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A theropod track assemblage including large deinonychosaur tracks from the Lower Cretaceous of Asia

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ABSTRACT

A total of more than 40 tridactyl and didactyl tracks were preserved as natural casts on four fallen blocks of sandstone representing the Lower Cretaceous Jiaguan Formation of Gulin County in southeastern Sichuan Province, China. While several trackways can be distinctly followed, others are isolated imprints only. All have been flattened by overburden pressures. Tridactyl tracks are present with three size-classes being <10 cm, 10–20 cm and >20 cm in length. Morphologically they are similar to the ichnogenus *Eubrontes*, considering the relatively weak mesaxony. Eight of the tracks on one of the blocks are clearly didactyl and are here interpreted as representing large and medium sized dromaeosaurids. The largest track is about ~30 cm long and comparable in size to the type of *Dromaeopodus* (~28 cm), from the Lower Cretaceous of Shandong Province, which was the largest dromaeosaurid track previously reported. This report adds new data to the growing number of dromaeosaurid tracksites reports from China, and from the Jiaguan Formation, suggesting that this theropod group had a preference for fluvial paleoenvironments.

1. Introduction

Lower Cretaceous theropod track assemblages with tridactyl representatives are common and widespread, whereas the presence of didactyl (deinonychosaur) tracks are mostly considered a peculiar feature. In this study we document both tridactyl tracks of the *Grallator-Eubrontes* plexus and didactyl forms co-occurring on the same surfaces. The didactyl tracks have a great length indicating the presence of large deinonychosaurs in the Jiaguan Formation.

Deinonychosauria (Colbert and Russell, 1969) is a diverse clade of theropod dinosaurs, and includes many famous Cretaceous predators like *Troodon* (Leidy, 1856), *Velociraptor* (Osborn, 1924), *Deinonychus* (Ostrom, 1969), *Utahraptor* (Kirkland et al., 1993), and *Microraptor* (Xu et al., 2000). Deinonychosauria is comprised of the dromaeosaurid and troodontid subclades, which are characterized by an enlarged and strongly curved claw on digit II. This claw could be retracted and held in a raised hyperextended position (Turner et al., 2012), and exquisitely preserved specimens of troodontids such as *Mei long* and *Sinornithoides youngi* reveal that digit II was held in this raised position even while a deinonychosaur was at rest (Xu and Norell, 2004).

Most Cretaceous deinonychosaurian skeletal fossils from China have been discovered from the Jehol Biota (Xu et al., 2003), in the area formerly called Jehol (now northern Hebei Province, western Liaoning Province and eastern Inner Mongolia). The body fossil record of deinonychosaurians is so especially rich in the Jehol region that the Shandong Tianyu Museum of Nature alone possesses about 700 specimens (Xing et al., 2015b). However, owing perhaps to the relative small size of most deinonychosaurians, their fossil record is scarce in other parts of China. However, the fossil track record has provided an important supplement to the known diversity and abundance of the Deinonychosauria throughout China, and suggests that the sickle-clawed predators were more prevalent

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than the skeletal record alone might suggest. For example, prior to this study Lockley et al. (2016a,b) identified at least 16 unequivocal examples of deinonychosaurian tracksites of which the majority (9) originate from the Lower Cretaceous of China.

Whereas footprints of dinosaurs from the Jiaguan Formation are well-preserved and abundant, their skeletons are all fragmentary and extremely rare. Zhen et al. (1994) first reported deinonychosaurian tracks from the Jiaguan Formation, in the E'mei Region of the Sichuan Basin. Since 1994, two sites in the Jiaguan Formation with *Velociraptorichnus* isp. and *Velociraptorichnus zhangi* (Xing et al., 2015b), and one site in the Feitianshan Formation, southern Sichuan Basin, with cf. *Dromaeopodus* (Xing et al., 2016), have been reported. Both are in the Lower Cretaceous. These tracks are the only record of deinonychosaurians in the Sichuan Basin and the Mishi (Xichang)-Jiangzhou Basin. The Jiaguan and Feitianshan formations are Type 1 and Type 2 deposits respectively (*sensu* Lockley, 1991; Lockley et al., 1994) in which tracks represent the only tetrapod evidence (Type 1) or in which tracks dominate over body fossils (Type 2).

In recent years, a number of dinosaur tracksites have been found in the Gulin region, including the Hanxi tracksite which contains the longest theropod trackway from East Asia, and a diverse sauropod-, theropod-, and ornithopod-track assemblage (Xing et al., 2015c). The Shimiaogou tracksite, which is 3.5 km away from the Hanxi tracksite, also contains a diverse track assemblage, including theropod, sauropod, ornithopod, and pterosaur footprints. In fall of 2015, Xu Ting, a resident in Guihua Township of Gulin region, found another dinosaur tracksite in Leibei of Guihua (GPS: 28°14′22.91″, 105°39′14.40″; Fig. 1). In November of 2015, Xu Ting and the Guihua Township Government invited some of the authors (LX, GP, YY, and SJ) to conduct a formal scientific investigation on these newly discovered tracks. The Leibei tracksite mainly yields tridactyl and didactyl theropod tracks, with unusual preservation. In the following we give a detailed description of this assemblage and discuss paleoecological implications.

Institutional abbreviations and acronyms
L/R = Left/right; T = Theropod; LB = Leibei tracksite, Gulin, Sichuan Province, China.

2. Geological setting

The Sichuan Basin is known for its large exposures of thick Mesozoic continental red beds (Gu and Liu, 1997). The Cretaceous sedimentary sequences consist of the Jiaguan Formation and the underlying Guankou Formation. Sandstones are prominent in the former and mudstones in the latter. The majority of the Cretaceous tracks are known from the Jiaguan Formation. The Jiaguan Formation is comprised primarily of meandering river deposits interbedded with occasional anastomosing river deposits in the upper member that was formed under semi-arid and semi-humid climatic conditions in a tropical or subtropical climate (Chen, 2009; see also; Wang et al., 2008). A set of thick, brick-red, feldspathic, quartz sandstones are highly characteristic of the Jiaguan Formation (Sichuan Provincial Bureau of Geology aviation regional Geological Survey team, 1976). The large thick sandstones produce large track-bearing blocks that contain well-developed wedge-shaped cross-stratification. On the track-preserving surfaces, mud cracks can be seen. Recent pollen studies indicate that the Jiaguan Formation is Barremian–Albian (Chen, 2009). The Leibei tracksite (Fig. 2) is a collapsed sandstone locality in the upper member of the Jiaguan Formation, and the collapsed blocks can be traced to their original level. A more detailed list and overview of Lower Cretaceous units in southwestern China and the present footprint taxa is given in Xing and Lockley, in press.

3. Materials and methods

The Leibei tracksite is situated in Leibei, Hanxi Village, Gulin County, within Guihua River Valley. Many tracks have been found

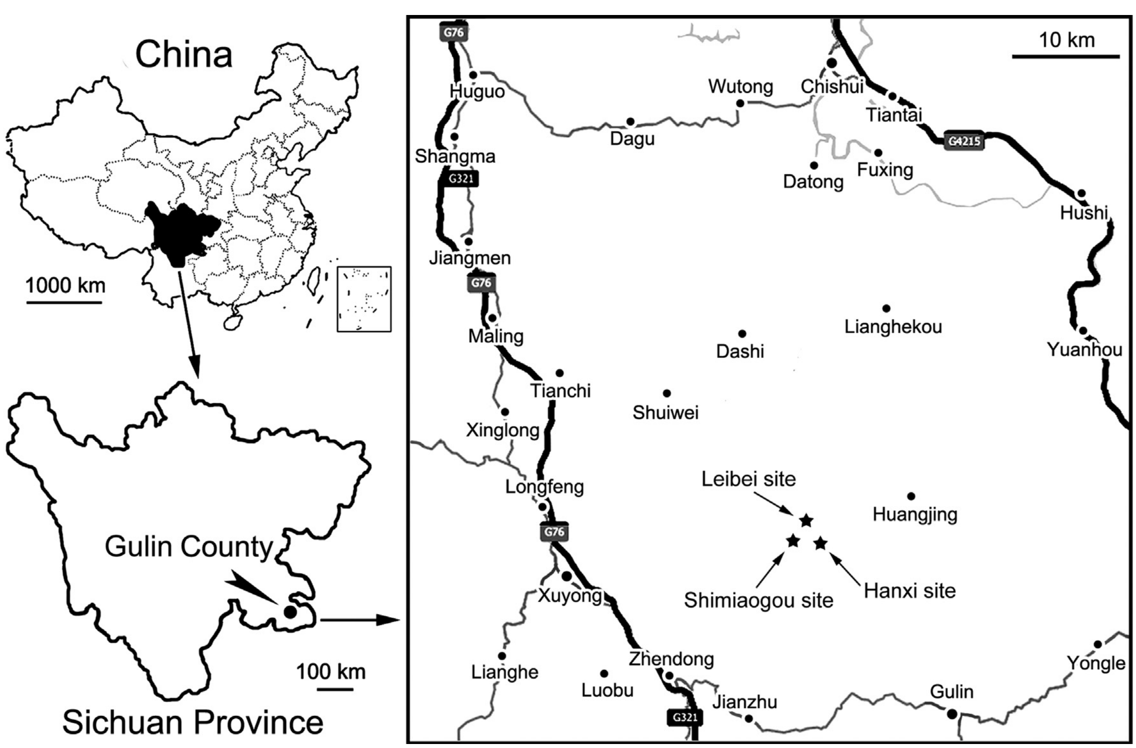

Fig. 1. Geographical setting showing the location (star icon) of the Leibei tracksite in Gulin County, Sichuan Province, China.

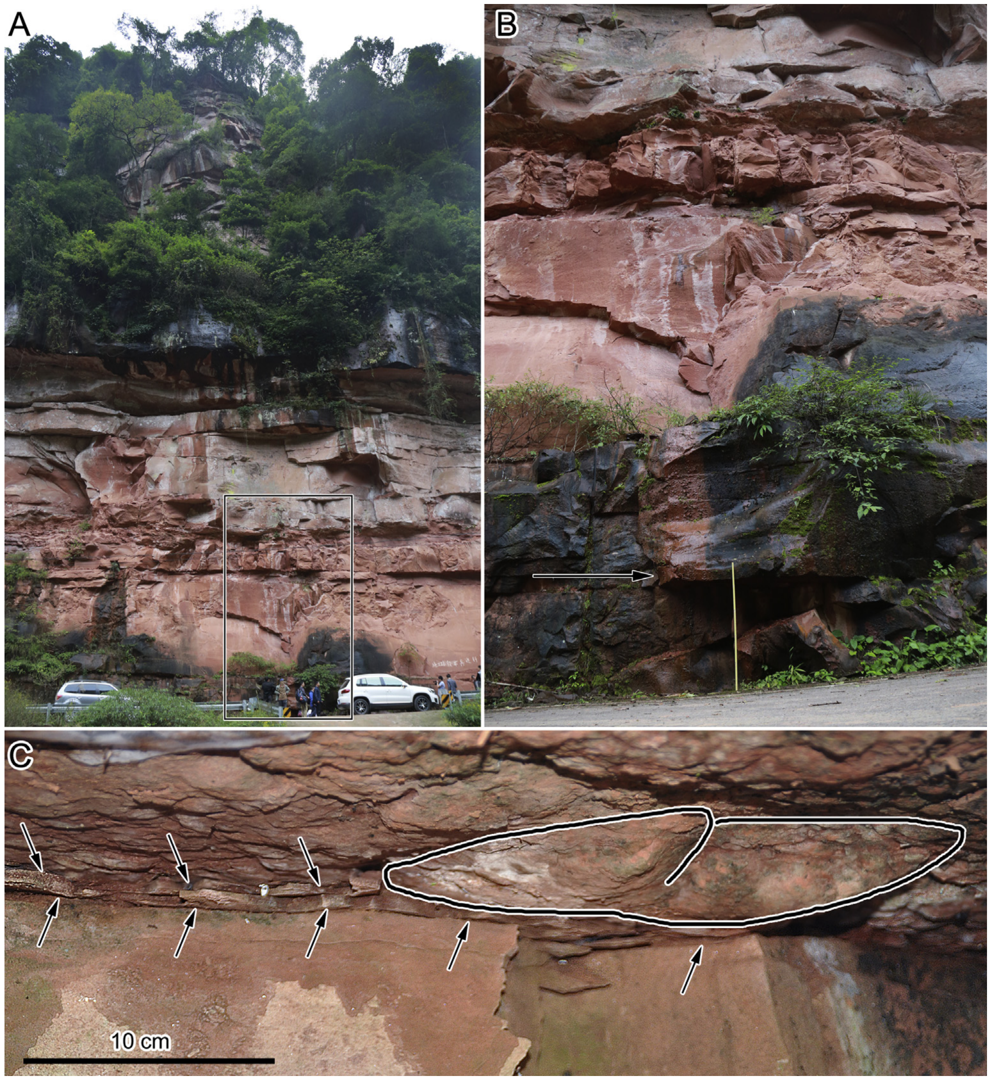

Fig. 2. General view of outcrop at the Leibei tracksite (A), close-up of the original track layer (B), arrows (C) indicate a thin muddy siltstone layer, outline drawing notes flattened track cast.

on collapsed rocks along the Guihua Creek, and the original levels of the tracks can be traced on rock sections beside the road, 10 m away.

Collapsed blocks are common at the Leibei tracksite and are scattered along the roadway on one side of the creek. Most of the blocks are covered with moss. At least four large blocks preserve tracks. Three additional tracks have been identified at the original, *in situ* level. All tracks are natural casts (convex hyporeliefs). Upon completion of track cleaning, the tracks were cataloged, photographed, and measured. A single image of the complete tracksite was formed using Adobe Photoshop Photomerge to combine several photos.

Maximum length (ML), Maximum width (MW), divarication angle (II–IV), pace length (PL), stride length (SL), pace angulation (PA), and rotation (R) were measured with the standard procedures established by Leonardi (1987) and Lockley and Hunt (1995). Methods proposed by Olsen (1980), Weems (1992), and Lockley (2009) were used to measure mesaxony (M) of tridactyl tracks (the degree to which the digit III protrudes anteriorly ahead of the digits II and IV). Speeds (v) of trackways were calculated using Alexander's (1976) formula: $v = 0.25g^{0.5} \cdot SL^{1.67} \cdot h^{-1.17}$, in which g = gravitational acceleration in m/s; SL = stride length; and h = hip height [based on the methods proposed by Alexander (1976) and Thulborn (1990)]. Moreover, in order to determine whether the trackmaker was walking, trotting or running, relative stride length (SL/h) was calculated using the method of Thulborn (1990).

Four well-preserved track-bearing blocks were discovered with identifiable tracks suitable for documentation. They are referred to as “blocks” 1–4, according to the sequence in which they are described. They display 14 trackways and a total number of 45 tracks.

Photogrammetric images were produced from multiple digital photographs which were converted into scaled, highly accurate 3D textured mesh models using Agisoft Photoscan (http://www.agisoft.ru/) (Falkingham, 2012). The mesh models were then imported into Cloud Compare (http://www.danielgm.net/cc/), where the models were rendered with accurately scaled color topographic profiles (Falkingham, 2012).

4. Track preservation

All tracks from Leibei tracksite are natural casts and most of them have features strongly suggestive of flattened tracks (Fig. 2C).

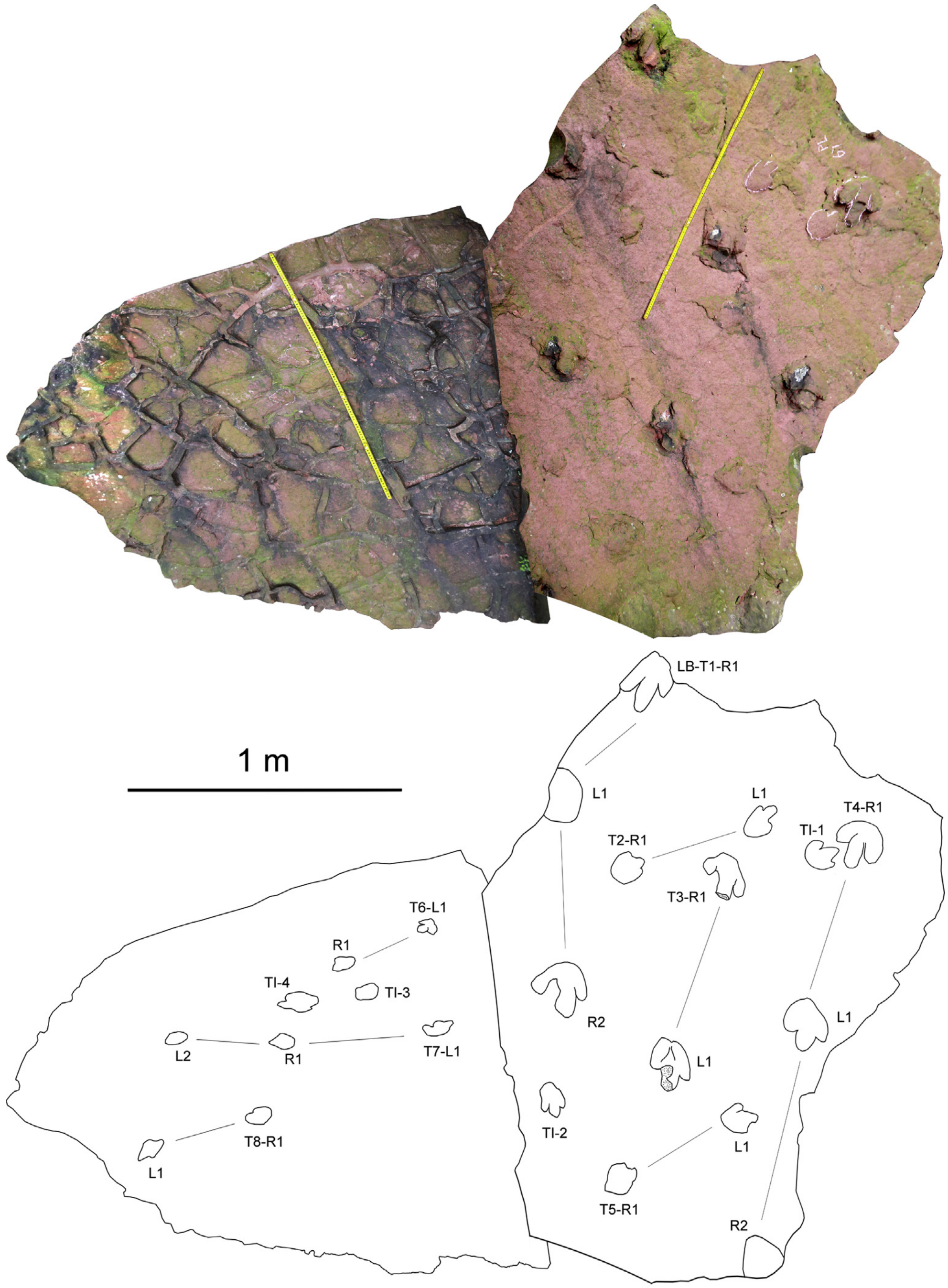

Fig. 3. Photograph and interpretative outline drawing of tridactyl theropod tracks from the Leibei tracksite block 1.

According to Lockley and Xing (2015), the most striking character of these flattened track casts is the widened appearance of all digits, especially the distal part of digit III and the reduced separation of digit traces by the reduction, or infilling of the inter-digit hypices by horizontal movement of the track fill or casting material by overburden pressures. Such flattening of digit casts is typical of sandstone casts that filled thin layers of fine, ductile sediment (silt or mud), deposited between thick sand units that are not as easily compacted as silt or mud.

Only one track can be attributed to the original level in the section. This flattened track cast, about 3.5 cm thick, occurs at the base of a thick sandstone layer (unit III). The underlying unit (II) is a thin (about 1 cm) muddy siltstone layer that was soft and ductile, which is in turn underlain by another thick sandstone unit (I). Such a silty mudstone layer sandwiched between massive sandstone units creates the perfect overburden conditions to produce flattened tracks. The trackmaker originally registered tracks on the upper surface of the silty mudstone of unit II, which was originally thicker than 1 cm, creating true tracks on unit II and perhaps undertracks on unit I. Then, the thick unit (III) of sandstone was deposited, filling the true tracks. Latter overburden pressures flattened out the softer and more ductile unit II between the thick sandstone units (I and III), and thus flattened the track infills on unit II.

The softer lithology of unit II is quite friable and prone to fragmentation. Therefore, although the weathering conditions exposed

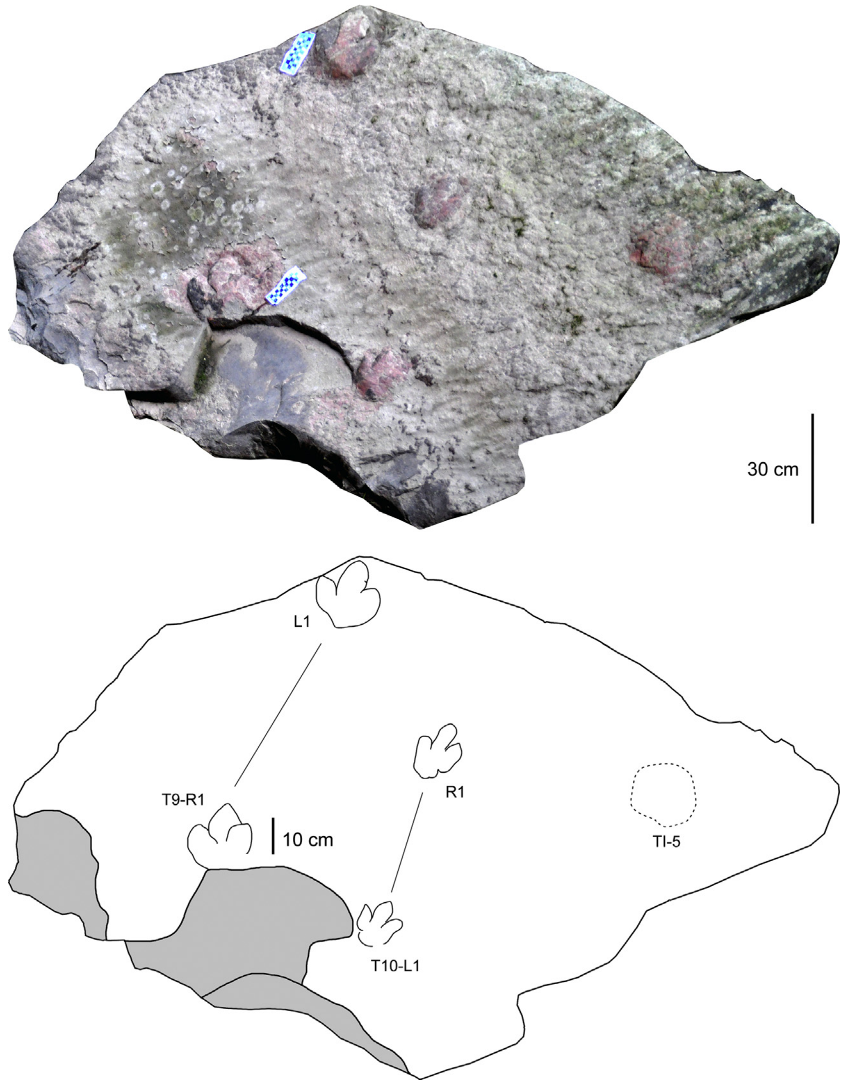

Fig. 4. Photograph and interpretative outline drawing of tridactyl theropod tracks from the Leibei tracksite block 2; showing two trackway segments of flattened tridactyl tracks.

the track casts, the track molds are seldom preserved intact and are weathered in most cases. However, the compressed flattened casts are resistant to weathering. No molds remain preserved on the surface of unit II, and undertracks can be found occasionally on the surface of unit I.

Similar to other tracksites in the Jiaguan Formation (e.g. Xing et al., 2015a), tracks at the Leibei tracksite may come from several levels. Unfortunately, the original position of tracks from blocks 1–4 cannot be traced back.

5. Theropod tracks

5.1. Tridactyl tracks

5.1.1. Description

Most Leibei tracks belong to tridactyl theropods. Well preserved tridactyl tracks are distributed on four fallen rocks which are cataloged as blocks 1–4, according to the sequence by which they were found. (Figs. 3–7).

Block 1 is comprised of two layers and preserves 14 tracks on the upper unit (Fig. 3). These tracks form five trackways: LB-T1–T5, comprised of 3, 2, 2, 3 and 2 tracks, respectively. The lower layer has highly developed mud cracks and preserves nine tracks that form three trackways: LB-T6–T8, comprised of 2, 3 and 2 tracks, respectively. Block 2 has five tracks, four of which form two paces: LB-T9–10 (Fig. 4). Block 3 preserves three tracks, two of which form a pace LB-T11 (Fig. 5) Block 4 preserves 13 tracks, among which four form two paces: LB-T12 and -T13, and three form trackway T14 (Fig. 6). Of the 27 tridactyl tracks, T4-R1, T6-R1 and TI-6 are the best preserved (Table 1).

T4-R1 (Figs. 3, 7) is 16.2 cm in length and has a L/W ratio of 1.2. Digit II is the shortest while digit III is the longest. The metatarsophalangeal pad is almost aligned with the middle axis of the track but deflects to digit IV slightly. The digit pads are indistinct. The divarication angle between digit II and digit IV is wide (61°), and the divarication angle between digit II and digit III (36°) is larger than that between digit III and IV (25°). The track rotates slightly inward. The pace length is roughly four times longer than the track. The value for M is 0.39.

T6-R1 (Figs. 3, 7) is 7.3 cm in length and has an L/W ratio of 1.2. Digit III is the shortest, while digit IV is the longest. The metatarsophalangeal pad deflects towards digit IV. The digit pads are indistinct. The divarication angle between digit II and digit IV is wide (71°), and the divarication angle between digit II and digit III

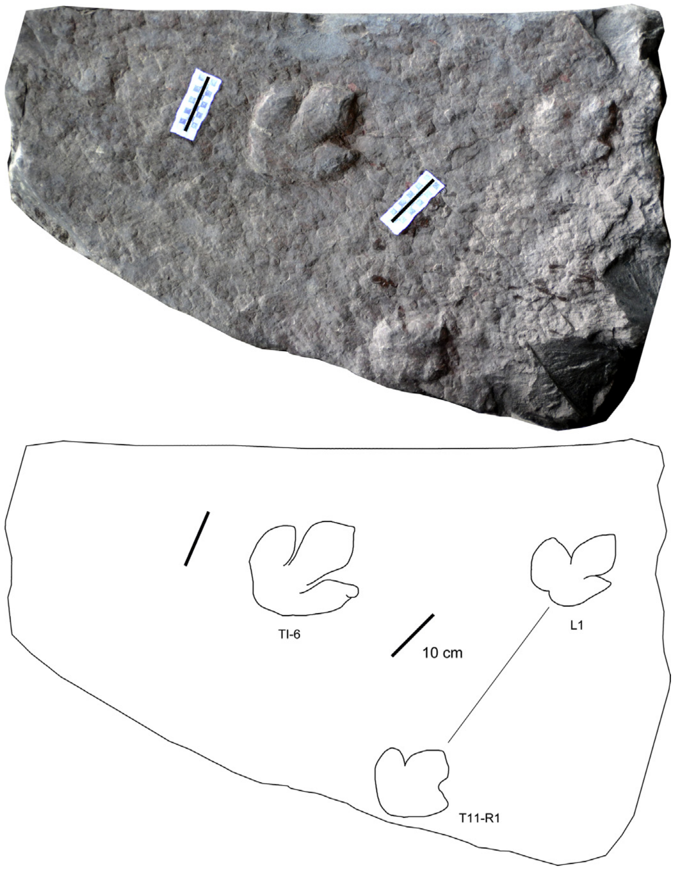

Fig. 5. Photograph and interpretative outline drawing of tridactyl theropod tracks from the Leibei tracksite block 3.

(43°) is larger than that between digit III and IV (28°). The track rotates inward towards the midline slightly. The pace length is roughly 4.8 times longer than the track. The value for M is 0.52.

The isolated TI-6 (Fig. 5) is 21 cm in length and the largest tridactyl track in Leibei tracksite. Its L/W ratio is 1.2. However, we stress that flattening of the tracks might have slightly distorted the true dimensions and therefore could influence these values. Digit II is the shortest, while digit III is the longest. The metatarsophalangeal pad is almost aligned to the middle axis of the track but deflects slightly towards digit IV. The digit pads are indistinct. Digit II and digit IV have visible claw marks and the divarication angle between them is wide (58°). The divarication angle between digit II and digit III (27°) is smaller than that between digit III and IV (31°). The value for M is 0.54. Pace lengths in LB-T1 are 67 and 68 and stride length is 132 cm. Pace length in T3 is 69 cm. Pace lengths in LB-T4 are 57 and 69 and stride length is 120 cm. Based on classic formulas of Thulborn (1990) and Alexander (1976), the relative stride length of 1.81 in LB-T1 suggests that the trackmaker was walking at a speed of about 6.48 km/h.

5.1.2. Discussion

The tridactyl tracks are identified as those of theropods based on (1) the distinct indentation of the posterior margin behind digit II, (2) claw marks, if preserved, showing a convergent margin or constriction at the junction with the digital pads (e.g. TI-6, T10), (3) a distinct metatarsophalangeal pad behind digit IV, whereas ornithopod tracks lack this feature, instead showing a large central pad behind digit III (Castanera et al., 2013).

In the Leibei tracks, lengths are larger than widths and L/W ratios of the anterior triangle are reflected by weak or moderate mesaxony, which are hallmarks of Eubrontidae (Lull, 1904). So they are provisionally referred to the *Eubrontes* morphotype. Generally *Eubrontes* was defined as a grallatorid track with relatively weak mesaxony and pes length being >25 cm (Olsen, 1980; Olsen et al., 1998). This was based on Lower Jurassic material from North America. In recent years, it has been evident that footprints similar to those of the *Eubrontes-Grallator* plexus also occur in stratigraphically younger strata, for example in the Lower Cretaceous (Xing et al., 2015d). Furthermore, *Eubrontes*-like tracks with weak mesaxony and pes lengths <25 cm are present as well.

Despite the small quantity, tracks from the Leibei tracksite reflect a diversity of trackmaker size. Track lengths fall in three classes: less than 10 cm, 10–20 cm and larger than 20 cm, and small-medium sized Eubrontid tracks dominate. Trackways LB-T1, T3 and T4 are parallel and are 30 cm and 45 cm apart from each other, probably representing group activity.

5.2. Deinonychosaurian tracks

5.2.1. Description

There are eight didactyl tracks on block 4 (Figs. 6, 8–9), five of which form two trackways: LB-T13 and T14.

LB-T14 is comprised of three tracks with a mean length of 30 cm and a mean L/W ratio of 2.7. However, we infer that LB-T14-L2 is missing or poorly preserved on the edge of the block (Fig. 6). The best preserved track is LB-T14-R2 (Fig. 8), whose length is 29.5 cm and L/W ratio is 2.8. Its digits III and IV are strong, elongated, parallel and almost equal length. There is no trace of digit II. Digital pads are unclear and no border between the heel and digital area can be seen. Relatively sharp distal digit traces (claw marks) are present. The other two tracks, LB-T14-R1 and L1, are poorly preserved and are similar to R2 in morphology, but smaller. The pace length is 2.7 times the track length. The tracks are rotated inwards towards the trackway midline by about 30°.

LB-T13 and isolated tracks TI-9, 10 and 11 are poorly preserved, are about 20 cm long (ranging from 19 cm to 22 cm), and their L/W ratios are 1.6–2.2, less than LB-T14 (2.8). Other features are the same as in LB-T14.

All the didactyl tracks from the Leibei tracksite are flattened. As described by Lockley and Xing (2015), the most striking character of these flattened tracks is the evident widening of the digit traces, which 'fuse' proximally due to filling of the hypices spaces. Distal parts of digits III and IV are also widened. These shapes are caused by overburden flattening and do not reflect true anatomy. Interestingly, the centers of the tracks have obvious pits, possibly due to the spaces between digits III, IV and the heel pad seen in *Dromaeopodus* (Li et al., 2008, and Fig. 9 herein).

In LB-T14, the pace length is 81 cm and the stride length is 163 cm. Based on the classic formula by Thulborn (1990) and Alexander (1976), the relative stride length of LB-T14 is 1.12, which indicates the trackmaker was walking at a speed of about 4.1 km/h.

5.2.2. Discussion

LB-T14 resembles typical deinonychosaur tracks, which currently include four ichnogenera (*Velociraptorichnus*, *Dromaeopodus*, *Dromaeosauripus*, and *Menglongipus*) (Xing et al., 2013a) (Figs. 8–9). Medium-large tracks include *Dromaeosauripus hamanensis* (Kim et al., 2008), *Dromaeosauripus yongjingensis* (Xing et al., 2013b), and *Dromaeopodus shandongensis* (Li et al., 2008). LB-T14 is most similar in size to *Dromaeopodus shandongensis* from Junan, Shandong, and cf. *Dromaeopodus* (BJB-TI1) from Bajiu tracksite, Sichuan (Xing et al., 2016). Length and position of the metatarsophalangeal region of LB-T14 is close to that of *Dromaeopodus*.

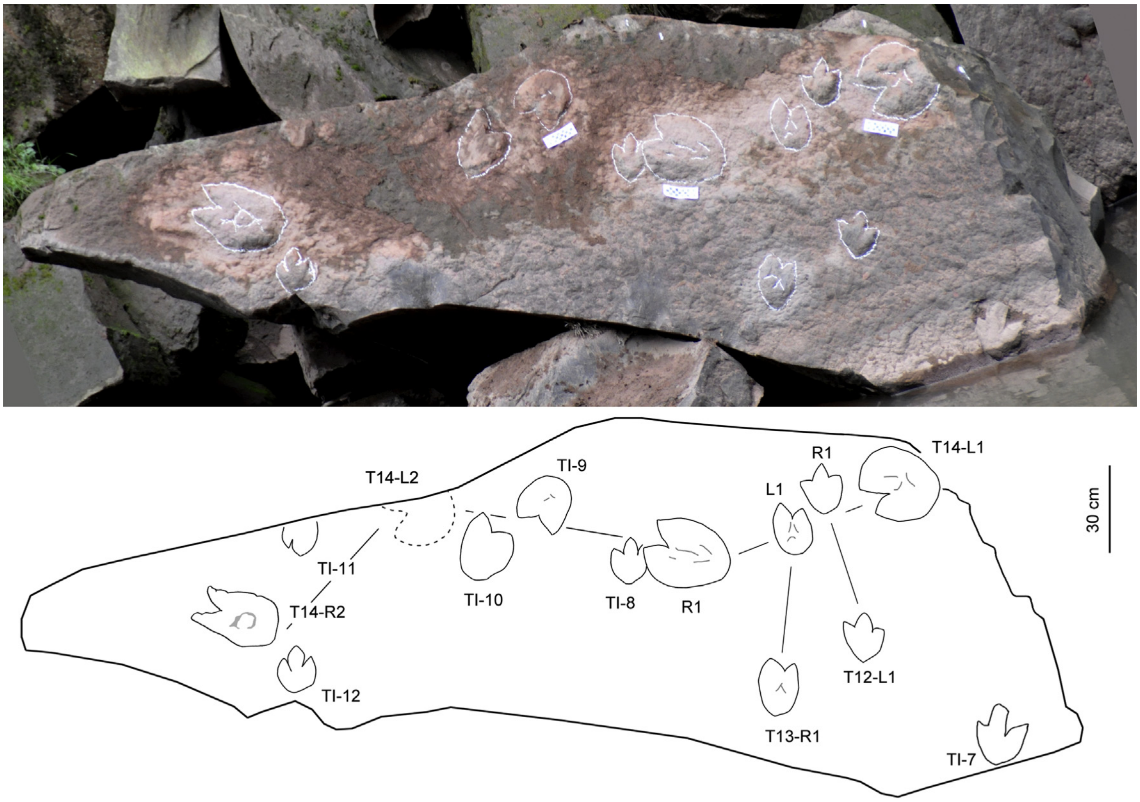

Fig. 6. Photograph and interpretative outline drawing of didactyl and tridactyl theropod tracks from the Leibei tracksite block 4.

Table 1
Measurements (in cm) of theropod tracks from track-bearing block 4 of Leibei tracksite, Sichuan Province, China.

Number.	ML	MW	II–IV	PL	SL	M	ML/MW
LB-T12-L1	16.5	15.0	61°	54.0	–	0.38	1.1
LB-T12-R1	17.5	14.5	60°	–	–	0.35	1.2
Mean	17.0	14.8	61°	54.0	–	0.37	1.2
LB-T13-R1	20.0	9.0	26°	–	–	–	2.2
LB-T13-L1	19.0	8.5	26°	55.5	–	–	2.2
Mean	19.5	8.8	26°	55.5	–	–	2.2
LB-T14-L1	29.5	10.5	21°	81.0	–	–	2.8
LB-T14-R1	30.5	11.0	20°	–	163.0	–	2.8
LB-T14-R2	29.5	10.5	21°	–	–	–	2.8
Mean	29.8	10.7	21°	81.0	163.0	–	2.8
TI-7	20.5	17.0	60°	–	–	0.41	1.2
TI-8	16.0	11.5	47°	–	–	0.35	1.4
TI-9	21.0	13.0	39°	–	–	–	1.6
TI-10	22.0	12.0	33°	–	–	–	1.8
TI-12	16.5	9.5	43°	–	–	0.44	1.7

Abbreviations: ML: Maximum length; MW: Maximum width (measured as the distance between the tips of digits II and IV); II–IV: angle between digits II and IV; PL: Pace length; SL: Stride length; PA: Pace angulation; ML/MW is dimensionless.

Flattening of the Leibei specimens impairs our ability to make further comparison. However, based on general size and shape and the knowledge that there are no other large didactyl tracks known form the Lower Cretaceous of China, or other regions, LB-T14 is here provisionally referred to cf. *Dromaeopodus* (Fig. 9).

The mean length of LB-T14 is 30 cm, slightly longer than *Dromaeopodus shandongensis* (~28 cm) and shorter than a unnamed, probable deinonychosaurian from Arches National Park, Utah (about ~28–?35 cm) (Lockley et al., 2004). This makes LB-T14 the largest deinonychosaurian track in Asia. However, again we emphasize that the size might be slightly incorrect by preservation and flattening effects. In large theropods, hip height is estimated to be 4.9 times the track length (Thulborn, 1990) and body length is estimated to be 2.63 times the hip height (Xing et al., 2009). In this way, the body length of the LB-T14 trackmaker can be roughly estimated at 3.9 m, which is larger than all known skeletons of deinonychosaurs from China (Xing Xu, pers. com.). The length is similar to that of *Deinonychus* (3.3–3.4 m) from the Lower Cretaceous (Middle Albian) of Montana (Ostrom, 1969), but smaller than that of *Utahraptor* (about 5.5 m) from the Lower Cretaceous (probably Barremian) of Utah (Kirkland et al., 1993).

6. Paleoecological inferences

The Jiaguan Formation has recently become known for many new dinosaur tracksite discoveries. As reported by Xing et al. (2016), nine of these sites have been described, and most are dominated by theropod and sauropod (saurischian) tracks, though ornithopod and pterosaur tracks occur in a few cases. Thus, the Leibei site is the tenth report, and is typical in being dominated by theropod tracks.

Lockley et al. (2016b) reported that of the16 previously documented tracksites with didactyl deinonychosaurid tracks 11 (69%) occur in Asia and 9 (56%) occur in China. The Leibei site changes these proportions to 12/17 (~71%) from Asia and 10/17 (59%) from China. There were two previous records of deinonychosaur tracksites from the Jiaguan Formation (Zhen et al., 1994; Xing et al., 2016). In both these cases the tracks are small sized and are referred to *Velociraptorichnus*. Cf. *Dromaeopodus* from the Leibei site represents the third site from this formation, all in all about 30% (3/10) of the Chinese localities. This is also the first large deinonychosaur tracksite found in Jiaguan Formation. This occurrence suggests a paleoecological pattern: i.e., the Jiaguan Formation

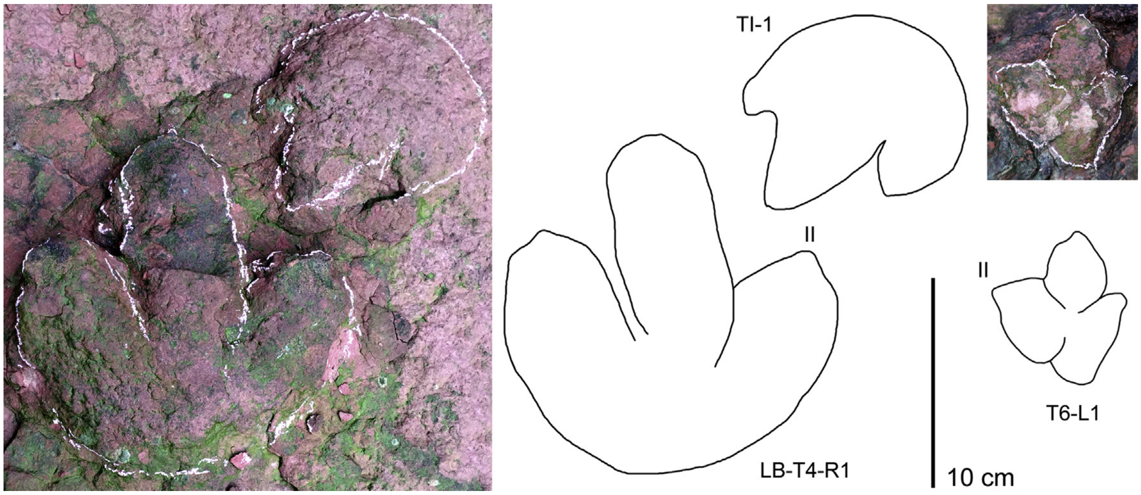

Fig. 7. Photograph and interpretative outline drawing of the well-preserved tridactyl theropod tracks from the Leibei tracksite block 1.

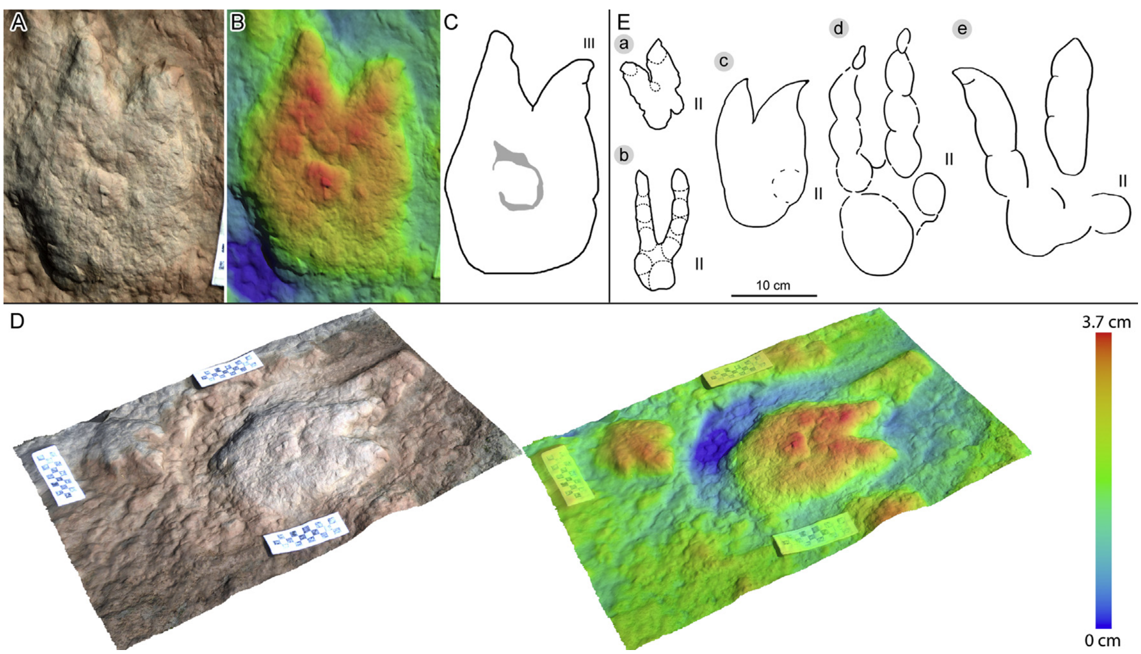

Fig. 8. Photograph (A), 3D image (B), interpretative outline drawing (C), and lower angle photograph and 3D image of didactyl deinonychosaur track T14-R2 (D) from block 4 at the Leibei tracksite. Interpretative outline drawings of dromaeopodid ichnotaxa drawn to the same scale (E): a, *Velociraptorichnus* (Zhen et al., 1994; Xing et al., 2009); b, *Dromaeosauripus yongjingensis* (Xing et al., 2013a); c, Jishan *Dromaeosauripus* isp. (Xing et al., 2013b); d, *Dromaeopodus shandongensis* (Li et al., 2007); e, cf. *Dromaeopodus* (Xing et al., 2016).

ichnofauna yields *Dromaeopodus*, *Velociraptorichnus*, *Minisauripus* and *Eubrontes* tracks, also bird tracks (*Koreanornis*) with distinct East Asian features (*sensu* Lockley et al., 2013, 2014) as in the Tianjialou Formation (Barremian–Albian, Kuang et al., 2013) ichnofauna described by Li et al. (2015) from Shandong. In addition, medium-sized deinonychosaur tracks and *Minisauripus* have been found in the Haman Formation (Aptian–Albian, Houck and Lockley, 2006) in South Korea (Kim et al., 2008), indicating a similar theropod fauna to that found in the Sichuan Basin. The Leibei discovery, therefore is consistent with the *Dromaeopodus-Velociraptorichnus-Minisauripus* assemblage dated as Barremian–Albian, which occurs in Shandong, in the Yishu fault zone (Xing et al., 2013a) and the Junan area (Li et al., 2015) and also in South Korea in the middle to late Early Cretaceous (Kim et al., 2008, 2012). Lockley et al. (2016a) argued that the majority of deinonychosaurian tracks sites are associated with Asian red bed and other inland fluvio-lacustrine paleoenvironments. The Leibei occurrence also indicates this same paleo-habitat preference.

7. Conclusions

1) The theropod ichnofauna described from the Leibei site is the tenth tracksite reported from the Lower Cretaceous red beds of the Jiaguan Formation, and includes both didactyl tracks cf. *Dromaeopodus* and tridactyl tracks assigned to *Eubrontes*.
2) This occurrence includes the third report of didactyl deinonychosaurian tracks from the Jiaguan Formation and the tenth from Lower Cretaceous red beds in China.
3) This is the first report of large didactyl tracks (cf. *Dromaeopodus*) from the Jiaguan formation, contrasting with two previous reports of smaller tracks assigned to the ichnogenus *Velociraptorichnus*.

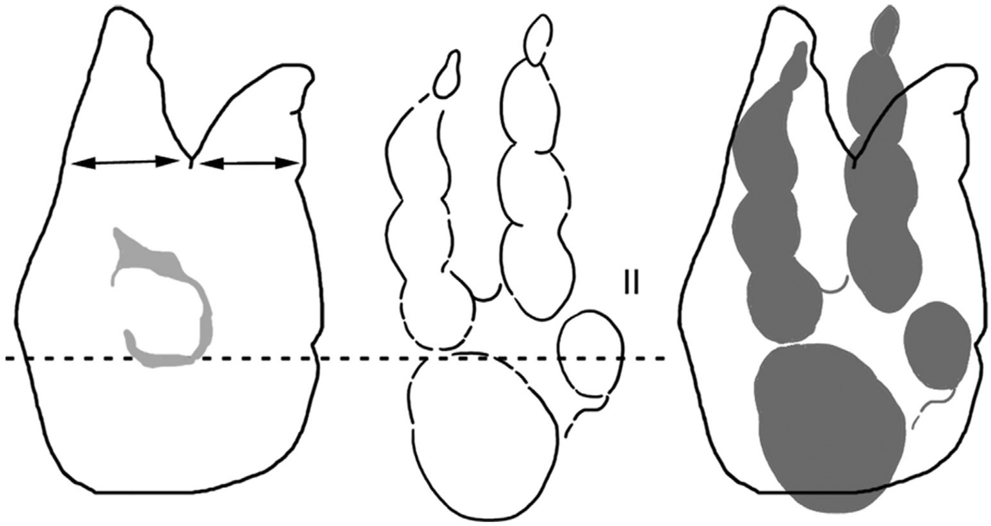

Fig. 9. Comparison between the flattened didactyl track T14-R2 (left) from block 4 at the Lebei tracksite and *Dromaeopodus shandongensis* holotype (center), after Li et al. (2008) with overlay of two tracks (right) to show similarity in size and general morphology.

4) The Leibei site tracks are all natural casts that have been flattened by overburden pressures.
5) The Leibei site is fairly typical of the Jiaguan Formation and other Lower Cretaceous red bed deposits of China in yielding a theropod- (saurischian-) dominated ichnofauna, in which deinonychosaur track occurrences are shown to be increasingly common.
6) The importance of these tracks as paleocological census proxies in the red beds of south China is much increased by the sparsity of skeletal remains in most of these deposits.

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