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Lida Xing & Martin G. Lockley

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Early Cretaceous dinosaur and other tetrapod tracks of southwestern China

Lida Xing · Martin G. Lockley

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Abstract In recent years the Lower Cretaceous red beds of southwestern China have yielded more than 20 significant dinosaur-dominated tracksites. More than half occur in the Jiaguan Formation with the remainder in the Feitianshan and Xiaoba formations. Collectively these sites provide evidence of at least 13 distinct dinosaurian trackmaker morphotypes, in addition to two avian theropod (bird) morphotypes and pterosaur and turtle tracks. Together these total 17 morphotypes provide a data base of 479 potential trackmakers, probably representing the same number of individuals. Such an ichnological database provides a useful proxy paleoecological census of tetrapod communities in the area during the Early Cretaceous, and is especially significant given the complete absence or scarcity of skeletal remains reported from these formations. The composition of ichnofaunas in all three formations is heavily saurischian (theropod and sauropod) dominated with a high diversity of distinctive theropod morphotypes, mostly assignable to known ichnogenera. Moreover, ichnofaunal data from multiple sites are generally consistent between sites and an indication of the reliability and repeatability of track census data. Such regionally-

L. Xing (🖂)

State Key Laboratory of Biogeology and Environmental Geology, China University of Geosciences, Beijing 100083, China e-mail: xinglida@gmail.com

L. Xing

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

M. G. Lockley (⊠) Dinosaur Trackers Research Group, University of Colorado Denver, PO Box 173364, Denver, CO 80217, USA e-mail: martin.Lockley@ucdenver.edu widespread data are rapidly superseding the information available from the skeletal record in the corresponding area, and must therefore be considered of high paleontological value.

Keywords Early Cretaceous · Dinosaur tracks · Southwestern China · Paleoecology

1 Introduction

A recent blitzkrieg in tracksite discoveries has brought on an ichnological renaissance in Chinese Mesozoic paleontology. Over 200 Mesozoic tetrapod tracksites were known in 2015 [1–3], compared with only 27 such sites in 1989 [4]. Most of the new sites were discovered and described by Sino-Japanese-American expeditions, between 1999 and 2006, and by Sino-American collaborative studies undertaken since 2012. The latter are characterized by strong international cooperation and multidisciplinary partnerships.

A great many of the newly discovered Chinese tracksites are Early Cretaceous in age, and have provided new insights into the fauna from this time. During the Early Cretaceous, the Earth experienced strong geologic and climactic changes, including the further separation and fragmentation of the continents, intense sea-floor spreading, abundant global volcanic activity [5], and a peak in the greenhouse climate [6]. Such environmental forces, fostered geographic isolation and drove organisms to evolve novel adaptations to the changing conditions, making the Early Cretaceous a key epoch in the study of Mesozoic biogeographic diversity [7].

Among China's Lower Cretaceous tracksites, those from Sichuan (with Chongqing, Northern Yunnan and Guizhou), Inner Mongolia, Gansu, and Shandong are among the richest, and record the greatest diversity. In particular, the track record of Gansu and Shandong, in the Sichuan-Yunnan Basin, have been critical in understanding the local palaeoecology, because equivalent-aged skeletal fossils have long been sparse or absent in the region [8].

2 Geological setting

In the Early Jurassic after coalification in terrestrial facies during Late Triassic, the studied areas experienced fluvio lacustrine deposition under drier climatic conditions. Ultrathick red clastic deposits constituted the framework of Sichuan Basin deposition and were widely distributed in Panxi (Panzhihua-Xichuang) area [8,9]. Deposition in the study area lasted from the Late Triassic to the end of the Oligocene [9].

The Cretaceous strata of Sichuan Province are concentrated in the Sichuan Basin, where they can be divided into three areas: the northern area (Tongxi-Bazhong region), the western area (Chengdu-Ya'an region), and the southwestern area (Yibin-Xishui region) (Fig. 1) [8]. The Sichuan Basin was under the influence of a tectonic belt in the north-northwest and a fault-fold belt in the southeast from the Cretaceous to the Paleogene. Deposition was volumetrically quite limited during the Early Cretaceous in the northern part of the basin while it was more rapid and continuous in the western and southwest parts from the Early Cretaceous to the Paleogene [9].

Most of the Cretaceous tracks have been discovered in the Jiaguan Formation, in the west and southwestern areas of the Sichuan Basin. Based on sporopollen assemblages, Chen [10] suggested that the Jiaguan Formation was formed in Barremian–Albian times, as fluvial facies under a tropical, or subtropical, semiarid and semi-humid climates.

The Southwest part of Sichuan Province is named Panxi. Compared with the Sichuan Basin, the area indicates relatively poor sedimentary continuity and displays the sedimentary characteristics of intermountain basin [9]. Panxi's largest basin is the Mishi-Jiangzhou Basin. Lower Cretaceous tracks there are mainly preserved in the Feitianshan Formation and the Xiaoba Formation. Tamai et al. [11] proposed that the Feitianshan Formation is Berriasian– Barremian age, based on paleomagnetism evidence. Lithological correlation shows that the Jiaguan Formation, in the Sichuan Basin, is comparable to the lower part of the Xiaoba Formation [12].

3 Dinosaur fauna

Twelve tracksites have been found in the Jiaguan Formation since 1971, and six and five, respectively, have been found in the Feitianshan Formation and Xiaoba Formation since 1991 (Table 1). The few dinosaur skeletal fragments found in the Jiaguan Formation, lack any description and discussion [8], and none is known from the Feitianshan Formation or Xiaoba Formation. All these tracksites, except Guanyuanchong [13] and Chuanzhu sites [14, 15], were found and described by the authors and colleagues since 2007 (Fig. 1) [16–33].

The Feitianshan Formation (Berriasian–Barremian) is older than the Jiaguan Formation (Barremian–Albian) [26]. Therefore, the known Cretaceous dinosaur records in the Mishi-Jiangzhou Basin begin in the Early Cretaceous and represent a greater span of time than presently known from the Sichuan Basin. Generally, the track record demonstrates a strong similarity between the dinosaur faunal assemblages from the Sichuan Basin and the Mishi-Jiangzhou Basin. Both include ornithopod, sauropod, nonavian theropod, and pterosaur tracks, while the Jiaguan Formation also yields thyreophora and bird tracks and the Feitianshan Formation yields possible turtle tracks (Table 1). The record from the Xiaoba Formation is far less diverse, and consists only of theropod and sauropod tracks. None of the formations has yielded crocodylian tracks.

Both the Sichuan and Mishi-Jiangzhou basins show a highly diversity of theropod tracks, including large, medium and small-sized tridactyl specimens, most of which are referred to *Grallator*-type and *Eubrontes*-type (Table 2). Both also yield significant didactyl tracks representing the Deinonychosauria: cf. *Dromaeopodus* from the Jiaguan and Feitianshan formations and *Velociraptorichnus* from the Jiaguan and Xiaoba formations. This indicates the success of deinonychosaurian trackmakers during the Early Cretaceous in the paleoenvironments represented by these deposits. In addition, the Jiaguan Formation has yielded unique specimens, including the world smallest theropod track *Minisauripus* and the bird tracks *Koreanaornis* and *Wupus*. The Feitianshan Formation also contains *Siamopodus*.

Brontopodus type tracks from the Feitianshan Formation are the first clearly described record of sauropod tracks in the Cretaceous strata of Sichuan Province. They are known from both the Jiaguan Formation and Xiaoba Formation. All sauropod tracks are referred to Brontopodus type, but the sauropods from the Jiaguan Formation appear to be more primitive than those in the Feitianshan Formation, as indicated by the consistentlynarrower trackway gauges seen in the Jiaguan Formation. Regarding the ornithischian track record, Caririchnium and Ornithopodichnus are represented by large and small ornithopod tracks in the Sichuan and Mishi-Jiangzhou basins. In many instances, the ornithopod trackways are parallel, suggesting gregarious behavior. The thyreophoran track Tetrapodosaurus has also been reported from the Sichuan Basin, but this is a rare occurrence based on limited material, and probably atypical. Pterosaur tracks, and probably atypical. Pterosaur





Fig. 1 Cretaceous sections and dinosaur footprint and bone distribution of Sichuan Basin (after [23]). Tracksites from Mishi-Jiangzhou Basin: 1, Sanbiluoga (I, II, IIN); 2, Jiefang; 3, Yangmozu; 4, Bajiu; 5, Mujiaowu; 6, Jierboshi; 7, Jierboshi II; 8, Zugu; 9, Yizi. Tracksites from Sichuan Basin: 1, Guanyuanchong; 2, Emei (Chuanzhu); 3, Lotus; 4, Baoyuan; 5, Hanxi; 6, Xinyang; 7, Longjing; 8, Tiger; 9, Shimiaogou; 10, Xinyang II; 11, Leibei; 12, Shihuawan. Bone sites (Green): 1, Sanxing site; 2, Renshou site; 3, Naxi site

tracks, belonging to *Pteraichnus*, have been found in both basins, and there is an isolated possible turtle track from the Feitianshan Formation. The Jiaguan Formation ichnofaunas are more diverse at the ichnogenus level than those from the Feitianshan and Xiaoba formations.

These occurrences point to a paleoecological pattern: i.e., the Jiaguan Formation ichnofauna yields *Dromaeopodus*, *Velociraptorichnus*, *Minisauripus* tracks (and bird tracks *Koreanaornis*) with distinct East Asian characteristics [34, 35] and is very similar in composition to the Tianjialou Formation ichnofauna described by Li et al. [36] from Shandong (Northeast China) and considered Barremian–Albian in age [37]. In this regard we have noted that, medium-sized deinonychosaur tracks and *Minisauripus* occur in the Haman Formation (Aptian–Albian, [38]) in South Korea [39], indicating a similar theropod-dominated ichnofauna to that found in the Sichuan Basin. Thus there appears to be a *Dromaeopodus-Velociraptorichnus-Minisauripus* assemblage dated as Barremian–Albian, which occurs in Shandong, in the Yishu fault zone [37, 40] and the Junan area [36] and also in South Korea in middle to late Early Cretaceous [34–39].

4 Dominant ichnotaxa

Sauropod tracks are usually preserved in coastal sediments and lakeshore sediments in tropical or subtropical, carbonate-generating areas at low latitudes or in river and lake sediments in more semi-arid, inland basin areas [41].

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Table 1	Composition of	f dinosaur-dominated	ichnofaunas i	n the	Jiaguan,	Feitianshan	and	Xiaoba	formations	of south	western	China
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Fm	Sites	Tm	The	Bi	Sa	Thy	Or	Pt	Tur
Jiaguan	Guanyuanchong [13]	3	100 %	_	_	_	_	_	_
	Emei [14–16]	24	87 %	5 %	_	8 %	_	_	_
	Lotus [17–19]	165	<1 %	18 %	10 %	_	68 %	3 %	_
	Tiger [20]	2	-	-	100 %	-	-	-	_
	Baoyuan [21]	9	100 %	-	-	-	-	-	-
	Xinyang [22]	5	80 %	-	20 %	-	-	-	-
	Xinyang II [16]	3	100 %	-	-	-	-	-	-
	Longjing [23]	4	-	-	75 %	-	25 %	-	-
	Hanxi [24]	20	35 %	-	40 %	-	25 %	-	_
	Shimiaogou [25]	38	32 %	-	26 %	-	37 %	5 %	-
	Leibei [16]	27	100 %	-	-	-	-	-	-
	Shihuawan [16]	1	-	-	100 %	-	-	-	-
	ALL SITES	301	-	-	-	-	-	-	-
Feitianshan	Sanbiluoga (I, II, IIN)* [26–28]	76	25 %	-	24 %	-	42 %	9 %	-
	Jiefang [29]	1	-	-	100 %	-	-	-	-
	Yangmozu [30]	22	100 %	-	-	-	-	-	-
	Bajiu [31]	24	63 %	-	33 %	-	-	-	4 %
	ALL SITES	123	-	-	-	-	-	-	-
Xiaoba	Mujiaowu[32]	10	90 %	-	10 %	-	-	-	-
	Jierboshi [33]	32	97 %	-	3 %	-	-	-	-
	Jierboshi II [33]	3	100 %	-	-	-	-	-	-
	Zugu [33]	4	-	-	100 %	-	-	-	-
	Yizi [33]	6	-	-	100 %	-	-	-	-
	ALL SITES	55	-	-	-	-	-	-	-

Note total estimate of trackmakers for each formation in bold

Fm formation, Tm estimated number of trackmakers, The non-avian theropod, Bi bird, Sa sauropod, Thy thyreophora, Or ornithopod, Pt pterosaur, Tur turtle

* Note that the data from Sanbiluoga sites I, II and IIN are poled together

Ornithopod tracks are generally preserved in humid environments with coal beds often in coastal plain paleoenvironments [41–43]. A typical example of these faunal/ environment correlations, is inferred in the Jurassic red beds of the Sichuan Basin where sauropods evidently thrived and ornithopods were comparatively scarce [44]. But this changed dramatically during the Early Cretaceous.

By assuming that each trackway segment and each additional isolated track most likely reflects one trackmaker, we can estimate the relative abundance of trackmakers and the proportions of different dinosaur groups in each tracksite. The Lotus and Shimiaogou sites from the Jiaguan Formation are dominated by ornithopods, which account for 69 % and 37 %, respectively. The Zhaojue Sanbiluoga site from the Mishi-Jiangzhou Basin is also dominated by ornithopod tracks (42 %). However, such ornithopod dominated Early Cretaceous tracksites are quite rare in China. Other important dinosaur-dominated track assemblages mainly consist of saurischian tracks, such as the Houzuoshan tracksite in the Tianjialou Formation, which primarily yields theropods (about 90 %). Saurischians account for 70 % (sauropod 38 % and theropods 32 %) at the Yanguoxia tracksite, Gansu Province. The Lower Cretaceous Jingchuan Formation strata from the Chabu tracksites region in Inner Mongolia lack identifiable ornithopod tracks and mainly yields sauropod-non avian theropod track assemblages with a significant number of avian theropod (bird) tracks [45].

The Jehol Biota is the most important and diverse Early Cretaceous dinosaur fauna known with birds accounting for 64.6 % and non-avian theropods accounting for 19.3 % [46]. However, as noted below in southwestern China, the track record exceeds the skeletal record significantly, making footprints of far greater importance for paleoecological census than previously supposed.

The faunal assessments in the abovementioned assemblages have almost certainly been influenced, to variable extents, by preservational and sampling biases related to distinctive facies assemblages and research preferences.



Trackmaker	Jiaguan Fm.	Feitianshan Fm.	Xiaoba Fm.	
Non-avian theropod	Grallator	Grallator-type	Grallator-type	
	Eubrontes	Eubrontes-type	Eubrontes-type	
	Minisauripus	Minisauripus	-	
	(cf. Irenesauripus)	_	-	
	Velociraptorichnus	_	Velociraptorichnus	
	cf. Dromaeopodus	cf. Dromaeopodus		
	Coelurosaurs tracks	_	-	
	_	Siamopodus	-	
Bird	Koreanornis	_	-	
	Wupus			
Sauropod	Brontopodus	Brontopodus	Brontopodus	
Thyreophora	(Tetrapodosaurus)	_	-	
Ornithopod	Caririchnium	Caririchnium	-	
	cf. Ornithopodichnus	_	-	
	_	Ornithopodichnus	-	
Pterosaur	Pteraichnus	Pteraichnus	-	
Turtle	-	cf. Emydipus	-	

Table 2 Comparison of dinosaur ichnofaunas from the Jiaguan, Feitianshan and Xiaoba formations (ichnogenera (in brackets) are rare or tentatively identified)

Nevertheless, it seems clear that the ornithopods that dominated some track assemblages in the Sichuan Basin and the Mishi-Jiangzhou Basin are atypical of Lower Cretaceous river–lake ichnofacies at low latitudes (Jiaguan deposition was located at 25.5° ancient north latitude, [47]). Nevertheless, the ichnofaunal distribution evidence demonstrates that the abundance of ornithopods was sometimes comparable to sauropod abundance in such environments.

Lockley et al. [35] suggested that the composition of China's Early Cretaceous ichnofaunas implies a distinctive regional signature: in short the aforementioned *Dromaeopodus-Velociraptorichnus-Minisauripus* assemblage is typical of East Asia but not of other regions. Track assemblages in the Sichuan-Yunnan Basin, such as the relatively rich deinonychosaur record, suggest that its Early Cretaceous dinosaurs may be more closely related to the Jehol Biota radiation than previously thought. If this is the case there are implications indicating that local geographical isolation, thought to have been brought on by the formation of mountains (Qinling–Dabie Mountains, [48]), was not as significant previously suspected.

In the early Lower Cretaceous (Neocomian) of the area the track assemblages are most often saurischian-dominated, mostly yielding avian and non-avian theropod and sauropod tracks with a significant number of pterosaur track occurrences. Relatively few ornithischian tracks occur until the post Neocomian (late Early Cretaceous). This pattern is confirmed by the abundance of ornithischian track assemblages in the post-Neocomian of northeastern China and Korea. A total of 128 papers have been published on Korean tracks since the 1980s: [49]. It has also recently been shown that there is no confirmed evidence of tracks of large aquatic crocodylians in the Cretaceous of China or Korea, [50] although small 'terrestrial' crocodilian tracks have very recently been reported from Korea [51]. This appears to reflect a regional lack of suitable habitat for large crocodylians. However, turtle tracks are known to occur at a small number of widely distributed sites.

5 Discussion

As shown in Table 2 the Jiaguan, Feitianshan and Xiaoba formations have yielded a total of about 17 named tetrapod ichnotaxa from 23 different sites with a widespread geographic distribution. Note, by comparison, that only three skeletal sites are known. These tracksites yield footprints that indicate the presence of diverse dinosaurian groups, avian theropods, turtles and pterosaurs. This indicates that despite the paucity of tetrapod skeletal remains, which are entirely lacking in the two latter formations, the ichnofaunas indicate a moderately high diversity of trackmakers, including about 13 attributed to non-avian dinosaurs. Likewise trackway numbers are significant. To date, an estimated 479 individuals are represented, based on discrete trackways each considered to represent a separate individual or trackmaker, as shown in Table 1. 301 of the all the 479 recorded trackways have been reported from the

Jiaguan Formnation with 123 and 55 respectively from the Feitianshan and Xiaoba formations.

Such abundant ichnological data from red bed sequences that are almost completely lacking in skeletal have great paleoecological significance. Following the classification of deposits (formations) on the basis of the relative abundance of tracks and bones, where type 1 deposits have only tracks, type 2 are track-dominated, type 3 tracks = bones, type 4 are bone dominated and type 5 have bones only [41, 52], the southwestern China ichnofaunas are all type 1 or 2. Not only does such data highlight the importance of tracks in the many deposits and regions where skeletal remains are sparse or absent, i.e., in the common situation where type 1 and type 2 deposits dominate the regional geology, such data also help to demonstrate whether individual ichnofaunas have consistent compositions from site to site in a given region. The data presented here shows that in the vast majority of cases the ichnofaunas from these three formations are saurischian (non-avain theropod and sauropod) dominated. Given that tracks are in situ evidence of the paleoenvironments frequented by trackmakers, we therefore regard the track record as a whole as a proxy paleoecological census representative of once living tetrapod faunas of the region. Moreover, sampling in the same formations produces repeatable results.

6 Conclusions

The faunal composition of the red bed deposits represented by the Jiaguan, Feitianshan and Xiaoba formations is evaluated on the basis of ichnofaunas reported from 23 sites. 12 sites from the Jiaguan were sampled yielding and estimated 301 trackways. Six and five sites respectively were sampled from the Feitianshan and Xiaoba formations with 123 and 55 trackways respectively recorded.

The Xiaoba Formation yields only theropods (from 3 sites), and sauropods (from 4 sites). Similarly three of the four Feitianshan Formation sites yield theropod and sauropod tracks with one site also yielding ornithopod, pterosaur tracks or turtle tracks (Table 1). Theropod tracks occur at 9 of 12 known Jiaguan sites (75 % of occurrences) making this track type the most-widely distributed. Sauropods tracks occur at 7 of 12 Jiaguan sites (\sim 58 %). Ornithopod tracks occur at 4 of the 12 sites (\sim 33 %), and dominate at only two of these. Bird and pterosaur track each occur at only 2 sites (\sim 17 %).

Thus the ichnofaunas from all three formations are saurischian (theropod and/or sauropod) dominated. In this regard it should be noted that the broad category of "theropod tracks" includes at least 6-8 distinct categories, including small and large tridactyl tracks in the *Grallator-Eubrontes* group, two didactyl morphotypes (*Velociraptorichnus* and *Dromaeopodus*), and the distinctive morphotype *Minisauripus*. Thus, not only are theropod tracks dominant in these ichnofaunas, they also represent significant diversity within the theropod clade.

We infer that the paleoecological census information derived from these type 1 and type 2 red bed deposits far exceeds anything currently available from the skeletal record. This pattern of "track only" and "track dominated" assemblages appears to be typical of Lower Cretaceous red bed deposition in southwestern China, and may prove that the utility of tracks far supersedes the skeletal record in providing paleoecological information on regional tetrapod abundance, diversity and distribution, that is often consistent and repeatable from site to site.

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Conflict of interest The authors declare that they have no conflict of interest.

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