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An unusual sauropod turning trackway from the Early Cretaceous of Shandong Province, China

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ABSTRACT

An unusual turning and a regular, straight sauropod trackway both left by small trackmakers, as well as additional isolated medium-sized to large sauropod tracks are described from the Early Cretaceous Dasheng Group of the Zhucheng Basin, Shandong Province, China. Based mainly on well-preserved tracks exhibiting three forwardly-directed digit/claw impressions and a pronounced heteropody, and to a lesser degree due to a predominantly narrow to medium trackway gauge, the two small trackways are assigned to the *Parabrontopodus* ichnotaxon. As there is no clear trackway and no well-preserved tracks amongst the medium-sized to large sauropod tracks, these tracks can only be identified as of sauropod origin but they cannot be assigned to an ichnotaxon. The unusual turning trackway is characterized by a highly variable trackway configuration (pes and manus outward rotation, gauge, pace, stride) and pattern (different degree of manus overprinting by pes tracks) along its course, evidently related to the narrow, semicircular turn to the left that the animal made. This is also associated with a pronounced change from a narrow–medium (in the straight part at the beginning) to a (very) wide (within the turn) gauge. This demonstrates that these two stances could have been used by one and the same sauropod trackmaker, even if in the present case associated with turning and not simply during straight progression, as it was already reported from a Late Jurassic tracksite from NW Switzerland and an Early Cretaceous tracksite from Spain. Such 'untypical' trackways provide important constraints for the reconstruction of locomotor characteristics of sauropods such as unsteady locomotion and changes in locomotor behavior, and they will be of particular interest in the future to model and understand the different 'locomotor styles/capabilities' sauropods were engaged in.

1. Introduction

Shandong Province is one of the most important Mesozoic vertebrate fossil producing areas in China. Body fossils (Hu, 1973), tracks (Young, 1960), and eggs (Chow, 1951) of dinosaurs are all known from Shandong's Mesozoic strata for a long time. The dinosaur track record includes tracks from the Upper Jurassic Santai Formation (Li et al., 2002), the Lower Cretaceous Laiyang Group (~130–120 Ma) and the upper Lower Cretaceous Dasheng Group (~110–100 Ma) (Kuang et al., 2013). The largest known tracksite is the Huanglonggou tracksite (theropod, sauropod, and turtle tracks, Li et al., 2011; Lockley et al., 2015) from the Laiyang Group. At the Wenxiyuan tracksite (also from the Laiyang Group), pterosaur tracks are preserved (Xing et al., 2012).

The tracksites of the Dasheng Group are primarily found along the Yishu Fault zone, which extends (north–northeast) from northwest Jiangsu Province into central Shandong Province (Zhucheng–Junan–Linshu–Tancheng). The so far described tracksites of the Dasheng Group (see Xing et al., 2015a: Fig. 1) include the Zhangzhuhewan (Xing et al., 2010a) and Tangligezhuang tracksites (Wang et al., 2013a) of Zhucheng; the Houzuoshan Dinosaur Park tracksite (Li et al., 2005a, 2005b, 2008; Lockley et al., 2007, 2008) of Junan; the Jishan tracksites I–VIII (Xing et al., 2013) of Linshu; the Beilin (Wang et al., 2013b; Xing et al., 2015a) and Qingquan tracksites (Xing et al., in press) of Tancheng; and the Nanguzhai tracksite of Donghai (Xing

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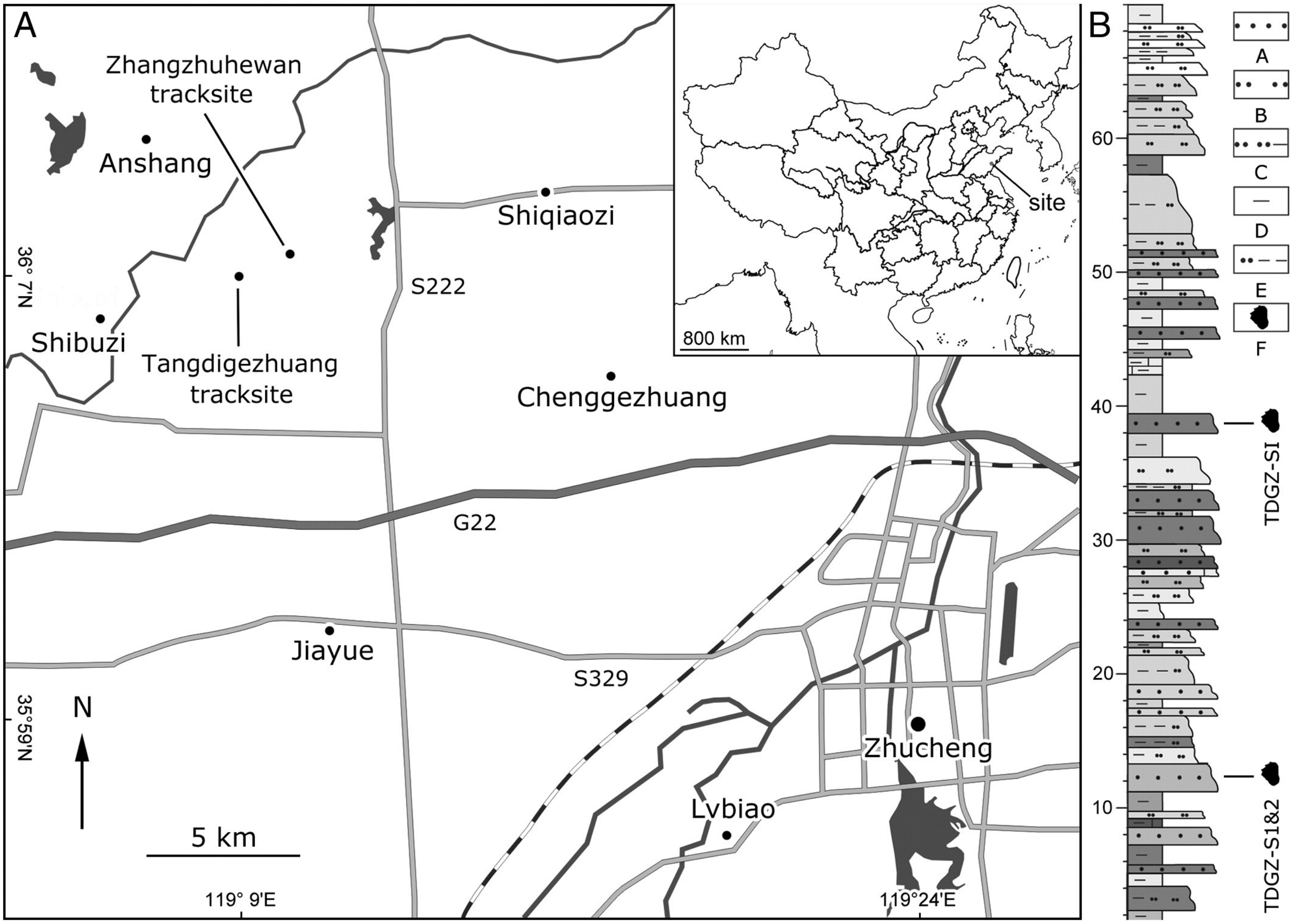

Fig. 1. Geographic position (A) and stratigraphic sections (B, Modified from Wang et al., 2013a) of the Tangdigezhuang dinosaur tracksite.

et al., 2010b). Except for the Houzuoshan Dinosaur Park tracksite, all these tracksites contain sauropod tracks, most of which were identified as small *Parabrontopodus* and large *Brontopodus* tracks (Xing et al., 2013). The largest trackway with a pes length of 84 cm is found at the Qingquan tracksite within the Dasheng Group, it is of the *Parabrontopodus*-/*Breviparopus*-type (Xing et al., in press).

Xing et al. (2010a) described the Zhangzhuhewan tracksite, which is close to the Tangdigezhuang tracksite, and reported tracks of sauropod, birds, and possibly ornithopods. Initially, the Zhangzhuhewan tracksite was thought to belong to the Laiyang Group. However, the latest geological survey showed that it to belongs to the Tianjialou Formation of the Dasheng Group (Kuang et al., 2013), and therefore has approximately the same age as the Tangdigezhuang tracksite.

Since 2000, Chen S. Q. from the Dinosaur Research Center of Zhucheng has discovered several new tracksites (Wang et al., 2013a), including the Tangdigezhuang tracksite, but lacking any detailed descriptions. Wang et al. (2013a) briefly described the Tangdigezhuang tracksite, but did not provide a morphological discussion. The first author inspected the Tangdigezhuang tracksite during 2013 and 2014, and here a detailed description, notably of the remarkable turning sauropod trackway, is provided for the first time.

2. Institutional and other abbreviations

I = Isolated tracks; L and R = left and right; NGZ = Nanguzhai tracksite, Jiangsu Province, China; P = pes impression; S = Sauropoda; T = track (single footprint); TDGZ = Tangdigezhuang tracksite, Shandong Province, China

3. Geological setting

Yanlu Fault is a large regional fault and significant geological characteristic of Eastern China. The portion of the Yanlu Fault within Shandong Province is called Yishu Fault zone, spanning 300 km in length and 20 to 60 km in width and consisting of four major, parallel faults all with approximately the same direction. The strata exposed in the Yishu Fault zone is divided into the Lower Cretaceous Laiyang, Qingshan and Dasheng groups, and the Upper Cretaceous Wangshi Group (T'an, 1923). Liu et al. (2003) divided the Dasheng Group into the Malanggou, Tianjialou, Siqiancun, and Mengtuan formations. However, Kuang et al. (2013) recently argued that the Malanggou and Siqiancun formations, and the Tianjialou and Mengtuan formations, respectively, are probably contemporaneous but developed in different facies. The Tianjialou/Mengtuan formations are composed of lacustrine facies deposits, dominated by detrital rocks, and with a thickness exceeding 500 m.

The Tangdigezhuang tracksite, situated 2 km to the north of the Zhangzhuhewan tracksite (Xing et al., 2010a) (Fig. 1A), belongs to Early Cretaceous Tianjialou Formation of the Dasheng Group, and is slightly younger than the strata exposed in the Zhangzhuhewan area. At the Tangdigezhuang tracksite, yellow–green and grayish green siltstones, fine sandstones and pelitic siltstones are exposed. These frequently exhibit small climbing ripple bedding, cross-bedding and parallel bedding, indicating that these are shallow lacustrine deposits (Wang et al., 2013a).

4. Material and methods

In 2014, due to the pronounced inclination (~45°) of the bedding planes at the Tangdigezhuang tracksite, the site was studied using a system of safety ropes, which were set up by technicians from Dinosaur Research Center of Zhucheng.

Wang et al. (2013a) have measured the geologic sections in Tangdigezhuang area, which has about 96 layers. Two dinosaur track-bearing levels are from the 11th and 46th layers within a ~30 m thick laminite interval (Wang et al., 2013a). TDGZ-S1 and S2 trackways are located on the same track level, whereas the medium-sized to larger sauropod tracks named TDGZ-SI tracks are located on a higher (~30 m) track level (Figs. 1B, 2). In order to produce accurate site and track(way) maps, all the tracks from both bedding planes were outlined with chalk, photographed (also for purposes of photogrammetry), and traced at a scale of 1:1 on large sheets of transparent plastic. Several photos were assembled to form a single overview image of the complete trackway, using Adobe Photoshop Photomerge (Fig. 3). All the tracings are reposited in the China University of Geosciences (Beijing).

For the two sauropod trackways (Table 1), 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 pes/manus 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 also 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 wide-gauge trackways, and trackways with a value higher than 2.0 are considered to be very wide gauge (Marty, 2008).

Terminology for trackway patterns (e.g., quadrupedal, pes/manus-dominated) is used according to Marty et al. (2006) and Marty (2008, fig. 2.16 on p. 39). Sauropod size classes are used according to Marty (2008, table 2.2. on p. 40): tiny: $P'L < 25$ cm; small: 25 cm $< P'L <$ 50 cm; medium-sized: $50 < P'L$ cm < 75; large: $P'L > 75$ cm.

Locomotion speed for the sauropod trackways was estimated using the formula of Alexander (1976). For sauropods, Alexander (1976) suggested that hip height (h) = 4 × foot length, whereas, later, Thulborn (1990) estimated h = 5.9 × foot length, and results for both of these factors are calculated and shown in Table 2. The relative stride length (SL/h) may indicate whether the animal was walking ($SL/h \leq 2.0$), trotting ($2 < SL/h < 2.9$), or running ($SL/h \geq 2.9$) (Alexander, 1976; Thulborn, 1990).

5. Description of sauropod tracks and trackways

5.1. Track preservation

All tracks are preserved as impressions (negative epirelief) in a finely-laminated siltstone (Fig. 4), which has a very fractured aspect and does not always split at the same level. Due to this reason, the tracks are cut by a fine network of fractures and generally not so well preserved, and it is difficult to identify the precise tracking surface respectively the “true track *sensu stricto*” (that surface that was in contact with the foot). Nonetheless, all tracks are considered as “true tracks” and not as undertracks or underprints (*sensu* Marty et al., 2009). Some of the tracks (notably the medium-sized to large ones)

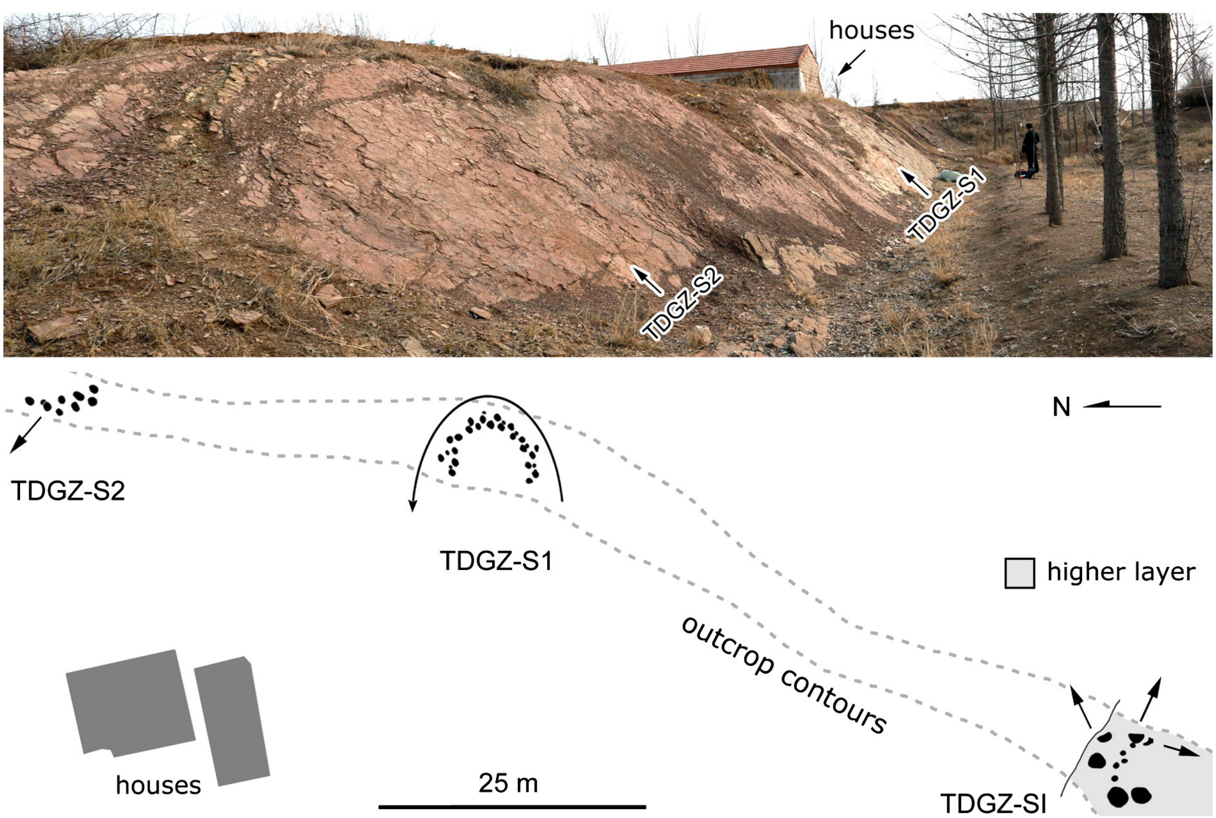

Fig. 2. Tangdigezhuang tracksite, Shandong Province, China. Schematic, interpretative outline drawing of the tracksite showing the three main, small sauropod trackways and some large isolated sauropod tracks (lower right) on two different track levels and in spatial relationship to each other.

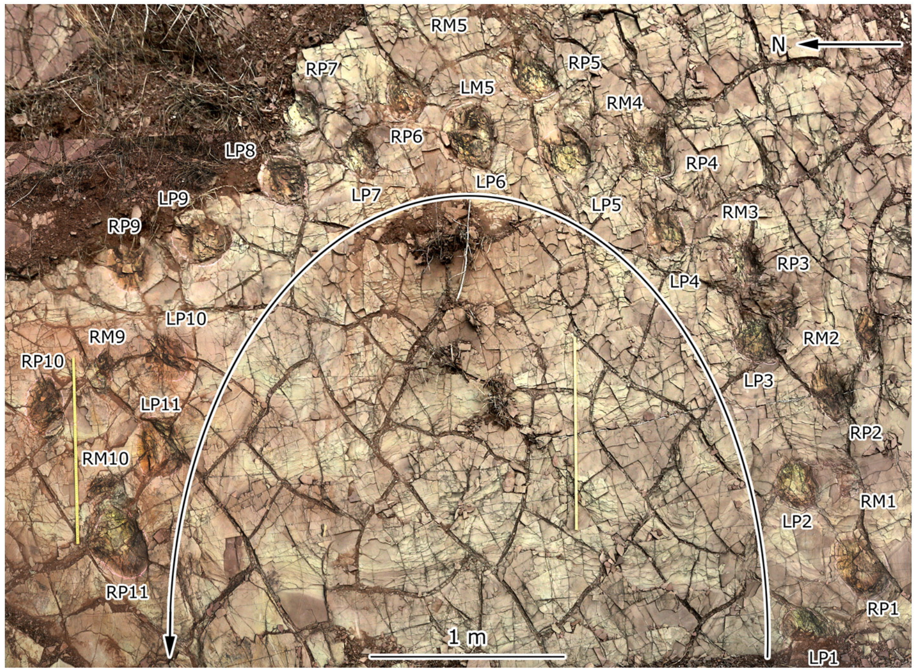

Fig. 3. Overview photograph of the turning TDGZ-S1 trackway from Tangdigezhuang tracksite, Shandong Province, China. Note the fine fracturation of the track level.

are surrounded by displacement rims and some of the pes tracks of trackways TGDZ-S1 & S2 exhibit some anatomical details of the foot, i.e. impressions of three prominent digits (pes track in Fig. 5A), also indicating that these tracks are "true tracks". Other tracks still bear parts of the track fill, while still others have a slightly collapsed aspect (manus track in Fig. 5B), suggesting that the substrate was soft and water-saturated at the time of track formation.

5.2. Track size classes and general morphology

The Tangdigezhuang tracks fall in two clearly different size categories: small and medium-sized to large tracks (sensu Marty, 2008, table 2.2).

The average pes length of the two small trackways is 30.4 cm (range 24.5 to 36.0 cm) for TDGZ-S1 and 38.5 cm (range 30.5 to 42.0 cm) for TDGZ-S2 (Table 1). Besides the TDGZ-S1 and S2 trackways, further small tracks are at least two isolated pes tracks numbered as TDGZ-SI 3p and 4p, respectively. These two tracks are located close to (in between) the medium-sized to large tracks.

The medium-sized to large tracks include only isolated tracks and these are numbered as TDGZ-SI1p–2p and 5p–7p (Fig. 6, Table 1). The maximum length of these tracks ranges between 70 (medium-sized) and 80 (large) cm.

Almost all of the small pes tracks of TDGZ-S1 and S2 are oval in shape and they are morphologically consistent. The best-preserved pes tracks exhibit three forwardly-directed digit/claw impressions, while well-preserved manus tracks are semicircular in shape and lack digit/claw (ungual) impressions. All these features identify the Tangdigezhuang tracks as of sauropod origin.

5.3. Trackway TDGZ-S1

This is a very special and rare turning sauropod trackway as it makes a pronounced and narrow, semicircular (180°) turn to the left so that the animal was heading back again after the end of the turn (Figs. 2, 3, 4A–B).

LP3 is the best-preserved pes track and has an elongated oval shape with three clear digit impressions that correspond to dI–dIII (Fig. 5).

This trackway exhibits a particular pes-dominated pattern because almost only right manus tracks are preserved. Only one single left manus track (LM5) is preserved.

The absence of most of the left manus tracks is possibly related to the pronounced and narrow turn to the left, which leads to a systematic overprinting of the left manus tracks by the left and/or right pes tracks. There is no evidence to assume that the absence of any of the left manus tracks may be related to a preservational issue (e.g., shallow, poorly visible tracks) or overburden. On the other hand, not all right manus tracks are visible neither, but this may be related to overburden and/or track fills that could not be removed.

Another particularity of this trackway is a pronounced negative (inward) rotation (against the direction of the turn) of the left pes tracks (LP4–LP9; range between −4° and −82°) in the middle of the trackway (respectively in the middle of the turn), while right pes tracks always have a positive (outward) rotation all along the trackway (respectively all along the turn, i.e. in the direction of the turn). With 71° for RP5 and 91° for RP6, respectively, the outward rotation of the pes is pronounced in the middle of the turn, but otherwise it has rather low, "typical" values in the range of 6–31°. All together this results in a mean pes outward rotation of 61° that may be little meaningful. The inward rotation of the left and outward rotation of the right pes also implies that – especially between LP5 and LP8 (i.e. in the middle of the turn) – the left and right pes tracks show the same orientation, which is very untypical for (straight) sauropod trackways.

All along the trackway, those right manus tracks that are preserved have a very pronounced outward rotation (mean of 103°; range between 75° and 130°). RM1 to RM4 are located on the inner side of the trackway, close to or sometimes almost touching (e.g.: RM2) the opposite left pes tracks. RM5 is located in line with RM1 to RM4 but as it is located in the middle of the turn, RM5 is located far away from the opposite left pes LP6. Instead, the left manus LM5 is present here in connection with LP6. RM6 to RM8 are not visible, most possibly because of the overburden. RM9 and RM10 are again present, but they are both poorly preserved. Both RM9 and RM10 are in an unusual position with respect to the preceding and subsequent pes tracks. RM10 located far in front of RP10, almost in connection with RP11. However, some of the pes positions at the end of the trackway

Table 1
Tangdigezhuang tracksite, Shandong Province, China. Measurements (in cm) for the two sauropod trackways TDGZ-S1 and S2 as well as for some isolated tracks from an upper track level. 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.

Number.	L	W	R	PL	SL	PA	L/W	WAP	WAP /P′L	WAM	WAM /M′W
TDGZ-S1-LP1	–	–	–	45.0	75.0	–	–	–	–	–	–
TDGZ-S1-LM1	–	–	–	–	–	–	–	–	–	–	–
TDGZ-S1-RP1	31.0	25.5	6°	56.0	93.0	113°	1.2	29.3	0.9	–	–
TDGZ-S1-RM1	12.5	14.5	93°	–	97.0	–	0.9	–	–	–	–
TDGZ-S1-LP2	27.5	23.5	45°	52.5	81.0	97°	1.2	35.9	1.3	–	–
TDGZ-S1-LM2	–	–	–	–	–	–	–	–	–	–	–
TDGZ-S1-RP2	29.0	21.5	23°	52.0	84.0	127°	1.3	21.2	0.7	–	–
TDGZ-S1-RM2	12.0	18.0	109°	–	77.0	–	0.7	–	–	–	–
TDGZ-S1-LP3	35.5	26.0	11°	41.0	74.0	114°	1.4	24.4	0.7	–	–
TDGZ-S1-LM3	–	–	–	–	–	–	–	–	–	–	–
TDGZ-S1-RP3	24.5	23.0	16°	46.0	78.0	116°	1.1	24.5	1.0	–	–
TDGZ-S1-RM3	10.5	15.0	130°	–	77.5	–	0.7	–	–	–	–
TDGZ-S1-LP4	25.0	23.0	−4°	45.0	68.0	95°	1.1	33.3	1.3	–	–
TDGZ-S1-LM4	–	–	–	–	–	–	–	–	–	–	–
TDGZ-S1-RP4	31.0	21.5	31°	46.5	76.0	103°	1.4	30.5	1.0	–	–
TDGZ-S1-RM4	10.5	17.0	110°	56.8	103.3	131°	0.6	–	–	22.8	1.3
TDGZ-S1-LP5	31.5	24.0	−32°	49.0	54.0	62°	1.3	44.3	1.4	–	–
TDGZ-S1-LM5	–	–	–	55.8	–	–	–	–	–	–	–
TDGZ-S1-RP5	31.0	24.5	71°	46.0	67.5	91°	1.3	32.6	1.1	–	–
TDGZ-S1-RM5	–	–	–	–	–	–	–	–	–	–	–
TDGZ-S1-LP6	34.5	29	−49°	44.0	59.0	82°	1.2	32.6	0.9	–	–
TDGZ-S1-LM6	–	–	–	–	–	–	–	–	–	–	–
TDGZ-S1-RP6	32.0	22.5	90°	39.0	63.0	88°	1.4	31.2	1.0	–	–
TDGZ-S1-RM6	–	–	–	–	–	–	–	–	–	–	–
TDGZ-S1-LP7	28.0	19.5	−74°	45.0	43.5	65°	1.4	35.4	1.3	–	–
TDGZ-S1-LM7	–	–	–	–	–	–	–	–	–	–	–
TDGZ-S1-RP7	36.0	30.5	–	36.0	–	–	1.2	–	–	–	–
TDGZ-S1-RM7	–	–	–	–	–	–	–	–	–	–	–
TDGZ-S1-LP8	28.0	25.0	−82°	–	64.0	–	1.1	–	–	–	–
TDGZ-S1-LM8	–	–	–	–	–	–	–	–	–	–	–
TDGZ-S1-RP8	–	–	–	–	–	–	–	–	–	–	–
TDGZ-S1-RM8	–	–	–	–	–	–	–	–	–	–	–
TDGZ-S1-LP9	27.0	32.0	−79°	44.0	65.0	78°	0.8	36.4	1.3	–	–
TDGZ-S1-LM9	–	–	–	–	–	–	–	–	–	–	–
TDGZ-S1-RP9	28.5	27.0	13°	58.0	96.0	89°	1.1	46.9	1.6	–	–
TDGZ-S1-RM9	11.0	17.0	75°	–	68.0	–	0.6	–	–	–	–
TDGZ-S1-LP10	30.0	20.5	31°	73.5	50.0	45°	1.5	68.2	2.3	–	–
TDGZ-S1-LM10	–	–	–	–	–	–	–	–	–	–	–
TDGZ-S1-RP10	31.0	23.5	27°	67.0	84.0	90°	1.3	40.7	1.3	–	–
TDGZ-S1-RM10	11.5	20.5	–	–	–	–	0.6	–	–	–	–
TDGZ-S1-LP11	32.0	24.5	–	51.0	–	–	1.3	–	–	–	–
TDGZ-S1-LM11	–	–	–	–	–	–	–	–	–	–	–
TDGZ-S1-RP11	34.0	25.0	–	–	–	–	1.4	–	–	–	–
TDGZ-S1-RM11	–	–	–	–	–	–	–	–	–	–	–
Mean-P	30.4	24.6	|40°|	49.3	70.8	91°	1.2	35.5	1.2	–	–
Mean-M	11.3	17	103°	56.3	84.6	131°	0.7	–	–	22.8	1.3
TDGZ-S2-RP1	42.0	31.0	42°	59.0	78.0	72°	1.4	53.0	1.3	–	–
TDGZ-S2-RM1	–	–	–	–	–	–	–	–	–	–	–
TDGZ-S2-LP1	37.5	37	−74°	70.0	83.0	82°	1.0	45.6	1.2	–	–
TDGZ-S2-LM1	–	–	–	–	–	–	–	–	–	–	–
TDGZ-S2-RP2	41.0	30.0	50°	53.0	82.0	78°	1.4	46.0	1.1	–	–
TDGZ-S2-RM2	10.0	20.0	60°	–	–	–	0.5	–	–	–	–
TDGZ-S2-LP2	42.0	28.0	−80°	73.0	78.0	72°	1.5	52.5	1.3	–	–
TDGZ-S2-LM2	–	–	–	–	–	–	–	–	–	–	–
TDGZ-S2-RP3	36.5	29.0	84°	60.0	76.0	72°	1.3	50.0	1.4	–	–
TDGZ-S2-RM3	–	–	–	–	–	–	–	–	–	–	–
TDGZ-S2-LP3	30.5	26.0	–	61.0	–	–	1.2	–	–	–	–
TDGZ-S2-LM3	–	–	–	–	–	–	–	–	–	–	–
TDGZ-S2-RP4	40.0	32.5	35°	–	101.0	–	1.2	–	–	–	–
TDGZ-S2-RM4	14.0	25.5	–	–	–	–	0.5	–	–	–	–
Mean-P	38.5	30.5	|61°|	62.7	83.0	75°	1.3	49.4	1.2	–	–
Mean-M	12.0	22.8	60°	–	–	–	0.5	–	–	–	–
TDGZ-S2-I1	50.5	36.3	–	–	–	–	1.4	–	–	–	–
TDGZ-SI1p	80.0	70.0	–	–	–	–	1.1	–	–	–	–
TDGZ-SI2p	70.0	58.0	–	–	–	–	1.2	–	–	–	–
TDGZ-SI3p	26.0	25.0	–	–	–	–	1.0	–	–	–	–
TDGZ-SI4p	32.0	26.0	–	–	–	–	1.2	–	–	–	–
TDGZ-SI5p	70.0	61.0	–	–	–	–	1.1	–	–	–	–
TDGZ-SI7p	>60	–	–	–	–	–	–	–	–	–	–
TDGZ-SI7m	19.0	37.0	–	–	–	–	0.5	–	–	–	–

Table 2
Estimation of locomotion speed of Tangdigezhuang sauropod trackmakers. Abbreviations: F, hip height conversion factors; SL/h, relative stride length; S, speed.

No.	F = 5.9		F = 4	
	SL/h	S (km/h)	SL/h	S (km/h)
TDGZ-S1	0.39	0.79	0.58	1.26
TDGZ-S2	0.34	0.72	0.50	1.12

(respectively at the end of the turn) are also unusual, as RP10 is located very far outside, giving the trackway a “wide-gauge” appearance between RP9 and LP11.

Apart from RM5, off-tracking (as described by Ishigaki and Matsumoto, 2009) is not visible for the right manus tracks, they are even located more inwards than in other “typical” sauropod trackways. Off-tracking may, however, be the reason why almost no left manus tracks were preserved but overprinted by the left pes, as they were left in a more interior position as usual

Contrary to the manus tracks, all pes tracks – except RP8 hidden below overburden – are visible. The configuration of the pes tracks is quite regular at the beginning (LP1–RP4), whereas the pace/stride diminishes in the middle of the trackway (respectively the middle of the turn) between LP5 and RP9 (deceleration). After RP9 the pace/stride increases again (acceleration). This is also expressed by a large range in pes pace length (39–73.5 cm), stride length (54–96 cm), and pace angulation (45°–127°).

The mean value for the (WAP/P′L)-ratio is 1.2, indicating that the trackway has a medium gauge. However, between LP1 and RP9, the trackway has a narrow to medium gauge and shifts to wide gauge after RP9, notably because of the track RP10, which is an “outlier”. This irregular configuration in trackway gauge (width) is obviously related to the narrow turn the animal makes. Similar pronounced shifts from a narrow to a very wide gauge along single trackways have also been reported by Marty et al. (2010b) for three, between 46 and 115 m long trackways (two of which with slight turns) from the Late Jurassic Courtedoux–Béchat Bovais taracksite (NW Switzerland). Marty et al.

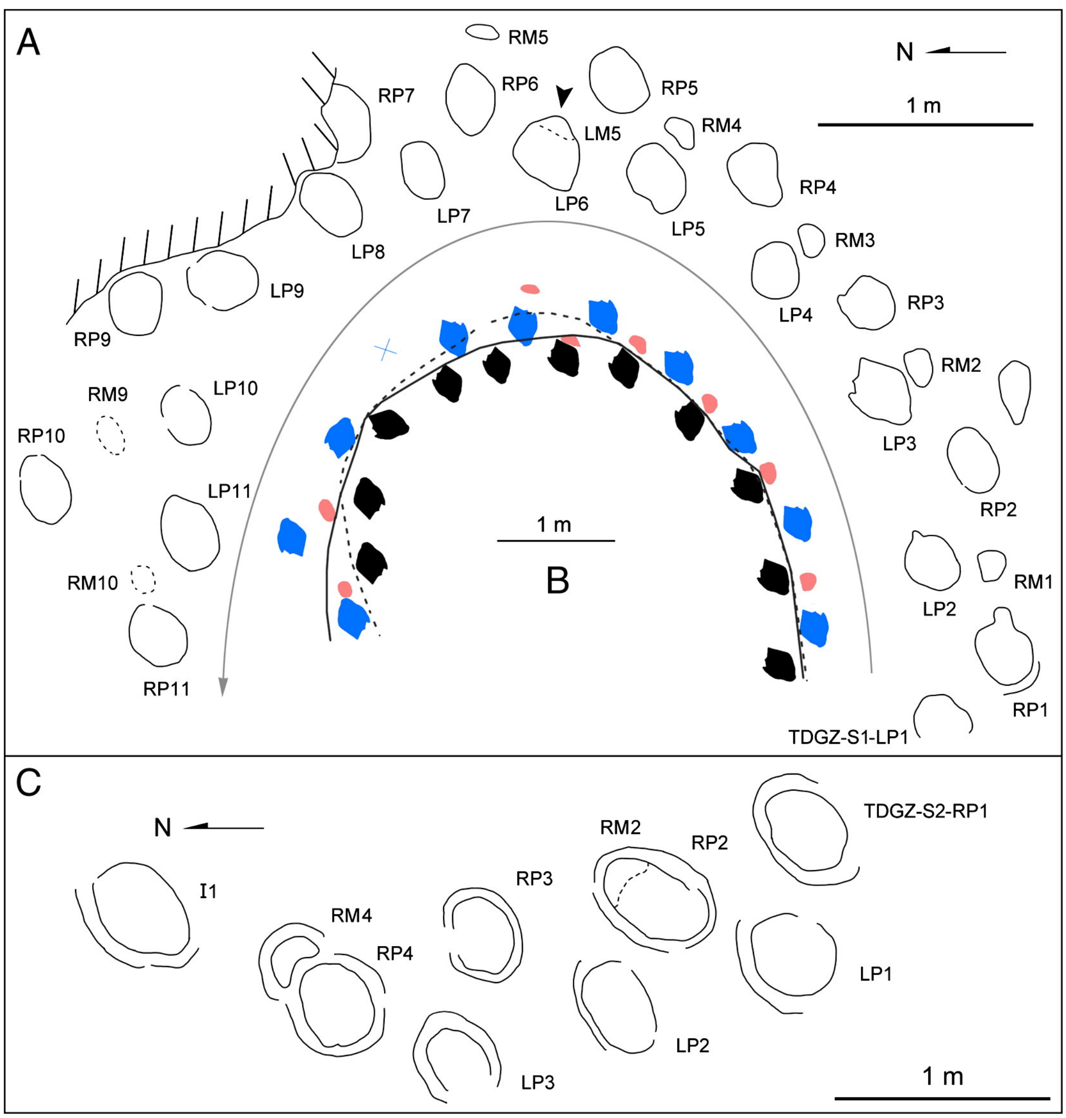

Fig. 4. Interpretative outline drawings of sauropod trackways from Tangdigezhuang tracksite. A, The turning TDGZ-S1 trackway; B, Schematic trackway based on A with idealized toe impressions, the blue tracks are the right pes tracks, while the black tracks are the left pes tracks; red tracks are right manus tracks; the solid line is the trackway midline of the pes while the dashed line is the (assumed) manus trackway midline. The offset between the pes (solid line) and right manus (dashed line) indicates the off-tracking phenomenon (Ishigaki and Matsumoto, 2009) of the manus with respect to the pes. It is assumed that all left manus tracks were systematically overprinted by left pes tracks. C, TDGZ-S2: this is a small, straight, pes-dominated trackway. Note the very pronounced inward rotation of the left pes tracks. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

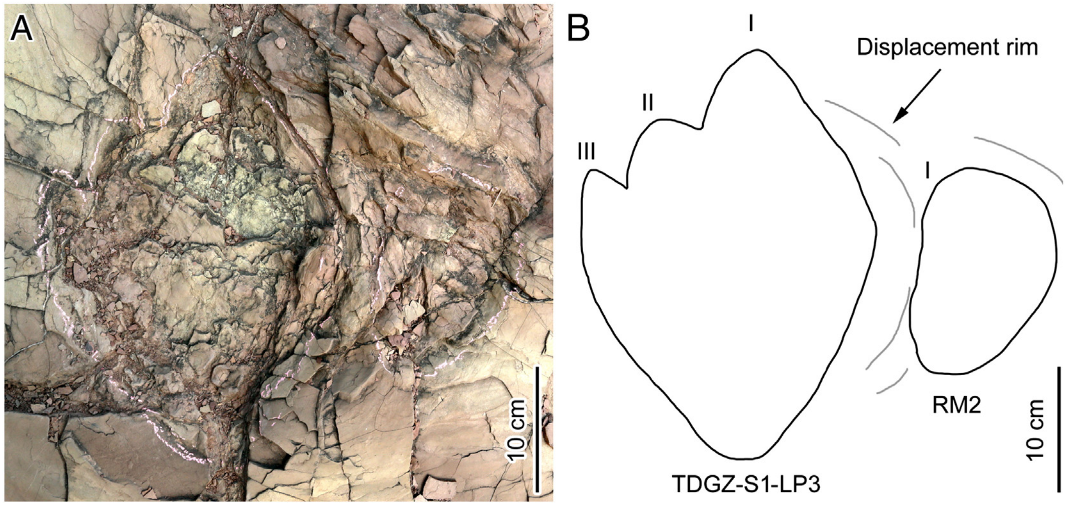

Fig. 5. Photographs (A) and interpretative outline drawings (B) of a well-preserved sauropod pes (TDGZ-S1LP3) and close by right manus (TDGZ-S1RM2) track.

(2010b) concluded that such a pronounced change between narrow and wide gauge over a couple of steps demonstrate that these two “locomotor styles” could have been used by one and the same sauropod trackmaker.

TDGZ-S1 is an obvious turning sauropod trackway. The turn itself is very narrow and consists of eleven pes and eight manus tracks. After a first slight turn after LP2, the trackmaker started turning even more after LP4.

The metatarsophalangeal region of LM5 is in contact with the interior, medial part of LP6, but the contact line is obscure. Unlike RM1–RM4, which are located in the inner side of the trackway, RM5 is located in the outer side (Fig. 3). The rotation angle of RP5–RP7 increases intensely, from 31° of RP4 to 71°–90°, whereas LP6–LP9 are turned inwards, with rotation angles from −4° to as high as −82°.

5.4. Trackway TDGZ-S2

TDGZ-S2 (Figs. 2, 4C) is a short, straight, pes-dominated sauropod trackway with a very pronounced pes track rotation, which is outward (positive values) for the right pes and inward (negative values) for the left pes tracks. While the outward rotation of the right pes tracks is considerable, the inward rotation of the left pes tracks can even be considered as extreme and very unusual (−74° for LP1 and −80° for LP2).

Even though the preserved part of trackway TDGZ-S2 is straight, it can not be excluded that it forms part of a larger turn. This could explain why the pes tracks exhibit such a pronounced (outward/inward) rotation. In the case of a turn, the isolated track TDGZ-S2-I1 at the end of the trackway could also be an additional pes track. However, this is difficult to confirm.

Although poorly-preserved and considerably weathered, the general outlines of most tracks are still recognizable. None of the tracks preserve distinct digit/claw impressions.

The only well-preserved manus track RM2 is semi-circular to slightly crescent in shape with an indentation at the rear end. RM4 may be slightly overprinted or deformed by RP4, and also shows a pronounced outward rotation, as does RP4. There are no left manus tracks preserved.

The mean value for the (WAP/P′L)-ratio is 1.2, indicating that the trackway has a medium (almost wide) gauge, even though the trackway dissembles a narrow gauge. However, the pes tracks actually intersect the trackway midline because of their extreme inward (left pes tracks) and outward (right pes tracks) rotation. This particular influence of track rotation on apparent trackway gauge was also discussed by Marty (2008).

5.5. Isolated, medium-sized to large tracks

TDGZ-SI1p–2p and TDGZ-SI5p–7p are isolated medium-sized to large sauropod tracks that are poorly preserved and considerably weathered (Fig. 6). All these tracks are interpreted as pes tracks.

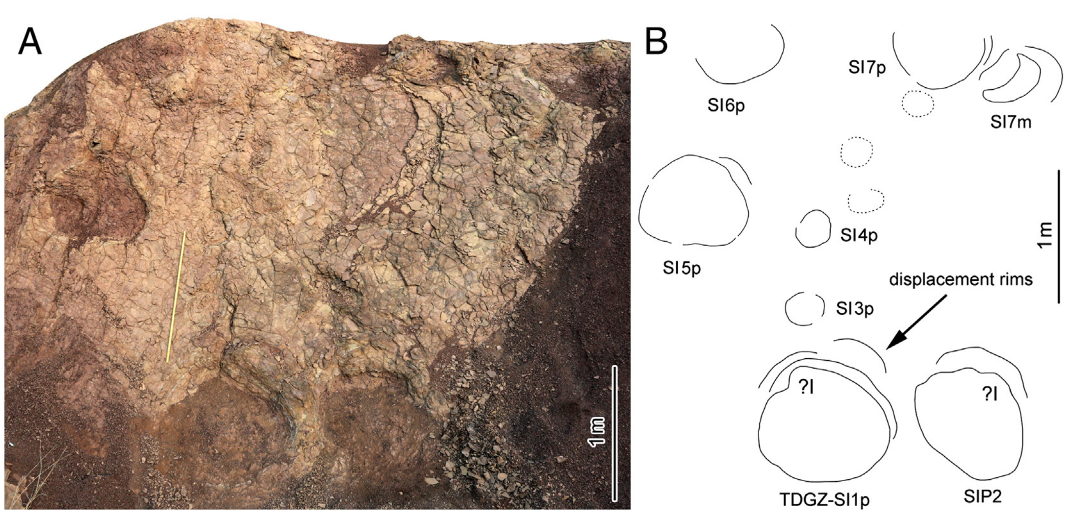

Fig. 6. Photographs (A) and interpretative outline drawings (B) of isolated sauropod track.

Of these tracks, the best-preserved track is SI1p. It is oval in shape with a length/width-ratio of 1.1 and with a single, poorly-preserved indentation at its anterior margin, possibly corresponding to digit I. The metatarsophalangeal pad impression is complete with smoothly-curved margins.

Close to the SI7p pes track a crescent-shaped impression labeled SI7m is located and this is possibly the corresponding manus track. However, due to its poor preservation and because of the absence of any clear trackway, this cannot unambiguously be confirmed.

These medium-sized to large tracks can be identified as sauropod pes tracks, but because of the lack of any substantial detail of the foot such as digit and claw impression and of any clear trackway, they cannot be assigned to any ichnotaxon. Nonetheless, they confirm the (more or less) coeval presence of small and medium-sized to large sauropod trackmakers in the same paleoenvironment.

5.6. Estimation of locomotion speed

The SL/h ratios of the TDGZ-S1 and S2 trackways are between 0.39–0.58 and 0.34–0.50 indicating a walking gait. Using the standard equation of Alexander (1976) to estimate speed from trackways, the mean locomotion speed of the trackmaker is between 0.79–1.26 km/h for TDGZ-S1 and 0.72–1.12 km/h for TDGZ-S2 (Table 2).

6. Discussion

6.1. Ichnotaxonomy

So far, most Early Cretaceous sauropod trackways in East Asia have been attributed either to the wide-gauge *Brontopodus* (Lockley et al., 2002) or the narrow-gauge *Parabrontopodus* (Xing et al., 2013) ichnotaxa. For instance, Xing et al. (2010b, 2013) assigned small sauropod trackways from the Nanguzhai and Jishan tracksites to *Parabrontopodus*, notably based on a clearly narrow gauge and a high heteropody. These trackways are very similar to the herein described trackways TDGZ-S1 and S2 from the Tangdigezhuang tracksite, even though both TDGZ trackways have a mean gauge that is rather medium than narrow.

A medium gauge category was proposed by Lockley et al. (1994) and Meyer et al. (1994), because based on gauge alone not all sauropod trackways could unambiguously be classified into either narrow or wide. By that time, these authors also stated that a formal classification of sauropod trackways on gauge alone was premature and that there is "a need to carefully describe well-preserved trackways and refine sauropod ichnotaxonomy …".

Nonetheless, today trackway gauge is commonly used in the classification of sauropod trackways (e.g. Santos et al., 2009; Mannion and Upchurch, 2010; Marty et al., 2010a; Castanera et al., 2014), even though the narrow to wide classification may be oversimplified (Castanera et al., 2012; Xing et al., 2015a), or it may reflect the fact that sauropods were able to change their habitual stance to a certain degree and when doing so leaving trackways that change from narrow to wide and may exhibit an overall (mean) medium-gauge (e.g., Marty et al., 2010b; Castanera et al., 2012).

While TDGZ-S2 is at the upper end of medium gauge (i.e. it is almost wide gauge), the (mean) medium-gauge of TDGZ-S1 seems to be related to the narrow turn (see discussion below). Actually, the straight part of TDGZ-S1 is best classified as (clearly) narrow gauge, but it becomes wider at the end of the turn. In any case, these trackways are both difficult to classify based on their (variable) gauge alone.

Wright (2005) has suggested classifying sauropod trackways mainly based on track morphology. This holds especially true for (medium gauge) trackways that cannot easily be classified based on their either (clearly) narrow or wide gauge. However, to do so "exquisitely"-preserved true tracks with substantial anatomical details (impressions of all digits, claws, other pads) are required and such tracks are typically rare in the fossil record.

Therefore, heteropody (difference in total track area between manus and pes tracks in a given quadrupedal trackway), which is very different between *Parabrontopodus* (high heteropody; 1:4 or 1:5 sensu Lockley et al., 1994) and *Brontopodus* (low heteropody; 1:3 sensu Lockley et al., 1994), is another good feature to distinguish sauropod ichnotaxa (Lockley et al., 1994). Heteropody is relatively easy to assess if completely preserved pes and especially manus tracks are available.

For both trackways TDGZ-S1 and S2, heteropody is clearly high, and therefore, we assign both small sauropod trackways of Tangdigezhuang to the *Parabrontopodus* ichnotaxon and do not consider an attribution to *Brontopodus* as very likely.

Another feature of both Tangdigezhuang trackways is a pronounced manus outward rotation (50°–110°), and this feature has a wide distribution in Early Cretaceous small sauropod trackways of China. In most cases, these small sauropod trackways are narrow to medium gauge, have a high heteropody, and are attributed to *Parabrontopodus* (Xing et al., 2010b, 2013).

Nonetheless, we suggest that future studies should be careful when classifying sauropod trackways, especially in the case of medium-gauge trackways, as these cannot be classified based on gauge, and/or if no well-preserved tracks with anatomical details are preserved. Also, it cannot be ruled out a priori, that certain medium-gauge, quadrupedal trackways with poorly-preserved tracks (that can not unambiguously be identified as of sauropod origin) may have been left by stegosaurian trackmakers (see also Cobos et al., 2010, p. 233).

The medium-sized to large sauropod tracks TDGZ-SI1p–2p, 5p–7p are poorly preserved and not associated in any clear trackway, and thus it is difficult to make any further ichnotaxonomical interpretations. TDGZ-SI 5p–7p may form a single trackway, which, if so, would be narrow gauge, with crescent-shaped manus tracks and a high heteropody, and thus, most likely resemble *Parabrontopodus*-like trackways (Santos et al., 2009; Marty et al., 2010a).

For a more detailed review of the *Parabrontopodus*, *Brontopodus* and other similar sauropod ichnotaxa, the reader is referred to Marty et al. (2010a).

6.2. Turning sauropod trackways

Sauropod trackways with turns (of various degrees) are known from the Central High Atlas Mountains, Morocco (Ishigaki and Matsumoto, 2009), from Copper Ridge, Utah, USA (Lockley, 1990, 1991), from Fenoglia Island, Croatia (Mezga and Bajraktarevic, 1999), from the Lommiswil tracksite, Switzerland (Meyer, 1990, 1993; Lockley and Meyer, 2000), from Lagosteiros Bay, Portugal (Meyer et al., 1994), from the Miraflores I tracksite, Spain (Castanera et al., 2014), from the Fumanya tracksite, Spain (Vila et al., 2008), from the Dazu tracksite, Chongqing, China (Lockley and Matsukawa, 2009), or from the Courtedoux—Béchat Bovais tracksite, NW Switzerland (Marty et al., 2010b). However, all these trackways exhibit rather slight (small) turns and do not represent narrow turns with a complete directional inversion ('turning around'), as it is reported here for the TDGZ-S1 trackway. Other similar trackways with such narrow turns and complete 'turning around' are so far only known from the Early Cretaceous Zhaojue tracksite (Sichuan Province, China; Xing et al., 2015b), and from the Late Jurassic Porrentruy–CPP tracksite (Canton Jura, NW Switzerland), but the latter is as yet not published (unpublished data of the Paleontology A16).

Ishigaki and Matsumoto (2009) have reported what they called an "off-tracking phenomenon" for the trackway 'Tu' of the Iouaridène tracksite (Late Jurassic, Morocco) and noted that this was also observable on a trackway from the Lommiswil tracksite (Late Jurassic, Switzerland) and possibly on a turning trackway from Copper Ridge (Late Jurassic, Utah, USA). Recently, the same phenomenon was described from the trackway no. 6 of the Zhaojue tracksite, where the trackway midline of pes and the manus tracks show a substantial degree of off-tracking (Xing et al., 2015b, fig. 11).

Ishigaki and Matsumoto (2009) have defined "off-tracking" as a pronounced gap (offset) between the pes and manus trackway midline at the turning point, analogous to the gap between the trace of the left (or right) front and rear wheels of a four-wheeled vehicle and this gap starts at the turning point (Fig. 7). However, the turning of a four-wheeled vehicle is completely mechanical and in the case of the old car illustrated in Fig. 7, the back wheels are fixed while only the front wheels do turn but still have a fixed position. For this reason, "off-tracking" of a four-wheeled vehicle is not the best analogue to explain the turning capabilities of sauropods, but it is a reasonably good term to describe quadrupedal trackways with a similar configuration.

An off-tracking of the manus is possibly also visible in trackway TDGZ-S1 after RP5, where RM5 is located much more outside with respect to the pes and with compared to all the other previous right manus tracks with respect to the corresponding pes tracks. This outlier can be explained by the fact, that the pes tracks started the curve at the same time as the manus tracks, similar to the gap between the trails of the left respectively right front and back wheels of a four-wheeled car (compare with Fig. 7C).

However, because only one left manus track is preserved and right manus tracks are missing between RM5 and RM9, the manus trackway midline shown in Fig. 4B is schematic only, and the degree of "manus off-tracking" is difficult to assess/quantify for trackway TDGZ-S1, when compared with trackway 'Tu' illustrated by Ishigaki and Matsumoto (2009, figs. 3 and 5).

Even if "off-tracking" is difficult to assess for TDGZ-S1, this trackway shows, how strong trackway parameters may vary along trackway course. This holds notably true for the pes trackway gauge, which varies between (very) narrow and wide gauge, but also for pes rotation, pace, and stride (Fig. 8). Obviously, these conspicuous irregularities in trackway configuration are linked to the turn and maybe an associated "hesitant" behavior. Consequently, the mean values become little meaningful and have to be looked at with care (step-by-step), especially when compared with values obtained from other "typical" straight sauropod trackways. In the latter case, comparisons should then be made mainly based on track morphology rather than on trackway parameters (including gauge).

In the context of varying trackway parameters, the change in pes rotation, notably for the left pes is worth mentioning. While sauropod trackways typically show a (pronounced) pes outward rotation (positive values) (e.g., Marty et al., 2010a), and while this "Charlie Chaplin stance" is also typically observed in both *Brontopodus* and *Parabrontopodus* Early Cretaceous Chinese sauropod trackways (Lockley et al., 2002; Xing et al., 2014), in TDGZ-S1, several inward rotated (negative values, Table 1) left pes tracks (between LP4 and LP9 respectively in the middle of the turn) do occur. Some of these are inward rotated to a considerable degree (up to −82°), and to our best of knowledge, such extremely high values (> −80°) for inward rotation have not been

Fig. 7. The "Off-tracking" phenomenon as demonstrated by a turning four-wheeled car (VW Polo, 1992, only front wheels turning). The speed of the car was constant and around 5–7 km/h. The trails were left in about 1 cm of dry snow on top of a hard surface, while the steering wheel was kept in the same position during the entire turn, resulting in a circular turn. Every single wheel leaves a continuous trail, of which each trail of left and right front and back wheels, are superimposed during straightforward progression. These initially superimposed trails of the left and right front and back wheels split up into four well-defined trails as soon as the car starts turning. i.e. at the beginning of the curve. In, the resulting "splitting-up" trace, the two trails of the back wheels start turning before the two trails of the front wheels resulting in an asymmetric pattern at the beginning of the curve (C). During this continuous turn, the four trails then retain a regular distance between each other (A, B). Note that the exterior trail of the (right) front wheel is most deeply impressed (A, B). The arrows in C indicate the trails of the back and front wheels. Also note that the mechanical car is not the best model to understand the turning locomotor capabilities of sauropods from a biomechanical point of view, but it is proposed to use the term "off-tracking" to describe quadrupedal trackways with a similar configuration.

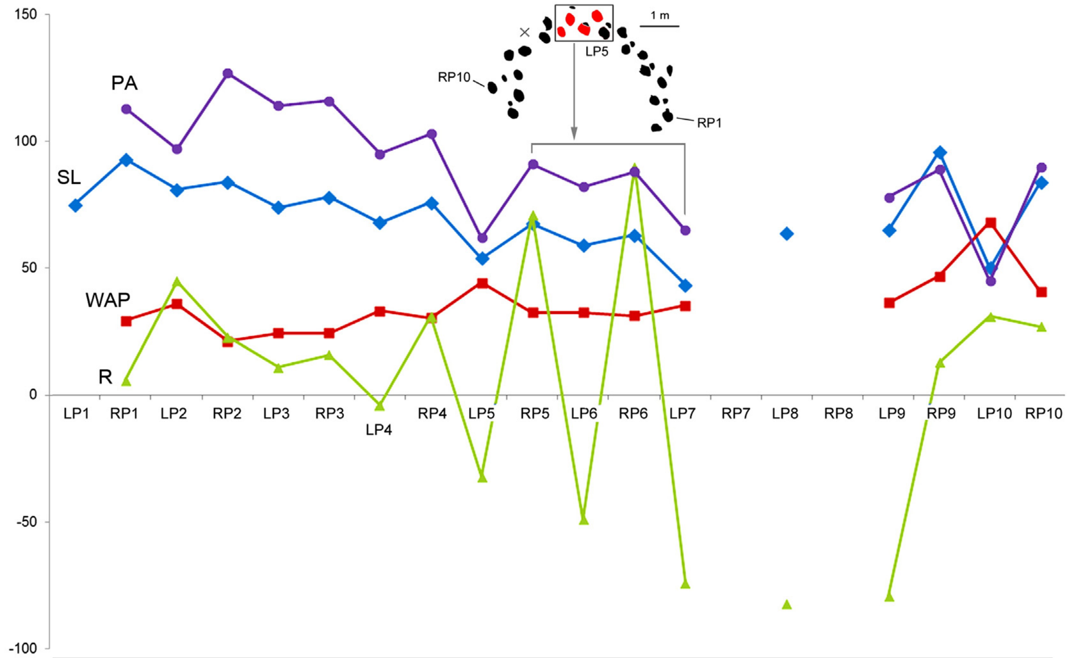

Fig. 8. Line chart indicating values for pes track rotation (R [°]), pace angulation (PA [°]), stride length (SL [cm]), and trackway gauge (WAP [cm]) along the course of trackway TDGZ-S1. Note that in the middle of the turn stride and pace lengths are decreasing, while trackway gauge is increasing from narrow–medium to wide gauge. In this part of the trackway, the pes rotation also shows an extreme variability with outward rotated right and inward rotated left pes tracks.

previously reported for any sauropod trackway. Evidently, this inward rotation must be associated with the turn to the left, as at the beginning and the end of the turn, the left pes tracks are outward rotated, as are all of the right pes tracks all along the trackway (and turn).

Finally, TDGZ-S1 also is a good example for a pes-dominated trackway, i.e. a trackway with clearly more pes than manus tracks preserved. While some of the right manus (RM5–RM9) tracks may be hidden under overburden, the absence of all but one left manus track cannot be explained by overburden and it is therefore striking. Since the animal was turning to the left, we assume that the left manus tracks came to lie in a position where they became systematically overprinted by the left pes, even though it can not be excluded that some may even have been overprinted by the right pes. Such overprinted tracks are an important constraint when it comes to the analysis of possible gaits that may have created such a trackway configuration and pattern (Stevens et al., in press).

6.3. Trackmaker behavior

The gait and heteropody patterns help distinguish different sauropod groups (Farlow, 1992; Lockley et al., 1994. Wilson and Carrano, 1999; Vila et al., 2013). The narrow to medium gauge TDGZ-S1 and S2 have been correlated with smaller narrow diplodocid-like trackmakers (Xing et al., 2015a).

Based on the study of recent mammal trackways around Lake Manyara in Tanzania, Cohen et al. (1993) distinguished two categories of trackways that are related to different behavior: (1) directional trackways, and (2) milling trackways. While travel across the site is directional movement and makes long, linear trackways, milling patterns are harder to decipher because they turn back and recross themselves many times (Cohen et al., 1993).

The turning trackway TDGZ-S1 clearly is not a directional trackway but rather falls in the latter milling category and indicates a special behavior, that is, however, impossible to assess. It has to be underlined that in the present case the part of the track level that is cropping out is well situated to capture the turn, but the track level is not exposed at the beginning and the end of the turn, and so we don't know what the animal did prior and after the turn. In order to really decipher a milling behavior, it would be required that the track level was cropping out over a much larger surface (see also Marty et al., 2012; Castanera et al., 2014).

7. Conclusions

The Tangdigezhuang tracksite is an important addition to the Chinese Early Cretaceous sauropod track record. We report two small trackways that share many similarities with the *Parabrontopodus* ichnotaxon, but that are not clearly narrow gauge, at least not along the entire trackway course. While this can be explained with a pronounced turn in one of the trackways, the other trackway is straight (even though not very long) and also shows a similar variability in gauge. Changes between narrow and wide gauge over a couple of steps demonstrate that these two locomotor styles could have been used by one and the same sauropod trackmaker, even if in the present case in one trackway in association with a narrow turn as well as pronounced shifts in pes rotation (from outward to inward).

The semicircular turn with complete 'turning around' as observed in TDGZ-S1 is very exceptional in the sauropod track record and as such important for future studies on sauropod locomotion capabilities (unsteady locomotion, ROM—range of motion), and the same holds true for other 'atypical' irregular trackways that exhibit highly variable trackway configuration such as changes in gauge, pace or stride, and such variable parameters. With growing trackway data, in the future, locomotor variation within ichnospecies may be addressed statistically, and ontogenetic effects of size on locomotor function may be analyzed.

It is proposed to use the term "off-tracking" as introduced by Ishigaki and Matsumoto (2009) to describe quadrupedal trackways with a similar configuration.

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