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Unusual deinonychosaurian track morphology (*Velociraptorichnus zhangi* n. ichnosp.) from the Lower Cretaceous Xiaoba Formation, Sichuan Province, China

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Abstract

A new Lower Cretaceous dinosaur footprint locality named the Mujiaowu tracksite in the Xiaoba Formation, Sichuan Province, has yielded a new assemblage containing the didactyl deinonychosaurian ichnogenus *Velociraptorichnus*. This is the eleventh report in the global record, the seventh from Asia and the fifth from China. All, except for an isolated report from Europe, occur in Lower Cretaceous deposits. Unlike previous reports of the ichnogenus, the Mujiaowu site has yielded both didactyl *Velociraptorichnus* tracks and tridactyl tracks which we interpret as a different expression of this same ichnogenus, caused by registration of digit II, either due to special substrate conditions or to less claw retraction. These tridactyl *Velociraptorichnus* footprints are assigned to the new ichnospecies *Velociraptorichnus zhangi*. Such tridactyl deinonychosaurid footprint morphology is predictable, but based on current ichnological evidence appears to be the

exception rather than the rule.

Keywords: Lower Cretaceous; Xiaoba Formation; deinonychosaurian track; *Velociraptorichnus*

1. Introduction

Because of its close phylogenetic relationship with birds, the Deinonychosauria clade (Gauthier, 1986) has been intensely studied in recent years. Deinonychosauria includes dromaeosaurids and troodontids, and the most iconic characteristic of the group is an enlarged pedal claw on digit II, which could be raised and held in a hyperextended position (Turner et al., 2012). Deinonchosaurians had four pedal digits including a short hallux that was not used functionally in locomotion (Turner et al., 2012). From both the track record and studies on functional morphology, it is evident that the distal part of digit II, which is characterized by a large claw, normally did not make contact with the substrate during locomotion (Li et al., 2007; Xing et al., 2013a; Lockley et al., in press). However, under certain conditions such as deeper substrate or variation in the posture of digit II, the latter could occasionally have left a distinct trace. Evidence from the Mujiaowu tracksite suggests that both didactyl and tridactyl expressions of the deinonychosaurian pes may be present in the Mesozoic track record.

Most phylogenetic studies have recovered a monophyletic Deinonychosauria comprising two subgroups, i.e., the Dromaeosauridae and Troodontidae (Gauthier, 1986; Holtz, 1998; Sereno, 1999; Turner et al., 2012; Agnolín and Novas, 2013), but other studies suggest that Deinonychosauria itself is paraphyletic, with troodontids being more closely related to birds than to dromaeosaurs (Forster et al., 1998; Godefroit et al., 2013) or vice versa (Xu et al., 1999; Norell et al., 2001). Furthermore, although many recent studies suggest that *Rahonavis*, other unenlagiids, and *Anchiornis* and its kin are deinonychosaurs (Makovicky et al., 2005; Hu et al., 2009; Xu et al., 2011; Senter et al., 2012; Turner et al., 2012), these taxa have been suggested to be basal avialans by other studies (Novas and Puerta, 1997; Forster et al., 1998; Xu et al., 2009; Agnolín and Novas, 2013; Godefroit et al., 2013). Finally, the iconic *Archaeopteryx* appears to possess a specialized pedal digit II (Mayr et al., 2005), though not as specialized as in Deinonychosauria. A hyper-extensible second pedal digit is thus likely to characterize a

clade more inclusive than the Deinonychosauria pending on the systematic positions of *Archaeopteryx* and other suggested basal avialans (Xu et al., 2011).

In 1994, Zhen et al. described three didactyl tracks from the Lower Cretaceous Jiaguan Formation and named them *Velociraptorichnus sichuanensis*, considering them to have been made by a dromaeosaur-type trackmaker on the basis of the didactyl foot morphology. This was the first documented instance of deinonychosaurian tracks. Presently, eleven deinonychosaurian track sites, all Cretaceous in age, are known: five from China, two from Korea, two from North America, and two from Europe. Most of these tracks have been assigned to four ichnogenera: *Velociraptorichnus, Dromaeopodus, Menglongipus*, and *Dromaeosauripus* (Lockley et al., in press) based on the configuration of digit pads and size.

In April 2014, Xiao-Min Zheng and Huan-Xin Zhang from Sichuan Bureau of Geological Exploration and Development of Mineral Resources discovered a new track site at Lewu Township (Fig. 1), which preserves an assemblage with theropod and sauropod tracks. These are described here in detail.

Institutional abbreviations

MJW = Mujiaowu tracksite, Xide County, Liangshan, China; SBGED = Sichuan Bureau of Geological Exploration and Development of Mineral Resources.

2. Geological setting

The Mujiaowu tracksite (GPS: 28°17'31.00"N, 102°39'2.00"E) near Mujiaowu Village, Lewu Township, Xide County, Liangshan, southwestern Sichuan Province, is an exposed light purplish red fine-grained feldspathic quartzose sandstone surface in the lower part of the Lower Cretaceous Xiaoba Formation. The area, which consists of Liangshan Autonomous Prefecture and Panzhihua City, is commonly known as the Panxi (Panzhihua–Xichang) region. The Panxi region is where the Cretaceous formations are most widely distributed in Sichuan Province other than in the Sichuan Basin. The largest basin in the Panxi region is the Mishi (Xichang)-Jiangzhou Basin (Luo, 1999).

Based on biostratigraphic evidence, from ostracods and stoneworts, the Cretaceous sediments of the Mishi-Jiangzhou Basin can be divided into the Lower Cretaceous Feitianshan and Xiaoba formations and the Upper Cretaceous–Paleogene Leidashu

Formation (Gu and Liu, 1997).

The Lower Cretaceous Xiaoba Formation is about 2434.5 m thick (SBGED, 2014) and formed primarily by purplish-red calcareous siltstone and mudstone (Gu and Liu, 1997), intercalated with carbonate and evaporite strata (SBGMR, 1991). The formative sedimentary systems have been interpreted as alluvial-fan, fluvial, and lacustrine environments (Chang et al., 1990). The First Member of the Xiaoba Formation is equivalent to the Jiaguan Formation from the Sichuan Basin (CGCMS, 1982).

3. Description of tracks and trackways

3.1. Didactyl deinonychosaur tracks

Material: Three natural molds of didactyl pes impressions, with slight sediment fill, cataloged as MJW-T2-L1–R1, MJW-TI4 from the Mujiaowu tracksite (Figs. 2-7, Table 1), and represented by plaster replicas SBGED-20141121-3 (MJW-T2-L1) and SBGED-20141121-4 (MJW-T2-R1).

Description: MJW-T2-L1 and R1 are preserved in a sandstone slab of the Mujiaowu tracksite, approximately 3 m away from the main track surface (in situ). Based on lithology, this slab is probably coincident with the main track surface. MJW-T2-L1-R1 is a single pace with a mean L/W ratio of 1.5. The pes tracks are elongate (average length 11.3 cm) with two digit impressions (digits III and IV) and a short rounded heel. A very faint trace of the digit II impression appears visible in T2-L1. The digit II impression connects with the impression of digit III at its proximomedial edge. The impressions of digits III and IV are roughly equal in length; however, those of digit IV are slightly more robust than those of digit III. The divarication angle between digits III and IV is 41°. In the trace of digit IV of MJW-T2-L1 two sub-rounded distal pads are visible. Claw impressions are relatively sharp, especially in digit III of L1. The large metatarsophalangeal region is semicircular and not separated from the digit traces by a distinct border. The absence of clear traces of accompanying digit II indicates the deinonychosaurian affinity of this trackway (Li et al., 2007; Lockley et al., in press). MJW-TI4 is a single track from the main track surface. Although the specimen is poorly preserved, the didactyl pes impression indicates the affinity with deinonychosaur tracks. Comparisons and discussion: Deinonychosaurian ichnotaxa (Fig. 5) currently consist of

four ichnogenera (Velociraptorichnus, Dromaeopodus, Dromaeosauripus, and Menglongipus). Xing et al. (2013b) divided these ichnogenera into small sized (mean pes length 10 cm); medium-sized (mean pes length 15 cm); large-sized (mean pes length of about 30 cm) tracks. T1-L1 belongs to the small sized tracks. Small sized deinonychosaurian tracks include Velociraptorichnus sichuanensis (Zhen et al., 1994; Xing et al., 2009), Velociraptorichnus isp. (Li et al., 2007), Menglongipus sinensis (Xing et al., 2009), Dromaeosauripus hamanensis (Kim et al., 2008) Dromaeosauripus jinjuensis (Kim et al., 2012), and Dromaeosauripus isp. indet. (Lockley et al., 2014). Among all these ichnotaxa, *Menglongipus sinensis* is extremely small (pes length of holotype is 6.3 cm; Xing et al., 2009) with digit IV being significantly shorter than digit III. Also it lacks a well-defined metatarsophalangeal pad. Dromaeosauripus tracks differ from the Mujiaowu tracks in being larger, up to about 20 cm long, and by the more slender shape with well-defined digital pad traces. Menglongipus sinensis also differs from the Mujiaowu tracks in size and by the shorter digit IV. The Mujiaowu tracks and *Velociraptorichnus sichuanensis* are similar in size and morphology to Velociraptorichnus sichuanensis. The length of the type specimen of V. sichuanensis is

11 cm, and that of Velociraptorichnus isp. from Shandong Province ~10 cm (Li et al.,

2007). *Velociraptorichnus* is characterized by relatively thick digits (compared with other deinonychosaurian tracks, such as *Dromaeosauripus*), and by the absence of well-defined digital pads, features seen also in the Mujiaowu tracks. Other similarities concern (1) the divarication angle between digits III and IV which is 30° and 27° in the *Velociraptorichnus* holotype and the Shandong specimen, respectively, and 41° in the Mujiaowu specimens, (2) a track length/single pace length ratio of 5 (55/11, based on the *Velociraptorichnus* paratype) vs. a track length/single step length ratio of 4.2 in the Mujiaowu tracks. An ichnospecific assignment cannot be given. Therefore, we refer the didactyl tracks from the Mujiaowu tracksite tentatively to *Velociraptorichnus* isp.

3.2. Systematic ichnology of tridactyl deinonychosaur tracks

Theropoda Marsh, 1881 Dromaeopodidae Li et al., 2007 Velociraptorichnus Zhen et al., 1994 Velociraptorichnus zhangi n. ichnosp. (Figs. 2-7, Table 1)

Etymology: The specific name is in honor of Dr. Jian-Ping Zhang, a well-known geologist and paleontologist who has contributed to the study of ichnology and application and construction of many Global and National Geoparks in China.

Holotype: One natural mold of tridactyl pes, cataloged as TI6 from the Mujiaowu tracksite Replica of holotype represented by SBGED-20141121-1. The original specimen remains in the field.

Paratypes: Specimen TI7 is a natural mold similar to the holotype. Replica of paratype represented by SBGED-20141121-2. As with the holotype, this specimen remains in the field.

Locality and horizon: Xiaoba Formation, Lower Cretaceous. Mujiaowu tracksite, Xide County, Sichuan Province, China.

Diagnosis: Small-sized (~10.4 cm long and ~9.4 cm wide) tridactyl theropod tracks with extremely low mesaxony. Digit II trace very narrow compared with other digits, approximately half the width of digit III; sharp claw impressions; large semicircular metatarsophalangeal region. The divarication angle between digits II and IV is 52°. The divarication angle between digits II and III is approximately half of that between digits III and IV.

Description: Compared with TI7, TI6 is better preserved with an L/W ratio of 1.1 (1.0 in TI7). It is tridactyl with digit III being slightly longer than other digits or subequal with digit II. Digits have sharp distal ends indicating the presence of acuminate claws, but digit pad traces are faint or indistinct, and still show residues of infilling sediment. The digit III trace is the widest, the digit II trace significantly narrower than other digits. The large metatarsophalangeal region is semicircular in shape. The divarication angle of digits II and IV is 52°, with the divarication angle between digits II and III being much smaller (17°) than that between digits III and IV (35°). The trace of the heel of TI6 is prominent

and probably formed by the dynamics of the foot registering on the sediment. TI7 is similar to TI6 in general morphology and was possibly left by a different individual as indicated by the smaller size.

Comparisons and discussion: According to Olsen (1980), Weems (1992), and Lockley (2009), theropod tracks can be differentiated on the basis of mesaxony: i.e., the degree to which the central digit (III) protrudes anteriorly beyond the medial (II) and lateral (IV) digits. Anterior triangle length/width ratios of TI6 and T17 are ~0.05 and ~0.10, respectively. Tracks with extremely low mesaxony as in the described specimens are not common. They are different from other known tridactyl theropod tracks from China and elsewhere. In this regard it is known that most deinonychosaurtracks have a digit IV almost as long a digit III. This type of morphology, by definition, leads to low mesaxony.

However, regardless of digit II, digits III and IV as well as the heel traces of TI6 and TI7 are similar in proportions and relative position to those seen in MJW-T2. For example, the divarication angles between digits III and IV are 35° (TI6) and 38° (TI7), close to 41° measured in MJW-T2, and the L/W ratios of TI6 and TI7 are 1.5–1.6, matching 1.5 of MJW-T2. All previously identified deinonychosaurian tracks are didactyl; however, we here consider TI6 and TI7 to be tridactyl versions of *Velociraptorichnus*. Although the large raptorialclaw borne on the highly modified second digit of deinonychosaurs is thought to have been held in a retracted position during locomotion, the digit was highly mobile and could have occasionally contacted the ground, leaving a distinct trace in a tridactyl track. We interpret the very narrow digit II impression observed in TI6 and TI7 as likely being the impression left by the large raptorial claw. The unusual preservation of the digit II claw impression may be attributed to substrate conditions where the tracks were registered that were different from those that prevailed at other *Velociraptorichnus* tracksites.

Similar track registration evidence appears to have been recorded in possible prosauropod tracks from the Late Triassic–Early Jurassic known as the ichnogenus *Evazoum* (Nicosia and Loi, 2003). Lockley and Lucas (2013) reported that *Evazoum* from North America includes a morphotype that is functionally didactyl, or pseudo-didactyl. These tracks in some cases preserve only the proximal pad trace of digit II as a swollen or enlarged pad, similar as in *Dromaeopodus* (Li et al., 2007); however, in other cases a faint trace of digit II is preserved, sometimes revealing only the distal trace of a claw. This

morphotype, which suggests a retractable digit II, has been illustrated on a number of occasions (Olsen et al., 1989; Gaston et al., 2003; Lockley et al., 2006) and recently formally described as the new ichnospecies *Evazoum gatewayensis* (Lockley and Lucas, 2013; Lockley et al., in press). We therefore predict that future finds of deinonychosaur tracks might show similar incomplete traces of digit II which would be intermediate in morphology between all previously-reported didactyl tracks and the tridactyl expression here designated as the ichnospecies *V. zhangi*.

3.3. Non-deinonchosaurian tridactyl tracks

Material: Seven natural molds of footprints, cataloged as MJW-T1-R1–R2, TI1–3, 5 from the Mujiaowu tracksite (Figs. 7, 8, Table 1). According to differences in morphology and mesaxony (Lockley, 2009), these tracks can be divided into two morphotypes.

Description, comparisons and discussion:

Morphotype A: Trackway MJW-T1 consists of three pes imprints that are rotated toward the midline (along digit III). They are small (13.3 cm long) and tridactyl. Manus and tail traces are absent. The length/width ratio of these tracks is 1.2. Track T1-L1 is the best representative of the track morphology. Digit III projects the farthest anteriorly. The digit impressions reveal indistinct pad impressions. The claw marks are relatively sharp. The proximal region of digits II and IV forms an indistinct U-shaped metatarsophalangeal region that lies in line with the axis of digit III. The footprints of trackway MJW-T1 have wide divarication angles $(62-79^\circ)$, show weak mesaxony, and have an anterior triangle length/width ratio of 0.49. Trackway MJW-T1 is narrow (pace angulation about 175°) and characterized by comparatively short stride lengths (70 cm). Morphotype A is morphologically similar to Anomoepus, i.e., similar size, wide divarication angles, weak mesaxony, and U-shaped metatarsophalangeal region. Anomoepus records in China are limited to the Jurassic, such as in Chongqing (Xing et al., 2013c) and North Shanxi (Xing et al., 2015a). Nevertheless, as Grallator-Eubrontes-Kayentapus assemblages, which were abundant during the Jurassic in North America, are also widely distributed in Cretaceous strata of China (Lockley et al., 2013), the Cretaceous occurrence of typical Jurassic Anomoepus would not be surprising. Therefore, we provisionally refer MJW-T1 to cf. Anomoepus isp.

Morphotype B: Among the isolated tracks TI1–3 and TI5, TI1 is the best preserved with an L/W ratio of 1.5 and an anterior triangle length/width ratio of 0.60. Two and three digit pads, respectively, are distinctly visible in digits II and III. The metatarsophalangeal pad of digit IV is relatively well-developed and positioned on the axis of digit III. Other tracks are poorly preserved and characterized by weak to moderate mesaxony (0.32–0.47), which is typical for footprints of the ichno- or morphofamily Eubrontidae Lull, 1904. However, a concrete ichnogeneric assignment cannot be given.

Most tridactyl tracks are oriented toward the west, perhaps indicating an ancient geographic constraint, such as a bank line (Lockley and Hunt, 1995).

3.4. Sauropod tracks

Material: Three natural molds of pes, cataloged as MJW-S1-LP1–LP3 from the Mujiaowu tracksite (Figs. 7, 9, Table 1).

Description: MJW-S1-LP1–LP2 is quite well preserved, but the right side of the track is covered by large collapsed rocks and vegetation, making it inaccessible. LP3 is poorly preserved, but appears to be in line with LP1 and LP2. These three tracks likely belong to the same trackway. All pes imprints lack associated manus prints.

The mean length of MJW-S1-LP1–LP2 is 44.2 cm, and the mean L/W ratio is 1.1. S1-LP1 is the best preserved and has a distinct displacement rim at the front of the track. The pes impression possesses four poorly defined indentations at its anterior margin, corresponding to the predicted positions of digits I to IV. The metatarsophalangeal pad impression is complete with smoothly curved margins.

Comparisons and discussion: Brontopodus (Farlow et al., 1989) is one of the most common and well known Cretaceous sauropod track types. Previously, most Early Cretaceous sauropod tracks in East Asia have been attributed to wide gauge *Brontopodus* (Lockley et al., 2002) and to narrow gauge *Parabrontopodus* (Xing et al., 2013b). Wide gauge or narrow gauge is an important distinguishing characteristic of sauropod trackways. Generally, *Brontopodus* represents distinct mid- or wide- gauge trackways whereas *Parabrontopodus* represents distinct narrow-gauge trackways (Lockley et al., 1994). As one side of the trackway is destroyed, gauge characteristics of MJW-S1 are difficult to determine. However, the length/width ratio of MJW-S1 is 1.1, and this ratio is coincident with that of typical sauropod tracks such as *Brontopodus* (~1.3, Farlow et al.,

1989) or Linshu *Brontopodus* isp. LSI-S1 (1.2, Xing et al., 2013b). The L/W ratio of typical *Parabrontopodus* appears to be larger (~1.4, Lockley et al., 1994), whereas the majority of *Parabrontopodus* isp. found in China are small and medium sized tracks (mostly smaller than 40 cm) (Xing et al., in press a). So, we tentatively refer MJW-S1 to *Brontopodus* isp.

6. Conclusions

As reviewed by Lockley et al. (in press) increased reports of deinonychosaurian tracks currently show that most sites occur in East Asia. Given that the here described tracks are the first to show both didactyl and tridactyl versions, we may roughly estimate that only about 10% of such tracks preserved the trace of the distal part of digit II. This suggests that most deinonychosaurs represented in the track record were habitually, functionally didactyl during progression, and therefore the registration of distal traces of digit II, as reported here, is the exception rather than the rule. Presumably, the registration of such digit II traces resulted from either unusual substrate conditions or behavior which led to less retraction of this digit. Assuming some morphological diversity among deinonychosaurians of the size of the *Velociraptorichnus* track makers reported from East Asia, it is possible that significant differences in the degree of retraction of pedal digit II were characteristic of different species, potentially contributing to different track morphotypes. Such inference could, in theory, be confirmed by finding skeletal remains indicating functionally different pedal configurations. The present report indicates that such difference might be sought in the skeletal record.

Currently, dinosaur tracks in the Mishi (Xichang)-Jiangzhou Basin are only found in the Early Cretaceous Feitianshan Formation. Several tracksites have been discovered, including Zhaojue tracksites I, II and IIN (Xing et al., 2013d, 2014, 2015b; Xing and Lockley, 2014), the Jiefanggou tracksite (Xing et al., 2015c), and the Yangmozu tracksite. Trackmakers include sauropods, theropods, ornithopods, and pterosaurs. This study documents the first dinosaur tracks from the Xiaoba Formation. Except for cf. *Anomoepus*, assemblages with *Velociraptorichnus* type, *Eubrontes* type, and *Brontopodus* type tracks have been found in contemporary strata of the Jiaguan Formation (Zhen et al., 1994; Xing et al., in press b). This indicates that the Early Cretaceous dinosaur faunas of the Sichuan and Mishi (Xichang)-Jiangzhou basins were

similar.

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References

- Agnolín, F.L., Novas, F.E., 2013. Avian ancestors: A review of the Phylogenetic relationships of the theropods Unenlagiidae, Microraptoria, *Anchiornis* and Scansoriopterygidae. SpringerBriefs in Earth System Sciences, 96 pp.
- CGCMS (Compiling Group of Continental Mesozoic Stratigraphy and Palaeontology in Sichuan Basin of China), 1982. Continental Mesozoic Stratigraphy and Palaeontology in Sichuan Basin of China. People's Publishing House of Sichuan Chengdu, 405 pp. (in Chinese).
- Chang, Y.H., Luo, Y.N., Yang, C.X., 1990. Panxi Rift and Its Geodynamics. Geological Publishing House, Beijing, 421 pp. (in Chinese).
- Farlow, J.O., Pittman, J.G., Hawthorne, J.M., 1989. *Brontopodus birdi*, Lower Cretaceous sauropod footprints from the US Gulf coastal plain. In: Gillette, D.D., Lockley, M.G. (Eds.), Dinosaur Tracks and Traces. Cambridge University Press, Cambridge, pp. 371–394.
- Forster, C.A., Sampson, S.D., Chiappe, L.M., Krause, D.W., 1998. The theropod ancestry of birds: new evidence from the Late Cretaceous of Madagascar. Science 279, 1915–1919.
- Gaston, R., Lockley, M.G., Lucas, S.G., Hunt, A.P., 2003. *Grallator*-dominated fossil footprint assemblages and associated enigmatic footprints from the Chinle Group (Upper Triassic), Gateway area, Colorado. Ichnos 10, 153–163.

Gauthier, J., 1986. Saurischian monophyly and the origin of birds. Memoirs of the

California Academy of Sciences 8, 1–55.

- Godefroit, P., Cau, A., Hu, D.Y., Escuillié, F., Wu, W.H., Dyke, G., 2013. A Jurassic avialan dinosaur from China resolves the early phylogenetic history of birds. Nature 498, 359–362.
- Gu, X.D., Liu, X.H., 1997. Stratigraphy (Lithostratic) of Sichuan Province. China University of Geosciences Press, Wuhan, 417 pp. (in Chinese).
- Holtz, T.R. Jr., 1998. A new phylogeny of the carnivorous dinosaurs. Gaia 15, 5-61.
- Hu, D.Y., Hou, L.H., Zhang, L.J., Xu, X., 2009. A pre-*Archaeopteryx* troodontid from China with long feathers on the metatarsus. Nature 461, 640–643.
- Kim, J.Y., Kim, K.S., Lockley, M.G., 2008. New didactyl dinosaur footprints (*Dromaeosauripus hamanensis* ichnogen. et ichnosp. nov.) from the Early Cretaceous Haman Formation, south coast of Korea. Palaeogeography, Palaeoclimatology, Palaeoecology 262, 72–78.
- Kim, J.Y., Lockley, M.G., Woo, J.O., Kim, S.H., 2012. Unusual didactyl traces from the Jinju Formation (Early Cretaceous, South Korea) indicate a new ichnospecies of Dromaeosauripus. Ichnos 19, 75–83.
- Li, R.H., Lockley, M.G., Makovicky, P.J., Matsukawa, M., Norell, M.A., Harris, J.D., Liu, M.W., 2007. Behavioural and faunal implications of Early Cretaceous deinonychosaur trackways from China. Naturwissenschaften 95, 185–191.
- Lockley, M.G., 2009. New perspectives on morphological variation in tridactyl footprints: clues to widespread convergence in developmental dynamics. Geological Quarterly 53, 415–432.
- Lockley, M.G., Hunt, A.P., 1995. Dinosaur Tracks and Other Fossil Footprints of the Western United States. Columbia University Press, New York, 360 pp.
- Lockley, M.G., Lucas, S.G., 2013. *Evazoum gatewayensis*, a new Late Triassic archosaurian ichnospecies from Colorado: Implications for footprints in the ichnofamily Otozoidae. New Mexico Museum of Natural History and Science, Bulletin 61, 345–352.
- Lockley, M.G., Farlow, J.O., Meyer, C.A., 1994. *Brontopodus* and *Parabrontopodus* ichnogen. nov. and the significance of wide- and narrow-gauge sauropod trackways. Gaia 10, 135–145.

Lockley, M.G., Wright, J., White, D., Li, J.J., Feng, L., Li, H., 2002. The first sauropod

trackways from China. Cretaceous Research 23, 363–381.

- Lockley, M.G., Lucas, S.G., Hunt, A.P., 2006. *Evazoum* and the renaming of northern hemisphere "*Pseudotetrasauropus*": implications for tetrapod ichnotaxonomy at the Triassic–Jurassic boundary. New Mexico Museum of Natural History and Science, Bulletin 37, 199–206.
- 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 87 (1), 1–20.
- Lockley, M.G., Gierlinski, G.D., Houck, K., Lim, J.D.F., Kim, K.S., Kim, D.Y., Kim, T.K., Kang, S.H., Hunt Foster, R., Li, R., Chesser, C., Gay, R., Dubicka, Z., Cart, K., Wright, C., 2014. New excavations at the Mill Canyon dinosaur track site (Cedar Mountain Formation, Lower Cretaceous) of eastern Utah. New Mexico Museum of Natural History and Science, Bulletin 62, 287–300.
- Lockley, M.G., Harris, J.D., Li, R.H., Xing, L.D., van der Lubbe, T., in press. Two-toed tracks through time: on the trail of "raptors" and their allies. In: Richter, A., Manning, P. (Eds.), Dinosaur Tracks: Next Steps. Indiana University Press, Bloomington.
- Luo, C.D., 1999. The Danxia landforms in southwestern Sichuan. Economic Geographya 19, 65–70 (in Chinese).
- Lull, R.S., 1904. Fossil footprints of the Jura-Trias of North America. Memoirs of the Boston Society of Natural History 5, 461–557.
- Makovicky, P.J., Apesteguía, S., Agnolín, F.L., 2005. The earliest dromaeosaurid theropod from South America. Nature 437, 1007–1011.
- Marsh, O.C., 1881. Principal characters of American Jurassic dinosaurs. Part V. The American Journal of Science and Arts, Series 3 (21), 417–423.
- Mayr, G., Pohl, B., Peters, S., 2005. A well-preserved *Archaeopteryx* specimen with theropod features. Science 310, 1483–1486.
- Nicosia, U., Loi, M., 2003. Triassic footprints from Lerici (La Spezia, northern Italy). Ichnos 10, 127–140.
- Norell, M.A., Clark, J.M., Makovicky, P.J., 2001. Phylogenetic relationships among coelurosaurian dinosaurs. In: Gauthier, J., Gall, L.F. (Eds.), New Perspectives on the Origin and Evolution of Birds. Yale University Press, New Haven, pp. 49–67.

- Novas, F.E., Puerta, P.F., 1997. New evidence concerning avian origins from the Late Cretaceous of Patagonia. Nature 387 (6631), 390–392.
- Olsen, P.E., 1980. Fossil great lakes of the Newark Supergroup in New Jersey. In: Manspeizer, W. (Ed.), Field Studies of New Jersey Geology and Guide to Field Trips. Rutgers University, New Brunswick, pp. 352–398.
- Olsen, P.E., Schlische, R.W., Gore, P.J.W. (Eds.), 1989. Tectonic, Depositional, and Paleoecological History of Early Mesozoic Rift Basins, Eastern North America. Vol. T351. American Geophysical Union, Washington, DC, 174 pp.
- Ostrom, J.H., 1969. Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. Peabody Museum of Natural History Bulletin 30, 1–165.
- SBGED (Sichuan Bureau of Geological Exploration and Development of Mineral Resources), 2014. Reports of 1:50000 Lianghekou, Bi'er, Mishi and Zhaojue Regional Geological Surveys Mapping of Wumengshan Area, Sichuan, China. Internal publications (in Chinese).
- SBGMR (Sichuan Bureau of Geology and Mineral Resources), 1991. Regional Geology of Sichuan Province. Geological Publishing House, Beijing, 264 pp. (in Chinese).
- Senter, P., Kirkland, J.I., DeBlieux, D.D., Madsen, S., Toth, N., 2012. New dromaeosaurids (Dinosauria: Theropoda) from the Lower Cretaceous of Utah, and the evolution of the dromaeosaurid tail. PLoS ONE 7 (9), e36790.
- Sereno, P.C., 1999. The evolution of dinosaurs. Science 284, 2137–2147.
- Turner, A.H., Makovicky, P.J., Norell, M.A., 2012. A review of dromaeosaurid systematics and paravian phylogeny. Bulletin of the American Museum of Natural History 371, 1–206.
- 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: Sweet, P.C. (Ed.), Proceedings 26th Forum on the Geology of Industrial Minerals. Virginia Division of Mineral Resources Publication 119, pp. 113–127.
- Xing, L.D., Lockley, M.G., 2014. First report of small *Ornithopodichnus* trackways from the Lower Cretaceous of Sichuan, China. Ichnos 21 (4), 213–222.
- Xing, L.D., Harris, J.D., Sun, D.H., Zhao, H.Q., 2009. The earliest known

deinonychosaur tracks from the Jurassic–Cretaceous boundary in Hebei, China. Acta Palaeontologica Sinica 48 (4), 662–671.

- Xing, L.D., Li, D.Q., Harris, J.D., Bell, P.R., Azuma, Y., Fujita, M., Lee, Y., Currie, P.J.,
 2013a. A new deinonychosaurian track from the Lower Cretaceous Hekou Group,
 Gansu Province, China. Acta Palaeontologica Polonica 58 (4), 723–730.
- Xing, L.D., Lockley, M.G., Marty, D., Klein, H., Buckley, L.G., McCrea, R.T., Zhang, J.P., Gierliński, G.D., Divay, J.D., Wu, Q.Z., 2013b. Diverse dinosaur ichnoassemblages from the Lower Cretaceous Dasheng Group in the Yishu fault zone, Shandong Province, China. Cretaceous Research 45, 114–134.
- 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., Wang, C.W., 2013c. Two theropod track assemblages from the Jurassic of Chongqing, China, and the Jurassic stratigraphy of Sichuan Basin. Vertebrata PalasiAtica 51 (2), 107–130.
- Xing, L.D., Lockley, M.G., Zhang, J.P., Milner, A.R.C., Klein, H., Li, D.Q., Persons, W.S. IV, Ebi, J.F., 2013d. A new Early Cretaceous dinosaur track assemblage and the first definite non-avian theropod swim trackway from China. Chinese Science Bulletin (English Version) 58, 2370–2378.
- Xing, L.D., Lockley, M.G., Zhang, J.P., Klein, H., Persons, W.S. IV, Dai, H., 2014. Diverse sauropod-, theropod-, and ornithopod-track assemblages and a new ichnotaxon *Siamopodus xui* ichnosp. nov. from the Feitianshan Formation, Lower Cretaceous of Sichuan Province, southwest China Palaeogeography, Palaeoclimatology, Palaeoecology 414, 79–97.
- Xing, L.D., Lockley, M.G., Tang, Y.G., Klein, H., Zhang, J.P., Persons, W.S. IV, Dai, H.,
 Ye, Y., 2015a. Theropod and ornithischian footprints from the Middle Jurassic
 Yanan Formation of Zizhou County, Shaanxi, China. Ichnos 22, 1–11
- Xing, L.D., Lockley, M.G., Marty, D., Piñuela, L., Klein, H., Zhang, J.P., Persons, W.S. IV, 2015b. Re-description of the partially collapsed Early Cretaceous Zhaojue dinosaur tracksite (Sichuan Province, China) by using previously registered video coverage. Cretaceous Research 52, 138–152.
- Xing, L.D., Lockley, M.G., Yang, G., Mayor, A., Klein, H., Persons, W.S. IV, Chen, Y., Peng, G.Z., Ye, Y., Ebi, J.F., 2015c. Tracking a legend: An Early Cretaceous sauropod trackway from Zhaojue County, Sichuan Province, southwestern China.

Ichnos 22, 22-28.

- Xing, L.D., Lockley, M.G., Bonnan, M.F., Liu, Y.Q., Klein, H., Zhang, J.P., Kuang, H.W., Burns, M.E., Li, N., in press a. Late Jurassic–Early Cretaceous trackways of medium-sized sauropods from China: new discoveries, ichnotaxonomy and sauropod manus morphology. Cretaceous Research.
- Xing, L.D., Lockley, M.G., Zhang, J.P., Klein, H., Marty, D., Peng, G.Z., Ye, Y., McCrea, R.T., Persons, W.S. IV, Xu, T., in press b. The longest theropod trackway from East Asia, and diverse sauropod-, theropod-, and ornithopod-track assemblages from the Lower Cretaceous Jiaguan Formation, southwest China. Cretaceous Research.
- Xu, X., Wang, X.L., Wu, X.C., 1999. A dromaeosaurid dinosaur with a filamentous integument from the Yixian Formation of China. Nature 401 (6750), 262–266.
- Xu, X., Zhao, Q., Norell, M.A., Sullivan, C., Hone, D., Erickson, G.M., Wang, X.L., Han,
 F.L., Guo, Y., 2009. A new feathered maniraptoran dinosaur fossil that fills a morphological gap in avian origin. Chinese Science Bulletin 54, 430–435.
- Xu, X., You, H.L., Du, K., Han, F.L., 2011. An *Archaeopteryx*-like theropod from China and the origin of Avialae. Nature 475, 465–470.
- Zhen, S.N., Li, J.J., Chen, W., Zhu, S., 1994. Dinosaur and bird footprints from the Lower Cretaceous of Emei County, Sichuan. Memoirs of the Beijing Natural History 54, 105–120 (in Chinese).

Figure captions

Fig. 1. Geographical setting showing the location (star icon) of the Mujiaowu dinosaur tracksite in Xide County, Sichuan Province, China.

Fig. 2. Photograph (A) and interpretative outline drawing (B) of didactyl and tridactyl theropod tracks from the Mujiaowu tracksite.

Fig. 3. Photograph (A) and interpretative outline drawing (B) of didactyl tracks from the

Mujiaowu tracksite.

Fig. 4. Photograph (A, C) and interpretative outline drawing (B, D) of tridactyl tracks from the Mujiaowu tracksite. (E) shows superimposed didactyl and tridactyl theropod tracks.

Fig. 5. Interpretative outline drawings of dromaeopodid ichnotaxa drawn to the same scale. (A) *Menglongipus* (Xing et al., 2009); (B) *Velociraptorichnus* from Shandong (Li et al., 2007); (C) *Velociraptorichnus* (Zhen et al., 1994; Xing et al., 2009); (D) Mujiaowu didactyl track (this study); (E) *Dromaeosauripus jinjuensis* (Kim et al., 2012); (F) *Dromaeosauripus yongjingensis* (Xing et al., 2013a); (G) *Dromaeosauripus hamanensis* (Kim et al., 2008); (H) Jishan *Dromaeosauripus* isp. (Xing et al., 2013b); (I) *Dromaeopodus shandongensis* (Li et al., 2007).

Fig. 6. Illustration of the foot of *Deinonychus antirrhopus* showing the derived pedal morphology characteristic of Deinonychosauria. (A) Dorsal view; (B) lateral view; (C) with digit II touching the ground. Modified from Ostrom (1969) and Turner et al. (2012).

Fig. 7. Interpretative outline drawing of sauropod and theropod tracks from the Mujiaowu tracksite.

Fig. 8. Photograph (A) and interpretative outline drawing (B) of theropod trackway from the Mujiaowu tracksite.

Fig. 9. Photograph (A) and interpretative outline drawing (B) of sauropod track from the Mujiaowu tracksite.

Table 1. Measurements (in cm) of the theropod and sauropod tracks from Mujiawu tracksite, Sichuan Province, China. Abbreviations: ML: maximum length; MW: maximum width (measured as the distance between the tips of digits II and IV); II-III, III-IV, II-IV: angle between digits II and III, digits III and IV, and digits II and IV; PL: pace length; SL: stride length; PA: pace angulation; M: mesaxony (length/width ratio for the anterior triangle). ML/MW is dimensionless.

Number	ML	MW	II-III	III-IV	II-IV	PL	SL	PA	М	ML/MW
MJW-T1-R1	13.1	10.3	30°	32°	62°	35.5	70.0	175°	0.49	1.3
MJW-T1-L1	13.5	12.3	34°	45°	79°	34.6	_	_	0.46	1.1
MJW-T1-R2	13.2	10.4	37°	30°	67°		_	_	0.52	1.3
Mean	13.3	11.0	34°	36°	69°	35.1	70.0	175°	0.49	1.2
MJW-T2-L1	11.4	6.4	_	34°		49.0	_	—		1.8
MJW-T2-R1	10.6	7.9		48°			_	-		1.3
Mean	11.0	7.2		41°		49.0		_		1.6
MJW-TI1	19.5	12.8	32°	29°	61°				0.60	1.5
MJW-TI2	12.9	9.1			55°	_		—	0.47	1.4
MJW-TI3	16.1	13.7			63°		_	_	0.32	1.2
MJW-TI4	10.1	6.0		36°						1.7
MJW-TI5	16.6	11.0			46°				0.35	1.5
MJW-TI6	10.4	9.4	17°	35°	52°			_	0.05	1.1
		6.7*								1.6
	8.5	8.4	19°	38°	57°		_	_	0.10	1.0
MJW-11/		5.4*								1.6
MJW-S1-LP1	43.5	42.7	_		_	143.0	_			1.0
MJW-S1-LP2	44.9	41.0	_		_			_		1.1
Mean	44.2	41.9		—	—		_		—	1.1

* The maximum width exclude the digit II.