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A NEW ORNITHISCHIAN–DOMINATED AND THEROPOD FOOTPRINT ASSEMBLAGE FROM THE LOWER JURASSIC LUFENG FORMATION OF YUNNAN PROVINCE, CHINA

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Abstract—Ornithischian- and theropod-dominated footprint assemblages from the Lower Jurassic Lufeng Formation of Yunnan Province, China, differ significantly from the skeletal record of the same region. Ornithischian tracks assigned to *Shenmuichnus wangi* are the most common track type (52%), while small *Anomoepus*-type tracks account for 31%. Large *Eubrontes*-like theropod tracks make up about 17% of the assemblage. The track record of the Lufeng Basin currently lacks evidence corresponding to basal sauropodomorphs and basal sauropods, even though they are the most abundant skeletal fossils.

INTRODUCTION

The Lufeng Basin of China contains many wide exposures of Mesozoic continental red beds rich in dinosaur and other vertebrate fossils, making the Lufeng Basin among the most famous dinosaur field research sites in the world (Dong, 1992; Luo and Wu, 1995). Jurassic strata are particularly abundant within the basin. The dinosaur fauna from the Lower Jurassic Lufeng Formation is frequently referred to as the Lufeng Saurischian Fauna or the *Lufengosaurus* Fauna (Young, 1951). Fossils from the Lower Jurassic Lufeng Formation have been found across Yunnan, including Lufeng, Yimen and Yuanmou areas.

Xing et al. (2009) described two theropod tracks assigned to the ichnospecies *Changpeipus pareschequier* from the Lower Jurassic Lufeng Formation of the Yaozhan tracksite, in Lufeng County. Theropod tracks were also discovered in the Lower Jurassic Fengjiahe Formation of the nearby Jinning Basin; these include *Eubrontes*, *Grallator*, and *Kayentapus* (Zhen et al., 1986; Lockley et al., 2013).

In 2014, Wang Tao, from the Lufeng Land and Resources Bureau, found an assemblage of large ornithischian tracks at the Dalishu tracksite, Lufeng County (Fig. 1). These tracks are the first evidence of large ornithischians in the Early Jurassic of Yunnan Province. Xing et al. (in press) described these specimens and assigned them to the new ichnospecies, *Shenmuichnus wangi*. In 2015, the first author of this paper and Dr. Hui Dai, Mr. Haiqian Hu from China University of Geosciences, Beijing found at least four other dinosaur track sites in the Lufeng Basin. The locality where the large ornithischian and theropod tracks were found is about 750 m northwest of the Dalishu tracksite near Dalishu village and is cataloged as Dalishu tracksite II (GPS: 24°56’14.54”N, 102° 0’32.49”E). The tracksite is within the protection of the Lufeng Dinosaur National Geological Park, Yunnan Province.

Abbreviations: **DLSII**, Dalishu track site II, Yunnan Province, China; **M**, manus prints; **P**, pes prints; **R/L**, right/left.

GEOLOGICAL SETTING

Lufeng Formation

The Lower Jurassic Lufeng Formation is part of the typical red beds of southwestern China (Sheng et al., 1962). Fang et al. (2000) divided the Lufeng Formation from base to top into the Shawan and Zhangjiaao members. The tracks are preserved in a layer within the lower Zhangjiaao Member. The Lufeng Formation includes shallow lacustrine strata, based on the chemical composition of deposits (Tan, 1997; Fang et al., 2000) (Fig. 2). The Dalishu track site II layer is at a slightly higher level than that of the previously described Dalishu track site, but both of them are preserved on a sandstone layer.

Invertebrate Traces

Dense invertebrate traces occur at Dalishu tracksite II, dominated by vertical burrows (Fig. 3). All these vertical burrows are in pairs and the U-shaped structure can be seen on one of the rock fracture surfaces. All these features are similar to *Diplocraterion* Torell 1870 (Fürsich, 1974). However, due to the small sample size (with U-shaped structure), it is difficult to discern systematic features, and thus the material is referred to cf. *Diplocraterion*.

Diplocraterion belongs to the *Skolithos* ichnofacies, which is mainly preserved in high energy, shallow marine substrates (Cornish, 1986; Šimo and Olšavský, 2007). In southern Sweden, *Diplocraterion* is also associated with some Early Jurassic tracks (Gierliński and Ahlberg, 1994). These Swedish sections have been interpreted as muddy shoreline deposits, gradually transgressed by low-energy brackish marine water (Ahlberg, 1990). *Diplocraterion* is also found in marginal lagoonal deposits of the Lower Cretaceous Wealden Group, southern England (Radley et al., 1998). Kim and Paik (1997) described *Diplocraterion* from nonmarine floodplain lake environments, representing paleoenvironments similar to those of the DLSII site (Tan, 1997).

MATERIALS AND METHODS

All tracks are preserved as natural impressions (concave epireliefs) and are distributed on three adjacent surfaces (different thin layers). The largest surface (Surface I), with two track-bearing levels, is about 130 m^2 and preserves 46 tracks (Fig. 4). After removing the withered vegetation and topsoil from the track surface, every footprint was numbered and outlined with chalk. And then we traced the outlines of the trackways in transparent plastic sheets. Maximum length, width,

FIGURE 1. Geographic map with the position of the Dalishu dinosaur footprint locality (indicated by footprint icon).

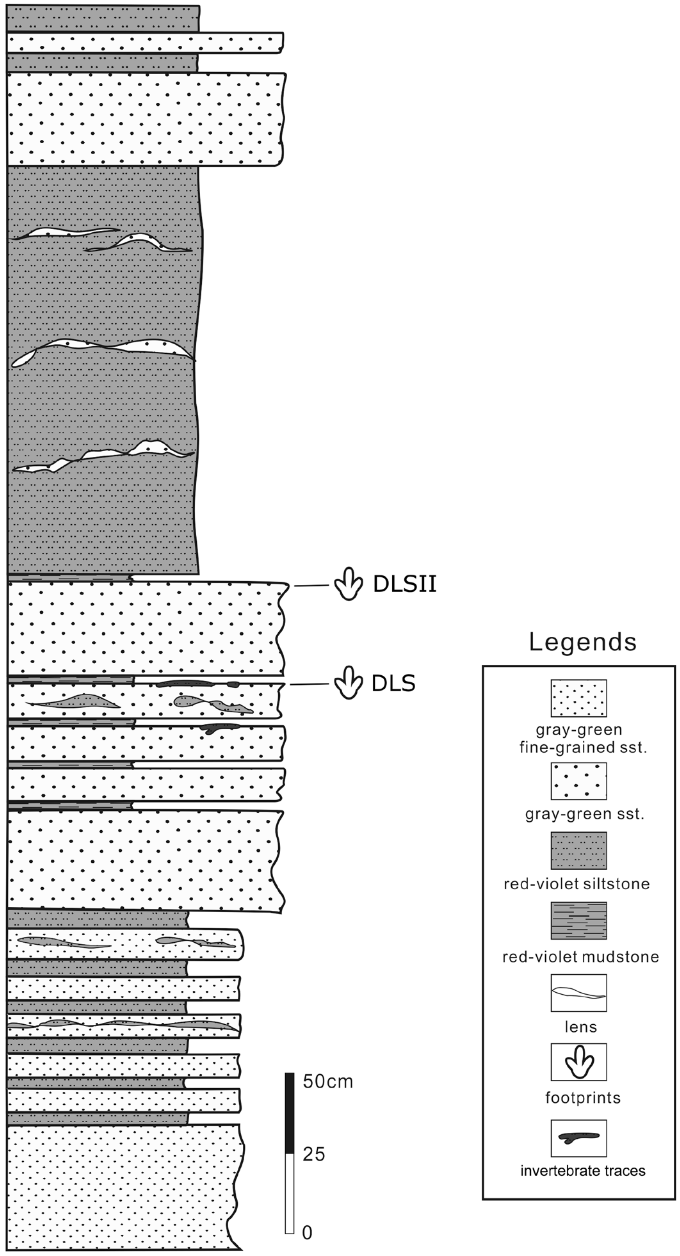

FIGURE 2. Stratigraphic section of the lower unit of the Lufeng Formation at the Dalishu track locality with position of DLS and DLSII track levels.

divarication angle, pace length, stride length, pace angulation and rotation were measured from original surface according to the standard procedures of Lockley and Hunt (1995) and Xing et al. (in press).

A distribution diagram (map) created on plastic film could not cover all tracks due to the 36 degree slope. Instead, the whole surface was recorded using a tele controlled four axis quadcopter aircraft (DJI Phantom 3) with a 12 mega-pixel camera, and the track distribution diagram was created based on the photographs, using Photoshop CS. Two other smaller surfaces span 4 m^2 and 9 m^2 with 10 and 8 tracks, respectively. Then, the small surfaces were covered by a single, large, transparent plastic sheets, on which the outlines of the tracks were traced. The plastic sheets are now stored in the collections of Yanqing Global Geopark, in Beijing.

DINOSAUR TRACKS

Ornithischian Tracks

Description and Comparisons

Nine ornithischian trackways are present at DLSII tracksite (Figs. 5-7, Table 1). DLSII-O3-RP5 and RM5, DLSII-O7-RP1 and RM1 are

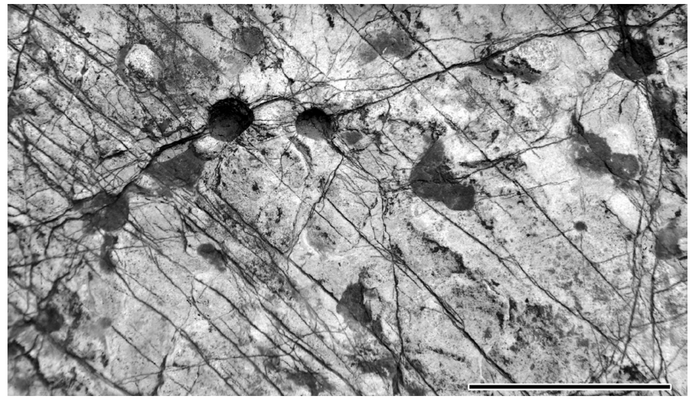

FIGURE 3. Photograph of invertebrate traces ?*Diplocraterion* Torell 1870 at Dalishu tracksite II.

the best-preserved tracks (Fig. 6). The pes prints are tridactyl, and their length nearly equals their width (L/W= 0.9/1.1). The trace of digit III is the longest, followed by digit IV, and digit II is shortest. The distal end of each digit trace is round and blunt, and the metatarsophalangeal region smoothly curved. The divarication between digits II and IV is wide (73° and 63°), and the anterior triangle length/width ratio of both pes imprints is 0.3.

The fan-shaped manus prints show a very wide digit divarication and a concave posterior margin formed between digits I and V. They are pentadactyl, symmetrical along digit III, and their width exceeds their length (L/W ratio 0.7). Digit proportions are subequal lengths of digits or digits I and V being slightly shorter than others (Table 1). O3-RM5 is positioned anterior to the corresponding pes trace, whereas in O7-RM1, the axis connecting the distal ends of digits I and V is aligned with the anterolateral margin formed by digits III and IV of O7-RP1 (i.e. parallel and anterolateral to the line connecting the tips of digits III and IV).

All manus imprints are outward rotated with digit V pointing backward, whereas the pes is inward rotated, relative to the midline. O7-RM1 is rotated approximately 29° outward from the trackway axis, whereas the inward rotation of the corresponding pes impression O7-RP1 is approximately 3°. The values in DLSII-O3-RP5 and RM5 are 22° outward for the manus, and 4° inward for the pes. The average pace angulation values of the pes traces are 112° (DLSII-O3), and 135° (DLSII-O7).

All other imprints of trackways O3 and O7 and in DLSII-O1, O2, O4–O6, O8, and O9, are consistent with these two tracks in morphology. Trackways are narrow-gauge, with the possible exception of DLSII-O9 (Fig. 7).

All tracks from DLSII-O1–O9 are consistent with *Shenmuichnus wangi* Xing et al. (in press) in size and morphology. *Shenmuichnus wangi* is similar to contemporary *Shenmuichnus youngteilhardorum* from Shaanxi Province (Li et al., 2012), but is obviously larger than the latter and has a different manus trace position (Xing et al., in press).

Three pes prints (DLSII-O3-RP1, DLSII-O5-LP1 and RP2; Fig. 5) show an elongated "heel" (metatarsal) trace. "Heel" traces here are not related to resting or crouching tracks and may instead be extramorphological variations, caused by deep and soft sediments (e.g., Gatesy et al., 1999; Xing et al., 2014a). Interestingly, these sedimentary conditions do not appear to have impacted the speed of the trackmakers (e.g. Xing et al., 2015a).

Theropod Tracks

Description and Comparisons

One incomplete natural mold from the Dalishu tracksite (Xing et al., in press) suggests that this specimen may similar to *Kayentapus* Welles, 1971 (Lockley et al., 2011) based on gracile digits and probably wider digit divarication. DLSII preserves at least four isolated theropod tracks (DLSII-TI1–TI4, Fig. 7), which are 28.5–36.4 cm long and substantially larger than *Shenmuichnus wangi* (18.2–21.5 cm). The L/W ratio is 1.3–1.6 and the divarication angles between digits II–IV are 35° and 63°, respectively.

DLSII-TI3 (Fig. 7) is the best preserved. It shows relatively slender digits. In LSII-TI3, digit II shows two digit pads, whereas in digits III and IV these are indistinct; a sub-ovoid metatarsophalangeal pad lies nearly in line with the axis of digit III, close to the proximal end of digit IV. The length/width ratio of the anterior triangle is 0.42;

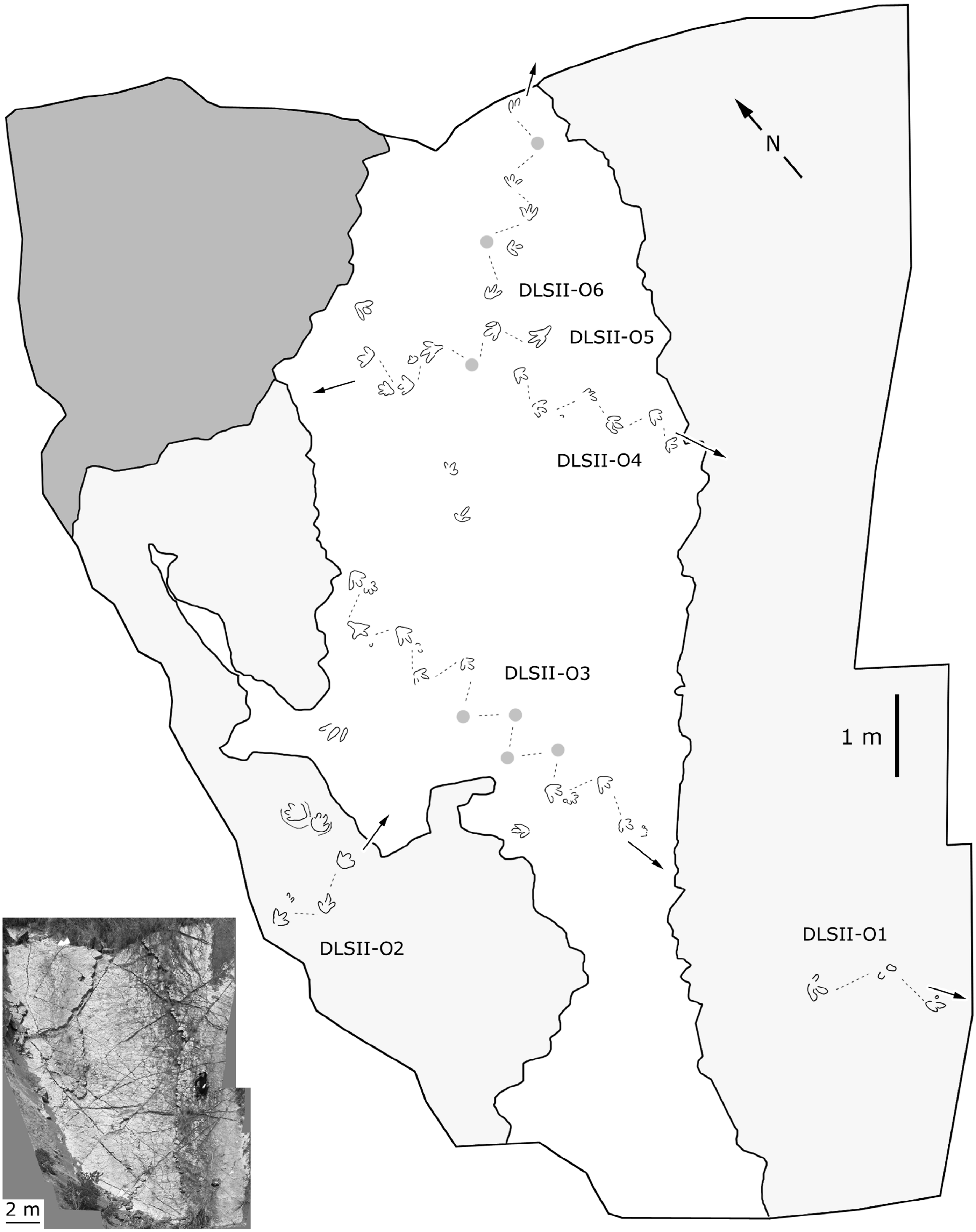

FIGURE 4. Photograph and interpretive outline drawing of track-bearing levels and surface I of Dalishu tracksite II.

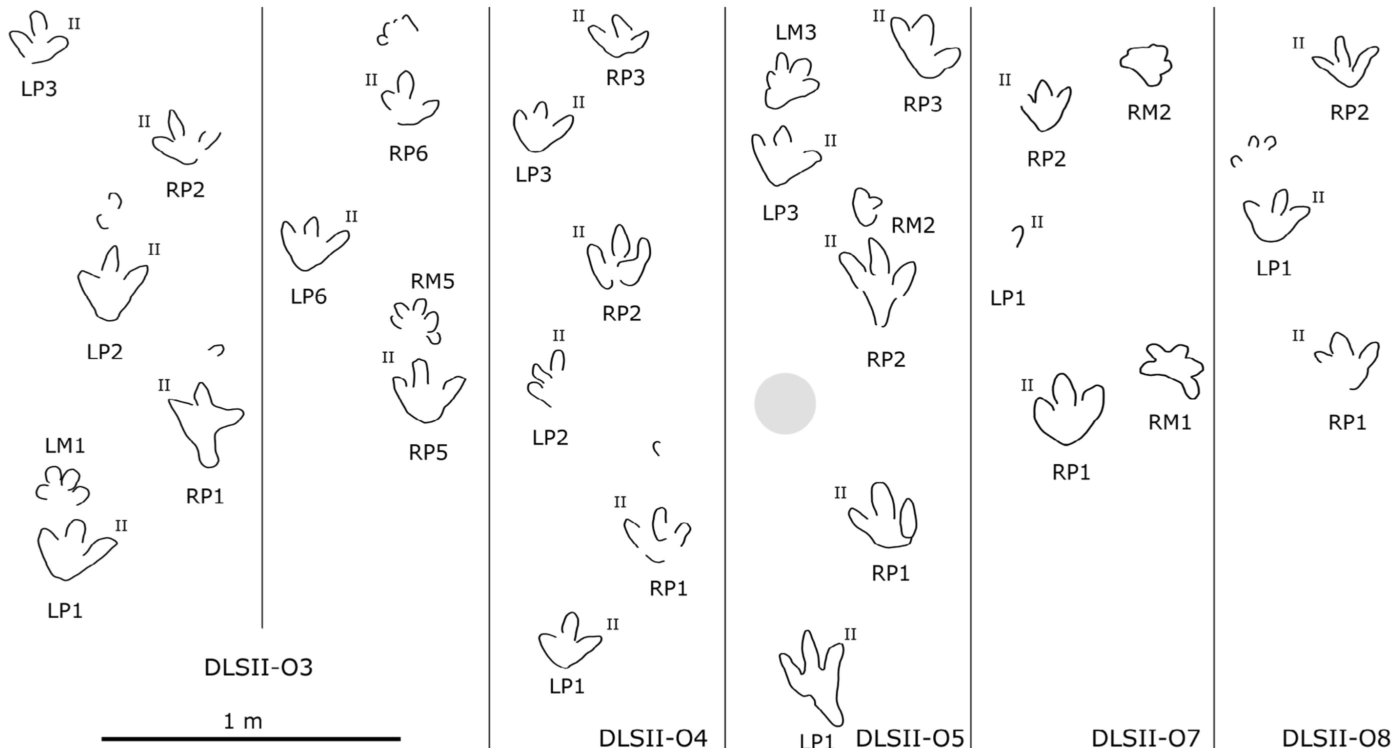

FIGURE 5. Interpretative outline drawings of *Shenmuichnus wangi* trackways described in this study. 1 m scale refers to all boxes with the trackways.

it is characterized by weak to moderate mesaxony. Some features are typically seen also in the ichnogenus *Kayentapus*, however, because of the only moderate preservation of the isolated imprints lacking more distinct traces of the pads, an assignment to *Kayentapus* seems to be doubtful. In addition, the metatarsophalangeal pad of digit IV well separated from the rest of the digit impressions (Lockley et al., 2011) is not among features of DLSII specimens.

Changpeipus carbonicus (Young, 1960) is another reasonably well-preserved theropod track that exhibits numerous distinctive features, such as its digital pad formula, which allies it to the *Grallator–Eubrontes* plexus (sensu Olsen, 1980). Some of the theropod tracks from the DLSII surfaces described here strongly resemble *Changpeipus*. Xing et al. (2009) introduced *Changpeipus pareschequier* as a new ichnotaxon based on material from the Lower Jurassic Lufeng Basin, Yunnan Province. Lockley et al. (2013) referred *Changpeipus pareschequier* to *Eubrontes pareschequier*. Xing et al. (2014a) reviewed and re-described all *Changpeipus* ichnospecies from China, and considered *Changpeipus* and *Eubrontes* to be similar ("sister") ichnotaxa. The most significant difference being the larger metatarsophalangeal pad and the wider digit II-IV divarication angle of *Changpeipus* (Xing et al., 2014a). DLSII-TI1–TI4 are similar to *Changpeipus carbonicus*, and also differ from *Eubrontes* in having a wider digit divarication (35°–63°) and larger and more V-shaped metatarsophalangeal pads. Therefore, we assign DLSII-TI1–TI4 to *Changpeipus carbonicus*.

Comparison of Skeletal and Track Records

As required by "2013 National Project for Preservation of Geologic Relics of Dinosaur in Lufeng" funded by the Ministry of Land and Resources of PRC, the Research Center for Geopark (Geoheritage) Investigation and Evaluation, China University of Geosciences conducted a geological relic investigation in Lufeng County and recorded numerous fossil sites and skeletal fossils. Skeletal records (Table 2) show that basal sauropodomorphs dominated the faunas of Lower Jurassic strata in the Lufeng Basin (87%), compared to basal sauropods (3%), theropods (8%) and basal thyreophorans (3%).

However, track records are significantly different from skeletal records (Table 3). Based on raw track data (not trackways) large theropod tracks consisting of *Eubrontes*-type tracks account for 17%, and small *Anomoepus*-type tracks account for 31%, while the large ornithischian *Shenmuichnus wangi* is the most common tack (52 %). The track record of the Lufeng Basin lacks evidence corresponding to basal sauropodomorphs and basal sauropods. Conversely, only two thyreophoran taxa are known representing single individuals (Table 3). It is tempting to attribute the *Shenmuichnus wangi* tracks to at least

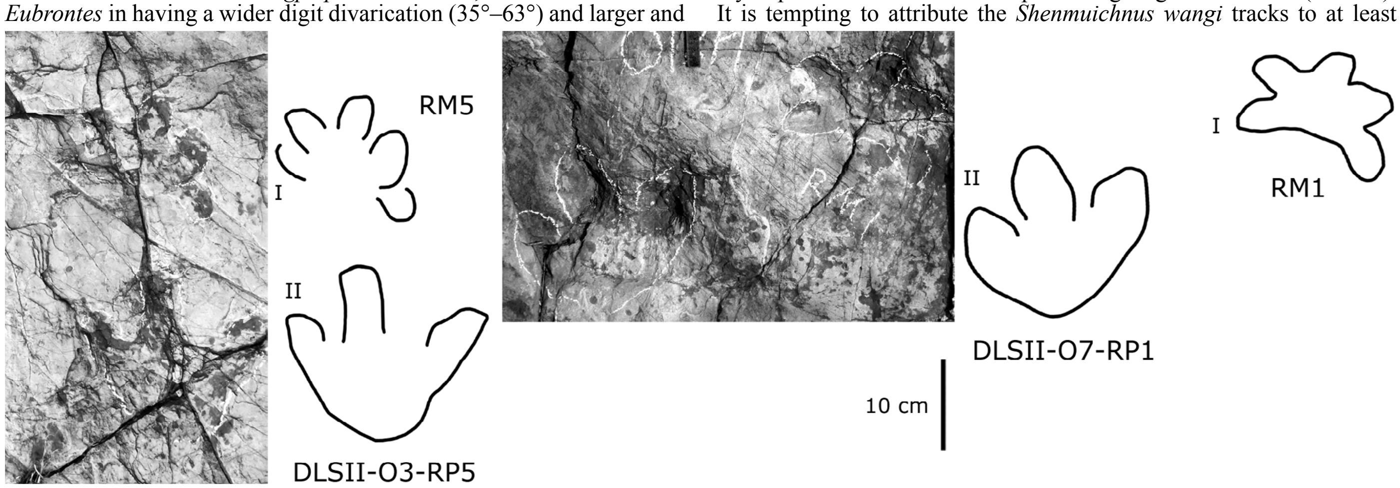

FIGURE 6. Photographs and interpretive outline drawings of best-preserved *Shenmuichnus wangi* tracks at Dalishu tracksite II.

TABLE 1. Measurements (in cm and degrees) of large ornithischian and theropod tracks from Dalishu tracksite II, Yunnan Province, China.

Number	ML	MW	L/W	II–IV	PL	SL	PA
DLSII-O3-LP1	20.8	26.4	0.8	78°	62.0	93.0	106°
DLSII-O3-LM1	14.6	—	—	—	—	—	—
DLSII-O3-RP1	28.7	25.9	1.1	—	54.5	92.2	125°
DLSII-O3-LP2	25.4	23.6	1.1	68°	49.4	83.7	105°
DLSII-O3-RP2	19.9	—	—	90°	56.3	—	—
DLSII-O3-LP3	17.6	20.3	0.9	95°	—	—	—
DLSII-O3-RP5	21.8	24.4	0.9	73°	59.2	97.2	112°
DLSII-O3-RM5	12.8	18.7	0.7	—	—	—	—
DLSII-O3-LP6	18.6	22.2	0.8	71°	57.8	—	—
DLSII-O3-RP6	17.9	19.3	0.9	88°	—	—	—
Mean-M	13.7	18.7	0.7	—	—	—	—
Mean-P	21.3	23.1	0.9	80°	56.5	91.5	112°
DLSII-O4-LP1	19.2	21.2	0.9	87°	46.1	84.2	98°
DLSII-O4-RP1	18.5	21.8	0.9	78°	64.2	96.3	107°
DLSII-O4-LP2	—	—	—	—	55.4	89.1	118°
DLSII-O4-RP2	21.8	19.3	1.1	64°	48.7	70.7	109°
DLSII-O4-LP3	17.6	19.3	0.9	71°	38.1	—	—
DLSII-O4-RP3	14.1	20.2	0.7	97°	—	—	—
Mean-P	18.2	20.3	0.9	79°	50.5	85.1	108°
DLSII-O5-LP1	34.0	21.3	1.6	—	55.0	—	—
DLSII-O5-RP1	22.9	20.6	1.1	65°	—	81.9	—
DLSII-O5-LP2	—	—	—	—	—	—	—
DLSII-O5-RP2	30.3	25.3	1.2	—	47.8	77.8	90°
DLSII-O5-LP3	20.6	24.8	0.8	82°	61.5	—	—
DLSII-O5-LM3	16.3	19.0	0.9	—	—	—	—
DLSII-O5-RP3	21.0	25.5	0.8	80°	—	—	—
Mean-M	16.3	19.0	0.9	—	—	—	—
Mean-P	25.7	23.5	1.1	76°	54.8	79.9	90°
DLSII-O7-RP1	20.5	22.0	0.9	63°	61.0	101.0	125°
DLSII-O7-RM1	12.0	18.5	0.6	—	—	99.0	—
DLSII-O7-LP1	—	—	—	—	53.0	—	—
DLSII-O7-RP2	20.5	19.0	1.1	—	—	—	—
DLSII-O7-RM2	13.0	18.0	0.7	—	—	—	—
Mean-M	12.5	18.3	0.7	—	—	99.0	—
Mean-P	20.5	20.5	1.0	63°	57.0	101.0	125°
DLSII-O8-RP1	19.5	>20	—	73°	51.0	107.5	134°
DLSII-O8-LP1	19.5	23.5	0.8	82°	65.5	—	—
DLSII-O8-RP2	22.5	26.5	0.8	87°	—	—	—
Mean-P	20.5	25.0	0.8	81°	58.3	107.5	134°
DLSII-TI1	36.1	23.1	1.6	55°	—	—	—
DLSII-TI2	28.5	18.7	1.5	45°	—	—	—
DLSII-TI3	36.4	29.1	1.3	62°	—	—	—
DLSII-TI4	29.9	22.7	1.3	63°	—	—	—

Notes: **ML**, maximum length; **MW**, maximum width; **PA**, pace angulation; **PL**, pace length; **SL**, stride length; **II–IV**: angle between digits II and IV; **L/W**: maximum length/maximum width.

TABLE 2. Statistics of species and specimens of Early Jurassic *Lufengosaurus* fauna in the Lufeng Basin.

Taxon	References	Number
Basal sauropodomorphs		
Lufengosaurus huenei	Young, 1941a	95*
Lufengosaurus magnus	Young, 1947	
Yunnanosaurus huangi	Young, 1942	
Lufengosaur type	Unidentified specimens# Reisz et al., 2013	5#
"*Gyposaurus*" (*Anchisaurus*) *sinensis*	Young, 1941b Galton and Upchurch, 2004	1
Jingshanosaurus xinwaensis	Zhang and Yang, 1995	2
Xixiposaurus suni	Sekiya, 2010	1
basal sauropods		
Chinshakiangosaurus chunghoensis	Dong, 1992 Upchurch et al., 2007	1
Kunmingosaurus wudingensis (nomen nudum)	Zhao, 1985	1
"*Yunnanosaurus*" *robustus*	Barrett, 1999	1
Yizhousaurus sunae	Chatterjee et al., 2010; Xing et al., 2015b	1
Theropods ##		
Megapnosaurus sp.	Irmis, 2004	1
Sinosaurus triassicus (= "*Dilophosaurus*" *sinensis*)	Xing, 2012; Xing et al., 2014c	5
Eshanosaurus deguchiianus	Xu et al., 2001	1
Panguraptor lufengensis	You et al., 2014	1
middle-sized theropod	Unidentified specimen	1
basal thyreophorans		
Tatisaurus oehleri	Simmons, 1965	1
Bienosaurus lufengensis	Dong, 2001	1
unnamed specimen	Dong Z.M., pers. comm.	1

* World Dinosaur Valley Park, Yunnan Province is exhibiting 45 and 47 skeletons of *Lufengosaurus huenei* and *L. magnus* respectively. The Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences preserves one skeleton of *L. huenei*. *Yunnanosaurus* is presented by two skulls, but some specimens may be referred to *Lufengosaurus magnus*. In general, all of available *Lufengosaurus* and *Yunnanosaurus* shall be further classified.

Lufeng Land and Resources Bureau and Lufeng Museum, respectively, conserve at least 2 unidentified Lufengosaur type skeletons, and an embryo is kept by Chuxiong Prefectural Museum (Reisz et al., 2013). In addition, there are countless other incomplete fragments.

Lukousaurus yini (Young, 1948) and "*Dianchungosaurus lufengensis*" (Yang, 1982) are referred to crocodylomorphs (Irmis, 2004; Barrett and Xu, 2005)

one of these taxa (*Tatisaurus oehleri* and *Bienosaurus lufengensis*), even though a correlation of ichnotaxa with distinct biological species cannot be proven. All in all, the track record is less diverse and assemblages different in composition when being compared to the present osteological record.

At last in east Asia, sauropod tracks are quite common in isolated inland basins with red bed deposits, where evaporation exceeded precipitation, such as in the Jurassic Sichuan Basin (Xing et al., 2014b). Body fossils and tracks suggest that sauropodomorphs flourished in the Jurassic Sichuan Basin.

It is puzzling as to why sauropodomorph tracks are not found in the Lufeng Basin. Their skeletal fossils are common in the mudstone sequences, whereas the ornithischian and theropod tracks described here are associated with sandstone units. However, these contextual facies differences are not considered to be of major significance. Track preservation generally requires a heterolithic alternation of sedimentary layers, particularly between sands and mud or silt, in order to create surfaces suitable for preservable tracks to be registered. Thus tracks may be made all over floodplains, but will not be well-preserved or noticed in continuous mud and silt sequences, whereas they may be more conspicuous and well-preserved where sand units are deposited. It is possible that some animals preferred river courses or other local paleoenvironments where sand layers were deposited or redistributed. They frequented for example lake shorelines, rather than parts of the

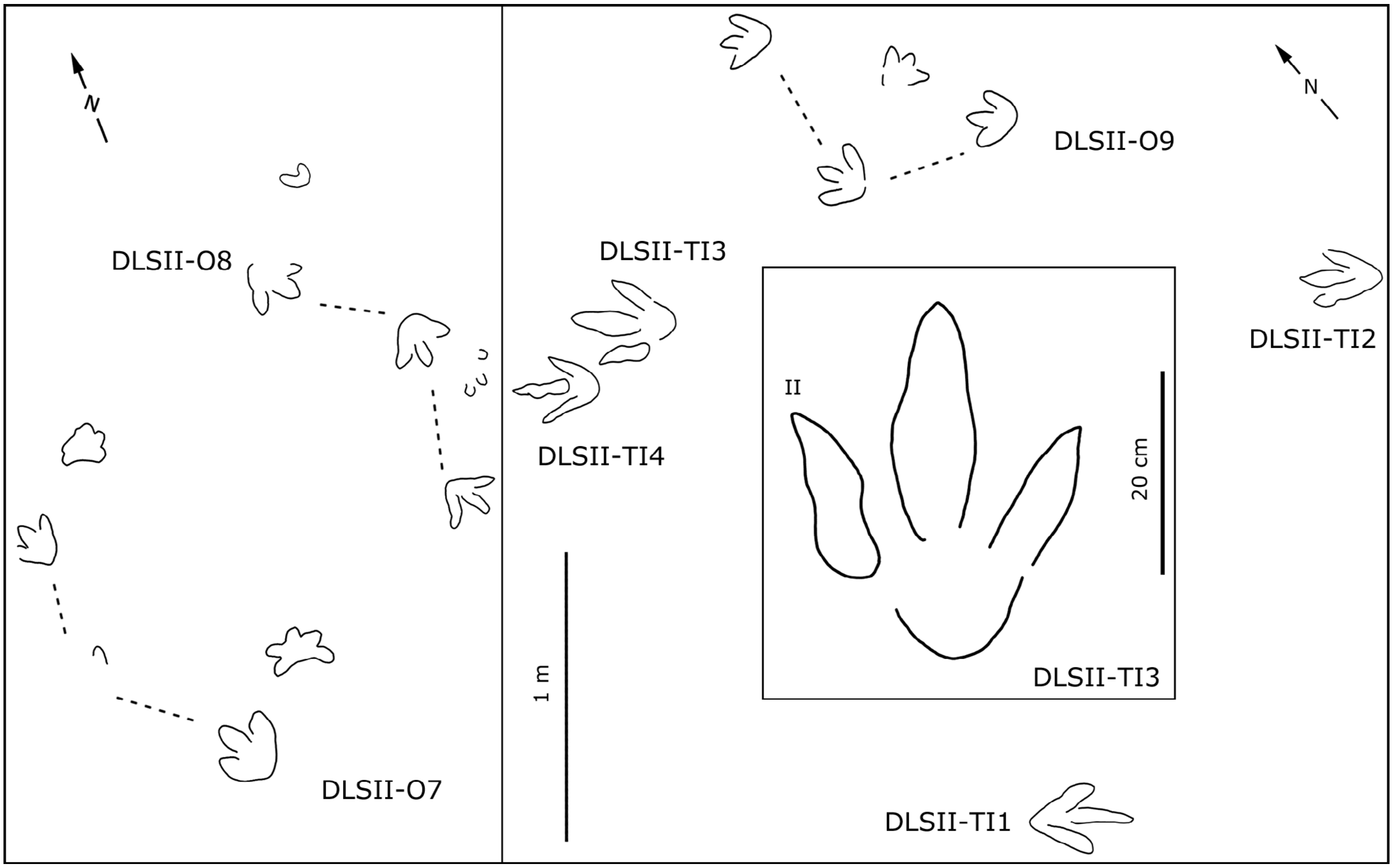

FIGURE 7. Map and interpretive outline drawings of track-bearing levels with surfaces II and III of Dalishu tracksite II showing ornithopod (*Shenmuichnus wangi*) and theropod (*Changpeipus carbonicus*) trackways.

TABLE 3. Statistics of Early Jurassic ichnotaxa and trackmakers in the Lufeng Basin.

Taxon	References	Trackmakers
Theropods		
? *Kayentapus*–type from DLS	Xing et al., in press	1
Changpeipus carbonicus from DLSII	this paper	4
Eubrontes pareschequier	Xing et al., 2009, 2014; Lockley et al., 2013	2
basal thyreophorans		
Shenmuichnus wangi DLS site	Xing et al., in press	4
DLSII site	this paper	18
Anomoepus-type tracks	unpublished data	13

floodplain where mud and silt deposition predominated. However, this is merely speculative, and any suggestions about differential preference of different local substrates by different animals is conjectural. It is more likely that taphonomic effects and different preservation potential, rather than preferred environments, controlled the track record in distinct substrates. This suggests that tracks that were subsequently preserved are a random sample of the animals that crossed areas with track preservation potential.

Lockley (1991) and Lockley et al. (1994) discussed the categorization of formations and facies according to the relative abundance (proportions) of trace (tracks) and body fossils. They defined Type 1 deposits as containing only tracks, Type 2 as track dominated, Type 3 as having tracks and bones in more or less equal abundance, Type 4 as bone-dominated and Type 5 as containing only bones. Deposits of Type 2, 3 and 4 may be subdivided in subcategory "a" where the track and bone evidence is consistent with regard to faunal elements or subcategory "b" where the evidence is inconsistent. It is clear from present evidence that the Lufeng Formation is a Type 3b or Type 4b deposit where both tracks and bones occur, with bones abundant, but indicating inconsistency in the evidence they provide of faunal elements. However, identifying such inconsistencies does not explain them. We can only infer that tracks indicate the animals that lived in or passed through the area, while bones indicate those that died in the area (if the bones were not transported), and may have lived in the area or nearby.

In the final analysis the combined evidence tells us more than the trace or body fossil evidence alone. Clearly, there are differential biases leading to the preservation of body fossils and tracks, and so the fossil record is very incomplete. However, the change in categorization of a deposit from either Type 1 or Type 5 to Types 2, 3 or 4, by definition, adds useful information. Likewise, in categorizing a Type 2b, 3b or 4b deposit, we also by definition recognize that the combined body and trace fossil record is necessary for a fuller description of the fauna. Such is the case in the recognition of ornithischian trackway components in the Lufeng Formation.

CONCLUSIONS

Ornithischian- and theropod-dominated footprint assemblages from the Dalishu tracksite representing the Lower Jurassic Lufeng Formation of Yunnan Province, China are dominated by the ichnospecies *Shenmuichnus wangi* (52%) with small *Anomoepus*-type tracks (31%) and *Eubrontes*-like theropod tracks (17%) of the assemblage. These data can be added to reports of the ichnospecies *Changpeipus pareschequier* from the Lower Jurassic Lufeng Formation at the Yaozhan tracksite, in Lufeng County (Xing et al., 2009) to give a more complete picture of the ichnofauna.

There is some consistency between the reports of relatively abundant thyreophoran trackways and rare thyreophoran body fossils. However, the track evidence contrasts with the skeletal record concerning sauropodomorphs, because the Lufeng Basin is dominated by abundant basal sauropodomorphs and basal sauropods which are as yet unknown from the track record. Due to these inconsistencies between the track and body fossil records, the Lufeng Formation can be classed as a Type 4b deposit: i.e., one in which bones predominate over tracks with significant inconsistencies between the two records in terms of the composition and relative abundance of the represented faunal components.

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