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# 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

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## Abstract

Tracks of large theropods and a single sauropod footprint are reported from red beds at Beikeshan locality in the Middle Jurassic Chuanjie Formation, of Lufeng County, near the large World Dinosaur Valley Park complex. The Chuanjie theropod tracks are assigned to the ichnogenus *Eubrontes* and the large sauropod track is given the provisional label *Brontopodus*. All occur as isolated tracks, i.e., trackways are not preserved. Saurischian dominated ichnofaunas are relatively common in the Jurassic of China. The producers of the Chuanjie tracks may have been similar to the basal tetanuran theropod *Shidaisaurus* and to mamenchisaurid sauropods, which were widely distributed throughout China, during the Jurassic, and are known from skeletal remains found in the same unit. Other potential sauropod trackmakers include titanosauriforms or as-yet-unknown basal eusauropods. The ichno- and skeletal records from the Jurassic of the Lufeng Basin are largely consistent, and both document the presence of middle-large sized theropods and sauropods.

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**Keywords:** Dinosaur tracks; World Dinosaur Valley Park; Beikeshan tracksite; *Eubrontes*; *Brontopodus*

## 1. Introduction

Abundant skeletal fossils of prosauropod and sauropod dinosaurs have been found in Lower and Middle Jurassic deposits of the Lufeng Basin (Young, 1951; Dong, 1992; Upchurch et al., 2007a). Although less abundant, theropod body fossils have also been discovered from the Lower–Middle Jurassic sediments, including complete specimens of *Sinosaurus triassicus* (Young, 1948) (= *Dilophosaurus sinensis* Hu, 1993)

(Xing, 2012; Xing et al., 2013a) and *Shidaisaurus jinae* (Wu et al., 2009).

Lü et al. (2006a) described the first dinosaur footprints from the Jurassic Lufeng Basin: an isolated large theropod track, which was named *Lufengopus dongi*. Xing et al. (2009a) described two theropod tracks from the Lower Jurassic Lufeng Basin, named *Changpeipus pareschequieri*. In a review of Chinese ichnotaxonomy, Lockley et al. (2013) assigned the former to cf. *Eubrontes* and the latter to *Eubrontes pareschequieri*. In a review of *Changpeipus*, Xing et al. (2014) considered *Changpeipus* and *Eubrontes* as similar (“sister”) ichnotaxa, on the basis of the large metatarsophalangeal pad positioned nearly in line with digit III, the digit proportions with IV > II, and the relatively large divarication angle between digits II and IV.

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In the summer of 2013, we investigated various dinosaur tracks in the Jurassic and Cretaceous of the Lufeng Basin. More theropod and sauropod tracks were discovered from the Middle Jurassic deposits.

Institutional abbreviations and acronyms. B = Beikeshan tracksite, China; HYMVC = The Collection from Heyuan Museum, Guangdong Province, China; T = Theropod; S = Sauropod; ZLJ = Lufeng Dinosaur Museum of World Dinosaur Valley Park, China.

## 2. Geological setting

The Red Beds of the Lufeng Series, in the Lufeng Basin, are approximately 750 m thick, and are conventionally divided into upper and lower units (Bien, 1941). Young (1951) determined the age of the Red Beds to be Late Triassic on the basis of the evolutionary ‘grades’ and stratigraphic correlations of its vertebrate fossils. Later, Sheng et al. (1962) proposed an Early Jurassic age for the Lower Lufeng Formation and a Middle Jurassic age for the Upper Lufeng Formation. Zhang and Li (1999) mapped Laochangjing, Chuanjie, and determined the relative stratigraphic positions of dinosaur fossils in the lower part of the Upper Lufeng Formation. Fang et al. (2000) restricted the name “Lufeng Formation” to what was previously called the Lower Lufeng Formation and further divided it into Shawan and Zhangjia’ao members. Fang et al. (2000) also assigned strata that had at various times been included in the Upper Lufeng Formation to the Chuanjie, Laoluocun, Madishan, and Anning formations. This most recent terminology scheme is followed here.

The new tracksite reported herein was discovered in Beikeshan (Shelled Hill) near Yaozhan, 1 km southeast of the World Dinosaur Valley Park, Lufeng County (GPS: 24°57'49.96" N, 102°4'41.14" E) (Fig. 1). The dinosaur footprint-bearing layer is 221.2 m thick and consists of thick-bedded purple mudstone and argillaceous siltstone mixed with thin purple deposits of fine-sandstone (Fig. 2). Although only a few isolated tracks occur at this site, the three theropod tracks illustrated here (Fig. 3) have been protected by the construction of concrete and brick shelters. Lü et al. (2006a) regarded the Beikeshan tracksite layer as positioned within the second member of the Upper Lufeng Formation (= Laoluocun Formation). However, later geological studies indicate that the Beikeshan tracksite layer is located at the top of the first member of the Upper Lufeng Formation (= Chuanjie Formation) (Fang and Li, 2008).

## 3. Ichnology

### 3.1. Theropod tracks

**Material:** Three natural molds (ZLJ BT1–3) from the Beikeshan tracksite (Fig. 3; Table 1). Protective coverings were built for each individual track. ZLJ BT1 was previously catalogued as No. L028; a cast of the specimen is stored in the Heyuan Museum, Guangdong Province, catalogued as HYMVC-1.

**Locality and horizon:** Chuanjie Formation, Middle Jurassic. Beikeshan tracksite, Lufeng County, Yunnan Province, China.

### Description and Comparison:

The three specimens (ZLJ BT1–3) are imperfectly preserved. The heel impression of ZLJ BT2 (Fig. 3C, D) is incomplete. ZLJ BT1 (Fig. 3A, B) is a tridactyl left pes, with a length/width ratio of 1.1. Digit II is the shortest and the most robust. The digit III impression constitutes approximately 61% of the footprint length. Each digit has a sharp claw mark. The claw marks of digit II and III point strongly inward. The borders of the digital pads of digit II and III are indistinct, with two or three pads observed. The phalangeal pads of digit IV are discernible; there are three digit pads and a relatively large metatarsophalangeal pad. The divarication between digit II and III is less than that between digit III and IV. The morphological characteristics of ZLJ BT2 and BT3 generally correspond with those of ZLJ BT1. However, the metatarsophalangeal pad of ZLJ BT3 is more developed, with a strong indentation behind digit II.

Lü et al. (2006a) previously described ZLJ BT1. However, our measurements indicate that the specimen is smaller than measured by these authors. ZLJ BT2 and BT3 are newly reported here.

ZLJ BT1 is similar to the *Eubrontes* morphotype in the following respects: ZLJ BT1 is a large (>25 cm long) functionally tridactyl footprint with a broad general shape; digit III is relatively short; there is no hallux trace; and the divarication of digits II and IV is on average 25°–40° (Olsen et al., 1998). Although the small sample size makes it difficult to identify systematic features, ZLJ BT1–3 are here referred to *Eubrontes* isp.

The *Eubrontes* morphotype is widely distributed in the Lower Jurassic deposits of China (Lockley et al., 2013). The earliest record of *Eubrontes* from China is *E. platypus* (Lull, 1904) from the Lower Jurassic Fengjiahe Formation of Jinning, Yunnan (Zhen et al., 1986). Subsequently, *Eubrontes monax* and *Eubrontes xiayangensis* (Lockley et al., 2013) were described from the Lower Jurassic of Jinning, Yunnan. *Eubrontes nianpanshanensis* has been reported from the Middle Jurassic strata of the Sichuan Basin (Yang and Yang, 1987; Lockley et al., 2013), which is situated close to the Lufeng Basin. Among these footprints only *E. platypus* and *E. xiayangensis* are represented by well-preserved specimens. All these tracks are attributable to *Eubrontes* based on the divarication of digits II–IV (37° and 21°) and the presence of a metatarsophalangeal pad that is positioned nearly in line with digit IV. More recently, a number of middle–large theropod tracks, from various other Jurassic sites have been assigned to *Eubrontes* (Lockley et al., 2013). In particular, the Xintiangou Formation of the Sichuan Basin has yielded a diverse assemblage of Middle Jurassic theropod footprints, which include *Eubrontes* and the ichnogenera *Grallator* and *Kayentapus* (Lockley and Matsukawa, 2009; Lockley et al., 2013; Xing et al., in press a). Although several other ichnogenera described based on this Xintiangou material (Yang and Yang, 1987) appear to be junior synonyms. The Xincun Formation in the Panxi region of the Sichuan Basin has yielded theropod tracks similar to *Kayentapus* (Xing et al., 2013b). The Middle Jurassic Shanshan tracksite, in the Turpan Basin (Xinjiang Uyghur Autonomous Region, northwestern China), Sanjianfang Formation, contains numerous theropod footprints that have been assigned to the ichnogenus *Changpeipus*, which is

Table 1

Measurements (in cm) of theropod and sauropod tracks from China.

Specimen	ML	MW*	LD II	LD III	LD IV	II–III	III–IV	II–IV	ML/MW
ZLJ BT1	37.8	34.7	21.9	22.6	24.4	28°	35°	63°	1.1
ZLJ BT2	47.2	33.9	24.6	28.9	26.3	27°	27°	54°	1.4
ZLJ BT3	43.6	31.7	26.9	26.9	21.6	27°	22°	49°	1.4
Mean	42.9	33.4	24.5	26.1	24.1	27°	28°	55°	1.3
ZLJ BS1	71.5	54.5	—	—	—	—	—	—	1.3

Abbreviations: ML: maximum length; MW: maximum width\*; LD II: length of digit II; LD III: length of digit III; LD IV: length of digit IV; II–III: angle between digits II and III; III–IV: angle between digits III and IV; II–IV: angle between digits II and IV; ML/MW: maximum length/maximum width. \* In ZLJ BT1–3 measured as the distance between the tips of digits II and IV.

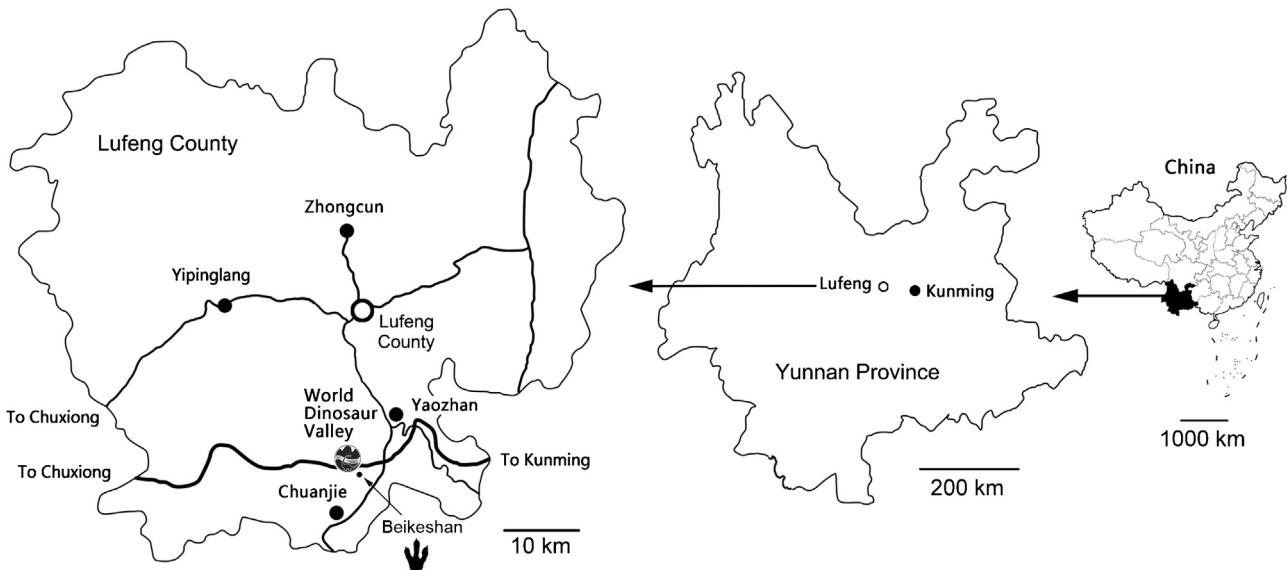


Fig. 1. Geographic map with the position of the Beikeshan dinosaur footprint locality (indicated by the footprint icon).

morphologically similar to, but still unique from, *Eubrontes* (Wings et al., 2007; Xing et al., 2014). From the Middle Jurassic Yan'an Formation of Zizhou County in Shaanxi Province, northern China, assemblages with *Eubrontes*, *Kayentapus*, and *Anomoepus* are known (Xing et al., in press b).

*Eubrontes*, *Grallator*, *Kayentapus*, and *Anomoepus* are typical components of the Lower Jurassic ichno-assemblages from North America (Lockley and Hunt, 1995; Olsen et al., 1998). However, in China, they occur not only in Lower Jurassic formations, but also in Middle and even Upper Jurassic strata. Thus,

theropod tracks from the Jurassic of China cannot be used for detailed biostratigraphy (Xing et al., 2013b). There are no significant morphological differences between *Eubrontes* isp. from the Middle Jurassic of the Beikeshan tracksite and *Eubrontes pareschequier* from the Lower Jurassic of the Lufeng Basin (Xing et al., 2009a; Lockley et al., 2013).

Other localities and stratigraphic units also provided Middle Jurassic footprint assemblages. At the Shanshan tracksite of the Turpan Basin (Xinjiang Uyghur Autonomous Region, north-western China), the Sanjianfang Formation yielded numerous

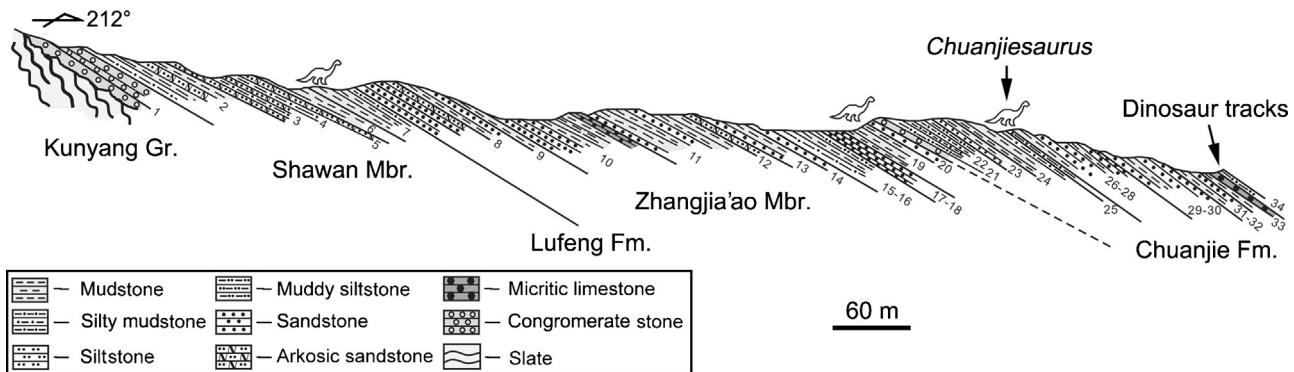


Fig. 2. Lithological section of the Chuanjie Formation and its related strata (modified from Fang et al., 2000; Sekiya, 2011).

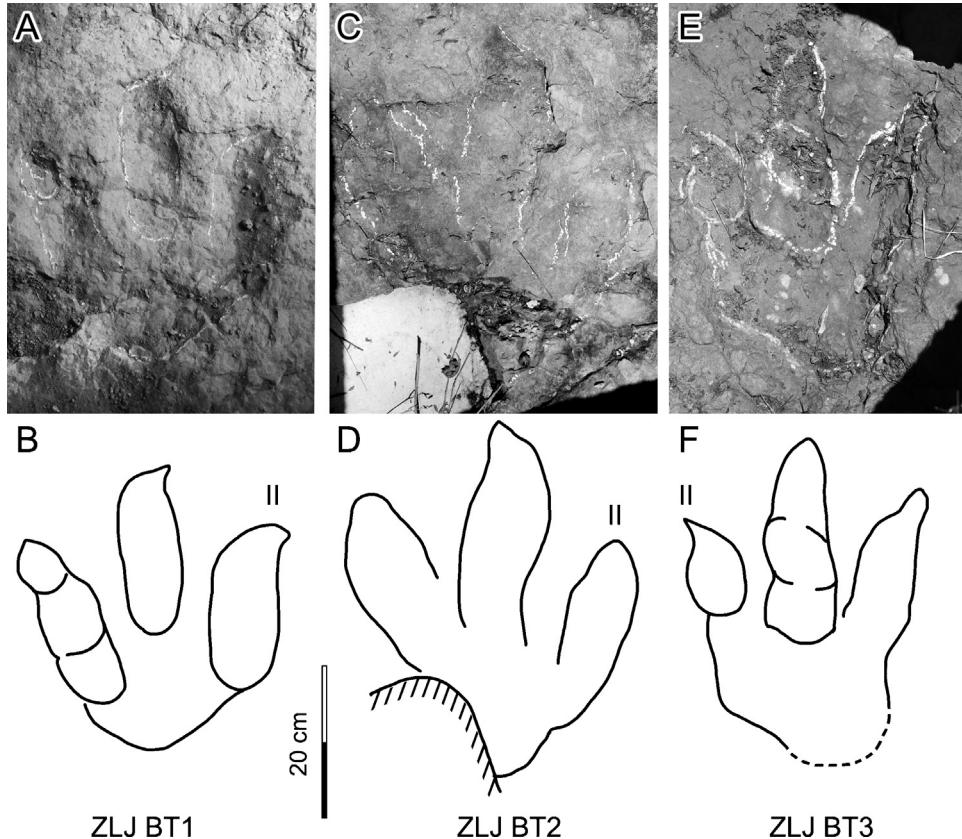


Fig. 3. Photographs and outline drawings of theropod tracks from the Beikeshan tracksite.

theropod footprints that have been assigned to the ichnogenus *Changpeipus*, which is morphologically similar to *Eubrontes* but also shows some distinguishing features (Wings et al., 2007; Xing et al., 2014). From the Middle Jurassic Yan'an Formation of Zizhou County in Shaanxi Province, northern China, assemblages with *Eubrontes*, *Kayentapus* (theropod), *Anomoepus*, and *Deltapodus* (ornithischian) footprints are known (Xing et al., in press b). One of the most important Middle Jurassic tracksites in North America, the Moab megatracksite in Utah (Entrada-Summit formations) shows thousands of theropod footprints similar to *Eubrontes* (Lockley, 1991; Lockley and Hunt, 1995). Middle Jurassic localities with theropod tracks are known from Europe (Lockley and Meyer, 2000; Day et al., 2004; Whyte et al., 2007), North Africa (Belvedere et al., 2011), Madagascar (Wagensommer et al., 2012), and South America (Leonardi, 1994).

### 3.2. Sauropod tracks

**Material:** One natural mold of pes, cataloged as ZLJ BS1 from the Beikeshan tracksite (Fig. 4).

**Locality and horizon:** Same as 3.1.

**Description and Comparison:**

After the discovery of the isolated pes ZLJ BS1, we attempted to expose more of the track layer. However, the tracksite is near a public road and it was difficult to do further excavation. ZLJ BS1 has a maximum, external diameter of 86 cm and a width of 70 cm, including the rim, with corresponding measurements

of 71.5 cm and 54.5 cm for the internal floor of the track. The track interior is partially filled by sediment. The pes impression possesses three to four poorly defined indentations at its anterior margin, corresponding to the predicted positions of digits I to III/IV. On this basis, ZLJ BS1 is probably a right pes track. The metatarsophalangeal pad impression is complete with smoothly curved margins.

*Brontopodus* (Farlow et al., 1989) is one of the most common and well known Cretaceous sauropod track types. Previously, most Early Cretaceous sauropod tracks in East Asia have been attributed to wide gauge *Brontopodus* (Lockley et al., 2002) and to narrow gauge *Parabrontopodus* (Xing et al., 2013c). ZLJ BS1 is an isolated pes, lacking an associated manus print, and thus it is difficult to make further comparison. However, the length/width ratio of ZLJ BS1 is 1.3, and this ratio is coincident with that of typical sauropod tracks such as *Brontopodus* (Farlow et al., 1989). An additional record of *Brontopodus* from China comes from the Upper Cretaceous Cangling area in Yunnan Province (Lockley et al., 2002). These Cangling tracks resemble ZLJ BS1 in morphology.

### 4. Track makers

In the Chuanjie Formation, the Chuanjie bonebed is the only horizon that has produced skeletal material of dinosaurs. The bonebed has yielded material from at least four individuals of the large sauropod *Chuanjiesaurus anaensis* (Fang et al., 2000; Sekiya, 2011), the theropod *Shidaisaurus jiniae* (Wu et al.,

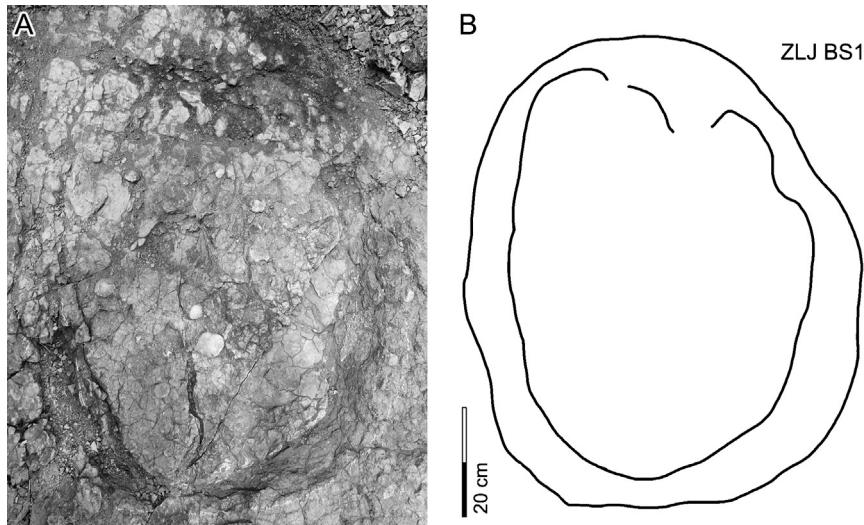


Fig. 4. Photograph and outline drawing of sauropod track from the Beikeshan tracksite.

2009), and a variety of turtles. Although no complete skeleton of *Chuanjiesaurus* is known, the body length is estimated at least 15 m (Toru Sekiya, pers. comm.). The body length of *Shidaisaurus* is approximately 5–6 m (Xiao-Chun Wu, pers. comm.).

Assuming a hip height/foot length ratio in the range of 4.0–5.9:1 for a sauropod (Alexander, 1976; Thulborn, 1989), the hip height of the Beikeshan sauropod trackmaker would be approximately 2.9–4.2 m. Body length/hip height ratio of *Shunosaurus* (a typical Middle Jurassic Chinese sauropod) is 3.7:1 (based on Farlow, 1992, Fig. 3). Assuming body proportions similar to those of *Shunosaurus*, the body length of the Beikeshan sauropod trackmaker is estimated to be 10.7–15.5 m. For theropod, using the average hip height/body length ratio of 1:2.63 (Xing et al., 2009b) and the formula hip height  $\approx 4 \times$  footprint length (Henderson, 2003) gives a body length estimation for the Beikeshan theropod of 4–5 m.

The Beikeshan sauropod track is the first sauropod track reported from the Chuanjie Basin. Only mamenchisaurid sauropod body fossils have been discovered in the local Middle Jurassic deposits, and the estimated size of the trackmaker is close to that calculated from the skeletons. A mamenchisaurid is, therefore, the most likely candidate for the Beikeshan sauropod trackmaker. The known distribution of mamenchisaurids spans across southwestern and northwestern China (from 25° to 44° N), making mamenchisaurids the most widely distributed sauropod group in China. Known mamenchisaurid genera include *Mamenchisaurus* (Young, 1954), *Omeisaurus* (Young, 1939), *Chuanjiesaurus* (Fang et al., 2000), *Yuannosaurus* (Lü et al., 2006b), and *Eomamenchisaurus* (Lü et al., 2008). Among these genera, *Mamenchisaurus* is the most abundant.

## 5. Palaeobiogeography of the Middle Jurassic sauropod tracks from southwestern China

Numerous sauropod fossils have been discovered in southwestern China. Continental Jurassic strata in Yunnan Province

are distributed mostly in the central subregions of Chuxiong and Kunming (Fang and Li, 2008). Vertebrate fossils are more abundant in the latter (Fig. 5). Both the Lufeng Basin and the Chuanjie Basin are situated in the Kunming Subregion.

The Jurassic strata of the Chuanjie Basin have produced the Lower Jurassic *Lufengosaurus* fauna, the Middle Jurassic *Chuanjiesaurus* fauna, and the Upper Jurassic *Mamenchisaurus* fauna (Fang et al., 2004). The basal sauropodomorph *Yimenosaurus* (Bai et al., 1990) and the basal sauropod *Chinshakiangosaurus* (Upchurch et al., 2007b) were discovered in Lower Jurassic deposits of the Chuxiong Subregion. The basal sauropodomorph *Yunnanosaurus* (Lü et al., 2007), the mamenchisaurids *Yuanmousaurus* (Lü et al., 2006b) and *Eomamenchisaurus* (Lü et al., 2008), and the basal eusauropod *Nebulasaurus* (Xing et al., in press c) come from the Middle Jurassic strata of the Chuxiong Subregion. Alongside the Chuanjie succession, the Jurassic Sichuan Basin has yielded the Lower Jurassic *Lufengosaurus* fauna, the Middle Jurassic *Shunosaurus* fauna, and the Upper Jurassic *Mamenchisaurus* fauna (Peng et al., 2005). Finally, the Changdu Basin in Tibet has yielded the Lower Jurassic *Lufengosaurus* fauna (Zhao, 1985) and the Middle Jurassic *Shunosaurus* fauna (Dong et al., 1983), but no Upper Jurassic fossils. Based on the compositional similarities of the Lower Jurassic and the Middle Jurassic faunas between the Changdu Basin and its neighboring regions, it would be expected that the Upper Jurassic fauna of the Changdu Basin also included mamenchisaurids.

Sauropod tracks from the Middle Jurassic of the Sichuan Basin were discovered at the Dazu tracksite in the Zhenzhuchong Formation (Fig. 6A). These tracks pertain to a wide gauge sauropod trackway, and were first reported by Yang and Yang (1987). They were later noted by Matsukawa et al. (2006) and briefly described by Lockley and Matsukawa (2009, fig. 7). This may be the oldest sauropod trackway known from China (Lockley and Matsukawa, 2009). The pes impressions of the Dazu tracks are relatively small. Taking the best-preserved pes track T2 as an example, it measures 34 cm in length, 25.4 cm in width, and has a length/width ratio of 1.3.

## Chuxiong Subregion

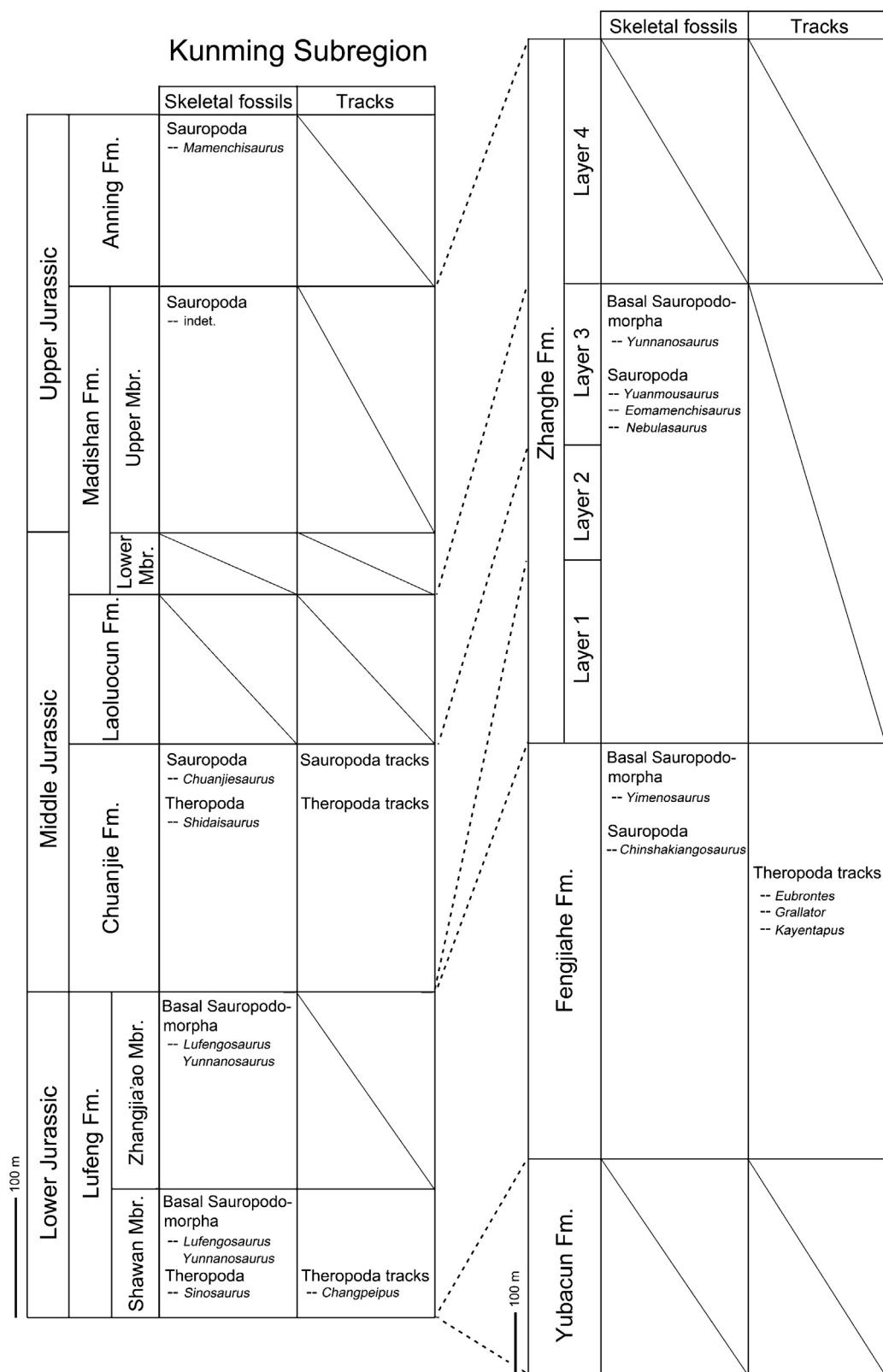


Fig. 5. Stratigraphic distribution of dinosaur skeletal fossils and footprints from the Jurassic of Kunming Subregion (including Chuanjie area, this study) and Chuxiong Subregion of Central Yunnan, China (stratigraphy modified from Fang and Li, 2008).

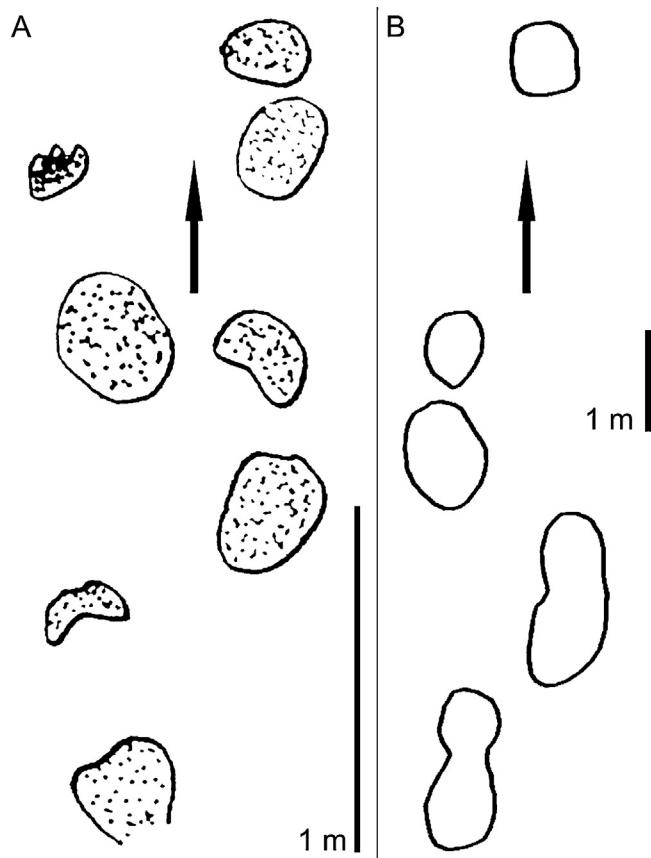


Fig. 6. A, sauropod trackway from Dazu tracksite, Sichuan Basin; B, sauropod trackway from Morong tracksite, Tibet.

Middle Jurassic sauropod tracks were also discovered in the Changdu Basin (Fig. 6B). At the Morong tracksite, eight tracks belonging to three sauropod trackways were discerned, and all resemble *Brontopodus* (Xing et al., 2011). These wide-(or medium)-gauge trackways suggest the presence of a large sauropod, possibly a titanosauriform (Xing et al., 2011) or an unknown basal eusaurod. The pes impressions of the Morong tracks are averaged 81 cm in length and 58.5 cm in width, and have a length/width ratio of 1.6—close to the proportions of the Beikeshan track. The most distinct characteristic of these sauropod trackways is their wide gauge pattern. Late Triassic–Early Jurassic sauropodomorph footprint assemblages are generally dominated by narrow-gauge trackways, such as the *Eosauropus* trackway from the Upper Triassic (Chinle Group) of Cub Creek (Lockley et al., 2006, 2011), trackways from the Lower Jurassic (Pliensbachian) of the Atlas Mountains, Morocco (Farlow, 1992), from the Lower Jurassic (Hettangian–Pliensbachian) of Lavini di Marco, Italy (Dalla Vecchia, 1994), and from several tracksites in the Lower Jurassic (Hettangian and Pliensbachian) of Poland (Gierliński, 1997; Gierliński and Sawicki, 1998; Gierliński and Pieńkowski, 1999; Gierliński et al., 2004, 2009).

In general, wide gauge sauropod trackways were left by titanosauriforms (Lockley et al., 1994; Wilson and Carrano, 1999) whereas narrow gauge trackways belong to basal sauropods, diplodocoids, and basal macronarians (Day et al., 2002). Henderson (2006) proposed the wide gauge pattern in

sauropods may be the consequence of the position of their center of mass and body weight distribution (cf. Lockley, 2007). The gait could have evolved more than once in sauropods. The osteological remains of basal eusaurodops such as *Patagosaurus*, *Volkheimeria*, *Cetiosaurus*, *Cetiosauriscus*, and *Turiasaurus* (Upchurch et al., 2004; Royo-Torres et al., 2006) suggest that these taxa were able to produce wide gauge trackways (Santos et al., 2009). Wide gauge ichnospecies *Polyonyx gomesi* was described by Santos et al. (2009) from the Middle Jurassic of Portugal, and the trackmaker probably pertains to non-neosauropod Eusaurodops.

Wide-gauge sauropod trackmakers emerged in southwestern China, presumably as a result of the Middle Jurassic radiation. The skeletal record of the Middle Jurassic Sichuan Basin is dominated by the eusaurodops *Shunosaurus* (Dong et al., 1983; Wilson, 2002; Peng et al., 2005). The body length of *Shunosaurus* is about 10 m. *Protognathosaurus* is a ‘cetiosaurid’ basal eusaurodops (Zhang, 1988), but this genus is known from only a fragmentary jaw, and more specimens are required to determine its validity. In addition, there are basal macronarians and mamenchisaurids, but these taxa lack skeletal characteristics (e.g., transversely wide sacrum, larger angle of limb elements in life position with respect to the sagittal plane, and increased curvature of the femoral midshaft; Santos et al., 2009) to indicate that they are potential producers of wide gauge trackways. Thus the trackmaker of the Dazu tracks probably pertains to an unknown basal eusaurodops.

The Morong *Brontopodus* tracks from the Changdu Basin are inferred to have been left by titanosauriforms (Xing et al., 2011). However, basal eusaurod trackmakers cannot be excluded. Fang et al. (2006) provided a preliminary document of the Changdu Region, in which the brachiosaurid macronarian *Microdontosaurus* and the ‘cetiosaurid’ basal eusaurod *Lancanjiangosaurus* were reported from the Middle Jurassic strata. Although these specimens lack a detailed description, they may represent potential makers of the Morong *Brontopodus* tracks.

The Beikeshan track is only an isolated pes imprint, and it is therefore difficult to offer further discussion. On the basis of a principal component analysis (PCA) of the femoral morphology, Sekiya (2010) proposed that *Chuanjiesaurus* is close to other titanosauriformes and was probably ancestor to later titanosauriformes. This proposal has not been supported by phylogenetic analysis (Sekiya, 2010), but it provides another possible wide gauge trackmaker for the Beikeshan sauropod track.

Sauropod body fossils occur throughout the Jurassic of the Lufeng area (Fig. 5), but until recently their tracks had not been reported. Theropod skeletal remains and tracks also occur in some of the older (Lower and Middle Jurassic) units. Thus, the track and bone records are broadly consistent. Lockley and Hunt (1994) proposed a scheme for evaluating the degree to which bone and track records are similar in any given formation. Formations where bones are more common than tracks are referred to as Category 4, with sub category “a” indicating similar faunas represented (in this case theropods and sauropods), as opposed to sub-category “b” where the tracks and bones represent different faunas.

An overview of the Middle Jurassic sauropod tracks of southwestern China indicates that there was a relatively higher degree of local sauropod diversity, probably including titanosauriforms, basal eusauropods, and mamenchisaurids.

## 6. Conclusions

The abundant sauropodomorph skeletal remains in the Lower and Middle Jurassic red beds of Yunnan Province and other regions of southern and western China are well-known. In addition, the theropod skeletal remains have been described. However, relatively little is known of the tracks from this region. This is probably due to the previous lack of study and to a lack of suitable facies for abundant track preservation. However, tracks do occur, and they appear to be more or less consistent, in general terms, with the skeletal fauna. Currently although sauropod skeletal diversity is relatively high, it is not possible to make any clear statements about diversity based on tracks.

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## References

- Alexander, R., 1976. Estimates of speeds of dinosaurs. *Nature* 261, 129–130.
- Bai, Z.L., Yang, J., Wang, G.H., 1990. A new genus of prosauropod from the Yuxi (region) of Yunnan Province. *Yuxi Cultural Organization* 1, 14–23 (in Chinese).
- Belvedere, M., Dyke, G., Hadri, M., Ishigaki, S., 2011. The oldest evidence for birds in northern Gondwana? Small tridactyl footprints from the Middle Jurassic of Msemrir (Morocco). *Gondwana Research* 19, 542–549.
- Bien, M.N., 1941. “Red Beds” of Yunnan. *Bulletin of the Geological Society of China* 21, 159–198.
- Dalla Vecchia, F.M., 1994. Jurassic and Cretaceous sauropod evidence in the Mesozoic carbonate platforms of the Southern Alps and Dinarids. *Gaia* 10, 63–73.
- Day, J.J., Upchurch, P., Norman, D.B., Gale, A.S., Powell, P.H., 2002. Sauropod trackways, evolution and behavior. *Science* 296, 1659.
- Day, J.J., Norman, D.B., Gale, A.S., Upchurch, P., Powell, H.P., 2004. A Middle Jurassic dinosaur trackway site from Oxfordshire, UK. *Palaeontology* 47 (2), 319–348.
- Dong, Z.M., 1992. *The Dinosaurian Faunas of China*. Springer-Verlag, Berlin, 188 pp.
- Dong, Z.M., Zhou, S.W., Zhang, Y.H., 1983. Dinosaurs from the Jurassic of Sichuan. *Palaeontologica Sinica, New Series C* 162 (23), 1–136 (in Chinese, with English summary).
- Fang, X.S., Li, P.X., 2008. *Jurassic Red Bed in the Central Yunnan of China*. Geological Publishing House, Beijing, 111 pp. (in Chinese, with English summary).
- Fang, X.S., Pang, Q.J., Lu, L.W., Zhang, Z.X., Pan, S.G., Wang, Y.M., Li, X.K., Cheng, Z.W., 2000. Lower, Middle, and Upper Jurassic subdivision in the Lufeng region, Yunnan Province. In: Editorial Committee of Proceedings of the Third National Stratigraphical Congress of China (Ed.), *Proceedings of the Third National Stratigraphical Congress of China*. Geological Publishing House, Beijing, pp. 208–214 (in Chinese, with English summary).
- Fang, X.S., Zhao, X.J., Lu, L.W., Cheng, Z.W., 2004. *Discovery of Late Jurassic Mamenchisaurus in Yunnan, southwestern China*. *Geological Bulletin of China* 12 (9–10), 1005–1009 (in Chinese, with English summary).
- Fang, X.S., Zhang, Z.J., Lu, L.W., Hang, Y.J., Zhao, X.J., Li, P.X., 2006. Collision between the Indian plate and the paleo-Asian plate and the appearance of Asian dinosaurs. *Geological Bulletin of China* 25 (7), 862–873 (in Chinese, with English summary).
- Farlow, J.O., 1992. Sauropod tracks and trackmakers: integrating the ichnological and skeletal record. *Zubia* 10, 89–138.
- Farlow, J.O., Pittman, J.G., Hawthorne, J.M., 1989. *Brontopodus birdi*, Lower Cretaceous sauropod footprints from the U.S. Gulf Coastal Plain. In: Gillette, D.D., Lockley, M.G. (Eds.), *Dinosaur Tracks and Traces*. Cambridge University Press, Cambridge, pp. 371–394.
- Gierliński, G., 1997. Sauropod tracks in the Early Jurassic of Poland. *Acta Geologica Polonica* 42 (4), 533–538.
- Gierliński, G., Pieńkowski, G., 1999. Dinosaur track assemblages from Hettangian of Poland. *Geological Quarterly* 43, 329–346.
- Gierliński, G., Sawicki, G., 1998. New sauropod tracks from the Lower Jurassic of Poland. *Geological Quarterly* 42, 477–484.
- Gierliński, G., Pieńkowski, G., Niedzwiedzki, G., 2004. Theropod track assemblage in the Hettangian of Soltyków, Poland, and its paleoenvironmental background. *Ichnos* 11, 95–213.
- Gierliński, G., Niedzwiedzki, G., Nowacki, P., 2009. Small theropod and ornithopod footprints in the Late Jurassic of Poland. *Acta Geologica Polonica* 59 (2), 221–234.
- Henderson, D.M., 2003. Footprints, trackways, and hip heights of bipedal dinosaurs — testing hip height predictions with computer models. *Ichnos* 10, 99–114.
- Henderson, D.M., 2006. Burly gaits: centers of mass, stability, and the trackways of sauropod dinosaurs. *Journal of Vertebrate Paleontology* 26 (4), 907–921.

- Hu, S.Y., 1993. A new theropod (*Dilophosaurus sinensis* sp. nov.) from Yunnan, China. *Vertebrata PalAsiatica* 31, 65–69 (in Chinese).
- Leonardi, G., 1994. Annotated Atlas of South America Tetrapod Footprints (Devonian to Holocene). CPRM, Brasilia, 247 pp.
- Lockley, M.G., 1991. The Moab megatracksite: a preliminary description and discussion of millions of Middle Jurassic tracks in Eastern Utah. In: Averitt, W.R. (Ed.), Guidebook for Dinosaur Quarries and Tracksites Tour, Western Colorado and Eastern Utah. Grand Junction Geological Society, pp. 59–65.
- Lockley, M.G., 2007. The morphodynamics of dinosaurs, other archosaurs and their trackways: holistic insights into relationships between feet, limbs and the whole body. In: Bromley, R., Melchor, R. (Eds.), Ichnology at the Crossroads: a Multidimensional Approach to the Science of Organism-substrate Interactions. Society of Economic Paleontologists and Mineralogists Special Publication 88, 27–51.
- Lockley, M.G., Hunt, A.P., 1994. A review of vertebrate ichnofaunas of the Western Interior United States: evidence and implications. In: Caputo, M.V., Peterson, J.A., Franczyk, K.J. (Eds.), Mesozoic Systems of the Rocky Mountain Region, United States. Rocky Mountain Section, Society for Sedimentary Geology, Denver, pp. 95–108.
- Lockley, M.G., Hunt, A.P., 1995. Dinosaur Tracks and Other Fossil Footprints of the Western United States. Columbia University Press, New York, 338 pp.
- Lockley, M.G., Matsukawa, M., 2009. A review of vertebrate track distributions in East and Southeast Asia. *Journal Paleontological Society of Korea* 25, 17–42.
- Lockley, M.G., Meyer, C., 2000. Dinosaur Tracks and Other Fossil Footprints of Europe. Columbia University Press, New York, 342 pp.
- Lockley, M.G., Farlow, J.O., Meyer, C.A., 1994. *Brontopodus* and *Parabrontopodus* ichnogen. nov. and the significance of wide- and narrow-gauge sauropod trackways. *Gaia* 10, 135–145.
- Lockley, M.G., Wright, J., White, D., Li, J.J., Feng, L., Li, H., 2002. The first sauropod trackways from China. *Cretaceous Research* 23, 363–381.
- Lockley, M.G., Lucas, S.G., Hunt, A.P., 2006. *Eosauropus* — a new name for a Late Triassic tracks: observations on the Late Triassic ichnogenus *Tetrasauropus* and related forms, with notes on the limits of interpretation. *New Mexico Museum of Natural History and Science, Bulletin* 37, 192–198.
- Lockley, M.G., Hups, K., Cart, K., Gerwe, S., 2011. A zone of sauropodomorph footprints in the basal Wingate Sandstone (Latest Triassic) of western Colorado and eastern Utah: is *Eosauropus* a common ichnogenus in this region? *New Mexico Museum of Natural History and Science, Bulletin* 53, 337–343.
- Lockley, M.G., Li, J.J., Li, R.H., Matsukawa, M., Harris, J.D., Xing, L.D., 2013. A review of the tetrapod track record in China, with special reference to type ichnospecies: implications for ichnotaxonomy and paleobiology. *Acta Geologica Sinica* (English Edition) 87 (1), 1–20.
- Lull, R.S., 1904. Fossil footprints of the Jura-Trias of North America. *Memoirs of the Boston Society of Natural History* 5 (11), 461–557.
- Lü, J.C., Azuma, Y., Wang, T., Li, S.X., Pan, S.G., 2006a. The first discovery of dinosaur footprint from Lufeng of Yunnan Province, China. *Memoir of the Fukui Prefectural Dinosaur Museum* 5, 35–39.
- Lü, J.C., Li, S.X., Ji, Q., Wang, G.F., Zhang, J.H., Dong, Z.M., 2006b. New eusaupod dinosaur from Yuanmou of Yunnan Province. *Acta Geologica Sinica* (English Edition) 80, 1–10.
- Lü, J.C., Li, S.X., Zhong, S.M., Azuma, Y., Fujita, M., Dong, Z.M., Ji, Q., 2007. New yunnanosaurid dinosaur (Dinosauria, Prosauropoda) from the Middle Jurassic Zhanhe Formation of Yuanmou, Yunnan Province of China. *Memoir of Fukui Prefectural Dinosaur Museum* 6, 1–15.
- Lü, J.C., Li, T.G., Zhong, S.M., Ji, Q., Li, S.X., 2008. A new mamenchisaurid dinosaur from the Middle Jurassic of Yuanmou, Yunnan Province, China. *Acta Geologica Sinica* (English Edition) 82 (1), 17–26.
- Matsukawa, M., Saiki, K., Ito, M., Obata, I., Nichols, D.J., Lockley, M.G., Kukihara, R., Shibata, K., 2006. Early Cretaceous terrestrial ecosystems in East Asia based on food-web and energy-flow models. *Cretaceous Research* 27, 285–307.
- Olsen, P.E., Smith, J.B., McDonald, N.G., 1998. Type material of the type species of the classic theropod footprint genera *Eubrontes*, *Anchisauripus*, and *Grallator* (Early Jurassic, Hartford and Deerfield basins, Connecticut and Massachusetts, U.S.A.). *Journal of Vertebrate Paleontology* 18 (3), 586–601.
- Peng, G.Z., Ye, Y., Gao, Y.H., Jiang, S., Shu, C.K., 2005. *Jurassic Dinosaur Faunas in Zigong*. People's Publishing House of Sichuan Province, Chengdu, 236 pp. (in Chinese, with English summary).
- Royo-Torres, R., Cobos, A., Alcalá, L., 2006. A giant European dinosaur and a new sauropod clade. *Science* 314, 1925–1927.
- Santos, V.F., Moratalla, J.J., Royo-Torres, R., 2009. New sauropod trackways from the Middle Jurassic of Portugal. *Acta Palaeontologica Polonica* 54 (3), 409–422.
- Sekiya, T., 2010. Re-examination of *Chuanjiesaurus ananensis* (Sauropoda, Dinosauria) from the Chuanjie Formation (Middle Jurassic) in Lufeng of Yunnan, China. *PhD Thesis*, Jilin University, 121 pp.
- Sekiya, T., 2011. Re-examination of *Chuanjiesaurus ananensis* (Dinosauria: Sauropoda) from the Middle Jurassic Chuanjie Formation, Lufeng County, Yunnan Province, southwest China. *Memoir of the Fukui Prefectural Dinosaur Museum* 10, 1–54.
- Sheng, S.F., Chang, L.Q., Cai, S.Y., Xiao, R.W., 1962. The problem of the age and correlation of the red beds and the coal series of Yunnan and Szechuan. *Acta Geologica Sinica* (English Edition) 42 (1), 31–56.
- Thulborn, R.A., 1989. The gaits of dinosaurs. In: Gillette, D.D., Lockley, M.G. (Eds.), *Dinosaur Tracks and Traces*. Cambridge University Press, Cambridge, pp. 39–50.
- Upchurch, P., Barrett, P.M., Dodson, P., 2004. Sauropoda. In: Weishampel, D.B., Dodson, P., Osmolska, H. (Eds.), *The Dinosauria* (Second Edition). California University Press, Berkley, pp. 259–322.
- Upchurch, P., Barrett, P.M., Galton, P.M., 2007a. A phylogenetic analysis of basal sauropodomorph relationships: implications for the origin of sauropod dinosaurs. In: Barrett, P.M., Batten, D.J. (Eds.), *Evolution and Palaeobiology of Early Sauropodomorph Dinosaurs*. Special Papers in Palaeontology 77, 57–90.
- Upchurch, P., Barrett, P.M., Zhao, X.J., Xu, X., 2007b. A re-evaluation of *Chinshakiangosaurus chunghoensis* Ye vide Dong, 1992 (Dinosauria, Sauropodomorpha): implications for cranial evolution in basal sauropod dinosaurs. *Geological Magazine* 144 (2), 247–262.
- Wagensommer, A., Latiano, M., Leroux, G., Cassano, G., D'Orazi Porchetti, S., 2012. New dinosaur tracksites from the Middle Jurassic of Madagascar: Ichnotaxonomical, behavioural and palaeoenvironmental implications. *Palaeontology* 55 (1), 109–126.
- Whyte, M.A., Romano, M., Elvidge, D.J., 2007. Reconstruction of Middle Jurassic dinosaur-dominated communities from the vertebrate ichnofauna of the Cleveland Basin of Yorkshire, UK. *Ichnos* 14 (1–2), 117–129.
- Wilson, J.A., 2002. Sauropod dinosaur phylogeny: critique and cladistic analysis. *Zoological Journal of the Linnean Society* 136, 217–276.
- Wilson, J.A., Carrano, M.T., 1999. Titanosaurs and the origin of “wide-gauge” trackways: a biomechanical and systematic perspective on sauropod locomotion. *Paleobiology* 25 (2), 252–267.
- Wings, O., Schellhorn, R., Mallison, H., Thuy, B., Wu, W.H., Sun, G., 2007. The first dinosaur tracksite from Xinjiang, NW China (Middle Jurassic Sanjianfang Formation, Turpan Basin) — a preliminary report. *Global Geology* 10 (2), 113–129.
- Wu, X.C., Currie, P.J., Dong, Z.M., Pan, S.G., Wang, T., 2009. A new theropod dinosaur from the Middle Jurassic of Lufeng, Yunnan, China. *Acta Geologica Sinica* (English Edition) 83 (1), 9–24.
- Xing, L.D., 2012. *Sinosaurus* from southwestern China. *University of Alberta, MS Thesis*, 286 pp.
- Xing, L.D., Harris, J.D., Toru, S., Masato, F., Dong, Z.M., 2009a. Discovery of dinosaur footprints from the Lower Jurassic Lufeng Formation of Yunnan Province, China and new observations on *Changpeipus*. *Geological Bulletin of China* 28 (1), 16–29.
- Xing, L.D., Harris, J.D., Feng, X.Y., Zhang, Z.J., 2009b. Theropod (Dinosauria: Saurischia) tracks from Lower Cretaceous Yixian Formation at Sihetun, Liaoning Province, China and possible track makers. *Geological Bulletin of China* 28 (6), 705–712.
- Xing, L.D., Harris, J.D., Currie, P.J., 2011. First record of dinosaur trackway from Tibet, China. *Geological Bulletin of China* 30 (1), 173–178.
- Xing, L.D., Bell, P.R., Rothschild, B.M., Ran, H., Zhang, J.P., Dong, Z.M., Zhang, W., Currie, P.J., 2013a. Tooth loss and alveolar remodeling in *Sinosaurus triassicus* (Dinosauria: Theropoda) from the Lower Jurassic

- strata of the Lufeng Basin, China. *Chinese Science Bulletin (English Version)* 58 (16), 1931–1935.
- Xing, L.D., Lockley, M.G., Li, Z.D., Klein, H., Zhang, J.P., Gierliński, G.D., Ye, Y., Persons IV, W.S., Zhou, L., 2013b. Middle Jurassic theropod trackways from the Panxi region, southwest China and a consideration of their geologic age. *Palaeoworld* 22, 36–41.
- Xing, L.D., Lockley, M.G., Marty, D., Klein, H., Buckley, L.G., McCrea, R.T., Zhang, J.P., Gierliński, G.D., Divay, J.D., Wu, Q.Z., 2013c. 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., Klein, H., Lockley, M.G., Wetzel, A., Li, Z.D., Li, J.J., Gierliński, G.D., Zhang, J.P., Matsukawa, M., Divay, J.D., Zhou, L., 2014. Changpeipus (theropod) tracks from the Middle Jurassic of the Turpan Basin, Xinjiang, Northwest China: new discoveries, ichnotaxonomy, preservation and paleoecology. *Vertebrata PalAsiatica* 52 (2), 233–259.
- Xing, L.D., Peng, G.Z., Ye, Y., Lockley, M.G., Klein, H., Persons IV, W.S., Zhang, J.P., Shu, C.K., Hao, B.Q., in press a. Sauropod and small theropod tracks from the Lower Jurassic Ziliujing Formation of Zigong City, Sichuan, China with an overview of Triassic–Jurassic dinosaur fossils and footprints of the Sichuan Basin. *Ichnos*.
- Xing, L.D., Lockley, M.G., Tang, Y., Klein, H., Zhang, J.P., Persons IV, W.S., Dai, H., Ye, Y., in press b. Theropod and ornithischian footprints from the Middle Jurassic Yanan Formation of Zizhou County, Shaanxi, China. *Ichnos*.
- Xing, L.D., Miyashita, T., Currie, P.J., You, H.L., Dong, Z.M., in press c. A new basal eusauropod from the Middle Jurassic of Yunnan, China, and faunal compositions and transitions of Asian sauropodomorph dinosaurs. *Acta Palaeontologica Polonica*. <http://dx.doi.org/10.4202/app.2012.0151>.
- Yang, X.L., Yang, D.H., 1987. *Dinosaur Footprints of Sichuan Basin*. Sichuan Publishing House of Science and Technology, Chengdu, 30 pp. (in Chinese).
- Young, C.C., 1939. On a new sauropoda, with notes on other fragmentary reptiles from Szechuan. *Bulletin of the Geological Society of China* 19 (3), 279–315.
- Young, C.C., 1948. On two new saurischians from Lufeng, Yunnan. *Bulletin of the Geological Society of China* 28 (1–2), 75–90.
- Young, C.C., 1951. The Lufeng saurischian fauna in China. *Palaeontologia Sinica, New Series C* 13, 1–96.
- Young, C.C., 1954. On a new saurod from Yiping, Szechuan. *Scinetia Sincia* 3 (4), 491–504.
- Zhang, Y., 1988. *The Middle Jurassic Dinosaur Fauna from Dashanpu, Zigong, Sichuan. Vol. II. Sauropod Dinosaurs (I)*. Sichuan Publishing House of Science and Technology, Chengdu, 89 pp. (in Chinese).
- Zhang, Z.X., Li, X.K., 1999. A study on the stratigraphic section bearing the new saurod fauna in Laohangjing, Lufeng. *Yunnan Geology* 18 (1), 72–82 (in Chinese).
- Zhao, X.J., 1985. The Jurassic Reptilia. In: Wang, S.E. (Ed.), *The Jurassic System of China. Stratigraphy of China* 11, 286–289 (in Chinese).
- Zhen, S.N., Li, J.J., Rao, C.G., Hu, S.J., 1986. Dinosaur footprints of Jinning County, Yunnan. *The Memoir of Beijing Natural History Museum* 33, 1–17 (in Chinese, with English abstract).