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Lower Cretaceous sauropod trackways from Lishui City and an overview of dinosaur dominated track assemblages from Zhejiang Province, China

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Abstract

A relatively small number of tetrapod tracksites from Zhejiang Province fills out the fossil record from that region, which is also known to have yielded both saurischian (titanosauriform, coelurosaur) and ornithischian (basal ornithopod, ankylosaurian) body fossils as well as dinosaurian eggs. We use photogrammetry and 3D imaging to reinterpret the sauropod tracks from Lishui City, which revealed the existence of trackways. The track record from three documented sites in Zhejiang Province includes avian and non-avian theropod, sauropod, ornithopod and pterosaur tracks. Previous work showed that the purported new bird ichnospecies *Dongyangornipes sinensis* is a synonym of *Uhangrichnus chuni*, while we here consider *Pteraichnus dongyangensis* as a *nomen dubium*. Such "provincial ichnotaxonomy" may mask similarities in the ichnofauna across large regions. In fact, we show that the ichnofauna is similar to that found in the Early Cretaceous elsewhere in China.

Keywords: Sauropod tracks, Theropod tracks, Bird tracks, Pterosaur tracks, Lishui Basin, Zhejiang Province

1 Introduction

In recent years, Zhejiang Province has become an important focus of study for China's Mesozoic vertebrates, especially the province's rich and diverse dinosaur egg fossils (Jin et al., 2012). Dinosaur skeletal fossils have also been found in several basins of Zhejiang Province, the material being attributed to titanosauriforms (Lü et al., 2008), ornithischians (Zheng et al., 2012), and ankylosaurians (Zheng et al., 2018). The first dinosaur tracks from Zhejiang were described by Matsukawa et al. (2009) from the Xiaqiao site in the south, which included sauropod tracks from the Lower Cretaceous Shouchang Formation. The Upper Cretaceous Jinhua Formation produced a rich track assemblage, including footprints of non-avian theropods, pterosaurs and birds (Lü et al. 2010; Azuma et al. 2013).

In May 2017, the first author of this study investigated the Xiaqiao site and used digital ortho-photography to reveal important new details of footprint morphology of sauropod trackways.

2 Geological setting

2.1 Cretaceous strata in Zhejiang Province

In Zhejiang Province, there are more than 30 basins with exposures of the Cretaceous terrestrial red beds. These basins are mainly distributed in the central and eastern areas and range from several to over 500 km^2 (Fig. 1). Their basements are formed by widely distributed volcanic rock series. Generally, the basins are dominated by fluvial–lacustrine detrital deposits, with a small quantity of pyroclastic components. However, the geologic classification of these strata has proven challenging. Different opinions exist, not only regarding the stratigraphic ages of different series, but also the categorization of the individual stratigraphic units (Jin et al., 2012; Fig. 2).

Zhejiang Bureau of Geology and Mineral Resources (1996) established the Upper Jurassic–Lower Cretaceous Jiande Group (Luocun, Huangjian, Shouchang and Hengshan Formations) and the Upper Cretaceous Qujiang

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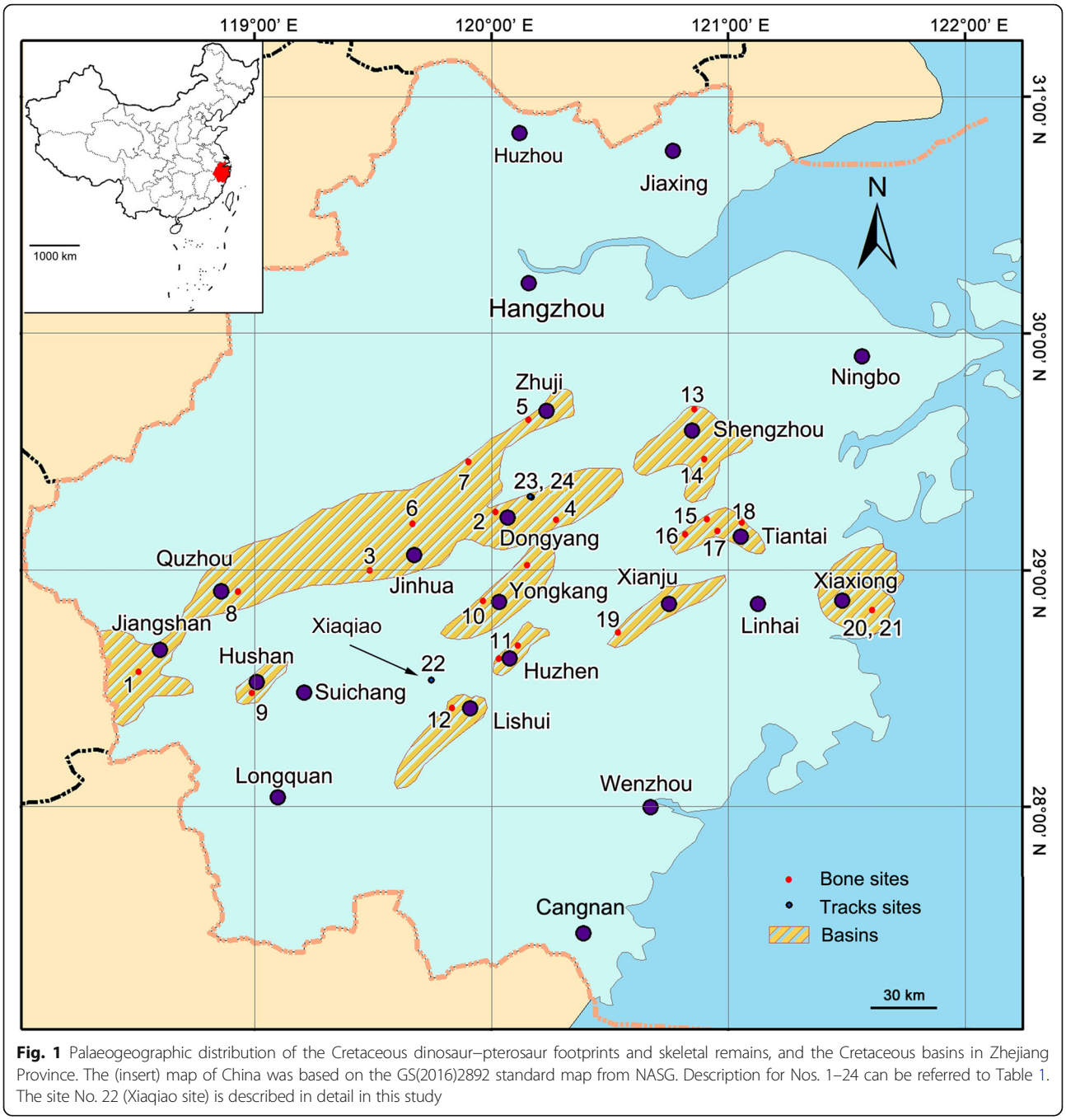

Fig. 1 Palaeogeographic distribution of the Cretaceous dinosaur–pterosaur footprints and skeletal remains, and the Cretaceous basins in Zhejiang Province. The (insert) map of China was based on the GS(2016)2892 standard map from NASG. Description for Nos. 1–24 can be referred to Table 1. The site No. 22 (Xiaqiao site) is described in detail in this study

Group (Zhongdai, Jinhua and Quxian Formations) and Tongxiang Formation, in the Yangtze stratigraphic area; and, the Upper Jurassic–Lower Cretaceous Moshishan Group (Dashuang, Gaowu, Xishantou, Chawan, Jiuliping and Zhucun Formations), the Lower Cretaceous Yongkang Group (Guantou, Chaochuan, Fangyan, Keshan and Xiaopingtian Formations) and the Upper Cretaceous Tiantai Group (Tangshang, Liangtoutang and Chichengshan Formations), in the Southeast China stratigraphic area (see Fig. 2). Chen (2000) divided the Cretaceous strata of Zhejiang Province into the Lower Cretaceous Luocun, Huangjian, Shouchang, Hengshan and Guantou Formations, and the Upper Cretaceous Chaochuan, Fangyan, Lanxi, Quxian and Tongxiang Formations. Based on a comprehensive analysis of lithostratigraphic sequence, paleontology, and isotope age, Cai and Yu (2001) suggested that the Yongkang, Tiantai and Hengjiang Groups are synchronous equivalents of different facies without overlap, accumulated between the late Early Cretaceous and the early Late Cretaceous. Cai and Yu (2001)

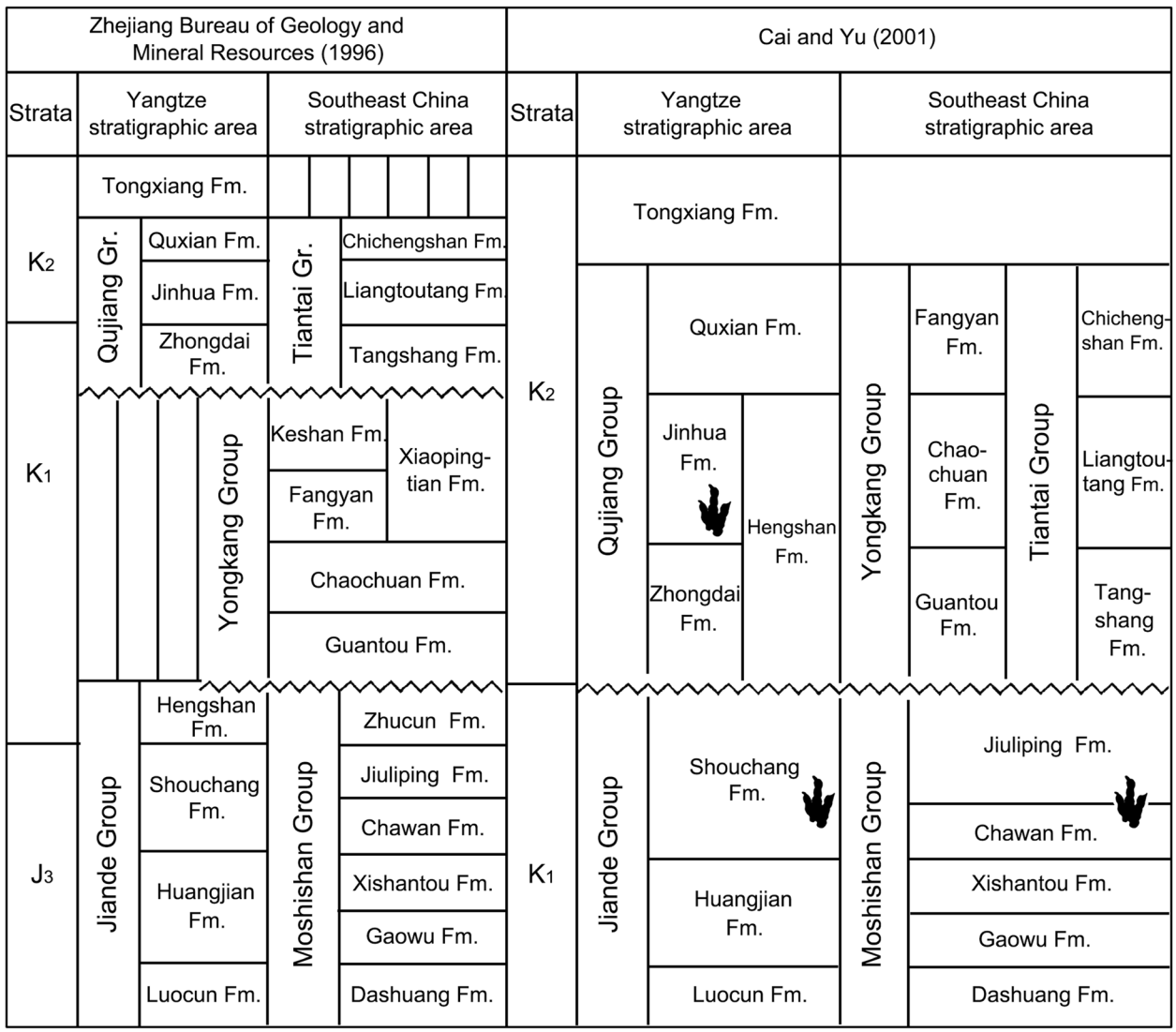

Fig. 2 An overview of the Upper Jurassic–Cretaceous stratigraphic units involved in the study area, after different researches and with demarcated track-bearing levels

re-established the Lower Cretaceous Jiande Group (Luocun, Huangjian, and Shouchang Formations) and the Upper Cretaceous Qujiang Group (Zhongdai, Jinhua, Hengshan [Zhongdai+Jinhua] and Quxian Formations) and the Tongxiang Formation, in the Yangtze stratigraphic area; and, the Lower Cretaceous Moshishan Group (Dashuang, Gaowu, Xishantou, Chawan and Jiuliping Formations), the Upper Cretaceous Yongkang Group (Guantou, Chaochuan and Fangyan Formations) and the Upper Cretaceous Tiantai Group (Tangshang, Liangtoutang and Chichengshan Formations), in the Southeast China stratigraphic area (Fig. 2).

2.2 Xiaqiao site

The dinosaur tracks were found beside a stream in Xiaqiao Village, Laozhu Town, Liantu District, Lishui City (GPS: 28°32′6.24″N, 119°44′39.18″E), at the northwestern edge of the Lishui Basin (No. 22 in Fig. 1 and Table 1). The Moshishan Group is dominated by acidic and intermediate-acidic volcanic rocks interbedded with sedimentary rocks; and mainly yields fossils of spores, stonewort, ostracods, conchostracans, bivalves, gastropods, insects, fish, and reptiles (Zhejiang Bureau of Geology and Mineral Resources, 1989; Wang, 2001). The Moshishan Group was previously designated as the Upper Jurassic on the basis of biostratigraphic comparisons (Gu, 1982). Through the zircon U–Pb dating of volcanic rocks, Li et al. (2014) demonstrated that these volcanic rocks were ~136–129 Ma in age, erupted in the Early Cretaceous. Zhang et al. (2012) confirmed isotopic ages of the Early Cretaceous for different formations of the Moshishan Group in eastern Zhejiang

Table 1 The distribution of dinosaur dominated track sites and dinosaur–pterosaur skeleton fossil records found from Zhejiang Province, China

No.	Specimens	Strata	Basin	Location
1	Titanosaurid *Jiangshanosaurus lixianensis* (Tang et al., 2001)	Upper Cretaceous Jinhua Formation	Jinqu	Lixian Village, Jiangshan City
2	Titanosaurid *Dongyangosaurus sinensis* (Lü et al., 2008)	Upper Cretaceous Fangyan Formation	Jinqu	Dongyang City
3	Therizinosaur "*Chilantaisaurus*" *zheziangensis* (Dong, 1979; Zanno, 2010)	"Mid" Cretaceous Chaochuan Formation	Jinqu	Zhongdai Village, Jinhua City
4	Ankylosaur *Dongyangopelta yangyanensis* (Chen et al., 2013a)	"Mid" Cretaceous Chaochuan Formation	Jinqu	Yangyan Village, Dongyang City
5	Hadrosaurid (Yu, 2013)	"Mid" Cretaceous Chaochuan Formation	Jinqu	Yinian Village, Zhuji City
6	Hadrosaurid (Yu, 2013)	Upper Cretaceous Zhongdai Formation	Jinqu	Shangfang Village, Lanxi City
7	Dinosaur fragments (Jin et al., 2012)	Upper Cretaceous Jinhua Formation	Jinqu	Pujiang County, Jinhua City
8	Dinosaur fragments (Yu, 2013)	Upper Cretaceous Jinhua Formation	Jinqu	Gaotangshi Village, Quzhou City
9	Theropoda tooth (Yu, 2013)	"Mid" Cretaceous Chaochuan Formation	Hushan	Xianglugang Village, Suichang County
10	Sauropod and theropod (Yu, 2013)	"Mid" Cretaceous Chaochuan Formation	Yongkang	Xishantou Village, Yongkang City
11	Ankylosaur *Jinyunpelta sinensis* (Zheng et al., 2018)	"Mid" Cretaceous Liangtoutang Formation	Huzhen	Lizhuang Village, Jinyun County, Lishui City
12	Ankylosaur *Zhejiangosaurus lishuiensis* (Lü et al., 2007)	"Mid" Cretaceous Chaochuan Formation	Lishui	Liancheng Town, Lishui City
13	Sauropod (Yu, 2013)	Upper Cretaceous Fangyan Formation	Xinsheng	Tinghu Village, Shengzhou City
14	Dinosaur fragments (Yu, 2013)	"Mid" Cretaceous Chaochuan Formation	Xinsheng	Shima Mountain, Shaoxing City
15	Hadrosaurid and basal ornithopod (Yu, 2013)	"Mid" Cretaceous Liangtoutang Formation	Tiantai	Huangmei Mountain, Tiantai County
16	Therizinosauroid "Tiantaiosaurus" (Qian et al., 2012)	"Mid" Cretaceous Chaochuan Formation	Tiantai	Fangshan Village, Tiantai County
17	Therizinosauroid (Yu, 2013)	"Mid" Cretaceous Liangtoutang Formation	Tiantai	Songliwan Village, Tiantai County
18	Basal ornithopod *Yueosaurus tiantaiensis* (Zheng et al., 2012)	"Mid" Cretaceous Liangtoutang Formation	Tiantai	Tiantai distillery, Tiantai County
19	Hadrosaurid (Yu, 2013)	"Mid" Cretaceous Chaochuan Formation	Xianju	Guanyin Mountain, Xianju County
20	Azhdarchidae *Zhejiangopterus linhaiensis* (Cai and Wei, 1994)	Upper Cretaceous Xiaoxiong Formation	Xiaoxiong	Aoli Village, Linhai City
21	Aves *Yandangornis longicaudus* (Cai and Zhao, 1999)	Upper Cretaceous Xiaoxiong Formation	Xiaoxiong	Aoli Village, Linhai City

Table 1 The distribution of dinosaur dominated track sites and dinosaur–pterosaur skeleton fossil records found from Zhejiang Province, China *(Continued)*

No.	Specimens	Strata	Basin	Location
22	Sauropod tracks (Matsukawa et al., 2009)	Upper Cretaceous Shouchang Formation	Lishui	Xiaqiao site, Lishui City
23	Pterosaurs, birds, small theropod, ornithopod, and sauropod tracks (Lü et al., 2010)	Upper Cretaceous Jinhua Formation	Jinqu	Fengchekou site, Dongyang City
24	Theropod, ?ornithopod, ?ankylosaurs, ?bird, and sauropods tracks (Du et al., 2015)	Upper Cretaceous Jinhua Formation	Jinqu	Guanyintang site, Yiwu City

Province: 139.9 Ma for the Dashuang Formation, 135–121.5 Ma for the Gaowu Formation, 132–116.4 Ma for the Xishantou Formation, 120–112.4 Ma for the Chawan Formation, and 121–109.3 Ma for the Jiuliping Formation. Ma et al. (2016) noted that the volcanic–sedimentary rock series in the Lishui Basin can be divided into three major stratigraphic units: the Lower Cretaceous Moshishan Group, the Upper Cretaceous Guantou–Zhaochuan Formations, and the Fangyan Formation. Matsukawa et al. (2009) believed that the Xiaqiao site belonged to the Upper Jurassic Shouchang Formation.

Isotope dating of volcanic rocks from the Jiande Group yields an age estimation of 134–115 Ma, indicating that the Jiande Group in this study area is similar to other Chinese Lower Cretaceous groups in age (Li et al., 2011). In addition, the Jiande biota is generally compared with the Jehol biota of the western Liaoning Province and the Jiande Group is also similar to its contemporaneous groups in the composition of biota, such as bivalves, gastropods, fish, insects, and plants (Zhejiang Bureau of Geology and Mineral Resources, 1996).

In terms of lithology and biological types, the Moshishan Group and the Jiande Group are particularly similar (Liu and Zhao, 1927; Zhejiang Bureau of Geology and Mineral Resources, 1996; Cai and Yu, 2001). Regardless of whether the Xiaqiao site belongs to the Shouchang Formation of the Jiande Group (125–121 Ma; Li et al., 2011) or to the Chawan–Jiuliping Formations of the Moshishan Group (120–109 Ma; Zhang et al., 2012), these dates indicate that the Xiaqiao site is the Aptian in age.

Table 2 Measurements (in cm) of the sauropod trackways from the Xiaqiao site, Zhejiang Province, China

Track	ML	MW	PL	SL	PA	ML/MW	WAP	WAP/P'ML
XQ-S1-RP1	49.4	32.8	101.8	174.7	124	1.5	45.3	0.9
XQ-S1-LP1	47.6	34.2	96.2	–	–	1.4	–	–
XQ-S1-RP2	44.4	32.9	–	–	–	1.4	–	–
Mean	47.1	33.3	99.0	174.7	124	1.4	45.3	0.9
XQ-S2-LP1	44.0	32.0	82.4	–	–	1.4	–	–
XQ-S1-RP1	–	–	–	–	–	–	–	–
XQ-S3-RP1	34.3	25.4	114.5	195.2	122	1.4	54.4	1.6
XQ-S3-LP1	38.3	24.1	108.8	157.5	94	1.6	71.8	1.9
XQ-S3-RP2	34.1	19.7	106.7	–	–	1.7	–	–
XQ-S3-LP2	40.8	21.7	–	–	–	1.9	–	–
Mean	36.9	22.7	110.0	176.3	108	1.6	63.1	1.7
XQ-SI2	53.5	40.0	–	–	–	1.3	–	–
XQ-SI3	34.7	38.4	–	–	–	0.9	–	–
XQ-SI4	30.4	21.3	–	–	–	1.4	–	–
XQ-SI5	34.5	30.9	–	–	–	1.1	–	–

Abbreviations: *ML* Maximum length, *MW* Maximum width, *PL* Pace length, *SL* Stride length, *PA* Pace angulation, *WAP* Width of the angulation pattern of pes (calculated value), *P'ML* Maximum length of pes. ML/MW and WAP/P'ML are dimensionless

3 Methods

Research data from the Xiaqiao site were collected using a digital SLR Canon camera (EOS 5D Mark III), with 14 photographs taken along the length of the track surface under natural lighting conditions. Photographic jpg image files were added to Agisoft Photoscan Professional Edition (version 1.2.6 build 2038 64 bit) to generate a dense point cloud of high resolution (1.3 mm average linear distance between points) and a digital elevation model (DEM). The DEM was opened in CloudCompare (version 2.8.0) to obtain a digital ortho-photograph and an ambient occlusion image. Additional images showing false-color elevation and contour lines (1 cm vertical equidistant) were used to visualize track depth, created in Paraview (version 5.0.0 64 bit).

Using the ratio between the width of the angulation pattern of pes (WAP) and the pes length (PL), gauge (trackway width) was quantified for pes and manus tracks in the trackways of quadrupeds (Marty, 2008; Marty et al., 2010). The pes tracks are likely to intersect the trackway midline if the (WAP/PL)-ratio is less than 1.0, which fits the definition of narrow-gauge (Farlow, 1992). Therefore, the (WAP/PL)-ratio of 1.0 is considered a threshold separating narrow-gauge from medium-gauge trackways, while 1.2 is considered the boundary between medium-gauge and wide-gauge trackways, with the boundary for defining very wide-gauge trackways set at values higher than 2.0 (Marty, 2008).

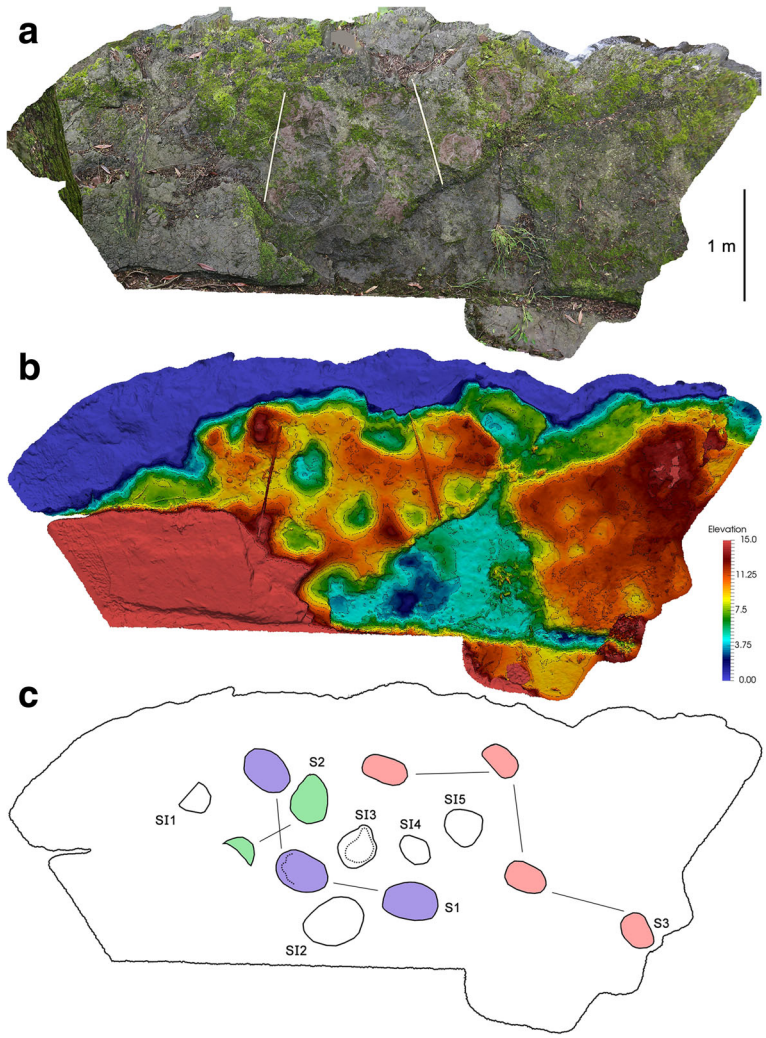

Fig. 3 **a** Field photograph from the Xiaqiao tracksite (XQ), Lishui City, Zhejiang Province; **b** 3D height map (warm colors = high areas, cool colors = low areas); **c** Interpretative outline drawing of Xiaqiao sauropod tracks (S1 = XQ-S1, SI1 = XQ-SI1)

4 Sauropod tracks of Lishui City

4.1 Description

Matsukawa et al. (2009) described these tracks but identified no trackway. However, the 3D photos analysed in this study are more discriminating in identifying track outlines and the patterns of trackways. On the mudstone level, we discovered at least 13 tracks. This is less than the 18 tracks identified by Matsukawa et al. (2009), and the reduced number is probably attributable to intervening weathering and damage caused by the roots of plants, which flourish in the wet environment near the river. However, among the 13 tracks, there were five isolated tracks (XQ-SI1–XQ-SI5; Table 2; Fig. 3) and three possible trackways (XQ-S1–XQ-S3; Table 2; Fig. 3). All tracks and trackways remain in situ.

Trackway XQ-S1 consists of three successive pes tracks and appears to be narrow-gauge, with a (WAP/P'ML)-ratio of 0.9 (P'ML stands for the maximum length of pes, Table 2; Marty, 2008). No manus impressions were recognized. The average length of the pes impressions is 47.1 cm, and the average (length/width)-ratio is 1.4. The pes impressions are oval and the metatarso–phalangeal region is smoothly curved. All tracks are poorly preserved without clear digit impression. The average pes pace angulation is 124°, which is relatively high for sauropods. Trackway XQ-S2 only preserves an incomplete single step and is morphologically similar to XQ-S1.

Trackway XQ-S3 consists of four poorly preserved pes tracks lacking distinct digit traces. The trackway pattern is between medium-gauge and wide-gauge (Marty, 2008), with a (WAP/P'ML)-ratio of 1.7. Impressions are oval in shape and have an average length of 36.9 cm and an average (length/width)-ratio of 1.6. The average pes pace angulation is 108°, which is characteristic of sauropods.

XQ-SI2 is 53.5 cm long and is the largest track at the Xiaqiao site. XQ-SI3 may be a manus impression with a (length/width)-ratio of 0.9 and is U-shaped with rounded marks inferred to represent traces of digits I and V. Only half of XQ-SI1 has been preserved. XQ-SI4 is only 30.4 cm long, possibly representing a smaller sauropod trackmaker. XQ-SI5 is 34.5 cm long with a (length/width)-ratio of 1.1, and may be a poorly preserved manus impression.

4.2 Comparisons and discussion

The morphology and trackway configuration of all the Xiaqiao tracks are typical of sauropods (Matsukawa et al., 2009). China's sauropod trackways are mostly wide- or medium-gauge and are therefore referred to the ichnogenus *Brontopodus* (Lockley et al., 2002). The Xiaqiao site sauropod trackways share numerous features with *Brontopodus* type tracks from the Lower Cretaceous of the USA (Farlow, Pittman and Hawthorne, 1989; Lockley, Farlow and Meyer, 1994). These features include: (1) probably U-shaped manus prints; (2) large and outwardly-rotated, oval pes tracks, with length greater than width; (3) wide-gauge. Overall, there is no discernable difference between the Xiaqiao *Brontopodus* tracks and other *Brontopodus* tracks widely distributed at China's Early and "Mid" Cretaceous tracksites, such as the Yanguoxia sites of the Hekou Group in northwestern China (Zhang et al., 2006; Xing et al., 2015a), more than 10 sites developed in Jiaguan, Feitianshan and Xiaoba Formations in southwestern China (Xing and Lockley, 2016), and more than a dozen sites of the Dasheng Group in eastern China (Xing et al., 2013a, 2015b). The wide-gauge of the *Brontopodus*-type trackways suggests titanosaurian sauropods as the most possible trackmakers (Wilson and Carrano, 1999; Lockley et al., 2002). Skeletal fossils of the titanosaurian *Jiangshanosaurus lixianensis* are known from the Jinhua Formation in eastern Zhejiang Province (Tang et al., 2001).

5 Dinosaur dominated track assemblages from Zhejiang Province

5.1 Dongyang sites of Jinhua Formation

In October 2008, researchers from the Institute of Geology, Chinese Academy of Geological Sciences, the Zhejiang Museum of Natural History, and the Dongyang Museum found numerous tracksites in Dongyang City. Some of these sites are very small, with only a few dinosaur tracks being preserved, as is the case with the Luoyanshan site, in Shanhuli Village. Larger sites are present on Fengchekou Mountain, in Wushan Village (No. 23 in Fig. 1 and Table 1), which produced a rich track assemblage, including theropod, pterosaur and bird tracks (Lü et al., 2010). The tracks were found in brownish-red siltstones of the Upper Cretaceous Jinhua Formation, Qujiang Group (the Jinhua Formation was once regarded as Fangyan Formation; see, Lü et al., 2008, 2010; Table 2).

Lü et al. (2010) briefly described the pterosaur, bird, small theropod, ornithopod, and sauropod tracks from Fengchekou site. The tracks were located at a construction site, and there were no large areas of exposed rocks. Except for the bird tracks, most tracks were observed in isolation and were not part of recognizable trackways.

Birds and sauropod tracks were rare and poorly preserved. Lü et al. (2010) provided two photos of theropod tracks, which were relatively well preserved. Although the lack of description makes further discussion difficult, these tracks are morphologically similar to *Asianopodus* (Matsukawa et al., 2005; Xing et al., 2014a) and *Jialingpus* (Zhen, Li and Zhen, 1983; Xing et al., 2014b; Fig. 4), and specifically share the traits of wide divarication angles and well-developed heels. In size, they are also similar to *Jialingpus*.

Azuma et al. (2013) described a bird footprint assemblage from Fengchekou site (GPS: 29°18′27.5″N, 120°9′54.7″E), and attributed them to *Dongyangornipes sinensis* and *Koreanaornis* cf. *hamanensis*. Buckley, McCrea and Lockley (2016), who looked into the main bird fauna based on multivariate statistical analyses, considered

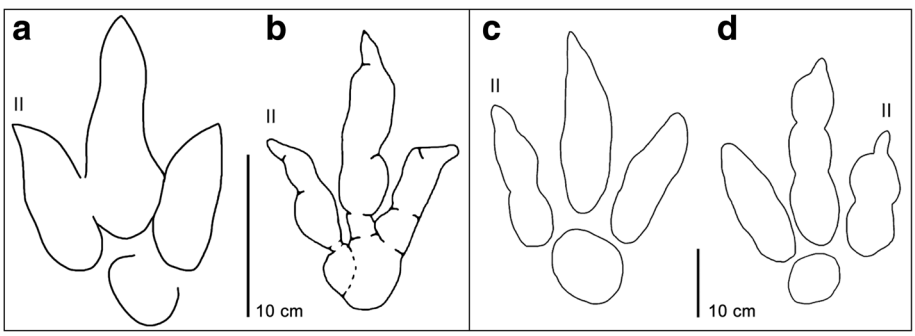

Fig. 4 Interpretative outline drawings of **a** The Cretaceous theropod track from the Fengchekou site based on the Fig. 3b in Lü et al. (2010); **b** The *Jialingpus* theropod track from Shaanxi Province (Xing et al., 2014b); **c–d** The *Asianopodus* tracks from Gansu Province (Xing et al., 2014a)

Dongyangornipes sinensis a subjective junior synonym of *Uhangrichnus chuni*. The latter is from lacustrine siliciclastic deposits of the Upper Cretaceous, purportedly Campanian, Uhangri Formation in South Korea (Yang et al., 1995).

Chen et al. (2013b) assigned the pterosaurs from the Fengchekou site to *Pteraichnus dongyangensis*. *Pteraichnus* is a classic pterosaur track and is relatively widely distributed in China (Lockley, Harris and Mitchell, 2008; Fig. 5). The first *Pteraichnus* specimen in China was found in the Yangouxia site, Gansu Province (Peng et al., 2004; Zhang et al., 2006; Xing et al., 2013b; Li et al., 2015), but has never been described in detail. *Pteraichnus* isp. Was also known from the Jimo site in the Laiyang Group of Shandong Province (Xing et al., 2012), from the Wuerhe site in the Tugulu Group of Xinjiang Uygur Autonomous Region (Xing et al., 2013c; He et al., 2013), from the Lotus site in the Jiaguan Formation of Chongqing Municipality (Xing et al., 2013b), from the Zhaojue site in the Feitianshan Formation of Sichuan Province (Xing et al., 2015c), from the Shimiaogou site in the Jiaguan Formation of Sichuan Province (Xing et al., 2016), and, the Yangmeikeng site in the Zhutian Formation of Guangdong Province (Xing et al., 2017). Except for the tracks from the Fengchekou and Yangmeikeng sites, all *Pteraichnus* specimens were the Early Cretaceous in age.

Sánchez-Hernández, Przewislik and Benton (2009) recognized that the ichnogenus *Pteraichnus* was over-split into five ichnospecies. They recognized only two of the six ichnospecies described from Spain, *P. longipodus* (Fuentes, Meijide and Meijide, 2004) and *P. parvus* (Meijide and Fuentes, 2001) as valid, and distinct from *P. saltwashensis* (Stokes, 1957) and *P. stokesi* (Lockley et al., 1995) which were named previously from North America. *P. nipponensis* (Lee et al., 2010) is also a distinct ichnospecies. Chen et al. (2013b) diagnosed *P. dongyangensis* as "*manus prints with 29° of divarication of digits II and III and that of the digits I and II is 52°. Ratio of width to length of the pes print is 0.17*". The divarication of digits I–II and II–III in manus prints of *Pteraichnus* vary largely depending on the quality of the

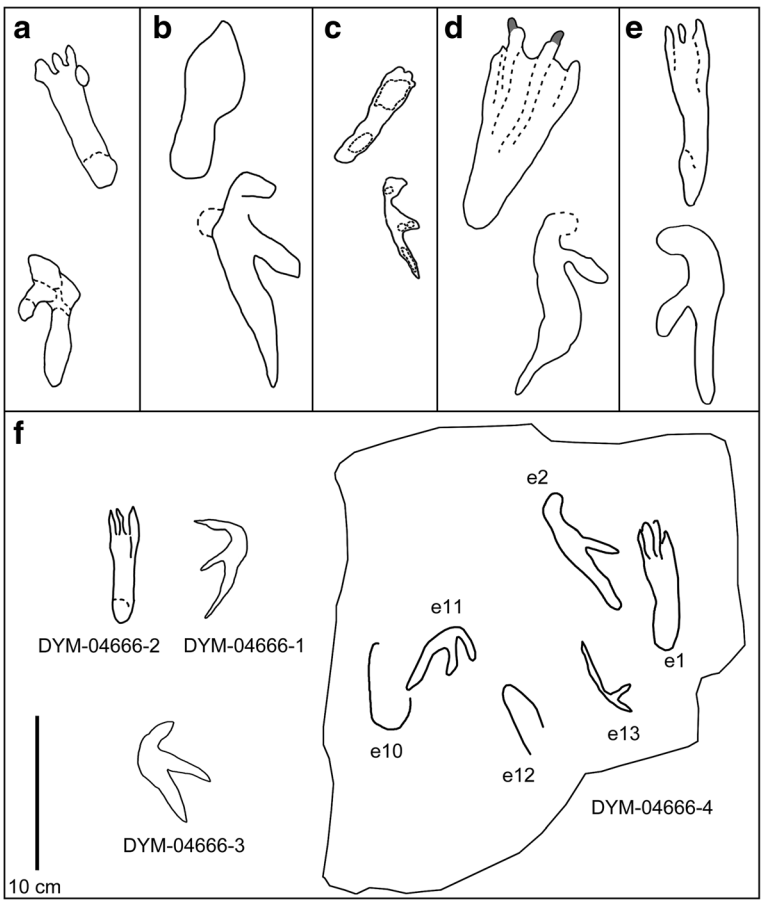

Fig. 5 The Cretaceous pterosaur tracks from **a** The Qijiang site (Xing et al., 2013b); **b** The Zhaojue site (Xing et al., 2015c); **c** The Jimo site (Xing et al., 2012); **d** The Wuerhe site (He et al., 2013); **e** The Liujiaxia site (Xing, unpublished data); **f** The Dongyang site (based on Chen et al., 2013b, their Figs. 3 and 4). Scale refers to **a–f**

sediment, as in the manus dominated *Pteraichnus* isp. From the Yangouxia site, Gansu Province (Li et al., 2015). Chen et al. (2013b) did not provide outlines of the manus, though Figs. 3 and 4 in Chen et al. (2013b) suggest variable values of divarication between manus digits. Thus, manus digit divarication cannot be used as a valid diagnostic character. There are two pes print specimens. They have four clear digits, just as in all *Pteraichnus* type tracks. Therefore, we here consider *P. dongyangensis* a *nomen dubium*.

5.2 Guanyintang site of Jinhua Formation

In 2010, researchers from the Institute of Geology, Chinese Academy of Geological Sciences, the Zhejiang Museum of Natural History, the Dongyang Museum and the Fukui Prefectural Dinosaur Museum discovered the Guanyintang site (GPS: 29°18′39.89″N, 120°9′42.11″E) on Houyantou Mountain, near Guanyintang Village of Jiangdong Subdistrict, Yiwu City (No. 24 in Fig. 1 and Table 1). In 2014, the Zhejiang Museum of Natural History found two pterosaur tracks, nearly 30 theropod dinosaur tracks, two ornithopod tracks, a group of possible ankylosaur tracks, a suspected bird track and more fragmented sauropod tracks, when excavating the Guanyintang site. These tracks are now covered by a shelter (GPS: 29°18′39.49″N, 120°9′37.85″E).

The Guanyintang site is located in the center of the Jinqu Basin, in the lower Upper Cretaceous Jinhua Formation. The sedimentation environment has been interpreted as coastal shallow–lake facies and fluvial delta, at the edge of a lake (Du et al., 2015). A total of 11 track-bearing layers are present in a 3 m-thick rock sequence.

Du et al. (2015) described the geological background of the Guanyintang site, and briefly described the specimens, but did not provide outline drawings, detailed comparisons, or ichnotaxonomic discussions. Judging from the illustrations of Du et al. (2015), the pterosaur tracks are morphologically consistent with the *Pteraichnus* type (Fig. 5). They are 17–19 cm long and similar in general morphology to those from the Dongyang sites. There is no detailed information about the other track types.

The reassignment of *Dongyangornipes sinensis* to *Uhangrichnis chuni*, and the evidence that *Pteraichnus dongyangensis* is indistinguishable from other *Pteraichnus* ichnospecies, indicates that the ichnospecies of Zhejiang Province are not distinct from others found from other localities in China and South Korea. It is obvious that previous work has created a misleading "provincial" ichnotaxonomy. The avian theropod and pterosaur tracks are in fact indistinguishable from previously named ichnotaxa in the region. Moreover, the erection of invalid ichnotaxa, not only obscures faunal similarities, but also can inflate diversity estimates, and confuse the regional palaeobiological–palaeoecological environment.

6 Conclusions

1) Lower Cretaceous (Aptian) ichnoassemblages from the Jiande Group and preserved at the Xiaqiao tracksite (Lishui City, southwestern Zhejiang Province) show typical *Brontopodus* tracks and trackways that can be attributed to titanosaurian sauropods. Skeletal fossils of the titanosaurian *Jiangshanosaurus lixianensis* are known from the stratigraphically younger (Upper Cretaceous) Jinhua Formation in eastern Zhejiang Province.
2) Upper Cretaceous ichnoassemblages with *Uhangrichnus* (bird) and *Jialingpus*-like (theropod) tracks, possible ornithopod and sauropod tracks, and *Pteraichnus* isp. (pterosaur) from the Jinhua Formation, at the Guanyintang and Dongyang sites, provide new information of tetrapod diversity in addition to dinosaur skeletal fossils found in Zhejiang Province. While theropod skeletal fossils are rare, track records indicate a higher theropod diversity and a greater abundance of pterosaurs.
3) Previously-proposed avian theropod (bird) and pterosaurian ichnospecies from these sites are ill conceived because they provide false information of a distinct provincial taxonomy, when in fact the ichnofaunas are similar to others from this region. Such ichnotaxonomy based on invalid ichnotaxa is misleading because it obscures true diversity patterns.
4) Dinosaur dominated track assemblages from the Upper Cretaceous Jinhua Formation are not significantly different from the typical Lower Cretaceous dinosaur-dominated ichnofaunas, such as those from the Liujixia sites (Gansu Province), Zhaojue sites (Sichuan Province), and Yishu fault zone area (Shandong Province). They are also similar to those from the Lower Cretaceous deposits of South Korea. Further discoveries in the Upper Cretaceous strata of Zhejiang Province will potentially include the typical Lower Cretaceous didactyl theropod tracks such as *Velociraptorichnus* or *Dromaeopodus*.

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Authors' contributions

LX and CC conceived and designed the experiments. CC, ML, AR, HK, NL and WP performed the experiments. LX, CC, and AR analyzed the data. LX, and

AR contributed reagents/materials/analysis tools. LX, CC, ML, AR, HK, NL and WP Wrote the paper. All authors read and approved the final manuscript.

Competing interests
The authors declare that they have no competing interests.

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References
Azuma, Y., J. Lü, X. Jin, Y. Noda, M. Shibata, R. Chen, and W. Zheng. 2013. A bird footprint assemblage of early late cretaceous age, Dongyang City, Zhejiang Province, China. *Cretaceous Research* 40: 3–9.

Buckley, L.G., R.T. McCrea, and M.G. Lockley. 2016. Analysing and resolving cretaceous avian ichnotaxonomy using multivariate statistics: Approaches and results. In *Dinosaur tracks: The next steps*, ed. P.L. Falkingham, D. Marty, and A. Richter, 258–308. Bloomington: Indiana University Press.

Cai, Z., and F. Wei. 1994. On a new pterosaur (*Zhejiangopterus linhaiensis* gen. Et sp. nov.) from upper cretaceous in Linhai, Zhejiang, China. *Vertebrata Palasiatica* 32: 181–194.

Cai, Z., and L. Zhao. 1999. A long tailed bird from the late cretaceous of Zhejiang. *Science in China, Series D-Earth Sciences* 42 (4): 434–441.

Cai, Z.Q., and Y.W. Yu. 2001. Subdivision and correlation of the upper beds of the cretaceous system in Zhejiang. *Journal of Stratigraphy* 25 (4): 259–266.

Chen, P.J. 2000. Comments on the classification and correlation of non-marine Jurassic and cretaceous of China. *Journal of Stratigraphy* 24 (2): 114–119.

Chen, R.J., J.C. Lü, Y.X. Zhu, Y. Azuma, W.J. Zheng, X.S. Jin, Y. Noda, and M. Shibata. 2013b. Pterosaur tracks from the early late cretaceous of Dongyang City, Zhejiang Province, China. *Geological Bulletin of China* 32 (5): 693–698.

Chen, R.J., W.J. Zheng, Y. Azuma, M. Shibata, T.L. Lou, Q. Jin, and X.S. Jin. 2013a. A new Nodosaurid ankylosaur from the Chaochuan formation of Dongyang, Zhejiang Province, China. *Acta Geologica Sinica (English Edition)* 87 (3): 658–671.

Dong, Z.M. 1979. Cretaceous dinosaurs of Hunan, China. In *Institute of Vertebrate Paleontology and Paleoanthropology, Nanjing Institute of Paleontology (Eds.). Mesozoic and Cenozoic Red Beds of South China: Selected Papers from the Cretaceous–Tertiary Workshop*, 342–350. Nanxiong: Science Press.

Du, T.M., H. Wu, X.S. Jin, G.Z. Jin, and Y.M. Sheng. 2015. The features of footprint fossils from Guanyintang Village, Yiwu City, Zhejiang Province and the suggestions for protection. *Research of Natural History and Museum* 2: 54–60.

Farlow, J.O. 1992. Sauropod tracks and trackmakers: Integrating the ichnological and skeletal record. *Zubia* 10: 89–138.

Farlow, J.O., J.G. Pittman, and J.M. Hawthorne. 1989. *Brontopodus birdi*. Lower Cretaceous sauropod footprints from the US Gulf coastal plain. In *Dinosaur Tracks and Traces*, ed. D.D. Gillette and M.G. Lockley, 371–394.

Fuentes, V.C., C.M. Meijide, and F.F. Meijide. 2004. Pteraichnus longipodus nov. ichno sp. in Oncala Mountain (Soria, Spain). *Stvdia Geol Salmant* 40: 103–114.

Gu, Z.W. 1982. *Stratigraphic correlation and description of the Jurassic strata in China*, 223–240. Beijing: Science Press.

He, Q., L.D. Xing, J.P. Zhang, M.G. Lockley, H. Klein, W.S.I.V. Persons, L.Q. Qi, and C. K. Jia. 2013. New early cretaceous pterosaur–bird track assemblage from Xinjiang, China — Palaeoethology and palaeoenvironment. *Acta Geologica Sinica (English Edition)* 87 (6): 1477–1485.

Jin, X.S., T. Du, W. Zheng, T. He, M. Ding, J. Xie, F. Yu, and Y. Sheng. 2012. *Dinosaurs walking in Zhejiang: Dinosaurs of Zhejiang Province*. Hangzhou: Zhejiang People's fine arts publishing house.

Lee, Y.N., Y. Azuma, H.J. Lee, M. Shibata, and J. Lü. 2010. The first pterosaur trackways from Japan. *Cretaceous Research* 31: 263–273.

Li, D.Q., L.D. Xing, M.G. Lockley, L. Piñuela, J.P. Zhang, H. Dai, J.Y. Kim, W.S.I.V. Persons, and D.L. Kong. 2015. A Manus dominated pterosaur track assemblage from Gansu, China: Implications for behavior. *Science Bulletin* 60 (2): 264–272.

Li, J.H., Z.L. Ma, Y.Q. Zhang, S.W. Dong, Y. Li, M.A. Lu, and J.P. Tan. 2014. Tectonic evolution of cretaceous extensional basins in Zhejiang Province, eastern South China: Structural and geochronological constraints. *International Geology Review* 56 (13): 1602–1629.

Li, X.H., S.D. Chen, J.H. Luo, Y. Wan, K. Cao, and L. Liu. 2011. Single zircon U–Pb isotope chronology of the early cretaceous Jiande group from western Zhejiang, SE China: Significances to stratigraphy. *Geological Review* 57 (6): 825–836 (in Chinese with English Abstract).

Liu, J.C., and Y.Z. Zhao. 1927. Geology of western Zhejiang. *Geological Report* 9: 51–73 (in Chinese with English Abstract).

Lockley, M.G., J.O. Farlow, and C.A. Meyer. 1994. *Brontopodus* and *Parabrontopodus* ichnogen. Nov. and the significance of wide- and narrow-gauge sauropod trackways. *Gaia* 10: 135–145.

Lockley, M.G., J.D. Harris, and L. Mitchell. 2008. A global overview of pterosaur ichnology: Tracksite distribution in space and time. *Zitteliana* B28: 187–198.

Lockley, M.G., T.J. Logue, J.J. Moratalla, A.P. Hunt, R.J. Schultz, and J.W. Robinson. 1995. The fossil trackway *Pteraichnus* is pterosaurian, not crocodilian: Implications for the global distribution of pterosaur tracks. *Ichnos* 4: 7–20.

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.

Lü, J.C., Y. Azuma, R.J. Chen, W.J. Zheng, and X.S. Jin. 2008. A new titanosauriform sauropod from the early late cretaceous of Dongyang, Zhejiang Province. *Acta Geologica Sinica (English Edition)* 82 (2): 225–235.

Lü, J.C., R. Chen, Y. Azuma, W. Zheng, I. Tanaka, and X. Jin. 2010. New pterosaur tracks from the early late cretaceous of Dongyang City, Zhejiang Province, China. *Acta Geoscientica Sinica* 31 (S1): 46–48 (in Chinese with English Abstract).

Lü, J.C., X.S. Jin, Y.M. Sheng, and Y.H. Li. 2007. New nodosaurid dinosaur from the late cretaceous of Lishui, Zhejiang Province, China. *Acta Geologica Sinica (English Edition)* 81 (3): 344–350.

Ma, Z., J. Li, Y. Zhang, S. Dong, C. Song, and Y. Li. 2016. Geochronological and structural constraints on the litho-stratigraphic units of the Lishui Basin, southeastern China. *Geology in China* 43 (1): 56–71 (in Chinese with English Abstract).

Marty, D. 2008. Sedimentology, taphonomy, and ichnology of Late Jurassic dinosaur tracks from the Jura carbonate platform (Cheveneze Combe Ronde tracksite, NW Switzerland) (PhD Thesis). In *Insights into the tidal-flat palaeoenvironment and dinosaur diversity, locomotion, and palaeoecology. GeoFocus 21*, 278. Fribourg: University of Fribourg.

Marty, D., M. Belvedere, C.A. Meyer, P. Mietto, G. Paratte, C. Lovis, and B. Thüring. 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.

Matsukawa, M., K. Hayashi, H.C. Zhang, J.S. Zhen, P.J. Chen, and M.G. Lockley. 2009. Early cretaceous sauropod tracks from Zhejiang Province, China. *Bulletin of Tokyo Gakugei University, Division of Natural. Sciences* 61: 89–96.

Matsukawa, M., K. Shibata, R. Kukihara, K. Koarai, and M.G. Lockley. 2005. Review of Japanese dinosaur track localities: Implications for ichno-taxonomy, paleogeography and stratigraphic correlation. *Ichnos* 12 (3): 201–222.

Meijide, C.M., and V.C. Fuentes. 2001. Huellas de pterosaurios en el Weald de Soria (Espana). In *Actas I Jornadas Internacionales sobre paleontología de dinosaurios y su entorno. Salas de los Infantes*, 397–406.

Peng, B.X., Y.S. Du, D.Q. Li, and Z.C. Bai. 2004. The first discovery of the early cretaceous pterosaur track and its significance in Yanguoxia, Yongjing County, Gansu Province. Earth Science — Journal of China University of Geosciences 29: 21–24.

Qian, M.P., Z.Y. Zhang, Y. Jiang, Y.G. Jiang, Y.J. Zhang, R. Chen, and G.F. Xing. 2012. Cretaceous Therizinosaurs in Zhejiang of eastern China. *Journal of Geology* 36 (4): 337–348.

Sánchez-Hernández, B., A.G. Przewislik, and M.J. Benton. 2009. A reassessment of the *Pteraichnus* ichnospecies from the early cretaceous of Soria Province, Spain. *Journal of Vertebrate Paleontology* 29 (2): 487–497.

Stokes, W.L. 1957. Pterodactyl tracks from the Morrison formation. *Journal of Paleontology* 31: 952–954.

Tang, F., X.M. Kang, X.S. Jin, F. Wei, and W.T. Wu. 2001. A new sauropod dinosaur of cretaceous from Jiangshan, Zhejiang Province. *Vertebrata PalAsiatica* 39 (4): 272–281.

Wang, Q.H. 2001. Discussion of ages of the Jiande group and the Moshishan Group in Zhejiang. *Volcanology and Mineral Resources* 22 (3): 163–169 (in Chinese with English Abstract).

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.

Xing, L.D., J.D. Harris, G.D. Gierliński, M.K. Gingras, J.D. Divay, Y.G. Tang, and P.J. Currie. 2012. Early cretaceous pterosaur tracks from a "buried" dinosaur tracksite in Shandong Province, China. *Palaeoworld* 21: 50–58.

Xing, L.D., D.Q. Li, M.G. Lockley, D. Marty, J.P. Zhang, W.S.I.V. Persons, H.L. You, C. Peng, and S.B. Kümmell. 2015a. Dinosaur natural track casts from the lower cretaceous Hekou Group in the Lanzhou–Minhe Basin, Gansu, Northwest China: Ichnology track formation, and distribution. *Cretaceous Research* 52: 194–205.

Xing, L.D., and M.G. Lockley. 2016. Early cretaceous dinosaur and other tetrapod tracks of southwestern China. *Science Bulletin* 61 (13): 1044–1051.

Xing, L.D., M.G. Lockley, H. Klein, G.D. Gierliński, J.D. Divay, S.M. Hu, J.P. Zhang, Y. Ye, and Y.P. He. 2014b. The non–avian theropod track *Jialingpus* from the cretaceous of the Ordos Basin, China, with a revision of the type material: Implications for ichnotaxonomy and trackmaker morphology. *Palaeoworld* 23: 187–199.

Xing, L.D., M.G. Lockley, H. Klein, J.P. Zhang, Q. He, J.D. Divay, L.Q. Qi, and C.K. Jia. 2013c. Dinosaur, bird and pterosaur footprints from the lower cretaceous of Wuerhe asphaltite area, Xinjiang, China, with notes on overlapping track relationships. *Palaeoworld* 22: 42–51.

Xing, L.D., M.G. Lockley, D.L. Li, H. Klein, W.S.I.V. Persons, Y. Ye, J.P. Zhang, and H. Ran. 2017. Late cretaceous Ornithopod-dominated, theropod, and pterosaur track assemblages from the Nanxiong Basin, China: New discoveries, ichnotaxonomy, and palaeoecology. *Palaeogeography, Palaeoclimatology, Palaeoecology* 466: 303–313.

Xing, L.D., M.G. Lockley, D. Marty, H. Klein, L.G. Buckley, R.T. McCrea, J.P. Zhang, G. D. Gierliński, J.D. Divay, and Q.Z. Wu. 2013a. Diverse dinosaur ichnoassemblages from the lower cretaceous Dasheng Group in the Yishu fault zone, Shandong Province, China. *Cretaceous Research* 45: 114–134.

Xing, L.D., M.G. Lockley, D. Marty, H. Klein, G. Yang, J.P. Zhang, G.Z. Peng, Y. Ye, W. S.I.V. Persons, X.Y. Yin, and T. Xu. 2016. A diverse saurischian (theropod-sauropod) dominated footprint assemblage from the lower cretaceous Jiaguan formation in the Sichuan Basin, southwestern China: A new ornithischian ichnotaxon, pterosaur tracks and an unusual sauropod walking pattern. *Cretaceous Research* 60: 176–193.

Xing, L.D., M.G. Lockley, D. Marty, L. Piñuela, H. Klein, J.P. Zhang, and W.S.I.V. Persons. 2015c. Re–description of the partially collapsed early cretaceous Zhaojue dinosaur tracksite (Sichuan Province, China) by using previously registered video coverage. *Cretaceous Research* 52: 138–152.

Xing, L.D., M.G. Lockley, L. Piñuela, J.P. Zhang, H. Klein, D.Q. Li, and F.P. Wang. 2013b. Pterosaur trackways from the lower cretaceous Jiaguan formation (Barremian–Albian) of Qijiang, Southwest China. *Palaeogeography, Palaeoclimatology, Palaeoecology* 392: 177–185.

Xing, L.D., D. Marty, K.B. Wang, M.G. Lockley, S.Q. Chen, X. Xu, Y.Q. Liu, H.W. Kuang, J.P. Zhang, H. Ran, and W.S.I.V. Persons. 2015b. An unusual sauropod turning trackway from the early cretaceous of Shandong Province, China. *Palaeogeography, Palaeoclimatology, Palaeoecology* 437: 74–84.

Xing, L.D., G. Niedźwiedzki, M.G. Lockley, J.P. Zhang, X.F. Cai, W.S.I.V. Persons, and Y. Ye. 2014a. *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.

Yang, S.Y., M.G. Lockley, R. Greben, B.R. Erickson, and S.K. Lim. 1995. Flamingo and duck-like bird tracks from the late cretaceous and early tertiary: Evidence and implications. *Ichnos* 4: 21–34.

Yu, F.M. 2013. Dinosaurs in Zhejiang — The Investigation and Research of Dinosaur Fossils from Zhejiang Province. Hangzhou: Zhejiang People's Publishing House, 254 pp.

Zanno, L.E. 2010. Osteology of Falcarius utahensis (Dinosauria: Theropoda): Characterizing the anatomy of basal therizinosaurs. *Zoological Journal of the Linnean Society* 158: 196–230.

Zhang, G.Q., Q.S. Wang, Y.P. Yu, C. Yang, and J. Xiao. 2012. Stratigraphic age and subdivision of volcanic rocks in eastern Zhejiang. *Journal of Stratigraphy* 3: 641–652 (in Chinese with English abstract).

Zhang, J., D. Li, M. Li, M.G. Lockley, and Z. Bai. 2006. Diverse dinosaur-, pterosaur- and bird-track assemblages from the Hakou formation, lower cretaceous of Gansu Province , northwest China. *Cretaceous Research* 27: 44–55.

Zhejiang Bureau of Geology and Mineral Resources. 1989. *Regional geology of the Zhejiang Province*, 166–188. Beijing: Geological Publishing House.

Zhejiang Bureau of Geology and Mineral Resources. 1996. *Stratigraphy (Lithostratic) of Zhejiang Province*, 1–236. Wuhan: China University of Geosciences Press.

Zhen, S.N., J.J. Li, and B.M. Zhen. 1983. Dinosaur footprints of Yuechi, Sichuan. *Memoirs of Beijing Natural History Museum* 25: 1–19 (in Chinese with English abstract).

Zheng, W.J., X.S. Jin, Y. Azuma, Q.Y. Wang, K. Miyata, and X. Xu. 2018. The most basal ankylosaurine dinosaur from the Albian–Cenomanian of China, with implications for the evolution of the tail club. *Scientific Reports* 8: 3711.

Zheng, W.J., X.S. Jin, M. Shibata, Y. Azuma, and F.M. Yu. 2012. A new ornithischian dinosaur from the cretaceous Liangtoutang formation of Tiantai, Zhejiang Province, China. *Cretaceous Research* 34: 208–219.