

记河北赤城上侏罗统-下白垩统土城子组 窄足龙-巨齿龙(兽脚类恐龙)足迹组合 及其古生态学意义¹⁾

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摘要:记述了河北省赤城县落凤沟化石点 163 个窄足龙足迹(*Therangospodus* isp.)。当该地区洪水泛滥时,同样的造迹者留下了 5 个游泳迹。一个异常大的足迹和一道疑似尾迹被归入巨齿龙足迹(*Megalosauripus* isp.)。土城子组 7 个主要足迹化石点表明,兽脚类的似鹫龙足迹型(*Grallator* morphotype)占据主导地位,这些足迹型的大小在各个足迹化石点都有着特定的范围。如果这些大小不同的足迹属于同一种造迹者,则暗示着同年龄的成员在特定年龄时会共同栖息在一起,在动物行为学上类似现生的一些蜥蜴和短吻鳄;如果这些足迹由不同的造迹者组成,则暗示着不同大小的种(主要表现在小型动物)可能拥有自己的领地,并特意避免与其他动物(特别是大型动物)相接触,在动物行为学上类似现生的肉食性哺乳动物。

关键词:河北赤城,侏罗-白垩纪界线,土城子组,窄足龙足迹,巨齿龙足迹,兽脚类游泳迹

中图法分类号:Q915.2 **文献标识码:**A **文章编号:**1000–3118(2011)04–0423–12

THERANGOSPODUS AND MEGALOSAURIPUS TRACK ASSEMBLAGE FROM THE UPPER JURASSIC-LOWER CRETACEOUS TUCHENGZI FORMATION OF CHICHENG COUNTY, HEBEI PROVINCE, CHINA AND THEIR PALEOECOLOGICAL IMPLICATIONS

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Abstract One hundred sixty-three footprints that pertain to *Therangospodus* have been found in the

1) 中国科学院脊椎动物进化系统学重点实验室开放课题基金资助。

Tuchengzi Formation at the Luofenggou track site in Chicheng County, Hebei Province, China. Five swim tracks were subsequently made by the same track makers after water submerged the region. In addition to the *Therangospodus* tracks, one exceptionally large theropod track and one possible trail trace are referred to *Megalosauripus* isp. Theropod tracks of the grallatorid morphotype predominate at this site and at six other known Tuchengzi Formation track sites; grallatorid tracks at each of these sites are dominated by individual specimens in particular size ranges. If the tracks were made by the same species of track maker, the variation in dominant track size among sites suggests that cohabiting groups were composed mainly of members of a single age class, ethologically similar to some extant lizards and *Alligator*. If the tracks were instead made by different species, their size distribution (favoring smaller species) suggests that species of different sizes may have preferred discrete territories or specifically avoided close contact with other (particularly larger) species, ethologically similar to modern carnivorous mammals.

Key words Chicheng, Hebei, China; Jurassic-Cretaceous boundary, Tuchengzi Formation, *Therangospodus*, *Megalosauripus*, Theropod swim tracks

1 Introduction

The Tuchengzi (also called Houcheng) Formation is one of the primary geologic units exposed in the Liaoxi-Jibei (western Liaoning-northern Hebei) area. This formation is primarily Early Cretaceous in age but spans the Jurassic-Cretaceous boundary (Davis, 2005; Sun et al., 2007; Zhang et al., 2009). Dinosaur tracks, primarily those of theropods, are abundant in this unit; the most common are basically of the grallatorid morphotype (Yabe et al., 1940; Shikama, 1942; Young, 1960; Zhang et al., 2004; Matsukawa et al., 2006; Fujita et al., 2007; Xing et al., 2009a; Sullivan et al., 2009). Grallatoridae is a massive ichnotaxon that encompasses many small to very large, narrow, tulip-shaped, functionally tridactyl tracks made by bipedal theropods (Olsen et al., 1998). Other Tuchengzi Formation tracks include didactyl *Menglongipus* tracks, attributed to Dromaeopodidae (Xing et al., 2009a), and bird tracks (Lockley et al., 2006).

The tracks discussed herein were discovered by Sun Denghai from the Chicheng County Vocational Education Center in February 2001. In April and October of that year, groups led by Dong Zhiming (Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China) and Azuma Yoichi (Fukui Prefectural Dinosaur Museum, Japan) examined the site. In 2008 and 2009, the senior author of the present paper was invited by the Chicheng County Bureau of Land and Resources to study dinosaur fossils from Tuchengzi Formation exposures in the area.

The track site is on a sloping surface and can be divided into lower and upper components, both in the same horizon and 5 m apart. The lower part of the track site (Fig. 1) is extensive and complete, with the exception of a discontinuous middle-lower portion. The upper part consists of several discrete track groupings, although their orientations are generally in accordance with those of the lower track site.

Institutional abbreviations FTS, Fuenteosalgo locality, Spain; HLT, Hailiutu, Nei Mongol, China; LF, Luofenggou Field, Hebei, China; MNTS, Museum of Nature and Technology in Starachowice, Poland.

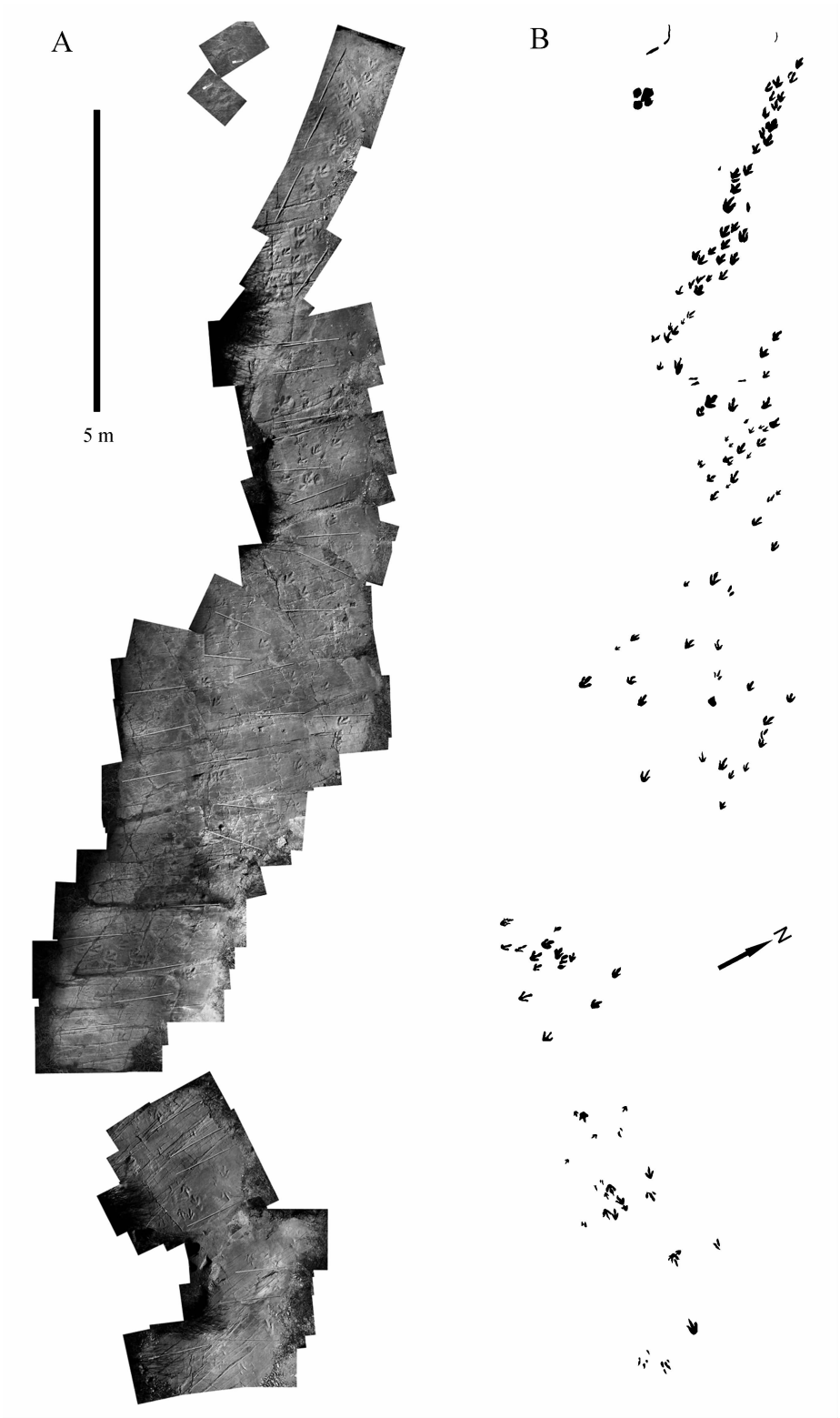


Fig. 1 Photograph (A) and outline drawing (B) of Luofenggou lower track site

2 Geological setting

The tracks were discovered at Luofenggou (which translates as “ravine of the fallen phoenix”), Zhanghao Village, Yangtian Township, Chicheng County, Zhangjiakou City, Hebei Province (40°50′53.03″N, 115°53′37.26″E). The fossil-bearing horizon is a grayish-purple, conglomeratic sandstone in the Tuchengzi Formation. The Tuchengzi Formation unconformably overlies the andesitic lavas of the Tiaoishan Formation and contacts the overlying high-Mg lavas of the Lower Cretaceous Zhangjiakou Formation in an angular unconformity (Davis, 2005). The Tuchengzi Formation in Hebei Province only partially overlaps in age the Tuchengzi Formation in western Liaoning Province (Swisher et al., 2002). This suggests that Tuchengzi sedimentation was probably diachronous (Davis, 2005). The minimum age of the Tuchengzi Formation was measured as 136 ~ 139 Ma (Swisher et al., 2002; Zhang et al., 2009), and its maximum age is 147 Ma (Zhang et al., 2009). The tracks occur in a horizon high in the Tuchengzi Formation, but it is not presently possible to determine whether the tracks are latest Jurassic or earliest Cretaceous in age.

3 Materials and methods

Luofenggou track sites have been exposed for decades, possibly even centuries, and therefore required extensive cleaning and preparation. A total of 168 tracks were measured with respect to the following parameters where possible: pes orientation, pes length and width, digit divarication, tail length and width, and trackway pace angulation.

4 Systematic ichnology

4.1 *Therangospodus isp.*

Material One hundred twenty-five footprints preserved as natural molds were found and remain in the field in the lower part of the Luofenggou track site. The tracks are cataloged individually as LF 1-LF 125 (Figs. 1, 2A, B, D, E; Table 1). In addition, thirty-eight complete natural molds were discovered in the upper part of the Luofenggou track site. The tracks are cataloged individually as LF 200-237 (Figs. 2C, F; Table 1).

Table 1 Measurements of Luofenggou Theropod tracks (cm)

Measurement	LF			
	1	2	211	126
Maximum length	16	17.7	22.9	38.3
Maximum width (distance between the tips of digits II and IV)	12.2	13.5	15.3	27.5
Length of digit II ¹⁾	7.4	7.4	10.2	16.1
Maximum width of digit II	2.7	4.3	4	12.3
Length of digit III ¹⁾	10.8	12.8	15.7	23.4
Maximum width of digit III	3.7	5.9	5	14.6
Length of digit IV ¹⁾	8.8	8.8	11.8	13.3
Maximum width of digit IV	2.6	2.9	4.4	9.8 *
Angle between digits II and III	35°	37°	27°	30°
Angle between digits III and IV	35°	29°	29°	23°
Angle between digits II and IV	70°	66°	56°	53°

1) Measured to the posterior margin of the posteriormost digital node; * Does not include the drag mark of digit IV.

Locality and horizon Tuchengzi Formation, Upper Jurassic-Lower Cretaceous (Tithonian-Valanginian). Luofenggou track site, Chicheng County, Hebei Province, China.

Description LF 1 and LF 2 from the lower part of the Luofenggou track site are the most complete and representative specimens of tridactyl theropod tracks from the site. The length: width ratios of LF 1 and LF 2 are both 1.3:1. Digit II is the shortest of the three digits and has two faint but discernible digital pads. Digit III is the longest digit and has three faint digital pads. Digit IV has three faint digital pads, but they are narrower than those of digits II and III. In all tracks, the divarication angle between digits II and III is equal to or greater than that between digits III and IV. LF 1 is more deeply impressed than LF 2 and has distinct claw marks. In deeply impressed specimens, the round metatarsophalangeal pad is aligned with the proximal ends of all three digits; discrete borders separate the metatarsophalangeal pad from digits II and III, but not digit IV.

The upper part of the Luofenggou track site produces tracks of the same general morphology as those from the lower track site, although they are more shallowly impressed. A typical example is specimen LF 211, for which the length: width ratio is 1.5:1. Its primary morphological characteristics are similar to those of LF 1 and LF 2. LF 211 is preserved somewhat differently than the other tracks: it consists of a dark stain on the sediment rather than an actual impression (Fig. 2F).

Despite the fact that LF 1, LF 2, and LF 211 pertain to same type of track, they exhibit differences in digital morphology. The distal ends of digits II and III enlarge markedly in LF 2, but not in LF 1 or LF 211. Digit III in LF 2 is 60% wider than its counterpart in LF 1; digit IV is also wider in the former specimen, but only by 10% (Fig. 2E).

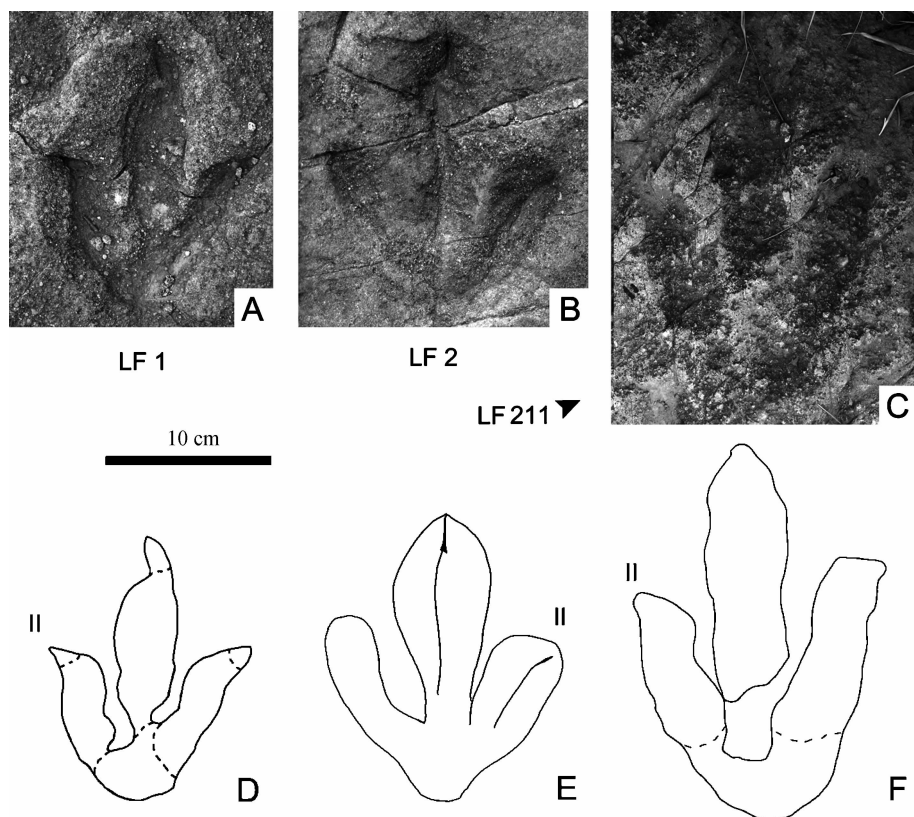


Fig. 2 Photographs (A-C) and outline drawings (D-F) of Luofenggou specimen LF 1, 2 and 211

None of the trackways in the upper and lower portions of the track site are long: they typically comprise 3 ~ 4 footprints. All exhibit a very narrow stance, with pace angulations of $170^{\circ} \sim 180^{\circ}$.

Discussion Tridactyl tracks such as those at Luofenggou are typically made by bipedal theropods. The Luofenggou tracks have less acute angles of divarication ($56^{\circ} \sim 70^{\circ}$) than those of either *Grallator* or *Eubrontes*. The divarication angles, as well as the lengths of the tracks accord with some characteristics of *Kayentapus*, in which angles of divarication between digits III and IV are greater than those between digits II and III (Piubelli et al., 2005). However, large, oblong centrally located proximal (metatarsophalangeal) pad and cigar-shaped phalangeal portion of digits with no discrete phalangeal pads well defined correspond with the *Therangospodus* morphotype described by Lockley et al. (1998b).

Lockley et al. (1998b) described the theropod ichnotaxon *Therangospodus* from Upper Jurassic of North America, Europe, and central Asia, for medium sized (averaging 28 cm long by 20.5 cm wide), elongate, asymmetric theropod tracks with coalesced, elongate, oval digital pads that are not separated into discrete phalangeal pads. Although the small-medium sized (range 8.4 ~ 30 cm in length) and several general morphological differences (Moratalla, 1993; Lockley et al., 1998b; Barco et al., 2006), the Luofenggou specimens are therefore referred to only as *Therangospodus* isp.

4.2 *Megalosauripus* isp.

Material One complete natural mold was found and remains in the field in the lower part of the Luofenggou track site. This track is cataloged individually as LF 126 (Fig. 3; Table 1).

Locality and horizon Tuchengzi Formation, Upper Jurassic-Lower Cretaceous (Tithonian-Valanginian). Luofenggou track site, Chicheng County, Hebei Province, China.

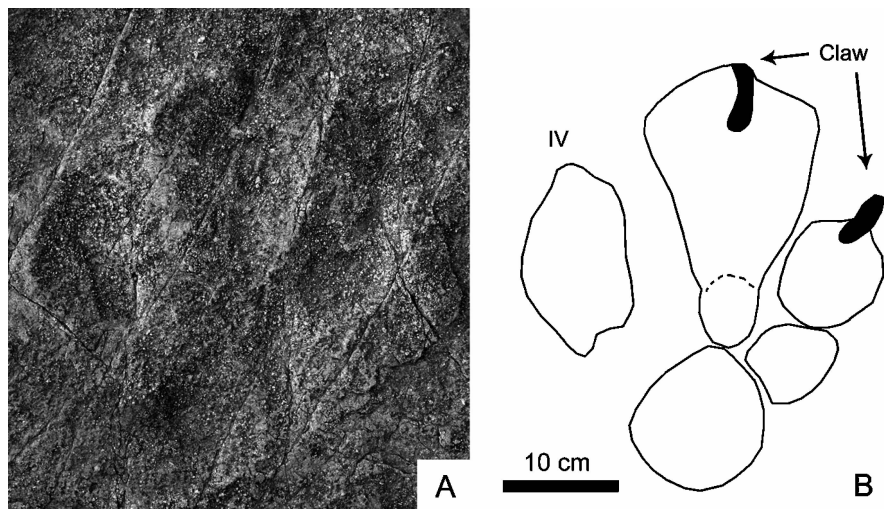


Fig. 3 Photograph (A) and outline drawing (B) of Luofenggou specimen LF 126

Description and discussion The largest track in either part of the Luofenggou track site, LF 126, is comparatively peculiar. Its length: width ratio is 1.2:1. The three digits and metatarsophalangeal pad are separate. The depth of LF 126 is similar to that of LF 2, and the distal end of digit III is also markedly enlarged. Its metatarsophalangeal region is large and round (maximum length 14.6 cm, maximum width 13.6 cm). Digits II and III possess long, sharp claw impressions, of which the claw of digit II is the longer: it is up to 10 cm in length, but

probably includes a drag mark.

A big footprint size, relatively large metatarsophalangeal area, discrete phalangeal pads, and digit III less projected than in other gallatorid tracks, all make this footprint very similar to *Megalosauripus* sensu Lockley et al. (1998a). Due to the small sample size and consequent inability to discern systematic features, LF 126 is referred to *Megalosauripus* isp.

A peculiar set of marks anterior to the isolated large track may constitute a tail trace. This enigmatic structure can be divided into two distinct regions: a wider posterior portion roughly 22 cm long and a narrower anterior portion roughly 33 cm long (Fig. 4). The two regions are separated by a 10 cm-long gap. The shorter, deeper posterior part is divided longitudinally into a pair of roughly equal troughs; the longer, shallower anterior part has no such structure. The ends of the two regions are collinear across the 10 cm gap, but the longer, shallower part abruptly angles to one side a short distance from the gap.

4.3 Swimming theropod tracks

Material Five complete natural molds of swimming theropod tracks were found in the field in the lower part of the Luofenggou track site. The tracks are cataloged individually as LF 127-131.

Locality and horizon Tuchengzi Formation, Upper Jurassic-Lower Cretaceous (Tithonian-Valanginian). Luofenggou track site, Chicheng County, Hebei Province, China.

Description and discussion Swimming theropod tracks were long considered rare to non-existent, and purported examples dubious. However, they have recently been recognized in large numbers, particularly in strata of Jurassic age, such as at the St. George Dinosaur Discovery Site at Johnson Farm (SGDS) in Utah, USA (Milner et al., 2006) and in the Cameros Basin, La Rioja, Spain (Ezquerro et al., 2007). The ichnogenus *Characichnos* was erected based on traces ascribed to a swimming theropod dinosaur (Whyte and Romano, 2001; Gierliński et al., 2004); such traces can be considered extramorphological variants of “walking” track types found associated with or near the swim tracks.

Five tracks are located in the middle (Fig. 5 C1) and lower (Fig. 5 C2) parts of the Luofenggou lower track site. The tracks from the middle part were made by a single track maker; those from the lower part were made by one or two track makers. These tracks differ in morphology from other Luofenggou tracks: they consist only of slender, tapering digit impressions and claw marks, and lack any impressions made by the metatarsophalangeal regions. The absence of

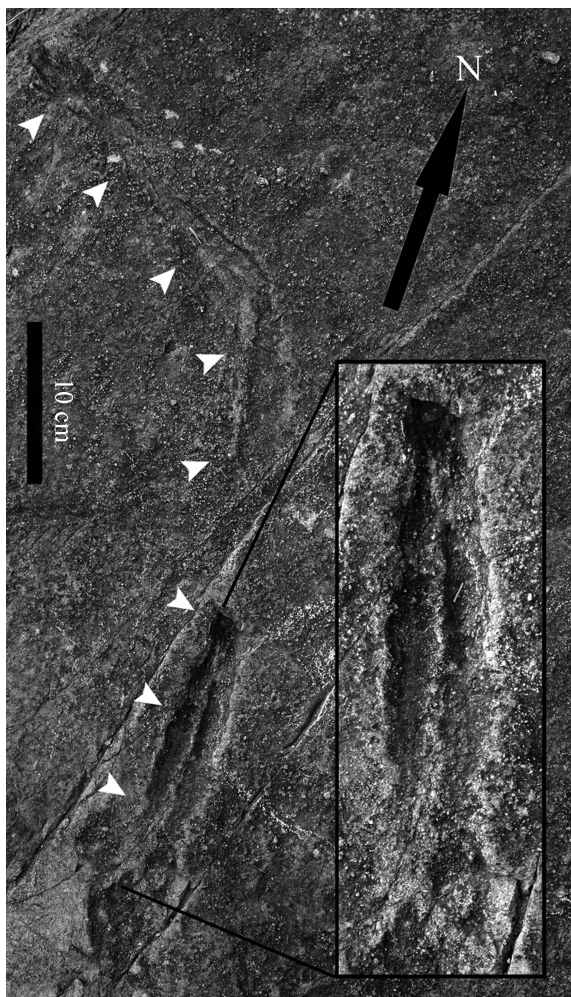


Fig. 4 Photograph of possible tail trace near Luofenggou specimen LF 126

metatarsophalangeal region impressions is common in swim tracks (Milner et al., 2006; Ezquerro et al., 2007). Specimen LF 127 is a representative specimen at the Luofenggou site, and its measurements are: digit III is 13.9 cm long, the digit to the left of digit III (whether this is digit II or IV is unclear) is 4.5 cm long, consisting only of an oval “digit pad”, and the digit to the right of digit III is 19.6 cm long, and curved. Generally speaking, these tracks are similar to prints 4, 5, and 6 from La Virgen del Campo track site zone 4 (Ezquerro et al., 2007), all of which are S-shaped scratch marks.

In LF 127-131, the anterior portions of the impressions are deepest, and the traces shallow posteriorly. These features indicate that greatest impact force was generated as the foot contacted the sediment; the foot was then lifted as it moved posteriorly, propelling the animal forward (Milner et al., 2006; Ezquerro et al., 2007).

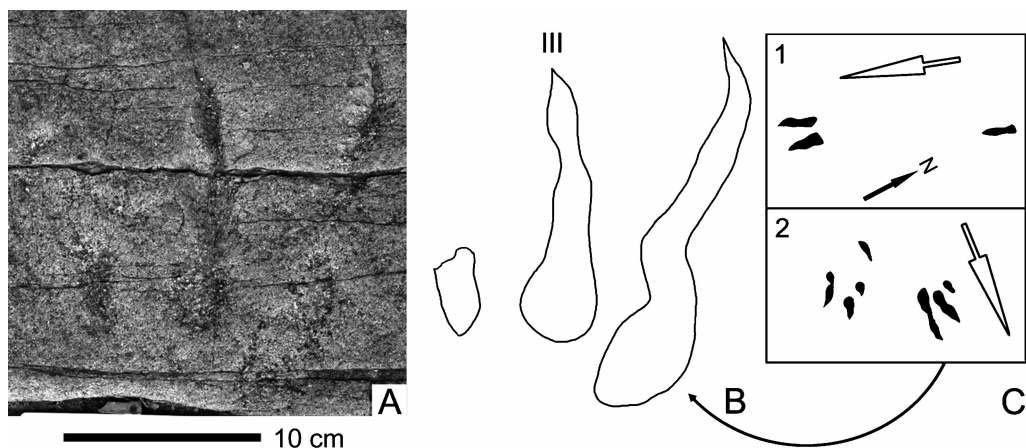


Fig. 5 Luofenggou swimming theropod track LF 127
A. Photograph; B. Outline drawing; C. Track distribution

5 Track orientation

The Luofenggou trackways exhibit a predominantly northwest orientation (Fig. 6). The variation in track morphologies, like LF 1, 2, and 211, suggests that at least three groups of dinosaurs passed through the area at different times. This interpretation implies that Luofenggou was probably a site frequently visited by *Therangospodus* track makers. The swimming tracks (LF 127-131), however, exhibit west-southwest (Fig. 5 C1) and southeast (Fig. 5 C2) orientations, indicating a different direction of travel for the swimming trace makers that passed through later.

6 Paleocological implications

Theropod tracks previously described from this region in China are primarily from the Tuchengzi Formation. Tuchengzi Formation theropod tracks are primarily of the grallatorid morphotype (Yabe et al., 1940; Shikama, 1942; Young, 1960; Zhang et al., 2004; Matsukawa et al., 2006; Fujita et al., 2007; Xing et al., 2009a); such tracks occur in the overlying, middle Early Cretaceous Yixian Formation as well (Xing et al., 2009b). The Luofenggou tracks of *Therangospodus* and *Megalosauripus* pertain to typical tridactyl theropod tracks as well.

At present, at least seven track sites have been discovered in the Tuchengzi Formation. In addition to the Luofenggou site, there are:

(1) Sijiazhi (Ssuchiatzu) track site, Yangshan area, near Chaoyang City, Liaoning Province (Yabe et al., 1940; Shikama, 1942; Young, 1960; Zhen et al., 1989; Matsukawa et al., 2006).

Tracks: *Grallator ssatoi*. Yabe et al. (1940) described some footprints from this site as a new ichnogenus and ichnospecies *Jeholosauripus ssatoi*. However, *Jeholosauripus* was considered a junior synonym of *Grallator* by Zhen et al. (1989). There are nearly 4000 tracks with lengths ranging from 7 ~ 12 cm (Yabe et al., 1940; Zhen et al., 1989), and their orientations are relatively consistent (Matsukawa et al., 2006, fig. 2).

(2) Sijiaban track site I, Nanbajiazi Township, near Beipiao City (Fujita et al., 2007).

Tracks: *Grallator*. Type A average length 4.5 cm (over 100 tracks); Type B average length 13.4 cm (3 tracks); Type C average length 16.7 cm (14 tracks). Orientations of the various types are relatively consistent (Fujita et al., 2007).

(3) Sijiaban track site II, Nanbajiazi County, near Beipiao City (Zhang et al., 2004).

Tracks: ? *Grallator*. 1 ~ 10 cm (8 tracks); 10 ~ 20 cm (30 tracks); 20 ~ 30 cm (9 tracks). The orientations of the tracks are consistent across all three size ranges (Zhang et al., 2004).

(4) Kangjiatun track site near Kangjiatun Village, Beipiao City (Lockley et al., 2006).

Tracks: *Pullornipes aureus*, bird tracks attributed to *Aquatilavipes* or cf. *Aquatilavipes*, and *Grallator*. The *Grallator* tracks were not described in detail.

(5) Nanshuangmiao track site in Chengde County, northern Hebei Province (Sullivan et al., 2009).

Tracks: *Anchisauripus*. Type A lengths range from 12.3 to 18.5 cm (8 tracks); Type B 28.8 cm long (1 track). The tracks are relatively consistent in orientation (Sullivan et al., 2009).

(6) Nijiagou track site, Chicheng County, Hebei Province. (Xing et al., 2009a).

Tracks: *Menglongipus*, *Grallator*-type. The *Grallator*-type tracks have an average length of 20 cm (roughly 40 tracks). Furthermore, there are two indistinct larger theropod tracks with lengths of 59 and 63 cm. The orientations of all the tracks are relatively consistent (Xing et al., 2009a).

As yet, no theropod body fossils have been discovered from the Tuchengzi Formation; the only dinosaur body fossils of any kind that have been recovered from the unit (including the Houcheng Formation) pertain to the basal ceratopsians *Chaoyangsaurus youngi* and *Xuanhuaceratops nei* (Zhao et al., 1999, 2006), and a brachiosaurid sauropod (Dong, 2001).

Tridactyl theropod tracks at each of these sites are dominated by individual specimens in particular size ranges (Fig. 7).

If the theropod tracks across all Tuchengzi Formation sites were made by the same species of track makers, the similar size distributions of the tracks within and across sites suggest that individuals normally cohabited with conspecifics of the same age class. Extant young iguanas will associate with each other after hatching (Burghardt et al., 1977), and young crocodylians may exhibit similar gregarious behavior (Coombs, 1990). Such activity may be seasonal, as in the case of aggregations of *Urosaurus ornatus* in winter (Elfström and Zucker, 1999). If this scenario is correct, then the few large footprints in the Tuchengzi Formation sample (at Sijiaban track site I and the Luofenggou track site) probably represent adult individuals. Evidence of social assemblages that include multiple age classes of theropods is scarce worldwide; the most prominent body fossil examples are aggregations of individuals of different ages of the giant carcharodontosaurid *Mapusaurus roseae* (Coria and Currie, 2006) and the tyrannosaurid *Albertosaurus* (Currie and Eberth, 2010). Stable social aggregations are rarely recorded in modern lizards, but have now been reported in several species of *Egernia* (Osterwalder et al., 2004). However, large individuals of *Alligator mississippiensis* have been observed cannibalizing large

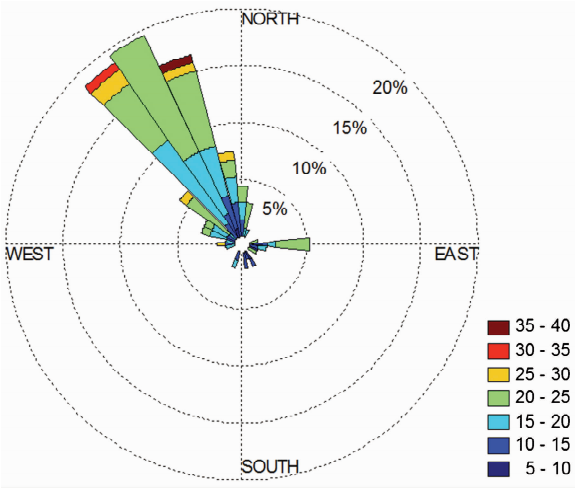


Fig. 6 Rose diagram showing the orientations of 131 footprints from the lower part of the Luofenggou track site

occurs in varieties of predators of similar sizes, such as coyotes and red foxes (Sargeant and Stephen, 1989).

juveniles and small adults (Rootes and Chabreck, 1993). Therefore it is possible that the presumed adult individuals were present at Tuchengzi track sites for the purpose of utilizing the juveniles as prey.

If the tracks were instead made by different species, their size distribution (dominated by smaller tracks) suggests that species of different sizes may have preferred discrete territories or specifically avoided close contact with other (particularly larger) species. This is ethologically similar to modern carnivorous mammals in which bigger species may expel smaller ones from a given territory, as has been observed between hyenas and lions (Trinkel and Kastberger, 2005). Among carnivorous mammals, range overlap

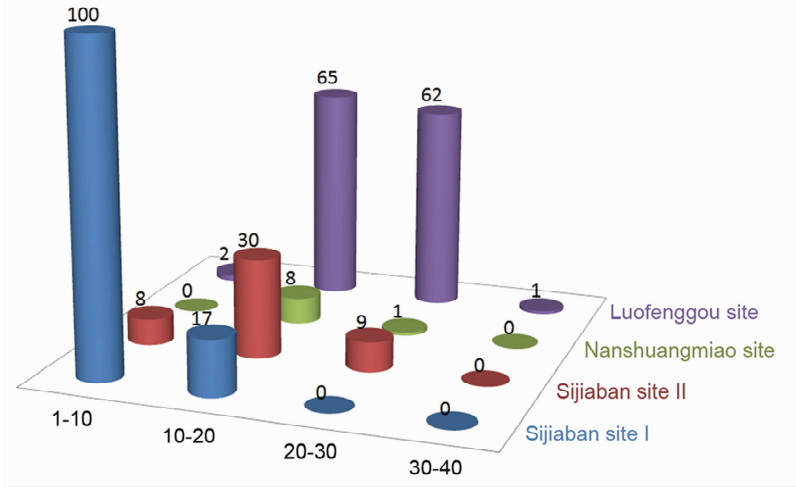


Fig. 7 Distributions of tracks in different size ranges at Sijiaban track sites I and II, the Nanshuangmiao track site, and the lower part of the Luofenggou track site

Acknowledgements We thank Philip J. Currie (University of Alberta, Edmonton, Alberta, Canada), Corwin Sullivan and Xu Xing (Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China), and Ran Hao (Key Laboratory of Ecology of Rare and Endangered Species and Environmental Protection, Guilin, China) for their critical comments and suggestions regarding early drafts of this paper. Corwin Sullivan helped to improve the English text. Thanks to Sun Denghai from the Chicheng County Vocational Education Center, Hebei Province for his participation in field research. Thanks to the Chicheng County Bureau of Land and Resources, which provided logistical support.

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