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Research Paper

Early Jurassic basal sauropodomorpha dominated tracks from Guizhou, China: Morphology, ethology, and paleoenvironment

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A B S T R A C T

The newly discovered large (350 m^2) Yantan dinosaur tracksite, in the Lower Jurassic Ziliujing Formation of Guizhou Province, China, reveals at least 250 footprints of which ~97 can be resolved into trackways of sauropodomorphs. All the trackways are sub parallel likely indicating gregarious behavior. One theropod track (cf. *Grallator*) was recorded. The sauropodomorph tracks predominantly represent quadrupedal progression (Morphotype A), and footprint morphology is similar to the ichnospecies *Liujianpusshunan*, characterized by outward pes rotation. Three trackways indicate bipedal progression, and two of these (Morphotype B) indicate inward pes rotation, accompanied by elongate pes digit scratch marks. For the latter phenomenon three possible scenarios are discussed: (1) significant rotation changes accompanying changes in gait, (2) swimming behavior, (3) formation of undertracks.

Sedimentological evidence indicates the tracks were made on a linguloid rippled, muddy, immature sandstone substrate characterized by significant differences in substrate consistency across the track-bearing surface. Microbially induced sedimentary structures (MISS) characterized by distinctive wrinkle marks indicate a stressed, probably semi-arid, paleoenvironment that was not conducive to habitation by invertebrate organisms. This is consistent with other evidence that Lower Jurassic sauropodomorph tracks are often associated with semi-arid paleoenvironments.

1. Introduction

Compared with the wide distribution of Late Triassic sauropodomorphs such as *Plateosaurus* in Europe (Sander, 1992), China lacks skeletal fossils of Late Triassic sauropodomorphs. The earliest skeletal records of Plateosauria in China are from the Early Jurassic (Young, 1951; Dong, 1992; Barrett et al., 2005). Also, no Late Triassic tracks of sauropodomorphs were found in China until 2014. One set of tracks resembling poorly preserved *Eosauropus* has been tentatively identified from the Xujiahe Formation at the Longguan site, Sichuan Province (Xing et al., 2014a). Better preserved sauropodomorph tracks were discovered in the Xujiahe Formation at the Yiguojiao site in south Sichuan Province, China, these tracks share a number of features in common with the ichnogenera *Eosauropus* (Late Triassic) and *Liujianpus* (Early Jurassic) (Xing et al., 2016a, 2018).

There are a few sauropodomorph tracksites in Early Jurassic formations of China: (1) Zhenzhuchong Formation of the Changhebian site, Dazu region of Sichuan Province (Lockley and Matsukawa, 2009; Xing et al., 2016b); (2) Ziliujing Formation of Gulin County, Sichuan Province (Xing, 2010; Xing et al., 2016a); (3) Ziliujing Formation of the Dazhuanwan site, Bijie City, Guizhou

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Province (Xing et al., 2017a). There are also some poorly preserved sauropodomorph undertracks from the Ziliujing Formation of the Hejie site, Zigong City, Sichuan Province (Xing et al., 2014b).

In 2013, Mr. Songbo Guo from Guizhou Diaoyutai State Guest Liquor Industry Co., Ltd discovered a group of regular indentations on cliff walls when laying construction foundations in Yantan Village, Maotai Town, Renhuai City, Guizhou Province, China (Fig. 1). After field examination in August 2017, the first author of this paper confirmed that they are truly dinosaur tracks. The site, now designated the Yantan site, was investigated again in December 2017 by the first, second and third authors.

Institutional and other abbreviations: UCM: University of Colorado Museum, USA. YT: Yantansite, Maotai Town, Guizhou Province, China.

2. Geographic and geologic setting

2.1. General setting

The tracksite reported in this study is located at the Diaoyutai brewery, Yantan Village, Maotai Town, Guizhou Province, China (27°53′59.13″N, 106°22′34.50″E). The track-bearing strata belong to the Lower Jurassic Ziliujing Formation. This formation lies disconformably and conformably between the underlying upper Triassic Erqiao Formation and the overlying middle Jurassic Xintiangou Formation, respectively. According to the Guizhou Bureau of Geology and Mineral Resources (1997), this formation has been subdivided into five members. In ascending order, they are Qijiang, Zhenzhuchong, Dongyuemiao, Maanshan and Daanzhai members (Fig. 2).

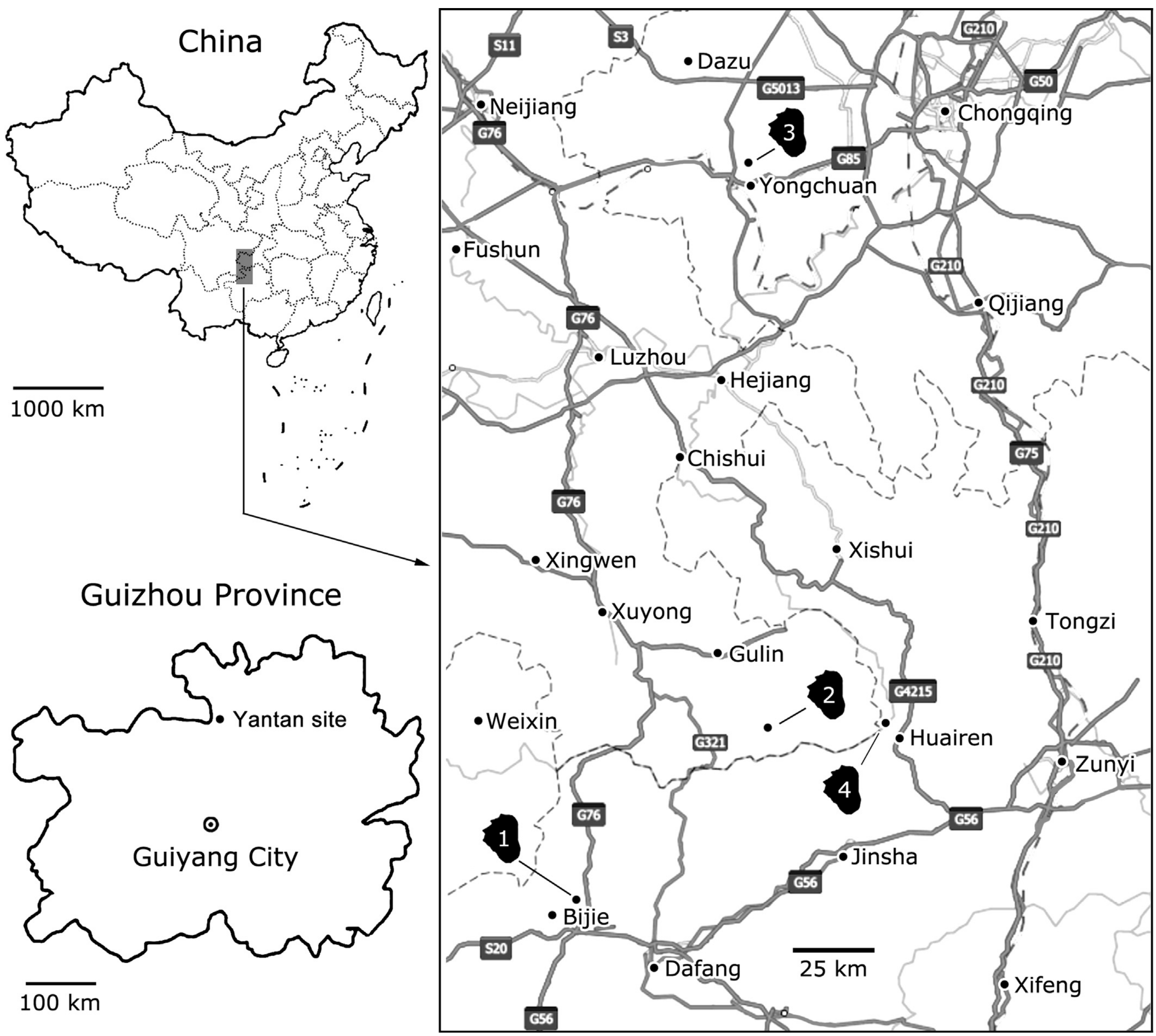

Figure 1. Map showing the location of sauropodomorph tracksites in southwestern China. (1) Dazhuanwan sites I and II, Bijie City, Guizhou Province; (2) Jiaoyuan tracksite, Gulin County, Sichuan Province; (3) Changhebian sauropod tracksite, Dazu County, Sichuan Province; (4) Yantan sauropod tracksite, Maotai Town, Guizhou Province, the location of the tracks described in this study. Modified from location of the tracks described in this study. Modified from Xing et al. (2013, 2016d, 2017a).

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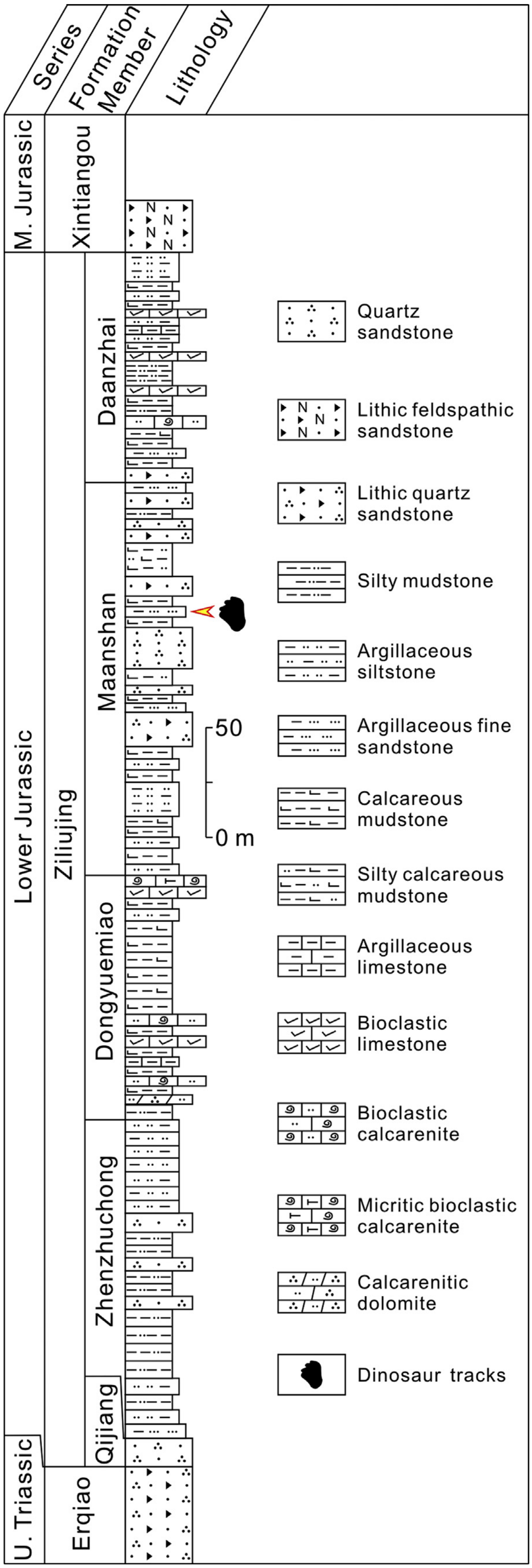

Figure 2. Stratigraphic section showing position of track-bearing level in the Maanshan Member of the Ziliujing Formation (Lower Jurassic).

In the northwest of Guizhou and southeast of Sichuan Provinces, the Ziliujing Formation is a set of purple red and dark purple grey medium-thick lithic sandstones, argillaceous siltstone, silty mudstone interbedded with grey-yellow to grey medium-thin argillaceous limestone, and shelly limestone, with a pale grey medium layer of quartz sandstone at the base (Zhang et al., 2016; Xing et al., 2016a, 2017a). Tracks from the Yantan site are preserved in medium-thick argillaceous lithic quartz sandstone of the Maanshan Member (the fourth member, Fig. 2). The frequent alternation of argillaceous siltstone, argillaceous sandstone, and conglomerate (Fig. 3A and B), and the occurrence of cross-bedding (Fig. 3C) and linguiod ripple marks (Fig. 3D), indicate a shallow to exposed lacustrine beach microfacies (Zhang et al., 2016).

2.2. Tracksite description

The main tracksite is a large exposed bedding plane (~25 m wide, ~14 m high) with a steep 45°–50° dip to the southwest (Fig. 4). The surface is characterized by linguoid ripples which are more or less uniform in appearance over the whole surface (~350 m^2). However, the distribution and depth of the tracks over the whole surface is variable, indicating significant variation in substrate conditions and track registration potential. Differences of track depth are generally ranging from ~10.0 cm to 20.0 cm; some are only ~1.0 cm deep, and others appear to be slightly raised compaction features, elevated ~1.0–2.0 cm above the surface.

Tracks from the Yantan site occur on at least three layers. The lowest sandstone layer has about 10 tracks which may be undertracks and only preserve indistinct oval outlines without any clear trackways. The middle sandstone layer has at least 250 tracks and the upper sandstone layer only yields an isolated pes track. The tracks in the middle layer are the best preserved of these layers. The trackways are conspicuous and generally deep and continuous over much of the main surface.

2.3. Sedimentary structures of microbial origin

Wrinkle structures, one type of microbially induced sedimentary structures (MISS), were observed on the ripple marked track-bearing surface (Fig. 3E). They occur within and around the tracks, being more frequent in the latter area. These structures are characterized by relatively short, oddly contorted, variably bifurcating, and minute-scale round-crested ridges. They are commonly 5–30 mm long, 1–3 mm wide, and 1–5 mm high. Similar structures have been reported in deposits of different ages and locations (e.g., Hagadorn and Bottjer, 1997, 1999; Porada and Bouougri, 2007). Within the tracks, the wrinkle structures are short, narrow, and low in relief, which is distinctively different from those around the tracks. The long axes of these structures have no preferred directions, but are often most prominent on ripple crest ridges and distributed in fan-like dentritic patterns on ripple mark slopes. In some ripple troughs the marks are lacking. Occasionally, wrinkle structures co-occur with sand cracks, which are another kind of MISS (Fig. 3F).

3. Methods

Scaffold covering the whole cliff wall was built due to the steepness of the main tracksite (~45°–50° dip to the S–SW), permitting examination of the tracks at close quarters, and allowing the making of chalk outlines, tracings, photographs and selected latex molds. Once outlines of the tracks over the whole outcrop had been chalked, eight large sheets of transparent plastic

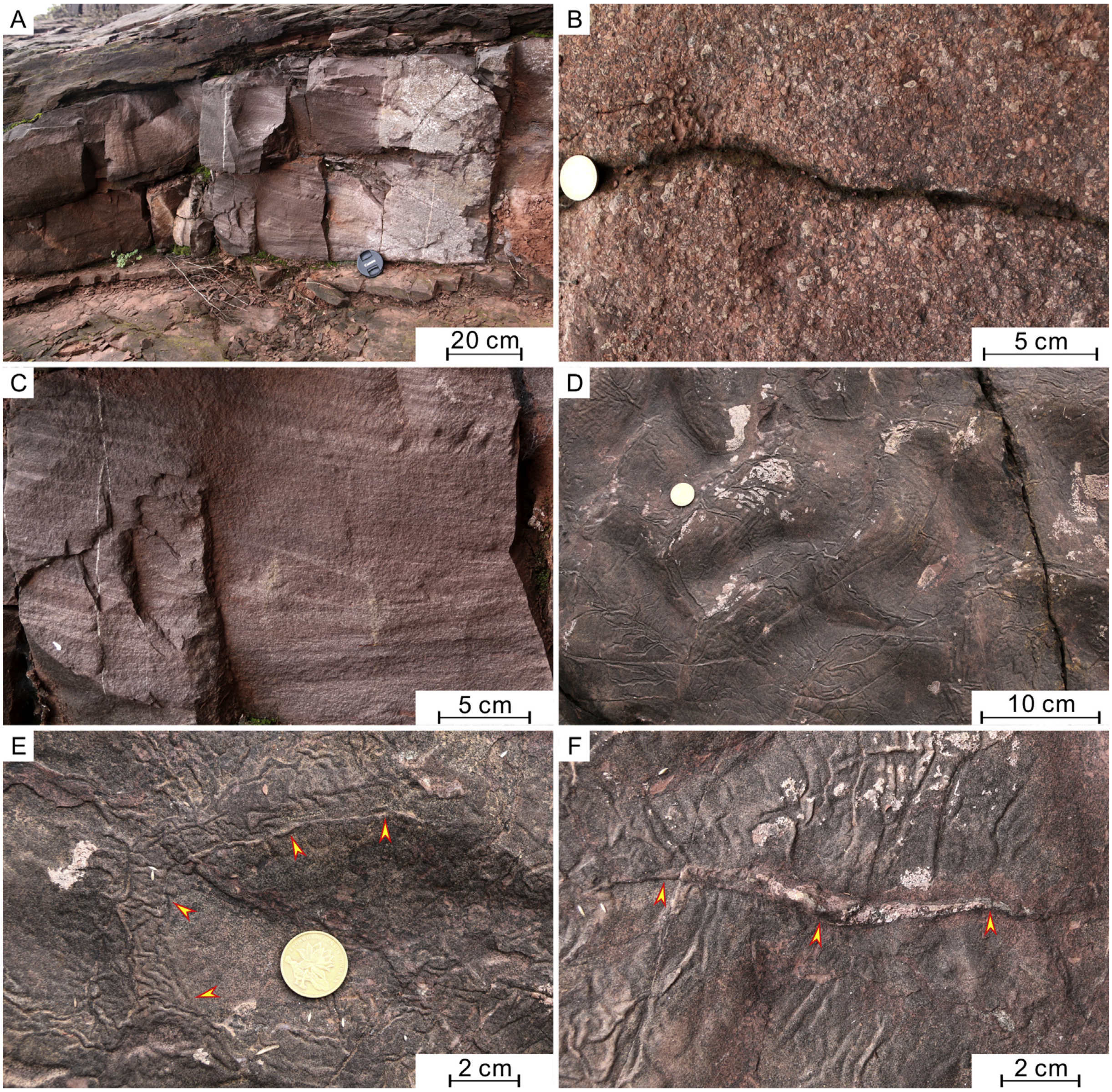

Figure 3. Sedimentary facies and structures associated with dinosaur tacks in the Yantan site. (A) Purple argillaceous sandstone interbedded with argillaceous siltstone. (B) Conglomerate. (C) Close-up view of argillaceous sandstone in Fig. 3A, showing cross bedding. (D) Linguoid ripple marks indicating a change from low to higher flow velocity. (E) Close-up view of ripple marks, showing microbially induced sedimentary structures, wrinkle structures, abundant on the crests of the ripple marks (arrows). (F) Co-occurrence of two types of microbially induced sedimentary structures, spindle-shaped sand crack (arrows) and wrinkle structures.

were used to trace most of the trackway segments. These were scanned and made into an overall track distribution map. All tracks and trackways remain *in situ*.

We obtained the following measurements of manus and pes imprints and trackways *in situ*: track length and width, rotation, pes – pes and manus – manus pace angulation, step, stride and inner and outer trackway width. Trackways were numbered YT-S1 to YT-S12 with "YT" indicating the Yantan tracksite and "S" the sauropod trackmaker.

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

4. Description of tracks

4.1. Sauropodomorph trackways

There are at least 14 trackways (YT-S1–YT-S14) and isolated tracks among the 252 tracks in the middle sandstone layer (Supplementary Table 1). These trackways are the main focus of this study. All the trackways are aligned from southwest to north-east. There are several trackway morphotypes present. The first morphotype A, YT-S1, S2, S4–S7, S9–S14, are characterized by an oval, outwardly rotated pes with four claw traces oriented sub-

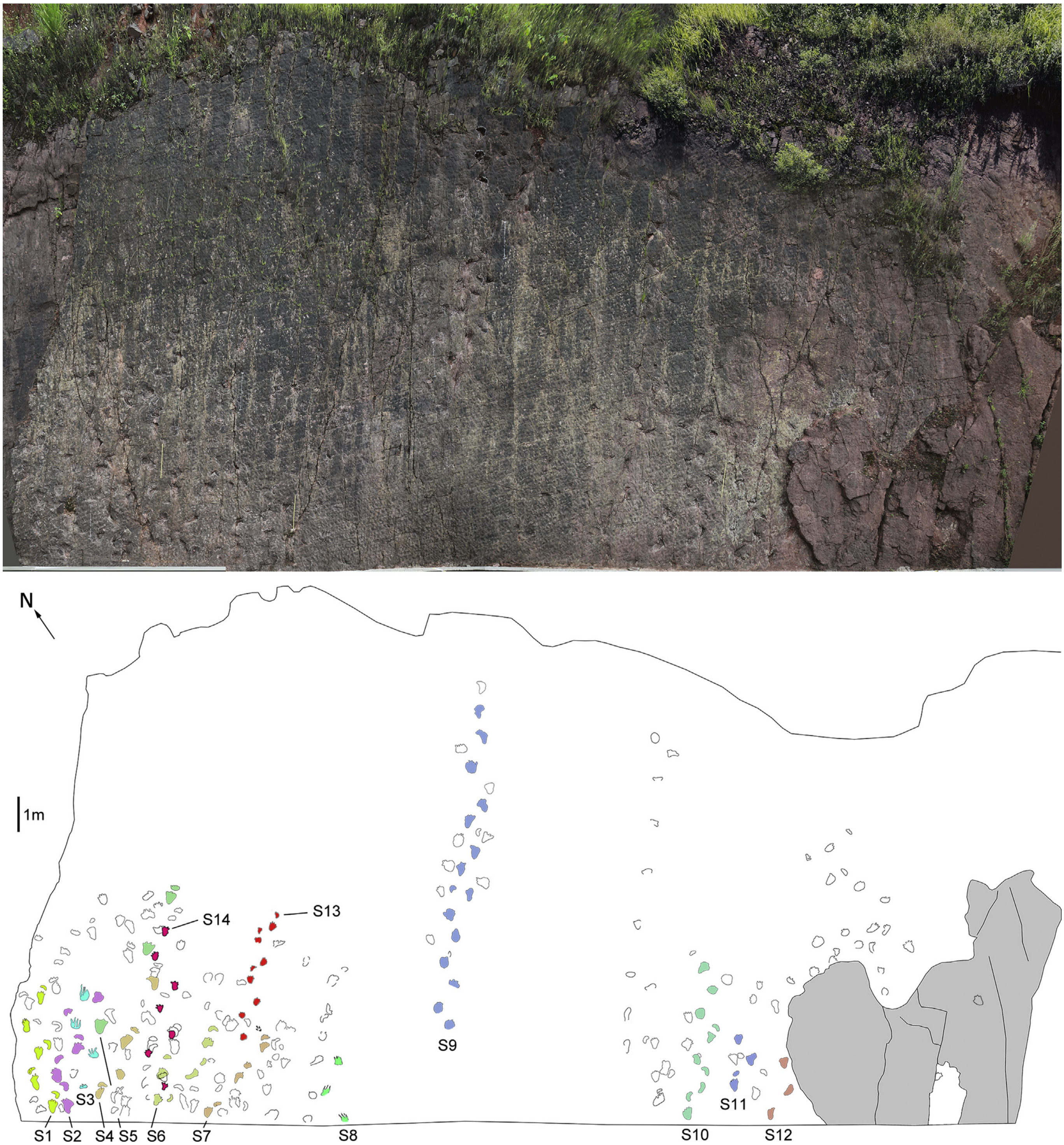

Figure 4. Photograph and interpretative outline drawing with distribution of sauropod trackways YT-S1–S14 (Morphotypes A and B) at the Yantan site. Notice abundant parallel trackways at lower left, possibly indicating gregarious behavior, with two trackways (Morphotype B; YT-S3 and YT-S8) preserved with inwardly rotated pes digit traces lacking a manus imprint.

parallel to the footprint axis, and with a semicircular to pentadactyl manus. Within this category most trackways indicate quadrupedal progression, but some trackways, notably S14, appear to belong tobipeds. The second morphotype B, YT-S3 and S8 preserve elongate claw marks with heel traces that are short or can be completely absent; manus imprints are missing. The trackway pattern is similar to morphotype A.

4.1.1. Morphotype A

The (WAP/PL)-ratios are no more than 1.0 in YT-S1, S2, S4, S9 and S10, meeting definition of narrow-gauge (Farlow, 1992), and are 1.5, 1.4, 1.2, 1.4 in S6, S11, S12, and S13, respectively, between medium-gauge and wide-gauge trackways, and 2.0 in S14, meeting definition of wide-gauge (Marty, 2008) (Fig. 5–7). YT-S1 and S6 are the best preserved in the 10 trackways.

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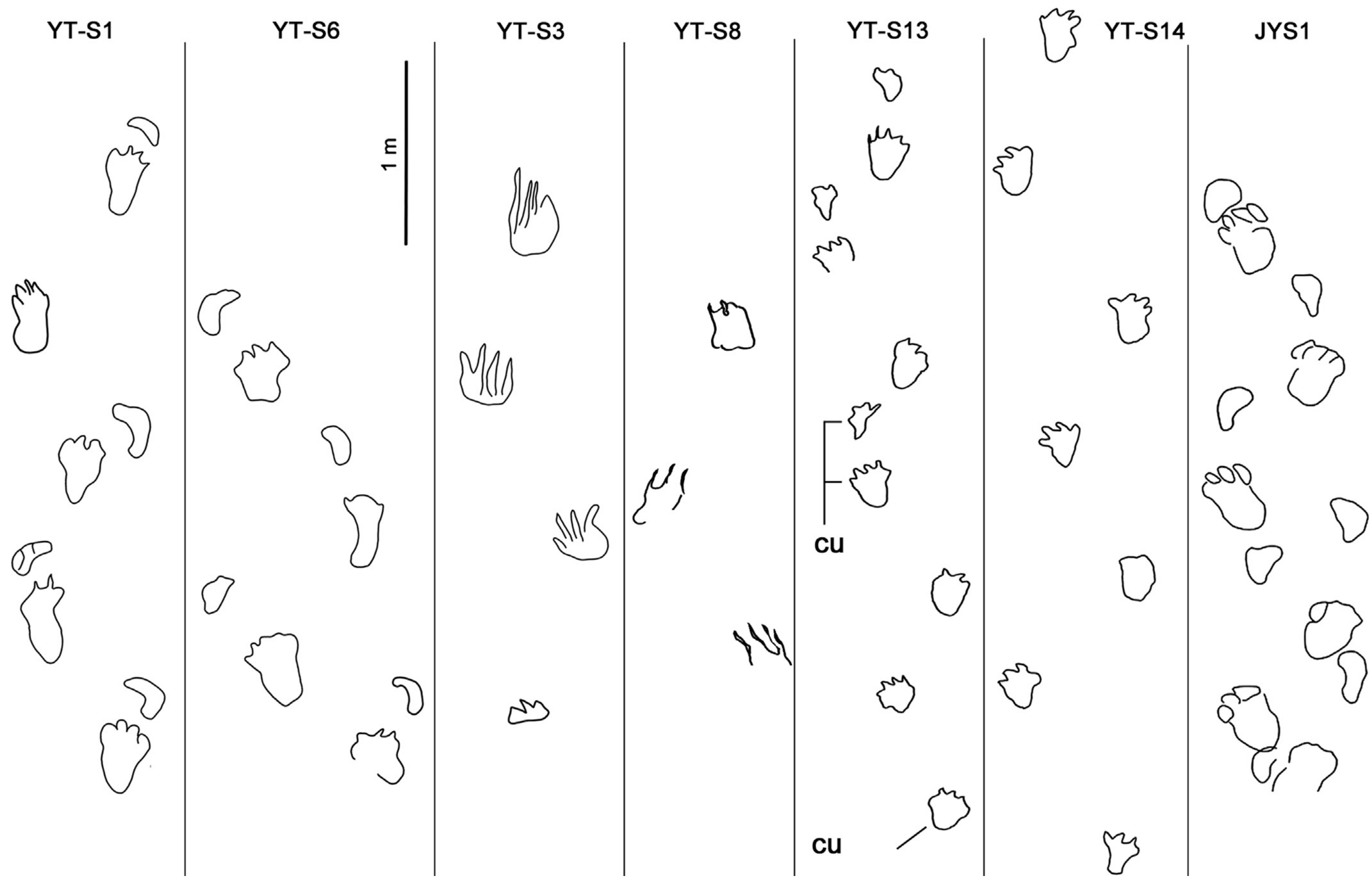

Figure 5. Interpretative outline drawings of best preserved sauropod trackways of the Yantan site, and *Liujianpusshunan* type trackway (YS1) for comparison. YT-S1, S6, S13, S14 (Morphotype A) and YT-S3, S8 (Morphotype B). Notice Morphotype B preserved with scratch-like, inwardly rotated pedal digit traces lacking a manus trace, and YT-S14 (Morphotype A) also lacking a manus trace.

The pes imprints are tetradactyl with their length and width ranging from about 32.5 to 39.0 cm and from 22.0 to 31.5 cm, respectively (average length/width ratio being 1.3). The digit traces (digit I–IV) are oriented subparallel to the pes axis. The sole area of the pes is divided by a transverse crease, situated almost midway along the length of the tracks: i.e. between about 46%–50% of the pes length from the anterior margin of the footprint (Fig. 6).

The manus is pentadactyl to semi-circular and wider than long, with a length that ranges between 9 and 18 cm and with a width that ranges between 20.5 and 27.0 cm (average length/width ratio of 0.6). The manus impressions of YT-S6 lie anterolateral to the pes impressions. The heteropody (ratio of manus to pes size) of YT-S6 is about 1:3–1:4.2. The manus impression is rotated approximately 63° outward from the trackway axis, which is much larger than the outward rotation of the pes impressions (approximately 32°). The average manus pace angulation is 87°, while the average pes pace angulation is 105°.

Morphotype A tracks from the Yantan site and the sauropodomorph tracks *Liujianpusshunan* from the Lower Jurassic Ziliujing Formation of the Jiaoyuan tracksite (Xing et al., 2016a) are very similar, and the two tracksites from which they are discovered are in close geographic proximity. The Jiaoyuan site is 43 km west of the Yantan site. Yantan Morphotype A tracks share diagnostic features with *Liujianpusshunan*, including (1) trackway of large quadruped with elongate, tetradactyl, outwardly-rotated pes imprints with digit proportions III > IV = II > I, and a sole area divided by a transverse crease; (2) manus pentadactyl to semi-circular and strongly rotated outward; (3) difference from other sauropodomorph tracks by the presence of four nearly equidimensional, elongate pes digit traces oriented subparallel to the pes axis and a sub-circular manus with five discrete blunt digit traces. Therefore, we refer Yantan Morphotype A tracks to *Liujianpusshunan*.

Trackway S14 appears to have been made by a biped. However, the pes morphology is not obviously different from other Morphoptype A trackways. The main difference is an extra-morphological (preservational) feature with imprints being preserved as raised pedestals, which we attribute to compaction of the sediment. This rare preservation as convex (instead of concave) epirelief occurs when the sediment is compressed under the weight of the animal and subsequently can resist erosional effects. Thus, there may also be a correlation between the mode of preservation and the apparent bipedal progression, however, presently it is not clear if this is truly a factor in obscuring manus tracks, which might otherwise be visible.

4.1.2. Morphotype B

YT-S3 and S8 tracks reveal great variation in morphological features (Figs. 5 and 8). Generally speaking, however, they only consist of slender, tapering, parallel pes digit imprints, and lack manus imprints or any imprints made by the heel area. Thus the most obvious difference between morphotypes A and B is that the former reflects a quadruped, the latter a biped. The pes imprints of YT-S3 are tetradactyl with their average length and width about 31.5 cm and 24.5 cm, respectively (average length/width ratio 1.4). YT-S3 has four elongated digit marks, among which digit I of RP1

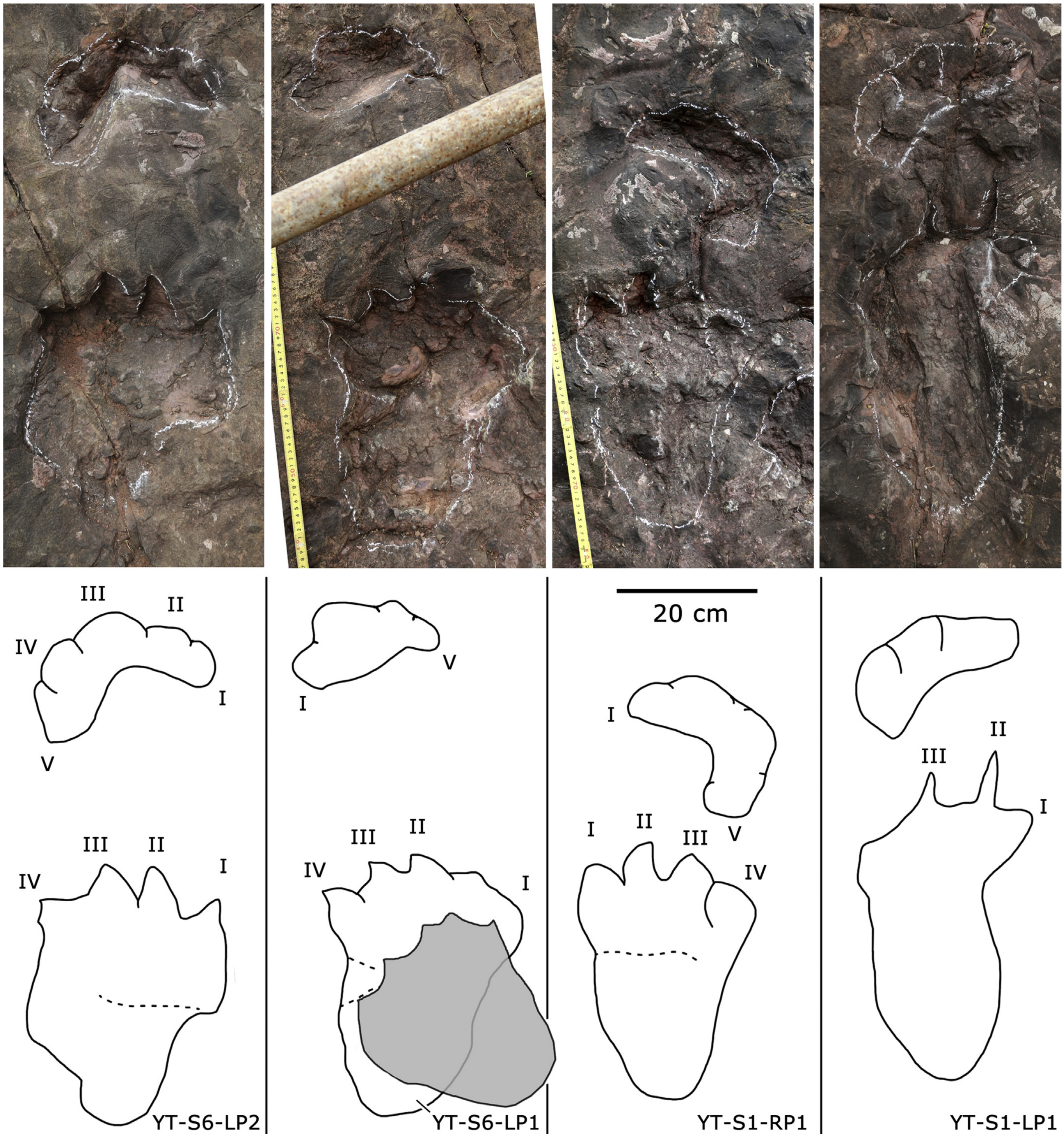

Figure 6. Photographs and interpretative outline drawings of best preserved sauropod tracks Morphotype A of Yantan site.

and RP2 of the right hindfoot are the shortest and four toes of LP2 of the left hindfoot are equal in length. Overall, the digit II–IV marks are longer and deeper, while the digits I marks are shorter and shallower. Elongated sand mounds are preserved at the posterior end of the YT-S3-LP2 and RP2, showing that substrate sediments were raked by the digits and pilled posteriorly.

Both of YT-S3 and S8 rotate medially to the trackway medianline by about 10°. This is a second striking difference between Morphotype A, which has an outwardly rotated pes. WAP/PL ratios of YT-S3 and S8 are 2.1 and 2.2. Such obvious difference in gauge of Yantan Morphotype B may be explained by lack of heel areas in some tracks. Generally, YT-S3 and S8 are narrow-gauge trackways.

4.2. Theropod track

A single small tridactyl track YT-TI1 (length 20.0 cm, width 12 cm: L/W = 1.67) was recognized (Fig. 7). The morphology is typical of *Grallator*. It is characterized by moderate mesaxony (0.60),

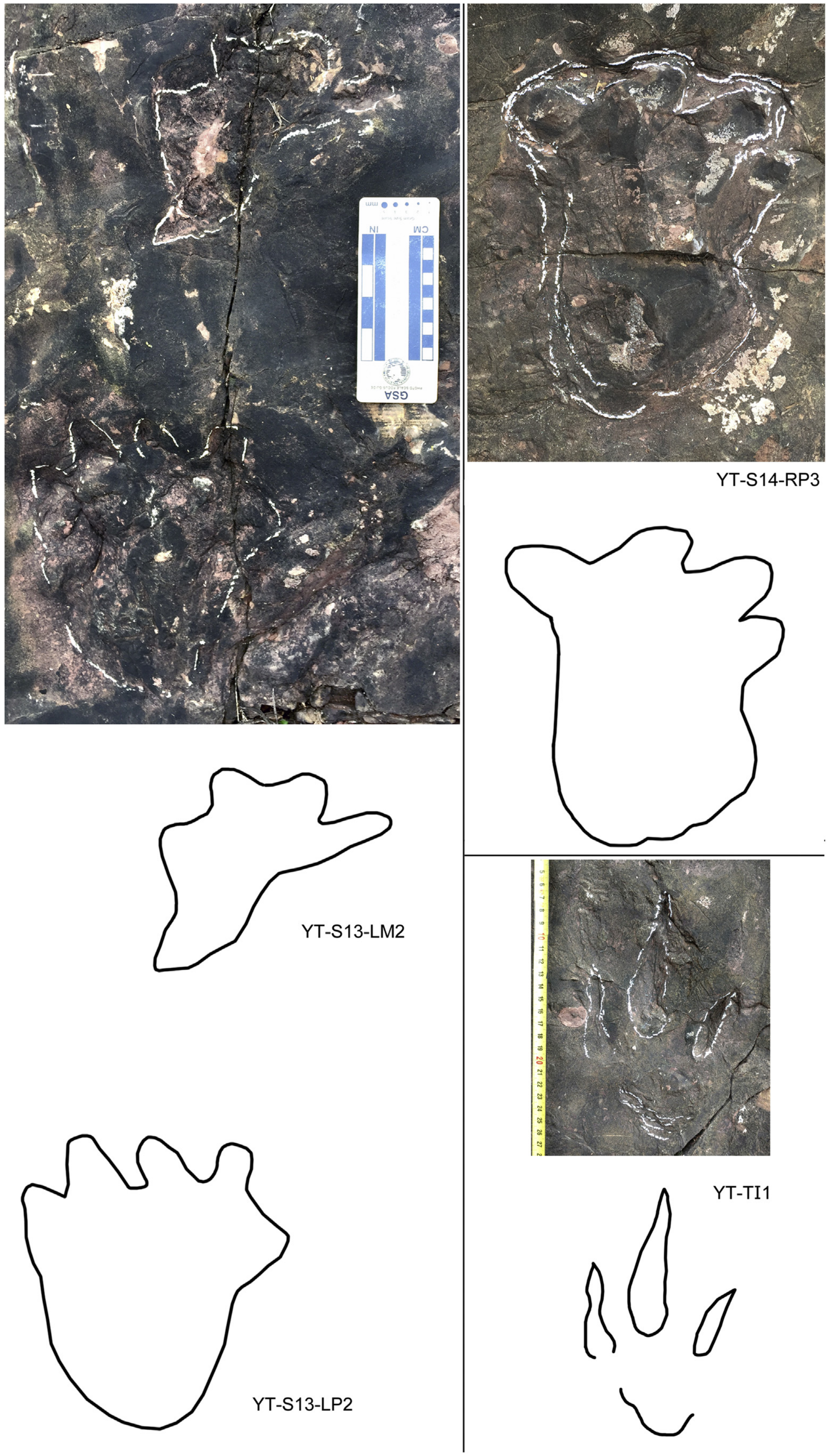

Figure 7. Photographs and interpretative outline drawings of small sized sauropod tracks and isolated theropod track (YT-TI1) of Yantan site.

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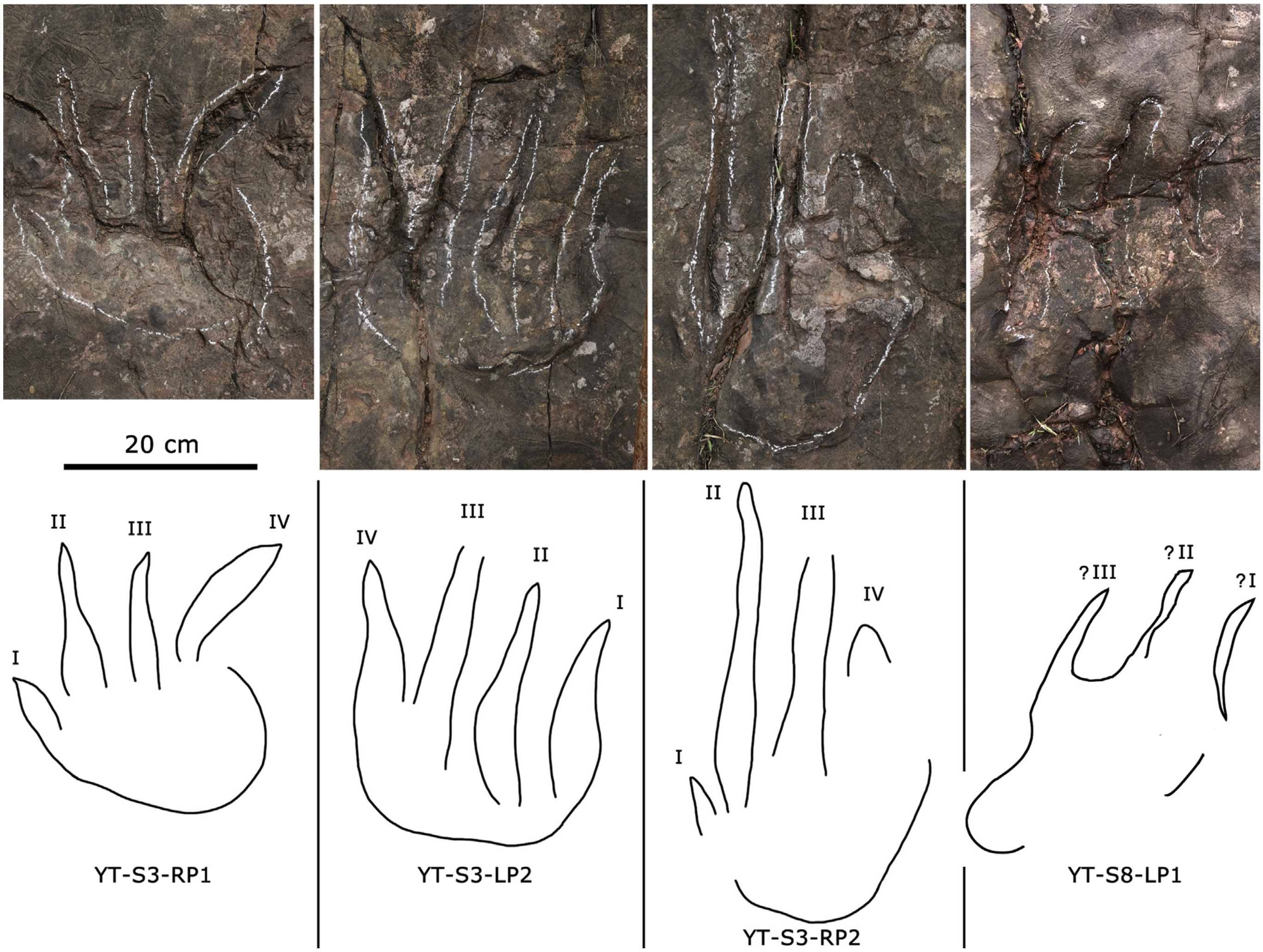

Figure 8. Photographs and interpretative outline drawing of best preserved sauropod Morphotype B pedal tracks of Yantan site. Notice scratch-like digit traces discussed here as (1) swim traces, (2) switch to bipedal movement, or (3) undertracks.

which is close to that in the typical *Grallator* from Zigong (average 0.63, in the range of 0.51–0.81, $N = 5$, Xing et al., 2014b) and the Jiaoyuan theropod track Type B from Gulin (Xing et al., 2017b). YT-TI1 has relatively wide divarication angles (47° between digits II and IV vs. 51° in the Hejie *Grallator* and 62° of the Jiaoyuan theropod track Type B). The metatarsophalangeal pad of digit IV of YT-TI1 is positioned in line with the long axis of digit III, this feature being much closer to that of *Jialingpus* from the Late Jurassic of Sichuan Province (Zhen et al., 1983; Xing et al., 2014c).

5. Discussion

In this section we consider both paleobiological and paleco-logical implications of preserved track surfaces.

5.1. Paleobiological implications

The first and most obvious feature of the Yantan site is that it exposes a large surface (~350 m^2) on which abundant tracks (~250) and recognizable trackways (~14) of large predominantly quadrupedal animals are oriented in similar NNE directions. This is strongly suggestive of progression by a group or groups of gregarious animals. This interpretation is supported to various degrees by the sedimentological evidence (see also below): i.e. deep and shallow trackways are concentrated in the same areas, suggesting most activity was made in a short period of time during which substrate conditions did not change markedly. In addition to the parallelism of most trackways, their distribution perpendicular to the direction of progression has paleobiological implications, indicating that at least 14 animals crossed an area little more than 20 m wide. In the NNW sector (Fig. 4) at least 10 of these animals crossed an area only ~10 m wide, with significant trackway overlap. This implies that in this sector they did not all cross "shoulder to shoulder" on a broad front (Lockley, 1989) but were following in line to some degree. To the ENE there are less trackways and they are more widely spaced.

As noted above biggest difference between Yantan Morphotype A and Morphotype B tracks is that the latter appear to represent bipedal animals that progressed with inward rotation of the pes, leaving elongate digit scratch marks, often less deeply registered than some of the deeper tracks in the Morphotype A group. Given that elongate scratch marks are characteristic of swim tracks this interpretation must also be considered. However, as noted in previous debates about swimming sauropodomorph dinosaurs, one of the main arguments against swimming sauropod scenarios based on tracks is that trackway spacing patterns (step length and gauge) in purported swim traces are often the same as in trackways made by normal walking animals. As discussed below, this appears to be the case here. Moreover, the slender, tapering, parallel digit traces associated with swim tracks have never been confirmed for sauropodomorphs, even though they are reported as a feature of swim tracks, attributed to theropods (Milner and Lockley, 2016).

However, while step length and gauge appear similar in both morphotypes A and B, the inward rotation of Morphotype B pes tracks is a notable difference. This raises the question of whether pes rotation may change as a given trackmaker switches from quadrupedal to bipedal progression or vice versa. Among dinosaur trackways it is generally well established that outward pes rotation is only pronounced in habitually quadrupedal Sauropoda. Conversely inward rotation of the pes is pronounced in Upper Triassic *Evazoum* trackways that have been assigned to bipedal prosauropod sauropodomorphs (Nicosia and Loi, 2003; Lockley et al., 2006), and in bipedal ornithischians, mainly ornithopods. Most other dinosaur trackways show little evidence of strong rotation towards either of these extreme rotational gaits. Lockley (2001, 2007) noted that *Otozoum* trackways exhibit both narrow- and wide-gauge gait patterns, but in the case of this ichnogenus, the corresponding variation in gauge-related, inward, pes track rotation is subtle. Unfortunately, there are no well-preserved trackways of quadrupedal *Otozoum*to further test the relationship between gait and rotation. However, a comparison between the trackways of *Otozoum*, which almost always represents a biped and the trackways of large quadrupedal sauropods (e.g., *Brontopodus*) does show the trend to outward pes rotation in the later quadrupedal forms. Lockley (1999) and Lockley and Jackson (2008) noted the polarity between inward versus less-inward pes rotation in erect-legged human trackmakers, and possible convergence with erect-limbed sauropods. In this case erect posture appeared to reduce inward rotation and be associated with a less entaxonic foot, whereas 'hunching' forward was correlated with outward rotation and a more entaxonic, sauropod-like foot.

The possibility that Morphotype B trackways could indicate swimming behavior cannot be ruled out completely. However, as discussed in a study of possible sauropod swim tracks based on the Yanguoxia digit-only sauropod pes tracks, from the Cretaceous of Gansu Province, toe-only traces may represent the penetration of claws into a track-bearing substrate without registration of the whole foot: i.e., the broader, fleshy part of the foot. In such cases claw penetration may serve a substrate gripping function. This could have been the case with Morphotype B trackways S3 and S8. In short, the digit-only sauropod pes trackways from Yanguoxia, previously thought to be evidence of swimming sauropod or sauropod walked in water (Li et al., 2006), are not evidence of swimming but rather evidence of claw penetration (Xing et al., 2016c). An interpretation of Morphotype B tracks as swim traces would require explaining why two of 14 subparallel trackways were made by swimmers, while the remainder indicate walking progression. It is possible that this was caused by fluctuating water levels (Romilio et al., 2013), and the nearly perpendicular orientation of the trackways to the flow direction could indicate that the sauropods were crossing a river. However, it has been pointed out that the archaic and largely discredited idea that sauropods could be bouyed up by water, only to touch toe tips to a subaqueous substrate (Bird, 1944), is conceptually similar to the scenario where toe tips penetrate the tracked surface to register on an underlayer (Lockley and Rice, 1990). The latter would be an alternative explanation for the formation of these traces, and the dynamics and outward rotation of the foot while sinking into the substrate, could also explain the inward pointing digit traces and scratches that were possibly registered on a deeper layer as undertracks. In this case Morphotype B traces were left after those of Morphotype A, and after the latter were covered by another sediment layer. It is important to note that several pes tracks of Morphotype A also show deep claw traces.

5.2. Paleoecological implications

The main track-bearing surface can be differentiated into several broad areas. Tracks are far more abundant and deeply impressed on the lower part of the dip slope (SW) than on the upper part of the surface (NE). The total number of tracks recorded on the entire area is ∼250 of which 97 are resolved into 14 sauropodomorph trackways (shown in color: Fig. 4) and ∼153 (uncolored) which are not easily resolved into trackways.

Using the base of the outcrop, now defined by the intersection of the road and bedding plane, a strike line drawn horizontally half way up the outcrop, ∼7.0 m above the road, separates the upper half of the outcrop with only ∼20 recognizable footprints mostly associated with a single trackway. This is in contrast to ∼250 tracks registered on the lower half of the outcrop which represent all the recognizable trackways.

The difference in distribution of tracks is clearly related to substrate conditions at the time of track registration. This conclusion is unambiguous because it is obvious that after making clear and mostly deep tracks in the southwesterly sector almost all the trackmakers, except S9, continued to the northeast without leaving clear footprints. This suggests that the substrate in this sector was much firmer, and resistant to deep impressions by all the trackmakers (except S9). As the entire surface is characterized by linguoid ripples, suggesting a predominant flow direction to the WNW, we may infer that the difference in substrate consistency was related to sediment saturation, and not to obvious differences in the distribution of sedimentary structures or flow regime indicators within the area.

In addition to being able to divide the area along a SW–NE 'dip' transect, based on track depth and frequency, there are also noticeable differences in track depth and frequency along a NNW–SSE 'strike' transect (Fig. 4). The NNW third of this transect contains registered trackways S1–S8 and S13–S14, whereas the middle third registered only trackway S9, and the ENE third registered trackways S10–S12. As noted above, this distribution suggests the lower density of tracks in the middle sector was the result of fewer trackmakers crossing the area, rather than differences in substrate conditions.

Close examination of the track-bearing surface indicates the important role played by microbially induced sedimentary structures (MISS). The morphology (type) of MISS are fundamentally controlled by their environment, and therefore could be used for paleoenvironmental reconstruction (Bose and Chafetz, 2009; Tang et al., 2011). Mainly two depositional settings favored the development of wrinkle structures have been suggested: offshore transition zones and foreshore environments (Mata and Bottjer, 2009; Noffke, 2009; Thomas et al., 2013). Since the formation of our wrinkle structures and sand cracks required exposure and dewatering, they much more likely formed in the foreshore environments (Bose and Chafetz, 2009; Tang et al., 2011). In the upper foreshore zone, owing to the long time exposure, commonly many types of sand cracks dominate this zone. Therefore, the wrinkle structures are most likely formed in the lower foreshore zone, with relatively short time for exposure and dewatering.

Although MISS, including wrinkle structures and sand cracks, were widespread in the Proterozoic (Hagadorn and Bottjer, 1997, 1999; Noffke et al., 2006; Schieber et al., 2007), they became restricted to highly stressed environments after the Cambrian (Hagadorn and Bottjer, 1999; Pruss et al., 2004; Sheehan and Harris, 2004; Chu et al., 2015). This has been attributed to the fact that development of microbial mats requires environments with low metazoan activity, e.g., burrowing or grazing (Pruss et al., 2004; Chu et al., 2015). Therefore, the abundant MISS in this study, indicate an environment with decreased grazing pressure, coupled with low-level bioturbation, which probably caused by hot climate and therefore high salinity in the intertidal environment during Jurassic. This interpretation finds general support in the lack of any clearly identifiable invertebrate trace fossils at the Yantan site. Likewise there is good evidence that many sauropodomorph dinosaur track assemblages are associated with deposits that represent semi-arid paleoenvironments.

Wrinkle structures are generally used as a collective term for a variety of small-scale crinkly texture on bedding surfaces, thus evoking the impression of a widespread participation of microbial mats during sedimentary deposition (Porada and Bouougri, 2007). Many mechanisms have been proposed to explain this type of MISS, such as loading and dewatering (Noffke et al., 2003), deformation by tide or storm current (Porada and Bouougri, 2007), and microbial mat growth (Gerdes et al., 2000). In this study, the random distribution of the long axes of wrinkle structures indicates that it is unlikely they originated from traction by tide, storm, or wind. The different density and morphology between local uplifted area (rich and large) and depression (scare and small) likely indicate that they were formed through dewatering and shrinkage. In the uplifted area, faster dewatering caused larger wrinkle structures, while in the topographically lower areas the situation is reversed due to the surfaces being wetter. The co-occurrence of sand cracks, possibly indicates that the genesis of these wrinkle structures was similar to that of sand cracks (Tang et al., 2011): as the exposure and dewatering continued further, sand cracks would be formed.

6. Conclusions

Sauropodomorph trackways from the Lower Jurassic Ziliujing Formation of Guizhou Province reveal at least 14 trackways of which the majority are attributable to the ichnospecies *Liujianpusshunan*, characterized by quadrupedal progression and outward pes rotation. The trackways are all subparallel indicating gregarious behavior. Two trackways indicate inward pes rotation, accompanied by elongate pes digit scratch marks and lack of manus imprints. Possible explanations of this phenomenon are: (1) switch from quadrupedal to bipedal progression and vice versa, (2) swimming behavior under fluctuating water levels, (3) presence of undertracks where the foot left traces of the toe tips on a deeper layer.

Distinctive microbially induced wrinkle marks indicate a stressed paleoenvironment that was probably semi-arid and not supportive of a diverse biota. This inference is consistent with other evidence that Lower Jurassic sauropodomorph tracks are often associated with semi arid paleoenvironments.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.gsf.2018.06.001.

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