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# Late Jurassic–Early Cretaceous trackways of small-sized sauropods from China: New discoveries, ichnotaxonomy and sauropod manus morphology

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## ABSTRACT

The growing database on sauropod tracksites, particularly from China, raises questions about hypotheses that wide-gauge sauropod trackways with low heteropody (*Brontopodus*) dominate the global sauropod track record in the Cretaceous. It also raises questions about the definition of narrow-, medium- and wide-gauge trackways and the quality of preservation needed to use such labels reliably. A number of Lower Cretaceous sauropod tracksites from China have yielded trackways of small-sized sauropods with pronounced heteropody that have been named *Parabrontopodus*. These co-occur with medium-sized to large *Brontopodus* trackways giving rise to at least two possible interpretations regarding sauropod trackmakers at these sites: 1) trackways were left by two different, smaller narrow gauge and larger wide gauge, taxonomic groups, 2) trackmakers belong to the same taxonomic group and were narrow gauge when smaller and wide gauge when larger, therefore not maintaining a constant gauge during ontogeny as inferred from some assemblages. The presence of different taxonomic groups is further evidence that narrow gauge trackmakers, previously considered typical of the Jurassic, persisted into the Early Cretaceous. This could be part of a regional trend in East Asia and some other regions such as the Iberian peninsula in Europe, where similar trackways have been found. Alternatively, this could reflect a previously unrecognized global trend. More track and skeletal data are needed to corroborate these hypotheses, because presently essential parameters are missing.



## 1. Introduction

In the Late Jurassic–Early Cretaceous, sauropods were widely distributed among several large dinosaur faunas of China, such as the Late Jurassic *Mamenchisaurus* fauna in the Sichuan and Dzungaria basins (Peng et al., 2005), the *Lanzhousaurus-Huanghetitan* fauna in the Lanzhou-Minhe Basin (You et al., 2006), and the Early Cretaceous Jehol biota in northeastern China (Wang et al., 2007). These sauropods, however, are all large-sized, generally ranging between 10 and 20 m, with no small-sized sauropods known.

Abundant sauropod tracks from the Late Jurassic–Early Cretaceous have been discovered in China, mostly from the Early Cretaceous, from sites such as Chabu, Inner Mongolia (Lockley et al.,

*Abbreviations:* BL, Beilin tracksite, Shandong Province, China; GDM-LT, Litan tracksite, Gansu, China; I, Isolated tracks; L and R, left and right; LG, Provisional Collection (Lin-shi Guancang, LG) of Zhucheng Municipal Museum, Shandong, China; LS, Jishan tracksite, Linshu, Shandong, China; NGZ, Nanguzhai tracksites, Jiangsu, China; P, pes impression; QJD, Qianjiadian tracksite, Beijing, China; S, Sauropod; TDGZ, Tangdigezhuang tracksite, Shandong, China; ZP, Zhongpu tracksite, Gansu, China.

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2002), Linshu, Shandong (Xing et al., 2013), and Zhaojue, Sichuan (Xing et al., 2014a). Among these tracksites, one type of tiny to small sauropod tracks is noteworthy. Commonly their pes prints are approximately 30 cm long, significantly smaller than other medium-sized sauropod tracks from China, such as those from Chabu (60 cm long; Lockley et al., 2002) and Linshu (53 cm long; Xing et al., 2013).

Most tracksites yielding tiny and small sauropod tracks are located within the Lower Cretaceous Dasheng Group of Shandong and neighboring northern Jiangsu Province (Fig. 1, Table 1). In addition, the same track types are also known from the Tuchengzi Formation of Yanqing, Beijing and the Hekou Group of Gansu (Xing et al., 2014b). In 2011, 2012, Wang et al. (2013a) discovered the Beilin tracksite in Tancheng County, Shandong, which is dominated by small sauropod tracks. The first author of this paper investigated the tracksite in 2013. Here, the tracksite is described in detail and tiny to small sauropod tracks from China are systematically reviewed, and discussed in the context of their global record.

There is no scientific reason that the growing track record of sauropods, and related questions of size distribution, morphology (heteropody) and gait (narrow, medium and wide gauge) should not attract as much serious attention as the skeletal record (e.g., Lockley et al., 1995). Indeed tracks may be the only evidence in some areas that lack sauropod body fossils. There is a general consensus that tracks are useful in distinguishing narrow and wide gauge trackmakers as reflected in the sauropodomorph ichnogenera *Parabrontopodus* and *Brontopodus*, respectively. The former have been correlated with diplodocoid sauropods, the latter with titanosauriform sauropods, proving that gait and heteropody patterns help distinguish different sauropod groups (Farlow, 1992; Lockley et al., 1994b. Wilson and Carrano, 1999; Wright, 2005; Henderson, 2006; Romano et al., 2007; Santos et al., 2009; Castanera et al., 2012, 2014; Vila et al., 2013). Ultimately a comprehensive global synthesis of all useful (morphologically diagnostic) sauropod trackway data is just as desirable as an equivalent synthesis of skeletal data. Ideally, the two data sets could be compared and should complement each other synergistically. However, this is a goal for future projects. Here we re-analyze selected sauropodomorph trackways from China and present different working hypotheses that need to be discussed in the future from both ichnological and osteological points of view.

## 2. Geological setting

The Lower Cretaceous Dasheng Group in Shandong represents a set of alluvial fan–fluvial–lacustrine facies of detrital rocks mixed with muddy limestone (Fig. 1). Liu et al. (2003) divided the Dasheng Group from base to top into the Malanggou, Tianjialou, Siqiancun and Mengtuan formations. However, Kuang et al. (2013) considered these units to have a different facies only, but to be contemporaneous. The Tianjialou and Mengtuan formations form the majority of the Jiaolai Basin deposits, which are a set of lacustrine facies deposits dominated by dark gray, yellow green, purple detrital rocks, occasionally mixed with dolomitic mudstones and micrite dolomite (dolomicrite), the thickness exceeding 500 m.

The sediments suggest a shallow lake environment with calcareous concretions horizons developed in the Tianjialou/Mengtuan formations (Kuang et al., 2013). Gymnosperms and ferns flourished indicating that the climate changed in the late Early Cretaceous from humid to arid and warm (Si, 2002). Based on regional geological surveys and biostratigraphy, Kuang et al. (2013)

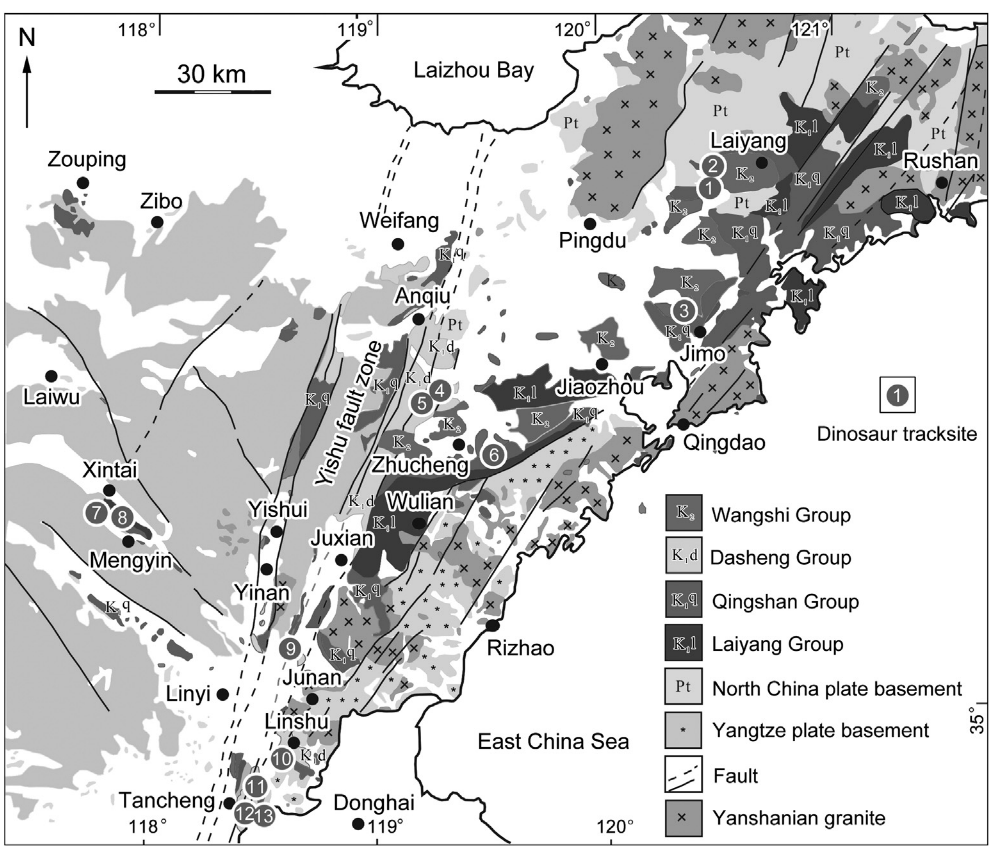


**Fig. 1.** Geographical and geological setting with the position of dinosaur tracksites in Shandong and northern Jiangsu provinces. 1, Shuinan, Laiyang; 2, Huangyandi, Laiyang; 3, Wenxiyuan, Jimo; 4, Zhangzhuhewang, Zhucheng; 5, Tangdigezhuang, Zhucheng; 6, Huanglonggou, Zhucheng; 7, Ningjiagou, Mengyin; 8, Yangzhuang, Mengyin; 9, Houzuoshan, Junan; 10, Jishan, Linshu; 11, Qingquansi, Tancheng; 12, Beilin, Tancheng (this study); 13, Nanguzhai, Donghai.

**Table 1**
Dinosaur tracksites from Shandong and northern Jiangsu Province.

| No. | Site | The type of tracks | Group | References |
|---|---|---|---|---|
| 1 | Shuinan, Laiyang | theropod | Lower Cretaceous<br>Laiyang Group | Li and Zhang, 2000<br>Xing et al., 2010a |
| 2 | Huangyandi, Laiyang | theropod<br>bird<br>crocodylian | Lower Cretaceous<br>Laiyang Group | Matsukawa et al., 2006<br>Lockley et al., 2010 |
| 3 | Wenxiyuan, Jimo | theropod<br>pterosaur | Lower Cretaceous<br>Laiyang Group | Xing et al., 2012 |
| 4 | Zhangzhuhewang, Zhucheng | sauropod<br>ornithopod<br>bird | Lower Cretaceous<br>Dasheng Group | Xing et al., 2010a |
| 5 | Tangdigezhuang, Zhucheng | sauropod | Lower Cretaceous<br>Dasheng Group | Wang et al., 2013a |
| 6 | Huanglonggou, Zhucheng | theropod<br>sauropod<br>turtle | Lower Cretaceous<br>Laiyang Group | Li et al., 2011<br>Lockley et al., 2012 |
| 7 | Ningjiagou, Mengyin | sauropod | Lower Cretaceous<br>Laiyang Group | Unpublished data |
| 8 | Yangzhuang, Mengyin | theropod | Middle-Upper Jurassic<br>Zibo Group | Li et al., 2002 |
| 9 | Houzuoshan, Junan | theropod<br>ornithopod<br>bird | Lower Cretaceous<br>Dasheng Group | Li et al., 2005a,b, 2007;<br>Lockley et al., 2007, 2008 |
| 10 | Jishan, Linshu | theropod<br>sauropod<br>ornithischian | Lower Cretaceous<br>Dasheng Group | Xing et al., 2013 |
| 11 | Qingquansi, Tancheng | sauropod | Lower Cretaceous<br>Dasheng Group | Xing et al., in press |
| 12 | Beilin, Tancheng | sauropod | Lower Cretaceous<br>Dasheng Group | Wang et al., 2013b<br>This text |
| 13 | Nanguzhai, Donghai | theropod<br>sauropod | Lower Cretaceous<br>Dasheng Group | Xing et al., 2010b |

considered that the Tianjialou/Mengtuan formations were formed in the late Aptian–Albian, about 110–100 Ma.

The Beilin tracksite is situated to the east of Beilin Village, Tancheng County, Shandong Province (Fig. 1). There are 19 dinosaur tracks exposed on an outcrop that is 4 m long and 2.5 m wide. The tracks at the Beilin tracksite are preserved in brick-red, medium-thick-bedded, medium, grained sandstone and siltstone, with medium-sized planar to wedge shaped bedding, and medium-small ripple marks that suggest delta plain deposits (Wang et al., 2013a).

## 3. Material and methods

The dip of the bedding planes of the Beilin tracksite is 25°, which allows easy access to the tracks for measurements and identification of the tracks. In order to make accurate maps, all the tracks from both sites were photographed, outlined in chalk, and traced on large sheets of transparent plastic. Videotaping was employed to convert the full size tracings to a digital format. All tracings are reposited in China University of Geosciences (Beijing).

For the trackways of quadrupeds, gauge (trackway width) was quantified for pes and manus tracks using the ratio between the width of the angulation pattern of the pes (WAP) or manus (WAM) and the pes length (P'L) or manus width (M'W), respectively (according to Marty, 2008; Marty et al., 2010a). The WAP/P′L-ratio and WAM/M'W-ratio were calculated from pace and stride length, assuming that the width of the angulation pattern intersects the stride at less than a right angle and at the approximate midpoint of the stride (Marty, 2008). If the WAP/P′L-ratio equals 1.0, the pes tracks are likely to touch the trackway midline. If the ratio is smaller than 1.0, tracks intersect the trackway midline, and are considered to be narrow-gauge (see Farlow, 1992). Accordingly, a value of 1.0 separates narrow-gauge from medium-gauge trackways, whereas the value 1.2 is arbitrarily used as the demarcation between medium-gauge and wide-gauge trackways, and trackways with a value higher than 2.0 are considered to be very wide-gauge (Marty, 2008) so that the classification of trackways based on gauge matches well with the one proposed by Romano et al. (2007).

For the classification of sauropod trackmaker size, the following sizes classes are used (Marty (2008; see also Castanera, 2012): tiny (P′L > 25 cm), small (25 cm ≤ P′L < 50 cm), medium-sized (50 ≤ P′L < 75 cm), large (P′L > 75 cm).

## 4. Beilin tracksite, Tancheng area

The Beilin tracksite yielded two small pes-only sauropod trackways, catalogued as BL-S1 and S2, respectively. In addition, there are isolated pes tracks, catalogued as SIP1–6. Some of the Beilin sauropod tracks even fall into the "tiny" (P′L < 25 cm) category. All tracks are natural impressions (concave epireliefs) (Figs. 2–3). However, most tracks are poorly-preserved due to backfilling of muddy sediments after foot withdrawal. Due to overprinting by the pes, manus prints are absent. This is a common phenomenon in the trackway record of sauropods (Lockley et al., 2012). Three pes tracks preserve more distinct morphological characteristics. The imprints BL-S1-RP4 and BL-SIP2 show three digit traces; the L/W ratio of these tracks is 1.2. Digit II of the pes is longer than the outer digits, whereas digit I is usually broader and more robust than the other two digits. The metatarsophalangeal pad region is smoothly curved. In BL-S2-LP3, some fine-grained, muddy sediment still adheres as infill to the impressions of digit I–III, leading to a deep pod-shaped structure. Three convex structures inside of the track probably represent three digits.

Both trackways are at the limit between narrow- and medium-gauge trackways, as indicated by a WAP/P′L-ratio of 1.0 (Table 2). In the trackways BL-S1 and S2, the pes tracks show a pronounced outward rotation relative to the midline (15° on average, ranging 6°–24°; 20° on average, ranging 4°–35°, respectively). The pace angulation is 92° (BL-S1)–99° (BL-S2). Using the equation to

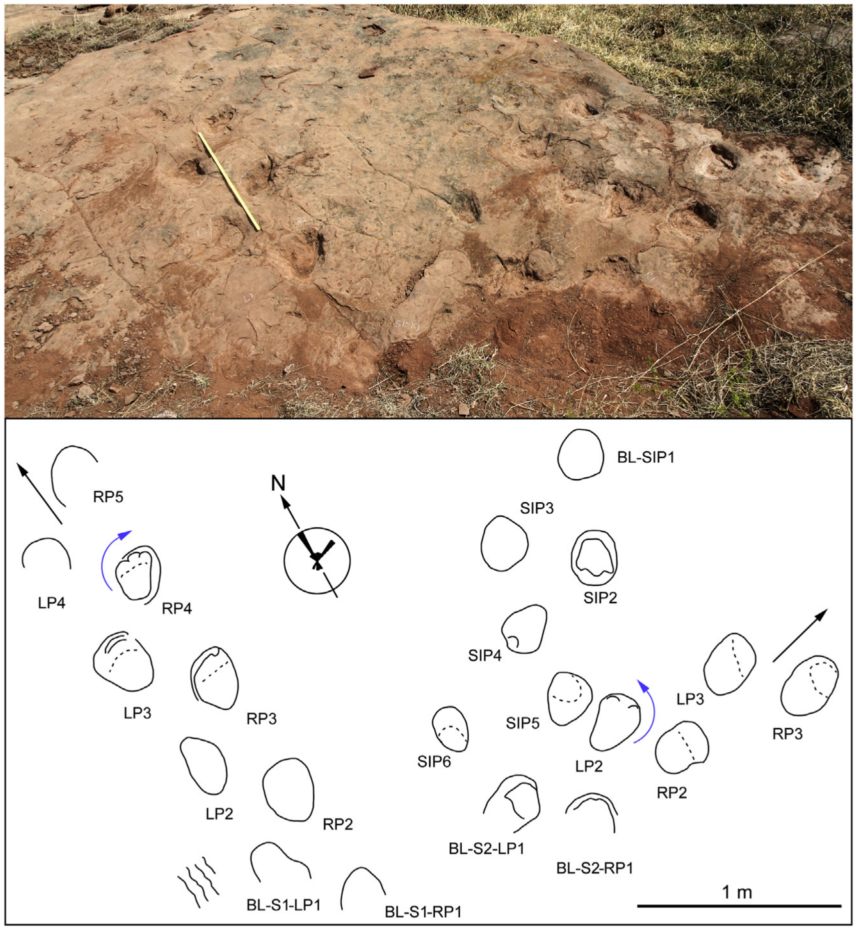


**Fig. 2.** Photograph and interpretative outline drawing of the track-bearing level at Beilin tracksite.

estimate speed from trackways (Alexander, 1976; Thulborn, 1990), the trackmakers are walking (SL/h $\leq$ 2.0); the mean locomotion speeds of the trackmakers are between 0.65 and 1.04 km/h and 0.68–1.08 km/h (Table 3).

The Beilin tracksite is situated approximately 1 km to the southwest of the Nanguzhai tracksite (Fig. 1), from where Xing et al. (2010a) described two different size classes of sauropod tracks and one theropod trackway. Regarding morphology, Beilin sauropod tracks are similar to the small-sized sauropod tracks NGZ-T2 and T3 at Nanguzhai (Fig. 4A). NGZ-T2 has six pes prints and one manus print, whereas T3 has one corresponding (partial) manus print for each pes, but some manus prints are poorly-visible dur to track fills (Xing et al., 2010a, Figs. 7B and 8).

## 5. Small sauropod tracks from China

Small sauropod trackways of the type found at the Beilin tracksite, often with strongly outwardly rotated manus prints (Fig. 4), appear to have a wide distribution in China. Besides the Beilin tracksite, this type of sauropod trackway occurs at seven other tracksites (Fig. 5, Table 4):

### 1) Nanguzhai tracksites, Jiangsu

The Nanguzhai tracksite is situated in Donghai County, Jiangsu Province, and belongs to the Lower Cretaceous Tianjialou Formation (upper Aptian–Albian), Dasheng Group. There are two well-preserved trackways (NGZ-T2 and T3) (Fig. 4A) and one poorly-preserved trackway (NGZ-T6). On the same stratum, large-sized sauropod tracks (roughly 50–60 cm long) and a theropod trackway are preserved. The orientation is basically bimodal to T2, T3 and T6.

NGZ-T2 and T3 are narrow gauge trackways. In the well-preserved manus prints NGZ-T3.6a, digits I–V are discernable. However, the soft sediments led to the infilling with mud that resulted in deformation at the border between digits II–IV, but most pes traces have distinct digits I–III. The metatarsophalangeal pad region of the pes is smoothly curved, and there is a constriction at the middle-posterior region of the track (at roughly 70% of the length). The heteropody of the well-preserved manus:pes track couplesis 1:3.7. Xing et al. (2010a) attributed the trackways to *Parabrontopodus* isp.

### 2) Zhangzhuhewan tracksite, Shandong.

The Zhangzhuhewan tracksite is situated in Zhucheng City, Shandong Province, and belongs to the Lower Cretaceous Tianjialou Formation, Dasheng Group. Xing et al. (2010b) described some tracks at the Zhucheng Dinosaur Museum from the Zhangzhuhewan tracksite. These tracks contain sauropod, bird, and possible ornithopod tracks (Xing et al., 2010b). The sauropod pes-dominated trackway of a small-sized individual LG.1 at the Zhangzhuhewan tracksite is poorly preserved and shows pes traces of oval shape which lack impressions of the digits (Fig. 4B).

### 3) Tangdigezhuang tracksite, Shandong

The Tangdigezhuang tracksite is located 2 km north of the Zhangzhuhewan tracksite, and belongs to the Lower Cretaceous

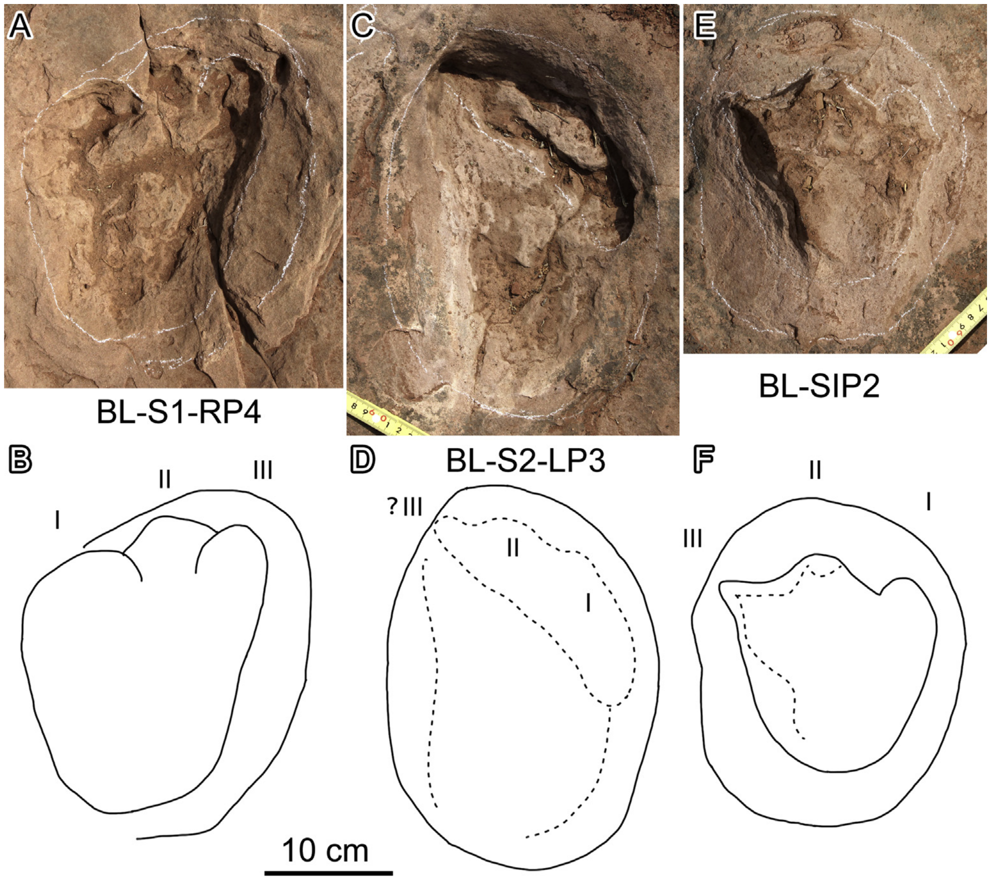


**Fig. 3.** Photographs (A, C, E) and interpretative outline drawings (B, D, F) of three well-preserved sauropod pes tracks from Beilin tracksite.

**Table 2**
Measurements (in cm) of the sauropod tracks from Beilin tracksite, Shandong Province, China.

| Number | L | W | R | PL | SL | PA | L/W | WAP | WAP/P'L |
|---|---|---|---|---|---|---|---|---|---|
| BL-S1-RP1 | – | – | – | 48.0 | 64.5 | – | – | – | – |
| BL-S1-LP1 | – | – | – | 42.5 | 63.2 | – | – | – | – |
| BL-S1-RP2 | 31.1 | 23.7 | 18° | 47.5 | 64.6 | 95° | 1.3 | – | – |
| BL-S1-LP2 | 31.1 | 18.0 | 6° | 42.5 | 62.0 | 90° | 1.7 | 30.4 | 1.0 |
| BL-S1-RP3 | 30.0 | 21.6 | 12° | 46.6 | 61.0 | 90° | 1.4 | 32.0 | 1.1 |
| BL-S1-LP3 | 30.5 | 26.0 | – | 44.0 | 60.0 | – | 1.2 | 32.8 | 1.1 |
| BL-S1-RP4 | 26.5 | 22.0 | 24° | 41.0 | 60.0 | – | 1.2 | – | – |
| BL-S1-LP4 | – | – | – | 45.6 | – | – | – | – | – |
| BL-S1-RP5 | – | – | – | – | – | – | – | – | – |
| Mean-P | 29.8 | 22.3 | 15° | 44.7 | 62.2 | 92° | 1.4 | 31.7 | 1.0 |
| BL-S2-LP1 | 30.3 | 23.0 | – | 38.0 | 63.0 | – | 1.3 | – | – |
| BL-S2-RP1 | – | – | – | 53.4 | 58.5 | – | – | – | – |
| BL-S2-LP2 | 30.0 | 21.2 | 35° | 39.5 | 63.0 | 94° | 1.4 | – | – |
| BL-S2-RP2 | 26.9 | 21.3 | 4° | 49.0 | 70.8 | 104° | 1.3 | 29.4 | 1.1 |
| BL-S2-LP3 | 30.2 | 20.2 | – | 43.0 | – | – | 1.5 | 27.6 | 0.9 |
| BL-S2-RP3 | 31.3 | 20.6 | – | – | – | – | 1.5 | – | – |
| Mean-P | 29.7 | 21.3 | 20° | 44.6 | 63.8 | 99° | 1.4 | 28.5 | 1.0 |
| BL-SIP1 | 24.0 | 22.4 | – | – | – | – | 1.1 | – | – |
| BL-SIP2 | 26.2 | 21.2 | – | – | – | – | 1.2 | – | – |
| BL-SIP3 | 26.0 | 21.5 | – | – | – | – | 1.2 | – | – |
| BL-SIP4 | 26.0 | 21.0 | – | – | – | – | 1.2 | – | – |
| BL-SIP5 | 25.7 | 21.0 | – | – | – | – | 1.2 | – | – |
| BL-SIP6 | 22.3 | 14.3 | – | – | – | – | 1.6 | – | – |

Abbreviations: L: Length; W: Width; R: Rotation; PL: Pace length; SL: Stride length; PA: Pace angulation; L/W: length/width; WAP: Width of the angulation pattern of the pes (calculated value); WAM: Width of the angulation pattern of the manus (calculated value); WAP/P'L and WAM/M'W are dimensionless.

Tianjialou Formation. Wang et al. (2013b) preliminarily described these tracks. The first author of this paper investigated these tracks in 2013, and a resulting description is in preparation. Besides the trackways of small-sized sauropods (TDGZ-S1 and TDGZ-S2) (Fig. 4C), large-sized sauropod tracks of 70–80 cm long were discovered at the Tangdigezhuang tracksite.

Differing from other trackways of small-sized sauropods, TDGZ-S1 and TDGZ-S2 are a rare example of turning trackways (e.g. Ishigaki and Matsumoto, 2009; Castanera et al., 2012, 2014), showing an increase of the footprint rotation angle during turn. Two trackways consist mostly of pes traces. In TDGZ-S1, the pes print TDGZ-S1-LP3 is well preserved with three discernable digital impressions. Most manus tracks in TDGZ-S1 are oval, narrowing at mid-length and the metacarpophalangeal pad region.

4) **Jishan tracksites, Shandong**

The Jishan tracksite is situated in Linshu County, Shandong Province, and belongs to the Lower Cretaceous Tianjialou Formation. Xing et al. (2013) described this assemblage, which includes trackways of small-sized and medium-sized sauropods

**Table 3**
Estimated data of the speed of Beilin sauropod trackmakers.

| No. | F = 5.9 | | F = 4 | |
|---|---|---|---|---|
| | SL/h | S (km/h) | SL/h | S (km/h) |
| BL-S1 | 0.35 | 0.65 | 0.52 | 1.04 |
| BL-S2 | 0.36 | 0.68 | 0.54 | 1.08 |

Abbreviations: F, hip height conversion factors; SL/h, relative stride length; S, speed.

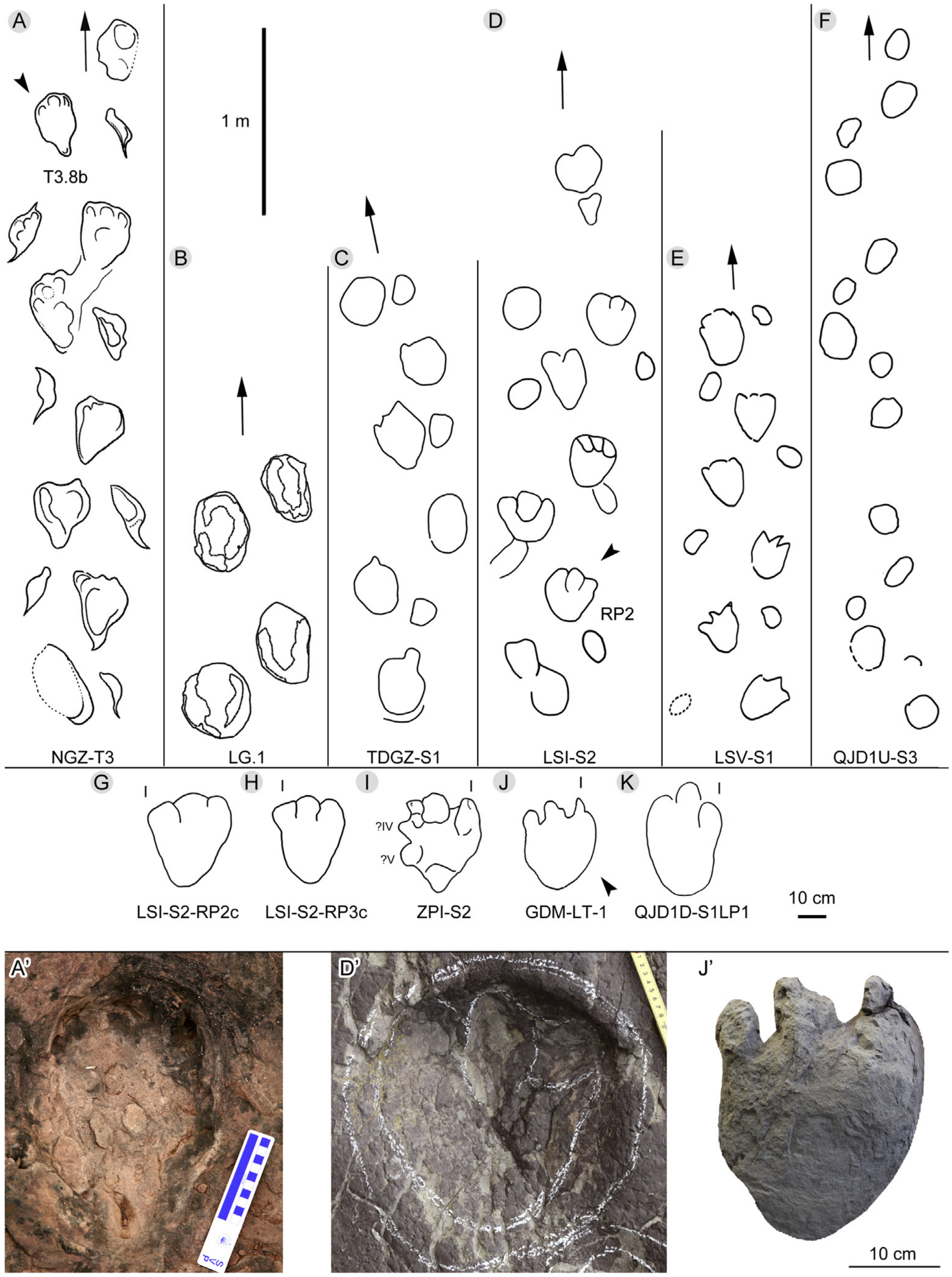


**Fig. 4.** Different tracks and trackways of small sauropods from China. A, NGZ-T3 from Nanguzhai tracksite, Donghai; B, LG.1 from Zhangzhuhewang tracksite, Zhucheng; C, TDGZ-S1 from Tangdigezhuang tracksite, Zhucheng; D and E, LSI-S2, LSV-S1 from Jishan traqcksite, Linshu; F, QJD1U–S3 from Qianjiadian tracksite, Beijing; G and H, LSI-S2-RP2c and LSI-S2-RP3c casts from Jishan tracksite, Linshu; I, ZPI-S2 mold from Zhongpu tracksite, Gansu; J, GDM-LT-1 cast from Litan tracksite, Gansu; K, QJD1D-S1LP1 mold from Qianjiadian tracksite, Beijing. Photographs of NGZ-T3-T3.8b (A′), LSI-S2-RP2 (D′) and GDM-LY-1 (J′).

(53.0–67.5 cm long). Theropod tracks and ornithischian tracks are also preserved.

In the trackways of small-sized sauropods, LSI-S2 (Fig. 4D) and LSV-S1 (Fig. 4E) are the best-preserved, and are narrow-gauge. LSI-S2 was preserved in soft sediments (imprints are up to 8–10 cm in depth), thus many details are preserved. Most manus traces are oval, narrowing at mid-length at the metacarpophalangeal pad region. All of the well-preserved pes tracks have three well-developed digit impressions. Digit I is usually broader and more robust than the other two digits, and digit III is longer than the outer digits. The metatarsophalangeal pad region is smoothly curved. Remarkably, LSI-S2 preserves three natural casts (Fig. 4G, H). No impressions of digits IV or V are preserved. LSI-S2 and LSV-S1 show a high heteropody, the surface area ratio of the manus:pes traces being 1:3.5.

When Xing et al. (2013) described the trackways of small-sized sauropods from the Jishan tracksite, differences to thyreophoran tracks (such as *Deltapodus* Whyte and Romano, 1994, 2001) were further analyzed. The latter usually lack a strong outward rotation of the manus traces (see Cobos et al., 2010), whereas sauropod trackways with strongly outwardly rotated manus traces are common (e.g., trackways of small sauropods from southern South

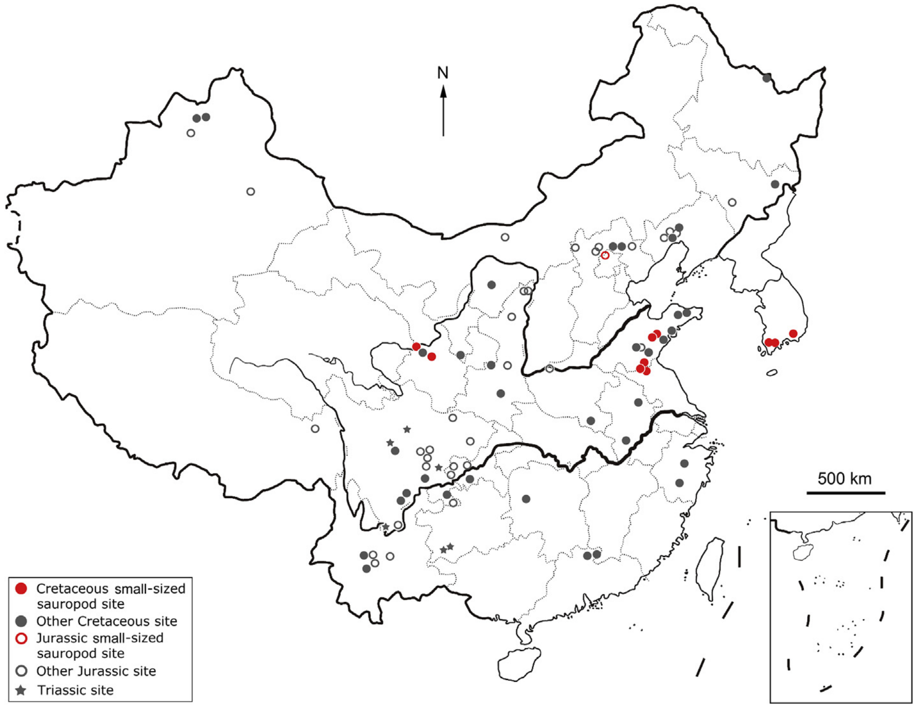


**Fig. 5.** Distribution of small sauropod tracks from China and South Korea.

**Table 4**
Measurements of small-sized sauropod tracks from China.

| Tracksite | Manus prints | | | Pes prints | | | | |
|---|---|---|---|---|---|---|---|---|
| | L (cm) | L/W | R | L (cm) | L/W | R | WR | H |
| Nanguzhai | 9.4 | 0.6 | 50°–70° | 35.1–35.7 | 1.4–1.5 | 24°–32° | 0.8 | 1:3.0 |
| Zhangzhuhewan | – | – | – | 37.4–44.5 | 1.4–1.5 | 6°–24° | 0.9 | – |
| Tangdigezhuang | 11.3–12.0 | 0.5–0.7 | 131° | 30.4–38.5 | 1.2–1.3 | 75°–91° | 1.2 | 1:3.4 |
| Jishan | 8.5–13.7 | 0.6–0.7 | 51°–53° | 27.0–27.1 | 1.0–1.3 | 16°–20° | 0.9 | 1:3.5 |
| Beilin | – | – | – | 29.7–29.8 | 1.4 | 15°–20° | 1.0 | – |
| Zhongpu | – | – | – | 29.5–33.7 | 1.2 | – | – | – |
| Litan | – | – | – | 29.5 | 1.3 | – | – | – |
| Qianjiadian | 11.6–16.5 | 0.6–0.7 | 65°–86° | 22.7–37.3 | 1.4 | 28°–39° | 1.3 | 1:2.2 |

Abbreviations: L: Length; L/W: length/width; R: Rotation; WR: WAP/P′L-ratio; H: heteropody.

Korea; Lim et al., 1989: Fig. 35.4A). The preservation of only three digital impressions is a widespread phenomenon in sauropod tracks but also in some thyreophorans as in stegosaurians. However, the strong outward rotation of the manus appears to be an anatomical signal indicating that the trackmakers of the Jishan trackways LSI-S2 and LSV-S1 are more likely sauropods than thyreophorans. They are assigned here to *Parabrontopodus* isp. on the basis of the narrow-gauge and the high heteropody.

5) **Zhongpu tracksite, Gansu**

The Zhongpu tracksite is situated in Zhongpu County, Gansu Province, and belongs to the Lower Cretaceous, the lower part of the 4th or 5th informal formation-level units of the Hekou Group (Barremian, Hayashi, 2006). In 2013, the first author investigated the tracksite, which contains sauropod and theropod trackways (Xing et al., 2014b). The sauropod tracks are small (29.5–33.7 cm) and large-sized (to 106.0 cm), but there are only two small sauropod tracks at the Zhongpu tracksite. No trackways could be identified. However, these tracks exhibit possible digit IV and V impressions. Digits I–?III of ZPI-S2 (Fig. 4I) resemble other small-sized sauropod tracks in morphology, but they may be affected by preservation. The lateral side of the track has two faint indentations, which might represent digits IV and V. The inferred trace of digit V is a round impression that probably represents a blunt pad or callosity.

The location of digits IV and V from the Zhongpu small-sized sauropod tracks differs from that in large-sized sauropod pes traces. Compared with well-preserved sauropod tracks, such as *Brontopodus birdi* (Farlow et al., 1989), their pes prints have four claw marks, claws I–II with an anterior orientation, and III–IV anterolaterally oriented. Contrary, the claw impressions of a typical sauropod pes are directed anterolaterally for digits I–III and laterally for digits IV–V, and they decrease in size laterally from digit I (Bonnan, 2005; Wright, 2005).

6) **Litan tracksite, Gansu**

The Litan tracksite is situated near Yanguoxia Town, Yongjing County, Gansu Province, and belongs to the Lower Cretaceous the 6th informal formation-level of Hekou Group. In 2013 one small-sized sauropod pes cast (GDM-LT-1) was discovered (Xing et al., 2015a) (Fig. 4J). The location of the three digits of GDM-LT-1 correspond to digits I–III. The claw mark of digit I is robust and has a tapering end, whereas that of digit II is round and blunt. Digit III is small but its terminal end is damaged.

There are at least two possible small-sized sauropod tracks at the Yanguoxia tracksite I (main site). These are pes tracks with three digit impressions in the sickle shaped structure (similar to BL-S2-LP3 from the Beilin tracksite). Their arrangement is similar to that in a trackway from the Beilin tracksite, which is presumed to represent undertracks.

7) **Qianjiadian tracksite, Beijing**

The Qianjiadian tracksite is situated in Yanqing County, Beijing, belonging to the Tuchengzi Formation at the Jurassic-Cretaceous boundary, which is the oldest stratum presently yielding small-sized sauropod tracks in China. The tracksite also yielded medium- and large-sized sauropod tracks (length ranges between 50.0 and 80.0 cm), theropod tracks in various sizes and possible ornithopod tracks.

Among the trackways of small-sized sauropods from Yanqing, QJD1D-S1 (Fig. 4K) and QJD1U–S3 (Fig. 4F) are the best preserved, representing narrow-gauge to medium-gauge trackways. The center of the pes tracks is positioned closer to the trackway midline than that of the manus tracks. In QJD1D-S1, the manus tracks are oval, narrowing at mid-length and the metacarpophalangeal pad region. All of the well-preserved pes traces have three well-developed digit impressions, which are consistent with other small-sized sauropod tracks in morphology.

Zhang et al. (2012) attributed Morphotype B to thyreophoran tracks, cf. *Deltapodus* isp. Xing et al. (2015b) attributed Morphotype B to small-sized sauropod tracks based on the general trackway pattern with the manus being strongly outward rotated. In terms of sheer numbers, the Qianjiadian tracksite preserves more of these track types than any other locality in China.

## 6. Comparison and discussion

Both narrow- and wide-gauge sauropod trackways (*Parabontopodus* and *Brontopodus* respectively) are relatively common in the Jurassic (e.g., Lockley et al., 1994a, b; Meyer and Pittmann, 1994, Meyer et al., 1994; Wilson and Carrano, 1999; Wright, 2005; Marty et al., 2010a), but *Parabrontopodus* is rare in the Cretaceous. *Parabrontopodus* exhibits high heteropody, whereas *Brontopodus* exhibits lower heteropody. Thus, the gauge differences first pointed out by Farlow (1992) helped defined a polarity, also integrating trends in heteropody, between narrow-gauge, small-manus morphotypes correlated with smaller narrow diplodocid-like trackmakers, and wide-gauge, large manus morphotypes correlated with brachiosaurid and titanosauriform trackmakers. It was argued that such polarities are evident in other non-sauropodomorph clades (Lockley, 2001, 2007), and therefore suggest that intrinsic morpholodynamic polarities reiterate across diverse clades. The implication is not that intermediate morphotypes do not exist. Rather the inference is that intermediates are not the result of random variation between polar extremes, but rather part of understandable reiterative processes. Despite recognizing both two fold morphological polarities in some clades and threefold organization, with intermediates in other clades. Lockley et al. (1994b) did not define a medium gauge category, as done by Meyer et al. (1994) and Marty (2008).

The updated track record from China supports previous evidence (Wright, 2005; Romano et al., 2007; Moratalla, 2009; Castanera et al., 2012, 2014), suggesting that the simplified polarity model, or framework, needs refinement. As noted above, as *Parabrontopodus* is recorded from the Cretaceous of China quite frequently. This raises questions for the (1) determination of narrow, medium and wide gauge (using pes and manus track configurations as explained above), (2) quality of preservation needed to assign tracks to one of these categories, (3) gauge as a possible function of size tending to be wider in larger individuals (cf. Lockley et al., 2002), (4) distinction between narrow and wide gauge tracks that could be blurred by the inclusion of the intermediate "medium gauge" category, and (5) abundance of narrow gauge sauropod trackways in the Cretaceous of China that could be due to regional variation instead of a global trend. While these questions cannot be answered here finally, they underline the importance of multiple working hypotheses that might be useful in future studies of sauropod trackways. In short, the two-fold polarity model fits morphological extremes of sauropodomorph morphology that can be correlated with the skeletal record, but we have yet to be able to determine whether intermediate morphotypes can be correlated with known skeletal morphologies. It is also currently impossible to say whether intermediate gauge and heteropody types can be understood in terms of the morphodynamic spectrum (sensu Lockley, 2001, 2007). While the polar extreme morphotypes are by definition extreme and so easily differentiated in a two-fold scheme, the middle or intermediate groups are by definition less easy to differentiate, and may in fact display behavioral vacillation or "switching" between extreme behaviors as the expression of a middle morphologies and behaviors in a threefold system.

### *6.1. Characteristics and distribution of small sauropod tracks from China and Korea*

In general, small sauropod tracks (25–40 cm) from China are characterized by.

1) narrow to medium gauge (WAP/P′L-ratio = 0.8–1.3);
2) high heteropody (1:2.2–1:3.5);
3) strongly outwardly rotated manus traces, approximately by 50°–130°;
4) pes traces with anteriorly directed, particularly well-developed digit impressions; in rare cases, digits IV and V left indistinct impressions.
5) extended stratigraphic range and distribution throughout the Early Cretaceous in northwestern, northern and eastern China, with a few occurrences at the Jurassic-Cretaceous boundary.

Thus far no body fossils corresponding to a potential quadrupedal dinosaur trackmaker have been discovered from the above-mentioned regions, which is unusual for China.

Xing et al. (2010, 2013) assigned the small-sized sauropod trackways from the Nanguzhai tracksite and the Jishan tracksite to *Parabrontopodus* isp. Based on the narrow-gauge and the high heteropody, the trackmakers are presumed to have been small sauropods.

Besides these records, there are also other small sauropod tracks discovered in China, including trackway 2 from the Du Situ River at the Chabu 6 sauropod tracksite from Inner Mongolia. The manus prints of the Chabu specimens only have a small outward rotation, approximately 12° (based on Lockley et al., 2002: Fig. 4). The trackways were attributed to *Brontopodus* (Lockley et al., 2002; Li et al., 2011), based on the relatively large manus (low heteropody), although it was noted that the trackway of the smallest trackmaker (no.2) was "essentially narrow gauge", whereas that of the larger one indicated a "wider gauge" (Lockley et al., 2002, p. 371). Therefore, the presence of *Parabrontopodus* isp. in the Chabu localities cannot be excluded.

Small quadrupedal trackways from China are mostly known from Shandong Province, the major region for track research in

China. With the exception of the Middle-Upper Jurassic Santai Formation yielding a small number of tracks (Li et al., 2002), the dinosaur tracks in Shandong were mostly discovered in two units of the Lower Cretaceous: the Laiyang Group (130–120 Ma), representing the lower subdivision of the Lower Cretaceous, and the Dasheng Group (110–100 Ma), representing the upper subdivision of the Lower Cretaceous (Kuang et al., 2013). No sauropod tracks have been discovered from the Middle-Upper Jurassic so far. The sauropod tracks from the Laiyang Group were discovered at two tracksites: Huanglonggou and Mengyin (Lockley et al., 2015). The sauropod tracks from the Dasheng Group are known from multiple localities except the Houzuoshan Dinosaur Park site (Table 1).

The sauropod tracks from the Dasheng Group are mostly distributed in the Yishu fault zone along an axis directed north-northeast, between northwestern Jiangsu and central Shandong provinces (Zhucheng– Junan– Linshu– Tancheng) (Table 1). Of these tracksites, the Jishan tracksite preserves the highest ichnodiversity of the Chinese tracksites. The Jishan sauropod tracks that can be assigned to the ichnogenera (*Parabrontopodus* and *Brontopodus)* (Xing et al., 2013).

Several trackways of smallmedium-sized sauropods are known from South Korea. One uncatalogued trackway from the Samcheonpo tracksite, Goseong (Lim et al., 1989: Fig. 35.4A), has a P'L of 19.2 cm. There are three digits discernable and the outward rotation of the pes traces is approximately 30°. The manus print is oval, its mean length is approximately 10.2 cm, and its outward rotation is approximately 29°. Although the pes prints resembles the small *Parabrontopodus* isp. from China in morphology, the outward rotation of the manus prints is smaller than in the specimens from China.

As shown by Lockley et al. (2006), the large Korean sauropod trackway assemblage from Goseong County is dominated by trackways of small sauropods. These have been assigned to *Brontopodus*, because like the larger trackways, they are consistently wide gauge. Thus, there is no compelling reason to infer different taxonomic groups of trackmakers.

### 6.2. Different ontogenetic stages or different species?

Almost all small sauropod tracks were preserved along with medium-sized to large sauropod tracks. Although the Litan, the Zhangzhuhewan, and the Beilin tracksites preserved small tracks only, medium-sized to large sauropod tracks were found in the same strata or nearby localities. These medium-sized to large sauropod tracks are attributed to *Brontopodus* (Xing et al., 2013). Typical examples are the Jishan and the Qianjiadian tracksite. There are at least two kinds of sauropod trackways showing different sizes and morphologies of tracks, suggesting that there may have been at least two different kinds of sauropods. Xing et al. (2010b) considered that the Nanguzhai small sauropod tracks were left by juvenile individuals of large sauropods. This possibility suggests that during ontogenetic growth, sauropod gauge may have changed from narrow to medium or wide. Alternatively, a reinterpretation based on increased sample size, suggests that differences in heteropody and gauge could indicate different taxonomic groups rather than juveniles and adults of the same trackmaker taxon.

According to Myers and Fiorillo (2009), juvenile and adult sauropods may have adopted different feeding and herding strategies, resulting in their segregation, which has been noted for example in titanosauriforms such as *Alamosaurus* and some diplodocids (see also Castanera et al., 2011, 2014). Sauropod skeletal fossils from China indicating this kind of behavior include the camarasauromorph *Bellusaurus sui* (Dong, 1990) from the Middle Jurassic Wujiawan Formation of the Dzungaria Basin, Xinjiang. 17 juvenile individuals of *Bellusaurus* with overall body lengths of 4–5 m have been found in the same bonebed (Dong, 1990). Most of the Early Cretaceous sauropods are attributed to Titanosauriformes (Weishampel et al., 2004; Rogers and Wilson, 2005). Vila et al. (2013) stated that the wide gauge condition reported from trackways of small and large titanosaurs implies similar body (trunk and limb) proportions despite large differences in body size. Contrary, at the Jishan and Qianjiadian tracksites, small sauropod trackways are narrow-to medium-gauge, whereas the medium-sized to large sauropod tracks are wide-gauge. This indicates that the trackmakers of medium-sized and large-sized sauropod trackways at these localities pertain to different taxonomic groups.

### 6.3. Walking gaits

Bonnan (2003) and Bonnan and Yates (2007) have suggested that pronation of the manus was a necessary adaptation in sauropods to allow for propulsion of the forelimb in concert with the hindlimb. Modeling of the forelimbs (Wilhite, 2003) and manus posture (Bonnan, 2003) in sauropods suggests that active pronation and supination of the manus were greatly restricted if not impossible. Manus movements themselves would have been largely restricted (Bonnan, 2003) because the known morphology of the carpal elements precludes extensive flexion and extension, let alone long-axis rotation. These morphological observations of limited manus mobility are supported by sauropod manus tracks that show the forefoot going into and out of the sediment without evidence of non-vertical movements (Milán et al., 2005; Romano and Whyte, 2012). Moreover, the radius morphology of sauropods does not resemble those of graviportal mammals wherein the radius crosses over the ulna to pronate the manus (VanBuren and Bonnan, 2013). Related morphometric studies on the forelimbs and hindlimbs of sauropods (Bonnan, 2004, 2007) further suggest that the greatest amount of movement occurred at the glenoid and acetabulum, with a more restricted range of movements occurring in the more distal elements.

Given these parameters, the strongly outwardly rotated manus prints (50°–130°) in trackways of small sauropods described here suggest the following. First, sauropod manus placement and orientation was not tightly constrained within individuals. Second, given the range of outward rotation of the manus in the prints described here and elsewhere (e.g., Santos et al., 1994), manus pronation was perhaps not as critical to locomotion as it appears to be in graviportal eutherian mammals (Hutson, in press; Bonnan, 2003). This suggests that propulsion of the forelimb did not require the degree of wrist flexion commonly observed in mammals. This is not to suggest that the forelimb played no role in moving the animal. Instead, the mechanics of the forelimb in sauropods must have differed from those of graviportal mammals, taxa often used as analogs for sauropod locomotion. Third, given what is known about movement in the sauropod forelimb, such variation and outward rotation of the manus in these trackways suggests movements of abduction, adduction, and long-axis rotation of the humerus about the glenoid occurred regularly in these sauropod trackmakers. This would follow from the observation that small movements proximally in a long forelimb would translate into more substantial movements distally (Carrano, 2005; Bonnan, 2007).

The orientation of the manus prints is intriguing to consider in light of recent studies by Holliday et al. (2010) and Bonnan et al. (2010, 2013) on archosaur articular cartilage. Unlike graviportal mammals in which a very thin layer of articular cartilage may constrain the range of movements to more stereotyped patterns to avoid joint injury (Bonnan et al., 2013), it is likely that sauropods retained centimeters of cartilage on their joints into adulthood

(Bonnan et al., 2010, 2013; Holliday et al., 2010). This difference in articular cartilage thickness may have had the effect of allowing for a greater range of “safe” orientations during locomotion, perhaps in relation to factors such as terrain topography and the properties of the sediment. In essence, the forelimb could perhaps passively adjust to the changing vagaries of the ground.

Overall, the data presented here suggest that sauropod forelimb posture and manus orientation were not tightly constrained. Perhaps passive adjustments and small proximal movements at the glenoid served functionally to ensure that such huge animals fully planted their manus in support during each footfall. These sauropod manus prints collectively suggest that pronation for propulsion, an apparent necessity for graviportal mammals, was a less significant factor in locomotion than simple support in sauropods.

### 6.4. *Endemic ichnofauna*

A number of recent studies have concluded that the Early Cretaceous ichnofaunas of East Asia are different from those found elsewhere. Specifically they point to an abundance of saurischian, especially grallatorid theropod tracks which appear reminiscent of Jurassic faunas. These are associated with other theropod ichnites (*Minisauripus* and dromaeosaurid tracks) not currently known from other regions. This prompts speculations, that in the Early Cretaceous East Asia represented a refuge of Jurassic faunas and/or region with a distinct endemic ichnofauna (Matsukawa et al., 2006; Lockley et al., 2002, 2013). It is possible that the high proportion of sauropod trackways with a more narrow gauge pattern (*Parabrontopodus*) reflects the persistence of more typical Jurassic ichnofaunas in this region. This conclusion is consistent with the observation that other saurischian- (theropod-) dominated assemblages from the Cretaceous of China contain abundant *Grallator* or grallatorid morphotypes reminiscent of Jurassic ichnofaunas.

## 7. Conclusions and perspectives

The occurrence of relatively narrow gauge trackways of small sauropods (*Parabrontopodus*) at a number of Lower Cretaceous sites in Shandong, and a few other Lower Cretaceous sites in China, where trackways of larger sauropods indicate wide gauge, raises some interesting questions:

1) why do narrow gauge sauropod trackways occur in significant numbers in this region during the Early Cretaceous, while globally the majority of sauropod trackways are reported to have been wide gauge (*Brontopodus*)?
2) do these tracks represent small or medium-sized biological taxa, different from those that made the larger wide-gauge trackways, and if so is it possible to correlate them with skeletal faunas as has been done for the more pronounced polar differences between extreme narrow and wide gauge forms? The alternative explanation is that the small tracks represent trackmakers that developed wide-gauge gaits during ontogenetic growth, or that some small and intermediate forms developed more variable gaits. Either interpretation does not change the evidence, which shows that the Shandong trackway samples appear different from well-preserved, similar aged (Early Cretaceous) trackway assemblages of Korea, where both small and large trackways are wide gauge (ichnogenus *Brontopodus*).

The present data suggest that one of several inferences is possible:

1) Narrow gauge trackways of medium-sized sauropods and wide gauge trackways of large-sized sauropods reflect different biological taxa.
2) The trackmaking taxon exhibited narrow-gauge gaits when small and medium-sized, but wide gauged when larger.
3) The higher frequency of narrow gauge sauropod trackways in the Cretaceous of China, is due to regional variation in sauropod trackmaker distribution and not typical of global trends (see Moratalla, 2009; Castanera et al., 2012, 2014).
4) Individual trackmakers may have shifted from narrow-gauge to wide-gauge due to behavior (gait) (see also Lockley, 2001, 2007; Marty et al., 2010b; Castanera et al., 2012)

Presently, the quality of preservation and limitation of sample size of these trackways prevents a more thorough corroboration of these hypotheses. The extent to which these hypotheses may be corroborated depends on constant evaluation of the growing track record of sauropods, and, importantly, the use of reliable data. All trackway samples, including those assigned to sauropods contain tracks with a large variation in the quality of track preservation. Currently, there is no generally accepted method of separating well-preserved trackways that allow reliable measurements, from those providing less trustable information. Previous syntheses of the global distribution of sauropod trackways with wide and narrow-gauge trackway configuration (Lockley et al., 1994b) were conducted at a time when many sauropod and non-sauropod ichnotaxa had been either misidentified, or named on the basis of incomplete and/or dubious material. Therefore, conclusions about a trend towards increasing dominance of wide-gauge (*Brontopodus*) trackways in the Cretaceous have to be seen cautiously. Subsequent attempts to test or challenge this interpretation (Wright, 2005; Mannion and Upchurch, 2010) have proved inconclusive, not least because of the quality of the ever-changing database. What is needed is a thorough review of all sauropod trackways where preservation is sufficiently good to measure gauge accurately. This task will be challenging because it will require familiarity with all suitable material, and the establishment of criteria for selecting suitable trackways for the database. Even then, any synthesis would need to be compared with the skeletal database of sauropods. Presently, we can only put forward these working hypotheses which may help to draw attention to the nature of the problem and the need for further work.

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