Xing, L, Lockley, MG, Klein, H, Falkingham, PL, Kim, JY, McRea, RT, Zhang, J, Persons IV, WS, Wang, T and Wang, Z

First early Jurassic small ornithischian tracks from Yunnan Province, Southwestern China

Xing, L, Lockley, MG, Klein, H, Falkingham, PL, Kim, JY, McRea, RT, Zhang, J, Persons IV, WS, Wang, T and Wang, Z (2016) First early Jurassic small ornithischian tracks from Yunnan Province, Southwestern China. PALAIOS, 31 (11). ISSN 0883-1351

PALAIOS
Emphasizing the impact of life on Earth's history

PALAIOS, 2016, v. 31, 516–524
Research Article
DOI: http://dx.doi.org/10.2110/palo.2015.074

1926 SEPM Society for Sedimentary Geology

FIRST EARLY JURASSIC SMALL ORNITHISCHIAN TRACKS FROM YUNNAN PROVINCE, SOUTHWESTERN CHINA

LIDA XING,[1] MARTIN G. LOCKLEY,[2] HENDRIK KLEIN,[3] PETER L. FALKINGHAM,[4,5] JEONG YUL KIM,[6] RICHARD T. MCCREA,[7] JIANPING ZHANG,[1] W. SCOTT PERSONS IV,[8] TAO WANG,[9] AND ZHENZHEN WANG[1]

[1]*School of the Earth Sciences and Resources, China University of Geosciences, Beijing 100083, China*
[2]*Dinosaur Tracks Museum, University of Colorado Denver PO Box 173364, Denver, Colorado 80217, USA*
[3]*Saurierwelt Paläontologisches Museum Alte Richt 7, D-92318 Neumarkt, Germany*
[4]*Structure and Motion Laboratory, Department of Comparative Biomedical Sciences, Royal Veterinary College, Hatfield AL97TA, United Kingdom*
[5]*Department of Ecology and Evolutionary Biology, Brown University, Providence, Rhode Island 02912, USA*
[6]*Department of Earth Science Education, Korea National University of Education, Cheongwon, Chungbuk 363-791, South Korea*
[7]*Peace Region Palaeontology Research Centre, Box 1540, Tumbler Ridge, British Columbia V0C 2W0, Canada*
[8]*Department of Biological Sciences, University of Alberta 11455 Saskatchewan Drive, Edmonton, Alberta T6G 2E9, Canada*
[9]*Lufeng Land and Resources Bureau, Lufeng 651200, China*
e-mail: xinglida@gmail.com

ABSTRACT: **In 2015, a group of small predominantly tridactyl tracks was discovered in the lower Shawan Member of the Lufeng Formation during an expedition to the Dalishu area, Lufeng County, Yunnan Province, China. The tracks are attributable to *Anomoepus*, and although mostly tridactyl, they include a few examples with characteristic tetradactyl morphology. Although considered a characteristic index ichnotaxon of a footprint-based Lower Jurassic biochron, *Anomoepus* has often been overlooked in assemblages dominated by theropod tracks. This is one of the earliest *Anomoepus* records from the Jurassic of China, and the fifth report of *Anomoepus* from China at all. To date, four reports represent sites inferred to be Lower or Middle Jurassic in age, with one dated as Upper Jurassic. It is an important component of Early Jurassic ichnofaunas because it points to the presence of ornithischian trackmakers, which are often rare or missing in the local skeletal faunas (*Lufengosaurus* faunas).**

INTRODUCTION

Anomoepus is a classic dinosaur ichnogenus. The first specimens were discovered from the Early Jurassic Newark Supergroup rift strata of the Connecticut Valley (Hartford and Deerfield basins) and were named by Hitchcock in 1848. Abundant well-preserved materials allowed the *Anomoepus* trackmaker to be recognized as an early ornithischian (Olsen and Rainforth 2003; Lockley and Gierliński 2006) and provided detailed information on morphological diagnostic characters such as manus impressions (e.g., Hitchcock 1858). Currently, the ichnogenus is known from eastern and western North America, Europe, southern Africa (Kent et al. 1995), and China (Lockley and Matsukawa 2009). The *Anomoepus–Grallator* (*Eubrontes*) Zone is considered a track assemblage typical of Liassic Age (Haubold 1984, 1986; Lucas 2007; Lockley et al. 2013).

In China, *Anomoepus* tracks are primarily found in Lower–Middle Jurassic formations in the southwest of Sichuan Province (Lockley and Matsukawa 2009) and in the Ordos Basin, including Jiaoping (Young 1966; Xing et al. 2015), Shenmu (Li et al. 2012), and Zizhou (Xing et al. 2015). Some tracks are also known from the Hailiutu Basin, near the Ordos Basin (Li et al. 2010). In China, *Anomoepus* tracks usually co-occur with *Grallator–Eubrontes–Kayentapus* and *Deltapodus* (Xing et al. 2015). The Upper Jurassic Nan'an site in Chongqing municipality, southwestern China, also preserves *Anomoepus* tracks (Xing et al. 2013).

In 2015, a fossil hunting expedition was launched into the Dalishu area in Lufeng County, in accordance with the "2013 National Project for Preservation of Geologic Relics of Dinosaurs in Lufeng" and funded by the Ministry of Land and Resources. Authors LX, TW, and ZW of this report were part of this expedition and discovered a group of tridactyl tracks approximately 600 m northwest of the main Dalishu tracksite, where large ornithischians and theropod tracks were discovered (Xing et al. 2016). The location was catalogued as Dalishu tracksite III (GPS: 24°56′30.65"N, 102° 0′23.26"E, WGS84) under the abbreviation DLSIII (Fig. 1A, 1B).

In the following we give a detailed description of this assemblage, which is important because it documents the presence of small ornithischians as a significant component of the Lower Jurassic Lufeng Formation, not reflected in the skeletal record thus far.

METHODS

The 3D photogrammetry image was compiled from 32 images (average elevation from subject was 1.01 m) taken with a Canon EOS 5D Mark III (Focal Lengths of 67, 70, 84, and 85 mm, resolution 3840 × 2560, pixel size 9.65398 μm) using Agisoft Photoscan Professional (v.1.0.4) model error 0.147 pix and Cloud Compare (v.2.5.3). Outline tracings of tracks on transparency film were taken from original specimens and digitized with vector-based drawing software. Measurements are based on standard parameters such as maximum length of footprint (ML), maximum width of footprint (MW), ML/MW ratio, divarication angle between digit traces II–IV, mesaxony value based on length/width of anterior triangle (AT) using the method of Weems (1992), pace length (PL), stride length (SL) and pace angulation (PA) (Table 1).

Published Online: November 2016

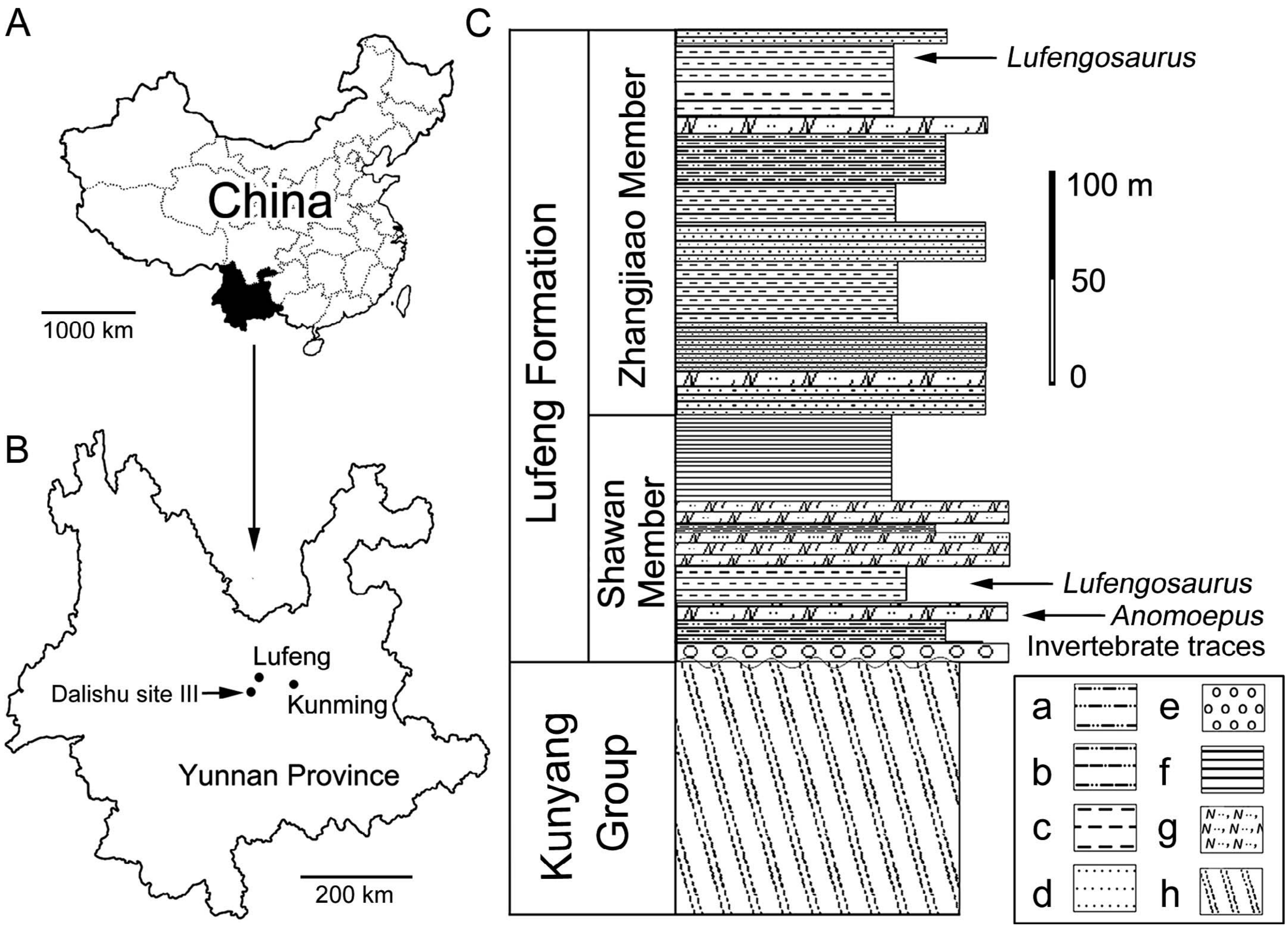

FIG. 1.—Location map. **A**, **B**) Location of Dalishu tracksite III in Yunnan Province, China. **C**) Stratigraphic section of Lower Jurassic–Cretaceous strata in the Lufeng Basin with position of track-bearing levels, invertebrate traces and skeletal remains (icons). Key: a = pelitic siltstone; b = sandy mudstone; c = mudstone; d = sandstone; e = conglomerate; f = shale; g = orthomicrite; h = fossiliferous orthomicrite. Lithological succession modified from Fang et al. (2000) and Sekiya (2011)

GEOLOGICAL SETTING

Lufeng Formation

The exposed Red Beds in the Lufeng Basin are from the Lufeng Series, which was previously divided into the Lower Jurassic Lower Lufeng Formation (dark purple beds) and the Middle Jurassic Upper Lufeng Formation (deep red beds) (Bien 1941; Sheng et al. 1962). Fang et al. (2000) subsequently studied the stratigraphic section at Lao Changqing–Da Jianfeng, in the Chuanjie Basin, and restricted the name "Lufeng Formation" to what was previously known as the lower Lufeng Formation. They divided the redefined Lufeng Formation into the Shawan and Zhangjia'ao Members (Fig. 1C). The Lufeng Formation is a succession of mudstone, siltstone, sandstone, and limestone deposited in piedmont plain, lake and fluvial environments (Luo and Wu 1995; Tan 1997).

Dalishu tracksite III is within the protection of Lufeng Dinosaur National Geological Park, Yunnan Province. It is located about 50 m west of the bonebed where the coelophysoid theropod dinosaur *Panguraptor* was found (You et al. 2014). The tracks are preserved in a fluvial sandstone layer within the lower Shawan Member. Biostratigraphic correlations (Luo and Wu 1995) indicate an early–middle Early Jurassic (Hettangian–Pliensbachian) age, whereas magnetostratigraphic analysis indicates a late Sinemurian–?Toarcian age (Huang et al. 2009).

Invertebrate Traces

cf. Gordia *ichnosp.*

Description.—Burrows (3–4 mm thick) preserved in convex hyporelief on siltstone beds in lacustrine deposits of the Lufeng Formation. The burrows are smooth, loosely winding, with a marked tendency to cross. Long diameter of a loop is up to 8.5 cm (Fig. 2).

Remarks.—Although the specimen resembles *Gordia arcuata* Ksiazkiewicz 1977, it is incomplete, and therefore identified only tentatively. The ichnogenus *Gordia* was originally defined based on its resemblance to *Gordius*, a freshwater worm usually called the hair-worm (Emmons 1844). *Gordia* is a facies-crossing form and ranges from Vendian (Narbonne and Hofmann 1987) to Holocene (Ratcliffe and Fagerstrom 1980).

Palaeophycus tubularis *Hall 1847*

Description.—Straight to slightly curved, generally smooth, horizontal, commonly collapsed cylindrical burrows, 2–3 mm in diameter and up to 30 cm long. Burrow density is more or less high. Wall-lining is thin, less than 1 mm. Burrow-fill is similar to host rock and typically massive. Burrow surfaces are typically smooth, but may be rugose in

TABLE 1.—*Measurements (in cm and degrees) of* Anomoepus *tracks from Dalishu tracksite III, Yunnan Province, China. Abbreviations: ML = maximum length; MW = maximum width; L/W = maximum length/ maximum width; II–IV = angle between digits II and IV; PL = pace length; SL = stride length; PA = pace angulation; * = maximum length without digit I trace.*

Number	ML	MW	L/W	II–IV	PL	SL	PA
DLSIII-O1-R1	10.5	11.0	1.0	115°	29.0	57.0	152°
	8.5*	11.0	0.8	—	—	—	—
DLSIII-O1-L1	11.0	10.0	1.1	91°	29.8	—	—
	9.5*	10.0	1.0	—	—	—	—
DLSIII-O2-L1	10.0	—	—	90°	30.6	—	—
DLSIII-O2-R1	10.0	11.5	0.9	92°	—	—	—
DLSIII-OI1	10.0	11.5	0.9	90°	—	—	—
DLSIII-OI2	13.5	14.0	1.0	77°	—	—	—
DLSIII-OI3	11.0	11.5	1.0	91°	—	—	—
DLSIII-OI4	10.5	11.5	0.9	89°	—	—	—
DLSIII-OI5	11.5	12.0	1.0	—	—	—	—
DLSIII-OI6	9.0	11.0	0.8	110°	—	—	—
DLSIII-OI7	9.0	11.5	0.8	109°	—	—	—
DLSIII-OI8	10.0	13.0	0.8	96°	—	—	—
DLSIII-OI9	10.5	12.0	0.9	96°	—	—	—
DLSIII-OI10	9.0	11.0	0.8	92°	—	—	—
DLSIII-OI11	9.3	16.0	0.6	100°	—	—	—
DLSIII-OI12	10.5	12.5	0.8	111°	—	—	—

places. The burrows are observed in convex hyporelief on the surfaces of siltstone beds (Fig. 2).

Remarks.—The thin wall-lining of *Palaeophycus tubularis* is distinct from that of other ichnospecies of *Palaeophycus*, *P. alternatus*, *P. herberti*, *P. striatus*, and *P. sulcatus*. *Palaeophycus* is a eurybathic form ranging from late Precambrian (Narbonne and Hofmann 1987) to Pleistocene (D'Alessandro and Bromley 1986).

Palaeophycus-*Gordia* assemblages represent a nearshore environment, belonging to the *Cruziana* ichnofacies (Zhang 1991). Based on the general chemical and trace element composition of its deposits, the lower part of the Lufeng Formation includes shallow lacustrine strata (Tan 1997).

SYSTEMATIC PALEOICHNOLOGY

Ornithischia Seeley 1887
?Thyreophora Nopcsa 1923
Ichnofamily Anomoepodidae Lull 1904
Anomoepus *Hitchcock 1848*

Diagnosis.—(After Olsen and Rainforth 2003). Small tracks (pes imprints < 20 cm long) of a facultative biped with wide digit divarication and weak mesaxony. Pes imprints tetradactyl, but functionally tridactyl. Sitting tracks with metatarsal and pentadactyl manus impressions. Metatarsal-phalangeal pad of digit IV almost directly in line with axis of digit III in walking tracks. Pedal digit I (hallux) relatively long and often at least partially impressed, especially in sitting tracks. In the manus, digit III longest with other digits decreasing in length symmetrically away from that digit. Tail trace usually present in sitting tracks. Fully bipedal as well as quadrupedal walking trackways occur.

Type Ichnospecies.—*Anomoepus scambus* Hitchcock 1848. *Anomoepus* isp.

Material.—All tracks are preserved as concave epireliefs and are distributed on two adjacent sandstone surfaces. Fifteen natural molds (14 in lower surface I, one in higher surface II) of small (9–13.5 cm in length) tri-tetradactyl footprints of bipedal dinosaurs from surface I of Dalishu tracksite III have been cataloged as DLSIII-O1-R1–R2, O2-L1–R1, and DLSIII-OI1–11 (Fig. 3; Table 1). Surface II is slightly higher and preserves only one track, which has been cataloged as DLSIII-OI12. DLSIII-OI12 was collected and, stored at the museum of Lufeng Dinosaur National Geological Park. All other tracks remain in the field.

Description and Comparisons.—Trackway DLSIII-O1 consists of three pes imprints and DLSIII-O2 of two pes imprints that are rotated toward the midline (as measured by inward rotation of the trace of digit III). Manus and tail traces are absent.

DLSIII-O1 tracks (Figs. 4, 5) are tetradactyl and the length/width ratios of these tracks range from 1.0 to 1.1. A soft substrate may explain the sub-optimal morphological features in the DLSIII-O1 tracks, which include the raised middle part and indistinct digital pads. However, all imprints preserve digit I (hallux) traces. The digit I traces are relatively long and clearly oriented backward and towards the median axis of the trackway. Digit III of DLSIII-O1-L1 shows inward displacement. Trackway DLSIII-O1 is narrow (pace angulation about 152°) and is characterized by comparatively short stride lengths (57 cm on average), given a mean footprint length of 10.8 cm.

Other tracks from surface I are tridactyl but, because they are relatively shallow, they have no clear digit pads and no distinct claw traces (Figs. 6, 7). However, they share the same overall morphology of the digit group II–IV with wide digit divarication angles (77°–115°) and weak mesaxony (0.41). Furthermore, the proximal region of digits II and IV form a U-shaped metatarsophalangeal region that is aligned with the axis of digit III. These features are diagnostic and support an assignment to *Anomoepus*.

DLSIII-OI12, from surface II, is the most representative of the track morphology (Fig. 6). The length/width ratio is 0.8; digit III projects the farthest anteriorly. Pads are preserved with the proximal one of digit III being well-rounded and nearly circular in shape. A phalangeal pad formula (including metatarso-phalangeal pad IV) of x-2-3-4-x is recognized. The claw traces are relatively blunt. The metatarsophalangeal pad of digit IV is located in line with the axis of digit III. The divarication angle is wide (111°), and the anterior triangle length/width ratio is 0.48.

The morphology of the small tridactyl tracks from DLSIII strongly resembles that of the ichnogenus *Anomoepus*, being similar in size and having wide divarication angles, weak mesaxony, and short stride lengths. Thus, the DLSIII tracks are assigned here tentatively to *Anomoepus* isp. The preservation does not allow a distinct ichnospecies determination.

ANOMOEPUS FROM CHINA

In China, most *Anomoepus* tracks are found in Lower–Middle Jurassic formations (Table 2). The first discovery was made by Lockley and Matsukawa (2009) at the Middle Jurassic Jinlijing site in Sichuan Province. The digit pads of Jinlijing *Anomoepus* isp. are indistinct as they are poorly preserved, but wide divarication angles and weak mesaxony together with inward rotation indicate that they belong to *Anomoepus*. Size differences demonstrate local *Anomoepus* trackmakers of variable size. In this same study these authors also recognized tetradactyl *Anomoepus* among specimens in the Chongqing Natural History Museum that were rescued from a site in the city since destroyed by construction (Xing et al. 2013).

In northern China, *Anomoepus* tracks are found at the Lower Jurassic Wulatezhongqi site in Inner Mongolia (Li et al. 2010), the Lower Jurassic Lijiananwa site in Shaanxi Province (Li et al. 2012), and the Middle Jurassic Huo and Wang sites in Shaanxi Province (Xing et al. 2015). Xing

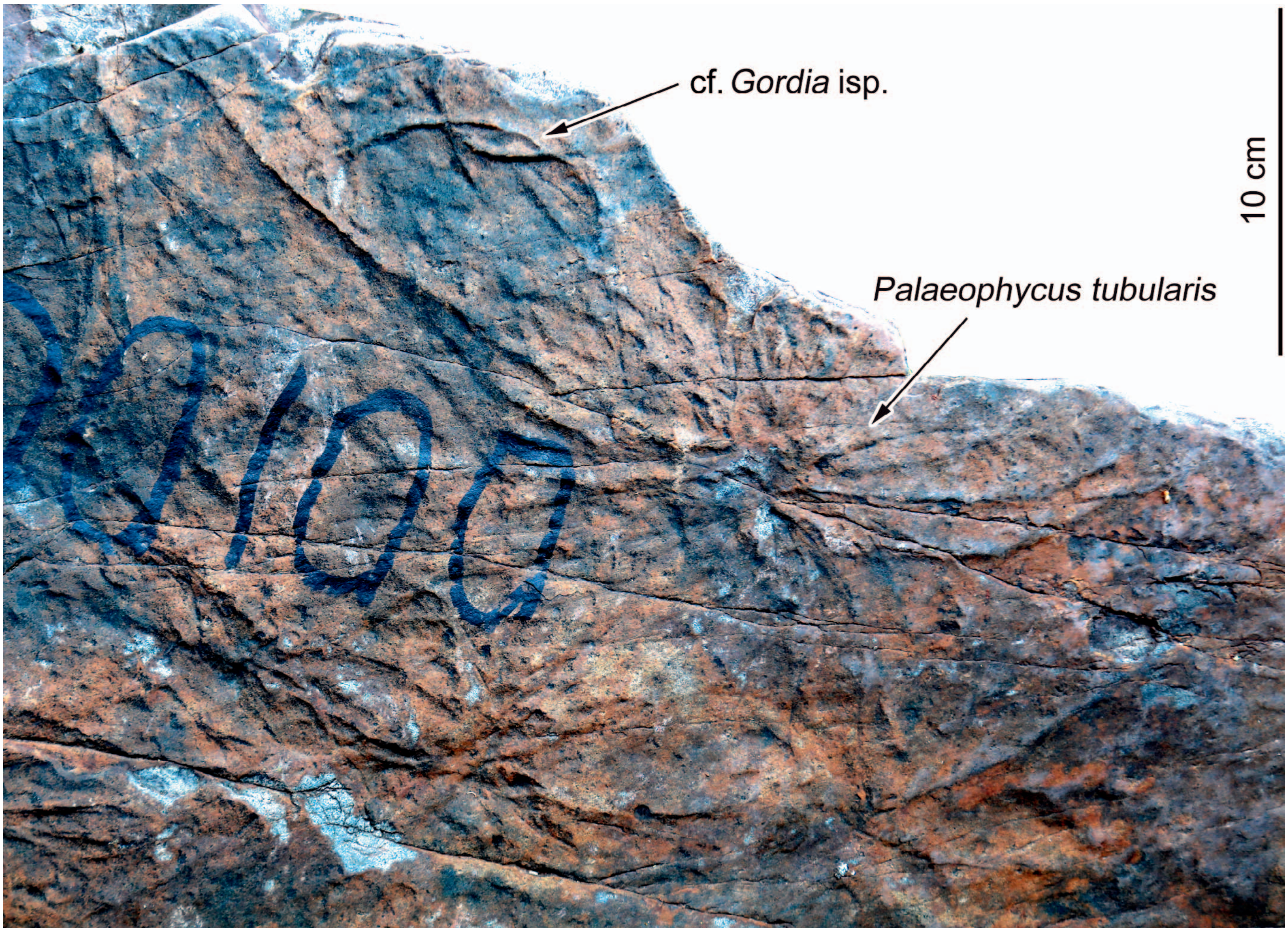

FIG. 2.—Photographs of invertebrate traces at Dalishu tracksite III.

et al. (2015) assigned *Shensipus tungchuanensis* Young 1966 from the Middle Jurassic Jiaoping Coal Mine site, Shaanxi Province, to *Anomoepus tungchuanensis* n. comb. All these tracks, except specimens from the Lijiananwa site, which have yet to be described in detail, have characteristics of *Anomoepus*, such as wide divarication angles (80°–91°) and weak mesaxony (0.40–0.60). WLT T7-12 from the Wulatezhongqi site has a metatarsal pad and a relatively long digit I trace (Fig. 8). Li et al. (2012) referred the Wulatezhongqi specimens to *Anomoepus intermedius* Hitchcock 1865. However, Olsen and Rainforth (2003) consider *A. intermedius* to be a subjective synonym of *A. scambus*. Generally, these records suggest that *Anomoepus* type trackmakers had a relatively wide distribution in the Ordos Basin and the nearby Hailiutu Basin during the Early–Middle Jurassic.

TABLE 2.—*Measurements (in cm and degrees) of* Anomoepus *tracks from China. Abbreviations: Fm = Formation; Gr = Group; ML = maximum length; L/W = maximum length/maximum width; II–IV = angle between digits II and IV; AT = anterior triangle length-width ratio; * = value from specimen with preserved metatarsophalangeal pad of digit IV is lower, about 87°; J1, 2, 3 = Lower/ Middle/ Upper Jurassic; HT = Huo and Wang sites; IVPP = Jiaoping Coal Mine site, Institute of Vertebrate Paleontology and Paleoanthropology; JLJ = Jinlijing site; LJNW = Lijiananwa site; V = Nan'an site; WLT = Wulatezhongqi site.*

Specimens	Age	Fm./ Gr.	ML	L/W	II–IV	AT
LJNW unnumbered track	J1	Fuxian Fm.	10.5	1.2	80°	0.60
WLT T7-12	J1	Zhaogou Fm.	18.0	1.8	91°	0.40
JLJ-O1-R7	J2	Xiashaximiao Fm.	13.1	0.8	99°*	0.47
JLJ-O2-L3	J2	Xiashaximiao Fm.	8.6	1.1	76°	0.50
IVPP V.3229-1	J2	Zhiluo Gr.	9.8	1.1	90°	0.42
HT1R2	J2	Yanan Fm.	12.5	1.0	88°	0.47
V1395-7	J3	Shangshaximiao Fm.	21.5	1.1	83°	0.58

cf. *Anomoepus* found at the Upper Jurassic Nan'an site of Chongqing municipality, in southwestern China, is larger in size (more than 20 cm) (Xing et al. 2013) and has an anterior triangle length/width ratio of 0.58, both of which differ from all Lower–Middle Jurassic *Anomoepus* known from China.

DLSIII *Anomoepus* isp. shows a length/width ratio and mesaxony similar to most *Anomoepus* from China, while its divarication angles between digits II and IV are larger. This discrepancy may reflect a preservation artifact or regional divergence in trackmaker types.

The records of both skeletal and track fossils suggest that the Lufeng Basin and the Sichuan Basin had similar dinosaur faunas during the Jurassic (Peng et al. 2005). Though the Sichuan Basin record lacks ornithischians from the Early Jurassic, it shows diversified small Neornithischia from the Middle Jurassic, including *Xiaosaurus* Dong and Tang 1983, *Agilisaurus* Peng 1990, and *Hexinlusaurus* Barrett et al.

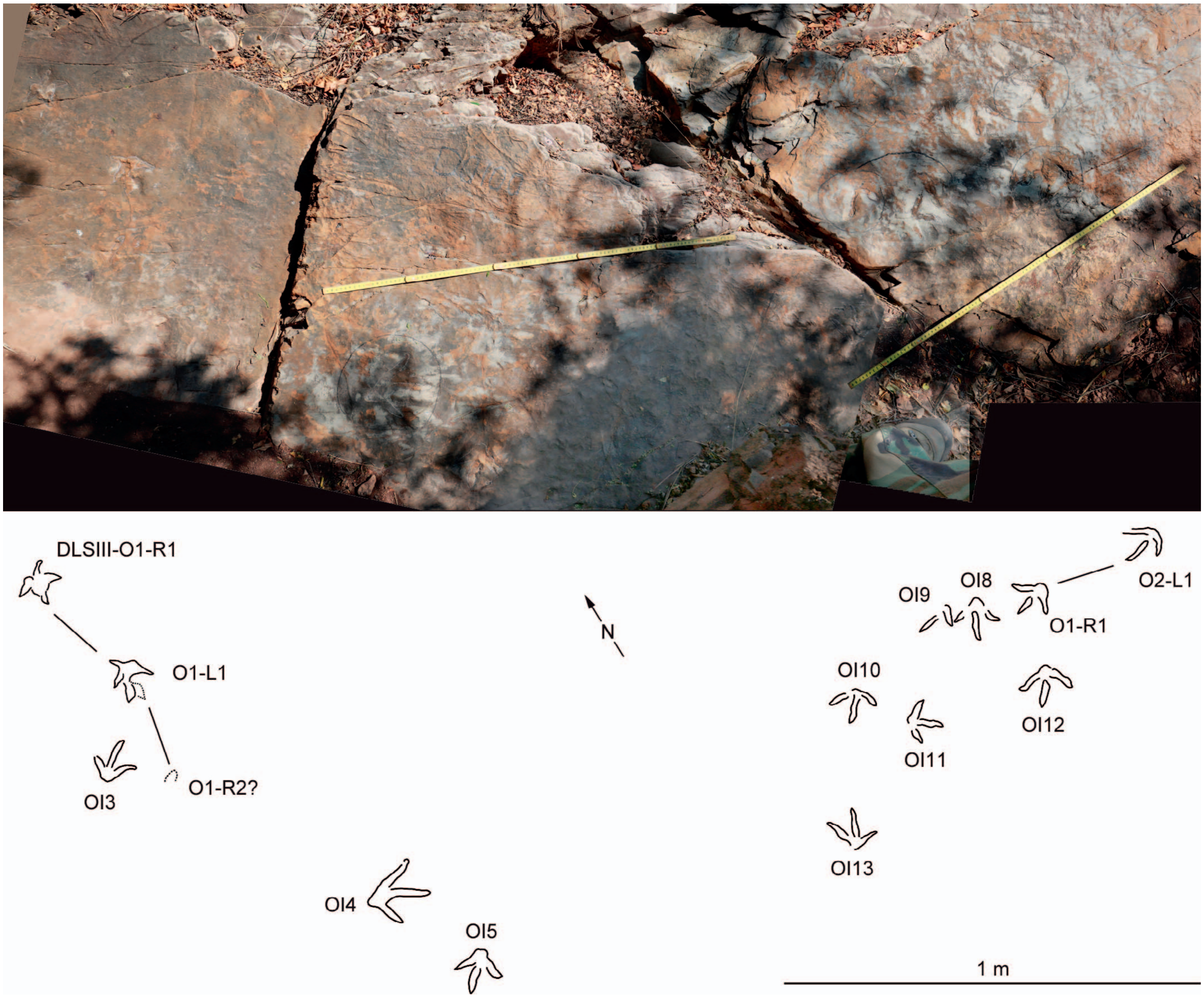

FIG. 3.—Photograph and interpretive outline drawing of track-bearing level at surface I of Dalishu tracksite III.

2005. All these taxa are 1.4–2 m long (Peng et al. 2005). Estimates from footprints are based on the hip height of small ornithopods, using 4.8× the maximum length of the pes trace as the hip height conversion factor (Thulborn 1990), and the average ratio of hip height to body length of 1:2.63 (Xing et al. 2009). The trackmakers of DLSIII *Anomoepus* isp. are thereby estimated to have been 1.3 m long, similar to those of Neornithischia from the Sichuan Basin.

Although *Anomoepus* was originally discovered in New England in the eastern United States (Hitchcock 1848) and has been repeatedly reported and described or re-described from that area (Olsen and Rainforth 2003), it was not widely recognized or described from other regions until quite recently, probably because it was often mistaken for a small theropod track. For example, despite abundant reports of classic Lower Jurassic *Grallator* and *Eubrontes* dominated assemblages in the western United States (Lockley and Hunt 1995; Lucas 2007), *Anomoepus* occurrences were not described or known in much detail from this area until 2006 (Lockley and Gierlinski 2006). Although *Anomoepus* is considered a characteristic track type of the Lower Jurassic ichnofaunal biochron (Lucas 2007), it also occurs in the Middle and Upper Jurassic of China and North America (Lockley and Gierlinski 2006). To date, *Anomoepus* tracks are poorly known from the Jurassic of Europe where they have mostly been reported from Poland as a Lower Jurassic record (Gierlinski and Pienkowski 1999; Gierlinski et al. 2004). Purported Triassic (?late Norian–Rhaetian) occurrences from Poland and Slovakia (Niedźwiedzki 2011) are doubtful. In China, *Anomoepus* was not recognized as a significant component of Jurassic ichnofaunas until 2009. Since then it has also been recognized as a component of Middle and Upper Jurassic assemblages in China and elsewhere (Lockley and Gierlinski 2006).

Based on its original occurrence in the Lower Jurassic of New England (Hitchcock 1848) and recurrence in other Lower Jurassic assemblages, *Anomoepus* was considered as a characteristic ichnogenus of the Lower Jurassic biochron of Lucas (2007). According to this author, it is the first ichnologically based biochron with a global distribution. This is confirmed by the aforementioned Lower Jurassic occurrences in Europe, Asia and North America, but it should be noted

FIG. 4.—Photograph and interpretive outline drawing of *Anomoepus* DLSIII-O1 trackway at Dalishu tracksite III.

that *Anomoepus* also occurs in the Middle and Late Jurassic, for example in the Late Jurassic of Spain (Lockley et al. 2008). Therefore, it is not an exclusively Lower Jurassic ichnogenus. In this regard we also note that *Anomoepus* is not a mono-ichnospecific ichnogenus as claimed by Olsen and Rainforth (2003); see Lockley and Gierlinski (2006) for discussion.

PRESERVATION

Some of the tracks exhibit a morphology associated with soft sediment collapse around digits. This is particularly evident for DSLIII-O1-R1 (Fig. 5). This track displays a raised area in the center of the track, at the convergence of the digit impressions. The raised portion within the track possesses two raised areas (Fig. 5A), and an inverted 'v' shape at the posterior end, a morphology highly similar to theropod tracks made in soft mud described by Gatesy et al. (1999, fig. 1c, d), and by Falkingham and Gatesy (2014, fig. 4) in simulated dry granular media. These were shown by those authors to be produced as the foot exits the sediment. The presence of this morphology suggests that the infill is likely to be part of the original track, and that the surface currently exposed may not be the original tracking surface.

CONCLUSIONS

Small predominantly tridactyl tracks from the lower Shawan Member of the Lufeng Formation in the Dalishu area, Lufeng County, Yunnan represent the fifth report of *Anomoepus* from the Jurassic of China. A few examples show a diagnostic tetradactyl morphology.

Most reports of *Anomoepus* from China are associated with sites dated as Lower or Middle Jurassic. This stratigraphic occurrence is consistent with the occurrence of the ichnogenus in the globally widespread Lower Jurassic biochron of Lucas (2007).

Anomoepus appears to be less common in the Jurassic than theropod tracks, which are ubiquitous in most regions. For this reason they may have been overlooked, and the increase in reports of *Anomoepus* in recent years may reflect improved ability by ichnologists to identify this ichnogenus.

The occurrences reported and reviewed here show that *Anomoepus* is an important component of Early Jurassic ichnofaunas indicating the presence of ornithischian trackmakers in biotas which locally lack or contain only rare ornithischian skeletal remains.

ACKNOWLEDGMENTS

The authors thank Xing Xu (Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences) for his critical comments and suggestions on this paper. This research was supported by the 2013 and

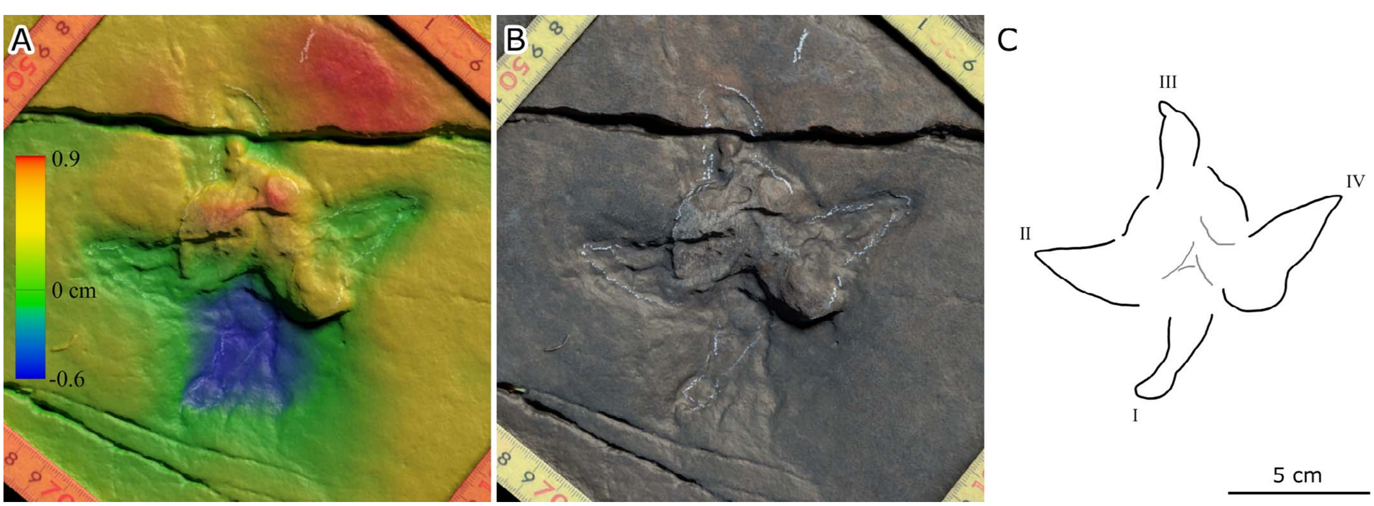

FIG. 5.—**A**) Photogrammetric color depth map of track DLSIII-O1-R1. **B**) Color orthophotograph of track DLSIII-O1-R1. **C**) Interpretive outline drawing of track DLSIII-O1-R1. The raised areas in the center of track likely formed as the digits exited the substrate. Scale bar = 5 cm. Color map ranges from –0.6 cm (blue) to 0.9 cm (red).

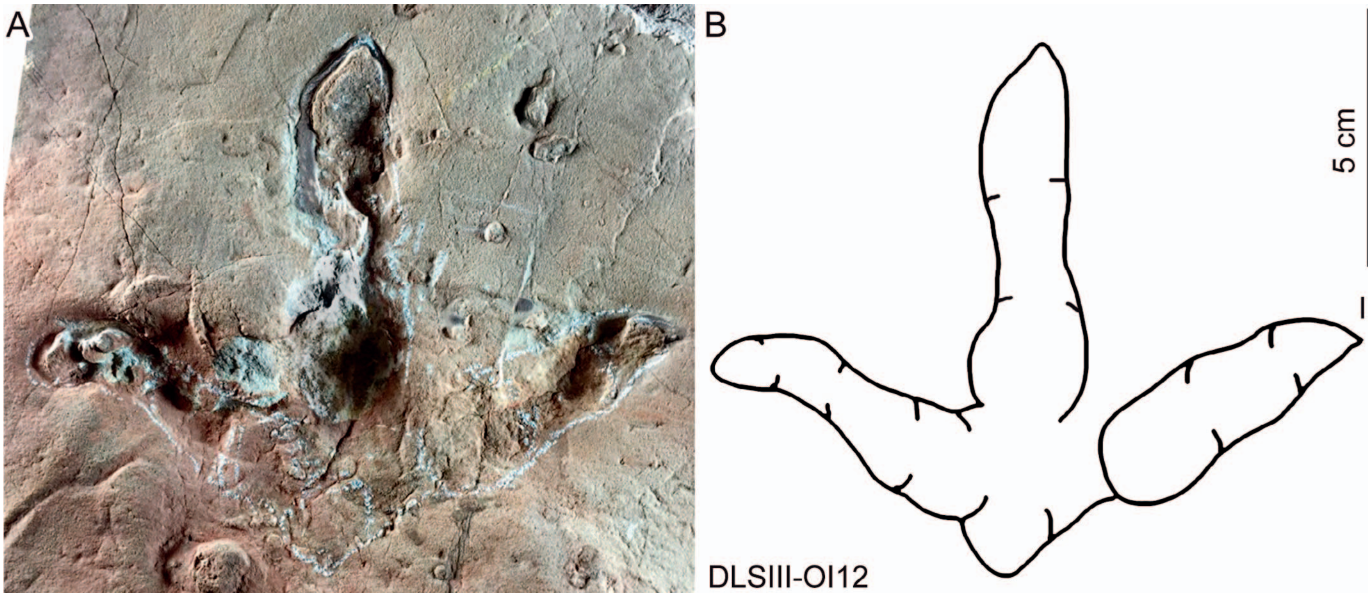

FIG. 6.—Photograph and interpretive outline drawing of *Anomoepus* DLSIII-OI12 at Dalishu tracksite III.

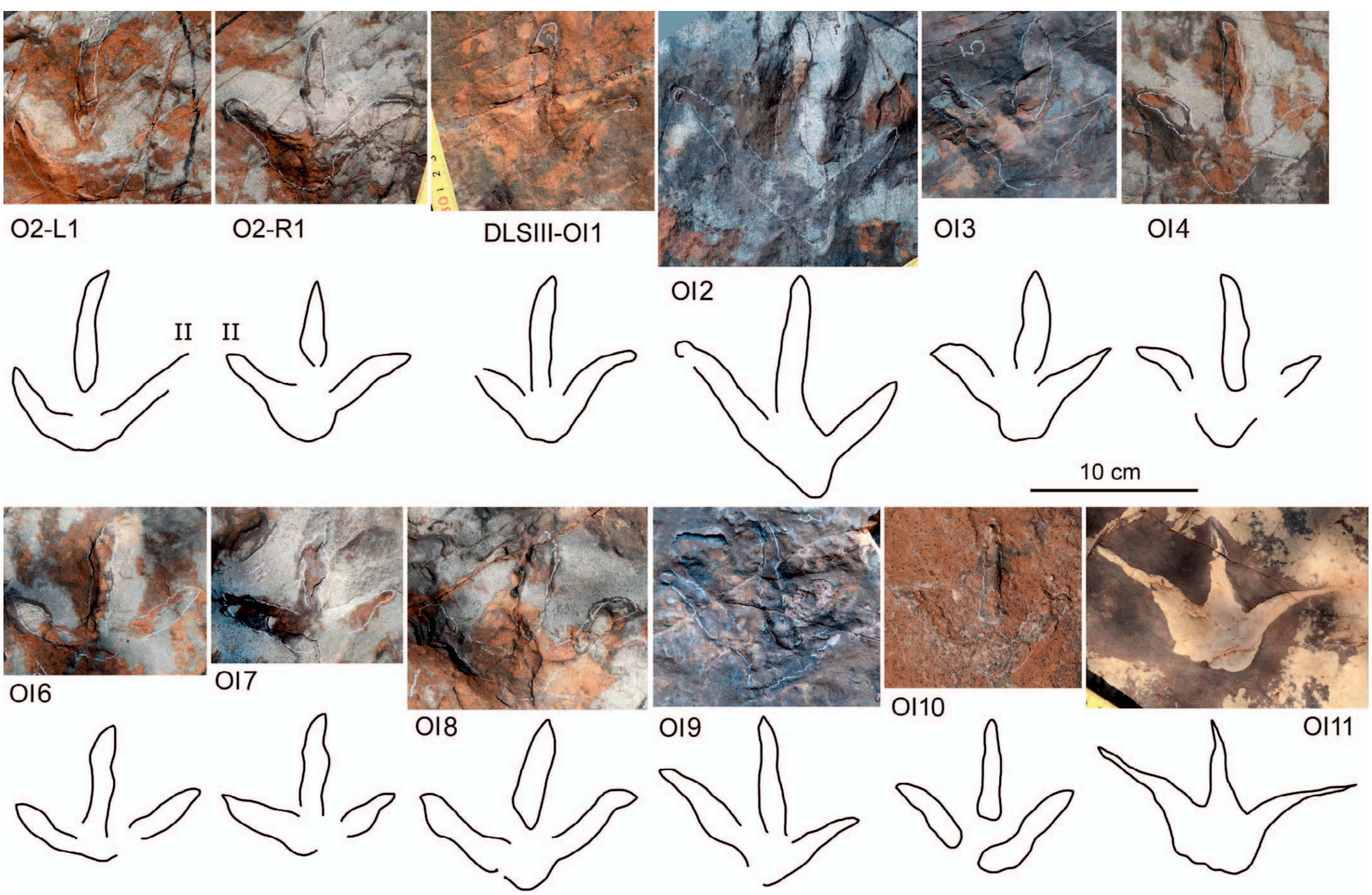

FIG. 7.—Photograph and interpretive outline drawings of *Anomoepus* tracks from trackway DLSIII-O2 and isolated imprints DLSIII-OI1–4 and DLSIII-OI6–11 at Dalishu tracksite III.

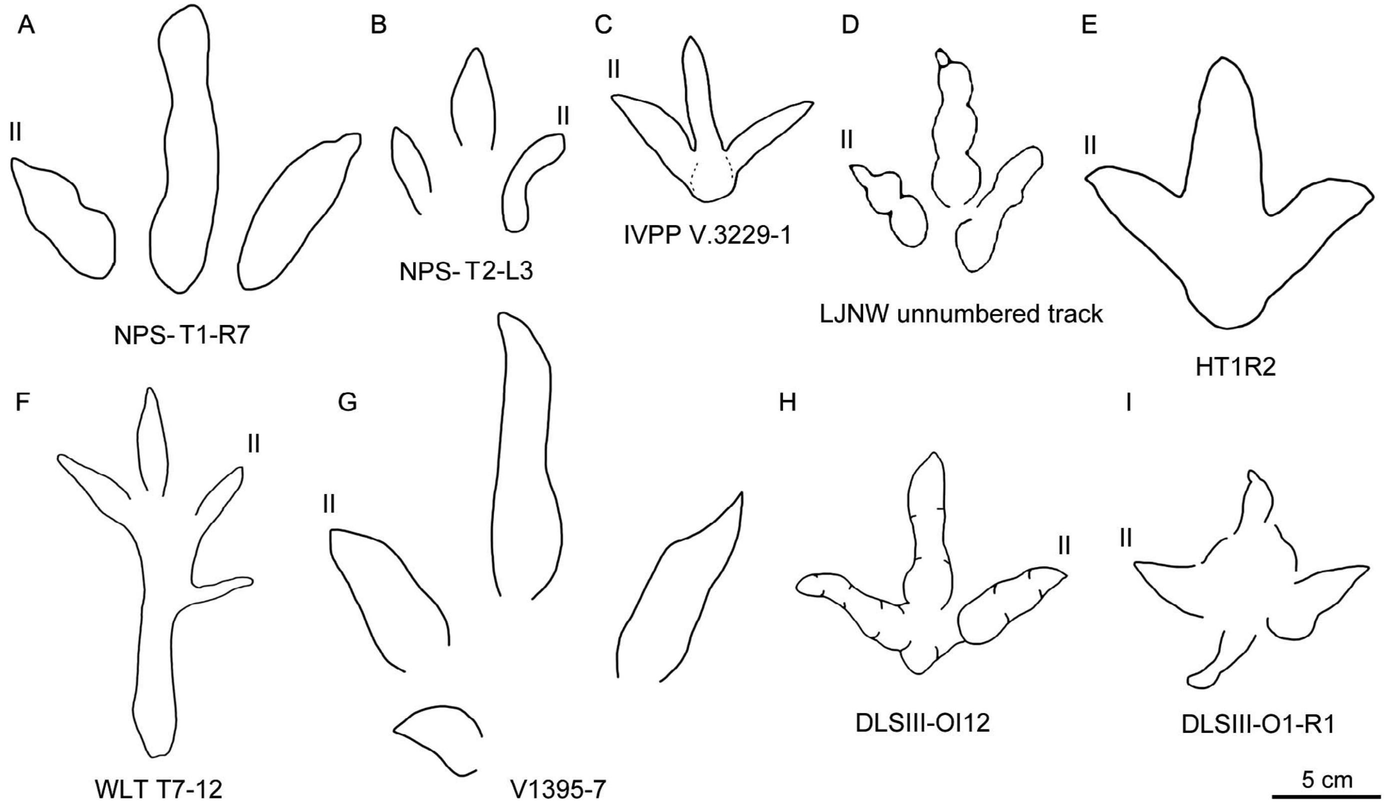

FIG. 8.—Schematic diagrams of *Anomoepus* ichnotaxa to the same scale. **A**, **B**) Middle Jurassic Jinlijing site, Sichuan Province. **C**) Middle Jurassic Jiaoping Coal Mine site, Shaanxi Province (Xing et al. 2015). **D**) Lower Jurassic Lijiananwa site from Shaanxi Province (Li et al. 2012). **E**) Middle Jurassic Huo and Wang sites from Shaanxi Province (Xing et al. 2015). **F**) Lower Jurassic Wulatezhongqi site from Inner Mongolia (Li et al. 2010). **G**) Upper Jurassic Nan'an site from Chongqing municipality (Xing et al. 2013). **H**, **I**) This paper.

2015 support fund for graduate students' science and technology innovation from China University of Geosciences (Beijing), China, and the World Dinosaur Valley Park, Yunnan Province, China. Reviewer B. Breithaupt, three anonymous reviewers, and editors A. Fiorillo and T. Olszweski are thanked for comments and suggestions that improved the paper.

REFERENCES

BARRETT, P.M., BUTLER, R.J., AND KNOLL, F., 2005, Small-bodied ornithischian dinosaurs from the Middle Jurassic of Sichuan, China: Journal of Vertebrate Paleontology, v. 25, p. 823–834.

BIEN, M.N., 1941, 'Red Beds' of Yunnan: Bulletin of the Geological Society of China, v. 21, p. 159–198.

D'ALESSANDRO, A. AND BROMLEY, R.G., 1986, Trace fossils in Pleistocene sandy deposits from Gravina area, Italy: Revista italiana di Paleontologia e Stratigrafia, v. 92, p. 67–102.

DONG, Z. AND TANG, Z., 1983, New ornithopod genus from the Middle Jurassic of Sichuan Basin, China: Vertebrata PalAsiatica, v. 21, p. 168–171.

EMMONS, E., 1844. The Taconic System: based on observations in New York, Massachusetts, Maine, Vermont and Rhode Island: Carrol and Cook, Albany, 68 p.

FALKINGHAM, P.L. AND GATESY, S.M., 2014, The birth of a dinosaur footprint: subsurface 3D motion reconstruction and discrete element simulation reveal track ontogeny: Proceedings of the National Academy of Sciences, v. 111, p. 18279–18284.

FANG, X.S., PANG, Q.J., LU, L.W., ZHANG, Z.X., PAN, S.G., WANG, Y.M., LI, X.K., AND CHENG, Z.W., 2000, Lower, Middle, and Upper Jurassic subdivision in the Lufeng region, Yunnan Province, *in* Proceedings of the Third National Stratigraphical Congress of China, Editorial Committee of Proceedings of the Third National Stratigraphical Congress of China: Geological Publishing House, Beijing, p. 208–214.

GATESY, S.M., MIDDLETON, K.M., JENKINS, F.A., AND SHUBIN, N.H., 1999, Three-dimensional preservation of foot movements in Triassic theropod dinosaurs: Nature, v. 399, p. 141–144.

GIERLIŃSKI, G. AND PIENKOWSKI, G., 1999, Dinosaur track assemblages from the Hettangian of Poland: Geological Quarterly, v. 43, p. 329–346.

GIERLIŃSKI, G., PIENKOWSKI, G., AND NIEDZWIEDZKI, G., 2004. Tetrapod track assemblage in the Hettangian of Soltykow, Poland, and its paleoenvironmental background: Ichnos, v. 11, p. 195–213.

HALL, J., 1847. Paleontology of New York, Volume I, Containing Description of the Organic Remains of the Lower Middle Division of the New York System (equivalent of the Lower Silurian rocks of Europe): C. van Benthuysen, Albany, 338 p.

HAUBOLD, H., 1984, Saurierfährten: Wittenberg Lutherstadt, A. Ziemsen Verlag, 231 p.

HAUBOLD, H., 1986. Archosaur footprints at the terrestrial Triassic–Jurassic transition, *in* K. Padian (ed.), The Beginning of the Age of Dinosaurs: Cambridge University Press, Cambridge, p. 189–201.

HITCHCOCK, E., 1848, An Attempt to Discriminate and Describe the Animals that Made the Fossil Footmarks of the United States, and Especially of New England: Memoirs of the American Academy of Arts and Sciences, Second Series, v. 3, p. 129–256.

HITCHCOCK, E., 1858, Ichnology of New England: A Report on the Sandstone of the Connecticut Valley, Especially its Fossil Footmarks: William White, Boston, 366 p.

HITCHCOCK, E., 1865, Supplement to the Ichnology of New England: Wright and Potter, Boston, 96 p.

HUANG, T.D., HUANG, C.L., LIN, C.T., KNELL, M.J., AND YANG, W.J., 2009, Exploring dinosaur strata of Yunnan via rare earth element analyses: Western Pacific Earth Sciences, v. 9, p. 15–36.

KENT, D.V., OLSEN, P.E., AND WITTE, W.K., 1995. Late Triassic–earliest Jurassic geomagnetic polarity sequence and paleolatitudes from drill cores in the Newark Rift basin, eastern North America: Journal of Geophysical Research, v. 100, p. 14965–14998.

KSIAZKIEWICZ, M., 1977, Trace fossils in the flysch of the Polish Carpathians: Palaeontologia Polonica, v. 36, p. 1–208.

LI, J.J., BAI, Z.Q., LOCKLEY, M.G., ZHOU, B., LIU, J., AND SONG, Y., 2010, Dinosaur tracks in Wulatezhongqi, Inner Mongolia: Acta Geologica Sinica, v. 84, p. 723–742.

LI, J.J., LOCKLEY, M.G., ZHANG, Y.G., HU, S.M., MATSUKAWA, M., AND BAI, Z.Q., 2012, An important ornithischian tracksite in the Early Jurassic of the Shenmu Region, Shaanxi, China: Acta Geologica Sinica, v. 86, p. 1–10.

LOCKLEY, M.G., GARCIA-RAMOS, J.C., LIRES, J., PINUELA, L. AND AVANZINI, M., 2008, A review of vertebrate track assemblages from the Late Jurassic of Asturias, Spain with comparative notes on coeval ichnofaunas from the western USA: implications for faunal diversity in association with siliciclastic facies assemblages: Oryctos, v. 8, p. 53–70.

Lockley, M.G. and Gierlinski, G., 2006, Diverse vertebrate ichnofaunas containing *Anomoepus* and other unusual trace fossils from the Lower Jurassic of the western United States: implications for paleoecology and palichnostratigraphy: New Mexico Museum of Natural History and Science Bulletin, v. 37, p. 175–191.

Lockley, M.G. and Hunt, A.P., 1995, Dinosaur Tracks and Other Fossil Footprints of the Western United States: Columbia University Press, New York, 338 p.

Lockley, M.G., Li, J.J., Li, R.H., Matsukawa, M., Harris, J.D., Xing, L.D., 2013, A review of the tetrapod track record in China, with special reference to type ichnospecies: implications for ichnotaxonomy and paleobiology: Acta Geologica Sinica (English edition), v. 87, p. 1–20.

Lockley, M.G. and Matsukawa, M., 2009, A review of vertebrate track distributions in East and Southeast Asia: Journal Paleontological Society of Korea, v. 25, p. 17–42.

Lucas, S.G., 2007, Tetrapod footprint biostratigraphy and biochronology: Ichnos, v. 14, p. 5–38.

Lull, R.S., 1904, Fossil footprints of the Jura-Trias of North Americ: Memoirs of the Boston Society of Natural History, v. 5, p. 461–557.

Luo, Z.X. and Wu, X.C., 1995, Correlation of vertebrate assemblage of the lower Lufeng Formation, Yunnan, China, *in* A.L. Sun and Y. Wang (eds.), Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biotas: China Ocean Press, Beijing, p. 83–88.

Narbonne, G.M. and Hofmann, H.J., 1987, Ediacaran biota of the Wernecke Mountains, Yukon, Canada: Journal of Paleontology, v. 30, p. 647–676.

Niedźwiedzki, G., 2011, A Late Triassic dinosaur-dominated ichnofauna from the Tomanová Formation of the Tatra Mountains, Central Europe: Acta Palaeontologica Polonica, v. 56, p. 291–300.

Nopcsa, F., 1923, The families of the Reptilia: Progress of Geology and Paleontology, v. 2, p. 1–210.

Olsen, P.E. and Rainforth, E.C., 2003, Early Jurassic ornithischian dinosaurian ichnogenus *Anomoepus*, *in* P.M. LeTourneau and P.E. Olsen (eds.), The Great Rift Valleys of Pangea in Eastern America, Volume 2, Sedimentology, Stratigraphy and Paleontology: Columbia University Press, New York, p. 314–368.

Peng, G.Z., 1990, A new small ornithopod (*Agilisaurus louderbacki* gen. et sp. nov.) from Zigong, China: Newsletter of the Zigong Dinosaur Museum (in Chinese), v. 2, p. 19–27.

Peng, G.Z., Ye, Y., Gao, Y.H., Jiang, S, and Shu, C.K., 2005, Jurassic dinosaur faunas in Zigong: People's Publishing House of Sichuan Province, Chengdu, 236 p.

Ratcliffe, B.C. and Fagerstrom, J.A., 1980, Invertebrate lebensspuren of Holocene floodplains: their morphology, origin and paleoecological significance: Journal of Paleontology, v. 54, p. 614–630.

Seeley, H.G., 1887, On the classification of the fossil animals commonly named Dinosauria: Proceedings of the Royal Society of London, v. 43, p. 165–171.

Sekiya, T., 2011, Re-examination of *Chuanjiesaurus ananensis* (Dinosauria: Sauropoda) from the Middle Jurassic Chuanjie Formation, Lufeng County, Yunnan Province, southwest China: Memoir of the Fukui Prefectural Dinosaur Museum, v. 10, p. 1–54.

Sheng, S.F., Chang, L.Q., Cai, S.Y., and Xiao, R.W., 1962, The problem of the age and correlation of the red beds and the coal series of Yunnan and Szechuan: Acta Geological Sinica, v. 42, p. 31–56.

Tan, X.H., 1997, Stratigraphy and depositional environments of the Lufeng Basin: Yunnan Geological Science and Technology Information, v. 1, p. 21–22.

Thulborn, T., 1990, Dinosaur Tracks: Chapman and Hall, London, 410 p.

Weems, R.E., 1992, A re-evaluation of the taxonomy of Newark Supergroup saurischian dinosaur tracks, using extensive statistical data from a recently exposed tracksite near Culpeper, Virginia, *in* P.C. Sweet (ed.), Proceedings of the 26th Forum on the Geology of Industrial Minerals: Virginia Division of Mineral Resources Publication, v. 119, p. 113–127.

Xing, L.D., Harris, J.D., Feng, X.Y., and Zhang, Z.J., 2009, Theropod (Dinosauria: Saurischia) tracks from Lower Cretaceous Yixian Formation at Sihetun, Liaoning Province, China and possible trackmakers: Geological Bulletin of China, v. 28, p. 705–712.

Xing, L.D., Lockley, M.G., Chen, W., Gierliński, G.D., Li, J.J., Persons, W.S. IV., Matsukawa, M., Ye, Y., Gingras, M.K., and Wang, C.W., 2013, Two theropod track assemblages from the Jurassic of Chongqing, China, and the Jurassic stratigraphy of Sichuan Basin: Vertebrata PalasiAtica, v. 51, p. 107–130.

Xing, L.D., Lockley, M.G., Tang, Y.G., Klein, H., Zhang, J.P., Persons, W.S. IV., Dai, H., and Ye, Y., 2015, Theropod and ornithischian footprints from the Middle Jurassic Yanan Formation of Zizhou County, Shaanxi, China: Ichnos, v. 22, p. 1–11.

Xing, L.D., Lockley, M.G., Zhang, J.P., You, H.L., Klein, H., Persons, W.S. IV., Dai, H., and Dong, Z.M., 2016, First Early Jurassic ornithischian and theropod footprint assemblage and a new ichnotaxon *Shenmuichnus wangi* ichnosp. nov. from Yunnan Province, Southwestern China: Historical Biology, v. 28, p. 721–723, http://dx.doi.org/10.1080/08912963.2015.1020424.

You, H.L., Azuma, Y., Wang, T., Wang, Y.M., and Dong, Z.M., 2014, The first well-preserved coelophysoid theropod dinosaur from Asia: Zootaxa, v. 3873, p. 233–249.

Young, C.C., 1966, Two footprints from the Jiaoping coal mine of Tungchuan, Shensi: Vertebrata PalAsiatica, v. 10, p. 68–71.

Zhang, X.P., 1991, Fossils from Tiaomajian Formation of Middle Devonian In Xinhua, Xiantan and other areas: Hunan Geology, v. 10, p. 97–104.

Received 30 September 2015; accepted 25 September 2016.