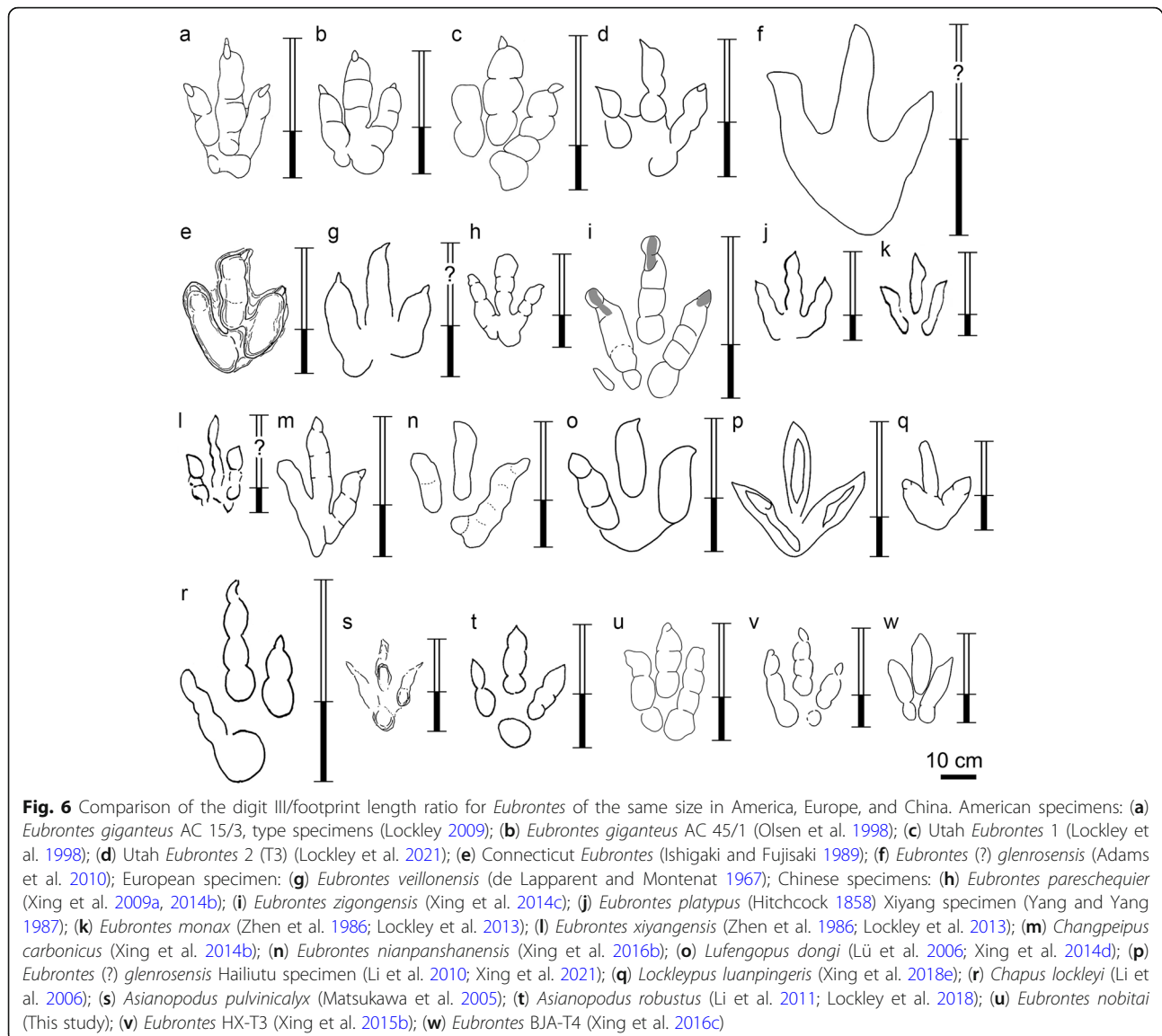
between digits II and III (19°) is smaller than that between digits III and IV (28°). The other JYX-T1 tracks are consistent with JYX-T1-L1 in all general features; the divarication angles between digit II and digit IV of these tracks range from 43° to 50°. All the tracks are rotated ~7° outwards from the trackway midline. The outer trackway width of JYX-T1, measured from the outside margin of the pes, is 33–37 cm. The average pace angulation is 160°, and the footprint length to pace length ratio is 1:2.6.

The stride length relative to pes length of the trackway JYX-T1 allows for a speed (v) calculation using the formula of Alexander (1976): $v = 0.25 g^{0.5} \times SL^{1.67} \times h^{-1.17}$, where g is the gravitational acceleration in m/s², SL is stride length, and h is hip height, which is estimated to

be 4.9 times the foot length using the ratio for large theropods proposed by Thulborn (1990). Then, we estimate a speed of ~1.08 m/s or ~3.89 km/h. The body length of the JYX-T1 track maker is approximately 4 m, further calculated using the average hip height to body length ratio of 1:2.63 (Xing et al. 2009c).

Comparison:

Eubrontes tracks were first discovered in the Connecticut River Valley of Massachusetts in the early nineteenth century, and were probably among the first non-avian dinosaur tracks discovered in North America (Hitchcock 1845; Lull 1904, 1953; Olsen et al. 1998). Hereafter, *Eubrontes* or *Eubrontes*-type tracks are commonly found in Lower Jurassic strata and have also been reported from the Jurassic series but less frequently from the



Cretaceous. They are also known from Upper Triassic strata (Lucas et al. 2006; Lagnaoui et al. 2012; Xing et al. 2013a, b; Zouheir et al. 2018).

Several large-sized theropod tracks from the carbonate bedrock of Paluxy River in the Albian Glen Rose Formation (Lower Cretaceous) in Texas, were assigned to *Eubrontes* (?) *glenrosensis* (Shuler 1935; Farlow et al. 2012), but were transferred into the ichnospecies *Irenesauripus glenrosensis* by Langston (1974).

Eubrontes-type tracks are very common in the Jurassic and have also been reported from the Cretaceous of China, including some ichnogenus with similar morphology such as *Chapus* from the Chabu site of Inner Mongolia (Li et al. 2006) and *Asianopodus* from Junan site of Shandong (Xing et al. 2014a; Li et al. 2015). Compared with the classical Early Jurassic *Eubrontes*–

Anchisauripus–*Grallator* assemblage (Olsen et al. 1998), Cretaceous *Grallator*–*Eubrontes* morphotypes from China have wider interdigital divarication (Lockley et al. 2013; Xing et al. 2016a), which can also be observed in Early Cretaceous theropod tracks from North America (Lockley et al. 1998).

The JYX-T1 track shows convergent traits with type *Eubrontes* tracks, such as the presence of a distinct metatarsophalangeal pad (MTP) trace posterior to digit II (MTP II). This characteristic is common in *Eubrontes* tracks, including type *Eubrontes* AC 151 (Olsen et al. 1998), and also distinguishes *Eubrontes* from *Chongqingpus*, a medium-large theropod track with a hallux impression (Xing et al. 2013a, b). This feature (MTP II) also distinguishes type *Eubrontes* and *E. nobitai* from most other *Eubrontes*, from common ichnogenus

Kayentapus of the Early–Middle Jurassic (Lockley et al. 2011; Xing et al. 2020), and from such Cretaceous ichnogenera as *Asianopodus* (Fig. 6).

The JYX-T1 track has weak mesaxony (0.37) and low length/width ratio (1.4), similar to those of type *Eubrontes* (Olsen et al. 1998; Lockley 2009). The mesaxony and length/width ratio are respectively 0.58 and 1.7 for *Eubrontes giganteus* from the Hitchcock collection (Lockley 2009) (Fig. 6a), suggesting that Hitchcock *Eubrontes* tracks are slightly more elongate. However, other local specimens assigned to *Eubrontes* display wider interdigital divarications and lower length/width ratios (Ishigaki and Fujisaki 1989; and see Lockley et al. 2021 for additional data). Overall, the length/width ratio, mesaxony and divarication angle (47°) of the JYX-T1 track are relatively lower and smaller than these three parameters of *Eubrontes* reported from the Lower Jurassic of Utah, USA (Lockley et al. 1998, Lockley et al. 2021; Lockley 2000, Fig. 7). *Eubrontes zigongensis* from

the Lower Jurassic Zhenzhuchong Formation of Sichuan Province, China (Fig. 6i) has stronger mesaxony (0.49) and wider divarication angle (55°) (Xing et al. 2014b). *Eubrontes nianpanshanensis* from the Middle Jurassic Xiashaximiao Formation of Sichuan Province (Fig. 6n) has much wider divarication angle (64°) (Yang and Yang 1987; Lockley et al. 2013; Xing et al. 2016c). *Eubrontes* HX-T3 tracks from the same Jiaguan Formation show similar mesaxony but wider divarication angles (53°–59°; Xing et al. 2016c) (Fig. 6v). *Eubrontes* BJA-T4, from the Lower Cretaceous Feitianshan Formation, has stronger mesaxony (Xing et al. 2016b) (Fig. 6w).

JYX-T1 also differs from all other *Eubrontes* tracks in two features. First, the metatarsophalangeal pad II of JYX-T1 is well developed, with a size similar to the phalangeal pad I of digit IV connected with the metatarsophalangeal pad IV; Second, JYX-T1 has a fairly long digit II, or shorter digit III. Excluding metatarsophalangeal pads and claw marks, the length of digit II is 85% as the

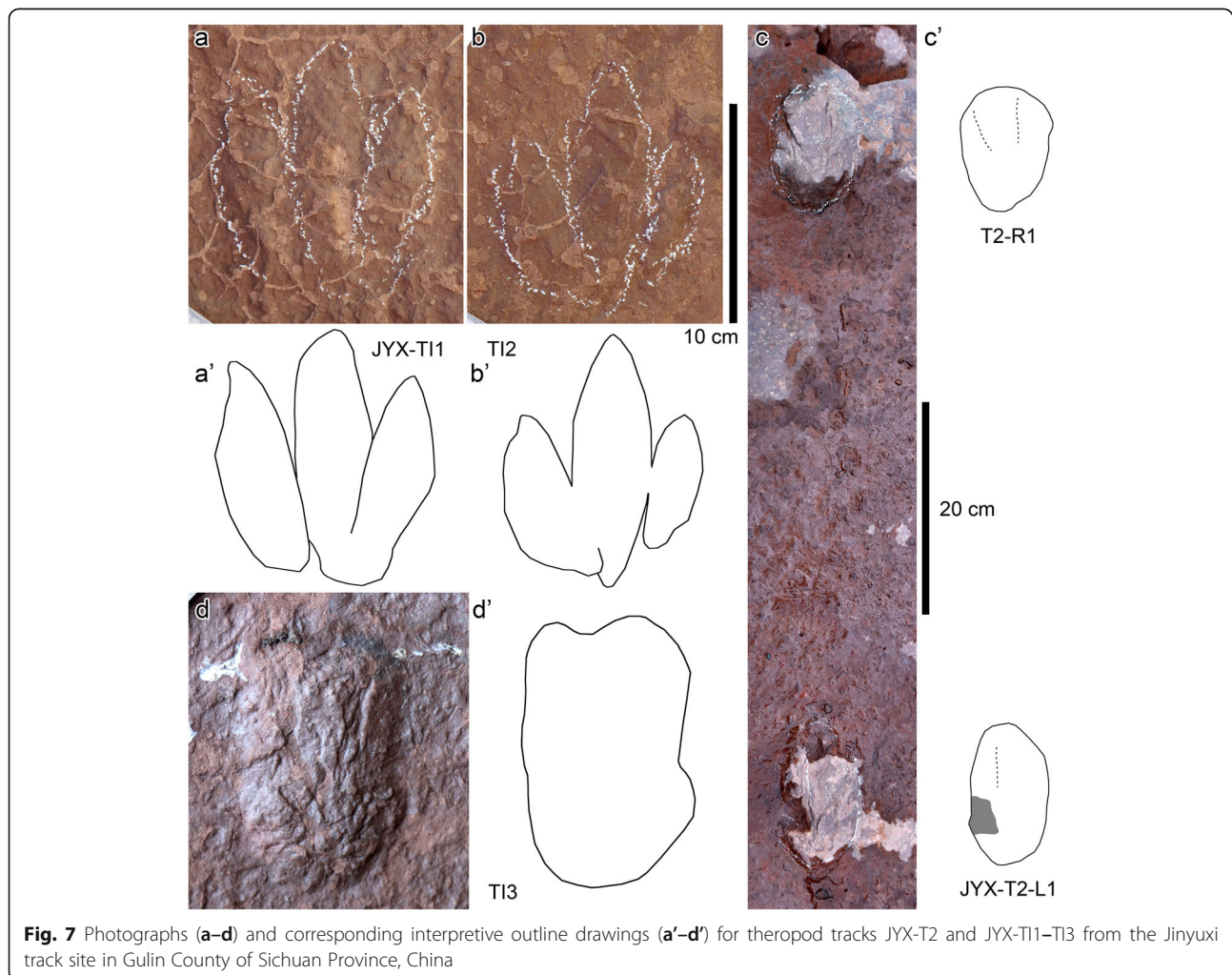


Fig. 7 Photographs (a–d) and corresponding interpretive outline drawings (a’–d’) for theropod tracks JYX-T2 and JYX-T11–T13 from the Jinyuxi track site in Gulin County of Sichuan Province, China

length of digit III. The length ratio (85%) is obviously different from the other aforementioned *Eubrontes*, of which only *E. nianpanshanensis* has a ratio of over 80%.

The length of digit III was measured in relation to the overall pes length (Demathieu 1990; Lockley 2000; Lockley et al. 2021) to show that the digit III/pes length ratio of the Early Jurassic *Eubrontes* was ~ 0.70 , compared with the ratio of ~ 0.60 for the Middle–Late Jurassic *Megalosauripus* (Lockley et al. 2021). A mean value of 0.64 was computed for the Early Jurassic *Eubrontes* from a large sample of well-preserved tracks from Utah, USA (Lockley et al. 2021). The digit III/pes length ratio has been calculated (Table 2) and illustrated (Fig. 6), mostly based on measurements obtained from individual tracks, for all the 23 morphotypes for the JYX-T1 series, including 18 morphotypes named at the ichnospecies level. The range of the digit III/pes length ratio varies from 0.57 to 0.71 with a mean value of about 0.65, indicating a slightly greater digitigrady than type *Eubrontes* but very close to the Utah sample. Meanwhile, the digit III/pes length ratio of the *E. nobotai* based on all tracks in the trackway is as similar as the case for *Eubrontes* Utah 2 (T3) (0.65 vs. 0.64). The relative length of digit III within the footprint is a potential measure of digitigrady. Arguably, the presence or absence of a digit II metatarsal phalangeal pad is also a measure of digitigrady and has been proved useful in ichnotaxonomic comparisons. For example, *E. nobotai* is closer to type *Eubrontes giganteus* than to other *Eubrontes* morphotypes in having a clear MTP II trace. For this reason, erecting the new ichnospecies under the unequivocal ichnogenus label *Eubrontes* is strengthened.

The Early Jurassic *Eubrontes veillonensis* tracks from Vendée, France (de Lapparent and Montenat 1967; Fig. 6g) are wider with stronger mesaxony. The Early Jurassic *Eubrontes platypus* (Hitchcock 1858) Xiyang specimen (Yang and Yang 1987) (Fig. 6j) and *Eubrontes xiyangensis* (Zhen et al. 1986; Lockley et al. 2013) (Fig. 6l) from Yunnan Province, China are poorly preserved, and then the original specimen needs more comparison. The Early Jurassic *Eubrontes* (?*Changpeipus*) *pareschequier* tracks (Xing et al. 2009b; Xing et al. 2014c) from Yunnan Province have stronger mesaxony and wider divarication angles. *Eubrontes* (?) *glenrosensis* (*Irenesauripus glenrosensis*, of Langston 1974) are larger than other *Eubrontes*, and have wider interdigital divarication angles.

4.5 Other theropod tracks

JYX-TI1 and JYX-TI2 (Figs. 2, 7) are small-sized tridactyl tracks located on one side of the same slab as the JYX-T1 trackway. The two footprints do not belong to the same trackway but are similar in morphology and length (12 cm and 11.3 cm). The tracks lack clear heel traces and thus have lower length/width ratios and wider

interdigital divarication angles, the former ratios are 1.3 and 1.4 respectively and the latter angles are 47° and 50°. The phalangeal pads of JYX-TI1 and TI2 are unrecognizable, and the tracks may therefore be undertracks. Considering the length/width ratios and the relatively sharp claw marks, JYX-TI1 and TI2 show an affinity with theropod tracks.

JYX-TI4 (Fig. 3) is well-preserved. Its length and width are 19.7 cm and 16.1 cm, respectively, and the mean length/width ratio is 1.2. Digit III projects the farthest anteriorly, followed by a smaller metatarsophalangeal pad posterior to digit II and another larger metatarsophalangeal pad posterior to digit IV. The larger metatarsophalangeal pad is closer to the line of the axis of digit III. Digit pad impressions are unambiguous only in digit II and III; the formula (including metatarsophalangeal pads II and IV) is $x-3-3-?-x$. Each digit has a sharp claw trace, and that of digit II is the clearest and longest. In general, the digits have relatively wide divarication angles between digits II and IV (61°). The tracks display weak mesaxony (0.40). Based on the pattern of metatarsophalangeal pads, JYX-TI4 is similar to Early Cretaceous Eubrontid tracks commonly known in the Jiaguan Formation (Xing et al. 2016a).

JYX-TI3, a single track and JYX-T2, a pair of tracks likely representing a step (Fig. 7) are clearly peculiar in morphology due to extramorphological (preservational) factors. All three tracks are longitudinal ovate casts without discernable morphological features. The more distal one of the two consecutive tracks in JYX-T2 shows faint traces of a tridactyl morphology, consistent with the length/width ratio, step and apparently narrow trackway. JYX-TI3 is 12.4 cm in length, with a length/width ratio of 1.7. There is a short, round impression on the right side of the track, near the heel. This could conceivably be interpreted as the short digit II trace characteristic of deinonychosaurian tracks. However, although variably, even poorly preserved deinonychosaurian tracks are known from similar facies in the Cretaceous of China (Zhen et al. 1994; Li et al. 2007; Xing et al. 2009a), the sample size and quality of preservation in JYX-TI3 and JYX-T2 do not allow such tenuous speculation.

The mean length of the two tracks included in JYX-T2 is 12.6 cm, and the mean length/width ratio is 1.6. There are some shallow longitudinal indentations on the JYX-T2 tracks, which may be interdigital gaps or folds formed by deposition or weathering. Both tracks lie on a straight line, with a pace length of 61.4 cm, and therefore have a high affinity with theropod tracks.

4.6 Sauropod tracks

4.6.1 Description

Sauropod trackways discovered at the Jinyuxi site (Figs. 8, 9 and 10) are imperfectly preserved and variable in

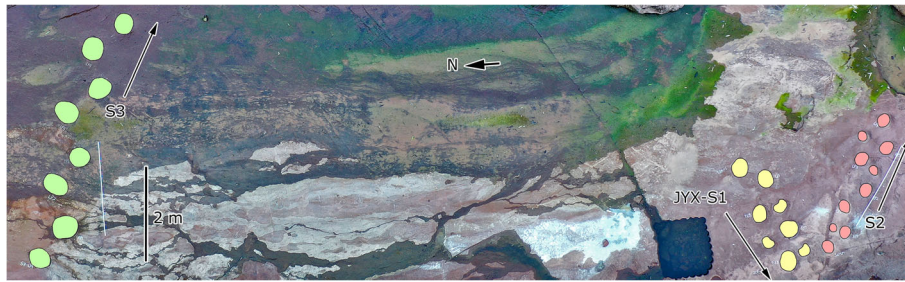


Fig. 8 Photograph and overlapped interpretive outline drawing with distribution of sauropod trackways from the Jinyuxi track site in Gulin County of Sichuan Province, China. The arrows indicate their walking directions

size. The mean length of the pes prints of JYX-S1–S4 is 37.4 cm, 31.2 cm, 49.0 cm, and 45.0 cm, respectively. The JYX-S1–S3 trackways contain tracks that are morphologically similar. The JYX-S2 and JYX-S3 trackways are both orientated from northwest to southeast. JYX-S1 is oriented from northeast to southwest. The slab bearing JYX-S4 (Fig. 10) has been stripped from the basement.

The newly exposed JYX-S4 is preserved best, consisting of a set of complete left tracks LP1–LM1, a set of complete right tracks RP2–RM2, and one incomplete right manus print RM1. The manus prints are oval, with obscure digit traces and metacarpophalangeal region. The pes prints are oval with long axes being outwardly rotated, and with anterior portion being wider than the posterior portion. The mean length of the pes and manus from the JYX-S4 trackway are 45.0 cm and 28.3 cm. The manus prints locate anteriorly to anteromedially to the pes prints. The mean length/width ratio of the manus and pes prints are 0.9 and 1.2 respectively. Traces of the claws on digits I–III are recognizable. Digit I is developed best with the deepest trace. There is an indentation in the middle of the trace, which may represent the gap between the phalangeal pad I and the claw.

The boundary between traces of digits I and II, and the boundary between traces of digits II and III are both obscure. The preservation of digit IV is different and shows that the track LP1 has a distinct digit trace while the trace of the RP2 is not so clear, and the metatarsophalangeal region is smoothly curved.

JYX-S1–S3 trackways have been seriously weathered and the JYX-S1 is relatively best preserved. Both JYX-S1 and JYX-S2 have pes prints with anterior manus prints, while JYX-S3 only has pes prints. Though JYX-S1–S3 trackways are different in size, their morphology is almost identical. The mean pes length respectively for the JYX-S1–S3 trackways is 37.4 cm, 31.2 cm and 49.0 cm. In the JYX-S1 trackway, the manus and pes prints are oval; digits I and V are discernible and the metatarsophalangeal region is smoothly curved but the claw traces are unidentifiable. The long axes of the pes prints are outwardly rotated by approximately 32° on average, and the anterior portion of the pes prints is wider than the posterior portion. The manus prints are rotated outward by approximately 17° on average from the trackway axis. The average pace angulation of the manus traces is 78°, while the average pes pace angulation is 99°. The mean

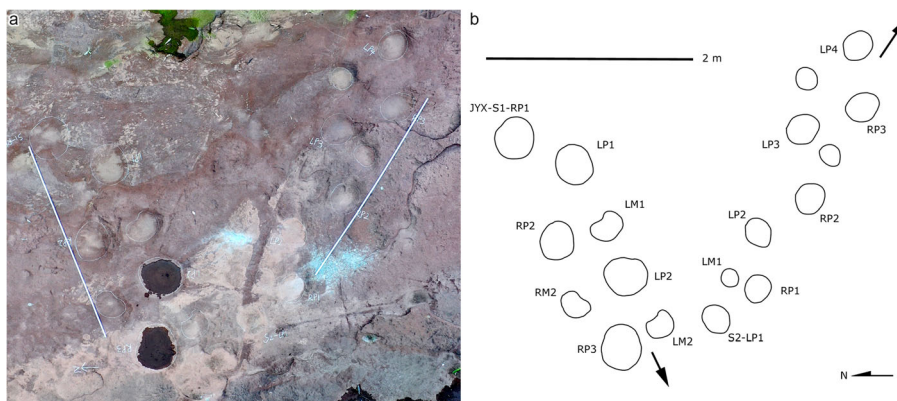


Fig. 9 Photograph (a) and interpretive outline drawing (b) of sauropod trackways JYX-S1 and JYX-S2 from the Jinyuxi track site in Gulin County of Sichuan Province, China. Note that the scale in a (white rules) and in b (black bar) are in an equal proportion (2 m)

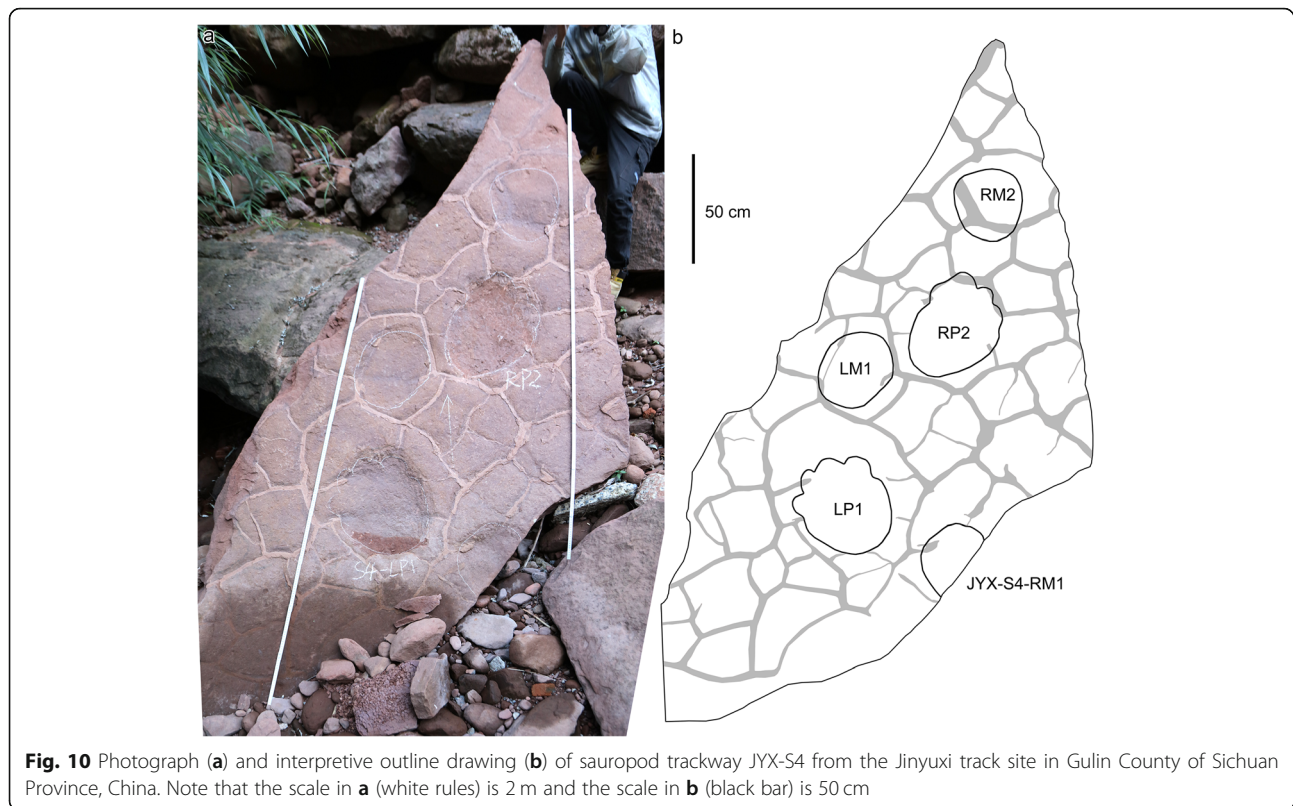


Fig. 10 Photograph (a) and interpretive outline drawing (b) of sauropod trackway JYX-S4 from the Jinyuxi track site in Gulin County of Sichuan Province, China. Note that the scale in a (white rules) is 2 m and the scale in b (black bar) is 50 cm

length/width ratios of the manus and pes prints of the JYX-S1 are 0.9 and 1.1, respectively. JYX-S2 and JYX-S3 are basically consistent with JYX-S1 in features and measurement data.

4.6.2 Comparison

Pes and manus morphology and trackway configuration of the quadruped trackways at Jinyuxi track site are typical of sauropods (Lockley and Hunt 1995; Lockley 1999, 2001). Three Jinyuxi sauropod trackways JYX-S1–S3 show definite WAP/P^{ML} ratios of 1.2, 1.2, and 1.1 respectively. According to Marty et al. (2010), the WAP/P^{ML} ratio of 1.0 differentiates sauropod trackways between the narrow-gauge and the medium-gauge, and the WAP/P^{ML} ratio of 1.2 is selected as a divide between the medium-gauge and wide-gauge trackways. Therefore, the JYX-S1–S3 trackways are the medium- to wide-gauge.

The mean heteropody (ratio of manus to pes size) of JYX-S1 is 1:2.1 (2.5, 1.9 and 1.8, $n = 3$), the mean heteropody of JYX-S2 is 1:2.2 (2.1, 2.1 and 2.5, $n = 3$), and that of JYX-S4 is 1:1.7 (1.6 and 1.8, $n = 2$). They are all lower than that of *Brontopodus birdi* (1:3) and of *Parabrontopodus* (1:4 or 1:5) (Lockley et al. 1994). Most sauropod trackways in China are medium- and/or wide-gauge and are therefore referred to the ichnogenus

Brontopodus (Lockley et al. 2002). The Jinyuxi sauropod trackways are consistent with the characteristics of *Brontopodus* type tracks like: (1) being medium- to wide-gauge; (2) having large outwardly directed pes tracks of which their length is longer than width; (3) having oval or U-shaped manus prints; (4) having a relatively low degree of heteropody (Farlow et al. 1989; Farlow 1992; Lockley et al. 1994; Santos et al. 2009; Xing et al. 2016a). *Brontopodus* trackmakers have long been considered to be Titanosauriformes (Wilson and Carrano 1999).

For sauropods, Thulborn (1990) estimated the hip height as: $h = 5.9 \times \text{foot length}$, while González Riga (2011) estimated the hip height as: $h = 4.586 \times \text{foot length}$. Further, the relative stride length (SL/h) is commonly used to determine whether an animal was walking ($SL/h \leq 2.0$), trotting ($2.0 < SL/h < 2.9$), or running ($SL/h \geq 2.9$) (Alexander 1976; Thulborn 1990). The SL/h ratios of the Jinyuxi sauropod trackways JYX-S1–S3 respectively range between 0.52–0.67, 0.54–0.7, and 0.51–0.66, accordingly suggesting that the sauropods were walking. Using the equation proposed by Alexander (1976) to estimate the speed from trackways, the mean locomotion speed of the trackmakers from JYX-S1–S3 is between 1.4 km/h and 2.12 km/h. This speed range is typical for sauropods, for which the estimated speed is always low.

5 Discussion

Among all the 23 *Eubrontes* occurrences listed in Table 2 and illustrated in Fig. 6, 15 of them originated from the Lower and Middle Jurassic. It was therefore clear that most well-defined examples of *Eubrontes*, including the type (*E. giganteus*) and five previously named ichnospecies from China (*E. zigongensis*, *E. pareschequier*, *E. nianshanensis*, *E. monax* and *E. xiyangensis*) as well as *E. veillonensis* from Europe, were from the Lower and Middle Jurassic. There were also abundant Triassic occurrences from North America, Europe and Africa (Lucas et al. 2006; Lagnaoui et al. 2012; Xing et al. 2013a, b; Zouheir et al. 2018). Of the eight occurrences from the Cretaceous, one morphotype reported from North America was transferred from ichnogenus *Eubrontes* (?) *glenrosensis* to *Irenesauripus* (Langston 1974). Other occurrences were listed simply as *Eubrontes* with no ichnospecies label.

After *Eubrontes* was first named by Hitchcock (1845) from the Lower Jurassic of New England, 17 ichnospecies were introduced (Chure and McIntosh 1989, p. 157), most of which were never adequately described, distinguished from other ichnospecies or identified elsewhere. Thus, with time it became accepted by most ichnological communities that only the type ichnospecies (*E. giganteus*) was widely recognizable (e.g. Lull 1953; Olsen et al. 1998) — few other *Eubrontes* ichnospecies were reported more than occasionally. This indicated a strong movement from a “splitter” to a “lumper” mentality. This trend was also applied to the ichnological record in China when it was recognized that the Jurassic tetrapod track record was seriously oversplit. Lockley et al. (2013) once pointed out “Jurassic theropod ichnotaxa reduced from 23 to only nine because most ichnogenera were subjective junior synonyms of *Grallator* and *Eubrontes*”.

To balance against this historical trend of early splitting and overcome it by later lumping, the increase of reports for track sites from China has led to acceleration in the scrutiny, renaming and reassessment of ichnospecies; while to identify new finds is also needed. This has transferred and redistributed at least six ichnospecies into *Eubrontes* (Lockley et al. 2013). In such cases, although the ichnogenus diversity is reduced, the diversity of ichnospecies increases. In this regard, the *Eubrontes* diversity is inflated by the reassignment of ichnospecies (names), even though some just survive in the literature regardless of the quality of the original ichnotaxomic research. This is somewhat obvious from Table 2, which shows that the Chinese ichnology still recognized six *Eubrontes* ichnospecies from the Jurassic. By contrast, only three *Eubrontes* occurrences were reported from the Cretaceous of China (Xing et al. 2015b; Xing et al. 2016b) — two without new ichnospecies labels, plus the

new ichnospecies *Eubrontes nobitai* described in this study. Xing et al. 2015b, Xing et al. 2016b) named cf. *Eubrontes* and a more broadly defined *Eubrontes*–*Megalosauripus* morphotype, both from Sichuan Province, further evidenced the reluctance to name new ichnotaxa. This cautious generalization trend is even more emphatically demonstrated by a survey on more than 130 *Eubrontes* track sites from the Lower Jurassic of western North America (Lockley et al. 2021; Lockley and Milner in press), which are simply labelled *Eubrontes*, with no ichnospecies labels. However, the discovery of well-preserved tracks such as characterizing the *E. nobitai* trackway makes it necessary to find suitable identifications.

Eubrontes nobitai, because of the fine preservation, appears to be one of the best-defined *Eubrontes* ichnospecies besides the type ichnospecies *E. giganteus*. Its occurrence in the Lower Cretaceous of Southwest China documents the long stratigraphic range and wide distribution of medium-sized theropods with well-padded feet and weakly projecting digit III. This supports the presence of a successful theropod line co-existing with the trackmakers of *Megalosauripus*-, *Changpeipus*-, *Therangospodus*- and other type tracks.

6 Conclusions

Eubrontes nobitai described firstly in this study is found in a well-defined trackway, comprising four extremely well-preserved tracks: 3 on the 0–1–2–3 scale proposed by Belvedere and Farlow (2016); and is the only Chinese theropod ichnotaxon that bears a close resemblance to type *Eubrontes*. Therefore, it is an important theropod morphotype with the potential to help better understand the morphological variation of *Eubrontes* and *Eubrontes*-like tracks in space and time. Ongoing studies (Xing et al. 2021; Xing et al. in press) have noted that the large theropod tracks *Asianopodus* and *Chapus* need to be compared with such widely distributed theropod ichnogenera as *Eubrontes* to conduct further research.

Sauropod tracks from the Jinyuxi track site are classified in *Brontopodus* type tracks. This is consistent with the previous sauropod track records of the Jiaguan Formation. Some poorly preserved tracks show the affinity of deinonychosaurian tracks, which are also clearly recorded in the Jiaguan Formation.

Abbreviations

JYX: The Jinyuxi, Gulin County, Sichuan Province, China; ZLJ-ZQK: The World Dinosaur Valley Park, Lufeng County, Yunnan Province, China

Acknowledgements

The author team thanks Xing Xu from the Key Laboratory of Evolutionary Systematics of Vertebrates, Chinese Academy of Sciences, Beijing and two anonymous reviewers for discussion and research support. We thank National Natural Science Foundation of China, and the 111 project, China.

Authors' contributions

LDX designed the project; LDX, MGL, LZ and AR performed the research and wrote the manuscript; HK, WSPIV and MYW contributed to reviewing the manuscript; LDX, GZP and YY participated in the field work, provided data, and investigated geological background. All authors read and approved the final manuscript.

Funding

The study is supported by the National Natural Science Foundation of China (Grant No. 41772008), the 111 project, China (Grant No. B20011), and the Fundamental Research Funds for Central Universities (Grant No. 265QZ201903).

Availability of data and materials

All data generated or analyzed during this study are included in this published article.

Declaration**Competing interests**

The authors declare that they have no competing interests.

Author details

¹State Key Laboratory of Biogeology and Environmental Geology, China University of Geosciences, Beijing 100083, China. ²School of the Earth Sciences and Resources, China University of Geosciences, Beijing 100083, China. ³Dinosaur Trackers Research Group, University of Colorado Denver, Denver 80217, USA. ⁴Saurierwelt Paläontologisches Museum Alte Richt 7, 92318 Neumarkt, Germany. ⁵Institute of Resources and Environment, Key Laboratory of Biogenic Traces and Sedimentary Minerals of Henan Province, Collaborative Innovation Center of Coalbed Methane and Shale Gas for Central Plains Economic Region, Henan Polytechnic University, Jiaozuo 454003, Henan Province, China. ⁶School of Biological Sciences, The University of Queensland, Brisbane, Queensland 4072, Australia. ⁷Mace Brown Museum of Natural History, Department of Geology and Environmental Geosciences, College of Charleston, Charleston 29401, USA. ⁸Zigong Dinosaur Museum, Zigong 643013, Sichuan Province, China.

Received: 14 January 2021 Accepted: 20 May 2021

Published online: 05 July 2021

References

- Adams, T.L., C. Strganac, M.J. Polcyn, and L.L. Jacobs. 2010. High resolution three-dimensional laser-scanning of the type specimen of *Eubrontes (?) glenrosensis* Shuler, 1935, from the Comanchean (Lower Cretaceous) of Texas: Implications for digital archiving and preservation. *Palaeontologia Electronica* 13.3 (1T): 1–11.
- Ahrens, J., B. Geveci, and C. Law. 2005. 36 — ParaView: An End-User Tool for Large-Data Visualization. In *Visualization Handbook*, ed. C.D. Hansen and C.R. Johnson, 717–731. Burlington: Butterworth-Heinemann <https://doi.org/10.1016/B978-012387582-2/50038-1>.
- Alexander, R. 1976. Estimates of speeds of dinosaurs. *Nature* 261: 129–130 <https://doi.org/10.1038/261129a0>.
- Belvedere, M., and J.O. Farlow. 2016. A numerical scale for quantifying the quality of preservation of vertebrate tracks. In *Dinosaur tracks — The next steps*, ed. P.L. Falkingham, D. Marty, and A. Richter, 92–99. Bloomington and Indianapolis: Indiana University Press.
- Chen, H.X. 2009. *Research of paleoenvironment and paleoclimate of Cretaceous in Ya'an area of western Sichuan Basin*. Master Thesis, 86. China: Chengdu University of Technology.
- Chen, L., T.Q. Lu, W. Guo, S. Li, Q.J. Chen, J.S. Zhang, and G.Q. Wang. 2019. Ichnofabrics and their environmental significance from the Upper Cretaceous Jiaguan Formation in Emei mt. Area, southwest Sichuan basin. *Acta Palaeontologica Sinica* 2: 222–231 (in Chinese with English Abstract).
- Chen, X.J. 1841. *Local chronicles of Renhuai Zhiliting*, 256. Guiyang: Guizhou Library.
- Chure, D.J., and J.S. McIntosh. 1989. Bibliography of the dinosauria exclusive of the Aves (1677–1986). *Museum of Western Colorado Paleontology Series* 1: 1–226.
- Cignoni, P., M. Callieri, M. Corsini, M. Dellepiane, F. Ganovelli, and G. Ranzuglia. 2008. In *MeshLab: An Open-Source Mesh Processing Tool*, ed. V. Scarano, R. De Chiara, and U. Erra, 129–136. Salerno: Sixth Eurographics Italian Chapter Conference.
- de Lapparent, A.F., and C. Montenat. 1967. Les empreintes de pas de reptiles de l'Infralias de Veillon (Vendée) [Reptile footprints from the lower Lias of Veillon (Vendée)]. *Mémoires de la Société géologique de France nouvelle série* 107: 1–44.
- Demathieu, G. 1990. Problems of discrimination of tridactyl footprints exemplified by the Hettangian trackways, the Causses, France. *Ichnos* 1: 97–110 <https://doi.org/10.1080/10420949009386339>.
- Ekdale, A.A., R.G. Bromley, and D.B. Loope. 2007. Ichnofacies of an ancient erg: A climatically influenced trace fossil association in the Jurassic Navajo Sandstone, southern Utah, USA. In *Trace fossils, concepts, problems, prospects*, ed. W. Miller, 562–574. Amsterdam: Elsevier.
- Farlow, J.O. 1992. Sauropod tracks and trackmakers: Integrating the ichnological and skeletal record. *Zubia* 10: 89–138.
- Farlow, J.O., M. O'Brien, G.J. Kuban, B.F. Dattilo, K.T. Bates, P.L. Falkingham, L. Pinuela, A. Rose, A. Freels, C. Kumagai, C. Libben, J. Smith, and J. Whitcraft. 2012. Dinosaur tracksites of the Paluxy River Valley (Glen Rose Formation, Lower Cretaceous), Dinosaur Valley State Park, Somervell County, Texas. In *Proceedings of the 5th International Symposium about Dinosaur Palaeontology and their Environment*, 41–69.
- Farlow, J.O., J.G. Pittman, and J.M. Hawthorne. 1989. Brontopodus birdi, Lower Cretaceous sauropod footprints from the U.S. Gulf Coastal Plain. In *Dinosaur Tracks and Traces*, ed. D.D. Gillette and M.G. Lockley, 371–394. Cambridge: Cambridge University Press.
- Gao, Y.H. 2007. New dinosaur footprint from Lower Jurassic of Weiyuan, Sichuan. *Vertebrata Palasiatica* 45 (4): 342–345.
- Geng, Q. 2011. Tectonic sequence stratigraphy and lithofacies paleogeography of Cretaceous–Paleogene in Sichuan Basin of China. *Journal of Chengdu University of Technology Science and Technology Edition* 38 (4): 394–401.
- González Riga, B.J. 2011. Speeds and stance of titanosaur sauropods: Analysis of Titanopodus tracks from the Late Cretaceous of Mendoza, Argentina. *Anais da Academia Brasileira de Ciências* 83 (1): 279–290 <https://doi.org/10.1590/S0001-37652011005000002>.
- Gu, X.D., and X.H. Liu. 1997. *Stratigraphy (Lithostratic) of Sichuan Province*, 417. Wuhan: China University of Geosciences Press.
- Hauck, T.E., S.E. Dashtgard, S.G. Pemberton, and M.K. Gingras. 2009. Brackish-water ichnological trends in a microtidal barrier island-embayment system, Kouchibouguac National Park, New Brunswick, Canada. *Palaios* 24: 478–496 <https://doi.org/10.2110/palo.2008.p08-056r>.
- Hitchcock, E.H. 1836. Ornithichnology — Description of the footmarks of birds, (Ornithichnites) on New Red Sandstone in Massachusetts. *American Journal of Science* 29 (ser. 1): 307–340.
- Hitchcock, E.H. 1845. An attempt to name, classify, and describe the animals that made the fossil footmarks of New England. Proceedings of the 6th Annual Meeting of the Association of American Geologists and Naturalists New Haven 6: 23–25.
- Hitchcock, E.H. 1858. *Ichnology of New England. A Report on the Sandstone of the Connecticut Valley, Especially Its Fossil Footmarks*, 220. Boston: William White.
- Hu, B., and X.T. Wu. 1993. Ichnocoenosis of alluvial Jiaguan Formation (Upper Cretaceous), Emei, Sichuan, China. *Acta Palaeontologica Sinica* 32 (4): 478–489 (in Chinese with English Abstract).
- Ishigaki, S., and T. Fujisaki. 1989. Three dimensional representation of *Eubrontes* by the method of Moire topography. In *Dinosaur Tracks and Traces*, ed. D.D. Gillette and G.G. Lockley, 421–425. Cambridge: Cambridge University Press.
- Lagnaoui, A., H. Klein, S. Voigt, A. Hminna, H. Saber, J.W. Schneider, and R. Werneburg. 2012. Late Triassic tetrapod-dominated ichnoassemblages from the Argana Basin (Western High Atlas, Morocco). *Ichnos* 19: 238–253 <https://doi.org/10.1080/10420940.2012.718014>.
- Lallensack, J.N., M. Buchwitz, and A. Romilio. 2020. Photogrammetry in ichnology: 3D model generation, visualisation, and data extraction. *Journal of Paleontological Techniques* <https://doi.org/10.31223/X5J30D>.

- Langston, W. 1974. Non-mammalian Comanchean tetrapods. *Geoscience and Man* 8: 77–102.
- Li, J., Z. Bai, M.G. Lockley, B. Zhou, J. Liu, and Y. Song. 2010. Dinosaur tracks in Wulatezhongqi, Inner Mongolia. *Acta Geologica Sinica* 84: 723–742 (in Chinese with English Abstract).
- Li, J.J., Z.Q. Bai, and Q.Y. Wei. 2011. *On the Dinosaur Tracks from the Lower Cretaceous of Otog Qi, Inner Mongolia*, 109. Beijing: Geological Publishing House.
- Li, J.J., M. Bater, W.-H. Zhang, B.-L. Hu, and L.-H. Gao. 2006. A new type of dinosaur tracks from Lower Cretaceous Otog Qi, Inner Mongolia. *Acta Palaeontologica Sinica* 45 (2): 221–234 (in Chinese with English Abstract).
- Li, R.H., M.G. Lockley, P.J. Makovicky, M. Matsukawa, M.A. Norell, J.D. Harris, and M. Liu. 2007. Behavioral and faunal implications of Early Cretaceous deinonychosaur trackways from China. *Naturwissenschaften* 95 (3): 185–191 <https://doi.org/10.1007/s00114-007-0310-7>.
- Li, R.H., M.G. Lockley, M. Matsukawa, and M. Liu. 2015. Important dinosaur-dominated footprint assemblages from the Lower Cretaceous Tianjialou Formation at the Houzuoshan Dinosaur Park, Junan County, Shandong Province, China. *Cretaceous Research* 52: 83–100 <https://doi.org/10.1016/j.cretres.2014.08.004>.
- Li, Y., S. Jiang, and X. Wang. 2020. The largest species of Asianopodus footprints from Junggar Basin, Xinjiang, China. *Chinese Science Bulletin* 65 (18): 1875–1887.
- Lockley, M.G. 1991. *Tracking Dinosaurs: A New Look at An Ancient World*, 238. Cambridge: Cambridge University Press.
- Lockley, M.G. 1999. *The Eternal Trail: A Tracker Looks at Evolution*, 334. Cambridge MA: Perseus Books.
- Lockley, M.G. 2000. Philosophical perspectives on theropod track morphology: Blending qualities and quantities in the science of ichnology. *Gaia: Revista de Geociencias, Museu Nacional de Historia Natural, Lisbon, Portugal* 15: 279–300.
- Lockley, M.G. 2001. Trackways and dinosaur locomotion. In *Palaeobiology II: A Synthesis*, ed. D.E.G. Briggs and P. Crowther, 412–416. Oxford: Blackwell Science <https://doi.org/10.1002/9780470999295.ch97>.
- 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., B. Breithaupt, N. Matthews, K. Shibata, and R. Hunt-Foster. 2021. A preliminary report on an Early Jurassic Eubrontes-dominated tracksite in the Navajo formation at the Mail Station Dinosaur Tracksite, eastern Utah. *New Mexico Museum of Natural History and Science Bulletin* 82: 195–208.
- Lockley, M.G., G.D. Gierlinski, and S.G. Lucas. 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., and A.P. Hunt. 1995. *Dinosaur Tracks and Other Fossil Footprints of the Western United States*, 360. New York: Columbia University Press <https://doi.org/10.7312/lock90868>.
- Lockley, M.G., J.J. Li, R.H. Li, M. Matsukawa, J.D. Harris, and L.D. Xing. 2013. A review of the tetrapod track record in China, with special reference to type ichnospecies: Implications for ichnotaxonomy and paleobiology. *Acta Geologica Sinica (English Edition)* 87 (1): 1–20 <https://doi.org/10.1111/1755-6724.12026>.
- Lockley, M.G., J.J. Li, L.D. Xing, B. Guo, and M. Matsukawa. 2018. Large theropod and small sauropod trackmakers from the Lower Cretaceous Jingchuan Formation, Inner Mongolia, China. *Cretaceous Research* 92: 150–167 <https://doi.org/10.1016/j.cretres.2018.07.007>.
- Lockley, M.G., C.A. Meyer, and V.F. dos Santos. 1998. Megalosauripus and the problematic concept of megalosaur footprints. *Gaia* 15: 313–337.
- Lockley, M.G., C.A. Meyer, A.P. Hunt, and S.G. Lucas. 1994. The distribution of sauropod tracks and trackmakers. *Gaia* 10: 233–248.
- Lockley, M.G., and A.R.C. Milner. in press. Eubrontes out west. The distribution morphology, ichnotaxonomy and associated ichnofauna of a large, Early Jurassic theropod trackmaker. In *Connecticut Dragons: The Dinosaurs of Dinosaur State Park and Their World*, ed. J.O. Farlow and J.A. Hyatt. Bloomington: Indiana University Press.
- Lockley, M.G., J. Wright, D. White, J.J. Li, L. Feng, and H. Li. 2002. The first sauropod trackways from China. *Cretaceous Research* 23: 363–381 <https://doi.org/10.1006/cres.2002.1005>.
- Lü, J., Y. Azuma, T. Wang, S. Li, and S. Pan. 2006. The first discovery of dinosaur footprint from Lufeng of Yunnan Province, China. *Memoir of the Fukui Prefectural Dinosaur Museum* 5: 35–39.
- Lü, J., X. Zhang, S. Jia, W. Hu, Y. Wu, and Q. Ji. 2007. The discovery of theropod dinosaur footprints from the Middle Jurassic Yima Formation of Yima County, Henan Province. *Acta Geologica Sinica (English Edition)* 81 (6): 439–445.
- Lucas, S.G., H. Klein, M.G. Lockley, J. Spielmann, G.D. Gierlinski, A.P. Hunt, and L.H. Tanner. 2006. Triassic–Jurassic stratigraphic distribution of the theropod footprint ichnogenus Eubrontes. *New Mexico Museum of Natural History and Science Bulletin* 37: 68–93.
- Lull, R.S. 1904. Fossil footprints of the Jura-Trias of North America. *Memoirs of the Boston Society of Natural History* 5: 461–557.
- Lull, R.S. 1953. Triassic life of the Connecticut Valley. *Bulletin of the Connecticut Geology and Natural History Survey* 181: 1–331.
- Marsh, O.C. 1881. Principal characters of American Jurassic dinosaurs. *Part V. American Journal of Science, Series 3* 21: 417–423.
- Marty, D., M. Belvedere, C.A. Meyer, P. Miotto, G. Paratte, C. Lovis, and B. Thüning. 2010. Comparative analysis of Late Jurassic sauropod trackways from the Jura Mountains (NW Switzerland) and the central High Atlas Mountains (Morocco): Implications for sauropod ichnotaxonomy. *Historical Biology* 22 (1–3): 109–133 <https://doi.org/10.1080/08912960903503345>.
- Matsukawa, M., K. Shibata, R. Kukihara, K. Koarai, and M.G. Lockley. 2005. Review of Japanese dinosaur track localities: Implications for ichnotaxonomy, paleogeography and stratigraphic correlation. *Ichnos* 12 (3): 201–222 <https://doi.org/10.1080/10420940591009231>.
- Olsen, P.E. 1980. Fossil great lakes of the Newark Supergroup in New Jersey. In *Field Studies in New Jersey Geology and Guide to Field Trips, 52nd Annual Meeting*, ed. W. Manspeizer, 2–39. Newark: New York State Geological Association, Newark College of Arts and Sciences, Rutgers University.
- Olsen, P.E., J.B. Smith, and N.C. McDonald. 1998. Type material of the type species of the classic theropod footprint genera Eubrontes, Anchisauripus and Gallator (Early Jurassic, Hartford and Deerfield Basins, Connecticut and Massachusetts, USA). *Journal of Vertebrate Paleontology* 18 (3): 586–601 <https://doi.org/10.1080/02724634.1998.10011086>.
- Santos, V.F., J.J. Moratalla, and R. Royo-Torres. 2009. New sauropod trackways from the Middle Jurassic of Portugal. *Acta Palaeontologica Polonica* 54 (3): 409–422 <https://doi.org/10.4202/app.2008.0049>.
- Shuler, E.W. 1935. Dinosaur tracks mounted in the bandstand at Glen Rose, Texas. *Field and Laboratory* 9: 9–13.
- Sichuan Provincial Bureau of Geology Aviation Regional Geological Survey Team. 1976. *Geological Map of the People's Republic of China, Xuyong Map Sheet. Sheet(H-48-XXXIV)*, 200000.
- Steering Group of Placenames in Gulin County Sichuan Province. 1983. *The Gazetteer of Gulin County Sichuan Province*, 490. Luzhou: Luzhou Printing Factory.
- Thulborn, T. 1990. *Dinosaur Tracks*, 410. London: Chapman and Hall <https://doi.org/10.1007/978-94-009-0409-5>.
- Wilson, J.A., and M.T. Carrano. 1999. Titanosaurs and the origin of “wide-gauge” trackways: A biomechanical and systematic perspective on auropod locomotion. *Paleobiology* 25: 252–267 <https://doi.org/10.1017/S0094837300026543>.
- Xing, L.D., H. Dai, M.G. Lockley, A. Romilio, H. Klein, Z.D. Li, X.F. Hu, G.Z. Peng, Y. Ye, and W.S. Persons IV. 2018b. Two new dinosaur tracksites from the Lower Cretaceous Jiaguan Formation of Sichuan Basin, China: Specific preservation and ichnotaxonomy. *Historical Biology* 30 (7): 976–984 <https://doi.org/10.1080/08912963.2017.1326113>.
- Xing, L.D., H. Dai, G.B. Wei, M.G. Lockley, H. Klein, W.S. Persons IV, M.Y. Wang, S.X. Jing, and H.Q. Hu. 2020. The Early Jurassic Kayentapus dominated tracks from Chongqing, China. *Historical Biology*. <https://doi.org/10.1080/08912963.2020.1769093>.
- Xing, L.D., J.D. Harris, X.Y. Feng, and Z.J. Zhang. 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., J.D. Harris, D.H. Sun, and H.Q. Zhao. 2009c. The earliest known deinonychosaur tracks from the Jurassic–Cretaceous boundary in Hebei, China. *Acta Palaeontologica Sinica* 48 (4): 662–671 (in Chinese with English Abstract).
- Xing, L.D., J.D. Harris, S. Toru, F. Masato, and Z.M. Dong. 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., H. Klein, M.G. Lockley, W. Chen, Y. Ye, M. Matsukawa, and J.P. Zhang. 2013a. Earliest records of theropod and mammal-like tetrapod footprints in the Upper Triassic of Sichuan Basin, China. *Vertebrata Palasiatica* 51: 184–198.
- Xing, L.D., H. Klein, M.G. Lockley, A. Wetzel, Z.D. Li, J.J. Li, G.D. Gierliński, J.P. Zhang, M. Matsukawa, J.D. Divay, and L. Zhou. 2014b. Changpeipus (theropod) tracks from the Middle Jurassic of the Turpan Basin, Xinjiang, Northwest China: Review, new discoveries, ichnotaxonomy, preservation and palaeoecology. *Vertebrata Palasiatica* 52 (2): 233–259.
- Xing, L.D., H. Klein, Z.H. Qin, W.S. Persons IV, and X. Xu. 2018e. Lower Cretaceous theropod tracks with the new ichnogenus and combination *Lockleypus luanpingensis* from the Dabeigou Formation of the Luanping Basin, Hebei Province, China. *Palaeoworld* 27: 482–489 <https://doi.org/10.1016/j.palwor.2018.09.004>.
- Xing, L.D., and M.G. Lockley. 2016. Early Cretaceous dinosaur and other tetrapod tracks of southwestern China. *Science Bulletin* 61 (13): 1044–1051 <https://doi.org/10.1007/s11434-016-1093-z>.
- Xing, L.D., M.G. Lockley, W. Chen, G.D. Gierliński, J.J. Li, W.S. Persons IV, M. Matsukawa, Y. Ye, M.K. Gingras, and C.W. Wang. 2013b. 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., M.G. Lockley, H. Klein, K. Niu, L. Zhang, C. Jia, L. Qi, C. Chou, A. Romilio, D. Wang, Y. Zhang, W.S. Persons IV, and M. Wang. in press. *Cretaceous bird-dominated, theropod, thyreophora, pterosaur and turtle track assemblages from the Tugulu Group*. Xinjiang: Ichnotaxonomy and palaeoecology. Peer J.
- Xing, L.D., M.G. Lockley, H. Klein, R. Zeng, S.F. Cai, X.C. Luo, and C. Li. 2018a. Theropod assemblages and a new ichnotaxon *Gigandipus chiappei* ichnosp. nov. from the Jiaguan Formation, Lower Cretaceous of Guizhou Province, China. *Geoscience Frontiers* 9: 1745–1754 <https://doi.org/10.1016/j.gsf.2017.12.012>.
- Xing, L.D., M.G. Lockley, D. Marty, J.P. Zhang, Y. Wang, H. Klein, R.T. McCrea, L.G. Buckley, M. Belvedere, O. Mateus, G.D. Gierliński, L. Piñuela, W.S. Persons IV, F.P. Wang, H. Ran, H. Dai, and X.M. Xie. 2015a. An ornithopod-dominated tracksite from the Lower Cretaceous Jiaguan Formation (Barremian–Albian) of Qijiang, South-Central China: New discoveries, ichnotaxonomy, preservation and palaeoecology. *PLOS ONE* 10 (10): e0141059 <https://doi.org/10.1371/journal.pone.0141059>.
- Xing, L.D., M.G. Lockley, T. Miyashita, H. Klein, T. Wang, W.S. Persons IV, S.G. Pan, J.P. Zhang, and Z.M. Dong. 2014d. Large sauropod and theropod tracks from the Middle Jurassic Chuanjie Formation of Lufeng County, Yunnan Province and palaeobiogeography of the Middle Jurassic sauropod tracks from southwestern China. *Palaeoworld* 23: 294–303 <https://doi.org/10.1016/j.palwor.2014.04.003>.
- Xing, L.D., M.G. Lockley, G.Z. Peng, Y. Ye, J.P. Zhang, M. Matsukawa, H. Klein, R.T. McCrea, and W.S. Persons IV. 2016b. *Eubrontes* and *Anomoepus* track assemblages from the Middle Jurassic Xiashaximiao Formation of Zizhong County, Sichuan, China: Review, ichnotaxonomy and notes on preserved tail traces. *New Mexico Museum of Natural History and Science Bulletin* 74: 345–352.
- Xing, L.D., M.G. Lockley, A. Romilio, H. Klein, J.Q. Zhang, H.Y. Chen, J.J. Zhang, M.E. Burns, and X.L. Wang. 2018c. Diverse sauropod-theropod-dominated track assemblage from the Lower Cretaceous Dasheng Group of Eastern China: Testing the use of drones in footprint documentation. *Cretaceous Research* 84: 588–599 <https://doi.org/10.1016/j.cretres.2017.12.012>.
- Xing, L.D., M.G. Lockley, Y.Z. Tang, A. Romilio, T. Xu, X.W. Li, Y. Tang, and Y.Z. Li. 2018d. Tetrapod track assemblages from Lower Cretaceous desert facies in the Ordos Basin, Shaanxi Province, China, and their implications for Mesozoic paleoecology. *Palaeogeography, Palaeoclimatology, Palaeoecology* 507: 1–14 <https://doi.org/10.1016/j.palaeo.2018.05.016>.
- Xing, L.D., M.G. Lockley, G. Yang, J. Cao, R.T. McCrea, H. Klein, J.P. Zhang, W.S. Persons IV, and H. Dai. 2016c. A diversified vertebrate ichnite fauna from the Feitianshan Formation (Lower Cretaceous) of southwestern Sichuan, China. *Cretaceous Research* 57: 79–89 <https://doi.org/10.1016/j.cretres.2015.08.005>.
- Xing, L.D., M.G. Lockley, and J.P. Zhang. 2016a. *Early Cretaceous dinosaur and other tetrapod tracks of southwestern China*, 410. Ningbo: Ningbo Publishing House ISBN 978-7-5526-2768-8 (in Chinese with English Abstract).
- Xing, L.D., M.G. Lockley, J.P. Zhang, H. Klein, D. Marty, G.Z. Peng, Y. Ye, R.T. McCrea, W.S. Persons IV, and T. Xu. 2015b. The longest theropod trackway from East Asia, and a diverse sauropod-, theropod-, and ornithopod-track assemblage from the Lower Cretaceous Jiaguan Formation, southwest China. *Cretaceous Research* 56: 345–362 <https://doi.org/10.1016/j.cretres.2015.05.008>.
- Xing, L.D., M.G. Lockley, J.P. Zhang, H. Klein, W.S. Persons IV, and H. Dai. 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. *Palaeogeography, Palaeoclimatology, Palaeoecology* 414: 79–97 <https://doi.org/10.1016/j.palaeo.2014.08.011>.
- Xing, L.D., M.G. Lockley, L.J. Zhang, A. Romilio, N. Namier, M.Y. Wang, and W. S. Persons IV. 2021. Tetrapod track assemblages from midwestern Inner Mongolia, China: Review and new observations. *New Mexico Museum of Natural History and Science Bulletin* 82: 525–541.
- Xing, L.D., A. Mayor, Y. Chen, J.D. Harris, and M.E. Burns. 2011. The Folklore of dinosaur trackways in China: Impact on Paleontology. *Ichnos* 18 (4): 213–220 <https://doi.org/10.1080/10420940.2011.634038>.
- Xing, L.D., G. Niedźwiedzki, M.G. Lockley, J.P. Zhang, X.F. Cai, W.S. Persons IV, and Y. Ye. 2014e. Asianopodus type footprints from the Hekou Group of Honggu District, Lanzhou City, Gansu, China and the "heel" of large theropod tracks. *Palaeoworld* 23: 304–313 <https://doi.org/10.1016/j.palwor.2014.08.003>.
- Xing, L.D., G.Z. Peng, Y. Ye, M.G. Lockley, R.T. McCrea, P.J. Currie, J.P. Zhang, and M.B. Burns. 2014c. Large theropod trackway from the Lower Jurassic Zhenzhuchong Formation of Weiyuan County, Sichuan Province, China: Review, new observations and special preservation. *Palaeoworld* 23: 285–293 <https://doi.org/10.1016/j.palwor.2014.10.010>.
- Xing, L.D., F.P. Wang, S.G. Pan, and W. Chen. 2007. The discovery of dinosaur footprints from the Middle Cretaceous Jiaguan Formation of Qijiang County, Chongqing City. *Acta Geologica Sinica* 81 (11): 1591–1602 (in Chinese with English Abstract).
- Yang, X., and D. Yang. 1987. *Dinosaur Footprints from Mesozoic of Sichuan Basin*, 30. Chengdu: Science and Technology Publications (in Chinese).
- Young, C.C. 1960. Fossil footprints in China. *Vertebrata Palasiatica* 4 (2): 53–67.
- Young, C.C. 1979. Footprints from Jinghong, Yunnan. *Vertebrata Palasiatica* 1 (2): 116–117.
- Zhen, S., J. Li, and C. Rao. 1986. Dinosaur footprints of Jinning, Yunnan. *Memoirs of the Beijing Natural History Museum* 33: 1–19.
- Zhen, S.N., J.J. Li, W. Chen, and S. Zhu. 1994. Dinosaur and bird footprints from the Lower Cretaceous of Emi County, Sichuan. *Memoirs of the Beijing Natural History Museum* 54: 105–120.
- Zouheir, T., A. Hminna, H. Klein, A. Lagnaoui, H. Saber, and J.W. Schneider. 2018. Unusual archosaur trackway and associated tetrapod ichnofauna from Irohalene Member (Timezgadiouine Formation, Late Triassic, Carnian) of the Argana Basin, Western High Atlas, Morocco. *Historical Biology*. <https://doi.org/10.1080/08912963.2018.1513506>.

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.