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First Early Jurassic Ornithischian and theropod footprint assemblage and a new ichnotaxon *Shenmuichnus wangi* ichnosp. nov. from Yunnan Province, southwestern China

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The new ichnospecies, *Shenmuichnus wangi* ichnosp. nov., is the first evidence for the presence of large ornithischians in the Early Jurassic of Yunnan Province, whereas the known skeletal record documents small species only. Until now *Shenmuichnus* was known from a single locality in Shaanxi Province by the ichnospecies *Shenmuichnus youngteilhardorum*. Compared with the latter, *Shenmuichnus wangi* is larger and shows a different trackway configuration, particularly in the relative position of manus and pes imprints. Palecologically, the occurrence of *Shenmuichnus wangi* in a red bed facies indicates the preference of distinctive environments of trackmakers of both ichnospecies, questioning former hypotheses of exclusivity of ornithischians in more humid climates. By abundance both skeletons and footprints of ornithischians suggest their role as a minor component in Early Jurassic saurischian dominated dinosaur faunas in this region.

Keywords: Early Jurassic; Lufeng Basin; dinosaur tracks; ornithischians; *Shenmuichnus*

1. Introduction

In southwestern China, the majority of Jurassic vertebrate fossils is known from the Lufeng (Young 1951) and Sichuan basins (Peng et al. 2005). Several vertebrate fossil discoveries were also made in the Changdu Basin of Tibet, however, detailed descriptions of these findings have yet to be published. Most dinosaur body fossils known from the Lufeng Basin come from Lower–Middle Jurassic sections, while in the Sichuan Basin the record essentially originates from Middle–Upper Jurassic strata. In particular, stegosaurs are abundant in the Middle–Upper Jurassic of the Sichuan Basin, whereas thyreophorans are rare in the Lower Jurassic of both basins (Simmons 1965; Dong 2001).

In February 2014, T. Wang, from Lufeng Land and Resources Bureau, discovered three trackways (19 pes–manus sets in total) of quadrupedal ornithischians in the Lower Jurassic Lufeng Formation at Dalishu, Konglongshan Town, Lufeng County (Figure 1). In the following these trackways, together with an isolated theropod pes imprint, are described.

The former are assigned to the ichnogenus *Shenmuichnus* and a new ichnospecies. *Shenmuichnus* was originally described and named based on material from the Lower Jurassic in the Shenmu area of Northern Shaanxi Province (Li et al. 2012). It is the first *Moyenisauripus* morphotype track reported from Asia. *Moyenisauripus* shows a wide range of preservational variations co-occurring on the same surface. This suggests to be cautious when assigning ornithischian footprints to distinct ichnotaxa such as *Sinoichnites* (Kuhn, 1958), *Moyenisauropus* (Ellenberger, 1974), *Deltapodus* (Whyte and Romano, 2001) and *Ravatichnus* (Gabouniya and Kurbatov, 1982).

Except *Shenmuichnus* and *Deltapodus*, before 2014, Early Jurassic ornithischian tracksites in China only included *Sinoichnites* from Shenmu, Shaanxi Province (Kuhn 1958), *Anomoepus* from Jinlijing, Sichuan Province (Lockley and Matsukawa 2009), and Wulatezhongqi, Inner Mongolia (Li et al. 2010).

The new record from the Lufeng Formation of Yunnan Province is the second occurrence of *Shenmuichnus* approximately 1700 km from the Shaanxi locality. These tracks are larger compared with those from Shaanxi Province and are preserved in typical red bed facies strata. They indicate the presence of large ornithischians in deposits otherwise known for abundant sauropodomorphs (Dong 1992).

Institutional abbreviations and acronyms: DLS, Dalishu tracksite, Yunnan Province, China; M, manus prints; P, pes prints; R/L, right/left.

2. Materials and methods

No permits were required to conduct this study. Three trackways and two isolated tracks are preserved as concave epireliefs on a surface that is approximately 4.5 m long and 2.5 m wide and that shows a dip of about 12°. High flood water or heavy rainfall has eroded an

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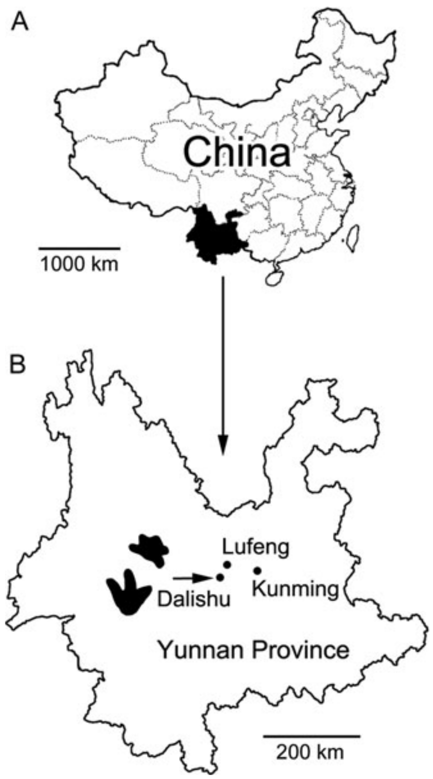

Figure 1. Geographic map with the position of the Dalishu dinosaur footprint locality (indicated by the footprint icon) (A, B).

overlaying layer of siltstone, exposing the lower track bearing sandstone layer. All pes traces are distinct, however, the manus traces are variably preserved as simply oval, crescentic or tridactyl–pentadactyl prints. These differences likely reflect preservational variation and may be due to the distinctive weight distribution between fore and hind limbs.

Tracks were individually catalogued and outlined with chalk. The complete track surface was traced on transparency film. Drawings (cataloged as CUGB-DLS) are housed at China University of Geosciences, Beijing. Tracks were measured and scanned following the procedures of Leonardi (1987), and a digital distribution pattern was made via Adobe PhotoShop CS6.

Besides maximum length (ML), maximum width (MW), divarication angles between digits (II–III, III–IV, II–IV), stride length (SL), pace length (PL) and pace angulation (PA), the mesaxony of pes imprints was calculated. This is the degree to which the central digit (III) protrudes anteriorly beyond the medial (II) and lateral (IV) digits. It can be measured as the ratio of the height of the anterior triangle (from base to apex at tip of digit III) over base (= width between tips of digits II and IV): i.e. height/base (L/W) *sensu* Weems (1992) and Lockley (2009).

For the trackways of quadrupeds, 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) and the pes length (ML) (according to Marty 2008; Marty et al. 2010). If the ratio is < 1.0, 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 > 2.0 are considered as very wide-gauge (Marty 2008).

3. Geological setting

In the Lufeng Basin, the red beds of the Lufeng Series are approximately 750 m thick, and are conventionally divided into upper and lower units (Bien 1941). Based on evolutionary ‘grades’ and stratigraphic correlations of vertebrate fossils, Young (1951) considered the red beds as Late Triassic in age. Later, Sheng et al. (1962) proposed an Early Jurassic age for the Lower Lufeng Formation and a Middle Jurassic age for the Upper Lufeng Formation. Zhang and Li (1999) mapped Lao Changjing, Chuanjie, and determined the relative stratigraphic positions of the dinosaur fossils in the lower part of the Upper Lufeng Formation. Fang et al. (2000) restricted the name ‘Lufeng Formation’ to what was previously called the Lower Lufeng Formation and further divided it into Shawan and Zhangjiaao members. The latter corresponds to the terminology scheme that we follow here.

The tracksite reported herein (GPS: 24°55′57.50″N, 102°0′51.53″E) was discovered in Dalishu, 7.5 km southwest of World Dinosaur Valley Park, Lufeng County (Figure 1). The tracksite is within the protection of the Lufeng Dinosaur National Geological Park, Yunnan Province. The tracks are preserved in a sandstone layer within the lower Zhangjiaao Member of the Lufeng Formation (Figure 2). Sauropodomorph (*Lufengosaurus*) skeletal fossils were discovered in both the upper and the lower units of the Dalishu tracks layer. Sauropod and theropod bones have also been found in the Middle Jurassic Chuanjie Formation (Xing et al. 2014) (Figure 2). The lower part of the Lufeng Formation includes shallow lacustrine strata. This is based on the chemical composition of deposits (Tan 1997). Higher levels are interpreted as being deposited in piedmont plain, lake and fluvial environments, based on the vertebrate record (Luo and Wu 1995).

4. Systematic palaeontology

Ornithischia Seeley, 1887

?Thyreophora Nopcsa, 1923

Ichnofamily Anomoepodidae Lull, 1904

Ichnogenus *Shenmuichnus* Li, Lockley, Zhang, Hu, Matsukawa and Bai, 2012

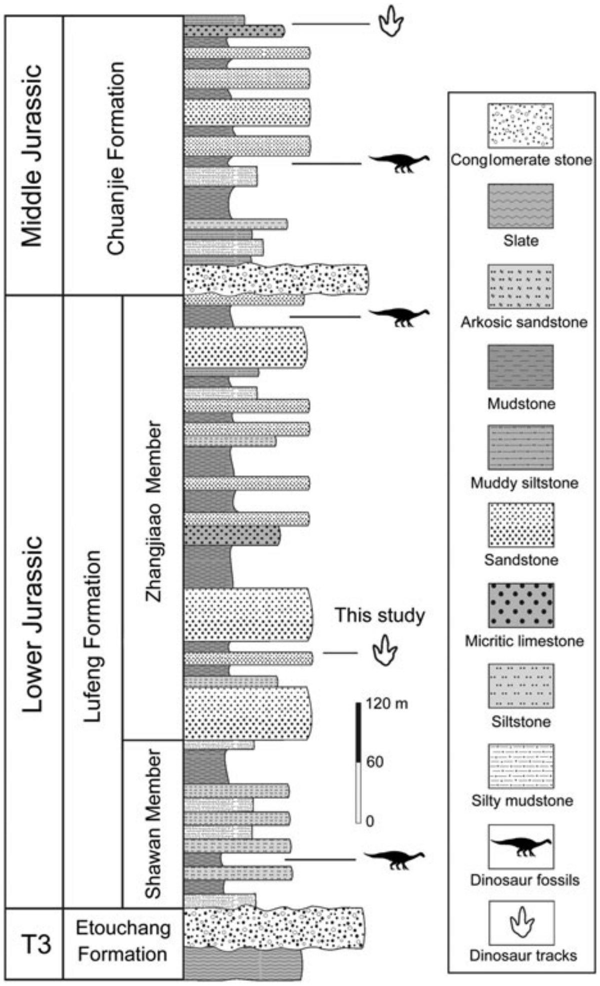

Figure 2. Lithological section of the Lufeng Formation and related strata (modified from Fang et al. (2000) and Sekiya (2011) showing levels with footprints and skeletal remains (icons).

Type ichnospecies *Shenmuichnus youngteilhardorum* Li, Lockley, Zhang, Hu, Matsukawa and Bai, 2012

Shenmuichnus wangi ichnosp nov

Figures 3–7, Table 1

Diagnosis: Narrow gauge trackways (WAP/ML = 0.94) showing large heteropody (1:1.48). Pes tracks tridactyl, large (22–23 cm long and 20–24 cm wide), with robust digits and weak mesaxony. Divarication between digits II and IV ranging 67–73°. Manus tracks pentadactyl and symmetrical along digit III, wider than long, with a length/width ratio of 0.6. Manus tracks aligned with antero-lateral margins of pes tracks formed by digits III and IV. Pes tracks rotated inward (22°), manus tracks rotated outward (35°), relative to trackway midline. Average pace angulation of manus tracks 92°, of pes tracks 125°. Short steps with pace length being 2.0–2.7 × footprint length.
Holotype: A trackway consisting of five successive pes–manus sets DLS1-RP1-RM1–DLS1-RP3-RM3.
Paratypes: Trackways DLS2 and DLS3 (consisting of eight and five track pairs, respectively), and the isolated set DLSI-RP1-RM1 from same surface are designated as paratypes. As with the holotype, these specimens (except DLSI) remain in the field. DLSI is stored in the Dinosaur Museum of Lufeng Dinosaur National Geological Park, Yunnan Province, China.
Etymology: The specific name is in honour of Mr Tao Wang, one of the best fossil hunters in China who has found nearly a hundred of *Lufengosaurus* skeletal remains and the tracks of this study.
Locality and horizon: Zhangjiaao Member of Lufeng Formation, Lower Jurassic. Dalishu tracksite, Lufeng County, Yunnan Province, China.
Description: DLS1-RP3 and RM3 are the best-preserved tracks. DLS1-RP3 is tridactyl and its length slightly exceeds its width (L/W = 1.05). The trace of digit III is longest, followed by digits II and IV which is shortest. The distal end of each digit trace is round, blunt, and the most deeply impressed part. The metatarsophalangeal region is smoothly curved. The divarication is wide (67° between digits II and IV), the divarication between digits III and IV being larger than that between digits II and III. The anterior triangle has a length width ratio of 0.3. Therefore, pes imprints are weakly mesaxonic. The heteropody (manus: pes) is 1:1.48. In addition, the quantified trackway gauge of DLS1 (WAP/ML) is 0.94, which corresponds to the definition of narrow-gauge (Marty 2008).

DLS1-RM3, which is the manus imprint of the holotype set, is relatively large and pentadactyl. It is symmetrical, with the axis being aligned with the antero-lateral margin formed by digits III and IV (i.e. opposite the line connecting the tips of digits III and IV) of the pes trace. The width of DLS1-RM3 exceeds the length (the ML/MW ratio is 0.6). Digits are fan-shaped and widely spread, with digit V pointing backward. Digits I and V are the most developed. All digits are subequal in length and show blunt ends without traces of the nails. The medial portion of the print is the deepest. DLS1-RM3 is rotated approximately 23° outward from the trackway axis, whereas the inward rotation of the corresponding pes impression DLS1-RP3 is approximately 13°. A few manus tracks are rotated inward relative to the trackway axis, as are all pes impressions, but precise rotation measurements are difficult to take due to the poor preservation of some imprints. The average pace angulation of the manus traces is 92°, while that of the pes traces is 125°.

The trackways DLS2 and DLS3 are slightly longer than DLS1 but are consistent with DLS1 in morphology. The step lengths of DLS2 and DLS3 trackways (62.6 and 56.6 cm, pes) are larger than in DLS1 (43.6 cm, pes); this is likely to reflect different speeds of different trackmaking individuals. However, the pace angulation of DLS2 and DLS3 trackways (127° and 129°, pes) is only slightly larger than in DLS1 (125°, pes).

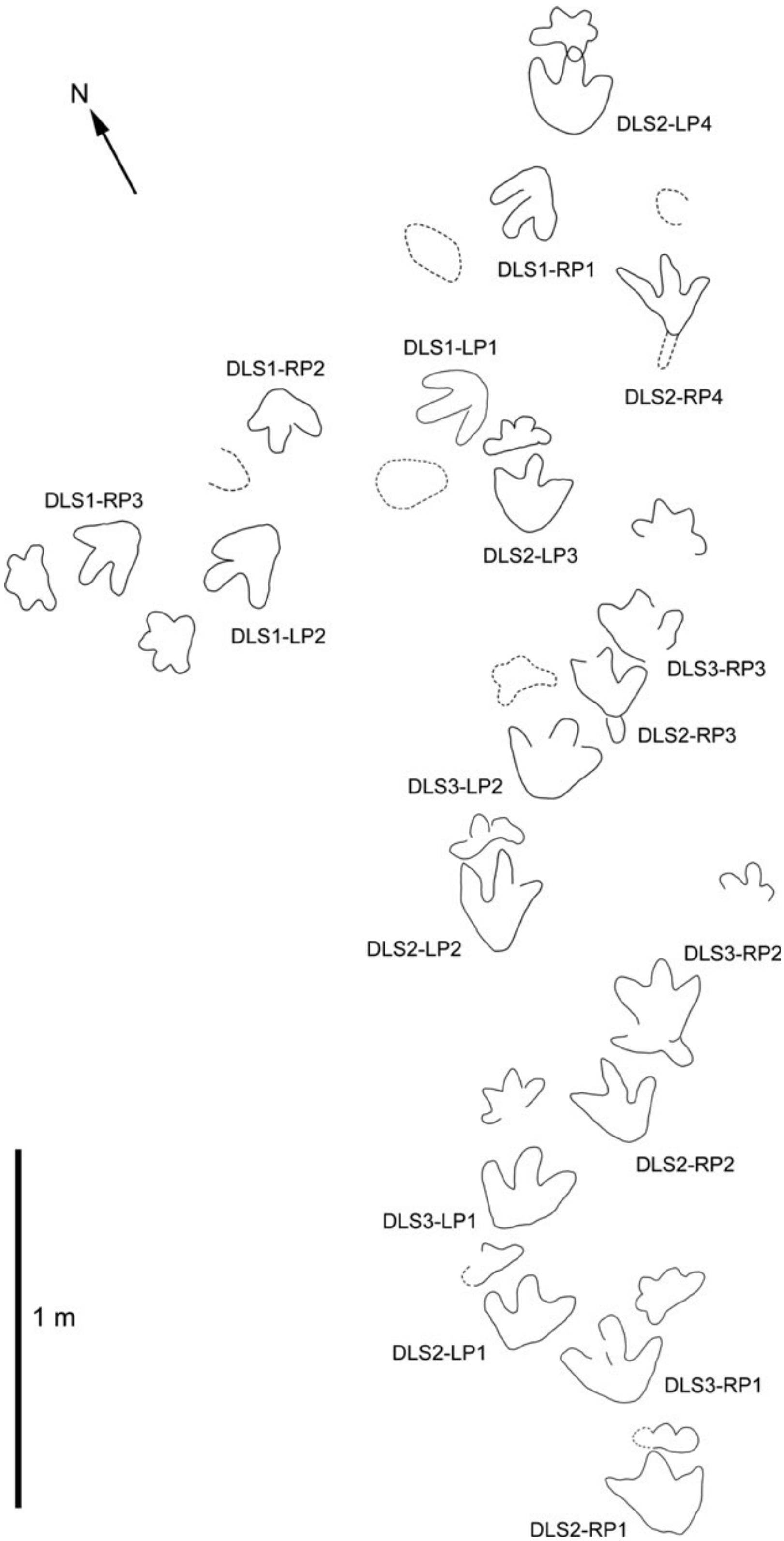

Figure 3. Map and interpretative outline drawing of track-bearing level at Dalishu tracksite showing trackways of a quadruped ornithischian DLS1–DLS3 assigned here to *Shenmuichnus wangi* ichnosp. nov. DLS1 represents the holotype trackway.

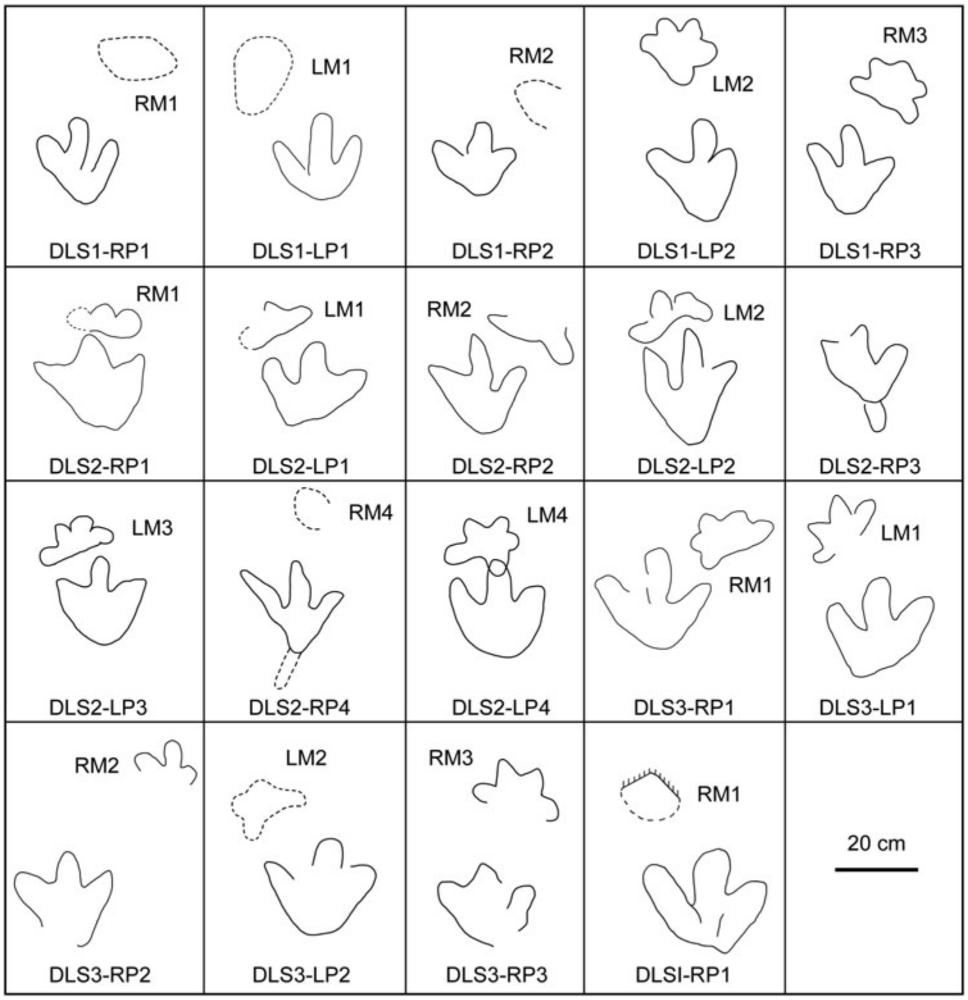

Figure 4. Interpretative outline drawings of *Shenmuichnus wangi* ichnosp. nov. tracks from the Dalishu tracksite. DLS1 represents the holotype.

RP3 and RP4 of DLS2 record elongated 'heel' (metatarsal pad) traces. The natural cast track DLSI1 (Figure 6) is an isolated pes–manus set, where the manus trace is an oval print with its axis also being aligned with the antero-lateral margin of the pes trace formed by digits III and IV. The pes trace is consistent with DLS1-RP3 in morphology.

Comparison and discussion: By the general pattern with imprints that reflect a functionally tridactyl pes which is rotated towards the midline, and by the pentadactyl, fan-shaped manus that often points outward, the Dalishu tracks resemble the ichnogenus *Anomoepus* Hitchcock, 1848 (Figure 8(A)). Further diagnostic features of *Anomoepus* such as the relatively wide digit divarication and the position of the metatarsophalangeal pad IV in line with digit III (Olsen and Rainforth 2003) are also present in the Dalishu tracks. *Anomoepus* was re-studied in detail and diagnosed by Olsen and Rainforth (2003). It is a typical ornithischian trackway attributed to a facultative biped. Its morphology is also similar to that of the ichnogenus *Moyenisauropus* (Figure 8(B)) that was originally described by Ellenberger (1974) from the Triassic–Jurassic Elliot Formation of the Stormberg Group of southern Africa and subsequently synonymised with *Anomoepus* by Haubold (1986), Olsen and Galton (1984) and Olsen and Rainforth (2003). Ellenberger (1970) named eight *Moyenisauropus* ichnospecies (Ellenberger 1970, 1972, 1974). As noted by Lockley and Gierlinski (2006), who examined the types of *Moyenisauropus* in the ichnological collections at Montpellier University, France, several of these ichnospecies represent *Anomoepus* and can be classified in the ichnofamily Anomoepodidae (Lull 1904). However, after Gierliński (1991, 1999) and Gierliński and Potemska (1987), the type ichnospecies *Moyenisauropus natator* is distinct from *Anomoepus*. Gierliński and Potemska (1987) were the first to recognise *Moyenisauropus* from Europe. The *Shenmuichnus* material described herein is similar to *Moyenisauropus natator* and

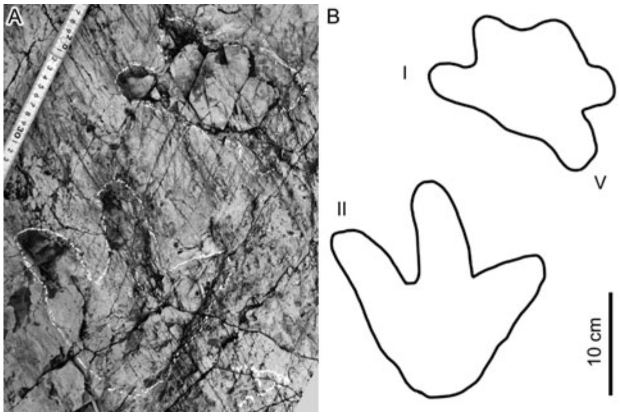

Figure 5. Photograph (A) and outline drawing (B) showing pes–manus set DLS1-RP3-RM3 and detail of the holotype trackway of *Shenmuichnus wangi* ichnosp nov. from the Dalishu tracksite.

Anomoepus, however, the latter two occasionally show a distinct hallux impression and sharp claws, whereas the Dalishu tracks are strictly tridactyl and claw traces are absent or indistinct. The latter feature could simply be related to preservation, whereas the lack of a hallux in all imprints is probably anatomically/gait controlled. Other differences of *Shenmuichnus* to *Moyenisauropus* and *Anomoepus* are the lack of occasional tail impressions, whereas short slender traces of the metatarsals, typically occurring in the latter two ichnotaxa, are present in the imprints DLS2 RP3 and RP4 (Figure 4). Extensive metatarsal impressions can be observed in *Moyenisauripus* and *Anomoepus* sitting tracks (Olsen and Rainforth 2003). However, a sitting behaviour is not documented in the Dalishu trackways.

Similarities of the Dalishu tracks with other ornithischian ichnotaxa such as *Deltapodus* Whyte and Romano, 1994 and *Tetrapodosaurus* Sternberg, 1932 (Figure 8(C),(D)) especially concern the shape of the manus imprints. The broadly crescentic outline with relatively short, blunt digit traces and the backward pointing digits I and V can be seen for example in *Deltapodus* and *Tetrapodosaurus* (Whyte and Romano 1994, 2001; McCrea et al. 2001; Xing, Lockley, McCrea, et al. 2013). However, a similar morphology occurs in *Moyenisauripus* (*Anomoepus*) tracks from the Upper Elliot Formation (Lower Jurassic) of southern Africa (Ellenberger 1974, sketches in pl. C–G, photographs in pl. XII; Figure 8(B)). Contrary, well-preserved manus traces of *Anomoepus* from the Newark Supergroup (Lower Jurassic) of North America exhibit long and slender digits with phalangeal pads and small claws (Olsen and Rainforth 2003). The shape of the manus traces in these ornithischian tracks is a function of extramorphological variation and different substrate conditions rather than an anatomical feature, and therefore cannot be used as a basis for ichnotaxonomic assignments.

Pes traces of the Dalishu tracks are different from *Tetrapodosaurus* by their tridactyly, whereas the latter is mostly tetradactyl (compare Figure 8(D),(F)). They are different from both *Tetrapodosaurus* and *Deltapodus* in (1) the shorter, posteriorly narrowing heel, whereas in the two latter ichnotaxa the plantar surface and heel area are relatively broad and largely elongated in *Deltapodus*; (2) the occasional occurrence of a slightly separated, slender and elongate trace of the metatarsals, whereas *Tetrapodosaurus* and *Deltapodus* lack this feature; (3) the distinct inward rotation of the pes imprints relative to the midline, while in *Tetrapodosaurus* and *Deltapodus* these are oriented parallel to the latter or slightly outward rotated (Whyte and Romano 1994, 2001; McCrea et al. 2001; Xing, Lockley, McCrea, et al. 2013). The short heel in the Dalishu tracks probably includes the metatarsophalangeal pad IV, which is positioned in line with digit III, a characteristic feature of *Anomoepus* (see above). This is suggested by the asymmetric posterior margin of the track showing an indentation at the posteromedial side (Figure 4).

When Li et al. (2012) described *Shenmuichnus youngteilhardorum* (type ichnospecies; Figure 8(E)) from the Fuxian Formation of Shenmu County, Shaanxi Province, an ornithischian ichnotaxon that they assigned to the ichnofamily Anomoepodidae Lull, 1904, the authors concluded that it differs from most other ornithischian tracks by the following characteristics: (1) habitually quadrupedal with tridactyl pes and blunt ungual traces, (2) large pentadactyl manus, (3) no hallux traces in pes, and blunt, rather than sharp pes and manus digit claw traces, and (4) absence of distinctive metapodial and tail traces characteristic of the ichnogenus *Moyenisauropus* Ellenberger, 1974. The Dalishu specimens generally share these four characteristics except the occurrence of a short metapodial trace in two tracks. Also, pes mesaxony (length/width ratio of the anterior triangle) is equal, about

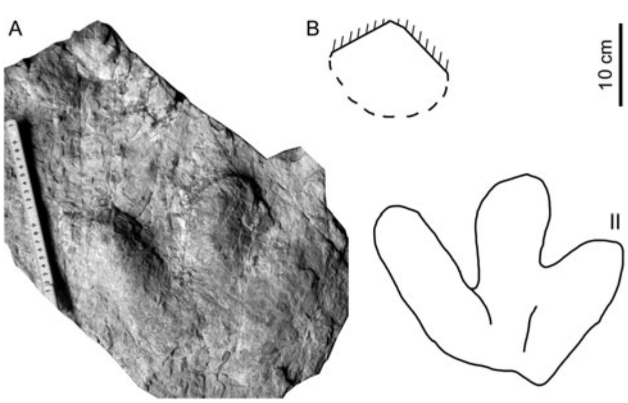

Figure 6. Photograph (A) and outline drawing (B) of paratype of *Shenmuichnus wangi* ichnosp. nov. DLSI-RP1 from the Dalishu tracksite.

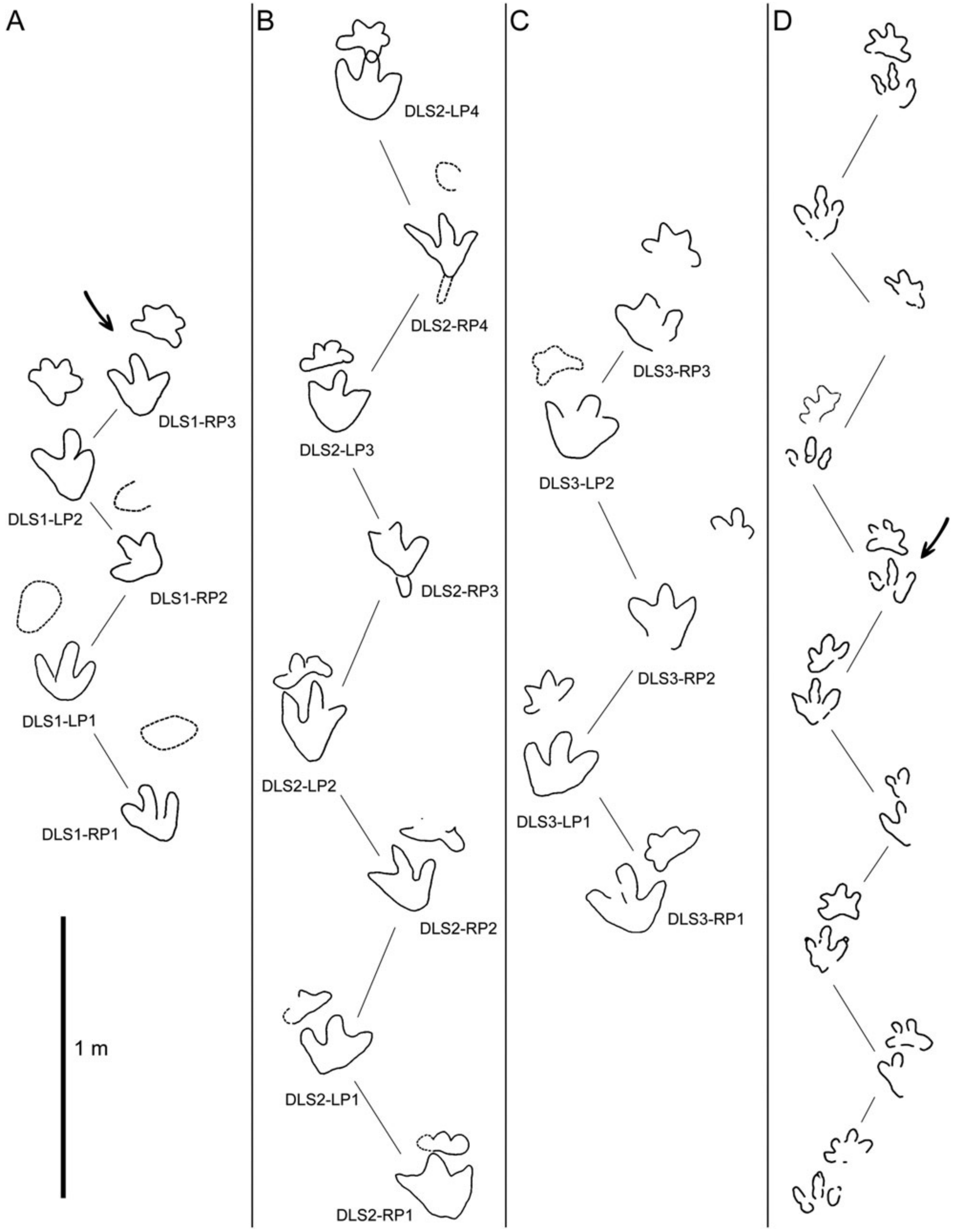

Figure 7. Interpretative outline drawings of *Shenmuichnus wangi* ichnosp nov. trackways described in this study (A–C) in comparison with *Shenmuichnus youngteilhardorum* trackway (D) from Lower Jurassic Fuxian Formation of Shaanxi Province. D modified from Li et al. (2012). Arrows indicate type specimens of *Shenmuichnus wangi* and *Shenmuichnus youngteilhardorum*.

Table 1. Measurements (in cm) of the *Shenmuichnus wangi* from Dalishu tracksite, Yunnan Province, China.

Number	ML	MW	II–III (°)	III–IV (°)	II–IV (°)	PL	SL	PA (°)	L/W
DLS1-RM1	10.5	19.0	–	–	–	65.5	84.5	92	0.6
DLS1-RP1	21.5	17.5	31	30	61	56.5	87.5	129	1.2
DLS1-LM1	13.5	19.0	–	–	–	51.0	81.0	102	0.7
DLS1-LP1	21.0	19.0	29	41	70	40.0	75.0	130	1.1
DLS1-RM2	–	–	–	–	–	52.0	60.0	83	–
DLS1-RP2	17.5	19.5	45	35	80	43.0	66.5	116	0.9
DLS1-LM2	10.0	19.5	–	–	–	43.0	–	–	0.5
DLS1-LP2	25.0	20.5	19	39	58	35.0	–	–	1.2
DLS1-RM3	9.5	18.5	–	–	–	–	–	–	0.5
DLS1-RP3	22.5	21.5	31	36	67	–	–	–	1.0
Mean-M	10.9	19	–	–	–	52.9	75.2	92	0.6
Mean-P	21.5	19.6	31	36	67	43.6	76.3	125	1.1
DLS2-RM1	7.5	18.0	–	–	–	71.5	–	105	0.4
DLS2-RP1	24.5	25.5	36	33	69	59.0	110.0	128	1.0
DLS2-LM1	9.5	19.0	–	–	–	–	119.5	107	0.5
DLS2-LP1	21.5	22.5	35	39	74	63.0	119.5	135	1.0
DLS2-RM2	–	–	–	–	–	–	–	–	–
DLS2-RP2	24.5	22.5	36	32	68	66.0	115.0	128	1.1
DLS2-LM2	8.5	21.0	–	–	–	–	111.5	–	0.4
DLS2-LP2	28.5	22.0	28	26	54	63.0	111.0	131	1.3
DLS2-RM3	–	–	–	–	–	–	–	–	–
DLS2-RP3	19.0	20.5	36	35	71	59.0	111.0	128	0.9
DLS2-LM3	9.0	19.0	–	–	–	75.0	113.5	110	0.5
DLS2-LP3	21.5	21.5	35	34	69	65.5	113.5	124	1.0
DLS2-RM4	–	–	–	–	–	69.0	–	–	–
DLS2-RP4	22.5	26.0	34	36	70	63.0	–	–	0.9
DLS2-LM4	9.5	19.0	–	–	–	–	–	–	0.5
DLS2-LP4	24.0	21.0	29	28	57	–	–	–	1.1
Mean-M	8.8	19.2	–	–	–	71.8	114.8	107	0.5
Mean-P	23.2	22.7	34	33	67	62.6	113.3	129	1.0
DLS3-RM1	10.5	18.0	–	–	–	71.5	115.0	94	0.6
DLS3-RP1	24.0	27.0	42	38	80	52.0	105.0	123	0.9
DLS3-LM1	11.0	20.0	–	–	–	89.0	116.0	86	0.6
DLS3-LP1	24.5	24.0	31	43	74	62.5	120.5	126	1.0
DLS3-RM2	12.5	15.5	–	–	–	89.0	101.5	91	0.8
DLS3-RP2	23.5	21.5	31	31	62	71.5	104.0	133	1.1
DLS3-LM2	11.0	17.5	–	–	–	62.0	–	–	0.6
DLS3-LP2	23.5	26.0	31	46	77	40.5	–	–	0.9
DLS3-RM3	12.0	21.0	–	–	–	–	–	–	0.6
DLS3-RP3	20.0	22.0	36	38	74	–	–	–	0.9
Mean-M	11.4	18.4	–	–	–	77.9	110.8	90	0.6
Mean-P	23.1	24.1	34	39	73	56.6	109.8	127	1.0
DLSI-LP1	23.0	27.0	35	38	73	–	–	–	0.9

Notes: 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.

0.3, in specimens from both sites. Therefore, the Dalishu tracks are assigned here to the ichnogenus *Shenmuichnus*. However, the Dalishu specimens differ from *Shenmuichnus youngteilhardorum* by the following characteristics: (1) Dalishu trackways are narrow-gauge (WAP/ML = 0.94), whereas the *Shenmuichnus youngteilhardorum* trackways are medium-gauge and wide-gauge (WAP/ML = 1.70); (2) the degree of heteropody of Dalishu specimens (1:1.48) is higher than in *Shenmuichnus youngteilhardorum* (1:0.90–1.07); (3) Dalishu tracks are larger than *Shenmuichnus youngteilhardorum* in absolute size (22–23 cm vs. 15–16 cm); (4) the relative pace length of the Dalishu specimens is shorter: PL = 2 × ML in DLS1, and 2.7 × ML and 2.5 × ML in DLS2 and DLS3, respectively, versus 3.3 times in *Shenmuichnus youngteilhardorum*; (5)the axis of the Dalishu manus traces always align with the antero-lateral margins of digits III and IV of the pes traces, while the axis of *Shenmuichnus youngteilhardorum* manus traces more often aligns with the antero-medial margins (digits II and III) of the pes traces (compare Figure 8(E),(F)). Especially the trackway gauge is an important (anatomically based) feature in quantified trackways. For example sauropod trackways

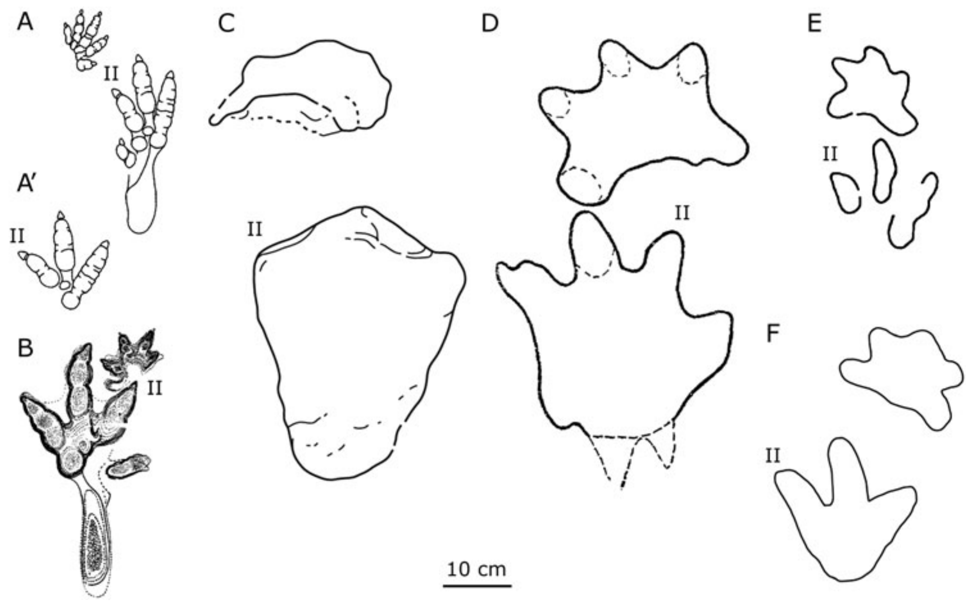

Figure 8. Schematic diagrams of Ornithischian ichnotaxa to the same scale. (A) *Anomoepus* manus and pes tracks with metatarsal impressions reflecting a sitting position, from the Newark Supergroup (Early Jurassic) of New England, North America (from Olsen and Rainforth 2003); (A′) idealised composite drawing of *Anomoepus* pes track reflecting walking movement, from the Newark Supergroup (Early Jurassic) of New England (from Olsen and Rainforth 2003); (B) *Moyenisauropus* pes–manus set with impression of the metatarsals, from the Upper Elliot Formation (Lower Jurassic) of southern Africa (from Ellenberger 1974); (C) *Deltapodus* pes–manus set from the Middle Jurassic of Great Britain (from Whyte and Romano 2001); (D) *Tetrapodosaurus* pes–manus set from the Lower Cretaceous of British Columbia (from Sternberg 1932); (E) *Shenmuichnus youngteilhardorum* pes–manus set from the Lower Jurassic of Shaanxi Province, China (from Li et al. 2012); (F) *Shenmuichnus wangi* pes–manus set (from this paper).

such as the wide-gauge *Brontopodus birdi* and the narrow-gauge *Parabrontopodus* reflect distinct osteo-taxonomic groups known from the skeletal record (Lockley, Farlow, et al. 1994). Based on differences in the trackway configuration, the Dalishu tracks are assigned here to the new ichnotaxon *Shenmuichnus wangi* ichnosp. nov. Bio-(ichno-)stratigraphically, it is important to note that all occurrences of *Shenmuichnus* are in Lower Jurassic strata.

Kuhn (1958) originally named and described the ornithopod ichnotaxon *Sinoichnites youngi* from the lower Upper Jurassic Anding Formation in Shenmu County, Shaanxi Province, China. *Sinoichnites* was assigned to Iguanodontidae by Young (1960), Kuhn (1963) and Zhen et al. (1989). Gierliński (1991) argued that *Sinoichnites youngi* resembles *Moyenisauropus karaszevskii* pes traces and that *Sinoichnites youngi* can be assigned to Thyreophora. Li et al. (2012) also mentioned that *Shenmuichnus youngteilhardorum* is possibly related to *Sinoichnites* and *Ravatichnus*. The latter is from Middle Jurassic fluvio deltaic deposits of Central Asia (Gabouniya and Kurbatov 1982). The Dalishu specimens resemble *Sinoichnites* in morphology. The digit divarication of *Sinoichnites* (approximately 89°) is slightly larger than that of DLSI (73°), but difficult to compare, because the *Sinoichnites* holotype is lost, and measurements can only be taken from photographs. The mesaxony of *Sinoichnites* is 0.4, which is also slightly larger than in the Dalishu specimens (0.3). The nearly isometric digits III and IV are consistent with the characteristics of the Dalishu specimens. Unfortunately, no further specimens of *Sinoichnites* from the type locality and horizon have been found and further comparisons, beyond the interpretations of Li are not possible (Li et al. 2012). Nevertheless, it is possible that the (lost) isolated pes of the *Sinoichnites* holotype and *Shenmuichnus* represent the same ichnotaxon. However, a synonymy and possible priority of the older name *Sinoichnites* (ICZN, 2000) cannot be proved, and therefore *Shenmuichnus* is a valid ichnogenus (Li et al. 2012).

Trackmakers: Trackmakers were habitual quadrupeds with a tridactyl pes, blunt unguals and a large pentadactyl manus. These features match the foot morphology of basal Thyreophora, such as *Scelidosaurus* (Norman et al. 2004; Li et al. 2012). Among quadrupedal dinosaurs, especially ceratopsians and thyreophorans, the ratio of hip height/foot length or width is not as clear as that of bipedal dinosaurs (Thulborn 1990). Therefore the common ratio, that is hip height = 4 × foot length (Alexander 1976) is provisionally adopted here. The hip height of the Dalishu trackmakers is estimated at 0.86–0.93 m. The ratio of hip height/body length of typical Jurassic–Cretaceous thyreophorans is here summarised in Table 2. From these data, it is clear that the ratio of the Early Jurassic *Scelidosaurus* (Owen 1859) is comparably low (1:3.7–4.0; Carpenter 2012), but this probably results from the incompleteness of

Table 2. Ratios of hip height to body length of six typical Thyreophora.

Typical Thyreophora	Age	Body length (m)	Hip height:body length	Reference
Scutellosaurus Colbert, 1981	J1	1.18	1:5.3	Colbert (1981)
Scelidosaurus Owen, 1859	J1	4.00	1:3.7–4.0	Carpenter (2012)
Huayangosaurus Dong, Tang and Zhou, 1982	J2	4.00	1:4.7	Zhou (1984)
Tuojiangosaurus Dong, Li, Zhou and Zhang, 1977	J3	7.00	1:4.8	Dong et al. (1977)
Sauropelta Ostrom, 1970	C1	5.50	1:5.0	Carpenter (2012)
Ankylosaurus Brown, 1908	C2	6.25	1:4.7	Carpenter (2004)

Note: Sources of measurements given in reference for each taxon.

the known *Scelidosaurus* caudal series and the error-prone reconstruction. The other Early Jurassic–Late Cretaceous species range from 1:4.7–5.3, with a mean of 1:4.8. Thus, the body length of the Dalishu trackmaker was probably up to 4.13–4.46 m.

Currently, only two thyreophoran specimens from southwest China have been named from skeletal remains: *Tatisaurus oehleri* (Simmons, 1965) and *Bienosaurus lufengensis* (Dong, 2001). The former (based on a partial lower jaw and teeth) was first interpreted as a hypsilophodontid (Simmons 1965). Later, *Tatisaurus* was reinterpreted as a stegosaurian by Dong (1990). Lucas (1996) reclassified *Tatisaurus* as a member of the genus *Scelidosaurus*. Most recently, Norman et al. (2007) considered *Tatisaurus* to be a dubious basal thyreophoran following this interpretation. *Tatisaurus* is one of the oldest members of the group. *Bienosaurus* is known only from axis and teeth, and was interpreted by Norman et al. (2004) as a basal thyreophoran. Both of these thyreophoran specimens come from individuals that did not far exceed 1 m in length, which is significantly smaller than the estimated size of the Dalishu trackmaker. Clearly, the disputed taxonomic status of these two species, based on relatively scant material, means that they are of limited palaeobiological utility, only pointing to the presence of ornithischians of dubious and disputed taxonomic affinity. The *Shenmuichnus wangi* footprints described here do not allow a trackmaker attribution more precise than ‘ornithischian’. The Early Jurassic age and the quadrupedal movement suggest basal thyreophorans as trackmakers (see also Olsen and Rainforth 2003). For *Shenmuichnus youngteilhardorum* more generally considered ornithischians as trackmakers (Lockley et al., 2013). Possibly, large-sized thyreophorans were present in the Early Jurassic of the Lufeng Basin, a faunal component that was not proved thus far by skeletons. No ornithischian skeletons have been found in the Middle Jurassic of the Lufeng Basin, where only theropods and mamenchisaurid sauropods have been found (Sekiya 2011). However, no significant geographical barrier divided the Early–Middle Jurassic Sichuan and Yunnan basins, and the same general faunas roamed the two (Peng et al. 2005). The trackmaker of the *Shenmuichnus* trackways most probably had affinities with the stegosaurs that flourished in the Middle–Late Jurassic Sichuan Basin such as *Huayangosaurus* (Dong, Tang and Zhou, 1982), and *Tuojiangosaurus* (Dong, Li, Zhou and Zhang, 1977).

Throughout the Jurassic, the Lufeng Basin was home to a flourishing population of sauropodomorphs, including the small (approximately 6–9 m long) prosauropods *Lufengosaurus huenei*, *Yunnanosaurus huangi*, *Yunnanosaurus magnus* and ‘*Lufengosaurus magnus*’ and a few sauropods, such as ‘*Kunmingosaurus wudingensis*’. More than a hundred *Lufengosaurus* specimens have been discovered in the Lufeng Basin, indicating the abundance of sauropodomorphs in the Early Jurassic in this region (Dong 1992). In terms of general size, *Lufengosaurus* and *Yunnanosaurus* are close to that estimated for the trackmaker of *Shenmuichnus* from the Dalishu site. The rarity of ornithischians in the skeletal fossil record may reflect their competitive exclusion by contemporaneous sauropodomorphs. From the track record, it seems that in the early Mesozoic ornithischian trackmakers were rare in comparison with saurischians, not just in China, but also in other parts of the globe such as in North America and Europe (Lockley and Hunt 1995; Lockley and Meyer 1999).

Theropoda Marsh, 1881

Theropod footprint indet

Material: One natural mould (DLST-1) from the Dalishu tracksite (Figure 9). The original specimens remain in the field.

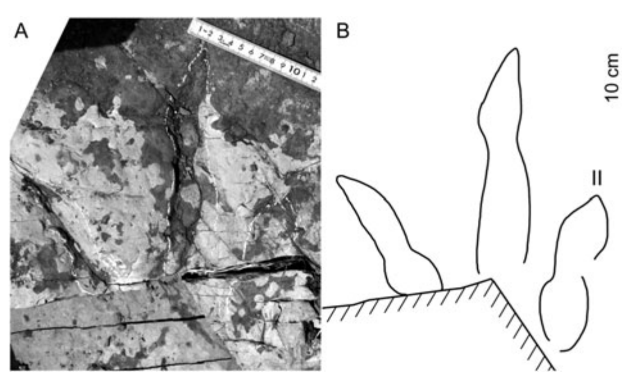

Figure 9. Photograph (A) and outline drawing (B) of theropod footprint indet. DLST-1 from the Dalishu tracksite.

Locality and horizon: Zhangjiaao Member of Lufeng Formation, Lower Jurassic. Dalishu tracksite, Lufeng County, Yunnan Province, China.

Description and comparison: DLST-1 is located on the same lower sandstone layer as the ornithischian tracks. The preserved portion of the track measures >27 cm in length and 23 cm in width. The trace of the proximal part and the 'heel' is missing, making its full length impossible to determine. The three preserved digits are long and slender. Digit II is estimated to have two pads, digit III to have at least two pads, but the real count is unknown. Its proximal portion is incomplete. Digit IV is also incomplete proximally. The slim digits and possible wide divarication of DLST-1 resemble the ichnogenus *Kayentapus* Welles, 1971 (Lockley et al. 2011). The latter is a characteristic, gracile, medium-sized theropod track in the Early–Middle Jurassic (Lockley et al. 2011; Xing, Lockley, Chen, et al. 2013; Xing, Lockley, Li, et al. 2013).

5. Palaeogeographical and palaeoenvironmental implications

After the Indosinian movement in the Middle–Late Triassic, connections formed between the Yangtze Platform and the North China Platform and between the Yangtze Platform and the Tarim Platform. This formed a wide continental environment. The ancient Kunlun and Qinling mountains traversed the continent from east to west, and caused a distinctive southern and northern palaeoclimate (Wang et al. 1985). The palaeoenvironment of the Early–Middle Jurassic Ordos Basin in northern China was warm and wet, and, therefore, a favourable environment for coal producing wetlands (Ma 1998; Zhang et al. 2008). The southern Chuandian (Sichuan-Yunnan) Basin (including the Lufeng Basin) was a tropical–subtropical humid-semiarid climate zone that produced the first Jurassic red beds (Gu and Liu 1995; Fang and Li 2008).

Shenmuichnus youngteilhardorum was discovered in the Fuxian Formation on the northeastern border of the Ordos Basin (Li et al. 2012). The Fuxian Formation consists of fluvial and lacustrine facies, located beneath the coal-bearing Yanan Formation sediments (Zhang et al. 2007). This suggests that the Jurassic ornithischians from the Ordos Basin inhabited humid coal-bearing, fluvio-deltaic facies (Li et al. 2012). In the Jurassic sediments of the Ordos Basin, the Early Jurassic *Shenmuichnus youngteilhardorum* and the Early–Middle Jurassic *Anomoepus* and *Deltapodus* tracks (Xing et al. 2014) are the only known evidences of ornithischians in this region.

Lockley, Meyer, et al. (1994) argued for a distinction between humid, clastic, coastal plain, coal-bearing facies dominated by ornithopods and ankylosaurs and semi-arid carbonate facies dominated by sauropods (McCrea et al. 2001). In this paper the majority of available evidence for coal-bearing ichnofaunas was taken from the Cretaceous. While the *Shenmuichnus youngteilhardorum* occurrence is consistent with this facies relationship, the *Shenmuichnus. wangi* report from the Lufeng Basin is not, and suggests that at least one form of large ornithischian from the Early Jurassic does not match this pattern. Obviously, the *Shenmuichnus wangi* trackmaker inhabited the same semi-arid environment as the sauropodomorphs.

6. Conclusions

(1) The ornithischian ichnogenus *Shenmuichnus* is reported for the first time from the Lower Jurassic of Yunnan Province on the basis of an assemblage of >30 manus and pes tracks comprising at least two diagnostic trackway segments.
(2) This is the second report of the ichnogenus from China and globally.
(3) The Yunnan trackways are assigned to the new ichnotaxon *Shenmuichnus wangi* ichnosp. nov. Compared with the ichnospecies *Shenmuichnus youngteilhardorum* from the Lower Jurassic of Shaanxi Province, the imprints are larger and display a different trackway pattern.
(4) An isolate large footprint without closer specification evidences the presence of theropods, their under-representation at this site is probably biased by preservational factors.
(5) The footprint assemblage enriches our knowledge about dinosaur communities in the Early Jurassic of East Asia, adding large ornithischians, possibly basal Thyreophora, as a further component. However, both the track record and skeletal record are consistent in indicating that ornithischian trackmakers were less abundant in the Yunnan region than saurischians, which are relatively well represented.
(6) Palaecologically the occurrence in red bed strata contradicts former hypotheses that ornithischian dinosaurs preferred more humid climates.

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Author contributions

Conceived and designed the experiments: L. Xing, M.G. Lockley, J. Zhang. Performed the experiments: L. Xing, M.G. Lockley, H. Klein, W.S. Persons IV. Analysed the data: L. Xing, M.G. Lockley, H. Klein. Contributed reagents/materials/analysis tools: L. Xing, Z. Dong. Wrote the paper: L. Xing, M.G. Lockley, J. Zhang, HY, H. Klein, W.S. Persons IV, Z. Dong.

Disclosure statement

No potential conflict of interest was reported by the authors.

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