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Diverse dinosaur ichnoassemblages from the Lower Cretaceous Dasheng Group in the Yishu fault zone, Shandong Province, China

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ABSTRACT

New dinosaur track assemblages were discovered recently in the Tianjialou Formation of the Lower Cretaceous Dasheng Group in Shandong Province, China. Theropods are represented by the trackways of two different medium-sized groups: (1) tridactyl tracks with a typical mesaxonic shape; (2) functionally didactyl tracks attributed to deinonychosaurian theropods. The latter report, the third from the Cretaceous of Shandong Province, enlarges the global record of didactyl theropod tracks, until now sparsely documented from only a few locations in Asia, North America and Europe. A number of features in the dromaeosaur trackway suggest the assignment to cf. *Dromaeosauripus*. Several medium-sized trackways resemble the narrow-gauge, small manus ichnogenus *Parabrontopodus*, and one large trackway is characterised by a wide-gauge and large manus, similar to *Brontopodus*. This suggests the co-occurrence of two different sauropod groups. A further component in these ichnoassemblages is a tetradactyl morphotype and trackways of ornithischian affinity that are tentatively attributed to psittacosaurs.

1. Introduction

The famous Tanlu fault zone, which extends NNE–SSW for more than 3000 km, forms a conspicuous geological feature along the northeastern margin of the Asian continent (Zhang et al., 2003: Fig. 1A). A series of folded mountain systems and basins extends along the middle Tanlu fault zone, called the Yishu fault zone (along Zhucheng–Junan–Linshu–Tancheng) between the Shandong Province and the Jiangsu Province, in eastern China.

Extensive outcrops of Cretaceous strata, bearing abundant dinosaur tracks, were discovered in the Yishu fault zone. The localities that have so far been described include the Houzuoshan Dinosaur Park, Junan County, Shandong Province (Li et al., 2005a,b, 2007; Lockley et al., 2007, 2008), the Zhangzhuhewan tracksite, Zhucheng City, Shandong Province (Xing et al., 2010a), and the Nanguzhai tracksites, Donghai County, Jiangsu Province (Xing et al., 2010b). Additionally, several tracksites have been discovered in the Jiaolai Basin, eastern Shandong Province, such as the Huanglonggou tracksite from Zhucheng City (Li et al., 2011). This latter tracksite was excavated in 2010, and thousands of tracks were discovered.

The tracksites we describe here were also discovered in the Yishu fault zone. In 2005, a number of tracks were found by local quarry workers at Ji Mountain (in Chinese: Jishan) at the northern margin of the Maling Mountain (in Chinese: Malingshan) range, Linshu County, Shandong Province, approximately 24 km north of the Nanguzhai tracksites (Fig. 1A). At the end of 2010, the Linshu Land and Resources Bureau organised the protection and excavation of the Jishan tracksites. In 2011, the first author was invited by the Linshu Municipal Bureau to study dinosaur track material from the exposures of the area. In 2012, financed by the Qijiang International Dinosaur Tracks Symposium, a detailed study of the tracksite was carried out.

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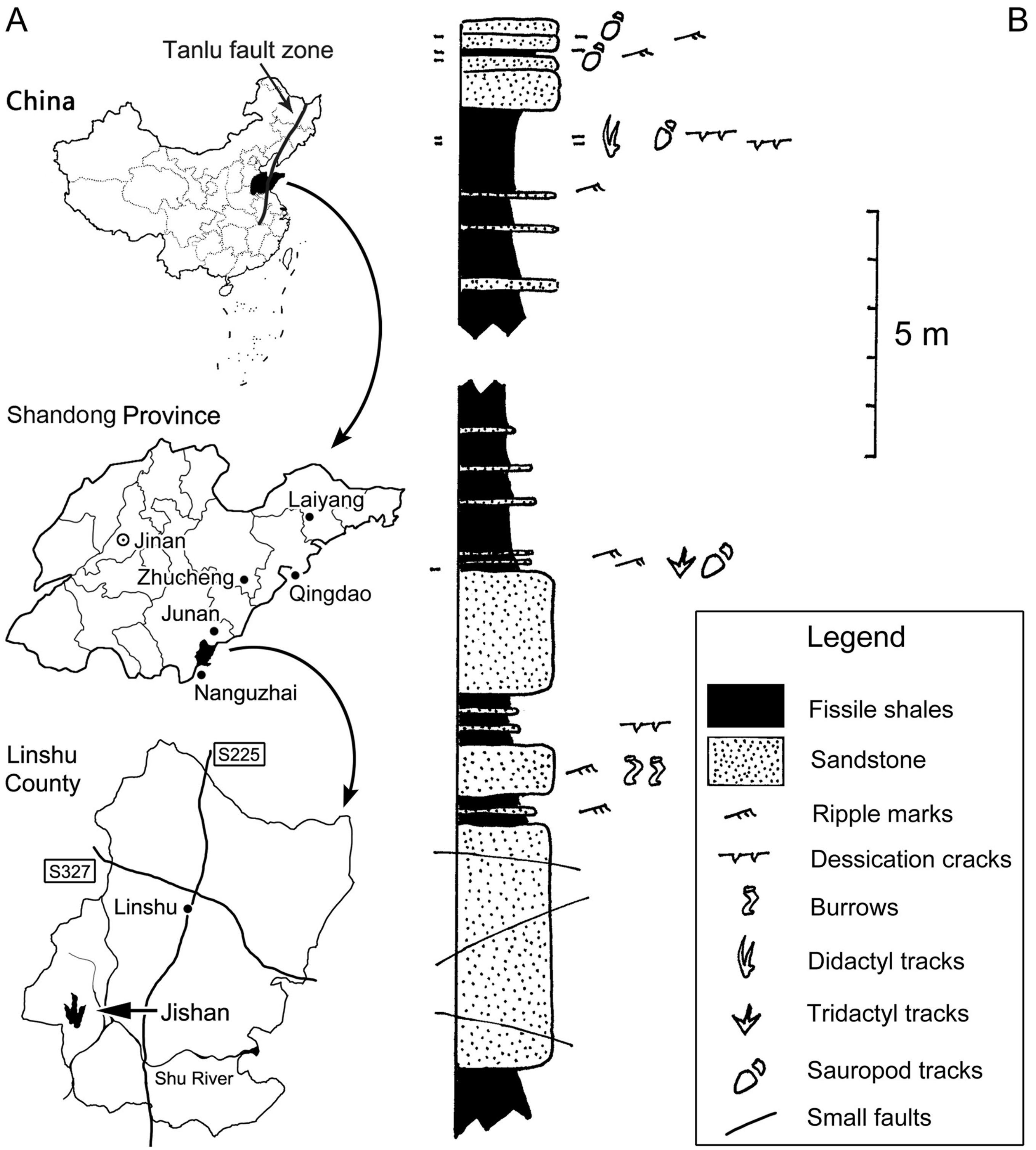

Fig. 1. Geographical setting (A) showing the location (footprint icon) of the Jishan dinosaur tracksites in Linshu County, Shandong Province, China. Stratigraphic section (B) of Lower Cretaceous strata as logged at the Jishan Site I with the position of the track-bearing levels.

2. Institutional abbreviations

CLS = Costalomo site, Burgos Province, Spain; HDT = Huaxia Dinosaur Tracks Research and Development Center, Gansu, China; LCU = Las Cuestas tracksite, Cameros Basin, Spain; LRH–dz = Li Rihui–Dasheng, Qingdao Institute of Marine Geology, China Geological Survey, China; LS = Linshu County Bureau of Land and Resources, Shandong, China; ZPAL = Institute of Palaeobiology of the Polish Academy of Sciences, Warsaw, Poland.

3. Geological setting

The Yimu fault zone and the Jialai Basin Cretaceous strata are divided into the Lower Cretaceous Laiyang and Qingshan groups and the Upper Cretaceous Wangshi Group (Tan, 1923). The Lower Cretaceous Dasheng Group was mainly developed from the Yimu fault zone. The succession consists of a sequence of alluvial fan-fluvio-lacustrine rocks mixed with marls and limestones, which are fractured due to tectonic activity. It is divided into (in ascending order): Malangou, Tianjialou, Siqiancun, and Mengtuan formations. The Dasheng and Qingshan groups are considered to be different contemporaneous facies resulting from the sedimentation of the same products (Liu et al., 2003). The recent field investigation concluded that the Lower Cretaceous Dasheng Group developed from the Yimu fault zone during an intensive subsidence stage, being subject to a set of lacustrine sedimentary sequences. The Siqiancun, Mengtuan and Xingezhuang formations (Liu et al., 2003) are probably different contemporaneous facies of sediments from the Malangou and Tianjialou formations. An alternative interpretation considers an independent origin (Kuang et al., 2013). Further studies are in progress.

The age of the Tianjialou Formation remains controversial. Sporopollen assemblages from the Tianjialou and Mengtuan formations were interpreted as being of Upper Cretaceous (Cenomanian–Turonian) age (Si, 2002). Based on conchostracans and the remains of the late Early Cretaceous ceratopsians *Psittacosaurus sinensis*, and *Psittacosaurus youngi* (Young, 1958; Zhao, 1962), Liu et al. (2003) considered the age of the Tianjialou Formation to be Barremian–Aptian. Liu et al. (2012) considered the tracksites of the Yishu fault zone as belonging to the late Lower Cretaceous Dasheng Group, the largest lacustrine deposit, the majority of which pertains to the Tianjialou Formation (Aptian–Albian, ~126–100 Ma in age). It is at least reliably established that the trace fossils of the Zhangzhuhewan–Linmu tracksite in Zhucheng (Xing et al., 2010a) are part of the Tianjialou Formation (Kuang et al., 2013), and this assignment is adopted in this paper. The dominant sediments of the Tianjialou Formation are a series of small bodies of lacustrine deposits (Liu et al., 2003), where tracks are often associated with ripple marks.

The tracks were discovered on several sites located in the Jishan Provincial Geopark, Caozhuang Town, Linshu County, Shandong Province (Fig. 1A). The tracksites are located close to each other and exhibit several track-bearing levels, which all belong to the same stratigraphic sequence of the Dasheng Group.

Site I (118°29′41.08″ E, 34°49′8.66″ N), which is the largest, comprises at least four layers of sandstone with dinosaur tracks on top, including a deinonychosaurian trackway, tridactyl theropod tracks, a large sauropod trackway and a medium-sized quadruped trackway also of probable sauropod affinity (Fig. 1B). Site II (118°29′51.98″E, 34°48′58.62″N) is situated 415 m southeast of Site I, and includes a tridactyl theropod trackway and several sauropod trackways. Sites III (118°29′50.41″E, 34°48′57.30″N) and IV (118°29′48.44″E, 34°48′57.62″N) are situated 60 m and 90 m southwest of Site II, respectively. These sites exhibit a high density of sauropod tracks and high degree of overprinting, making the identification of trackways a difficult task. Site V (34°49′15.81″E, 118°29′41.16″N) has several trackways of quadrupedal dinosaurs and a poorly-defined dinosaur trackway with tetradactyl tracks. Sites VI and VII are not discussed in further detail due to the lack of useful information. Site VIII (34°49′37.24″N 118°29′46.69″E) has two wide-gauge sauropod trackways and one quadrupedal dinosaur trackway of unknown affinity.

Because the reported tracksites from Jishan have all been discovered in recent years by road construction and mining, they were only exposed to recent weathering for a short time period. Therefore, in some tracks, the fills are amalgamated to the track, making it difficult to separate them mechanically. Nevertheless, several well-preserved track casts were recovered.

4. Methodology

At all sites tracks were examined by a majority of authors, photographed and, in many cases, outlined with chalk. At several sites with steeply inclined surfaces, ladders and mechanical devices ("cherry pickers") were used to allow researchers to access the tracks without climbing. All trackways and track assemblages were traced on transparent plastic and acetate sheets.

Using a combination of photographs and tracings, maps of the more important surfaces and trackway segments were produced. Standard measurements including track length, track width, dimensions of individual toe impressions, footprint rotation, step, stride, pace angulation and trackway width were obtained directly from trackways as well as from tracings.

Individual tracks and trackways were given prefix designations which identify the various Linshu sites (LSI, LSII etc.,) followed by an abbreviation for the trackway (D for didactyl, S for sauropod, T for tridactyl, O for ornithischian) designations for individual trackways (S1, S2 etc.) and tracks (R1, L1 etc. for right and left pes in the case of bipedal trackways and RP1 and RM1 to distinguish manus and pes in the case of quadrupedal trackways). As far as possible all relevant track labels are shown on the accompanying maps and diagrams.

For the quadrupedal trackways, gauge (trackway width) was quantified for pes and manus tracks by using the ratio between the width of the angulation pattern of the pes (WAP) or manus (WAM) and the pes length (ML) or manus width (MW), respectively (according to Marty, 2008; Marty et al., 2010). In the case of manus tracks, the manus width is used instead of its length because manus tracks are often incomplete due to overprinting by the subsequent pes or due to a more digitigrade impression; for this reason, the manus length is subjected to a high variability, and the width represents the size of the manus more accurately than the length (Marty et al., 2010). The (WAP/ML)-ratio and (WAM/MW)-ratio were calculated with the Pythagoras' theorem from pace and stride length, assuming that the width of the angulation pattern intersects the stride under a right angle and approximately at the midpoint of the stride (Marty, 2008, p. 37). While these data are not based on a direct measurement of the width of the angulation pattern in the field, the obtained values are a good approximation for the trackway gauge. If the [WAP/ML]-ratio equals one (i.e., ML = WAP), the pes tracks are likely to touch the trackway midline. If the ratio is smaller than one, tracks intersect the trackway midline, which corresponds to the definition of narrow-gauge (see Farlow, 1992). Accordingly, a value of 1.0 separates narrow-gauge from medium-gauge trackways, whereas the value 1.2 is fixed between medium-gauge and wide-gauge trackways, and trackways with a value higher than 2.0 are considered as very wide-gauge (Marty, 2008).

Due to the patchiness of the outcrops and the widespread visible tectonic features such as folding and faults, it was not possible to correlate track-bearing surfaces between the various outcrops (Sites I–V and VIII) described here. However a section was measured at Site I, which has the most extensive outcrops as well as four track-bearing levels (Fig. 1B).

5. Description of tracks and trackways

5.1. Didactyl tracks

Description

One single trackway, composed of five consecutive pes tracks, catalogued individually as LSI-D1-R1, L1, R2, L2, R3 (Figs. 2 and 3; Table 1). The original trackway remains on Site I, where it is even possible to excavate more tracks at the end of the trackway. A

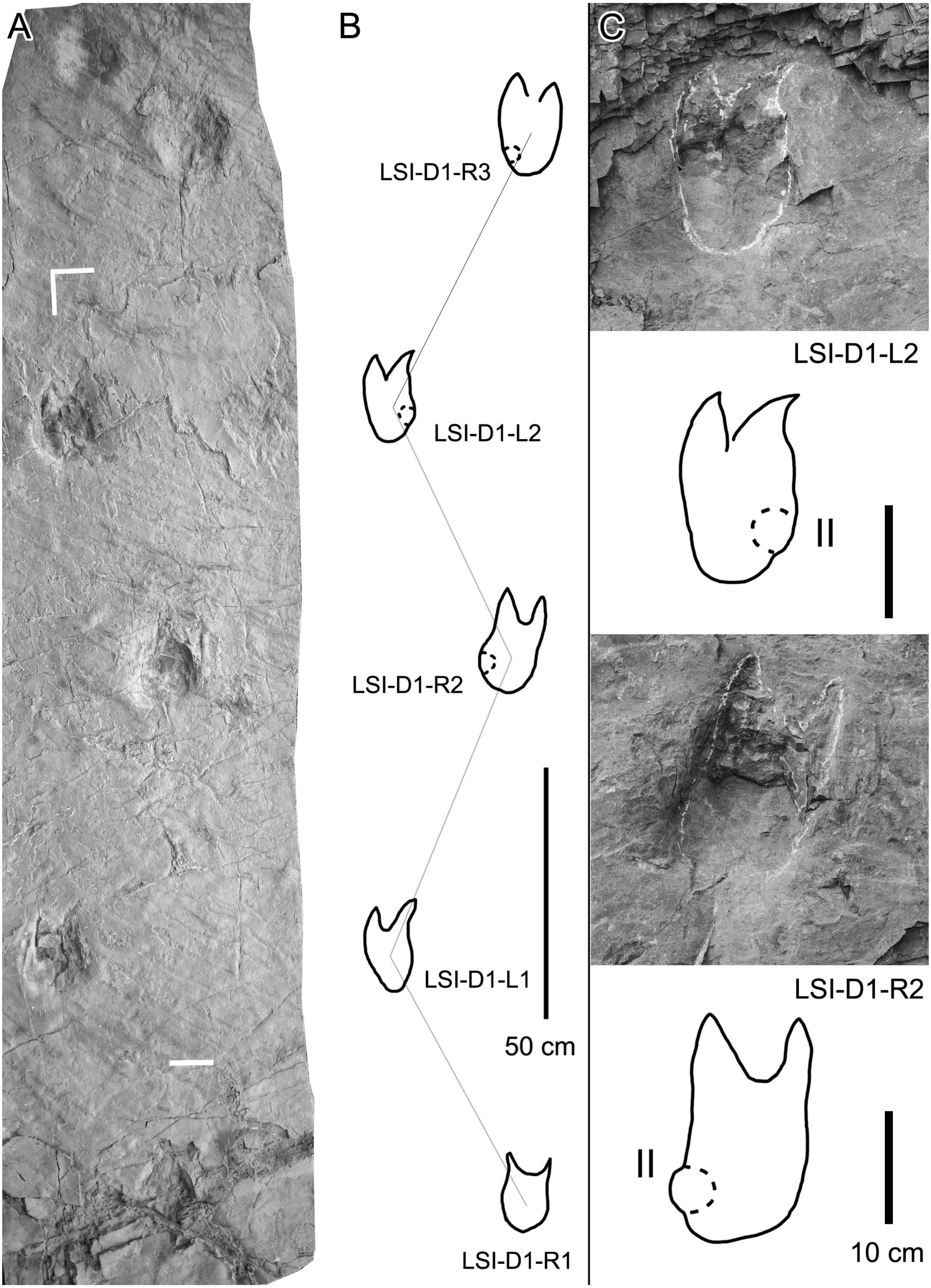

Fig. 2. Didactyl theropod tracks from the Jishan tracksite I. A and B overview with photograph and interpretative outline drawing of the five successive pes tracks. C. Detailed photographs and interpretative outline drawings. Note the recurrent, small notch interpreted as digit II.

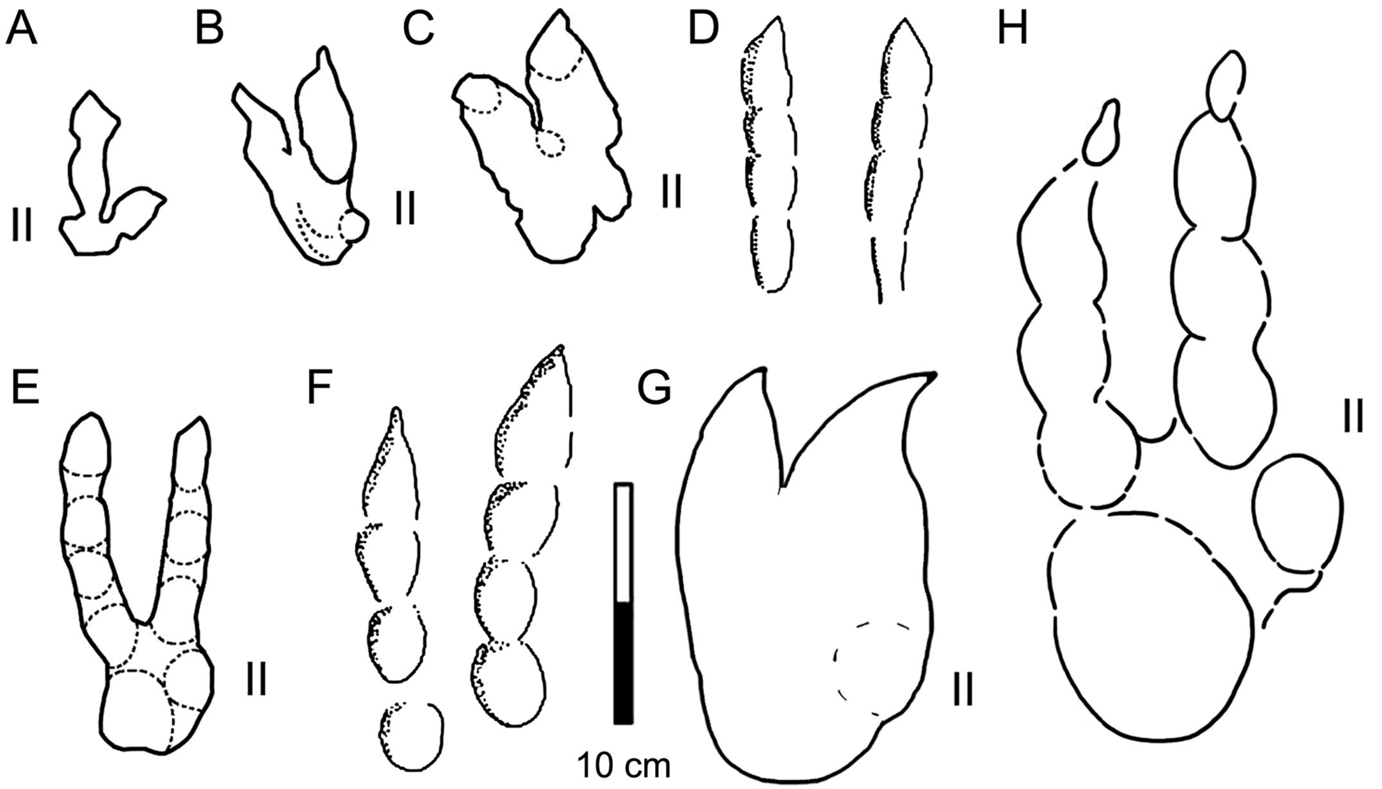

Fig. 3. Interpretative outline drawings of dromaeopodid ichnotaxa drawn to the same scale. A. *Menglongipus* (Xing et al., 2009); B. *Velociraptorichnus* from Shandong (Li et al., 2007); C. *Velociraptorichnus* (Zhen et al., 1994; Xing et al., 2009); D. *Dromaeosauripus jinjuensis* (Kim et al., 2012); E. *Dromaeosauripus yongjingensis* (Xing et al., 2012); F. *Dromaeosauripus hamanensis* (Kim et al., 2008); G. Jishan didactyl tracks (this study); H. *Dromaeopodus shandongensis* (Li et al., 2007).

replica was made by the Linshu Land and Resources Bureau, Shandong Province.

The pes tracks (19.5 cm length on average) are elongate with a rounded and quite deep (mean 3.8 cm, range 3–4.4 cm) depression (concave epirelief) comprising the central area and the heel and constituting the major part of the track. It is connected with two slender, elongated comparatively shallow impressions of digits III and IV. The short, round impression of digit II is best visible in LSI-D1-R2 and LSI-D1-L2. Compared with digits III and IV, the impression of digit II is more shallow and indistinct. Digit II impressions are partially embedded within the impression of digit III at its proximomedial edge. The impressions of digits III and IV are nearly parallel, those of digit III are more robust and longer than those of digit IV. Digital pads are indistinct or completely absent, claw impressions sharp and turned inward on both digit III and digit IV. The large metatarsophalangeal region is semicircular and not separated from the digits by a distinct border. The mean outward rotation of the tracks is 14° (LSI-D1-R1–L2: 15°, 13°, 14°, 17°, 11°). The trackway LSI-D1 shows no evidence of manus impressions or tail traces.

Ichnotaxonomy and trackmaker identification

The two digit impressions are interpreted as traces of digits III and IV, and this clearly indicates a deinonychosaurian affinity of this trackway (Li et al., 2007).

Deinonychosaurian ichnotaxa (Fig. 3) comprise four ichnogenera (*Velociraptorichnus*, *Dromaeopodus*, *Dromaeosauripus* and *Menglongipus*). A considerable size range is represented by these

Table 1
Measurements (in cm) of the dinosaur tracks from the Jishan tracksites.

Number	ML	MW	LD II	LD III	LD IV	II–III	III–IV	II–IV	SL	PL	PA	L/W
LSI-D1-R1	17.1	10.0	–	3.8	4.0	–	29°	–	110.7	55.1	134°	1.71
LSI-D1-L1	19.3	10.6	–	4.3	4.5	–	24°	–	110.5	65.2	135°	1.82
LSI-D1-R2	21.1	11.2	–	5.0	6.3	–	22°	–	118.0	55.5	135°	1.88
LSI-D1-L2	18.3	10.5	–	4.5	4.9	–	26°	–	–	72.0	–	1.74
LSI-D1-R3	21.5	12.0	–	4.7	5.3	–	22°	–	–	–	–	1.79
Mean	19.5	10.9	–	4.5	5.0	–	25°	–	113.0	62.0	135°	1.79
LSII-T1-L1	26.4	22.5	9.2	15.6	–	36°	34°	70°	180.0	104.0	169°	1.17
LSI-T20	28.3	24.0	11.2	21.2	14.8	43°	35°	78°	–	–	–	1.18
LSV-O2-T1	19.2	18.4	–	–	–	–	–	–	108.1	58.4	171°	1.04
LSV-O2-T2	27.7	20.0	–	–	–	–	–	–	–	50.0	–	1.39
LSV-O2-T3	19.2	12.5	–	–	–	–	–	–	–	–	–	1.54

Abbreviations: R/L: Right/Left; LD I: length of digit I; LD II: length of digit II; LD III: length of digit III; LD IV: length of digit IV; ML: maximum length; MW: maximum width*; PA: pace angulation; PL: pace length; SL: stride length; II–III: angle between digits II and III; III–IV: angle between digits III and IV; II–IV: angle between digits II and IV; L/W: maximum length/maximum width. *Dinosaur tracks measured as distance between the tips of digits II and IV (LSIT1.1–1.4 between the tips of digits II and III).

tracks: they include small sized-tracks (mean pes length 10 cm) such as *Velociraptorichnus sichuanensis* (Zhen et al., 1994; Xing et al., 2009), *Velociraptorichnus* isp. (Li et al., 2007), *Menglongipus sinensis* (Xing et al., 2009), and *Dromaeosauripus jinjuensis* (Kim et al., 2012); medium-sized tracks (mean pes length 15 cm) such as *Dromaeosauripus hamanensis* (Kim et al., 2008), *Dromaeosauripus yongjingensis* (Xing et al., 2012), and 21 cm-long didactyl tracks from Utah labelled *Dromaeopodus* (Cowan et al., 2010; Lockley et al., 2013); large-sized tracks (mean pes length of about 30 cm) such as *Dromaeopodus shandongensis* (Li et al., 2007).

Other didactyl tracks of uncertain affinity include *Paravipus didactyloides* from the Middle Jurassic of Niger (Mudroch et al., 2011), and a didactyl footprint from the Lower Jurassic of Morocco (Ishigaki and Lockley, 2010) that may be an extra-morphological variant of a tridactyl track: see Lockley et al. (2013) for review. *Paravipus* is no deinonychosaurian track (Lockley et al., 2013) and may be a swim track (Milner A.R.C. pers. comm.).

Generally, the Jishan tracks are similar to *Dromaeosauripus* (Kim et al., 2008, 2012; Xing et al., 2012) based on the following characteristics: (1) similar size in comparison with *D. yongjingensis* and *D. hamanensis*; (2) claw marks large and discernible in comparison with *D. jinjuensis* and *D. hamanensis*; (3) digit II present only as an inconspicuous posteromedial trace associated with the impression of the proximal part of digit III, see *D. yongjingensis*; (4) large semi-circular, metatarsophalangeal region, similar to *D. yongjingensis*.

The lack of distinct digital pad traces and the large metatarsophalangeal portion, which is not separated from the digit traces by a distinct border, can be explained by their preservation as deep tracks in fine water-saturated lacustrine sediment. Thus, they do not show much anatomical detail when compared to shallower tracks. Because these tracks are quite deep, the central part of the track and the heel area is strongly rounded and morphologically rather indistinct.

When compared with other *Dromaeosauripus* tracks the most distinctive features of the Jishan specimens are the large, bulbous posterior or metatarsal–phalangeal impressions. However as these appear to be mostly extramorphological features, their ichnotaxonomical significance is uncertain. Likewise the low pace angulation may also be due to progression over a soft substrate. Thus we refer to the Jishan tracks only as cf. *Dromaeosauripus* isp. In comparison, *D. yongjingensis* from Gansu lacks sharp claw marks, and has a higher mean pace angulation (162°). *D. jinjuensis* and *D. hamanensis* both lack a well-defined metatarsophalangeal pad, and have larger mean pace angulations (180° and 175°, respectively), and therefore differ from the Jishan tracks.

Compared with *Dromaeopodus shandongensis* (Li et al., 2007), the largest known dromaeosaur tracks, the smaller Jishan tracks show less defined digital and metatarsophalangeal pad traces. In the former, the trace of digit II is more distinctly medially offset. The pace angulation (134.5°) is again much lower than in *Dromaeopodus* (170°).

With a mean pes length of 19.5 cm, the Jishan didactyl tracks are in the medium size range of known deinonychosaurian tracks, and thus significantly differ from *Velociraptorichnus* and *Menglongipus* tracks, which are smaller in size; the mean pes length of the *Velociraptorichnus sichuanensis* type being 11 cm, that of the *Menglongipus sinensis* type being 6.3 cm (Xing et al., 2009).

The relative stride length ($SL/h = 1.32$, SL, stride length; h, hip height) indicates that the Jishan trackmaker was walking, and using the hip height conversion factor 4.6 (Thulborn, 1990) and Alexander's (1976) equation, a velocity of 1.15 m/s can be calculated. This is faster than that of *Dromaeosauripus yongjingensis* (0.75 m/s, Xing et al., 2012), slower than that of *Dromaeopodus shandongensis* (1.63 m/s; Li et al., 2007; Kim et al., 2008), and much slower than *Dromaeosauripus hamanensis* (4.86 m/s, Kim et al., 2008).

Amongst deinonychosaurian trackways, the Jishan specimen has the lowest pace angulation (134.5°), and also shows the deepest imprints. As inferred above, this could be related to a facultative behaviour under soft substrate conditions. However, we cannot rule out the possibility that the gait could also reflect particular anatomical or locomotor characteristics of the trackmaker.

5.2. Tridactyl tracks

Description

An isolated natural mold at Jishan Provincial Geopark Site I catalogued individually as LSI-T20 (Fig. 4D; Table 1), and a trackway composed of three consecutive natural molds (with partial natural casts) at Jishan Provincial Geopark Site II, catalogued individually as LSII-T1-L1–L2 (Fig. 4A–C and 5; Table 1). The original tracks all remain in the geopark, while replicas have been recovered and are deposited in the Linshu Land and Resources Bureau, Shandong Province.

The single trackway LSII-T1 at Site II shows three successive tridactyl tracks. Of these, LSII-T1-L1 (Fig. 4A–C) is the best preserved with well-defined pad impressions. A few metatarsophalangeal pads are preserved in LSII-T1-L2, while LSII-T1-R1 is seriously damaged. The mean pace angulation of 169° indicates a trackmaker with a narrow stance typical of theropods. The isolated track LSI-T20 (Fig. 4D) is well preserved, and is similar to LSII-T1-L1 regarding general track morphology.

Generally, digit III is the longest, followed by digits IV and II. Sharp claw impressions are visible, and those on digit III and IV are quite robust. The digital pad impressions and the metatarsophalangeal region are indistinct. The digits have a high divarication angle with the mean divarication angle between digits II and III being higher than between digits III and IV.

LSII-T1-L1 is preserved with a partial natural cast of digit III that remained in the concave epirelief (Fig. 4A). Also, it shows lateral scratch lines at the medial and lateral sides that were produced when individual scales dragged through the sediment. Remarkably, the natural cast of digit III preserved with a 3D cast of the claw (Fig. 4A–C). The border between the trace of the sheath of the claw and the pad is very distinct. The claw is 5.1 cm in length and approximately 2 cm at its widest point. An elongated, round, shallow concavity was observed in medial view. Medially, the scale scratch lines near the claw are quite deeply imprinted, averaging 2.5 mm in width and in a density of 3–4 lines per centimetre. The scale scratch lines near the preserved metatarsophalangeal pad II are considerably narrower, averaging 1.5 mm in width. They occur in a density of 4–5 lines per centimetre. Laterally, the scale scratch lines average 1.2 mm in width, and they occur in a density of 6–7 lines per centimetre. This likely indicates the general size (diameter) of scale traces on the trackmaker's foot.

It is important to note that striations on SII-T1-L1 (Fig. 4A) occur on the sides of the sandstone fill (or cast) representing the wall of the track created by the registration of digit III. This is common in casts. However in this case part of the cast remained in the footprint. This means we can see the foot-sediment contact both on the floor and the wall of the track. It also clearly implies that the track was made by penetrating through a layer of mud that was deposited above the presently exposed sandstone bedding plane and that is now eroded (Fig. 4E). On the floor of the track, the foot pushed the mud downward to the contact with the underlying sand: i.e., to the sand–mud bedding plane interface. However, the wall of the tracks shows a different interface where the foot slid through the mud leaving striations above the lower bedding plane. When the track was subsequently filled up by sand, a new interface was created between the mud and the overlying sand. Subsequent erosion has removed the mud except for a thin veneer at the lower sand mud interface that can be seen as a chocolate-brown mud-

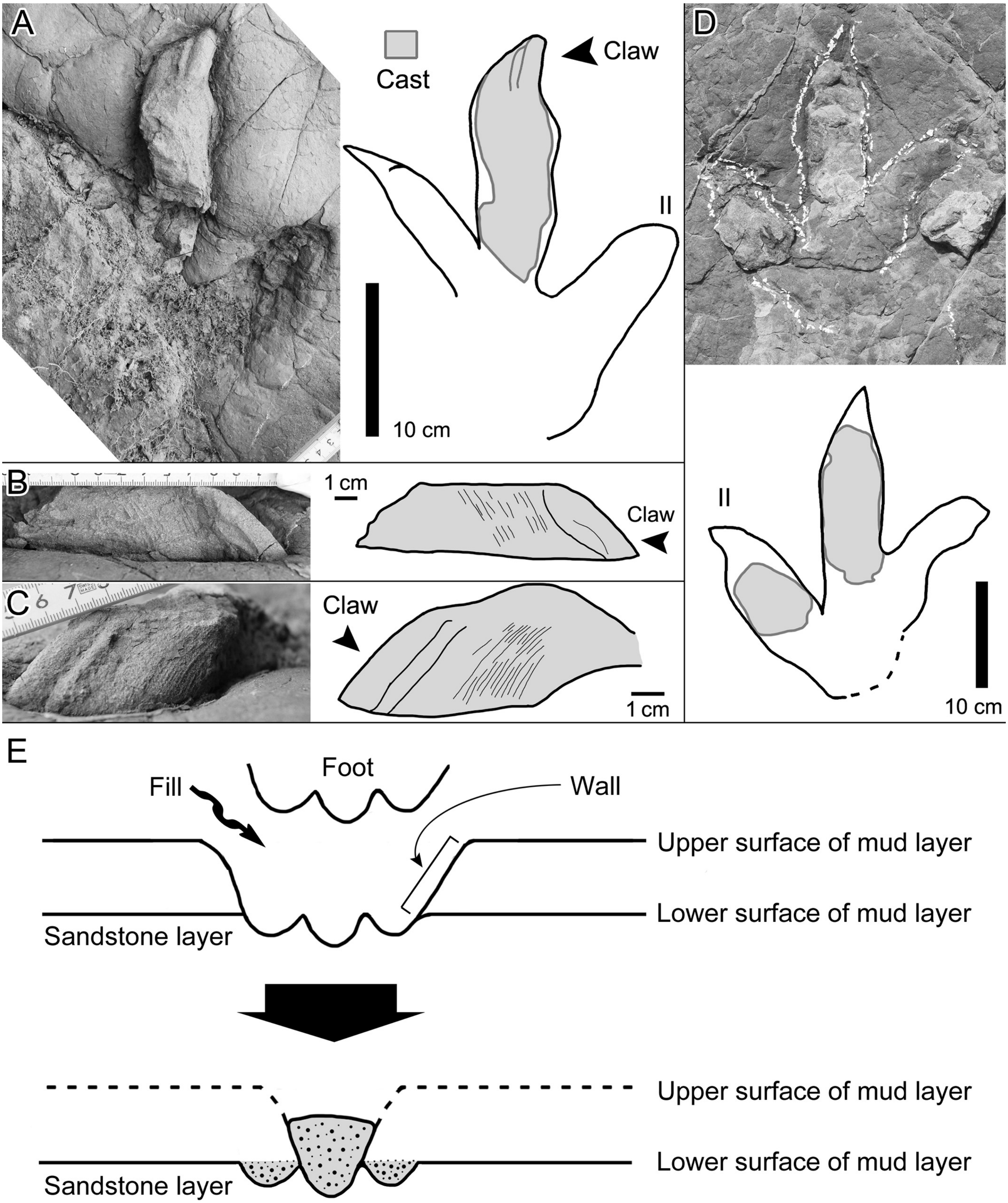

Fig. 4. Tridactyl theropod tracks from the Jishan tracksite I and II. A. Photograph and sketch of left pes track L1 of trackway LSII-T1. B and C. Photographs and sketches showing details of A with claw impression and lateral scratch lines. D. Photograph (track outlined with white chalk) and interpretative outline drawing of isolated pes track LSI-T20. E. Schematic diagram showing how slide marks were preserved and cast in sandstone on the walls of a mud layer that has since eroded away: see text for details.

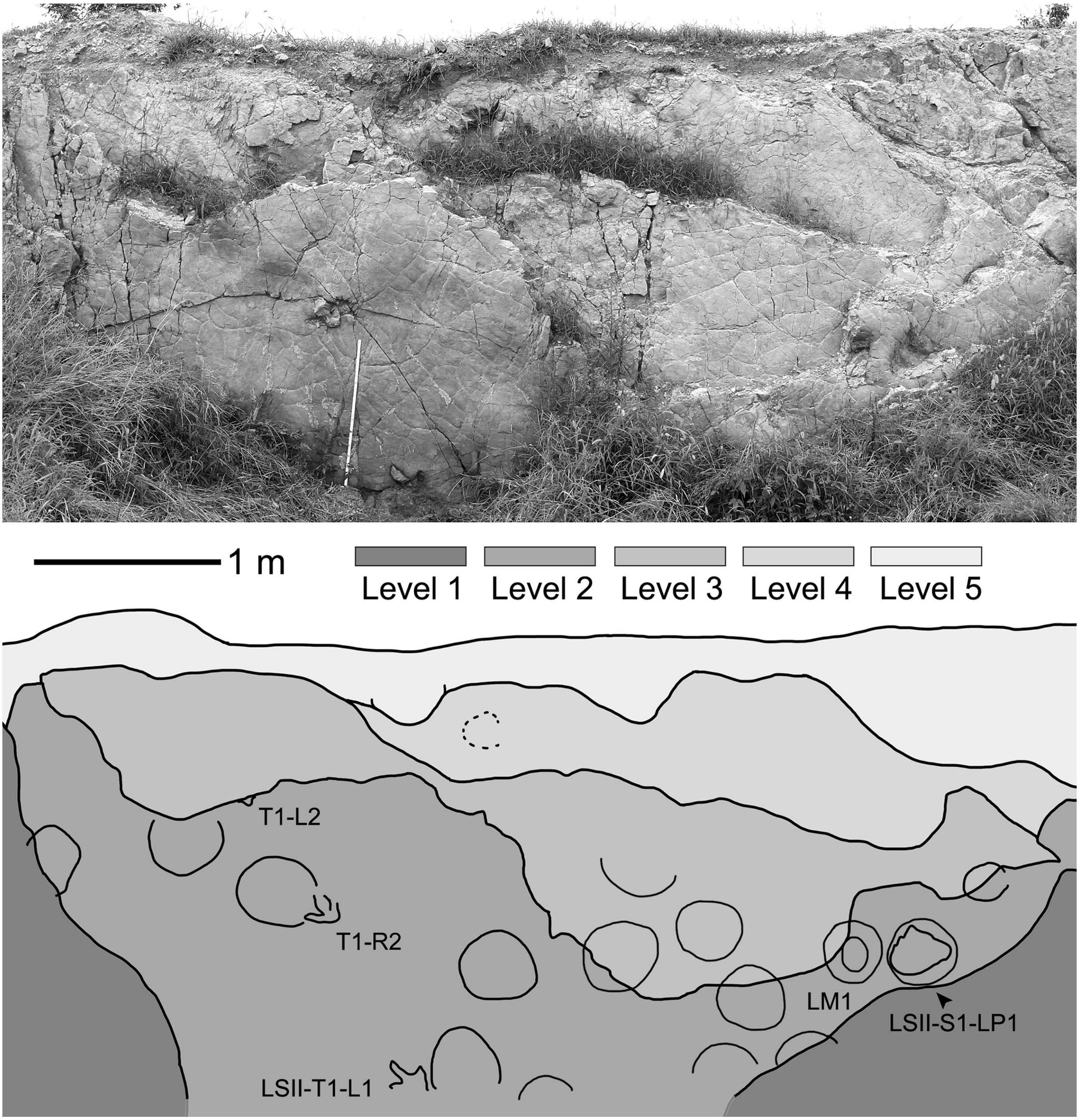

Fig. 5. Photograph and interpretative outline drawing of different levels at Jishan Tracksite II with a sauropod (LSII-S1) and theropod (LSII-T1) trackway.

cracked surface presently exposed as "background" around the track and between the digit traces. This leads to the conclusion that we can simultaneously see the "lower" sand–mud interface (the exposed background bedding plane) and a representation (i.e., cast) of the surface within the mud layer that once filled up became the "upper" mud–sand interface where the track was registered on mud now removed by erosion. The two interfaces (i.e., the upper and lower surface of the mud layer) coincide under the track where the foot pushed the mud down to the lower interface. However, where the striations are preserved as casts on the track wall, the upper interface between mud and overlying sand is preserved. This means that although the mud layer is *not* preserved, and may originally have been compacted considerably, it is possible to infer the original thickness of the mud from the depth of the sandstone cast, which due to the grain–grain contact in sand deposits cannot have been significantly compacted. Thus, we infer that the mud in which the theropod originally stepped was at least 3 cm deep (Fig. 4E).

Ichnotaxonomy and trackmaker identification

Because of the small number of tracks, an assignment to a particular ichnotaxon cannot be given. However, the tracks are similar to *Therangospodus* from the Upper Jurassic of North America and Asia and the Lower Cretaceous of Europe (Lockley et al., 2000) based on (1) their medium size (26 cm in length), (2) the lack of distinct phalangeal pads, and (3) the narrow trackway pattern with a mean pace angulation averaging 170°.

In the Jishan tridactyl tracks, the hypex between digits II and III is more posteriorly positioned compared with that between digits III and IV, which is unusual for theropod tracks. The opposite is the case for example in *Chapus lockleyi* (Li et al., 2006: Fig. 2). Theropod tracks that are similar to LSII-T1-L1 and LSI-T20 in this respect include *Siamopodus khaoyaiensis* (Early Cretaceous, ?Neocomian), and a large trackway from Phu Faek (Early Cretaceous, ?Berriasian), Thailand (Lockley et al., 2006: Fig. 7). Other tridactyl theropod tracks from China, comparable to those from Jishan are also known from Junan (Li et al., 2005a) and from the Nanguzhai (Xing et al., 2010b) and Huanglonggou (Zhuchang, Shandong) tracksites (Li et al., 2011) (see Fig. 1 for location). The latter comes from the Dasheng Group.

The Nanguzhai tracks are poorly preserved. They have a mean length of 22.8 cm, relatively widely-divaricated digits (mean 45°), and a mean pace angulation of 171.5° (Xing et al., 2010a,b). The unnamed large theropod tracks from the Huanglonggou tracksite are also sturdy, but they have an oval metatarsophalangeal pad of digit IV (Li et al., 2011). The Junan specimens lack detailed descriptions, but they have a similar size-range (15–26 cm in length; Li et al., 2005a) and shape with robust digits. The Junan theropod tracks can probably be referred to *Asianopodus* (R.H. Li, pers. comm.).

The direction of scratch lines of LSII-T1-L1 conforms to entry striations of digits when the pes moved forward and deeper into the substrate (Gatesy, 2001). Similar scale scratch lines are also found in theropod tracks from other tracksites (e.g., Avanzini et al., 2011). The relative amount of scratch lines has probably no relation to the track size (Xing et al., 2013b). It seems that the tip of the claw of LSII-T1-L1 was not sharp, probably having been worn down. This is common for modern terrestrial birds, such as ostriches (ref). A similar detailed preservation of claws is rare but can be observed in specimens (CLS-F-6 and CLS-F-7) from the Pinilla de los Moros Formation (Upper Hauterivian–Lower Barremian), Burgos, Spain (Huerta et al., 2012).

5.3. *Trackways and isolated tracks of large quadrupeds*

Description

Five complete pes–manus track pairs of a trackway at Jishan Provincial Geopark Site I, are catalogued as LSI-S1-RM1–RM3, LP2–RP3 (Fig. 6; Table 2). Another trackway from a different level at Site I comprises what we interpret as three pes–manus undertrack pairs catalogued as LSI-S9-RM1–RM2, LP2–LP3 (Fig. 7; Table 2), and one isolated pes undertrack catalogued as LSI-T21 (Fig. 7; Table 2). Additionally, there are a number of isolated tracks that cannot be attributed to distinct trackways at Jishan Provincial Geopark Site III (Fig. 8) and Site IV, the latter being better preserved. Two more trackways (LSVIII-S1 and S3) are found at Jishan Provincial Geopark Site VIII (Fig. 9). All tracks remain in the Geopark.

The LSI-S1 tracks show two different areas: the internal portion consists of the true track *sensu stricto*, while the external part is marked by sediment displacement rims around the track, as shown in Fig. 6. The length:width ratios of the LSI-S1 tracks are very similar. In LSI-S1, the pes track LSI-S1-LP3 and the manus track LM3 are the best-preserved tracks.

The manus track LSI-S1-LM3 is sub-circular in shape and lacks discernible claw marks. A circular mark situated laterally to the track could correspond to the delineations of the foot callosity of digit V. The metacarpophalangeal pad region is concave.

The pes track LSI-S1-LP3 is of oval shape. The distance to the manus track LM3 is 21 cm. Digits I and II have well-developed claw marks, digits III and IV have small nail marks or depressions made by small unguals or foot callosities. Digit V is indicated by a small lateral lobe. The three inner claw marks are directed laterally. The metatarsophalangeal pad region is smoothly curved.

Other pes–manus pairs from the LSI-S1 trackway generally have a morphology similar to that of LP3 and LM3. The other manus tracks are just sub-circular impressions, while the pes tracks still have discernible claw marks on digits I and II.

The manus tracks are rotated outward relative to the trackway axis by an average of 33.6° (with a range between 24° and 46°); this value is larger than the outward rotation of the pes tracks (29.3° on average with a range between 21° and 38°). The inner trackway width between the manus tracks and between the pes tracks ranges from 40.5 to 51.5 cm and 14.6 to 18.3 cm, respectively.

In addition, two trackways (LSVIII-S1 and S3) at Jishan Provincial Geopark Site VIII are both composed of 6 complete pes–manus track pairs (Fig. 9). These tracks have a general morphology similar to the tracks of the LSI-S1 trackway. However, due to the inaccessibility of the site, the trackway parameters could not be measured in the field.

The LSI-S9 and S10 trackways (Fig. 7) are located at the top of the Site I stratigraphic sequence (Fig. 1). These trackways are preserved in association with ripple marks and are relatively shallow in comparison with other trackways from Site I. They show very few morphologic characteristics, and are therefore considered to be undertracks that formed in a well-laminated sediment. In support of this interpretation it is interesting to note that the ripple marks are less well defined than they are in the surrounding sediment. This is consistent with the undertrack interpretation, suggesting that the transmitted force of track registration on a higher surface blurred or partially obliterated the ripple marks on the buried undertrack surface. The track sizes of LSI-S9 equal the external diameter of LSI-S1 (see Table 2). This suggests that they were probably made by a similar-sized trackmaker.

Furthermore, there was an isolated pes impression LSI-T21, near the LSI-S9 trackway (Fig. 7A), with a partial natural cast showing a convex anterior end that may represent a digit claw mark. LSI-T21 is the largest track from this locality, being approximately 79 cm in length.

A number of other poorly-preserved tracks or undertracks similar to those of LSI-S9 are common at sites I, III and IV, however, they cannot all be attributed to distinct trackways. The tracks at site III (Fig. 8) are more scattered and less well preserved than those on site IV. There are several possible trackways at this site, including the better-preserved tracks of this locality.

Ichnotaxonomy and trackmaker identification

The pes and manus morphology and trackway configuration of the LSI-S1 trackway is typical for sauropod trackways. This trackway is clearly wide-gauge, as is also indicated by the (WAP/ML)-ratio (Table 2) and the track morphologies are consistent with what is known of most Cretaceous sauropod trackways (Lockley, 1999, 2001).

Most wide-gauge sauropod trackways from China have been referred to the ichnogenus *Brontopodus* (Lockley et al., 2002). The large-sized sauropod tracks are most similar to *Brontopodus* based on the following features: wide- (or medium-) gauge; a ratio of manus to pes size of 1:1.5, U-shaped manus tracks, pes tracks longer than broad with large, outwardly directed claw marks on digits I–III, a small trace of digit IV and a small callosity or pad mark *representing* digit V. Because of their rather low heteropody (manus:pes = 1:1.5) the large Jishan sauropod tracks are similar to *Polyonyx gomesi* with a low heteropody of 1:2 (Santos et al., 2009;

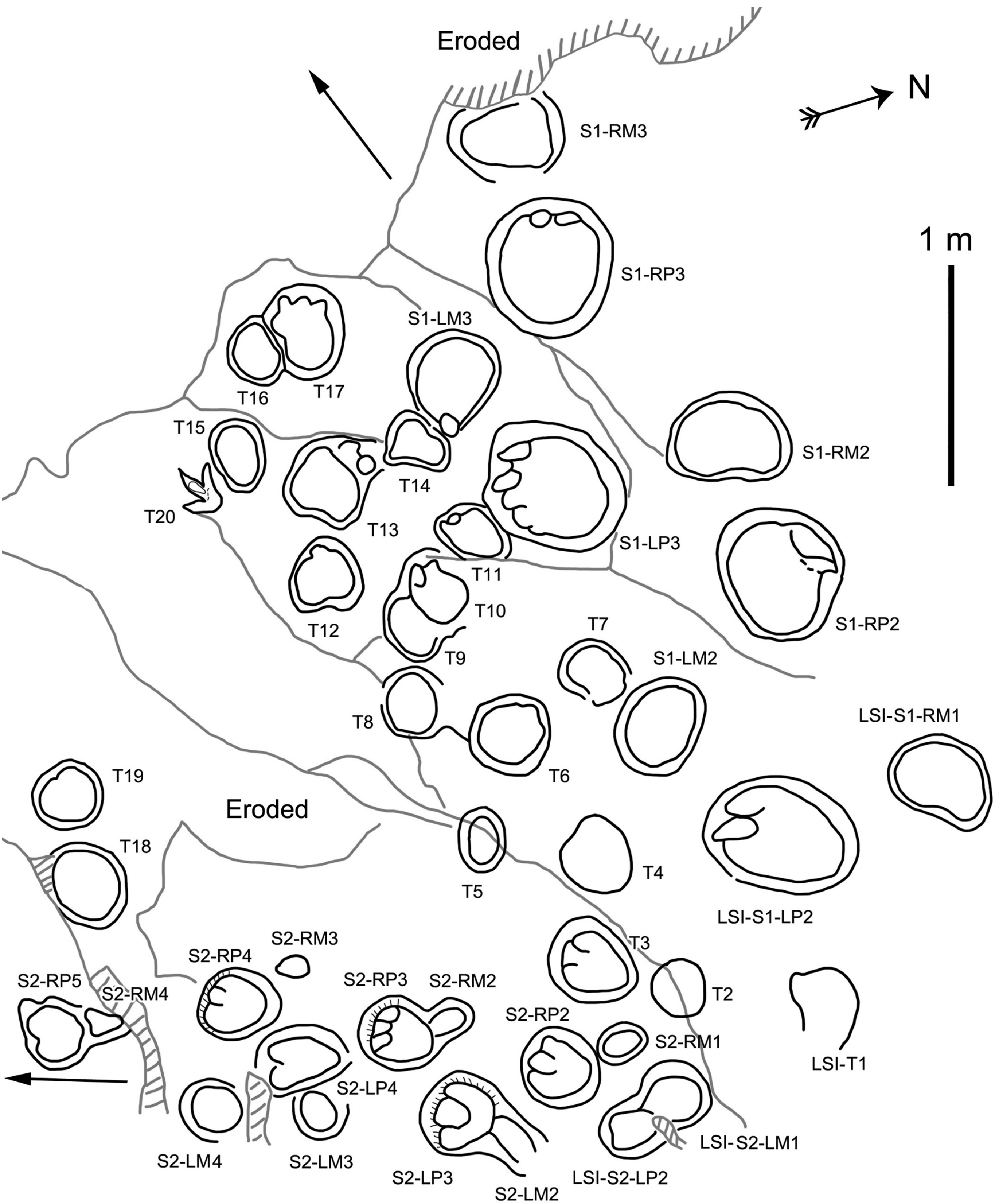

Fig. 6. Interpretative outline drawing of track-bearing level at Jishan tracksite I with trackways and isolated tracks of large sauropods, medium-sized ?sauropods and theropods.

Table 2
Measurements (in cm, except PA in degrees) of the large- and medium-sized quadrupedal trackways from the Jishan tracksites.

Number	ML	MW	SL	PL	PA	L/W	WAP	WAM	WAP/ML	WAM/MW
LSI-S1-RM1	28.8	42.0	173.0	124.2	88°	0.69	–	89.1	–	2.1
LSI-S1-LP2	56.0	38.8	180.5	115.7	108°	1.44	72.4	–	1.3	–
LSI-S1-LM2	28.5	37.4	177.9	125.7	91°	0.76	–	88.8	–	2.4
LSI-S1-RP2	48.4	46.4	175.3	107.5	110°	1.04	62.2	–	1.3	–
LSI-S1-RM2	29.5	45.6	174.5	124.3	89°	0.65	–	88.5	–	1.9
LSI-S1-LP3	55.5	44.4	–	105.0	–	1.25	–	–	–	–
LSI-S1-LM3	33.5	38.8	–	115.3	–	0.86	–	–	–	–
LSI-S1-RP3	52.0	47.0	–	–	–	1.11	–	–	–	–
LSI-S1-RM3	29.0	42.0	–	–	–	0.69	–	–	–	–
Mean-M	29.9	41.2	175.1	122.4	89°	0.73	–	88.8	–	2.2
Mean-P	53.0	44.2	177.9	109.4	109°	1.21	67.3	–	1.3	–
LSI-S2-LM1	20.0	23.5	76.5	34.0	94°	0.85	–	–	–	–
LSI-S2-LP2	21.0	22.5	72.7	41.2	111°	0.93	19.4	–	0.9	–
LSI-S2-RM1	10.0	17.0	78.0	66.5	76°	0.59	–	53.9	–	3.2
LSI-S2-RP2	27.8	25.8	71.4	47.0	104°	1.08	30.8	–	1.10	–
LSI-S2-LM2	12.0	21.0	84.5	59.3	–	0.57	–	41.6	–	2.0
LSI-S2-LP3	27.4	29.5	78.9	43.5	117°	0.93	18.3	–	0.7	–
LSI-S2-RM2	10.0	16.0	74.0	20.0	106°	0.63	–	–	–	–
LSI-S2-RP3	28.0	23.8	78.8	49.0	129°	1.18	29.1	–	1.0	–
LSI-S2-LM3	14.8	19.0	45.7	65.8	38°	0.78	–	61.7	–	3.3
LSI-S2-LP4	32.3	22.2	–	38.2	–	1.45	–	–	–	–
LSI-S2-RM3	11.0	15.0	92.5	72.7	81°	0.73	–	56.1	–	3.7
LSI-S2-RP4	27.2	26.4	86.9	–	–	1.03	–	–	–	–
LSI-S2-LM4	20.0	23.5	–	69.0	–	0.85	–	–	–	–
LSI-S2-RM4	12.0	17.5	–	–	–	0.69	–	–	–	–
LSI-S2-RP5	25.8	26.5	–	–	–	0.97	–	–	–	–
Mean-M	13.7	19.1	75.2	55.3	79°	0.71	–	53.3	–	3.1
Mean-P	27.1	25.2	77.7	43.8	115°	1.08	24.4	–	0.9	–
LSI-T1	35.0	28.5	–	–	–	1.23	–	–	–	–
LSI-T2	23.5	26.5	–	–	–	0.89	–	–	–	–
LSI-T3	31.0	26.4	–	–	–	1.17	–	–	–	–
LSI-T4	32.0	30.0	–	–	–	1.07	–	–	–	–
LSI-T5	14.2	24.0	–	–	–	0.59	–	–	–	–
LSI-T6	25.7	29.8	–	–	–	0.86	–	–	–	–
LSI-T7	26.0	19.0	–	–	–	1.37	–	–	–	–
LSI-T8	22.2	25.0	–	–	–	0.89	–	–	–	–
LSI-T9	27.3	16.5	–	–	–	1.65	–	–	–	–
LSI-T10	30.5	24.0	–	–	–	1.27	–	–	–	–
LSI-T11	28.3	18.0	–	–	–	0.16	–	–	–	–
LSI-T12	26.5	26.3	–	–	–	1.01	–	–	–	–
LSI-T13	32.8	28.2	–	–	–	1.16	–	–	–	–
LSI-T14	24.3	19.0	–	–	–	1.28	–	–	–	–
LSI-T15	19.0	29.5	–	–	–	0.64	–	–	–	–
LSI-T16	18.6	24.4	–	–	–	0.76	–	–	–	–
LSI-T17	38.0	27.9	–	–	–	1.36	–	–	–	–
LSI-T18	34.6	29.8	–	–	–	1.16	–	–	–	–
LSI-T19	24.5	28.6	–	–	–	0.86	–	–	–	–
LSI-T21	79.0	62.2	–	–	–	–	–	–	–	–
LSI-S9-RM1	–	–	189.3	113.5	120°	–	–	62.6	–	–
LSI-S9-LP2	58.3	51.2	197.0	105.2	122°	1.14	36.9	–	0.6	–
LSI-S9-LM2	38.6	56.9	–	103.0	–	0.68	–	–	–	–
LSI-S9-RP2	65.3	51.8	–	117.0	–	1.26	–	–	–	–
LSI-S9-RM2	–	–	–	–	–	–	–	–	–	–
LSI-S10-LP1	78.8	62.7	–	–	–	–	–	62.6	–	–
Mean-M	38.6	56.9	189.3	108.3	120°	0.68	–	62.6	–	–
Mean-P	67.5	55.2	197.0	111.1	122°	1.20	36.9	–	0.6	–
LSV-S1-LM1	7.4	13.5	87.8	67.5	88°	0.55	–	51.3	–	3.8
LSV-S1-RP1	27.7	20.1	75.0	40.0	119°	1.38	13.9	–	0.5	–
LSV-S1-RM1	9.0	12.0	86.5	58.0	86°	0.75	–	38.7	–	3.2
LSV-S1-LP2	28.0	22.0	80.2	47.0	119°	1.27	24.5	–	0.9	–
LSV-S1-LM2	8.0	14.8	82.0	68.0	82°	0.54	–	54.3	–	3.7
LSV-S1-RP2	25.0	18.3	76.3	46.0	128°	1.37	25.7	–	1.0	–
LSV-S1-RM2	10.2	14.3	77.7	56.2	96°	0.71	–	40.6	–	2.8
LSV-S1-LP3	26.0	20.8	78.0	39.0	135°	1.25	–	–	–	–
LSV-S1-LM3	9.0	15.7	–	48.2	–	0.57	–	–	–	–
LSV-S1-RP3	25.5	21.5	–	45.5	–	1.19	–	–	–	–
LSV-S1-RM3	7.5	13.0	–	–	–	0.58	–	–	–	–
LSV-S1-LP4	30.0	21.5	–	–	–	1.40	–	–	–	–
Mean-M	8.5	13.9	83.5	59.6	88°	0.62	–	46.2	–	3.4
Mean-P	27.0	20.7	77.4	43.5	125°	1.31	21.4	–	0.8	–

Abbreviations: WAP: width of the angulation pattern of the pes (calculated value); WAM: width of the angulation pattern of the manus (calculated value); WAP/ML and WAM/MW are dimensionless.

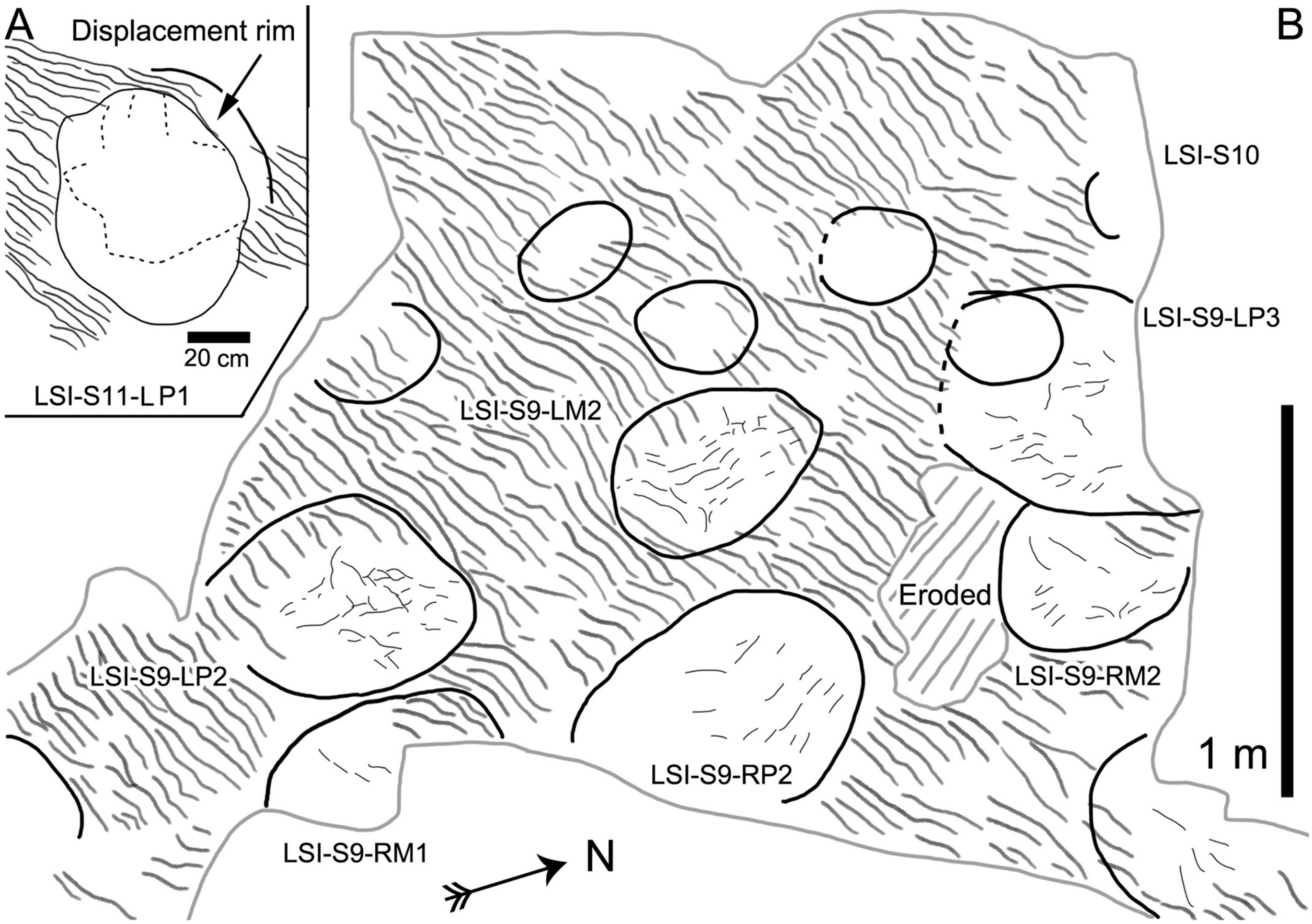

Fig. 7. Interpretative outline drawing of sauropod trackways on the upper level of Jishan Site I. A. Isolated track (S11) showing displacement rim. B. Sketch of sauropod trackways LSI-S9, S10.

Lockley et al., 1994), and appear different from *Brontopodus birdi* tracks from Texas with a high heteropody of 1:3 (Farlow et al., 1989; Lockley et al., 1994).

In contrast, LSI-S9 could be a narrow-gauge trackway (Table 2). However, it is composed of poorly-preserved undertracks showing very few distinct morphological characteristics. Therefore, trackway features are variable and trackway gauge is not easy to determine.

Generally speaking, Chinese sauropod trackways tend to be wide- or medium-gauge with relatively small heteropody, as is also observed on the Chabu (Inner Mongolia Autonomous Region) tracksites, and the Chuxiong (Yunnan Province) tracksite (1:1.9 and 1:2.9) (Lockley et al., 2002).

5.4. Trackways of medium-sized quadrupeds

Description

In the Jishan Provincial Geopark Sites I and V, two trackways composed of eight and six complete pes–manus track pairs, respectively, are catalogued as LSI-S2-LM1–RM4, LP2–RP5 (Figs. 6 and 10D) and LSV-S1-LM1–RM3, RP1–LP4 (Fig. 10B; Table 2). Two natural casts from the pes of LSI-S2-RP2 and RP3 are designated as LSI-S2-RP2c and RP3c (Fig. 10A). Some isolated tracks forming poorly-defined trackways are preserved in the Jishan Provincial Geopark Sites I and V, and are numbered as isolated tracks LSI-T1–T19 (natural-mold tracks), and LSV-T1–T9 (natural-cast tracks) (Figs. 6 and 10C). A pair of well-preserved, isolated pes–manus tracks at the Jishan Provincial Geopark Site II are catalogued individually as LSII-S1-LP1 and LM1 (Fig. 5). One trackway (LSVIII-S2) is preserved in the Jishan Provincial Geopark Site VIII (Fig. 9). Additionally, there are some tracks that do not comprise discernible trackways preserved in the Jishan Provincial Geopark Sites I–IV. All original specimens remain in the geopark.

The best-preserved trackways of these medium-sized quadrupeds are LS1-S2 from site 1 (Figs. 6 and 10D) and LSV-S1 from site V (Fig. 10B) both of which were accurately traced in the field.

The centre of the pes tracks is positioned somewhat closer to the trackway midline than that of the manus tracks. In the trackways LSI-S2 and LSV-S1, the manus tracks show a pronounced outward rotation relative to the midline (53° on average, ranging 47°–65°; 51° on average, ranging 40°–68°, respectively). On the contrary, the pes tracks are less outwardly rotated (16° on average, ranging 11°–25°; 20° on average, ranging 18°–27°, respectively). The inner trackway width between pes tracks averages 5.3 cm, ranging 4–6 cm.

In the LSI-S2 and LSV-S1 trackways, most manus tracks are oval, narrowing at mid-length, and the metacarpophalangeal pad region (i.e., the posterior border of the track is slightly concave). All of the well-preserved pes tracks have three particularly well-developed digit impressions. For some tracks such as LSI-S2-RP2c and RP3c (Fig. 10A) the middle digit of the pes is slightly longer than the outer digits, while the inner digit, probably corresponding to digit I, is

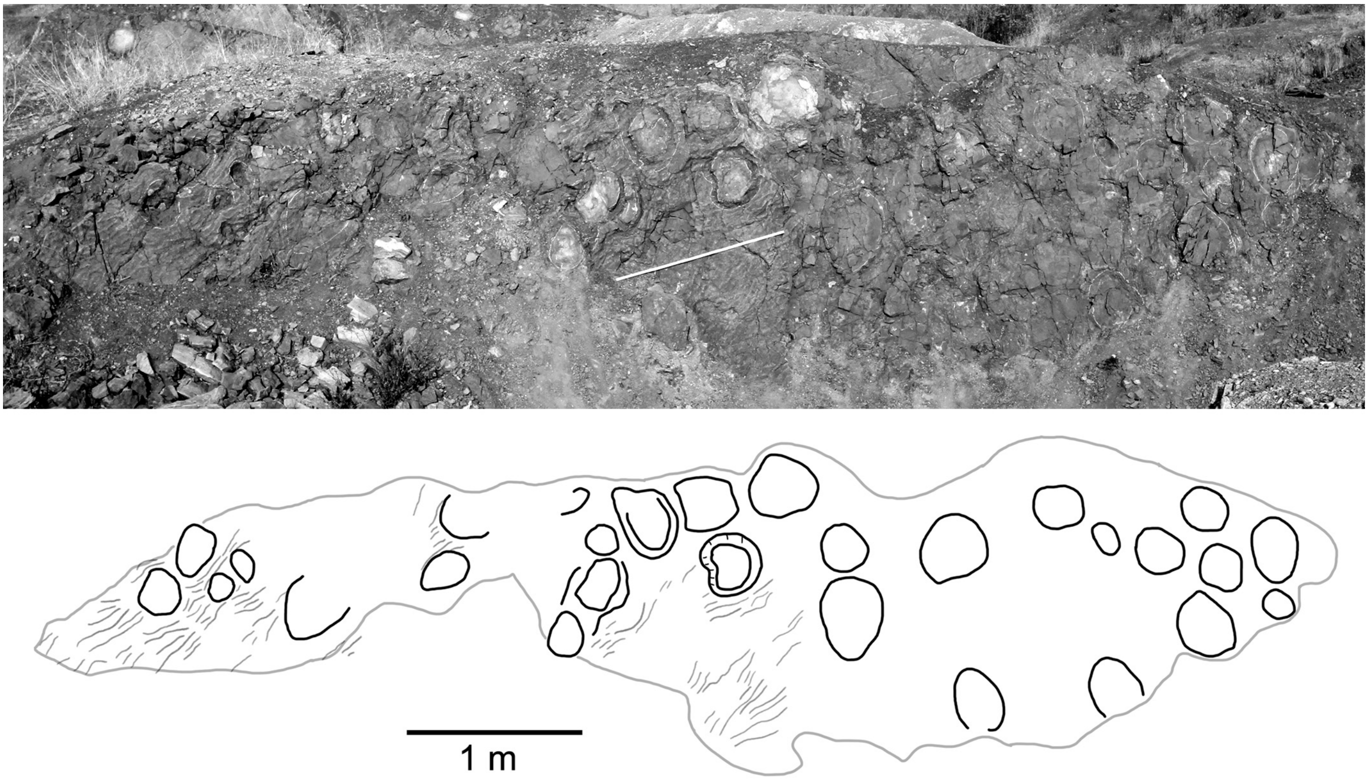

Fig. 8. Photograph and interpretative outline drawing of scattered sauropod tracks at Jishan Site III.

usually broader and more robust than the other two digits. The metatarsophalangeal pad region is smoothly curved.

Tracks LSI-T1–T19 are isolated, without a discernible trackway pattern, but the orientation of the tracks is generally consistent with the orientation of trackway LSI-S1. Most tracks are similar in morphology to the LSI-S2 tracks, among these, T17 with three well-defined and sharp digit marks, successively decreasing in size medially (7.5 × 6.4, 6.2 × 5.3, and 6.7 × 4.0). LSV-T1–T9 are also isolated tracks, without any discernible trackways. The semicircular track T4 shows four convex impressions, which may either correspond to manus digit impressions (see Santos et al., 2009, Fig. 8) or represent extramorphological or preservational features. Some pes–manus pairs were observed, such as T8 and T9.

At Site II (Fig. 5) there are essentially round impressions with diameters ranging from 37 to 45 cm. Among these, LSII-S1-LP1 and LM1 show some detail. Three outwardly rotated digits are present in S1-LP1. The similar sizes of the external diameters of these tracks suggest sauropod affinity. For example, in the LSI-S10 trackway from Site I (Fig. 7), the smaller undertracks are oval impressions (~30 × 21 cm). The pace angulations of LSI-S10 are 122° and 126°, similar to pes track pace angulations of LSI-S2 and LSV-S1.

Ichnotaxonomy and trackmaker identification

Identification of the medium-sized trackways of quadrupeds from Jishan is ambiguous, because the three digit impressions of the pes tracks may either represent digits I–III of sauropods or II–IV of thyreophorans.

The LSI-S2 trackway was preserved in soft sediments (deep tracks, up to 8–10 cm in depth). The three digits of LSI-S2 are round and blunt and similar to the short, bluntly rounded digit impressions of *Deltapodus* (Whyte and Romano, 1994, 2001; Milàn and Chiappe, 2009; Cobos et al., 2010; Mateus et al., 2011; Xing et al., 2013a), whereas the three distinct, sharper impressions in the LSV-S1 trackway (Fig. 10B), which were registered on firmer sediments (creating shallower tracks, approximately 4 cm deep), are similar to typical sauropod claw marks as seen in many sauropod pes tracks from the Cretaceous of Korea (Lim et al., 1989; Lockley et al., 2006).

Typical thyreophoran tracks, such as *Metatetrapous*, *Stegopodus*, *Deltapodus*, *Apulosauripus*, and *Tetrapodosaurus*, possess straight (and not curved) digital impressions ranging from moderately elongate to quite short and blunt (Gierliński and Sabath, 2008). The larger tridactyl pes tracks sometimes show elongated heel traces and associated large pentadactyl or crescentic manus tracks (Lockley et al., 2012a,b). In some respects, the medium-sized trackways of quadrupeds from Jishan are indeed similar to the above-mentioned thyreophoran tracks, especially to *Deltapodus*. For example, LSI-S2 (Fig. 10D) shows large tridactyl pes tracks, an elongated heel and crescentic manus tracks. However, most thyreophoran tracks such as *Metatetrapous* (Nopcsa, 1923), *Tetrapodosaurus* (Sternberg, 1932), *Deltapodus* (Whyte and Romano, 1994, 2001; Gierliński and Sabath, 2008; Xing et al., 2013a), *Apulosauripus* (Nicosia et al., 1999), and *Shenmuichnus* (Li et al., 2012) lack strongly outwardly rotated manus tracks. Instead, the axis of the manus track is nearly parallel to the axis of digit III of the pes track in these thyreophoran ichnotaxa, whereas the outward rotation of the manus tracks of the Jishan specimens is strongly pronounced and can reach up to 51°–53°. However, this could possibly be related to a particular gait or behaviour, and thus not be considered as a diagnostic feature for ichnotaxonomy. However, most thyreophoran manus tracks, even those that are not well preserved show distinct digits traces, rather than the semicircular manus tracks of sauropods. The lack of any such manus digit traces in the Jishan assemblages argues against a thyreophoran interpretation.

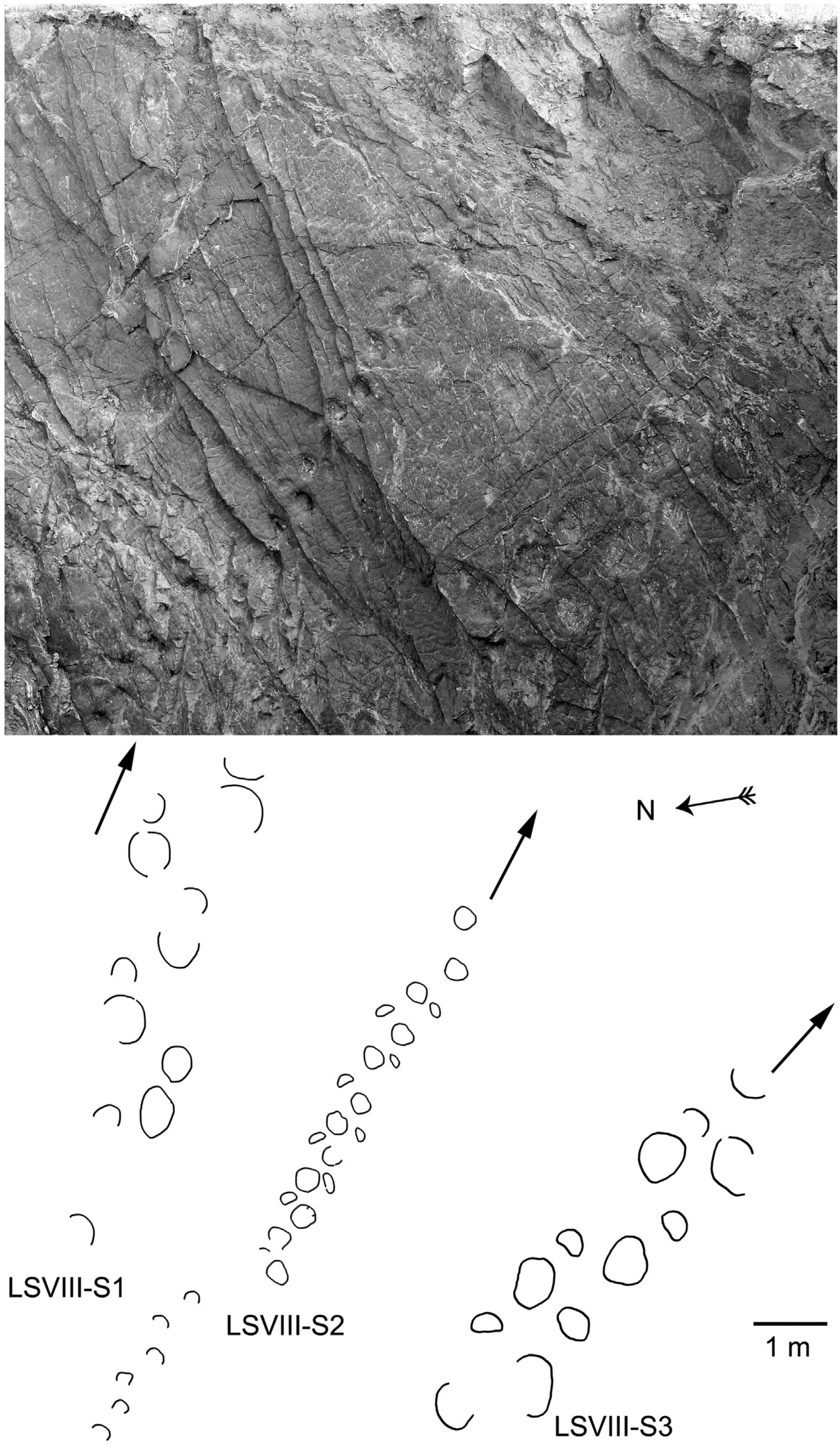

Fig. 9. Sauropod trackways and medium-sized quadruped (?sauropod) trackway at Jishan Site VIII. Note that the outline drawing is based on the photograph only, and not on a mapping of the surface which could not be accessed.

Sauropod pes tracks may show two to four claw impressions, but usually three, and the pedal claw impressions of a typical sauropod pes are directed laterally or anterolaterally and decrease in size laterally from digit I (Bonnan, 2005; Wright, 2005). Thus, traces of digits IV and V are typically short, blunt and inconspicuous rounded impressions (Lockley and Hunt, 1995; Marty et al., 2010). The pes tracks of the Jishan trackways are directed anterolaterally, and preserve separate impressions of rounded toes. Sauropod pes

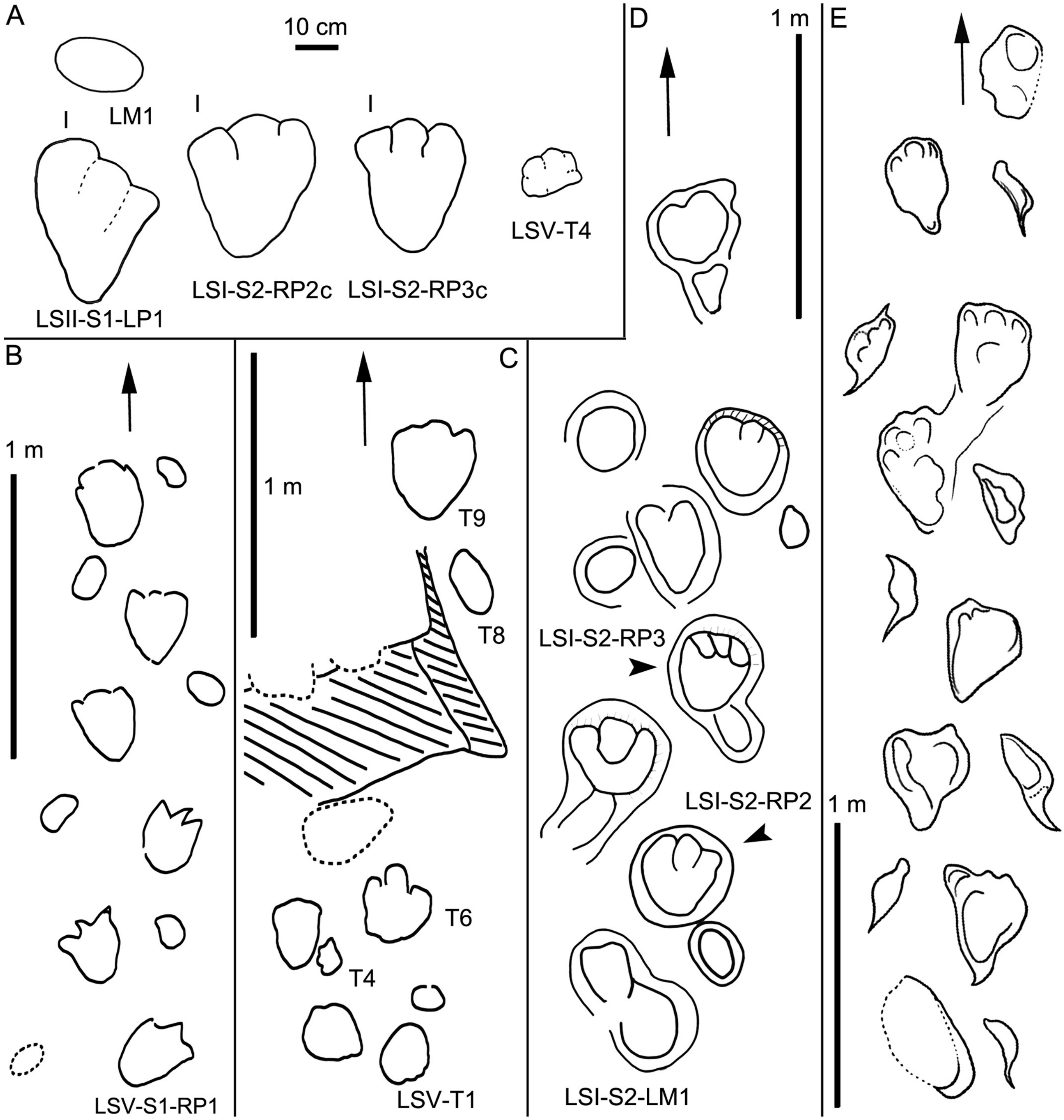

Fig. 10. Interpretative outline drawings of narrow-gauge quadruped (?sauropod) trackways. A. Well-preserved manus and pes track pair from Jishan tracksite I, II and V; B. Trackway (LSV-S1) from Jishan tracksite V; C. Isolated tracks (LSV-T1–T9) from Jishan tracksite V; D. Trackway (LSI-S2) from Jishan tracksite I; E. Trackway (T3) from Nanguzhai tracksite III for comparison.

tracks with three digital impressions are common, for example in the trackways of small sauropods from South Korea (Lim et al., 1989: Fig. 35.4A; Lockley et al., 2006), several specimens of *Parabrontopodus macintoshi* from Colorado (Lockley et al., 1994), *P. frenki* from Chile (Moreno and Benton, 2005: Fig. 6), “brontosaur” trackways from Crayssac, France (Lange-Badré et al., 1996; Lockley and Meyer, 2000: Fig. 7.20), trackway 2 from the Du Situ River from the Chabu 6 sauropod tracksite from Inner Mongolia (Lockley et al., 2002: Fig. 4), the *Polyonyx gomesi* trackways from Portugal (Santos et al., 2009: Fig. 5), Late Jurassic trackways from the Swiss Jura Mountains (Marty et al., 2010: fig. 5), or the sauropod trackways from the Las Cerradicas tracksite, Spain (Castanera et al., 2012: Fig. 8). The age of these tracks ranges from Middle Jurassic to the Early Cretaceous, representing different ichnogenera and suggesting that three digital impressions is a typical morphological characteristic of sauropod pes tracks. A sauropod pes cast LCU-I-37-12p from the Early Cretaceous (Berriasian) of the Cameros Basin, Spain (Castanera et al., 2012: Fig. 5) is notable in that it preserves a shorter digit III, similar to the round and blunt digit IV of typical sauropod tracks. If the anterior ends of these two digit traces merge, the impression maybe similar to LSI-S2-RP2c, RP3c (compare with Fig. 10A).

In general, later sauropods such as titanosauriformes possess more developed digits I–III with claws, but less-well developed digits IV–V (Bonnan, 2005), although, how these osteological features were expressed in the soft tissue is not known with any certainty. Digits IV–V of the trackmaker of the Jishan tracks were probably short, like those of most sauropods, and their impressions would be observed only in exceptionally well-preserved tracks. On the other hand, the Jishan tracks possess a relatively robust middle digit, with a relatively long ungual as was also observed in titanosauriformes (Averianov et al., 2002).

The co-occurrence of sauropod trackways of different-sized animals on the same track level is common (e.g., Lockley et al., 2002; Marty et al., 2003; Marty, 2008). However, the co-occurrence of sauropod and thyreophoran tracks on the same track level has so far only been reported from the Cal Orcko site in Bolivia (Meyer et al., 2001). Also, skeletal remains of a large titanosauriform, *Euhelopus zdanskyi*, were found in the Early Cretaceous of the Shandong Province (Barremian–Aptian, ca. 130–112 Ma) (Wiman, 1929; Wilson and Upchurch, 2009), while no thyreophoran skeleton has been discovered thus far. Therefore, the authors consider that the trackmaker of the Jishan tracks are more likely sauropods than thyreophorans.

The medium-sized Jishan trackways (e.g., LS1-S2 and LSV-S1) are clearly narrow-gauge and have a high heteropody. The surface ratio of the manus:pes is ~1:3.5 in comparison with the 1:1.5 ratio for the large trackmaker LS1-S1 from Site 1. The higher heteropody values are also greater than the 1:1.5 ratio of the large-sized sauropod tracks from Jishan and closer to those of typical *Parabrontopodus* tracks (1:3, Lockley et al., 1994). Nonetheless, because the preservation is suboptimal, we refrain from formally assigning the Jishan trackways to *Parabrontopodus* simply based on these characteristics. We also note that the global spatial and temporal distribution of wide- and narrow-gauge sauropod trackways (Lockley et al., 1994) indicates that *Parabrontopodus* was almost exclusively confined to the Jurassic. However, at that time many of the newly found sauropod tracksites from China and other regions were not known. These remain to be analysed for trackway gauge, heteropody values and then added to an updated global database. The presence of two kinds of sauropod trackways of different size and different pes morphology at a single tracksite (LS1) and more generally in the Linshu assemblages, suggests that there may have been at least two different kinds of sauropods. This raises the question of whether they represent different ontogenetic stages or different species. On balance differences in heteropody and gauge would seem to suggest different species rather than juveniles and adults of the same species. According to Myers and Fiorillo (2009), juvenile and adult sauropods may have adopted different feeding and herding strategies, resulting in their segregation. Nevertheless, for the Linshu assemblage, the presence of different size-classes cannot be completely excluded.

The association of the Jishan large- and medium-sized sauropod trackways is similar to the Nanguzhai tracksites yielded from the same stratum, in Donghai County, Jiangsu Province (Xing et al., 2010a,b). There, a total of six trackways occur at the Nanguzhai site III, among which T1 pertains to a theropod, T2, 3, 6 to smaller sauropods, and T4 and 5 to larger sauropods, an association consistent with that of the Jishan site I. The large sauropod and theropod tracks at the Nanguzhai site III are poorly-preserved, but in the smaller sauropod trackways (Fig. 10E), the size (35.1 × 24.9 cm for pes), pace angulation (94° for the manus, 117°–124° for the pes), and the outward rotation (50°–70° for the manus, 16°–19° for the pes) is similar to the Jishan medium-sized sauropod trackways. Length:width ratios (1.41–1.47 for the manus, 0.56 for the pes) are slightly larger in specimens from Nanguzhai site III than in those from Jishan, which may be due to the muddy and soft Nanguzhai sediments leading to longer "heel" impressions (Xing et al., 2010b). All of these characteristics suggest that the Nanguzhai medium-sized sauropod tracks and the Jishan medium-sized trackways could pertain to the same trackmakers. Significantly, a manus (T3.6a) and a pes (T3.8b) from the Nanguzhai site III preserve fine details: in T3.6a, digits I–V can be observed as being similar to LSV-T4 in morphology. In T3.8b from Nanguzhai, digits I–IV are visible with digits III–IV being very close to each another; for another pes of the same trackway, digits III–IV are usually combined as a large impression. However, all of these characteristics were observed on wetter and muddier sediments, and more reliable evidence is required.

Several medium-sized sauropod tracks from the Zhangzhuhewan tracksite, Zhucheng City, Shandong Province (Xing et al., 2010a) have similar sizes to that of the Jishan specimens (42.1 × 29.3 cm). Xing et al. (2010a) interpreted these specimens as pes-only sauropod trackways, with an average pace angulation in LG1.1–1.4 of 101°, which lies in the range of LSI-S2, LSI-S10, and LSV-S1 pes track pace angulations. This indicates that the medium-sized sauropod trackways from Zhangzhuhewan, Nanguzhai and Jishan probably pertain to the same kind of widely-distributed trackmakers.

Xing et al. (2010b) assigned the Nanguzhai tracks to *Parabrontopodus* isp., and thus, this kind of track-type might have had a wider distribution. For example, trackways of small sauropods from southern South Korea (Lim et al., 1989: Fig. 35.4A) have similar pace angulations: 110° for the manus, 125° for the pes. Furthermore, Kim et al. (2012) noted that the rotation angles of the manus impressions of sauropod tracks from the Cretaceous Jindong Formation of Korea (Lim et al., 1989), the Jurassic of Portugal (Santos et al., 1994), and the Jurassic and Cretaceous of Italy and Croatia (Dalla Vecchia, 1994) are up to 45°, which is similar to that of the Jishan specimens.

5.5. Tetradactyl tracks

Description

Two trackways, one composed of three tracks at Jishan Provincial Geopark Site V, catalogued as LSV-O2-T1–T3 (Figs. 11 and 12; Table 1). Another possible trackway near LSV-S1 is composed of four poorly-preserved impressions, catalogued as LSV-T1–T3, T5 (Fig. 12), and one isolated indentation LSV-T6 (Fig. 12). Both trackways appear narrow as if made by bipeds, although the trackway segments are too short and incomplete to support this inference with certainty. All original specimens remain in the Geopark.

T1 and T2 of the LSV-O2 trackway are well preserved and similar in morphology, even though that T2 possesses a more elongated "heel". T1 has a sediment displacement rim on what is inferred to be the medial side based on the short digit trace representing digit I, (the digital lengths from medial to lateral are 3.6, 7.9, 7.4, 4.4 cm). T2 has sediment displacements rims both medially and laterally. Assuming T2 represents the next footprint in a linear, narrow trackway the lateral digit is the shortest (and digit trace lengths from the medial to the lateral are 8.1, 9.0, 8.5, 2.5 cm). Given these inferences, the T1–T3 track configuration probably constitutes a left–right–left sequence.

Digit I is the shortest and has a sharp claw mark. Digit II is the longest and the most forward projecting, digit III is slightly shorter than digit II. Digits II–IV lack distinct claw marks, they are round and blunt terminally, and merge proximally in a smoothly curved heel region. The total divarication angle between digits I and IV is 73°, it is the largest between digits I and II (I 29°II 24°III 20° IV).

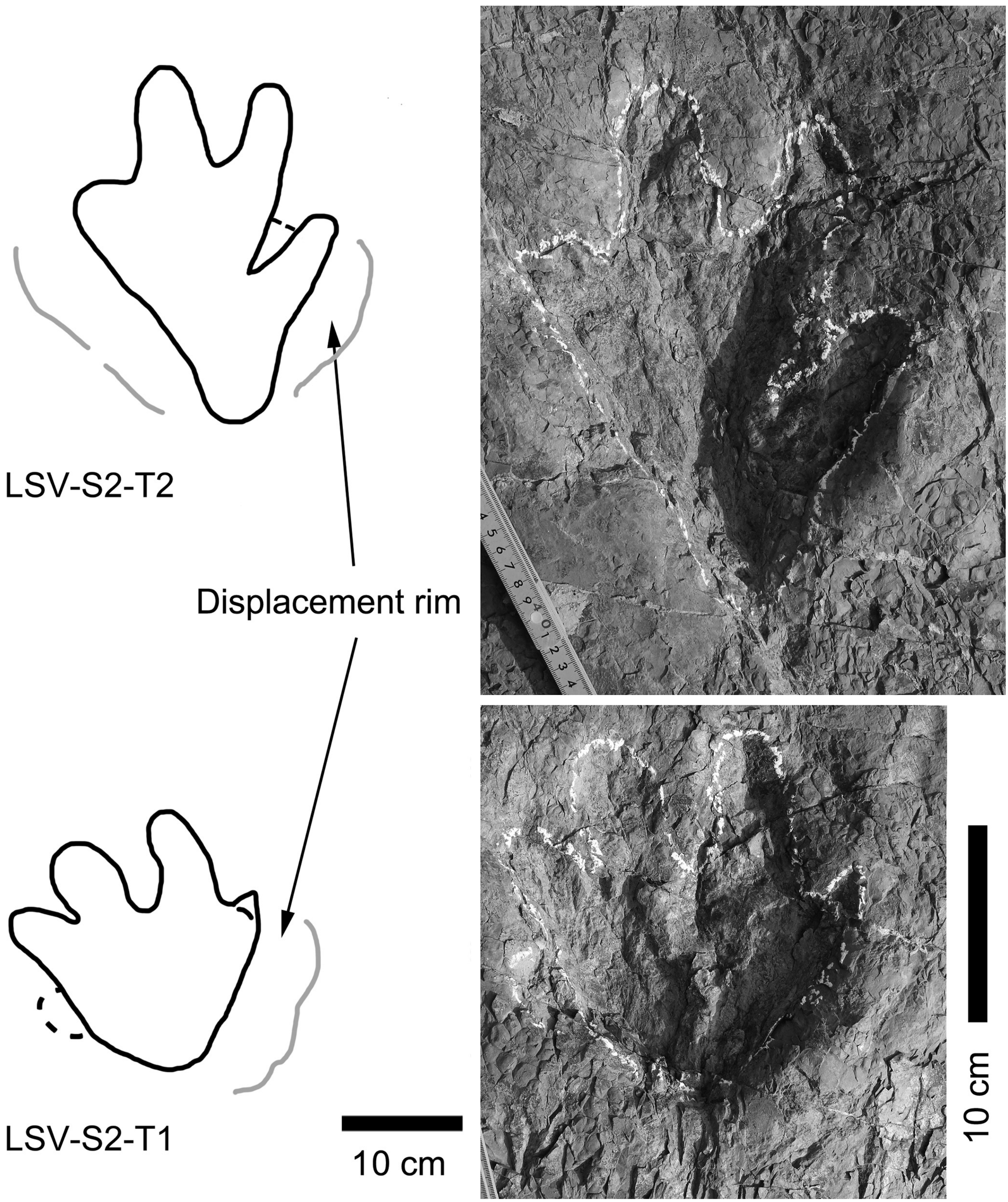

Fig. 11. Photographs and interpretative outline drawings of tetradactyl tracks at Jishan tracksite V belonging to a possible psittacosaur trackway (LSV-O2-T1–T2).

LSV-O2-T2 shows a longer heel trace in comparison with T1. Traces of T2 digits I–III are similar to those in T1, but digit IV appears shorter than in T1. Proximally, digit IV has projecting sediment displacements rims, indicating that this difference may be extramorphological. The terminal heel region is U-shaped. In T2 the divarication between digits I and IV is only 57° (I 20°II 18°III 19°IV), but here again, the largest divarication is between digits I and II. LSV-O2-T3 lacks detailed morphological characteristics.

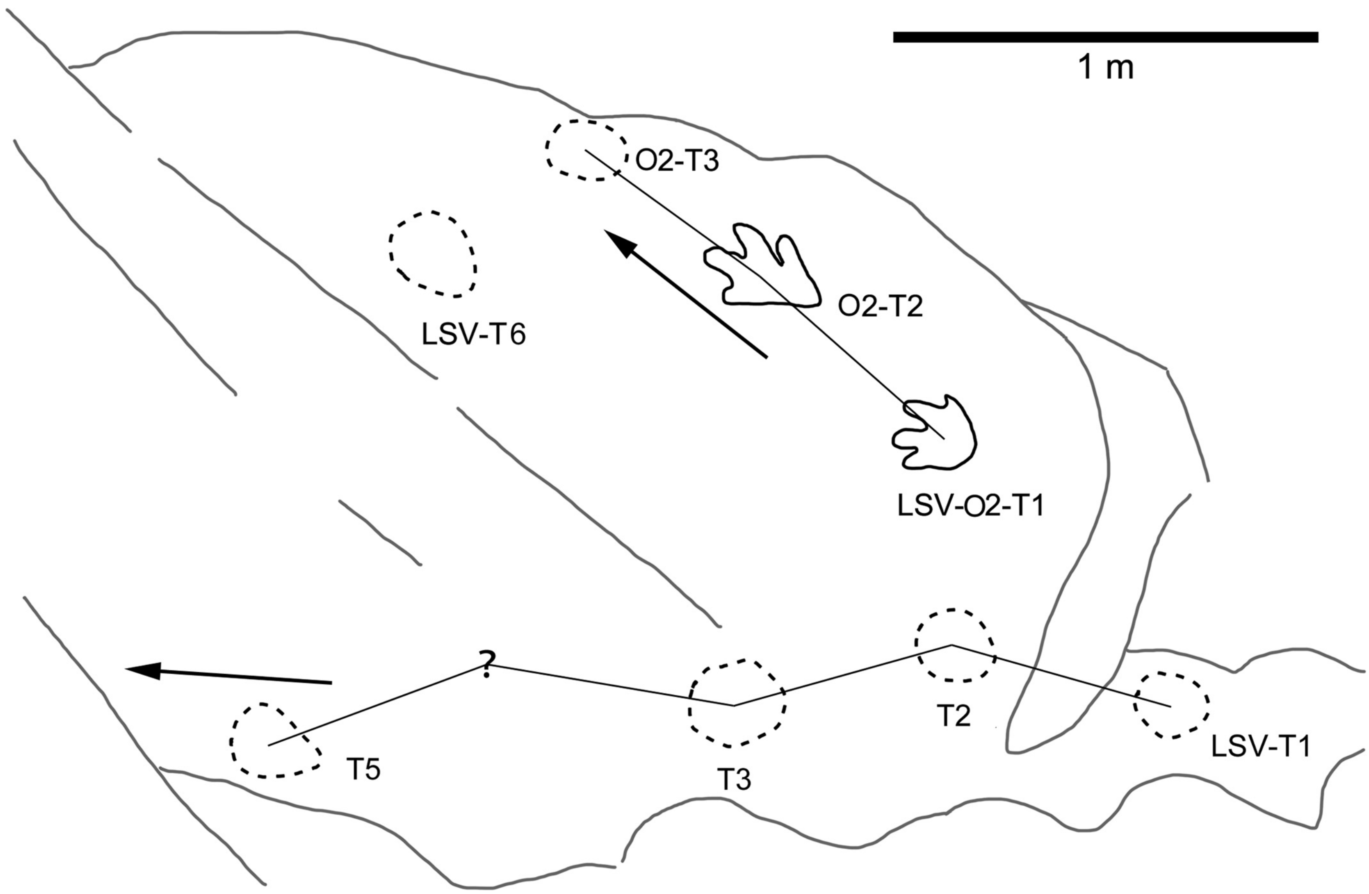

Fig. 12. Interpretative outline drawing with overview of possible psittacosaur trackway with tetradactyl tracks (LSV-O2-T1–T3) above and indistinct trackway LSV-T1–T3, T5 (undertracks) below at Jishan tracksite V.

As shown in Fig. 12, LSV-T1–T3, T5 probably constitutes a single trackway. The pace of T1–T3 is 53.0 and 56.1 cm, the stride 103.3 cm, and the pace angulation is 142°. The stride of T3–T5 is 111.5 cm. These measurements are similar to those of the LSV-O2 trackway, indicating that the tracks were left by the same kind of trackmakers.

Ichnotaxonomy and trackmaker identification

The Jishan tracks are morphologically consistent with the pes skeletons of some thyreophorans (see Apesteguia and Gallina, 2011: Fig. 4). The fifth digit of the pes was strongly reduced and probably left no impression. The track surface has been eroded away at a distance of 30 cm alongside the trackway (Fig. 12). Assuming that the track sequence LSV-O2 represents only one half of a trackway, the other portion should be preserved within the exposed area, because trackways of quadrupedal thyreophorans tend to be rather narrow-gauge; but this is not the case. We therefore infer that LSV-O2-T1 and T2 are successive pes tracks of a narrow-gauge ornithischian trackway.

Tetradactyl pes tracks with round and blunt digits are for example present in the ichnogenera *Tetrapodosaurus* (Sternberg, 1932; McCrea et al., 2001) and *Ceratopsipes* (Lockley and Hunt, 1995). Although, based on respective type specimens, digits are much blunter in the latter ichnogenus. Traditionally, *Ceratopsipes* is interpreted as a ceratopsian track (Lockley and Hunt, 1995), and *Tetrapodosaurus* as an ankylosaurian track. However, Gierliński and Sabath (2008) considered *Tetrapodosaurus* to be closer to the ceratopsian pedal pattern than to the ankylosaurian pes, which may even be tridactyl. The first pedal digit was well developed in basal neoceratopsians like *Protoceratops* (Granger and Gregory, 1923; Niedźwiedzki et al., 2012) and *Psittacosaurus* (Osborn, 1923; Russell and Zhao, 1996). A rare association of a track with an articulated *Protoceratops* skeleton from Mongolia indicates that the pes track of *Protoceratops* looks like a smaller, more gracile and digitigrade version of the large- and semi-plantigrade *Tetrapodosaurus* (Niedźwiedzki et al., 2012).

In contrast, several typical ornithischian morphotypes contain functionally tridactyl footprints, lacking a strong hallux, or have one that is clearly shorter than the main digit group II–IV (Niedźwiedzki et al., 2012). For example, *Deltapodus* and *Apulosauripus*, considered as thyreophoran, generally have tridactyl pes tracks (Gierliński and Sabath, 2008).

LSV-O2-T1 and T2 *are* similar to *Tetrapodosaurus* and *Ceratopsipes* in morphology. The latter is a quadruped trackway of average size (40 × 52 cm in the holotype pes) only reported from the Late Cretaceous. For pes tracks, width usually exceeds length, unlike in LSV-O2-T1 and T2. *Tetrapodosaurus* is restricted to the Middle Cretaceous (Aptian through Cenomanian) of the North American Cordilleran. The geological age is similar to that of LSV-O2-T1 and T2. Digit I is also the shortest in both *Tetrapodosaurus* and LSV-O2-T1 and T2. Aside from size (*Tetrapodosaurus* is ∼34 cm in length), the divarication of digits I 14° II 21° III 32° IV (Sternberg, 1932) in the pes track of *Tetrapodosaurus* significantly differs from LSV-O2-T1 and T2. Moreover, LSV-O2-T1 and T2 lack manus tracks. On the other hand, morphologically, LSV-O2-T1 and T2 respectively are similar to the *Protoceratops* footprint ZPAL MgD-II/3 from the Djadokhta Formation (Upper Cretaceous) of Mongolia, and *Tetrapodosaurus* CU-MWC 209.33 from the Dakota Group (Middle

Cretaceous) of Colorado (Gierliński and Sabath, 2008; Niedźwiedzki et al., 2012), for instance, by the relatively short length of digit I and the long digit IV.

Ankylosaurians and thyreophorans are unknown from the Cretaceous of Shandong Province and neighbouring regions. However, abundant psittacosaur (ceratopsians) remains were found in nearby Early Cretaceous deposits. Young (1958) described these specimens and named them *Psittacosaurus sinensis*. *P. youngi*, (Zhao, 1962) is generally considered a junior synonym of *P. sinensis* (Sereno, 1990). On the other hand, ceratopsians such as *Zhuchengceratops* (Xu et al., 2010a,b) were also discovered in Upper Cretaceous strata of Shandong, indicating that ceratopsians were probably quite abundant in the Early and Late Cretaceous of Shandong.

Psittacosaurus including its pes structure is well known, and we have compared the pes of *Psittacosaurus neimongoliensis* (Russell and Zhao, 1996) with the best-preserved LSV-O2-T1 (Fig. 13), and conclude that the morphologies are consistent. Supposing that the trackmaker of LSV-O2-T1 is *Psittacosaurus*, then it is not surprising that LSV-O2-T1 and T2 lack manus tracks. The forelimbs of *Psittacosaurus* were too short to reach the ground and could neither be pronated nor generate propulsive force for locomotion, suggesting that *Psittacosaurus* was entirely bipedal (Senter, 2007).

On the other hand, assuming a foot length:hip height ratio in the range of 4–4.6 for a small bipedal dinosaur (Thulborn, 1990; Henderson, 2003), the hip height of the LSV-O2-T1 trackmaker would be approximately 0.76–0.88 m. The hip height:body length ratio of *Psittacosaurus* is 1:2.8 (based on Lucas, 2006: Fig. 1), so the body of the LSV-O2-T1 trackmaker may have been 2.13–2.46 m long. This length falls within the known length span of *Psittacosaurus*, for example *P. mongoliensis* reached 2 m in length (Sereno, 1997).

Given the age and location at which these tracks were found it is tempting to infer that they may be of psittacosaurian affinity. However, it is still a puzzle that tracks that are confidently attributable to psittacosaurs or protoceratopsians have never been identified confidently except in one isolated example pertaining to the latter group (Niedźwiedzki et al., 2012). This demonstrates that track and bone assemblages may indicate different faunal distributions and abundances.

6. Vertebrate tracks from Shandong Area

Vertebrate tracks in Shandong Province are mainly present in the Lower Cretaceous Laiyang and Dasheng Groups. Abundant dinosaur body fossils were found in the Upper Cretaceous Wangshi Group (such as the hadrosaurid *Shantungosaurus* Hu et al., 2001, the ceratopsid *Sinoceratops* Xu et al., 2010a,b, and the tyrannosaurid *Zhuchengtyrannus* Hone et al., 2011). Compared to the Upper Cretaceous Wangshi Group, vertebrate fossils are comparably rare in the Lower Cretaceous Laiyang and the Dasheng Groups, and thus tracks are ideal complements.

Laiyangpus liui (Young, 1960) has been named from the Laiyang Group, based on a now lost holotype assemblage of three- and four-toed parallel trackways from a lacustrine depositional environment in Laiyang City, interpreted to represent crocodylians (Lockley et al., 2010). The medium-sized grallatorid *Paragrallator* (Li and Zhang, 2000; Xing et al., 2010a,b), the robust tridactyl theropod track *Corpulentapus* (Li et al., 2011), a pterosaur track attributed to *Pteraichnus* isp., and unnamed tridactyl theropod tracks from Jimo City (Xing et al., 2012) are also known from the Laiyang Group. The Huanglonggou tracksite of the Laiyang Group (Li et al., 2011) near Zhucheng, where more than 2000 tracks have been mapped (Lockley et al., 2012a,b) is particularly spectacular, with an ichnofauna that is saurischian-dominated.

From the tracksites of the Dasheng Group, the Houzuoshan Dinosaur Park shows the most diverse ichnoassemblage. Named tracks from this site include large didactyl deinonychosaurian tracks (*Dromaeopodus*), small didactyl deinonychosaurian tracks (*Velociraptorichnus*), small tridactyl theropod tracks (*Minisauripus*), the avian track *Koreanaornis* and the distinctive zygodactyl avian track *Shandongornipes* (Li et al., 2005a,b; Lockley et al., 2007, 2008). Unnamed tracks include quadrupedal ornithopod trackways (Matsukawa and Lockley, 2007).

Two other tracksites of the Dasheng Group are the Zhangzhuhewan and the Nanguzhai tracksites. The former includes medium-sized sauropod tracks, iguanodon–hadrosaur morphotype ornithopod tracks and isolated shorebird tracks (Xing et al., 2010a,b). They were first attributed to the Yangjiazhuang Formation of the Laiyang Group. However, based on ongoing geological investigations, the specimens should pertain to the Tianjialou Formation of the Dasheng Group (Kuang et al., 2013). The Nanguzhai tracksites include two different sizes of sauropod tracks and one poorly-preserved theropod trackway (Xing et al., 2010b). The Nanguzhai tracksites (Xing et al., 2010a), and the Jishan tracksites also exhibit numerous sauropod trackways, with different morphotypes suggesting that at least two different groups of sauropods were present in the Dasheng Group of the Yishu fault zone. The presence of deinonychosaurian tracks also indicates that deinonychosaurians had a wider distribution in the Lower Cretaceous Shandong Province. Non-deinonychosaurian theropod tracks frequently co-occur alongside medium-sized sauropod tracks. The

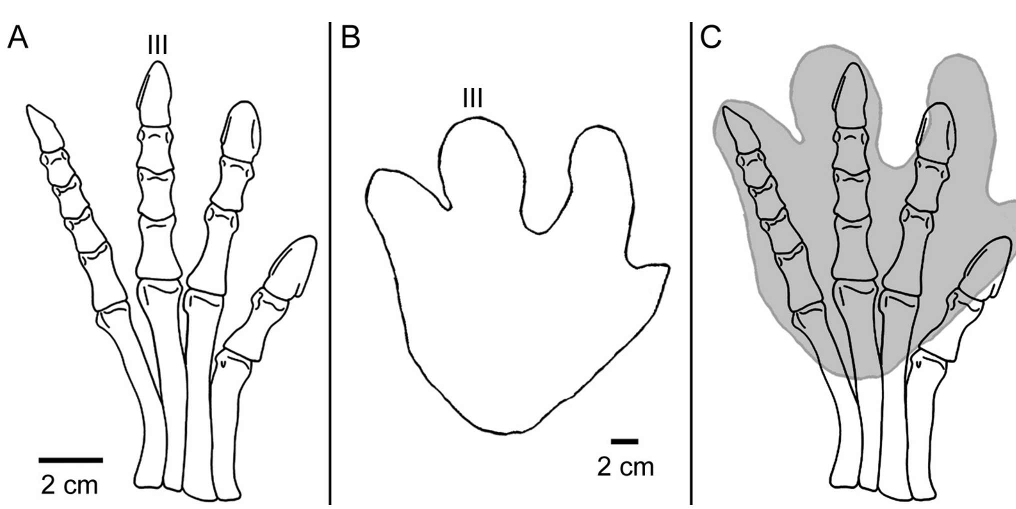

Fig. 13. A. Pes skeleton of *Psittacosaurus* (Russell and Zhao, 1996); B. Tetradactyl track (LSV-O2-T1) from this study; C. Pes skeleton (A) superimposed on a tetradactyl track (B).

deinonychosaurian and tridactyl theropod tracks from the Jishan sites again support the conclusions of Matsukawa et al. (2006) that the Early Cretaceous ichnofaunas of northeast China are dominated by theropod and bird tracks, in broad concordance with the body fossil record. *Psittacosaurus* is common in Early Cretaceous sediments in Asia (You and Dodson, 2004) and possible *Psittacosaurus* tracks from the Tianjialou Formation are reported in this study.

On the other hand, some ichnotaxa of the Yishu fault zone are comparable with those from the Early Cretaceous of South Korea (such as *Minisauripus*; Lockley et al., 2008). The geological age of the Tianjialou Formation was adjusted from Barremian–Aptian to Aptian–Albian (Kuang et al., 2013), which is consistent with the Haman Formation of South Korea. Similar track associations may indicate that similar palaeoenvironments pre-dominated in the two areas. However, this requires further comparisons.

7. Conclusions

The new dinosaur ichnofauna from the Lower Cretaceous Dasheng Group of Shandong Province shows a remarkable diversity. It is a characteristic assemblage, comparable with others from coeval localities in the Yishu fault zone of eastern China.

Typical are trackways of large- and medium-sized sauropods that show some similarities with wide- and narrow-gauge ichnogenera such as *Brontopodus* and *Parabrontopodus*, and that possibly reflect different sauropod trackmaker groups, co-occurring with medium-sized tridactyl theropod tracks.

Peculiarities are (1) the presence of a didactyl trackway (cf. *Dromaeosauripus*) that can be attributed to a deinonychosaurian theropod, (2) the co-occurrence of functionally didactyl and tridactyl theropod footprints, (3) the presence of tetradactyl ornithischian, possible psittacosaur tracks.

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