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Diverse sauropod-, theropod-, and ornithopod-track assemblages and a new ichnotaxon *Siamopodus xui* ichnosp. nov. from the Feitianshan Formation, Lower Cretaceous of Sichuan Province, southwest China

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ABSTRACT

Copper mining activities in a huge quarry in the fluvial–lacustrine Lower Cretaceous Feitianshan Formation near Zhaojue, Sichuan Province have temporarily exposed large track-bearing surfaces that require rapid documentation before they are subject to erosion or damage from collapse or destruction by mining. Due to the urgent need to document these sites several preliminary studies of representative material have been completed, and more than 1000 tracks have been observed. Here we present maps of two large surfaces, with a combined area of ~1000 m^2, representing the same stratigraphic level, and yielding multiple trackways of measurable quality, including at least 8 theropod, 7 sauropod, and 22 ornithopod trackways. Additional trackmakers of the two latter groups are also well-represented by natural casts derived from an overlying unit disturbed by quarrying. The sauropod tracks are assigned to the ubiquitous ichnogenus *Brontopodus*. The ornithopod tracks belong to the ichnogenera *Caririchnium*, attributed to quadrupeds or facultative bipeds, and *Ornithopodichnus*, corresponding to smaller bipeds. Based on size and morphology the theropod trackways appear to represent diverse morphotypes, including one attributed to the new ichnospecies *Siamopodus xui*. The Feitianshan Formation ichnofauna, which also includes pterosaur tracks from other nearby surfaces, is moderately diverse and indicates an abundant presence of archosaurs in the region during the Early Cretaceous.

1. Introduction

The Early Cretaceous dinosaur fauna of China is famous for its biological diversity. For example, the Jehol Biota of northeastern China contains a higher number of dinosaur species than any other known contemporaneous fauna (Zhou and Wang, 2010). The high diversity of Chinese Early Cretaceous dinosaurs is reflected in both the skeletal and ichnofossil record. Localities such as the Yanguoxia tracksites of Gansu Province (Zhang et al., 2006; Xing et al., 2013a), the Chabu tracksites of Inner Mongolia (Lockley et al., 2002; Li et al., 2011a), the Junan (Li et al., 2005, 2007) and Linshu tracksites (Xing et al., 2013b) of Shandong Province, the Qijiang Lotus tracksite of Chongqing Municipalities (Xing et al., 2007, 2013c), the Wuerhe (also "Urho") tracksites of Xinjiang (Xing et al., 2011a, 2013d), all indicate a rich biodiversity with at least three or more types of dinosaur, bird, pterosaur and turtle tracks. The abundant dinosaur tracks have also greatly contributed to the reconstruction of dinosaur faunas in areas where skeletal fossils have yet to be discovered.

Historically, Zhaojue County, Sichuan Province is a traditional settlement region for the Yi people. Within Zhaojue County three major dinosaur tracksites have been recently discovered: The Zhaojue tracksite (Xing et al., 2013e; Xing and Lockley, in press; Xing et al., in press-a); the Jiefanggou tracksite (Xing et al., in press-b), and the Yangmozu tracksite (unpublished data). The Zhaojue site (ZJ) is the largest of the three (Fig. 1), and was discovered in September, 1991, after being exposed by large-scale quarrying at a copper mine. It is subdivided into several constituent tracksites. Tracksite ZJI preserved the largest number of tracks, but collapsed between 2006 and 2009, and the tracks were nearly all destroyed. Based on video recording made prior to 2006 and on surviving fragments, the lead author and colleagues described the footprints from ZJI (Xing et al., in press-a). These include theropod, sauropod and ornithopod tracks as well as pterosaur footprints. Zhaojue tracksites ZJII and ZJIIN show theropod, sauropod, and ornithopod tracks. Ornithopod tracks are the most abundant and pterosaur tracks have not been discovered at either of these. Xing et al. (2013e) preliminarily described the dinosaur track assemblage of ZJII, including the first definitive non-avian theropod swim trackway from China based on the lower part of the tracksite only. Adequate data were not obtained until the area was made accessible with the aid of professional rock

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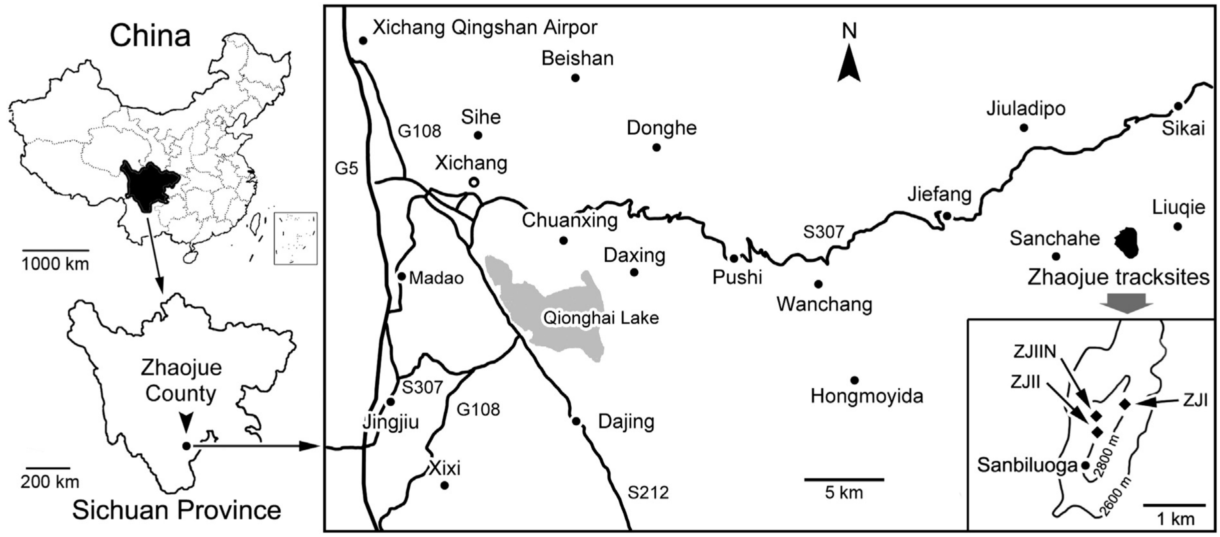

Fig. 1. Geographic map indicating the location of the Zhaojue dinosaur tracksite localities in Liangshan Yi Autonomous Prefecture, Zhaojue County, Sichuan Province, China. ZJI = Zhaojue tracksite I; ZJII = Zhaojue tracksite II; ZJIIN = Zhaojue tracksite II North.

climbers. By these means it was possible to map, trace, and measure representative tracks directly. Parallel trackways of small ornithopods, referable to the ichnogenus *Ornithopodichnus*, and with a walking gait pattern similar to ornithopod tracks reported from South Korea were discovered and described from ZJIIN, (Xing and Lockley, in press). The descriptions herein provide details of the track assemblages from Zhaojue tracksites ZJII and ZJIIN. Both sites represent large areas that belong to the same surface. ZJII includes a mapped area of over 500 m^2, while ZJIIN comprises a mapped area of over 400 m^2. In Xing and Lockley (in press), the three main outcrops ZJI, ZJII, and ZJIIN are designated as tracksites I, II and IIN (N = north).

The aim of this study is to provide a more detailed documentation of tracksites ZJII and ZJIIN and the unique material in view of progressive mining activity and erosion threatening a destruction and loss of valuable data. Here we describe and discuss a diverse ichnoassemblage that moreover allows some conclusions about paleoecology, paleobiogeography and radiation of dinosaur faunas in East Asia.

1.1. Institutional and location abbreviations

AMNH = American Museum of Natural History, New York, USA; CUGB = China University of Geosciences, Beijing, China; HDT = Huaxia Dinosaur Tracks Research and Development Center, Gansu, China; Muz. PIG = Geological Museum of the Polish Geological Institute, Warsaw, Poland; NGMC = National Geological Museum of China, Beijing, China; UCM = University of Colorado Museum of Natural History, Boulder, USA; ZDM = Zigong Dinosaur Museum, Sichuan, China.

1.2. Ichnological abbreviations

LM = left manus; LP = left pes; RM = right manus; RP = right pes; ML = maximum length; MW = maximum width; P′ML = maximum length of pes; P′MW = maximum width of pes; M′ML = maximum length of manus; M′MW = maximum width of manus; R = rotation of tracks relative to midline; SL = stride length; PL = pace length; PA = pace angulation; *h* = height at the hip; WAM = width of the manus angulation pattern; WAP = width of the pes angulation pattern. MPL = distance between center of manus to center of pes.

2. Geological setting

2.1. Feitianshan Formation

The Zhaojue site is a large active copper mine quarry in the upper member of the Feitianshan Formation (Lower Cretaceous) of Sichuan Province. The Feitianshan Formation was originally considered to be Late Jurassic in age, but subsequently, due to the discovery of a *Minheella–Pinnocypridea* ostracod assemblage in the lower part, and a *Cypridea–Latonia* assemblage in the upper part, only the former was assigned to the Late Jurassic, whereas the upper member was assigned to the Early Cretaceous (Wei and Xie, 1987). When Tamai et al. (2004) discussed the paleomagnetics of the Chuan (=Sichuan) and Dian (=Yunnan) fragments of the Yangtze Block, they proposed a Berriasian to Barremian age for the Feitianshan Formation.

The outcrops in the area are dominated by alternating successions of thick sandstones with minor siltstones and shale and successions of thick brick red siltstones containing thin sandstone layers (Fig. 2). The quarry sequence reveals tracks at several levels, including both true tracks and undertracks as concave epireliefs on the surfaces of sandstone beds, and natural casts (convex hyporeliefs) on the underside of shale or silt beds where sand has filled in tracks. The exposed sandstone surfaces are extensive and reveal many tracks, ripple marks, desiccation cracks and other biogenic and non-biogenic sedimentary features. The preservation quality of the tracks is variable, but generally good.

2.2. Paleoecology and sedimentary features

The common presence of ripple-marks and mud-cracks suggest shallow water and intermittent desiccation. Invertebrate traces are preserved in the argillaceous siltstone and include *Beaconites* and *Scoyenia*. The trace makers of *Beaconites* and *Scoyenia* are probably arthropods (Graham and Pollard, 1982; Frey et al., 1984). Both of these ichnogenera pertain to *Scoyenia* ichnofacies (Yang et al., 2004) and both are fodinichnia type traces. In general, *Scoyenia* ichnofacies represents intermittent emergence and shallow flooding in low-energy non-marine facies, typical for river floodplains or lakeshore regions (Yang et al., 2004).

The surface of site ZSIIN (Figs. 3–4) exhibits a low, convex-up or domed area about 8 m in diameter. This represents the remnant of an overlying bed that was partially eroded. It was part of a sandstone bed that filled a depression or paleochannel, and originally may have been

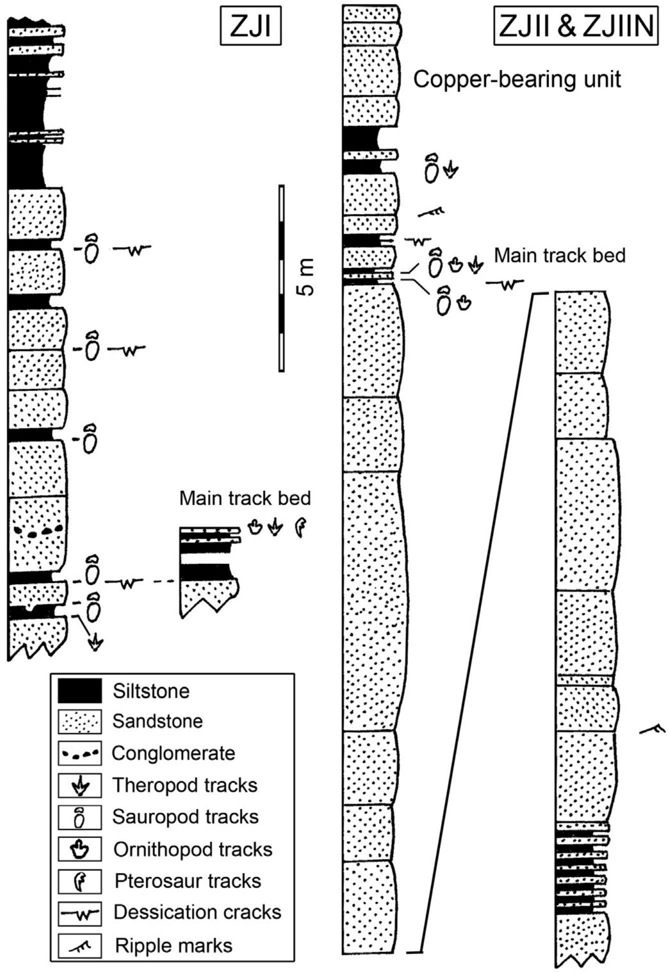

Fig. 2. Stratigraphic sections of dinosaur tracksites ZJI, ZJII and ZJIIN.

thicker in this area. Subsequent erosion cut into both the filling of the depression, and the underlying bed, leaving a rippled marked surface on which tracks were registered. Large linguoid and smaller current ripples indicate that the direction of the last flow. When the tracks were left, was towards the east around the domed area that may have been emergent during the waning stage. This would also explain why this part was not eroded, thus remaining as a local topographic high.

3. Materials and methods

Tracksites ZJI and ZJII are about 450 m apart. According to Liu et al. (2009), before it collapsed, tracksite I initially revealed about 1000 tracks. After our calculation, their number determined from photos and the video was at least 632 (Xing et al., 2013c, in press-a), although some were too small to see or count confidently. After the collapse an additional 90 tracks, not included in the count, were recorded in the southern corner of tracksite I (Xing et al., in press-a). This gives a minimum estimate of 722 tracks for ZJI. ZJII revealed 141 tracks on the surface and 15 more preserved on fallen blocks, while ZJIIN revealed 193 tracks including fallen casts. Thus a total of at least 1071 tracks have been reported from the three quarry sites. ZJIIN is situated roughly fifty meters north of ZJII, and an eight-meter wide mine road intervenes between the two sites. In the areas where tracks have been discovered, quarrying has been shut down, but the tracks remain exposed and unprotected. Moreover, the area is mountainous with a relief around the quarry area up to 2800 m.

At the time they were studied, ZJII and ZJIIN displayed impressive track-rich surfaces. Due to being underlain by a massive sandstone unit almost 30 m meters in thickness (Fig. 2) and with a dip of ~45–50° the overlying layers which consist of alternations of siltstone and sandstone, including a copper-rich unit, that was the target of quarrying operations, were susceptible to easy removal by erosion and quarrying. As described below, the larger area (ZJII: Fig. 5) consisted of several thousand square meters of surface, of which it was possible to map ~500–525 m^2. The smaller area (ZJIIN: Fig. 4) of about 400–415 m^2 was completely mapped. The total mapped are is therefore between ~900 and 940 m^2.

The main exposures of track-rich bedding planes in Figs. 4–5 were, and in places still are, overlain by other layers with tracks. This is particularly significant in the case of site ZJIIN because immediately above the mapped surface (Fig. 4), is a relatively thin (30–50 cm thick) siltstone–sandstone couplet in which tracks penetrated from the upper surface, impacting and penetrating the underlying silts almost as far as the sand of the main track layer. As this upper sandstone eroded, it produced many natural casts, some of which are described here in conjunction with the natural true tracks from the main track surface, which records footprints made on much thicker sandstone, without soft siltstone immediately below it (Fig. 2). Only a few shallow undertracks were observed, penetrated from the upper sandstone, and deep enough to make mappable impressions on the main surface. Nevertheless, such complex multiple track-bearing units indicate the need for caution in track interpretation. Although largely eroded, remnants of the upper track-bearing layer have yielded casts which give insight into some of the complexities of track formation noted below.

Due to the steepness of the bedding planes (40–50°) at tracksites ZJI, ZJII and ZJIIN, it was necessary to use safety ropes during the study of the track-bearing surfaces. In order to make accurate maps, especially in areas scheduled for destruction by quarry operations, tracks were photographed, outlined with chalk, and traced on large sheets of transparent plastics. Videotaping was employed to convert the full size, tracing maps into a digital format (Figs. 4–5). In addition, a representative area of well-preserved tracks was mapped manually using a simple chalk grid. Several natural casts were collected from fallen rubble, and latex molds of representative tracks were made. Furthermore, more detailed tracings of selected tracks were made on transparent acetate film, reposited at UCM. Latex molds, plaster replicas, and most tracings are reposited at HDT and UCM.

Maximum length (ML), maximum width (MW), divarication angle (II–IV), pace length (PL), stride length (SL), pace angulation (PA) and rotation of tracks (R) were measured according to the standard procedures of Leonardi (1987) and Lockley and Hunt (1995).

Mesaxony of tridactyl tracks was calculated according to the methods of Olsen (1980), Weems (1992), and Lockley (2009). This is the degree to which the central digit (III) protrudes anteriorly beyond the medial (II) and lateral (IV) digits. It can be measured as the ratio of the height of the anterior triangle (from base to apex at tip of digit III) over base (= width between tips of digits II and IV): i.e., height/base (L/W).

The distance between centers of pes and manus imprints (MPL) was calculated in trackways of quadrupedal ornithischians. In sauropod trackways, the distance between the proximal margin of the manus and the distal margin of the pes was measured due to difficulties in determining the centers of imprints.

For the trackways of quadrupeds, gauge (trackway width) was quantified for pes and manus tracks using the ratios WAP/P′ML and WAM/M′ML (see Marty, 2008 and Marty et al., 2010). They were calculated from pace and stride length, assuming that the width of the angulation pattern intersects the stride at a right angle and at the approximate midpoint of the stride (Marty, 2008). If the (WAP/P′ML)-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 fixed between medium-gauge and

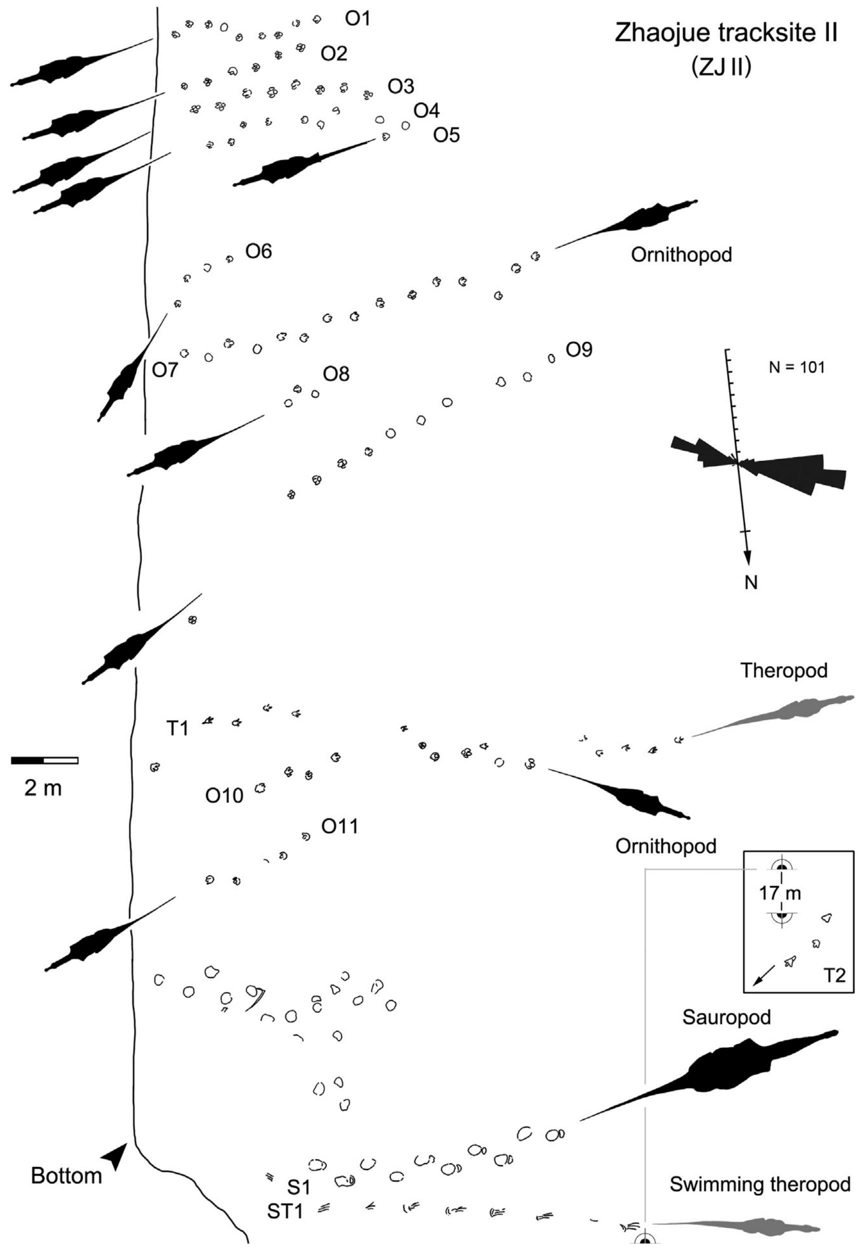

Fig. 3. Map of track-bearing level at tracksite ZJII with trackways and isolated tracks of sauropods, ornithopods and theropods. O1–11 = ornithopod trackways; S1 = sauropod trackway; ST1 = swimming theropod trackway; T1 = theropod trackway.

wide-gauge trackways, and trackways with a value higher than 2.0 are considered to be very wide-gauge (Marty, 2008).

For calculation of hip heights and speed estimates of sauropods derived from the trackways, controversial methods of Alexander (1976), Thulborn (1990) and González Riga (2011) were adopted. Different values from these were juxtaposed but left undiscussed.

4. Tracks and trackways

4.1. Ornithopod tracks

4.1.1. Description

Zhaojue tracksite ZJII reveals eleven ornithopod trackways, cataloged as ZJII-O1–O11; some isolated ornithopod tracks and partial trackways were also preserved on the collapsed rocks (Figs. 4–8, Table. 1). ZJII-O98–O99 are the best-preserved examples of Zhaojue ornithopod tracks, revealing the mostcomplete sequential manus-pes sets (Fig. 6). ZJIIN preserved nine ornithopod trackways, cataloged as ZJIIN-O1–O9 (Fig. 4). Except for an isolated cast collected by the Zigong Dinosaur Museum from ZJIIN (cataloged as ZDM201306–4), all tracks remain in situ.

Ornithopods at ZJII and ZJIIN are divisible into two morphotypes. Morphotype A, is represented by thirteen trackways at ZJII (ZJII-O1–O11, O98–O99) and by a single trackway at ZJIIN (ZJIIN-O8). Morphotype A pes traces are mesaxonic, functionally tridactyl and plantigrade with a length estimated at 20–30 cm, and the average and median ML/MW ratios are both of 1.3. The pes-manus association ZJII-O98-LP1 and LM1 (Fig. 6A–B) is the best-preserved representative of morphotype A. The pes trace shows quadripartite morphology, consisting of impressions of three digits and a heel pad separated by pronounced ridges. The ML/MW ratio is 1.6 while the anterior triangle L/W ratio is 0.37. Digit II trace is the shortest, while traces of digits III and IV are almost equal in length. Each digit trace has a strong and blunt claw or ungual mark. The heel is triangular. There is a distinct border between the heel and the three digits. The interdigital divarication II–IV is 47°. The manus trace is oval, with no discernable claw marks. The short axis of the oval manus trace aligns with the antero-lateral margins of the pes trace

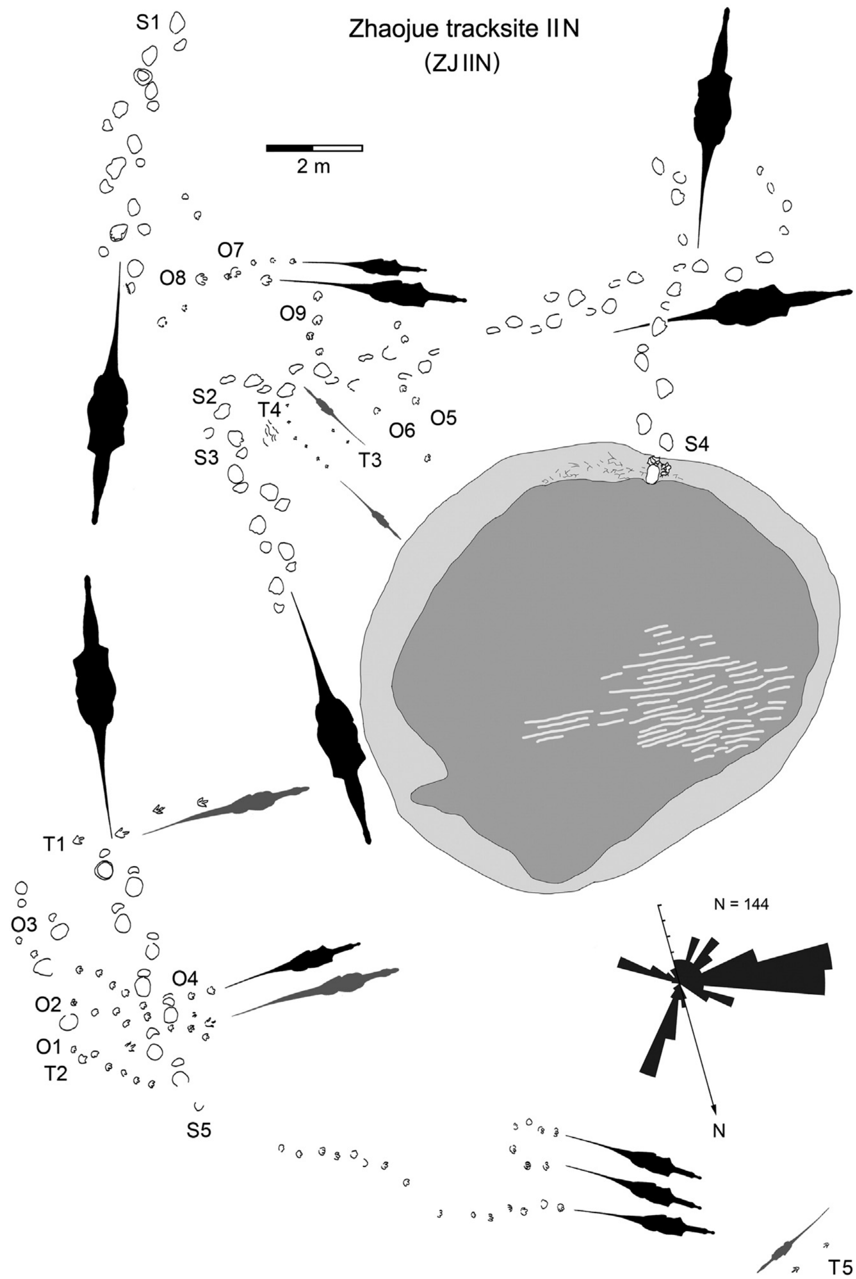

Fig. 4. Map of track-bearing level at Zhaojue tracksite ZJIIN with trackways and isolated tracks of sauropods, ornithopods and theropods. Notice large circular area at center right (in gray) that represents a remnant of an eroded upper layer (see detail in Fig. 5).

(i.e., opposite the line connecting the tips of digits III and IV). The ratio of manus center-pes center distance/pes trace length (MPL/P′ML) is 1.1. ZJII-O99 tracks (Fig. 6C) are basically consistent with ZJII-O98 morphology, with an average ML/MW ratio of 1.6 and average anterior triangle L/W ratio of 0.36 (ranging between 0.34 and 0.38). However, in ZJII-O99, the pes ungual trace of digit III is blunter, the manus trace is much closer to the pes trace, and the MPL/P′ML ratio is 0.6. ZJII-O99 PL is 3.1 × P′ML.

Tracks from ZJII show considerable morphological variation, which is probably due to the original substrate being wet and slippery. Well-preserved tracks, such as ZJII-O2-L3, O9-R9, and ZJII-O98-LP1 are similar in most respects, but only ZJII-O2-L3 preserves distinct claw marks (Fig. 8). Except for ZJII-O98 and O99, all other ornithopod tracks at ZJII are without manus traces, perhaps because the original tracks were too shallow to be preserved. In the trackway sample ZJII-O1–O11 trackways O1–O3, O7, and O9 are well-preserved (Figs. 7A, 8). The average PA of these well-preserved trackways is 155° (range between 134° and 166°). Based on trackways ZJII-O1–O3, the pes traces show consistent inward rotation mean 8°, 18° and 19° (Fig. 7A).

Morphotype B is only represented at ZJIIN by trackways ZJIIN-O1–O7 (Figs. 7B, 8). Pes tracks are mesaxonic, functionally tridactyl and plantigrade, with ML being 13–18 cm and with an average and median ML/MW ratio of 1.1. ZJIIN-O1-L3 (Fig. 6D) is the best-preserved representative. The ML/MW ratio is 1.1 while the anterior triangle L/W ratio is 0.21. Digit II is the shortest, while digit IV is the longest. Digital pads are absent. Digit traces are deeply impressed distally. Claw marks are round and blunt. There is no border between the heel and the three digits. The interdigital divarication II–IV is 58°. ZJII-O1 PL is 3.1 × P′ML. The average PA is 157°. Based on trackways ZJIIN-O1–O3, the pes traces show consistent inward rotation, respectively of 7°, 10°, and 14° (Fig. 7B).

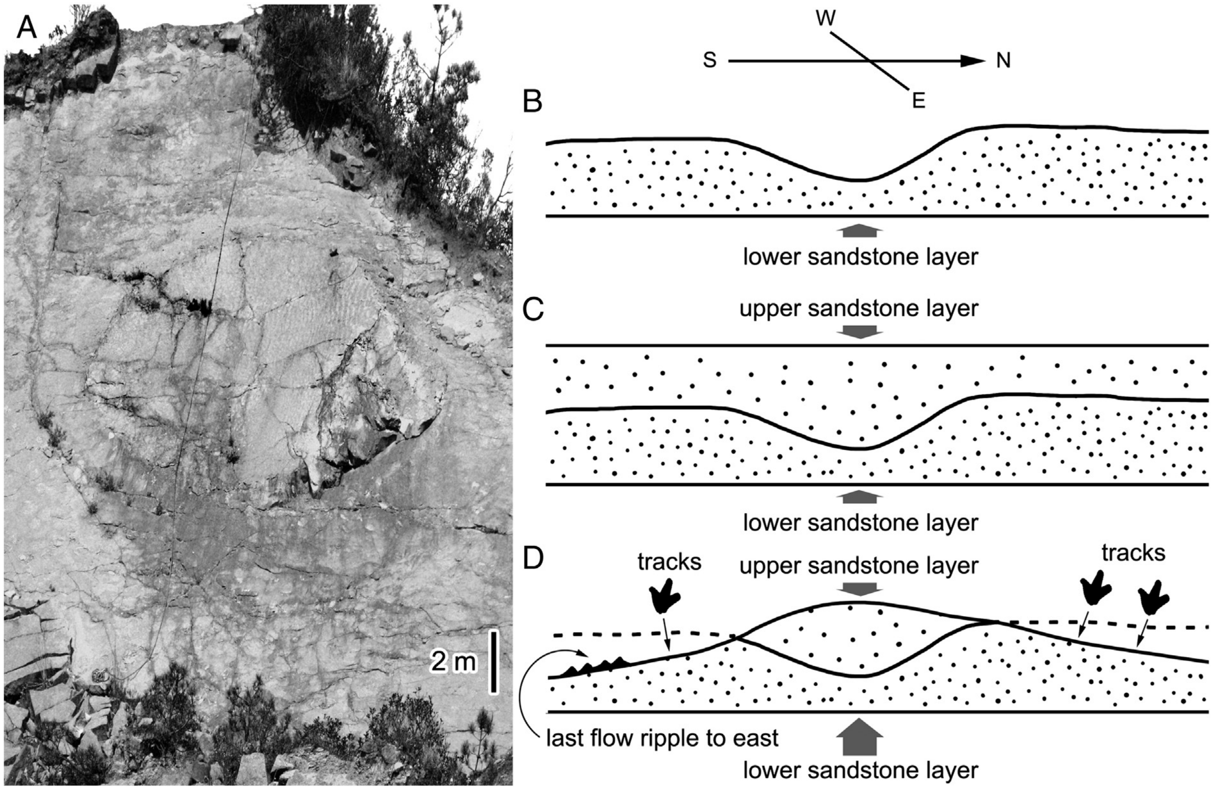

Fig. 5. Large domed area at ZJIIN and mapped in Fig. 4. A. Photograph. B–D. Schematic drawings demonstrating formation of the structure by infilling of a channel and erosion of upper sandstone layer.

4.1.2. Comparisons and discussion

Lower Cretaceous ornithopod trackways are well-known from Europe, North America, and East Asia. To date, six valid ornithopod ichnogenera have been named from the Cretaceous: *Amblydactylus* (two ichnospecies), *Caririchnium* (three ichnospecies), *Iguanodontipus*, and *Ornithopodichnus* from the Lower Cretaceous and *Hadrosauropodus* (two ichnospecies) and *Jiayinosauropus* (Lockley et al., in press) from the Upper Cretaceous.

Morphotype A from ZJII and ZJIIN resembles *Caririchnium*, an ichnogenus originally described from the Antenor Navarro Formation, Brazil, and defined by Leonardi (1984). Lockley et al. (in press) described the pes trace as possessing a sub symmetric, quadripartite morphology consisting of impressions of three digits, and a heel pad separated by pronounced ridges. Either, the pes was functionally plantigrade, or the impression of the heel pad is related to the softness of the substrate. In life, these ridges would have represented concave-up creases separated by convex-down pads. The ungual traces reported in Leonardi (1984) occur within, not distal to, the traces of digits II–IV. The manus traces of the type ichnospecies *C. magnificum* from Brazil are irregular in size and shape ("L" shaped to oval or sub-circular). In two other ichnospecies, *C. leonardii*, from Colorado, USA (Lockley et al., 2001), and *C. lotus*, from China (Xing et al., 2007), the manus traces are irregular and sub-oval, respectively. The P′ML/P′MW ratio of *C. magnificum* is 1.4 and the anterior triangle L/W ratio is 0.31 (based on Leonardi, 1984: Plate XI).

This distinctive morphology of *Caririchnium* (quadripartite pes and small oval manus) is also seen in the Zhaojue ornithopod morphotype A. Both the P′ML/P′MW ratio and the anterior triangle L/W ratio of the holotype of *Caririchnium magnificum* are similar to those of morphotype A. However, being limited to a small number of manus traces and lacking a well-preserved trackway, morphotype A is difficult to compare.

In 2009 Kim et al. named the ichnogenus *Ornithopodichnus* based on large footprints from the Lower Cretaceous of Korea which exhibit distinctively weak mesaxonic and broad, transverse pes imprints that are wider than long. Much smaller *Ornithopodichnus* trackways were later described from the Upper Cretaceous of Korea including several parallel trackways of bipeds, assumed to have been gregarious ornithopods (Lockley et al., 2012). *Ornithopodichnus* type trackways are also known from the Houzuoshan Dinosaur Park, Shandong Province, China (Matsukawa and Lockley, 2007; Lockley, 2009). At least three parallel small ornithopod trackways (ZJIIN-O1–O3) from ZJIIN show the same morphology and gait pattern as the small *Ornithopodichnus* trackways from South Korea (Xing and Lockley, in press). Similar to the trackways from South Korea, morphotype B from ZJIIN also exhibits a transverse shape and has a consistent tendency towards the inward rotation typical of ornithopods (Lockley et al., 2012; Xing and Lockley, in press). Therefore, we assign morphotype B from Zhaojue tracksite IIN to the ichnogenus *Ornithopodichnus* (Xing and Lockley, in press).

In general, the Early Cretaceous ornithopod tracks from China are morphologically similar. Traces of a quadripartite pes and small oval manus were observed in the sample of middle-sized tracks (20–30 cm in length), with only the degree of mesaxony differing. Morphotype A from the Zhaojue tracksites shows a strong mesaxony (0.37), close to specimens from the Yanguoxia tracksite, Gansu Province (Zhang et al., 2006) that have a slightly stronger mesaxony (0.41, based on Zhang et al., 2006: Fig. 12) and a P′ML/P′MW ratio of 1.5. Other Chinese ornithopod track types have weaker mesaxony. For example, the ornithopod tracks from Houzuoshan in Shandong Province have values of 0.20 and 0.23 (Lockley, 2009). The footprint from the Luanping tracksite (Hebei Province) is approximately 28 cm long, with a P′ML/P′MW ratio of 1.1, a weak mesaxony of 0.29, and the oval manus trace is situated anterior to digit III and digit IV of the pes (based on Matsukawa et al., 2006, Fig. 3).

4.1.3. Speed estimates

For small ornithopods (P′ML < 25 cm), Thulborn (1990) suggests that $h = P'ML^{1.08} \times 3.97$. The relative stride length (SL/h) may be

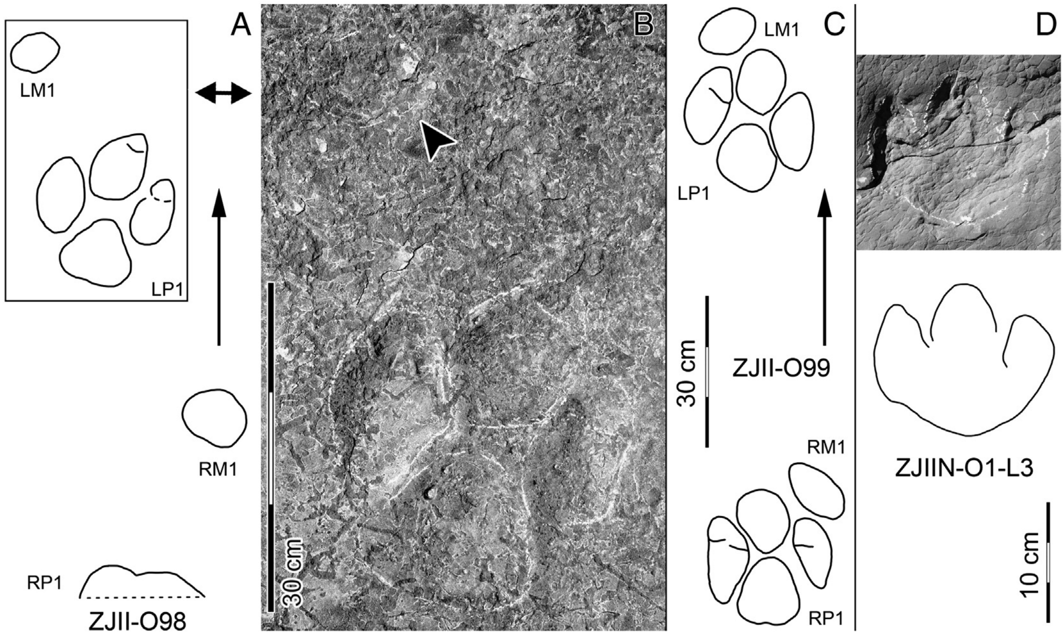

Fig. 6. Ornithopod tracks at tracksites ZJII and ZJIIN. A, B) photograph and interpretative outline drawing of ZJII-O98 with manus pes sets; C) interpretative outline drawing of ZJII-O99 with manus pes sets; D) photograph and interpretative outline drawing of ZJIIN-O1-L3. Arrow in B points to manus.

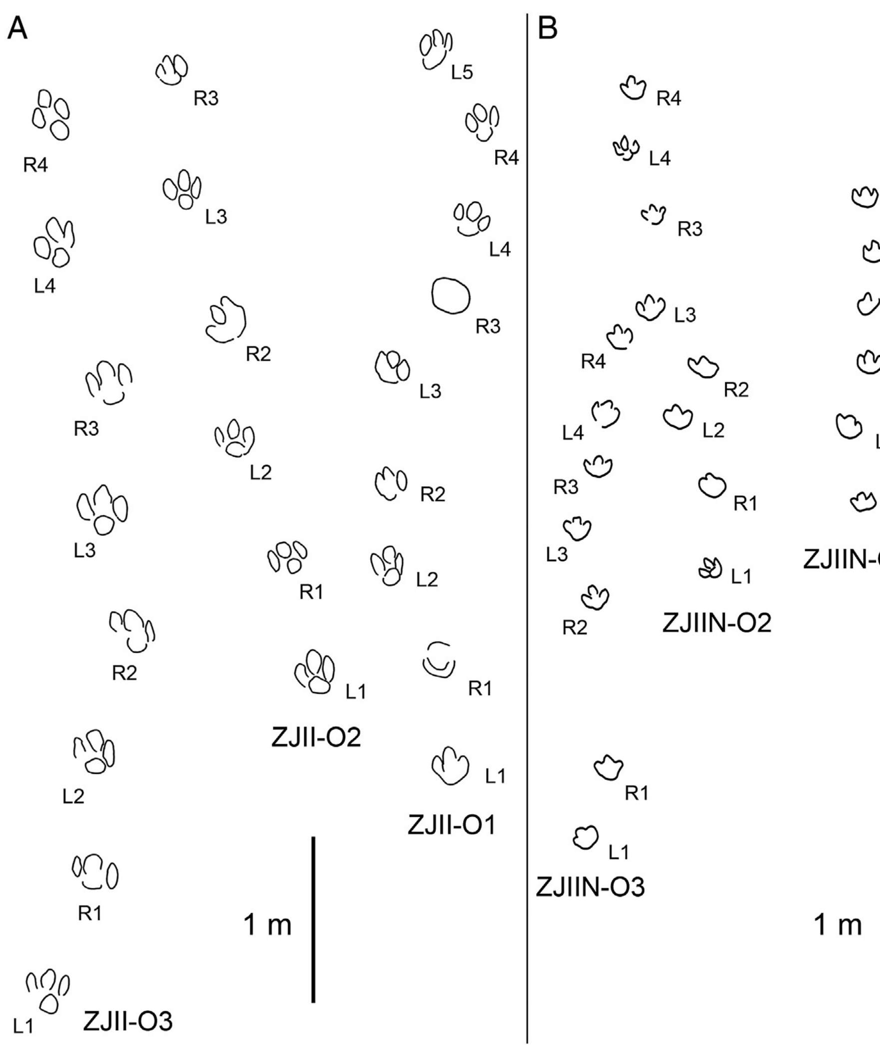

Fig. 7. Interpretative outline drawings of ornithopod trackways from tracksites ZJII (A) and ZJIIN (B).

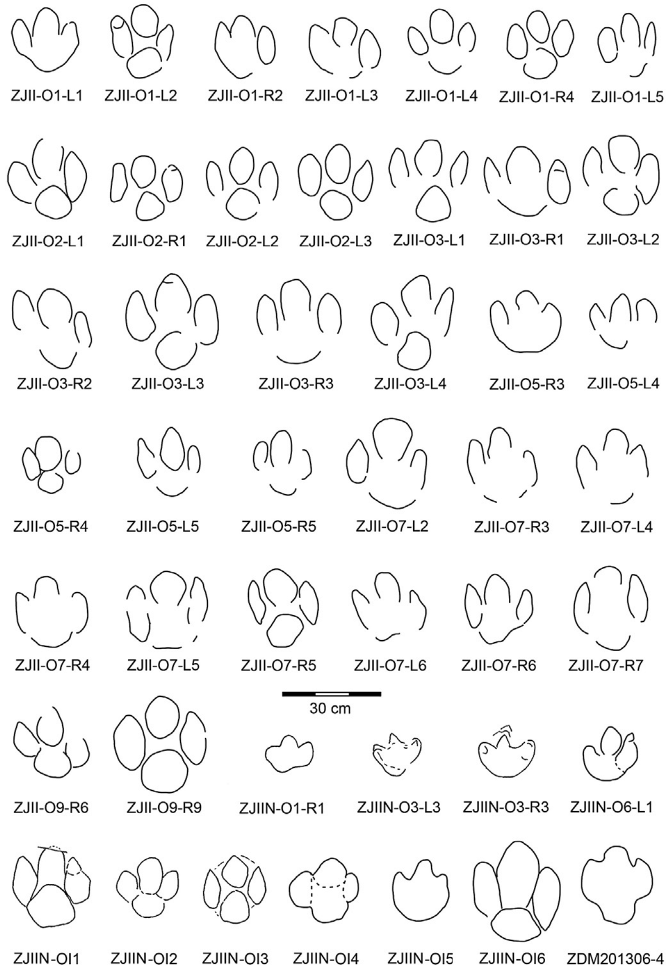

Fig. 8. Interpretative outline drawings of ornithopod tracks from tracksites ZJII and ZJIIN.

used to determine whether the animal is walking (SL/h ≤ 2.0), trotting (2 < SL/h < 2.9), or running (SL/h ≥ 2.9) (Alexander, 1976; Thulborn, 1990). The SL/h ratios of the Zhaojue ornithopod trackways morphotype A ZJII-O1–O3, O7, O9, O10 range 1.02–1.48 (Table. 2) and accordingly suggest a walking gait. Using the formula of Alexander (1976), the speed of these six trackways ranges between an estimated 3.02–6.01 km/s (Table. 2). Taking ZJIIN-O1 and O2 as examples, morphotype B indicates a walking speed of 3.31 and 3.56 km/s, respectively (Xing and Lockley, in press).

4.2. Theropod tracks

4.2.1. Description

ZII and ZJIIN yielded eight theropod trackways, ZJII-T1, T2, ST1, ZJIIN-T1, T2, T3, T4, T5 (Figs. 4, 5, 9–11). Several isolated theropod tracks were also discovered in the collapsed debris. All other tracks remain in situ.

Ichnosite ZJII preserves three theropod trackways: ZJII-T1, T2, and ST1 (swim trackway), respectively made of 12, 3 and 8 individual tracks. ZJII-T1 is a typical tridactyl trackway, and it crisscrosses with an ornithopod trackway (ZJII-O10). ZJII-T1-L6, R8 and L9 are well-preserved tracks. The most remarkable characteristics of these trackways are different extramorphological variations, which are attributable to the wet and soft sediments. The phalangeal pad traces of each digit are indistinct and shrink toward the footprint axis, which makes the digits look more slender (dotted line in Fig. 9). A larger metatarso-phalangeal area and "heel" is preserved in L6, due to the softer sediments, but is absent in R8 and L9.

ZJII-T2 is situated at a small outcrop at the northern extremity of the ZJII; the distance between ZJII-T2 and ZJII-ST1 is about 17 m, so there is no display on Fig. 5. ZJII-T2 tracks are poorly-preserved, possibly a result of long-term weathering. However, ZJII-T2 shows one of the largest theropod tracks from the two tracksites. ZJII-T2-R2 is the best-preserved, measures 28.4 cm in total length, and is similar to ZJII-T1-R8 in general morphology (Fig. 9). The interdigital divarication II–IV is wide (71°), a big heel trace is preserved, which probably retains a partial metatarsal pad that is 13 cm long. ZJII-TI1 is an isolated right track (Fig. 9). Abundant invertebrate traces surround ZJII-TI1. Digit II of ZJII-TI1 has two preserved phalangeal pad traces, digit III has two or three preserved phalangeal pads, and the phalangeal pads of digit IV are indistinct. A metatarso-phalangeal pad is visible close to the axis of digit III but more developed laterally toward digit IV.

Ichnosite ZJIIN preserves five theropod trackways: ZJIIN-T1–T5, which consist of four, three, two, six, and two tracks, respectively (Fig. 4). ZJIIN-T1 and T2 resemble ZJII-T1 in morphology, but without the influence of the wet and soft original substrate. ZJIIN-T1-L2 (Fig. 9) is the best-preserved track. It has a P′ML/P′MW ratio of 1.3, all three digits present sharp claw marks, and the interdigital divarications are 32° of II-III, 24° of III-IV and 56° of II-IV. The metatarso-phalangeal pad of digit IV is positioned near the axis of digit III but slightly more close to digit IV. The average PA of ZJIIN-T1 is 154°, slightly larger than in ZJII-T1 (146°).

ZJIIN-T5 is a single pace trackway made of two poorly-preserved tracks. ZJIIN-T1-L1 is quite well-preserved, with a strong indentation behind digit II (Fig. 9). The most significant difference between L1 and other Zhaojue theropod tracks is the very slender digits of the former, which may reflect partial collapse of the track wall in a relatively deep track.

4.2.2. Comparisons and discussion

Among Zhaojue theropod tracks, ZJIIN-T5 has moderate mesaxony (0.71). It resembles the widely-discovered *Grallator* morphotype from Liaoning, northern China. Early Cretaceous small theropod tracks from China are dominated by the *Grallator* morphotype, which includes *Jialingpus* (a form with exceptionally large, sometimes compound, metatarso-phalangeal pads) (Xing et al., 2014). For the specimens at the Sihetun site (NGMC V2115A and B), the anterior triangle L/W ratio is also approximately 0.7 (based on Xing et al., 2009, Fig. 3). The Sihetun tracks could have been made by an oviraptosaur (Xing et al., 2009), and the trackmaker of ZJIIN-T5 was probably a small non-avian theropod, possibly belonging to the same group. However, as noted by Gierliński and Lockley (2013) some orviraptosaurs had tetradactyl feet and could have left tetradactyl tracks, in which the trace of digit I, as well as digits II–IV, was registered. However, as digit I is short in oviraptosaurs, its trace may not have registered in shallow tracks.

The average anterior triangle L/W ratio of ZJII-T1, T2, ZJII-TI1 and ZJIIN-T1 is 0.37, which is typical of the values reported for the morphofamily Eubrontidae (Lull, 1953). These tracks are basically consistent in morphology with theropod tracks from Zhaojue tracksite ZJI (Xing et al., in press-a). In addition, ZJII-ST1 is the first definite non-avian theropod swim trackway (ichnogenus *Characichnos*) from China (Xing et al., 2013e). Based on similarity of the track widths (16.0 cm from ZJII-ST1 vs. 16.9 cm from ZJII-T1), ZJII-ST1 and ZJII-T1 were probably left by the same kind of trackmaker. ZJII-T1 is also comparable to *Irenesauripus* Sternberg, 1932, 1932 (Xing et al., 2011b; Xing et al., 2013e; Lockley et al., 2014a, b; McCrea et al., 2014) an ichnogenus in need of revision. *Irenesauripus* tracks are widespread in Early Cretaceous (and early Late Cretaceous) assemblages (Currie, 1983; Gangloff and May, 2004; Gierliński et al., 2008; Xing et al., 2011b). Taking the best-preserved track, ZJIIN-T1-L2 (Fig. 9) as an example, its morphology is similar to *Irenesauripus* AMNH 3065 from Comanche series (Aptian–Albian) of Dinosaur Valley State Park, Texas, to a similar ichnite from the Cameros Basin, Enciso Group (Aptian) of Los Cayos site, Spain, and to *Irenesauripus* sp., Muz. PIG 1704.II.2 from Maastrichtian Gaizes of Potok, Roztocze, Poland (see Gierliński et al.,

Table 1
Measurements (in cm) of ornithopod tracks from Zhaojue tracksite ZJII and ZJIIN, Sichuan Province, China.

Number	ML	MW	II–IV	PL	SL	PA	ML/MW
ZJII-O1-L1	22.4	17.5	50°	63.1	126.0	159°	1.3
ZJII-O1-R1	22.0	19.0	–	65.2	108.5	153°	1.2
ZJII-O1-L2	23.6	17.6	45°	47.1	115.4	178°	1.3
ZJII-O1-R2	20.2	13.5	43°	69.1	118.5	142°	1.5
ZJII-O1-L3	19.3	14.7	48°	57.0	101.5	157°	1.3
ZJII-O1-R3	20.0	22.8	–	47.6	104.9	172°	0.9
ZJII-O1-L4	21.1	18.4	61°	57.9	106.0	139°	1.1
ZJII-O1-R4	22.4	17.0	49°	52.4	–	–	1.3
ZJII-O1-L5	23.2	13.7	31°	–	–	–	1.7
Mean	21.6	17.1	47°	57.4	111.5	157°	1.3
ZJII-O2-L1	27.5	17.7	46°	66.2	144.7	168°	1.6
ZJII-O2-R1	20.5	14.6	50°	78.6	147.0	160°	1.4
ZJII-O2-L2	22.3	19.4	55°	69.0	152.0	163°	1.1
ZJII-O2-R2	24.5	20.5	57°	83.1	151.1	169°	1.2
ZJII-O2-L3	23.0	17.8	51°	69.1	–	–	1.3
ZJII-O2-R3	18.0	11.0	39°	–	–	–	1.6
Mean	22.6	16.8	50°	73.2	148.7	165°	1.4
ZJII-O3-L1	26.7	22.1	53°	72.7	143.5	161°	1.2
ZJII-O3-R1	21.2	21.9	63°	73.3	145.9	164°	1.0
ZJII-O3-L2	25.3	19.5	52°	73.9	144.7	148°	1.3
ZJII-O3-R2	26.0	22.3	55°	75.5	148.5	163°	1.2
ZJII-O3-L3	29.2	22.4	48°	73.6	162.6	159°	1.3
ZJII-O3-R3	26.7	21.0	50°	91.4	165.6	164°	1.3
ZJII-O3-L4	30.2	22.5	50°	76.2	–	–	1.3
ZJII-O3-R4	32.6	14.5	32°	–	–	–	2.2
Mean	27.2	20.8	53°	76.7	151.8	160°	1.4
ZJII-O4-L1	22.3	19.2	–	65.0	–	–	1.2
ZJII-O4-R1	25.3	18.5	–	–	131.7	–	1.4
ZJII-O4-L2	–	–	–	–	–	–	–
ZJII-O4-R2	–	–	–	63.5	97.7	–	–
ZJII-O4-L3	–	–	–	55.5	–	–	–
ZJII-O4-R3	20.5	17.5	54°	–	10.4	–	1.2
ZJII-O4-L4	–	–	–	–	–	131°	
ZJII-O4-R4	16.8	15.5	55°	–	76.3	136°	1.1
ZJII-O4-L5	–	–	–	–	–	–	
ZJII-O4-R5	18.0	14.5	50°	64.2	117.9	–	1.2
ZJII-O4-L6	21.2	18.7	55°	65.2	–	–	1.1
ZJII-O4-R6	20.5	15.5	–	–	–	–	1.3
Mean	20.7	17.1	54°	62.7	86.8	134°	1.2
ZJII-O5-L1	21.0	17.0	51°	–	–	–	1.2
ZJII-O6-R1	19.2	16.0	52°	72.2	140.0	173°	1.2
ZJII-O6-L1	22.4	18.0	–	68.3	139.1	138°	1.2
ZJII-O6-R2	22.5	14.0	43°	79.5	–	–	1.6
ZJII-O6-L2	20.9	16.6	54°	–	–	–	1.3
Mean	21.3	16.2	50°	73.3	139.6	156°	1.3
ZJII-O7-L1	22.5	17.5	50°	74.8	133.2	137°	1.3
ZJII-O7-R1	21.8	21.8	–	78.9	142.3	142°	1.0
ZJII-O7-L2	29.8	19.8	53°	82.0	153.9	136°	1.5
ZJII-O7-R2	24.7	24.5	–	81.7	138.3	146°	1.0
ZJII-O7-L3	27.3	17.4	–	65.5	142.9	135°	1.6
ZJII-O7-R3	24.0	17.2	52°	89.5	157.3	141°	1.4
ZJII-O7-L4	24.6	17.8	53°	76.7	–	167°	1.4
ZJII-O7-R4	23.0	19.4	63°	86.2	185.7	166°	1.2
ZJII-O7-L5	24.2	20.8	53°	101.0	183.2	155°	1.2
ZJII-O7-R5	25.8	19.7	48°	84.0	157.2	–	1.3
ZJII-O7-L6	24.2	19.0	61°	78.4	–	–	1.3
ZJII-O7-R6	22.5	22.6	66°	–	167.5	–	1.0
ZJII-O7-L7	–	–	–	–	–	–	
ZJII-O7-R7	28.0	18.5	45°	65.2	–	–	1.5
ZJII-O7-L8	23.2	20.5	57°	–	–	–	1.1
Mean	24.7	19.8	55°	80.3	156.2	147°	1.3
ZJII-O8-L1	18.4	19.7	–	50.9	80.4	110°	0.9
ZJII-O8-R1	20.2	15.7	50°	50.9	–	–	1.3
ZJII-O8-L2	20.6	20.6	–	–	–	–	1.0
Mean	19.7	18.7	50°	50.9	80.4	110°	1.1
ZJII-O9-R1	17.3	24.1	–	88.3	162.8	153°	0.7
ZJII-O9-L1	21.9	25.9	–	78.3	–	–	0.8
ZJII-O9-R2	20.1	27.0	–	–	171.2	–	0.7
ZJII-O9-L2	–	–	–	–	–	–	–
ZJII-O9-R3	27.3	26.1	–	93.2	192.6	167°	1.0
ZJII-O9-L3	26.4	28.6	–	100.0	187.1	165°	0.9
ZJII-O9-R4	25.9	26.6	–	88.6	–	165°	1.0
ZJII-O9-L4	24.9	17.0	64°	95.4	180.4	170°	1.5
ZJII-O9-R5	29.0	17.2	44°	92.3	186.0	178°	1.7
ZJII-O9-L5	24.4	19.5	48°	93.3	–	–	1.3
ZJII-O9-R6	21.6	19.3	–	–	–	–	1.1
Mean	23.9	23.1	52°	91.2	180.0	166°	1.1
ZJII-O10-R1	24.2	19.8	57°	–	–	–	1.2
ZJII-O10-R3	–	95.0	43°	148.4	–	138°	–
ZJII-O10-L3	23.6	18.6	60°	59.0	151.0	133°	1.3
ZJII-O10-R4	22.3	16.2	43°	99.0	–	–	1.4
ZJII-O10-L4	26.5	19.8	53°	–	–	–	1.3
ZJII-O10-R6	20.9	15.5	45°	94.4	189.5	158°	1.3
ZJII-O10-L6	28.9	20.5	52°	95.4	186.0	169°	1.4
ZJII-O10-R7	25.1	–	–	90.0	–	–	–
ZJII-O10-L7	27.0	21.8	56°	–	–	–	1.2
Mean	24.8	18.9	51°	88.8	168.7	150°	1.3
ZJII-O11-R1	–	–	–	87.8	145.3	–	–
ZJII-O11-L1	22.5	18.6	66°	57.6	156.7	–	1.2
ZJII-O11-R2	–	–	–	98.8	166.5	–	–
ZJII-O11-L2	18.7	16.8	66°	74.4	–	–	1.1
ZJII-O11-R3	23.2	16.5	46°	–	–	–	1.4
Mean	21.5	17.3	59°	79.7	156.2	–	1.2
ZJII-O98-RM1	11.1	13.7	–	84.5	–	–	0.8
ZJII-O98-LP1	32.1	20.4	47°	89.0	–	–	1.6
ZJII-O98-LM1	8.6	12.4	–	–	–	–	0.7
Mean	17.3	15.5	47°	86.8	–	–	1.0
ZJII-O99-RM1	7.4	13.2	–	89.0	–	–	0.6
ZJII-O99-RP1	26.0	18.0	46°	84.0	–	–	1.4
ZJII-O99-LM1	7.8	12.4	–	–	–	–	0.6
ZJII-O99-LP1	27.0	15.5	40°	–	–	–	1.7
Mean	17.1	14.8	43°	86.5	–	–	1.1
ZJIIN-O1-R1	11.0	12.5	75°	47.2	88.0	159°	0.9
ZJIIN-O1-L1	13.5	13.1	59°	41.5	75.0	166°	1.0
ZJIIN-O1-R2	12.5	12.9	63°	35.5	67.3	171°	1.0
ZJIIN-O1-L2	13.0	12.5	–	34.0	66.3	162°	1.0
ZJIIN-O1-R3	14.3	13.7	67°	32.0	–	–	1.0
ZJIIN-O1-L3	13.5	12.7	58°	–	–	–	1.1
ZJIIN-O1-L7	11.9	10.2	62°	39.6	87.4	157°	1.2
ZJIIN-O1-R8	13.0	11.2	70°	49.0	80.4	158°	1.2
ZJIIN-O1-L8	13.5	13.0	–	33.4	70.0	157°	1.0
ZJIIN-O1-R9	14.9	13.0	–	38.0	61.0	–	1.1
ZJIIN-O1-L9	14.4	14.0	–	30.0	69.5	–	1.0
ZJIIN-O1-R10	–	–	–	44.0	99.6	–	–
ZJIIN-O1-L10	13.0	14.0	–	60.0	–	–	0.9
ZJIIN-O1-R11	12.5	13.3	71°	–	95.5	–	0.9
ZJIIN-O1-L12	12.2	–	–	–	76.0	–	–
ZJIIN-O1-L13	10.0	9.9	69°	38.5	79.8	141°	1.0
ZJIIN-O1-R14	11.5	–	–	45.0	76.0	146°	–
ZJIIN-O1-L14	11.2	–	–	35.3	81.1	–	–
ZJIIN-O1-R15	14.9	12.3	58°	49.0	82.2	–	1.2
ZJIIN-O1-L15	15.8	–	–	36.6	–	–	–
ZJIIN-O1-R16	16.0	10.6	–	–	–	–	1.5
Mean	13.1	12.4	65°	40.5	78.4	157°	1.1
ZJIIN-O2-L1	13.5	13.4	62°	52.0	95.0	156°	1.0
ZJIIN-O2-R1	14.6	14.6	58°	46.0	72.1	128°	1.0
ZJIIN-O2-L2	14.6	13.8	73°	35.0	69.1	110°	1.1
ZJIIN-O2-R2	13.4	16.6	87°	50.0	97.7	138°	0.8
ZJIIN-O2-L3	16.1	13.7	64°	56.0	98.0	155°	1.2
ZJIIN-O2-R3	13.2	14.2	74°	44.0	79.5	152°	0.9
ZJIIN-O2-L4	13.9	13.8	63°	38.0	–	–	1.0
ZJIIN-O2-R4	14.5	13.4	76°	–	–	–	1.1
ZJIIN-O2-L15	14.8	13.9	67°	45.0	81.4	135°	1.1
ZJIIN-O2-R15	14.0	11.5	–	43.5	–	–	1.2
ZJIIN-O2-L16	14.0	15.5	–	–	–	–	0.9
Mean	14.2	14.0	69°	45.5	84.7	139°	1.0
ZJIIN-O3-L1	13.3	14.8	70°	50.0	–	–	0.9
ZJIIN-O3-R1	14.7	15.7	74°	–	104.4	–	0.9
ZJIIN-O3-L2	–	–	–	–	–	–	–
ZJIIN-O3-R2	16.4	15.6	72°	44.0	81.0	151°	1.1
ZJIIN-O3-L3	15.2	15.7	71°	41.0	75.5	171°	1.0
ZJIIN-O3-R3	15.0	16.3	76°	34.8	81.2	180°	0.9
ZJIIN-O3-L4	15.8	14.2	54°	47.4	–	–	1.1
ZJIIN-O3-R4	14.8	13.5	69°	–	–	–	1.1
ZJIIN-O3-R17	10.5	11.0	–	33.8	60.2	135°	1.0
ZJIIN-O3-L18	12.5	–	–	30.0	60.1	160°	–
ZJIIN-O3-R18	13.1	12.0	–	30.2	–	–	1.1
ZJIIN-O3-L19	10.0	13.5	–	–	–	–	0.7
Mean	13.8	14.2	69°	38.9	77.1	159°	1.0

(continued on next page)

Table 1 (*continued*)

Number	ML	MW	II–IV	PL	SL	PA	ML/MW
ZJIIN-O4-R1	16.0	13.5	73°	45.1	–	–	1.2
ZJIIN-O4-L1	17.6	14.5	63°	–	–	–	1.2
Mean	16.8	14.0	68°	45.1	–	–	1.2
ZJIIN-O5-R1	16.4	16.5	69°	44.4	–	–	1.0
ZJIIN-O5-L1	19.9	16.7	68°	–	–	–	1.2
Mean	18.2	16.6	68°	44.4	–	–	1.1
ZJIIN-O6-L1	13.4	13.9	–	–	–	–	1.0
ZJIIN-O6-L3	13.5	12.9	69°	–	–	–	1.0
Mean	13.5	13.4	69°	–	–	–	1.0
ZJIIN-O7-R1	12.2	11.0	70°	–	–	171°	1.1
ZJIIN-O7-L1	13.0	–	–	–	–	–	–
ZJIIN-O7-R2	14.5	–	–	–	–	–	–
Mean	13.2	11.0	70°	–	–	171°	1.1
ZJIIN-O8-R1	25.1	19.3	55°	78.6	143.0	157°	1.3
ZJIIN-O8-L1	22.2	19.0	52°	67.5	–	–	1.2
ZJIIN-O8-R2	25.4	19.0	–	–	–	–	1.3
Mean	24.2	19.1	54°	73.1	143.0	157°	1.3
ZJIIN-OI1	25.2	16.1	41°	–	–	–	1.6
ZJIIN-OI2	18.5	16.1	59°	–	–	–	1.2
ZJIIN-OI3	20.4	14.9	47°	–	–	–	1.4
ZJIIN-OI4	19.8	14.5	52°	–	–	–	1.4
ZJIIN-OI5	19.0	14.0	51°	–	–	–	1.4
ZJIIN-OI6	30.5	20.2	47°	–	–	–	1.5
ZDM201306-4	23.9	15.0	40°	–	–	–	1.6

Abbreviations: ML: maximum length; MW: maximum width (measured as the distance between the tips of digits II and IV); II–IV: angle between digits II and IV; PL: pace length; SL: stride length; PA: pace angulation; ML/MW is dimensionless.

2008, Figs. 2, 4A–B). The trackmaker of *Irenesauripus* was potentially the carcharodontosaurian *Acrocanthosaurus* (Langston, 1974; Farlow, 2001; Lockley et al., 2014a, b). However, the Zhaojue theropod specimens are smaller (P′ML = 27.9 cm) than *Irenesauripus* (P′ML = 40.6 cm in *I. mclearni* Sternberg, 1932). The heel of the holotype of *Irenesauripus* is more developed than that of the Zhaojue specimens. In general, "*Irenesauripus*" from East Asia needs further comparison.

4.2.3. New ichnotaxon

In introducing the new ichnospecies of *Siamopodus* proposed below, we note that the original description of *Siamopodus khaoyaiensis* (Lockley et al., 2006) involved a proof error as follows. The ichnospecies name, while appearing in the abstract and figure captions, was omitted from the section on Systematic Ichnology (Lockley et al., 2006, p. 140). Thus, the ichnospecies description and ichnogenus diagnosis, while presented as separate paragraphs, appear sequentially under the same heading, without the ichnospecies name and etymology (meaning from Khao Yai National Park) inserted before the description.

Theropoda Marsh, 1881
Ichnofamily indet.
Genus *Siamopodus* Lockley et al., 2006
Type ichnospecies: *Siamopodus khaoyaiensis* Lockley et al., 2006
Siamopodus xui ichnosp. nov.
(Fig. 11A–C)

Table 2
Estimated data of the speed of Zhaojue ornithopod morphotype A trackmakers.

No.	SL/h	S (km/h)
ZJII-O1	1.02	3.02
ZJII-O2	1.30	4.64
ZJII-O3	1.10	3.89
ZJII-O7	1.25	4.57
ZJII-O9	1.48	6.01
ZJII-O10	1.34	5.15

Abbreviations: SL/h, relative stride length; S = absolute speed.

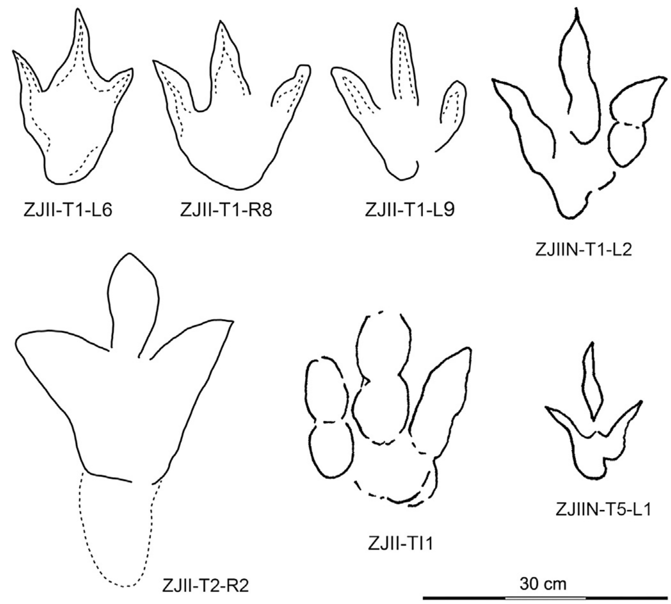

Fig. 9. Photograph and interpretative outline drawings of well-preserved theropod tracks from tracksites ZJII and ZJIIN.

Etymology: The specific name is in honor of Dr. Xing Xu, a distinguished paleontologist who contributed greatly to the study of dinosaurs in China.

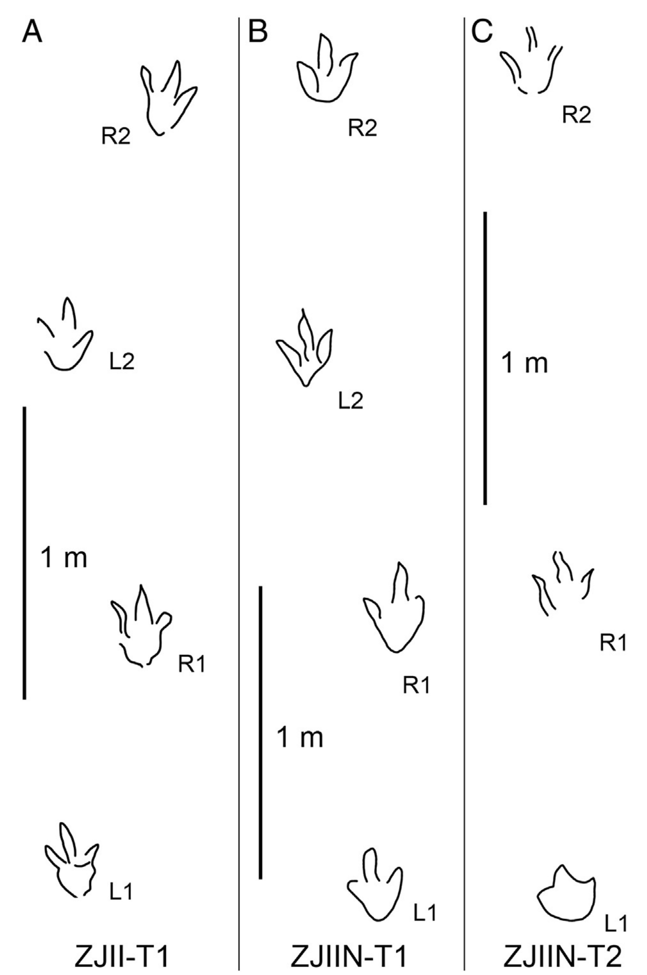

Fig. 10. Interpretative outline drawings of theropod trackways from tracksites ZJII and ZJIIN.

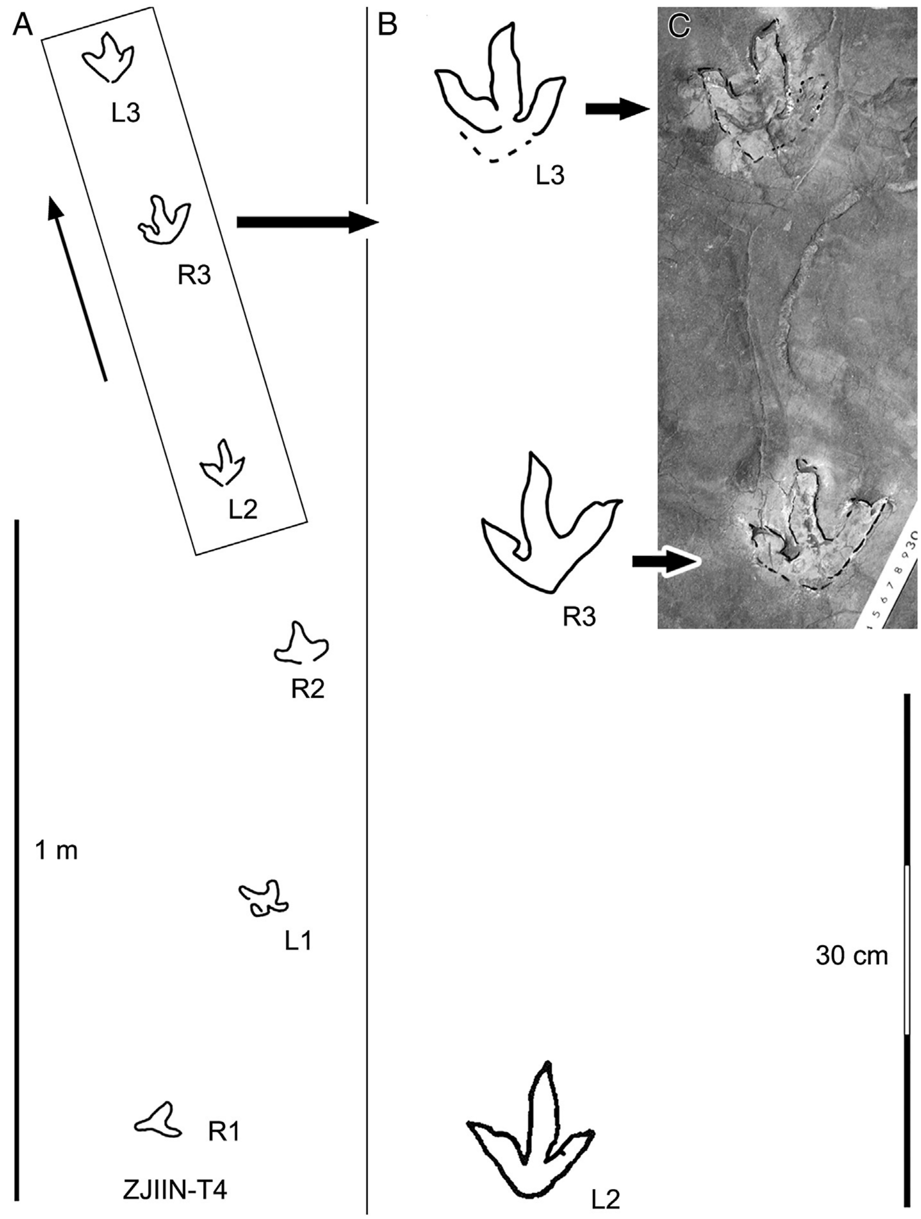

Fig. 11. Photograph (C) and interpretative outline drawings (A–B) of *Siamopodus xui* ichnosp. nov. holotype trackway ZJIIN-T4 based on UCM 214.268 and CU GB-ZJIIN-T4. B–C show details of portion demarcated by rectangle in A.

Holotype: six natural-mold tracks, organized in a trackway and cataloged as ZJIIN-T4-R1–L3 from the Zhaojue tracksite ZJIIN (Fig. 11). The original specimens remain in the field. Replicas of the last three tracks (L2, R3 and L3: Fig. 11A–B) cataloged as UCM 214.268 and also as CUGB-ZJIIN-T4.

Locality and horizon: The Feitianshan Formation, Lower Cretaceous. Zhaojue tracksites ZJII and ZJIIN, Sichuan Province, China.

Diagnosis: Small-sized theropod trackway with a functionally tridactyl, digitigrade and mesaxonic pes. Inner hypex between digits II and III is situated posterior to outer hypex between digits III and IV. The metatarso-phalangeal pad of digit IV is situated in alignment with the track axis, without distinctive bilobed sub-symmetric heel. The trackway is narrow, with a pace angulation of ~170°.

Description: Trackway ZJIIN-T4 shows functionally tridactyl, digitigrade and mesaxonic pes imprints that have an average ML and MW of 8 cm and 7.1 cm. The tracks are characterized by straight, comparatively slender digital traces, with slight inward curvature of the distal claw trace of digit III; claw marks of the three digits are sharp and distinct. The phalangeal pads are partly obscured by infilling sediment. The last three tracks in the six track series (L2, R3 and L3) are preserved as replicas (UCM 214.268 and CUGB-ZJIIN-T4). Of these, R3 is the best preserved with a ML/MW ratio of 0.9. Digit II is the shortest and digit III the longest. The metatarso-phalangeal pad is situated in alignment with the track axis. The hypex between digits II and III is situated posterior to the hypex between digits III and IV. The distance from the inner hypex (between digits II and III) to heel /pes length is 30%. The distance from the outer hypex (between digits III and IV) to heel /pes length is 40%. There is a wide divarication angle (80°) between digit II and digit IV, and the interdigital divarication II–III (36°) is smaller than III–IV (44°). The tracks are rotated slightly inwards towards the axis of the trackway. However the mean rotation angle is difficult to determine accurately because the trackway is curved and the first three footprints are poorly preserved. The average anterior triangle L/W ratio is 0.49 (N = 3). The average PA is 170°.

Table 3
Measurements (in cm) of the theropod tracks from Zhaojue tracksite ZJII and ZJIIN, Sichuan Province, China.

Number	ML	MW	II-IV	PL	SL	PA	ML/MW
ZJII-T1-L1	21.4	18.8	75°	83.0	178.0	146°	1.1
ZJII-T1-R1	23.3	18.7	67°	103.0	180.0	137°	1.3
ZJII-T1-L2	24.1	14.5	61°	90.0	–	–	1.7
ZJII-T1-R2	26.2	17.5	51°	–	–	–	1.5
ZJII-T1-R4	20.3	16.2	–	69.8	–	–	1.3
ZJII-T1-L5	18.0	18.2	70°	–	185.3	–	1.0
ZJII-T1-L6	22.6	15.2	52°	–	–	–	1.5
ZJII-T1-L8	–	14.9	–	63.2	130.2	125°	–
ZJII-T1-R8	20.3	19.6	62°	82.0	162.0	166°	1.0
ZJII-T1-L9	23.5	17.8	64°	80.7	161.7	154°	1.3
ZJII-T1-R9	22.0	14.5	–	85.5	–	–	1.5
ZJII-T1-L10	24.5	–	–	–	–	–	–
Mean	22.5	16.9	63°	82.1	166.3	146°	1.3
ZJII-ST1-L1	37.0	17.6	–	142.5	281.4	180°	2.1
ZJII-ST1-R1	28.7	19.8	–	138.5	275.0	185°	1.4
ZJII-ST1-L2	33.7	12.2	–	136.5	258.0	182°	2.8
ZJII-ST1-R2	32.0	14.0	–	121.1	262.5	180°	2.3
ZJII-ST1-L3	41.0	16.0	–	141.2	274.0	183°	2.6
ZJII-ST1-R3	41.4	14.0	–	133.0	250.0	181°	3.0
ZJII-ST1-L4	21.0	–	–	117.0	–	–	–
ZJII-ST1-R4	33.5	18.3	–	–	–	–	1.8
Mean	33.5	16.0	–	132.8	266.8	182°	2.3
ZJII-T2-R1	–	–	–	92	182	180°	–
ZJII-T2-L1	–	–	–	92	–	–	–
ZJII-T2-R2	28.4	26.8	71°	–	–	–	1.1
ZJIIN-T1-L1	25.4	19.0	62°	96.5	187.0	153°	1.3
ZJIIN-T1-R1	29.4	21.0	56°	97.4	187.5	155°	1.4
ZJIIN-T1-L2	27.4	20.5	56°	95.5	–	–	1.3
ZJIIN-T1-R2	23.4	19.0	70°	–	–	–	1.2
Mean	26.4	19.9	61°	96.5	187.3	154°	1.3
ZJIIN-T2-L1	20.6	19.2	78°	106.5	–	–	1.1
ZJIIN-T2-R1	22.0	22.6	–	–	182.2	–	1.0
ZJIIN-T2-R2	23.2	22.4	65°	–	–	–	1.0
Mean	21.9	21.4	72°	106.5	182.2	–	1.0
ZJIIN-T3-R1	6.8	8.2	87°	–	–	–	0.8
ZJIIN-T3-L1	8.8	7.5	92°	45.7	–	–	1.2
Mean	7.8	7.9	90°	45.7	–	–	1.0
ZJIIN-T4-R1	5.2	7.0	–	37.2	75.0	152°	0.7
ZJIIN-T4-L1	6.3	7.8	115°	39.0	70.0	175°	0.8
ZJIIN-T4-R2	6.7	8.3	122°	32.3	74.9	173°	0.8
ZJIIN-T4-L2	7.8	7.8	84°	42.7	69.6	180°	1.0
ZJIIN-T4-R3	7.9	8.8	80°	26.6	–	–	0.9
ZJIIN-T4-L3	8.9	8.0	90°	–	–	–	1.1
Mean	7.1	8.0	98°	35.6	72.4	170°	0.9
ZJII-TI1	24.0	19.0	54°	–	–	–	1.3
ZJIIN-T5-L1	16.8	11.6	65°	–	–	–	1.4

Abbreviations: ML: maximum length; MW: maximum (measured as the distance between the tips of digits II and IV); II–IV: angle between digits II and IV; PL: pace length; SL: stride length; PA: pace angulation; ML/MW is dimensionless.

Comparisons and discussion: theropod tracks and tridactyl tracks are often difficult to assign to known ichnotaxa with confidence. This is also the case with trackway ZJIIN-T4. However, it is distinctive by i) being significantly smaller than all the other 20–30 cm long theropod tracks at ichnosites ZJII and ZJIIN, an ii) having the hypex between digit traces II and III more posterior that between digit traces III and IV, as noticeble by comparing ZJIIN-TI (Fig. 9) to ZJIIN-T4 (Fig. 11). This feature alone draws attention to the similarity with *Siamopodus khaoyaiensis* (Lockley et al., 2006) from the Cretaceous of Thailand. Other similarities include the comparatively low ML/MW ratio and wide interdigital divarication angles, as well as the anterior triangle L/W ratio (0.49 vs. 0.47) based on Lockley et al. (2006, fig. 5A). The large pes (P′ML = 30 cm of the holotype of *Siamopodus khaoyaiensis*) has more or less parallel sided digit traces, although the digit traces in the smaller paratypes (P′ML = 14–17 cm) taper more sharply. Differences include size, which is not an important diagnostic factor for ichnotaxonomy (Lockley and Hunt, 1995), and the lack of a bilobed heel trace in the Chinese specimen. Other differences are of little obvious diagnostic utility. The Chinese specimen, herein named *S. xui* has a pace angulation of 170°. However, the possible trackway segments and the single, uncertain pace angulation given for *S. khaoyaiensis* are insufficient to provide useful information for comparative analysis.

Thus, the trackway described here is readily distinguished from all other tracks preserved at the Zhaojue sites (ZJ I, ZJII, and ZJIIN) both in size and morphology, especially the configuration of the two hypices. As noted in a previous section, tracks of the *Grallator* morphotype are relatively common in the Cretaceous of China (Lockley et al., 2013). However the morphotype described here (Fig. 11) reveals much lower ML/MW ratios than *Grallator*, both for the whole track and the anterior triangle (see Table 3). Regarding the ML/MW ratio of ZJIIN-T4, the Chinese specimen (here named *S. xui*) has a "proportionally shorter digit III" (sensu Olsen and Rainforth, 2003, p. 314) making it more like *Anomoepus*: i.e., with weak mesaxony (sensu Lockley, 2009). However, in most other diagnostic features, including the lack of a diagnostic manus and hallux trace, or the configuration of the hypices, it is fundamentally different from *Anomoepus*. It is pertinent to note that some small theropod tracks from China, including *Corpulentapus* (Li et al., 2011b) have very low ML/MW and anterior triangle L/W ratios (~1.1 and 0.31 respectively: see Lockley, 2009). Thus, we argue that *S. xui* is different from either the grallatorid and the anomoepid morphotypes, but nevertheless shows diagnostic theropodian attributes. Its most diagnostic feature, the configuration of the hypices, allies it most closely with *Siamopodus*. Differences are noteworthy, but it is premature to erect a new ichnogenus, especially in the light of recent efforts to reduce the number of indistinguishable theropodan ichnogenera reported from the ichnological literature on the Mesozoic of China (Lockley et al., 2013). In this regard however, it has been stated that Cretaceous theropod ichnotaxa are more differentiated, distinct and diverse than those in the Jurassic. This inference requires further testing by careful comparative study. The distinctive morphotype is assigned here to the new ichnospecies *Siamopodus xui*.

4.3. Sauropod tracks

4.3.1. Description

Tracksites ZJII and ZJIIN preserve six large quadruped trackways: ZJII-S1, ZJIIN-S1, S2, S3, S4, and S5 (Figs. 4, 5, 12–14, Table 4). Several isolated tracks were also discovered in the collapsed debris. Except for ZDM201306-1–3 (Fig. 11), which are housed at the Zigong Dinosaur Museum, all other tracks and trackways remain in situ.

Trackway ZJII-S1 is situated near the trackway of the swimming theropod, which was briefly described in Xing et al. (2013e). That description focused on the tracks from the lower part of the tracksite. The manus impressions of ZJII-S1 (Fig. 12A) lie slightly anteromedially to the pes impressions. The average length/width ratios of the manus and pes impressions are 0.6 and 1.3 respectively. Taking the best-preserved manus-pes association RP5- RM5 (Fig. 11), the manus imprints show oval digit impressions, while the claws and the metacarpo-phalangeal region are indistinct. The pes impression is oval, digits I and II have incomplete claw marks, and the metatarso-phalangeal region is smoothly curved. The manus impression is rotated approximately 19° outward from the trackway axis, which is smaller than the outward rotation of the pes impressions (approximately 28°). The average manus PA is 119°, while the average pes PA is 120°.

The better-preserved trackways at tracksite ZJIIN are S1, S2, S3, and S5 (Fig. 12B–D), among which S1, S3, and S5 resemble the ZJII-S1 trackway both in size and morphology (Table 4). Digits I, II and III of some of the best preserved pes traces of the Zhaojue quadruped trackways have well-developed claw marks. In some instances, digits IV have small nail marks or depressions made by small unguals or foot callosities, as in ZJIIN-S1-RP4 and ZJIIN-S3-LP1 (Fig. 13). The manus traces are usually oval or U-shaped, partial well-preserved manus traces with rounded marks of digits I and V, as in ZJIIN-S5-LM1 (Fig. 13). The outward rotation of ZJIIN-S1 is slightly larger than that of ZJII-S1, being 30° in the manus and 32° in the pes on average.

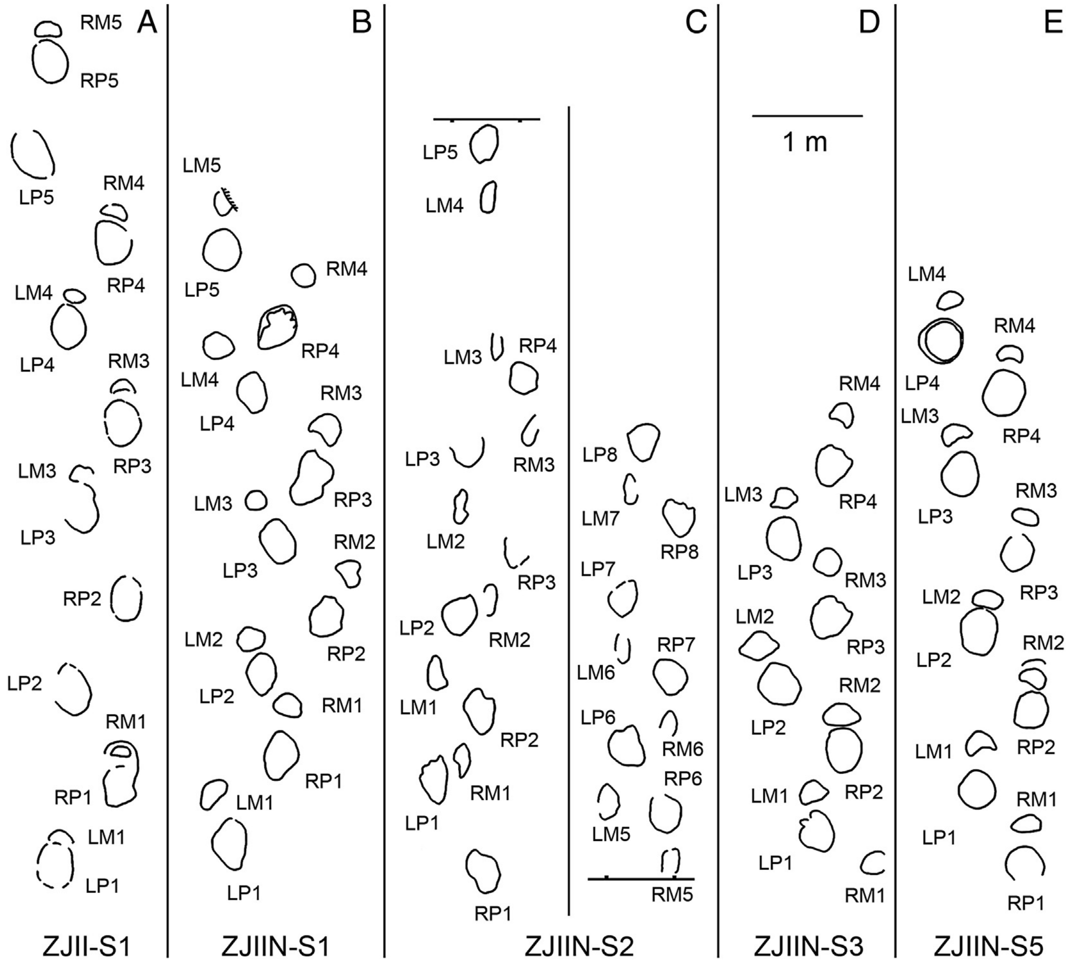

Fig. 12. Interpretative outline drawings of sauropod trackways from tracksites ZJII and ZJIIN. A–E share the same scale bar.

Trackway ZJIIN-S2 is the most unusual (Fig. 12C). The manus traces are strongly rotated outwards from the trackway axis by 80° on average. The pes trace rotations are similar to those of other trackways, that is 28°. LM1 and LP1 (Fig. 13) are the best preserved. The LM1 manus trace is oval, digit traces I and V are discernable, and the outward rotation is up to 122°. The traces of digits I–IV of the pes LP1 are distinct, with that of digit I being the sharpest and digit IV being the weakest. In LP1, the metatarso-phalangeal has partially collapsed, likely due to the wet and soft sediments; the proximal end is smoothly curved; and the outward rotation is 21°. Among all other sauropod tracks from Zhaojue tracksites II and IIN, the distance between the manus and the pes ranges between 6 and 24 cm, which is less than P′ML. Whereas, the distance between ZJIIN-S2-LM1 and ZJ-S2-LP1 is up to 61.7 cm, that is 1.7 times that of the length of the latter.

ZDM201306-1 is an incomplete specimen, other ZDM specimens and ZJIIN-SI1, 3–7 (Figs. 13–14) are well-preserved. All these pes prints are longer than wide, with many preserving large, outwardly directed claw marks of digits I–III, the small claw mark of digit IV, and a small callosity or pad mark of digit V. The "medial digit" of ZJIIN-SI1 is larger than the "outer digits". The "medial digit" is probably caused by the lack of a border between digit II and III.

4.3.2. Comparisons and discussion

The pes and manus morphology and trackway configuration of the Zhaojue large quadruped trackways are typical of sauropods (Lockley and Hunt, 1995; Lockley, 1999, 2001). Most sauropod trackways in China are wide- (or medium-) gauge and are therefore referred to the ichnogenus *Brontopodus* (Lockley et al., 2002). The Zhaojue sauropod trackways are between medium-gauge and wide-gauge trackways, with a WAP/P′ML ratio of 1.0 to 1.3 (Marty, 2008).

The Zhaojue sauropod trackway configurations are also consistent with the characteristics of *Brontopodus* type tracks from the Upper Jurassic of Portugal and Switzerland (Meyer and Pittman, 1994; Santos et al., 2009) and from the Lower Cretaceous of the USA (Farlow et al., 1989; Lockley et al., 1994). These features are 1) wide-gauge; 2) pes tracks that are longer than wide, and large and outwardly directed; 3) U-shaped manus prints; and 4) a high degree of heteropody (ratio of manus to pes size). The mean heteropody of the well-preserved ZJI sauropod tracks is 1:2.3 (2.1, 2.3, and 2.5, $n = 3$). This is close to *Brontopodus birdi* (1:3) but significantly less than in the narrow-gauge ichnotaxa *Breviparopus* (1:3.6) or *Parabrontopodus* (1:4 or 1:5) (Lockley et al., 1994). The wide-gauge of the *Brontopodus*-type trackways suggests that the tracks were left by titanosaurian sauropods (Wilson and Carrano, 1999; Lockley et al., 2002).

Because of the lack of significant details within the tracks and the absence of additional trackway data, the isolated pes tracks cannot be assigned to a distinct ichnogenus, nor can they be attributed accurately to a trackmaker. However, compared with the imprints of the sauropod trackways from tracksites ZJII and ZJIIN, these isolated tracks probably pertain to *Brontopodus*, due to the digital morphology and ML/MW ratios.

4.3.3. Speed estimates

For sauropods, Alexander (1976) first suggested that hip height $h = 4 \times$ foot length, whereas, later, Thulborn (1990) estimated $h = 5.9 \times$ foot length. González Riga (2011), proposed a formula for titanosaurid tracks based on anatomical and ichnological evidences as $h = 4.586 \times \mathrm{FL(ML)}$.

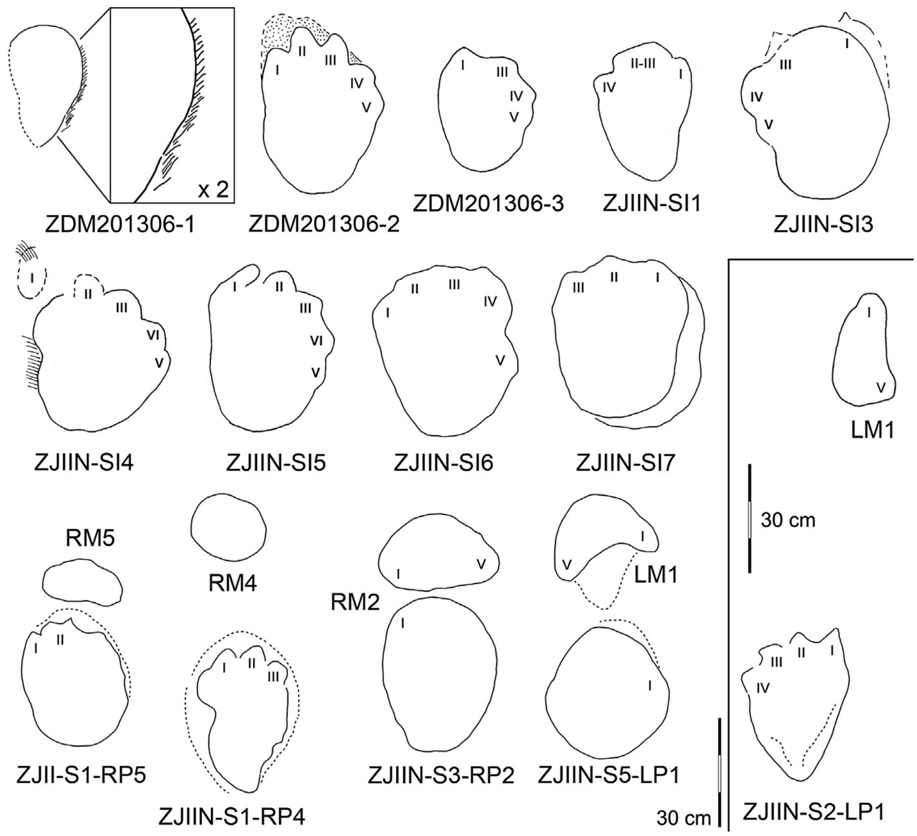

Fig. 13. Interpretative outline drawings of well-preserved sauropod tracks from tracksites ZJII and ZJIIN.

The relative stride length (SL/h) may be used to determine whether the animal is walking (SL/h ≤ 2.0), trotting (2 < SL/h < 2.9), or running (SL/h ≥ 2.9) (Alexander, 1976; Thulborn, 1990). The SL/h ratios of the Zhaojue sauropod trackways are between 0.51–0.74 and 0.75–1.09 (Table 5) and accordingly suggest walking. Using the equation to estimate speed from trackways (Alexander, 1976), the mean locomotion speed of the trackmaker is between 1.44–2.38 km/h and 2.27–3.74 km/h.

The unusually long distance between the pes and manus in ZJIIN-S2 is difficult to understand. Although the estimated speed calculated from ZJIIN-S2 is the fastest (Table 5), the speed difference cannot explain the considerable distance between the pes and manus, in comparison with the other trackways (S1, S3 & S5). The speed of the ZJIIN-S5 trackmaker was only slightly slower, but the distances between its pes and manus tracks are much shorter (Fig. 12). A more likely explanation is that the trackmaker of ZJIIN-S2 had longer limbs. For the super-large titanosaur *Argentinosaurus huinculensis* (estimated to be 40 m long), the length of the forelimb and hindlimb is probably similar (based on Sellers et al., 2013, Fig. 2). Computer simulations indicate that, at low speed, *A. huinculensis* created trackways similar to those of traditional titanosaurs, with short distances between the manus and pes (see Sellers et al., 2013, Fig. 12). Contrary, brachiosaurids, with their forelimbs being longer than their hind limbs (Gunga et al., 1995), are expected to place their manus and pes at a greater distance from each other, while walking. Therefore, ZJIIN-S2 can possibly be attributed to a brachiosaur, while all other trackways might belong to titanosaurs. However, this cannot be proved with certainty.

4.3.4. Integument scratch lines and special preservation

Some isolated sauropod tracks, such as ZDM201306-1 and ZJIIN-SI4, preserve integument or skin scratch lines made when individual pedal skin tubercles or 'scales' dragged through the sediment (Fig. 13). The scale scratch lines of typical tracks average 5–10 mm in width, and there are 9–12 lines per 10 cm. The size of these scale scratches is slightly smaller than typical scales from sauropod skin impressions. For example, the sauropod skin impressions from the Lower Cretaceous Haman Formation of Gainri and Sinsu Island, South Korea, reveal large pentagonal and heptagonal scale impressions (size 2.0–2.5 cm) (Kim et al., 2010). Another specimen from the Upper Jurassic Morrison Formation, Wyoming, U.S.A., shows scales of 0.75–1.2 cm size (Platt and Hasiotis, 2006). However, while skin polygons can be 2.0–2.5 cm in diameter, this does not mean that the vertical striations or scratch marks they create will also be separated by similar distances: different irregularities in skin texture and relief will be superimposed by the dynamics of the foot penetrating the sediment and creating a striated track wall. In this manner the striations cannot be more widely separated that the polygon widths but more closely spaced.

Track ZJIIN-SI3 (Figs. 13–14) is an unusual natural cast of a right pes, approximately 10 cm deep, and is divided into distinct upper and lower parts, presumably representing different phases of track registration. There is no distinct border between digits I–III at either level, and a trace of digit II is not preserved. Distinct impressions of digits IV and V are present laterally, at the lower level, but not at the upper level. A slope to the wall of the track cast indicates the angle at which the foot registered on the substrate. Seen "upside down" the cast appears as a pedestal and probably owes its preservation to having penetrated through and impacted on two layers of sediments of different hardness and moisture content. The surface sediments were drier or firmer and the claw marks were therefore preserved as they cut through the exposed layers, while sediments underneath may have been softer, yielding to the weight of the sauropod as it pushed the upper layer downward. The sediment making up the floor of the footprint is likely in part a "strip" of the upper layer pushed aside, while a certain amount of softer sediment flowed in above it. After the whole track was filled in by the next layer of sand "a sandwich effect" was created, which, after

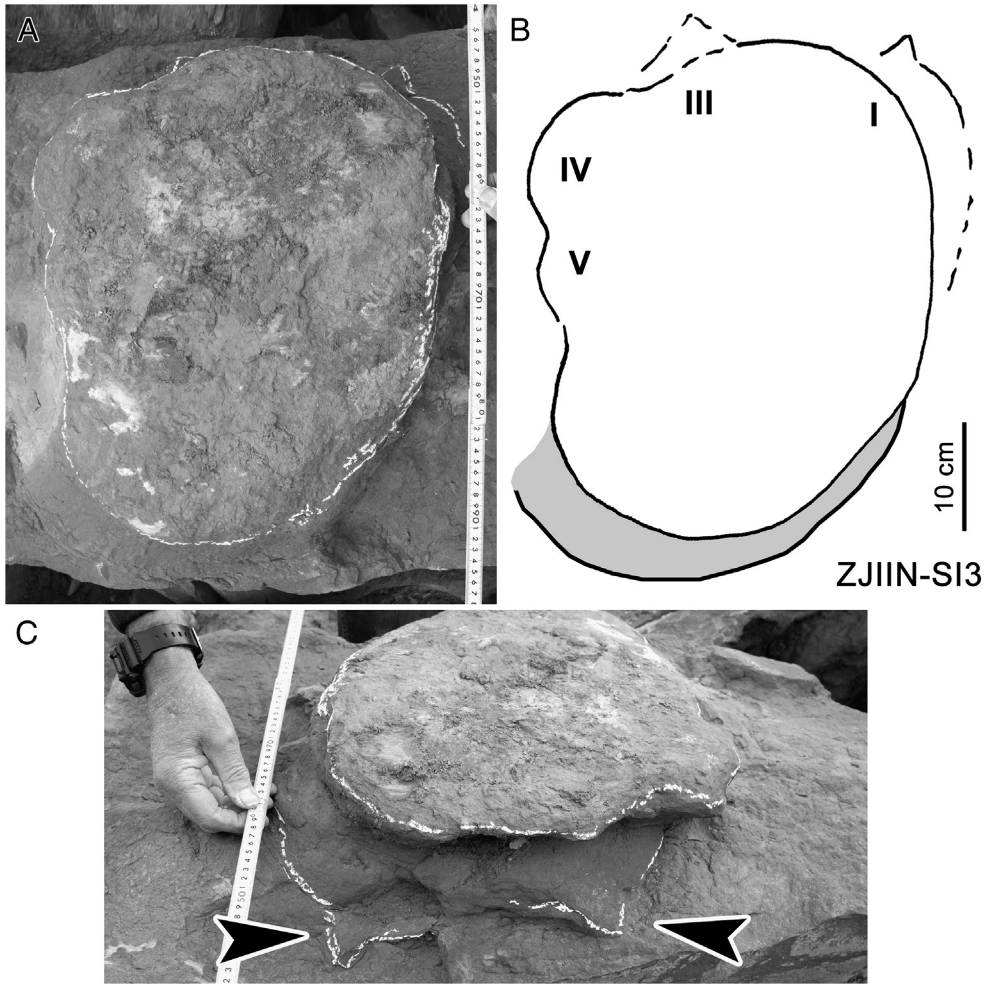

Fig. 14. Photograph (A, C) and interpretative outline drawing (B) of the sauropod infill ZJIIN-SI3 from tracksite ZJIIN, showing peculiarities of preservation. Black arrows in (C) indicate digit I and III impressions.

exhumation and erosion, produced this pedestal feature. This inference is strongly supported by the fact that the main track layer is overlain by a thin silt layer that, in turn, is over-lain by a track-rich sandstone from which most of the casts originate (see Fig. 2 and explanation above).

5. Lower Cretaceous dinosaur ichnoassociations from China and paleoecological implications of the Feitianshan Formation

Remarkably, all ornithopod tracks at Zhaojue tracksite ZJII are similar in size and all conform to the *Caririchnium* morphotype. The trackways are generally parallel, consistent in direction, and all reflect walking individuals. This suggests that the area was probably used as a common passage for ornithopods that probably lived in herds.

Most ornithopod tracks at Zhaojue tracksite ZJIIN are small-sized *Ornithopodichnus*, only one larger *Caririchnium* morphotype trackway was discovered. This suggests that different ornithopods probably assembled in different species groups of different sizes, and in locally different areas.

The appearance of middle-large-sized theropod trackway among those of the ornithopods (Fig. 5) may suggest that theropod predators were active in the region where potential prey species (ornithopods) were common. Similar behavioral interpretations have been made based on the Early Cretaceous (Aptian–Albian) *Amblydactylus* and *Irenesauripus* assemblages from Peace River Canyon, Canada (Currie, 1983). However, trackway patterns and the estimated speeds of the trackmakers show no evidence of direct confrontations, and it is difficult to determine whether representatives of the two groups were both in the tracked areas at precisely the same time.

The appearance of *Grallator*, *Eubrontes* or *Irenesauripus* morphotypes and other theropod tracks such as *Siamopodus xui* at Zhaojue tracksites ZJII and ZJIIN suggests a high diversity of local theropods. *Asianopodus* tracks have been reported from China and Thailand (Matsukawa et al., 2006), but this ichnogenus was not identified in the present study. The diversity and abundance of theropod tracks in the Lower Cretaceous of China is considerable (Matsukawa et al., 2006), with distinctive new ichnotaxa such as *Corpulentapus* having been reported quite recently (Li et al., 2011b). However, as yet there has been no regional synthesis with confident identification of a larger number of theropod tracks at the ichnogenus level to demonstrate the relative abundance and distribution of the different types at a regional level.

The sauropod track sample from the Zhaojue tracksites is proportionally larger (more abundant) than any among the Early Cretaceous Sichuan Basin sites, and far exceeds the sauropod track sample from the Lotus tracksite near Qijiang, Chongqing City, where they are represented by undertracks and isolated casts (unpublished data). Likewise at the Jiefang tracksite from the Zhaojue area, only one trackway is known (Xing et al., in press-b). These discoveries have altered the previous interpretations by Xing et al. (2011b) that the dinosaur track record from the Cretaceous Sichuan Basin is dominated by theropods and ornithopods. It suggests that titanosaurian sauropods were also abundant.

In general, the three tracksites in Zhaojue (ZJI, ZJII and ZJIIN) document a high dinosaurian biodiversity, including sauropods, theropods,

Table 4
Measurements (in cm) of the sauropod trackways from Zhaojue tracksites II and II N, Sichuan Province, China.

Number	ML	MW	R	PL	SL	PA	ML/MW	WAP	WAP/P′ML	WAM	WAM/M′MW
ZJII-S1-LM1	10.3	20.0	–	95.0	–	105°	0.5	–	–	–	–
ZJII-S1-LP1	40.9	32.5	31°	94.5	158.3	113°	1.3	–	–	–	–
ZJII-S1-RM1	9.2	16.5	–	–	–	–	0.6	–	–	–	–
ZJII-S1-RP1	38.5	30.0	25°	93.1	168.7	122°	1.3	51.7	1.3	–	–
ZJII-S1-LM2	–	–	–	–	–	–	–	–	–	–	–
ZJII-S1-LP2	46.0	33.5	37°	97.8	169.0	121°	1.4	47.6	1.0	–	–
ZJII-S1-RM2	–	–	–	–	–	–	–	–	–	–	–
ZJII-S1-RP2	40.0	26.8	21°	93.3	162.2	125°	1.5	46.4	1.2	–	–
ZJII-S1-LM3	13.2	21.6	16°	90.4	164.1	126°	0.6	–	–	–	–
ZJII-S1-LP3	41.3	30.9	23°	87.5	168.9	124°	1.3	40.5	1.0	–	–
ZJII-S1-RM3	11.7	22.4	5°	91.9	158.9	125°	0.5	–	–	40.5	1.8
ZJII-S1-RP3	41.3	32.0	18°	101.5	164.5	123°	1.3	44.2	1.1	–	–
ZJII-S1-LM4	12.0	19.5	–	86.5	–	–	0.6	–	–	40.1	2.1
ZJII-S1-LP4	39.5	30.0	16°	85.8	158.6	109°	1.3	44.8	1.1	–	–
ZJII-S1-RM4	11.1	21.9	36°	–	178.6	–	0.5	–	–	–	–
ZJII-S1-RP4	37.5	32.6	49°	106.5	174.3	124°	1.2	57.4	1.5	–	–
ZJII-S1-LM5	–	–	–	–	–	–	–	–	–	–	–
ZJII-S1-LP5	49.0	32.0	–	86.9	–	–	1.5	45.0	0.9	–	–
ZJII-S1-RM5	13.7	23.0	–	–	–	–	0.6	–	–	–	–
ZJII-S1-RP5	39.2	31.5	–	31.5	31.5	–	1.2	–	–	–	–
Mean (M)	11.6	20.7	19°	91.0	167.2	119°	0.6	–	–	40.3	2.0
Mean (P)	41.3	31.2	28°	87.8	150.7	120°	1.3	47.2	1.3	–	–
ZJIIN-S1-LM1	16.6	32.0	51°	108.5	152.4	108°	0.5	–	–	–	–
ZJIIN-S1-LP1	45.7	31.5	36°	97.0	167.8	135°	1.5	–	–	–	–
ZJIIN-S1-RM1	21.6	26.3	0°	70.7	139.4	95°	0.8	–	–	30.0	1.1
ZJIIN-S1-RP1	45.9	29.9	6°	81.5	140.2	115°	1.5	31.4	0.7	–	–
ZJIIN-S1-LM2	22.8	25.2	18°	110.5	134.0	72°	0.9	–	–	55.6	2.2
ZJIIN-S1-LP2	40.5	27.5	24°	80.0	128.8	92°	1.5	41.9	1.0	–	–
ZJIIN-S1-RM2	19.0	26.0	66°	109.5	–	84°	0.7	–	–	86.1	3.3
ZJIIN-S1-RP2	41.5	29.8	49°	87.0	139.8	115°	1.4	55.4	1.3	–	–
ZJIIN-S1-LM3	19.5	19.5	14°	93.1	150.7	82°	1.0	–	–	74.2	3.8
ZJIIN-S1-LP3	41.8	27.2	31°	73.5	–	112°	1.5	41.4	1.0	–	–
ZJIIN-S1-RM3	21.6	27.5	48°	127.3	147.8	76°	0.8	–	–	79.5	2.9
ZJIIN-S1-RP3	50.5	32.0	46°	96.6	144.8	115°	1.6	45.6	0.9	–	–
ZJIIN-S1-LM4	29.2	24.5	12°	102.0	–	–	1.2	–	–	87.3	3.6
ZJIIN-S1-LP4	38.0	23.5	–	65.7	–	–	1.6	40.0	1.1	–	–
ZJIIN-S1-RM4	19.8	23.1	–	–	–	–	0.9	–	–	–	–
ZJIIN-S1-RP4	44.8	30.2	–	97.0	–	–	1.5	–	–	–	–
ZJIIN-S1-LM5	–	–	–	–	–	–	–	–	–	–	–
ZJIIN-S1-LP5	36.0	36.0	–	–	–	–	1.0	–	–	–	–
Mean (M)	21.3	25.5	30°	103.1	144.9	86°	0.9	–	–	68.8	2.8
Mean (P)	42.7	29.7	32°	84.8	144.3	114°	1.5	42.6	1.0	–	–
ZJIIN-S2-RM1	15.5	22.3	41°	82.0	145.0	126°	0.7	–	–	–	–
ZJIIN-S2-RP1	–	–	–	–	–	–	–	–	–	–	–
ZJIIN-S2-LM1	16.2	29.9	122°	84.5	152.9	125°	0.5	–	–	37.1	1.2
ZJIIN-S2-LP1	37.2	27.5	21°	77.0	148.9	134°	1.4	–	–	–	–
ZJIIN-S2-RM2	11.0	17.2	–	89.0	155.0	120°	0.6	–	–	39.0	2.3
ZJIIN-S2-RP2	40.6	17.5	–	86.5	150.5	–	2.3	32.0	0.8	–	–
ZJIIN-S2-LM2	8.9	30.5	–	95.0	150.0	114°	0.3	–	–	–	–
ZJIIN-S2-LP2	31.8	32.0	–	80.8	150.3	–	1.0	–	–	–	–
ZJIIN-S2-RM3	12.1	28.0	–	86.0	–	–	0.4	–	–	–	–
ZJIIN-S2-RP3	–	100.0	–	151.6	–	–	–	–	–	–	–
ZJIIN-S2-LM3	9.5	26.3	–	–	136.0	–	0.4	–	–	–	–
ZJIIN-S2-LP3	31.0	28.5	–	79.5	–	–	1.1	–	–	–	–
ZJIIN-S2-RM4	–	–	–	–	–	–	–	–	–	–	–
ZJIIN-S2-RP4	27.0	25.0	–	–	–	–	1.1	–	–	–	–
ZJIIN-S2-LM4	13.3	29.3	73°	–	–	118°	0.5	–	–	–	–
ZJIIN-S2-LP4	–	–	–	–	–	–	–	–	–	–	–
ZJIIN-S2-RM5	15.0	24.0	–	78.2	123.1	97°	0.6	–	–	43.2	1.8
ZJIIN-S2-RP5	–	–	–	–	–	–	–	–	–	–	–
ZJIIN-S2-LM5	20.0	28.5	84°	85.8	143.1	113°	0.7	–	–	–	–
ZJIIN-S2-LP5	30.0	26.4	17°	90.2	147.8	132°	1.1	–	–	–	–
ZJIIN-S2-RM6	14.5	–	–	84.0	–	–	–	–	–	47.7	–
ZJIIN-S2-RP6	31.0	27.3	25°	89.0	125.7	133°	1.1	33.2	1.1	–	–
ZJIIN-S2-LM6	12.6	30.0	78°	–	145.3	–	0.4	–	–	–	–
ZJIIN-S2-LP6	38.7	30.0	51°	75.3	136.5	113°	1.3	40.7	1.1	–	–
ZJIIN-S2-RM7	–	–	–	–	–	–	–	–	–	–	–
ZJIIN-S2-RP7	32.5	28.0	5°	81.8	145.5	112°	1.2	45.2	1.4	–	–
ZJIIN-S2-LM7	12.8	26.6		–	–	–	0.5	–	–	–	–
ZJIIN-S2-LP7	29.8	26.2	27°	89.5	145.5	121°	1.1	–	–	–	–
ZJIIN-S2-RM8	–	–	–	–	–	–	–	–	–	–	–
ZJIIN-S2-RP8	30.0	29.2	–	86.6	134.8	–	1.0	41.5	1.4	–	–
ZJIIN-S2-LM8	–	–	–	–	–	–	–	–	–	–	–
ZJIIN-S2-LP8	32.6	28.0	–	75.2	142.4	–	1.2	–	–	–	–
ZJIIN-S2-RM9	–	–	–	–	–	–	–	–	–	–	–

Table 4 (*continued*)

Number	ML	MW	R	PL	SL	PA	ML/MW	WAP	WAP/P′ML	WAM	WAM/M′MW
ZJIIN-S2-RP9	36.9	30.5	–	–	–	–	1.2	–	–	–	–
ZJIIN-S2-LM9	–	–	–	–	–	–	–	–	–	–	–
ZJIIN-S2-LP9	32.5	23.5	–	76.8	–	–	1.4	–	–	–	–
Mean (M)	13.5	26.6	80°	85.6	143.8	116°	0.5	–	–	41.8	1.8
Mean (P)	33.0	27.1	28°	83.7	143.6	124°	1.2	38.5	1.2	–	–
ZJIIN-S3-RM1	24.5	20.2	–	87.0	144.7	120°	1.2	–	–	–	–
ZJIIN-S3-RP1	–	–	–	–	–	–	–	–	–	–	–
ZJIIN-S3-LM1	19.4	22.0	4°	78.8	148.3	111°	0.9	–	–	40.0	1.8
ZJIIN-S3-LP1	40.0	26.4	10°	83.7	143.8	115°	1.5	–	–	–	–
ZJIIN-S3-RM2	21.9	33.0	7°	97.5	147.0	91°	0.7	–	–	46.7	1.4
ZJIIN-S3-RP2	42.6	30.6	11°	80.5	125.2	90°	1.4	44.9	1.1	–	–
ZJIIN-S3-LM2	22.6	28.0	46°	100.5	142.0	107°	0.8	–	–	68.1	2.4
ZJIIN-S3-LP2	42.5	32.5	50°	78.0	141.0	108°	1.3	56.0	1.3	–	–
ZJIIN-S3-RM3	23.1	24.0	25°	71.5	140.2	111°	1.0	–	–	48.5	2.0
ZJIIN-S3-RP3	38.0	34.0	33°	85.4	143.1	112°	1.1	49.5	1.3	–	–
ZJIIN-S3-LM3	19.5	23.5	–	94.1	–	–	0.8	–	–	44.3	1.9
ZJIIN-S3-LP3	40.4	28.1	–	79.0	–	–	1.4	47.1	1.2	–	–
ZJIIN-S3-RM4	20.0	20.0	–	–	–	–	1.0	–	–	–	–
ZJIIN-S3-RP4	36.3	29.0	–	–	–	–	1.3	–	–	–	–
Mean (M)	21.6	24.4	21°	88.2	144.4	108°	0.9	–	–	49.5	1.9
Mean (P)	40.0	29.7	26°	78.9	140.1	106°	1.4	49.4	1.2	–	–
ZJIIN-S4-LP1	45.2	26.8	23°	75.0	116.2	105°	1.7	–	–	–	–
ZJIIN-S4-RP1	40.6	29.5	16°	65.6	121.3	98°	1.4	42.7	1.1	–	–
ZJIIN-S4-LP2	45.4	30.0	8°	89.0	137.5	108°	1.5	48.7	1.1	–	–
ZJIIN-S4-RP2	44.8	34.3	19°	77.8	135.8	111°	1.3	47.6	1.1	–	–
ZJIIN-S4-LP3	42.9	28.0	–	83.4	–	–	1.5	46.1	1.1	–	–
ZJIIN-S4-LM3	17.5	23.8	–	–	–	–	0.7	–	–	–	–
ZJIIN-S4-RP3	37.9	28.1	–	–	–	–	1.3	–	–	–	–
Mean (M)	17.5	23.8	–	–	–	–	0.7	–	–	–	–
Mean (P)	42.8	29.5	17°	78.2	127.7	106°	1.5	46.3	1.1	–	–
ZJIIN-S5-RM1	18.0	25.1	7°	90.8	141.6	109°	0.7	–	–	–	–
ZJIIN-S5-RP1	38.1	34.0	–	85.0	149.6	111°	1.1	–	–	–	–
ZJIIN-S5-LM1	21.0	27.2	20°	80.2	137.9	109°	0.8	–	–	46.4	1.7
ZJIIN-S5-LP1	36.2	31.5	41°	91.8	153.4	110°	1.1	47.8	1.3	–	–
ZJIIN-S5-RM2	18.5	25.3	32°	87.4	156.3	126°	0.7	–	–	45.7	1.8
ZJIIN-S5-RP2	37.3	28.0	42°	90.6	153.4	118°	1.3	50.4	1.4	–	–
ZJIIN-S5-LM2	18.5	24.5	29°	87.8	162.8	114°	0.8	–	–	37.2	1.5
ZJIIN-S5-LP2	45.0	30.8	10°	84.3	152.0	114°	1.5	43.2	1.0	–	–
ZJIIN-S5-RM3	15.2	23.9	28°	102.9	160.0	103°	0.6	–	–	48.5	2.0
ZJIIN-S5-RP3	38.0	29.8	27°	90.5	154.7	112°	1.3	45.9	1.2	–	–
ZJIIN-S5-LM3	19.8	27.5	32°	95.0	129.4	95°	0.7	–	–	59.2	2.2
ZJIIN-S5-LP3	43.1	33.4	20°	88.2	131.8	97°	1.3	50.5	1.2	–	–
ZJIIN-S5-RM4	17.5	22.0	–	74.5	–	–	0.8	–	–	54.5	2.5
ZJIIN-S5-RP4	45.0	35.5	–	75.5	–	–	1.3	54.2	1.2	–	–
ZJIIN-S5-LM4	15.3	25.6	–	–	–	–	0.6	–	–	–	–
ZJIIN-S5-LP4	37.4	33.4	–	–	–	–	1.1	–	–	–	–
Mean (M)	18.0	25.1	25°	88.4	148.0	109°	0.7	–	–	48.6	1.9
Mean (P)	40.0	32.1	28°	86.6	149.2	110°	1.3	48.7	1.2	–	–
ZDM201306-2	46.4	31.6	–	–	–	–	1.5	–	–	–	–
ZDM201306-3	34.9	27.1	–	–	–	–	1.3	–	–	–	–
ZJIIN-SI1	38.0	27.0	–	–	–	–	1.4	–	–	–	–
ZJIIN-SI3	47.2	38.3	–	–	–	–	1.2	–	–	–	–
ZJIIN-SI4	43.3	36.8	–	–	–	–	1.2	–	–	–	–
ZJIIN-SI5	45.4	35.0	–	–	–	–	1.3	–	–	–	–
ZJIIN-SI6	47.5	38.4	–	–	–	–	1.2	–	–	–	–
ZJIIN-SI7	44.7	37.9	–	–	–	–	1.2	–	–	–	–

Abbreviations: ML: maximum length; MW: maximum; R: rotation; PL: pace length; SL: stride length; PA: pace angulation; WAP: width of the angulation pattern of the pes (calculated value); WAM: width of the angulation pattern of the manus (calculated value); ML/MW, WAP/P′ML and WAM/M′MW are dimensionless.

Table 5
Estimated data of the speed of Zhaojue sauropod trackmakers.

No.	F = 5.9		F = 4		F = 4.586	
	SL/h	S (km/h)	SL/h	S (km/h)	SL/h	S (km/h)
ZJII-S1	0.62	1.98	0.91	3.10	0.80	2.66
ZJIIN-S1	0.57	1.76	0.84	2.77	0.74	2.38
ZJIIN-S2	0.74	2.38	1.09	3.74	0.95	3.17
ZJIIN-S3	0.59	1.80	0.88	2.84	0.76	2.45
ZJIIN-S4	0.51	1.44	0.75	2.27	0.65	1.94
ZJIIN-S5	0.63	2.02	0.93	3.17	0.81	2.70

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

and ornithopods. The assemblage resembles that from the Lower Cretaceous Hekou Group (Aptian–Albian) at the Yanguoxia site of northwest China (Zhang et al., 2006), from the Lower Cretaceous Jiaguan Formation (Barremian–Albian) at the Lotus site of Chongqing (Xing et al., 2007), and the Lower Cretaceous Tianjialou Formation (Aptian-Albian; Kuang et al., 2013) at Houzuoshan–Linsu sites. In contrast, the assemblage from the Lower Cretaceous Jingchuan Formation at the Chabu site, Inner Mongolia (Li et al., 2011a) lacks any confidently identified ornithopod tracks. However the Zhaojue ichnofaunas differ from the Yanguoxia assemblages in lacking evidence of didactyl dromaeosaurs and avian theropods (birds). In this regard they also differ from many of the Lower Cretaceous ichnofaunas from Shandong, which also yield dromaeosaur and bird tracks (Li et al., 2007; Xing et al., 2013b;

Li et al., in press). The Emei tracksite also yields dromaeosaur and bird tracks (Zhen et al., 1994).

The Zhaojue tracksite (Xing et al., 2013e, in press-a, in press-b; Xing and Lockley, in press, and this study) and the Qijiang tracksite (Xing et al., 2007, 2013c), are similar in revealing abundant ornithopod-rich ichnofaunas. However, other assemblages from the Lower Cretaceous are different. Thus overall, Early Cretaceous ichnofaunas of China still indicate a strong regional variation in composition and a certain provinciality (Lockley et al., in press). There are similarities in sedimentary geology across the Early Cretaceous Sichuan–Yunnan Basin of Southwest China, which pertains to inland basin fluvial–lacustrine deposits, however it remains to be shown how much this influences uniformity in the ichnofaunas.

The Qinling–Dabie Mountains (Wang, 1985) may have been a biogeographic barrier to dinosaur migration. For example, south of the mountain, within the Ordos Basin, neither tracks nor skeletons of iguanodontids have been found up to date. However, at the Hexi Corridor Basin near the Ordos Basin (including Lanzhou–Minhe Basin) and the Yishu fault zone areas from Shandong Province, eastern China, ornithopod tracks are more abundant. In this regard, the Yanguoxia track assemblages from the Lanzhou–Minhe Basin resemble those of the Sichuan–Yunnan Basin, at least with respect to the tracks of larger dinosaurs that have a greater potential for preservation. The preservation of the tracks of smaller animals, such as birds and pterosaurs, may also be biased by preservational factors, such as fine-grained sediment and its plasticity. The basins north of the ancient Qinling–Dabie Mountains were closely related to the flourishing Jehol Biota, and the local dinosaur assemblages are basically consistent (Chen, 1988). Thus, the track assemblages from the Sichuan–Yunnan Basin indicate that the relation between the Early Cretaceous dinosaur assemblages and the radiation of the Jehol Biota is probably closer than expected. Thus, it might infer that biogeographic obstacles created by the mountain ranges were not as severe as has been supposed. Because the Early Cretaceous Sichuan–Yunnan Basin sediments lack fossil skeletons, the track record has played an important role in assessing the paleoecology, and will continue to do so.

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