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ORIGINAL RESEARCH

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Theropod tracks from the Jurassic–Cretaceous boundary, Tuchengzi Formation, Chengde, China: Review and new observations

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ABSTRACT

Previously known theropod dinosaur footprints preserved as natural casts in the Tuchengzi Formation, on a rock wall beside the railway in Nanshuangmiao Village, Shangbancheng Town, Chengde City, were originally assigned to ichnogenus *Anchisauripus* and tentatively attributed to oviraptosaurs. The assemblage was restudied in more detail by examining the entire assemblage of 55 tracks associated with two horizons. The size range of the 27 measured tracks suggests a more diverse grallatorid–eubrontid assemblage and potentially greater diversity of theropod trackmakers. The label *Anchisauripus*, which has fallen into disuse in some recent literature, implies trackmakers of medium shape and size in the grallatorid–eubrontid morphological spectrum. However, given the presence of other theropod ichnotaxa in the Jurassic to Early Cretaceous strata of the Tuchengzi Formation and time equivalent units we suggest that explicit reference to the *Grallator-Anchisauripus-Eubrontes* (GAE) plexus, or simply the term *Grallator-Eubrontes* plexus be confined to Lower Jurassic assemblages as originally defined and intended. Further study centered on the 16 known Tuchengzi assemblages and older theropod ichnfaunas is necessary to confirm or refute the degree to which grallatorid–eubrontid assemblages from these different epochs are similar or convergent. Even if the tracks are morphologically very similar inferences regarding trackmaker identity are problematic because the same theropodan trackmaker species, genera or even families were not present in both epochs.

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1 Introduction

In recent years, numerous dinosaur track sites have been found in Hebei Province and Beijing City. Except for the Lower Cretaceous Dabeigou Formation Jingshang site (Xing et al., 2018) and the Xiguayuan Formation Qiaomaigou and Sangyuan sites from Luanping (Xing et al., 2019), these track sites all come from the Tuchengzi Formation, which spans the Jurassic–Cretaceous boundary. Among these Tuchengzi sites are the Luofenggou sites from Chicheng (Xing et al., 2009a, 2011, 2012), Madigou and Chengde Mountain Resort and its Outlying Temples site (Xing et al., 2020), the Nanshuangmiao site from Chengde (Sullivan et al., 2009), and the Qianjiadian sites from Beijing (Xing et al., 2015). Together with the contemporary tracksites from Liaoning Province, in Northeast China, these sites reveal the relatively diverse Tuchengzi dinosaur ichnofauna (Yabe et al., 1940; Shikama, 1942; Young, 1960; Zhang et al., 2004; Matsukawa et al., 2006; Fujita et al., 2007), which is saurischian-dominated and includes tridactyl and didactyl non-avian theropods, birds, sauropods, and possible small ornithopods. The faunal composition indicated by the track record differs substantially from the local skeleton records, which only consist of the basal ceratopsians *Chaoyangsaurus youngi* and *Xuanhuaceratops niei* (Zhao et al., 1999, 2006) and a brachiosaurid sauropod (Dong, 2001). The degree of correspondence between body fossils and tracks (Lockley, 1991; Lockley et al., 1994) makes the Tuchengzi dinosaur ichnofauna a Type 2b deposit, where the fossil track record dominates, and bone evidence is inconsistent with the track fauna. To date 16 track sites have been reported from the Tuchengzi Formation (Xing et al., in review).

In 2007, Changshu HAN discovered eight dinosaur footprints on the rock wall beside the railway in Nanshuangmiao Village, Shangbancheng Town, Chengde City (Fig. 1). Sullivan et al. (2009) described these tracks, assigned them to *Anchisauripus*, and tentatively inferred the trackmaker to represent a small-sized oviraptor such as *Caudipteryx*. However, they stated (p. 36) that "this interpretation remains uncertain." As noted below this interpretation is questionable.

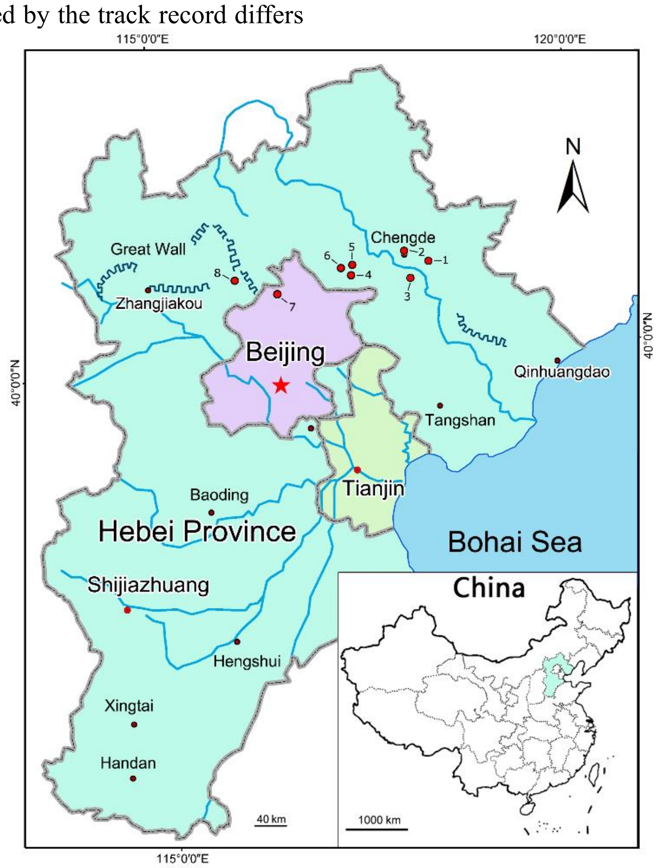

Figure 1. Location of Madigou (1), Chengde Mountain Resort and its Outlying Temples (2), Shangbancheng (Nanshuangmiao) (3), Jingshang (4), Qiaomaigou (5), Sangyuan (6), Qianjiadian (7) and Luofenggou (8) track sites in Hebei Province and Beijing City, China (Modified from Xing et al., 2019: Fig 1).

2 Geological setting

Sullivan et al. (2009) and Xu et al. (2014)

considered the Nanshuangmiao site to be located in the lowermost Houcheng (Tuchengzi) Formation of Hebei Province. The age of the tuff in this area was determined by using the U-Pb (SHRIMP) method is 152.3±2.9 and 151.8±3.3 Ma (Cope et al., 2007). The age, as determined by U-Pb (LA-ICP-MS) dating methods, is 146.5±1.7 Ma (Zhang et al., 2008). Cope et al. (2007) suggested that the steeply dipping coarse fluvial deposits in this region represent the distal toe of a large alluvial system that fed into the region from the north. The tracks occur in a layer of mudstone a few centimeters thick that probably represents a mud drape on a fluvial gravel bar (Sullivan et al., 2009). Evidence for a fluvial facies association includes pervasive cross stratification and numerous scour surfaces that occur within the coarse sandstone and conglomerate beds surrounding the tracks (Sullivan et al., 2009).

3 Material

The specimen described by Sullivan et al. (2009) was designated IVPP VC15815 and consists of a plaster replica of a portion of the original surface with eight sandstone track casts (convex hyporeliefs). This replica cast was created from the latex mold that replicated the original positive track impressions as they would have appeared in the muddy substrate. Sullivan et al. (2009) also mentioned specimen IVPP V15816, a portion of the track-bearing layer that was collected in blocks, but no photos or data were provided, and they stated (p. 37) that "the tracks reproduced on the cast are clearer and better-preserved than those on the portion of the track-bearing layer that was actually collected."

The Nanshuangmiao Site is actually located in Huangqiwanzi Village, Shangbancheng Town, thus the track site is hereafter referred to as the Shangbancheng Site. During 2020 fieldwork, the authors discovered 55 tracks at the site (Fig. 2), which represent two layers. There are 6 tracks in the lower (Layer I), three of which compose one trackway designated SBC-T1, and 49 isolated tracks in the upper (Layer II).

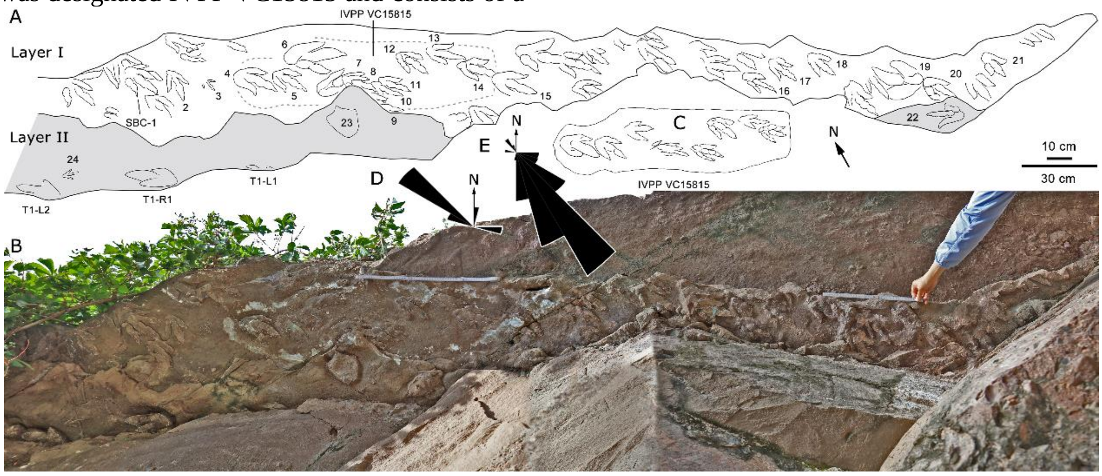

Figure 2. The interpretative outline drawing (A), photograph (B) of the track surface, and outline drawings of the IVPP specimen (C), wind-rose diagram of Layer II of trackmakers walking direction (D), and Layer I (E), from Shangbancheng site.

4 Morphology

4.1 General features

All 55 tracks are tridactyl with sharp claw marks, which is typical of theropod tracks (Figs. 3, 4, 5). The wind-rose diagram shows that most tracks from Layer I are oriented northwest and most tracks from Layer II are oriented southeast. The authors measured the 25 best preserved footprints, of these the average length is 16.1 cm, the maximum length is 25.2 cm, the minimum length is 6.4 cm, and the length/width ratios have an average value of 1.7 (ranging from 1.4 to 2.4): Table 1. Sixteen of them show well-preserved interdigital angles. The divarication angle between digit II and IV of these sixteen tracks is average 49°. that between digits II and III (26°) being similar with than between digits III and IV (23°). The divarication angles between digits II and III of six tracks are larger than those between digits III and IV. Eleven other tracks have wider angles between the medial and outer digits.

The length of the IVPP VC15815 tracks range from 12.3 cm to 18.5 cm, the length/width ratios have an average value of 1.8, and range from 1.5 to 2.3 (Sullivan et al., 2009). Sullivan et al. (2009) also mentioned that the best-preserved track on the collected slabs is even larger (28.8 cm).

4.2 Trackway SBC-T1

SBC-T1 is the only trackway at the

Shangbancheng site and consists of three tracks. Of those three, only SBC-T1-R1 is nearly complete, lacking distal ends of digit IV. SBC-T1-R1 is the 21.1 cm long and ~7.9 cm wide. The average pace length of SBC-T1 is 46.4 cm, 2.2 times the track length. The stride length is 92.6 cm, and the pace angulation is 178°. SBC-T1 is notably narrow.

The preservation of SBC-T1 is unique: two tracks are preserved in a pit of incompletely weathered argillaceous sediments (the gray part of Figure 2). There are mud cracks near the footprints and at the proximal ends of digit IV of SBC-T1-R1. SBC-T1-R1 may be vertically compressed (slightly flattened) especially digit III, giving the footprint 'fleshy' appearance, and removing traces of digital pads. The unusual preservation of trackway SBC-T1 is similar to that of the theropod trackway XY-T1 from the Jiaguan Formation in the Sichuan Basin, Southwest China (Lockley & Xing, 2015; Xing et al., 2016), which has been interpreted as a special kind of preservation.

	L	W	L/W	PL	SL	PA	M	II-III	III-IV	II-IV
SBC-1	16.8	10.4	1.6	—	—	—	0.58	29	21	50
SBC-2	13.8	9.1	1.5	—	—	—	0.74	27	29	56
SBC-3	—	5.3	—	—	—	—	0.61	—	—	—
SBC-4	18.9	10.9	1.7	—	—	—	0.67	23	26	49
SBC-5	15.5	9.9	1.6	—	—	—	0.64	25	28	53
SBC-6	25.2	12.7	2.0	—	—	—	0.51	22	18	40
SBC-7	20.4	—	—	—	—	—	—	—	—	—
SBC-8	14.8	—	—	—	—	—	—	—	—	—
SBC-10	13.9	—	—	—	—	—	—	—	—	—
SBC-11	14.2	—	—	—	—	—	—	—	—	—
SBC-12	15.1	8.3	1.8	—	—	—	0.61	22	25	47
SBC-13	16.5	9.9	1.7	—	—	—	0.77	25	27	52
SBC-14	—	8.9	—	—	—	—	—	—	—	48
SBC-15	16.9	—	—	—	—	—	—	—	—	—
SBC-16	15.4	6.3	2.4	—	—	—	0.81	21	16	37
SBC-17	13.8	8.1	1.7	—	—	—	0.59	25	24	49
SBC-18	13.7	8.8	1.5	—	—	—	0.62	26	26	52
SBC-19	21.2	12.7	1.7	—	—	—	0.56	14	36	50
SBC-20	15.2	8.2	1.8	—	—	—	0.74	25	21	46
SBC-21	13.0	9.0	1.4	—	—	—	0.46	25	29	54
SBC-22	15.3	10.5	1.5	—	—	—	0.65	25	28	53
SBC-24	6.4	4.1	1.6	—	—	—	0.70	26	29	55
SBC-T1-L1	—	—	—	48.7	92.6	178	—	18	—	—
SBC-T1-R1	21.1	—	—	44.0	—	—	—	—	—	—
SBC-T1-L2	17.8	—	—	—	—	—	—	—	—	—

Table 1. Measurements (in centimeter, degree and square centimeter) of the theropod tracks from Nanshuangmiao site, Hebei Province, China. **Abbreviations**: L: Maximum length; W: Maximum width; PL: Pace length; SL: Stride length; PA: Pace angulation; L/W is dimensionless; M: Mesaxony; II–III, III–IV, II–IV: the divarication angle of digits II–IV.

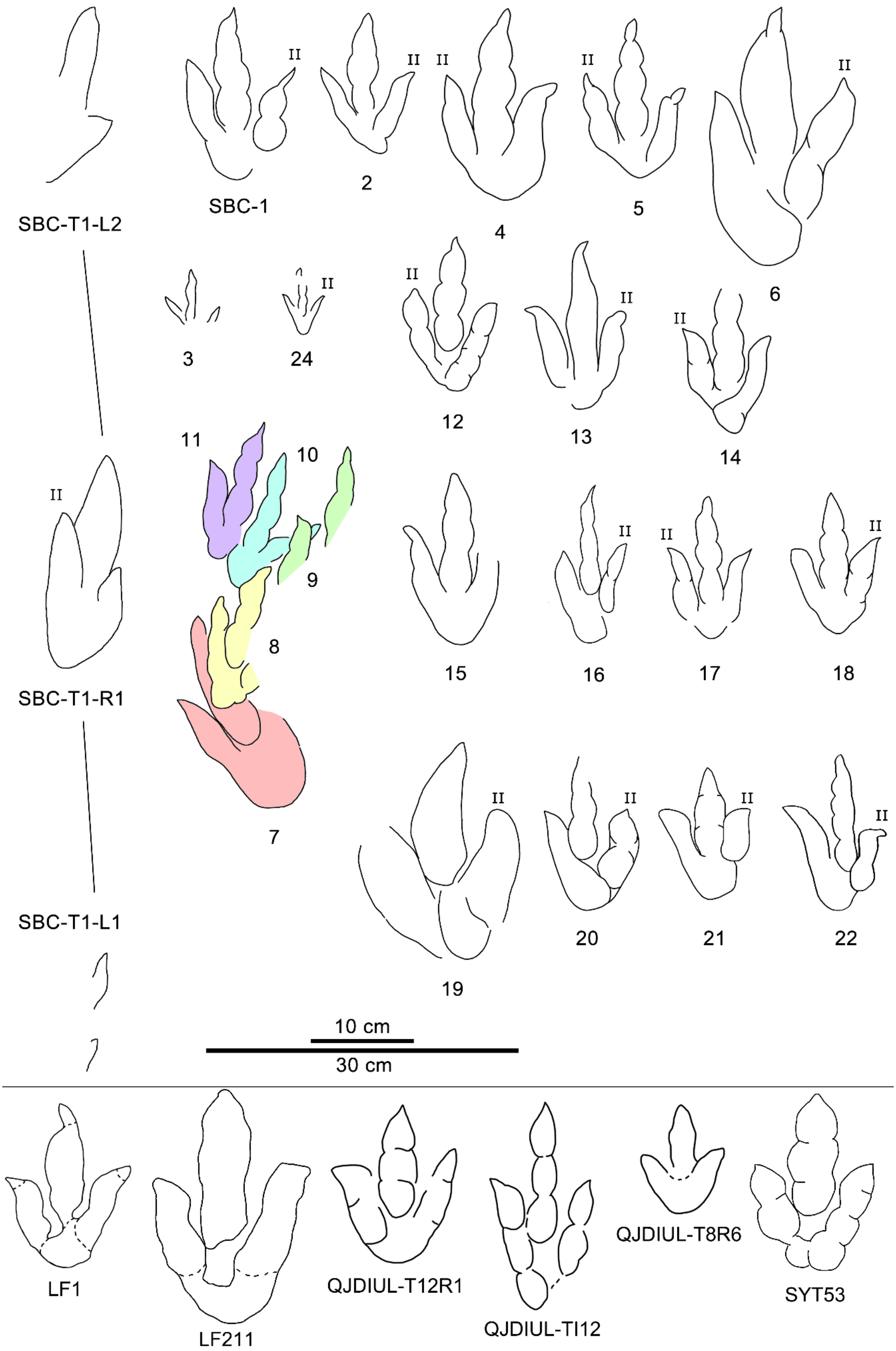

Figure 3. The interpretative outline drawings of the theropod tracks from Shangbancheng site, and other theropod tracks from Tuchengzi Formation.

4.3 Isolated tracks

The best-preserved footprint from Shangbancheng site is SBC-12 which is a left imprint. SBC-12 is 15.1 cm long and 8.3 cm wide, with a length/width ratio of 1.8. SBC-12 is mesaxonic with digit III projecting the farthest anteriorly, followed by digits II and IV. The phalangeal pad formula is easily discerned and diagnostic of theropods: i.e., with 2, 3, 4, pads respectively on digit II–IV. Claw marks are sharp, especially in digits II and III. The metatarsophalangeal pad of digit IV is positioned in line with the axis of digit III. The divarication angle of II–IV is wide (47°), that between digits III and IV (22°) is similar to that between digits II and III (25°). The mesaxony value is 0.61. Other well-preserved tracks, such as SBC-1, 2, 4, 5, 13, 14, 15, 17, 18, 20, 21, 22, have the same characteristics as SBC-12. SBC-16 is similar to SBC-12 in length (15.4 cm), but has a higher length/width ratio (2.4) and mesaxony (0.81). In SBC-16 the divarication angle of II–IV is relatively narrow (37°).

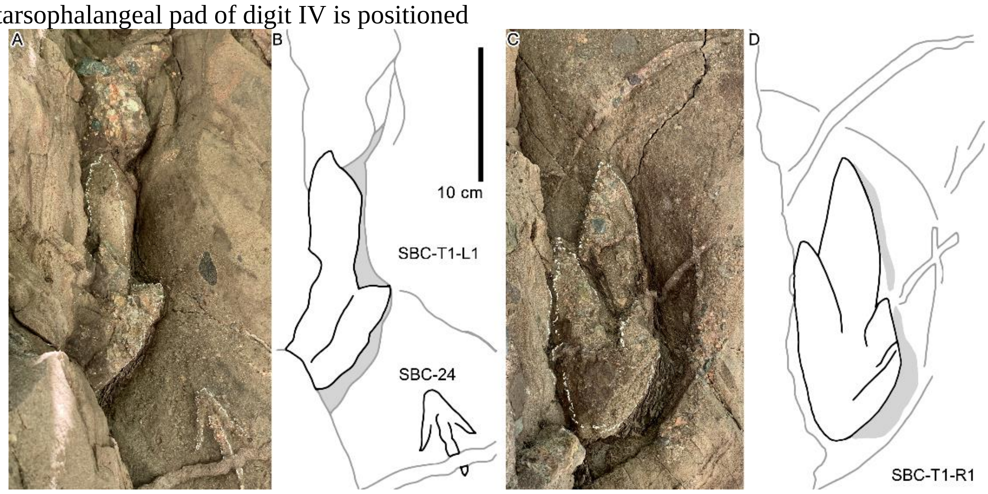

Figure 4. Photograph (A and C) and interpretative outline drawings (B and D) of the theropod from Shangbancheng site Layer II.

SBC-6 is well-preserved, 25.2 cm long and 12.7 cm wide, with a length/width ratio of 2.0. The phalangeal pad traces of digits III and IV are not clearly registered. Digit II has two phalangeal pads. Claw marks are sharp, especially that of digit III. The metatarsophalangeal pad of digit IV is positioned in line with the axis of digit III. The divarication angle II–IV is wide (40°), that between digits III and IV (22°) being similar with than between digits II and III (18°). The mesaxony value is 0.51. SBC-19 is also large, 21.2 cm in length. It lacks traces corresponding to the distal ends of digit IV, and the II–IV divarication angle is wider (50°) than SBC-6.

SBC-3 and SBC-24 are small-sized tracks, both less than 7 cm long. SBC-3 is incomplete, lacking a heel trace : the width of 5.3 cm. SBC-24 is well-preserved, 6.4 cm long and 4.1 cm wide. The length/width ratio is 1.6. The phalangeal pad formulae of digits II and IV were indistinctly registered. The digit III traces have three phalangeal pads, with its midsection destroyed by a mud crack. All claw marks are sharp. The metatarsophalangeal pad of digit IV is in line with the axis of digit III. The II–IV divarication angle is wide (55°), that between digits III and IV (26°) being more similar to that between digits II and III (29°). The mesaxony value is 0.70.

SBC-7 and SBC-11 overlap each other., SBC-8 overlays SBC-7 and 10. SBC-9 overlays SBC-10, and SBC-10 overlays SBC-11. These overlapping tracks indicate that (1) the tracks were probably made in a near-optimum substrate for track registration (neither too wet nor too dry) and (2) multiple dinosaurs were active in this area during a short time interval.

5 Discussion

Considering the classic “brontozoid” ichnites (*Grallator*, *Anchisauripus* and *Eubrontes*), Sullivan et al. (2009) assigned eight tracks from IVPP VC15815 to *Anchisauripus*, according to the morphology of the track, notably the length/width ratio, interdigital divarication and projection ratio (Olsen et al., 1998). In this paper, mesaxony (anterior triangle L/W ratio) is a substitute for projection ratio. According to the new statistics，the Shangbancheng tracks have a length/width ratio of 1.7 (N=15), an overall (II–IV) divarication angle of 49° (N= 16), and moderate mesaxony (0.64, N= 16). These measurements differ from those of Sullivan et al (2009): a length/width ratio of 1.8 (N=5), and an outer divarication angle of 30.5° (N= 7). Lockley (2009) provided the length/width ratio and mesaxony of *Grallator–Anchisauripus–*

Eubrontes plexus: 2.64 (1.22), 1.90 (0.68), and 1.70 (0.58). The Shangbancheng specimens have the same length/width ratio as *Eubrontes*, with the mesaxony ranging between *Anchisauripus* and *Eubrontes*. Taking SBC-12, the best-preserved track, as an example, the length/width ratio (1.8) and mesaxony (0.61) are closer to those of *Eubrontes*. Only the measurements of SBC-16, 2.4 (0.81), are closer to *Grallator*, which may be due to the external morphological changes caused by a wet substrate. The small-sized SBC-24, with the value of 1.6 (0.70), shows similarity with SBC-12. The consistency of the features of the large and small tracks suggests that the two sizes may belong to adult and juvenile trackmakers of similar genera. But there are too few small tracks for further comparisons.

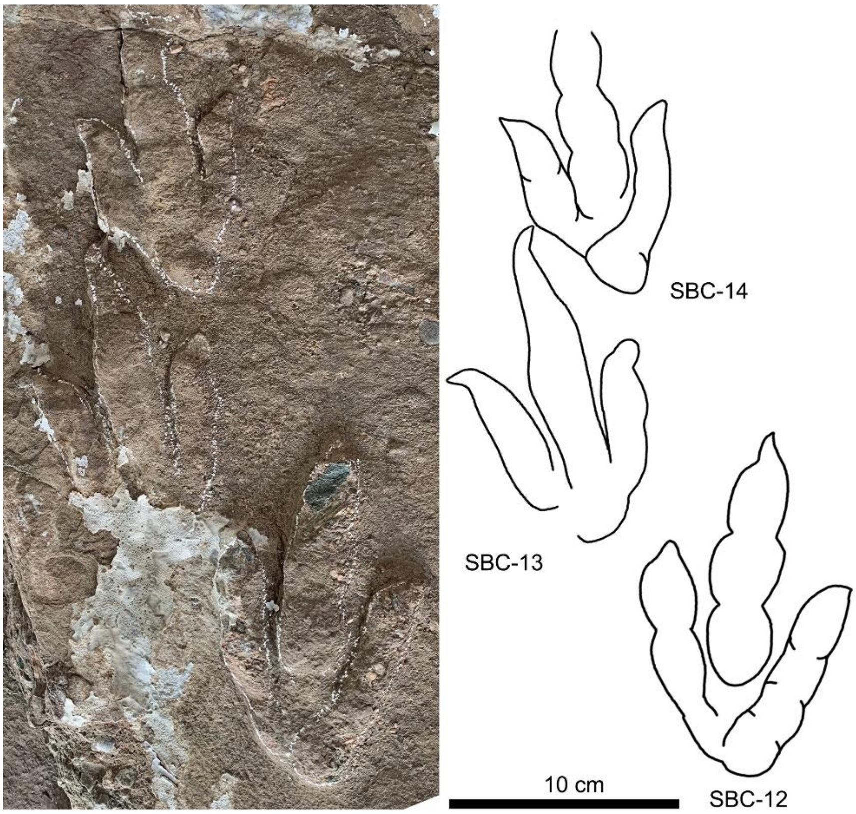

Figure 5. Photograph (A) and interpretative outline drawings (B) of the well-preserved theropod from Shangbancheng site Layer I.

When describing the *Grallator–Anchisauripus–Eubrontes* plexus, Olsen et al. (1998) provided three ranges of length and interdigital angle: <15 cm (10°–30°), 15–25 cm (20°–35°), >25 cm (25°–40°). This is consistent with the observation that the larger members of this plexus, i.e., *Eubrontes*, are proportionally wider than the smaller ichnotaxa (Olsen, 1980; Lockley, 2009; Farlow et al., 2018) The Shangbancheng specimens fall with the length range of *Anchisauripus* and the divarication angle wider than that of *Eubrontes*.

Classic *Grallator–Anchisauripus–Eubrontes* plexus from the Lower Jurassic of the United States of America is not fully comparable with Jurassic–Cretaceous tridactyl theropod tracks from China. In many regions, notably Europe and North America the *Grallator–Anchisauripus–Eubrontes* (GAE) plexus has been identified (Lockley & Hunt, 1995; Lockley & Meyer, 2000) in the Lower Jurassic. However, in China in the Jurassic–Lower Cretaceous transition, *Grallator* has often been reported (Yabe et al 1940; Lockley et al., 2015) although *Eubrontes* is less often recorded, and reports of *Anchisauripus* are rarer. The Cretaceous ichnogenus *Asianopodus* has also been reported from several sites (Matsukawa et al., 2005; Li et al., 2015) but is as yet unknown from the Jurassic. Nevertheless, theropod tracks in the size range of the *Grallator–Anchisauripus–Eubrontes* plexus, including *Asianopodus*, are common, in the Jurassic–Cretaceous transition and the Lower Cretaceous of China and show something of the continuous allometric changes, of the 'Jurassic' plexus. Lockley et al. (2013) and Xing et al. (2016) mentioned that the Jurassic–Cretaceous *Grallator* and *Eubrontes* of China, show a wider interdigital angle. Some records represent small-sized *Eubrontes* (Qianjiadian and

Sichuan sites, Xing et al., 2015 and in press respectively) or large-sized *Grallator* (Tongfosi site, Xing et al., 2017, and the Hunaglonggou site, Lockley et al., 2015). Thus, at most track sites researchers have not recognized *Anchisauripus*, thus making the report of Sullivan et al., (2009) somewhat anomalous. It has recently been noted that there have been very few reports of *Anchisauripus* in the theropod track literature (Lockley & Milner, in revision; Lockley & Xing, in review). This appears to be due to the tendency of observers to more easily recognize morphological end members than intermediate forms (Stoddard et al., 2017), but it also implies that *Anchisauripus* and *Grallator* are very similar as the relevant studies show (Olsen et al., 1998)

The Tuchengzi Formation yields fairly abundant theropod tracks. Specimens from Liaoning Province and some specimens from Hebei Province were assigned to *Grallator ssatoi* (Yabe et al., 1940; Shikama, 1942; Young, 1960; Zhen et al., 1989; Matsukawa et al., 2006). However, theropod tracks from several sites in Liaoning remain undescribed.

Xing et al. (2011) assigned 163 theropod tracks from the Luofengpo tracksite, Chicheng County, Hebei Province to *Therangospodus* isp. based on their identification as medium sized, elongate, asymmetric theropod track with coalesced, elongate, oval digital pads, not separated into discrete phalangeal pads (Lockley et al., 1998). Theropod tracks from the Shangyi tracksite, Zhangjiakou City, Hebei Province were also assigned to *Therangospodus* isp. based on similar features (Xing et al., 2014). At the Qianjiadian site (Beijing area), most of the well-preserved theropod tracks are of the grallatorid–eubrontid type (Xing et al., 2015). Tentatively, the Shangbancheng specimens can also be labelled as a grallatorid–eubrontid assemblage. As noted above the presence of tracks assigned to *Asianopodus* and *Therangospodus* in association *Grallator* and *Eubrontes* in a number of Lower Cretaceous ichnofaunas indicates the need for more detailed research to distinguish between individual theropod track morphotypes and the differing composition of Lower Jurassic, *Grallator–Eubrontes* plexus ichnofaunas, and those ostensibly more diverse ichnofaunas from the Lower Cretaceous.

Overall, records from Liaoning province need more study, but until then we note that theropod tracks from the Tuchengzi Formation are dominated by an assemblage resembling, or convergent with widespread grallatorid–eubrontid ichnofaunas, with other tridactyl forms reported including *Therangospodus* isp. (Xing et al., 2011), didactyl *Menglongipus* (Xing et al., 2009a) and *Velociraptorichnus* (Xing et al., 2019). The assemblage suggests some points of comparison with the thriving theropod fauna of the later Jehol Biota, which includes didactyl dromaeosaurs and troodontids assemblage and tridactyl oviraptorosaurs, compsognathids, ornithomimosaurs, therizinosaurs and tyrannosauroids (Xu et al., 1999, 2000, 2012; Zhou, 2014). For consistency with the interpretation of Sullivan et al. (2009) that the narrow Shangbancheng *Anchisauripus* tracks might be attributable to an oviraptosaur, it should be noted that Gierlinski and Lockley (2013) explicitly inferred that oviraptosaurids might have registered the widely splayed tetradactyl theropod track *Saurexallopus* reported from the Late Cretaceous (Maastrichtian) of North America: see Lockley et al. (2018) for review. While there may have been some significant variation in the size age and morphology of oviraptosaurid feet, there are no obvious similarities between *Anchisauripus*, typical of the Lower Jurassic and *Saurexallopus* from the Late Cretaceous. It is also important to stress that if Tuchengzi *Anchisauripus* is attributed to an oviraptosaurid, the logical inference that an identical Lower Jurassic *Anchisauripus* might be made by an oviraptosaurid is untenable on evolutionary grounds and can only be addressed by speculating on possible convergence. Again, for consistency with the inferences of Sullivan et al. (2009) Xing et al. (2009b) suggested *Grallator* from the Lower Cretaceous Yixian Formation at Sihetun, Liaoning Province, might be attributable to oviraptorosaurian trackmakers. However, Yixian *Grallator* shows certain differences from the Tuchengzi *Grallator*, e.g., the mesaxony (0.77) of the former is approximately 0.51 times of that of *Grallator ssatoi* (Shikama, 1942). Thus, we must recognize the correlation between oviraptosaurid tracks and named theropod ichnotaxa remains tentative and ambiguous, even when tracks and potentially corresponding trackmakers are represented in rocks of comparable age.

6 Conclusions

There are at least 16 known theropod dominated track sites reported from the Tuchengzi Formation (Xing et al., in review). The degree of correspondence between the body and trace fossil records for the formation as a whole, makes the Tuchengzi dinosaur ichnofauna a Type 2b deposit, (Lockley, 1991; Lockley et al., 1994) where the fossil track record clearly dominates, and the very sparse skeletal body fossil evidence is entirely inconsistent with the ichnofauna. Our restudy of the Shangbancheng ichnofauna (one of the 16 sites) provides more morphometric detail and suggests a grallatorid–eubrontid assemblage, with a range of theropod track sizes. We question the previous conclusion of Sullivan et al., (2009) that the only identifiable ichnotaxon is *Anchisauripus.* Likewise, the suggestion of these authors that the tracks may plausibly, but at the same time uncertainly, be attributed to an oviraptosaurid trackmaker, highlights the perennial uncertainly surrounding attempts to identify theropod trackmakers, even when coeval skeletal equivalents are known from the same units, which is *not* the case here. While a wide range of potential trackmakers (including dromaeosaurs, troodontids oviraptorosaurs, compsognathids, ornithomimosaurs, therizinosaurs and tyrannosauroids) can be inferred from our general knowledge of the later Jehol biota, no such skeletal fauna is known from the track-rich type 2b desposit which constitutes the Tuchengzi Formation. Likewise attributing a theropod ichnotaxon based on a Lower Jurassic assemblage to a Cretaceous theropod family raises an obvious chronological problem that can only be addressed by speculating on biological convergence.

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References

Cope, T. D. & Graham, S. A. (2007). Upper crustal response to Mesozoic tectonism in western Liaoning, North China, and implications for lithospheric delamination, Geological Society, London. Special Publications, 280(1), 201-222. https://doi.org/10.1144/SP280.10

Dong, Z.M. (2001). A forefoot of sauropod from the Tuchengzi Formation of Chaoyang area in Liaoning, China. In Deng, T. & Wang, Y. (Eds.), Proceedings of the 8th Annual Meeting of the Chinese Society of Vertebrate Paleontology (pp. 29-33). Beijing: China Ocean Press.

Farlow, J. O., Coroian, D. & Currie, P. J. (2018). Noah's ravens: interpreting the makers of tridactyl dinosaur Footprints (p.643). Bloomington: Indiana University Press.

Fujita, M., Azuma, Y., Lee, Y.N., Lü, J.C., Dong, Z.M., Noda, Y.& Urano, K. (2007). New theropod track site from the Upper Jurassic Tuchengzi Formation of Liaoning Province, northeastern China. Memoir of the Fukui Prefectural Dinosaur Museum, 6, 17-25.

Gierlinski, G. & Lockley M. G. (2013). A trackmaker for *Saurexallopus*: ichnological evidence for oviraptosaurid tracks from the Upper Cretaceous of western North America. Chapter 23, *In* Titus, A. & Loewen, A. (eds). At the Top of the Grand Staircase (p. 526-529). Indiana University Press.

Li, R., Lockley, M. G., Matsukawa & Liu, M. (2015). Important Dinosaur-dominated footprint assemblages from the Lower Cretaceous Tianjialou Formation at the Houzuoshan Dinosaur Park, Junan County, Shandong Province, China. Cretaceous Research 52, 83-100. https://doi.org/10.1016/j.cretres.2014.08.004

Lockley, M.G. (1991). Tracking dinosaurs: a new look at an ancient world. Cambridge, NY: Cambridge University Press.

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.& Xing, L.D. (2015). Flattened fossil footprints: implications for paleobiology. Palaeogeography, Palaeoclimatology, Palaeoecology, 426, 85-94. https://doi.org/10.1016/j.palaeo.2015.03.008

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

Lockley, M.G., Hunt, A.P. & Meyer C. (1994). Vertebrate tracks and the ichnofacies concept: implications for paleoecology and palichnostratigraphy. In Donovan S. (Eds.), The paleobiology of trace fossils (p. 241-268). New York (USA): Wiley and Sons.

Lockley, M.G., Meyer, C.A.& Moratalla, J.J. (1998). *Therangospodus*: trackway evidence for the widespread distribution of a Late Jurassic theropod dinosaur with well-padded feet. Gaia, 15, 339-353.

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), 87(1), 1-20. https://doi.org/10.1111/1755-6724.12026
Lockley, M.G., Li, R., Matsukawa, M., Xing, L. Li, J., Liu, M., & Xing, X. (2015). Tracking the yellow dragons: Implications of China's largest dinosaur tracksite (Cretaceous of the Zhucheng area, Shandong Province, China). Palaeogeography, Palaeoclimatology, Palaeoecology, 423, 62-79. https://doi.org/10.1016/j.palaeo.2015.01.028
Lockley, M. G. & Meyer, C. A. (2000). Dinosaur Tracks and other fossil footprints of Europe. Columbia University Press.
Lockley, M. G. & Milner, A. R. C. (In revision). *Eubrontes* out west. In Farlow, J.O. (ed.) Indiana University Press.
Lockley, M. G., Simmons, E. & Hirschfield, S. (2018). A new Dinosaur track locality in the Late Cretaceous (Maastrichtian) Laramie Formation of Colorado. New Mexico Museum of Natural History and Science, Bulletin, 79, 395-406.
Lockley, M. G. & Xing, L. (In review). A review of the non-avian theropod track record and the implications for the Ontogenetic Niche Shift model. Earth Science Reviews.
Matsukawa, M., Shibata, K., Kukihara, R., Koarai, K. & Lockley, M. G. (2005). Review of Japanese Dinosaur Track localities: implications for ichnotaxonomy, paleogeography and stratigraphic correlation. Ichnos, 12, 201-222. https://doi.org/10.1080/10420940591009231
Matsukawa, M., Lockley, M.G. & Li, J.J. (2006). Cretaceous terrestrial biotas of East Asia, with special reference to dinosaur-dominated ichnofaunas: towards a synthesis. Cretaceous Research 27, 3-21. https://doi.org/10.1016/j.cretres.2005.10.009
Olsen, P.E. (1980). Fossil great lakes of the Newark Supergroup in New Jersey. *In* Manspeizer, W. (Ed), Field studies in New Jersey geology and guide to field trips (p. 352-398). 52nd Annual Meeting of the New York State Geological Association, Rutgers University, Newark College of Arts and Sciences, Newark.
Olsen, P.E., Smith, J.B.& McDonald, N.G. (1998). Type material of the type species of the classic theropod footprint genera Eubrontes, Anchisauripus and Grallator (Early Jurassic, Hartford and Deerfield basins, Connecticut and Massachusetts, U.S.A.). Journal of Vertebrate Paleontology, 18 (3), 586-601. https://doi.org/10.1080/02724634.1998.10011086
Shikama, T. (1942). Footprints from Chinchou, Manchoukuo, of Jeholosauripus, the Eo-Mesozoic dinosaur. Bulletin of the Central National Museum Manchoukuo, 3, 21-31.
Stoddard, M.C, Yong, E.H., Akkaynak, D., Sheard, C., Tobias, J.A. & Mahadevan, L. (2017). Avian egg shape: Form function and evolution. Science, 356, 1249-1254. https://doi.org/10.1126/science.aaj1945
Sullivan, C., Hone, D.W.E., Cope, T.D., Liu, Y. & Liu, J. (2009). A new occurrence of small theropod tracks in the Tuchengzi Formation of Hebei Province, China. Vertebrata Palasiatica ,47, 35-52.
Xing, L.D., Harris, J.D., Sun, D.H.& Zhao, H.Q. (2009a). The Earliest Known Deinonychosaur Tracks from the Jurassic–Cretaceous boundary in Hebei, China. Acta Palaeontologica Sinica, 48(4), 662-671.
Xing, L.D., Harris, J.D., Feng, X.Y. & Zhang, Z.J. (2009b). Theropod (Dinosauria: Saurischia) tracks from Lower Cretaceous Yixian Formation at Sihetun, Liaoning Province, China and Possible Track Makers. Geological Bulletin of China, 28(6), 705-712.
Xing, L.D., Harris, J.D.& Gierliński, G.D. (2011). Therangospodus and Megalosauripus track assemblage from the Upper Jurassic–Lower Cretaceous Tuchengzi Formation of Chicheng County, Hebei Province, China and Their Paleoecological Implications. Vertebrata PalasiAtica, 49(4), 423-434
Xing, L.D., Gierliński, G.D., Harris, J.D.& Divay, J.D. (2012). A Probable Crouching Theropod Dinosaur Trace from the Jurassic–Cretaceous Boundary in Hebei, China. Geological Bulletin of China, 31(1), 20-25
Xing, L.D., Liu, Y.Q., Kuang, H.W., Klein, H., Zhang, J.P., Burns, M.E., Chen, J., Wang, M.W.& Hu, J. (2014). Theropod and possible ornithopod track assemblages from the Jurassic–Cretaceous boundary Houcheng Formation, Shangyi, northern Hebei, China. Palaeoworld, 23, 200-208. https://doi.org/10.1016/j.palwor.2013.10.002
Xing, L.D., Zhang, J.P., Lockley, M.G., McCrea, R.T., Klein, H., Alcalá, L., Buckley, L.G., Burns, M.E., Kümmell, S.B.& He, Q. (2015). Hints of the early Jehol Biota: important dinosaur footprint assemblages from the Jurassic–Cretaceous Boundary Tuchengzi Formation in Beijing, China. PLOS ONE, 10(4), e0122715. https://doi.org/10.1371/journal.pone.0122715
Xing, L.D., Lockley, M.G.& Zhang, J.P. (2016). Early Cretaceous dinosaur and other tetrapod tracks of southwestern China. Ningbo: Ningbo Publishing House.

Xing, L.D., Lockley, M.G., Kim, K.S., Klein, H., Matsukawa, M., Lim, J.D., Persons, W.S.IV. & Xu, X. (2017). Mid-Cretaceous dinosaur track assemblage from the Tongfosi Formation of China: comparison with the track assemblage of South Korea. Cretaceous Research, 74, 155-164. https://doi.org/10.1016/j.cretres.2017.02.019

Xing, L.D., Klein, H., Qin Z.H., Persons, W.S.IV. & Xu, X. (2018). Lower Cretaceous theropod tracks with the new ichnogenus and combination Lockleypus luanpingensis from the Dabeigou Formation of the Luanping Basin, Hebei Province, China. Palaeoworld, 27, 482-489. https://doi.org/10.1016/j.palwor.2018.09.004

Xing, L.D., Lockley, M.G., Qin, Z.H., Klein, H., Romilio, A., Persons, W.S.IV., Nie, X.& Wan, X.Q. (2019). Dinosaur tracks from the Lower Cretaceous Xiguayuan Formation in the Luanping Basin, Hebei Province, China. Cretaceous Research. https://doi.org/10.1016/j.cretres.2019.06.009

Xing, L.D., Lockley, M.G., Du, T.M., Zhang, L.J., Klein, H., Romilio, A., Persons, W.S.IV., Wang, K., Li, Z.Y.& Wan, X.Q. (2020). Dinosaur tracks from the Jurassic-Cretaceous boundary Tuchengzi Formation (Hebei Province, China) used as building stones in the Chengde imperial summer resort: age, ichnology, and history. Cretaceous Research. https://doi.org/10.1016/j.cretres.2019.104310

Xing, L., Lockley, M.G., Klein, H., Zhang, L., Romilio, A., Persons, W.S.IV, Peng, G., Ye, Y.& Wang, M. (in press). The new ichnotaxon *Eubrontes nobitai* ichnosp. nov. and other Saurischian tracks from the Lower Cretaceous Jiaguan Formation of Sichuan Province, China

Xing, L., Lockley, M.G., Mao, Z., Gu., Z., Bai, C., Qiu, L., Klein, H., Liu, Y., Wang, M., Romilio, A., Persons, W.S.IV & Wan., X. (in review). A large dinosaur track site from the Jurassic-Cretaceous boundary in the Tuchengzi Formation, Hebei Province, China: morphology, ontogeny and paleocommunity structure.

Xu, H., Liu, Y.Q., Kuang, H.W. & Peng, N. (2014). Age of the Tuchengzi Formation in northern China and the terrestrial Jurassic-Cretaceous boundary in China. Earth Science Frontiers, 21 (2), 203-215 (in Chinese with English abstract).

Xu, X., Zhou, Z.& Wang, X. (2000). The smallest known non-avian theropod dinosaur. Nature, 408, 705-708. https://doi.org/10.1038/35047056

Xu, X., Wang, K., Zhang, K., Ma, Q., Xing, L., Sullivan, C., Hu, D., Cheng, S.& Wang, S. (2012). A gigantic feathered dinosaur from the Lower Cretaceous of China. Nature, 484, 92-95. https://doi.org/10.1038/nature10906

Xu, X. ; Tang, Z.L.& Wang, X.L. (1999). A therizinosauroid dinosaur with integumentary structures from China. Nature, 399 (6734), 350-354. https://doi.org/10.1038/20670

Yabe, H., Inai, Y. & Shikama, T. (1940). Discovery of dinosaurian footprints from the Cretaceous of Yangshan, Chinchou: preliminary note. Proceedings of the Imperial Academy Japan 16, 560-563.

Young, C.C. (1960). Fossil footprints in China. Vertebrata Palasiatica, 4, 53-66. https://doi.org/10.2183/pjab1912.16.560

Zhang, Y.Z., Zhang, J.P., Wu, P., Zhang, X.B. & Bai, S. (2004). Discovery of dinosaur tracks from the Middle-Late Jurassic Tuchengzi Formation in the Chaoyang area, Liaoning Province. International Geology Review, 50, 561-566.

Zhang, H., Wang, X.M., & Liu, X. M. (2008). Constraints on the upper boundary age of the Tiaojishan Formation volcanic rocks in West Liaoning-North Hebei by LA-ICP-MS dating. Chinese Science Bulletin, 53(22), 3574-3584. https://doi.org/10.1007/s11434-008-0287-4

Zhao, X., Cheng, Z.& Xu, X. (1999). The earliest ceratopsian from the Tuchengzi Formation of Liaoning, China. Journal of Vertebrate Paleontology, 19, 681-691. https://doi.org/10.1080/02724634.1999.10011181

Zhao, X., Cheng, Z., Xu, X.& Makovicky, P.J. (2006). A New Ceratopsian from the Upper Jurassic Houcheng Formation of Hebei, China. Acta Geologica Sinica, 80, 467-473. https://doi.org/10.1111/j.1755-6724.2006.tb00265.x

Zhen, S.N., Li, J.J., Rao, C.G., Mateer, N.J., & Lockley, M.G. (1989). A review of dinosaur footprints in China. In: Gillette, D.D. and Lockley, M.G. (eds) Dinosaur Tracks and Traces (p. 187-197). Cambridge University Press, Cambridge.

Zhou, Z. H. (2014). The Jehol biota, an early cretaceous terrestrial lagerstätte: New discoveries and implications. National Science Review, 1, 543-559. https://doi.org/10.1093/nsr/nwu055

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