

江苏下白垩统孟瞳组的恐龙足迹群及 蜥脚类足迹形态的多样性

邢立达^{1,2)}* 杰瑞德 D 哈里斯³⁾ 贾程凯⁴⁾

1) 阿尔伯塔大学生物科学系, 加拿大埃德蒙顿 T6G 2E9, Xinglida@gmail.com;

2) 中国科学院脊椎动物进化系统学开放实验室, 北京 100044;

3) 迪克西州立学院自然科学系, 美国犹他 84770;

4) 新疆油田公司勘探开发研究院, 新疆克拉玛依 834000

摘要 中国江苏省东海县南古寨孟瞳组发现了数种恐龙足迹, 包括兽脚类足迹和蜥脚类足迹。这些足迹出现在同一层位的四个相邻的足迹化石点。这些足迹化石点至少保存了三种不同形态的兽脚类足迹和未成年—成年的蜥脚类足迹。南古寨三号足迹化石点的兽脚类足迹和蜥脚类足迹出现了“回填”现象, 这是在足迹所附带的沉积物与基底地面相互作用下, 产生的流体和塑性行为下形成的。

关键词 蜥脚类足迹 似雷龙足迹未定种 兽脚类足迹 孟瞳组 早白垩世

DINOSAUR TRACKS FROM THE LOWER CRETACEOUS MENG TUAN FORMATION IN JIANGSU, CHINA AND MORPHOLOGICAL DIVERSITY OF LOCAL SAUROPOD TRACKS

XING Li-da^{1,2)}, Jerald D HARRIS³⁾, JIA Cheng-kai⁴⁾

1) Department of Biological Sciences, University of Alberta, 11145 Saskatchewan Drive, Edmonton,
Alberta T6G 2E9, Canada, Xinglida@gmail.com;

2) Key Laboratory of Evolutionary Systematics of Vertebrates, Chinese Academy of Sciences,
PO Box 643, Beijing 100044, China;

3) Physical Sciences Department, Dixie State College, 225 South 700 East, St. George, Utah 84770, USA;

4) Research Institute of Petroleum Exploration and Development, Karamay 834000, Xinjiang, China

Abstract Diverse dinosaur (theropod and sauropod) tracks from the Nanguzhai track locality in Donghai County, Jiangsu Province, China occur in the Lower Cretaceous Mengtuan Formation. The locality is subdivided into four adjacent track sites at the same stratigraphic level. The sites preserve at least three track types pertaining to theropods to juvenile-adult sauropods. “Backfilled” theropod and sauropod tracks at Nanguzhai Site III are the products of appendage-sediment interactions where the substrate was fluid and behaved plastically.

Key words Sauropod tracks, *Parabrontopodus* isp., theropod tracks, Mengtuan Formation, Early Cretaceous

1 INTRODUCTION

Donghai County is situated in the northeast of Jiangsu Province, and borders on Tancheng County and the Maling Mountains in the west. The Maling Mountains stretch more than 60 km from north to south, demarcating the Tanlu fault zone. Uplift of the batholith coring the mountains has exposed Cretaceous continental sedimentary strata. Beginning in the late 1970s and continuing through the early 1980s, dinosaur footprints were reported near Nanguzhai village, Shanzuokou township, Donghai County to the Archaeological Team from Nanjing Museum and Institute of Vertebrate Palaeontology and Paleoanthropology, Academia Sinica. In 1996, when Zhen *et al.* (1996) summarized dinosaur tracks in China, they attributed these tracks, with lengths up to 82 cm, to the biggest dinosaurs in China. Today, the fossils have been intensely weathered, and only two remain well enough to discern detail.

In 2005, new tracks were discovered by Mr. Tang Yonggang (an amateur fossil collector) at the original site. The tracks are preserved in grayish purple silty shale of the Mengtuan Formation (Dasheng Group). Abundant theropod and ornithomimid tracks have also been discovered in the Tianjialou Formation (Barremian—Aptian) in Houzuoshan Dinosaur Park, Junan County, Shandong Province (Li *et al.*, 2005a), approximately 70 km northwest of Nanguzhai. These include *Shandongornipes muxiai* (Li *et al.*, 2005b; Lockley *et al.*, 2007), *Dromaeopodus shandongensis* (Li *et al.*, 2007), and *Minisauripus zhenshuonani* (Lockley *et al.*, 2008). The Tianjialou Formation is also a member of the Dasheng Group, though it underlies the Mengtuan Formation, which is the uppermost unit in the Dasheng Group. Thus, two Dasheng Group units are now known to preserve fossil footprints.

2 INSTITUTIONAL ABBREVIATIONS

HDT=Huaxia Dinosaur Tracks Research and

Development Center, Gansu, China. LRH-dz=Li Rihui-Dasheng, Qingdao Institute of Marine Geology, China Geological Survey, China. ROLM=Rovereto Lavini Marco, Italy. ZDM=Zigong Dinosaur Museum, Sichuan Province, China.

3 GEOLOGICAL SETTING

The Dasheng Group was originally designated for strata at Mazhan, Anqiu City, in central Shandong Province. These lacustrine sediments had previously been encompassed as an upper unit of the Lower Cretaceous Qingshan Group (Hao *et al.*, 2000). Dasheng Group strata represent a lateral, correlative facies of Qingshan Group strata (Liu *et al.*, 2003). The Dasheng Group is divided into six formations (in ascending order): Xiaodian, Datuling, Malangou, Tianjialou, Siqiancun, and Mengtuan.

The age of the Mengtuan Formation remains controversial. Based on gastropod fossils from the unit at Qiancao, Zhucheng City, Pan (1983) assigned the unit a middle-late Lower Cretaceous age. Sporopollen assemblages from the Tianjialou and Mengtuan formations were interpreted as Cenomanian-Turonian in age (Si, 2002). Liu *et al.* (2003) questioned the lateral correlation of the Dasheng and Qingshan groups and determined that the Linjiazhuang and Xingezhuang formations, which had previously been considered part of the Wangshi Group, were identical to the Siqiancun and Mengtuan formations, respectively; all were considered Lower Cretaceous. This age assignment for the Mengtuan Formation is adopted in this paper.

4 DISTRIBUTION OF TRACKS

The tracks were discovered at four sites located at the northwest end of Nanguzhai Village, Shanzuokou Township, Donghai County, Jiangsu Province (Fig. 1). The four track sites are adjacent to one another and at the same stratigraphic level.

Site I (118°25'43"E, 34°36'25"N) is the locali-

ty where sauropod tracks were discovered in the 1980s. A maximum of 20 footprints were originally preserved in a single row. Currently, only one largely complete pes print and an incomplete manus print remain. Site II ($118^{\circ}25'41''\text{E}$, $34^{\circ}36'26''\text{N}$) is situated 46 m northwest of Site I; it also preserves one pes print and one manus print. Site III ($118^{\circ}25'38''\text{E}$, $34^{\circ}36'19''\text{N}$) lies 150 m south of Site II. This site, which is the largest, exposes roughly 46 footprints (Fig. 2). Site IV is separated by a stream from Site III but is on the same bedding plane; it preserves nine tracks.

5 SYSTEMATIC ICHNOLOGY

5.1 Theropod tracks

Material Four complete natural molds found at Nanguzhai Site III are cataloged individually as T1.1—1.4. (Fig. 3, Plate II, figs. A—D, Table 1). A cast of specimen T1 is curated in the HDT, where it is cataloged as HDT. 201—204. The original tracks were not collected and are still in the field.

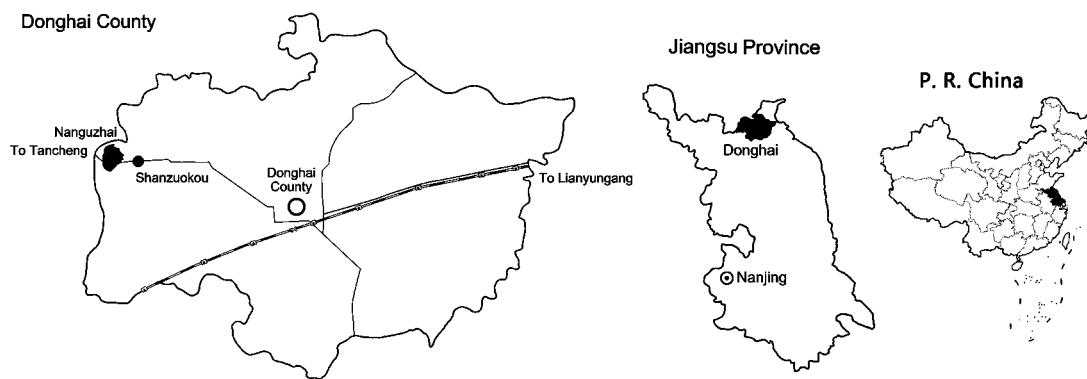


Fig. 1 Geographic map indicating the location (footprint icon) of the Nanguzhai dinosaur footprint locality in Donghai County, Jiangsu Province, P. R. China

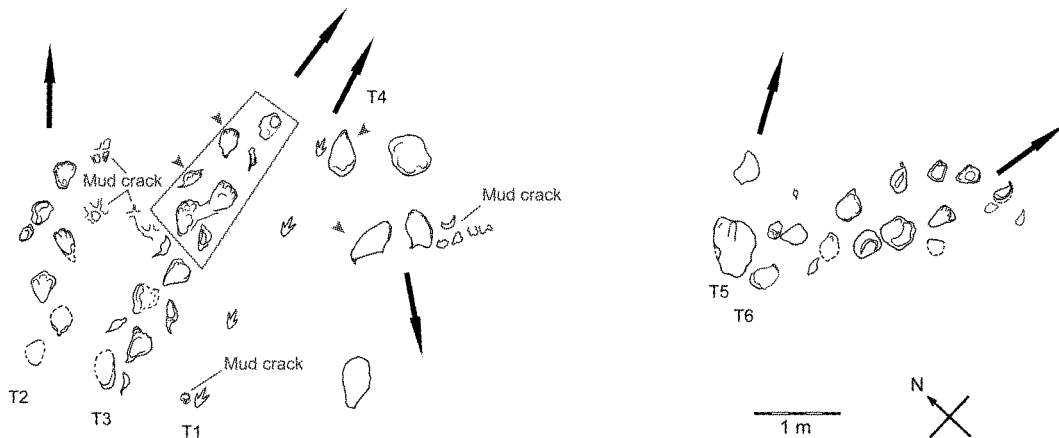


Fig. 2 Distribution of footprints at Nanguzhai Site III

Close-ups of footprints indicated by red arrows are provided in Figs. 5 and 6.

Description Four tridactyl theropod footprints are preserved in a single trackway at Site III (T1 in Fig. 2). Of these, T1.1 is the best preserved. Pace angulation measurements of the trackway are all 171° — 172° , indicating the track maker possessed the very narrow stance typical of

theropods.

The length : width ratios of T1.1—3 average $1.92 : 1$. In each track, digit III projects the farthest anteriorly, followed by digits IV and II. In each track, the distances from the caudal end of the print to the tips of digits II and IV are about

60% the distance from the posterior end of the print to the tip of digit III. Digit pad impressions are indistinct. Each digit has a sharp claw mark; the one on digit III is the best defined. The metatarsophalangeal region is indistinct, so the presence of one or more pads there cannot be confirmed. In T1. 1—2, the distolateral portions of digit II are laterally convex. Pace lengths are: T1. 1—2: 1.0 m; T1. 2—3: 1.25 m, T1. 3—4: 1.01 m. Stride lengths are: T1. 1—3: 2.2 m, T1. 2—4: 2.2 m.

Discussion The relative lack of definition of theropod tracks T1. 1—1. 4 makes it impossible to attribute them to a particular ichnotaxon. However, the lack of definition is itself informative. The deepest portions of each track are on the opposite sides of each foot but on the same sides of the trackway overall - that is, digits IV in T1. 1 and T1. 3 and digits II in T1. 2 and T1. 4. This seems to indicate either that the track maker was off balance or that the sediment to one side of the animal was more easily deformed than on the other.

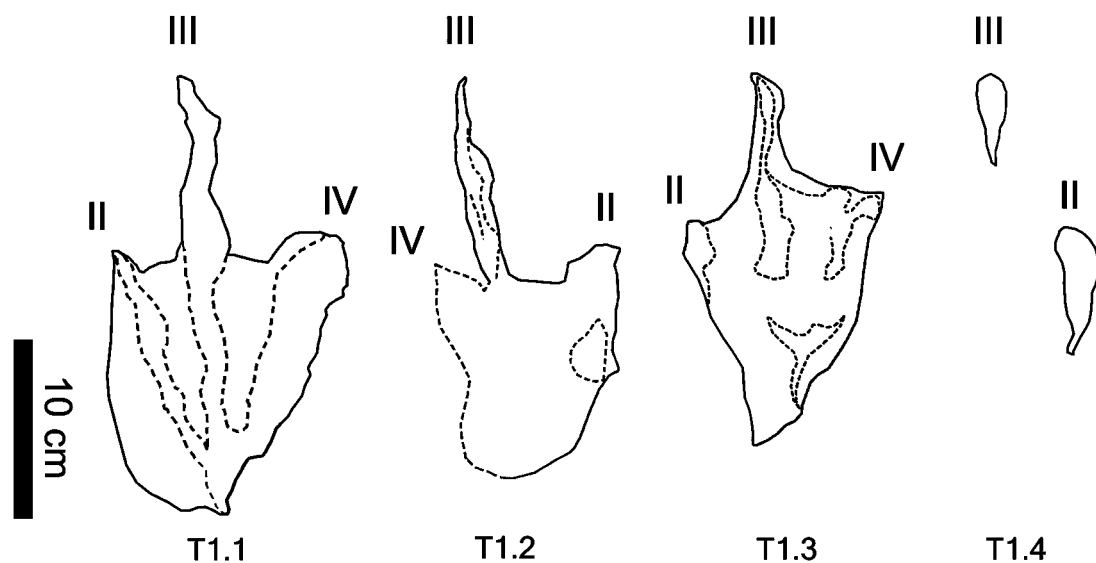


Fig. 3 Outline drawings of Nanguzhai Site III theropod tracks T1. 1—1. 4

Dashed lines within the footprint delineate concavities within each footprint; dashed footprint outlines indicate indistinct footprint borders.

Table 1 Measurements (in cm; ° as noted) of Nanguzhai Site III theropod tracks T1. 1—1. 4

Measurement	T1.			
	1	2	3	4
Maximum length	24.71	22.65	21.06	-
Maximum width(distance between the tips of digits II and IV)	12.8	10?	11.06	-
Length of digit II*	16.18	14.29?	12.98	6.99
Length of digit III*	24.71	22.65	21.06	5.07
Length of digit IV*	16.91	12.65?	15.96	-
Angle between digits II and III	17°	30°	17°	17°
Angle between digits III and IV	30°	13°?	28°	-
Angle between digits II and IV	47°	43°	45°	-

* Digit length measured to the posterior margin of the metatarsophalangeal region.

5.2 Sauropod tracks

5.2.1 Site I

Material One complete pes impression and one half manus impression of sauropod tracks have

been found as natural molds at Nanguzhai Site I (the first site reported in the 1980s). The tracks are cataloged individually as T7. 1a (manus) and T7. 1b (pes) (Fig. 4, Plate II, fig. G, Table 2).

Casts of the specimens are curated in the HDT, where they are cataloged as HDT. 205a and

HDT. 205b, respectively. The original tracks remain in the field.

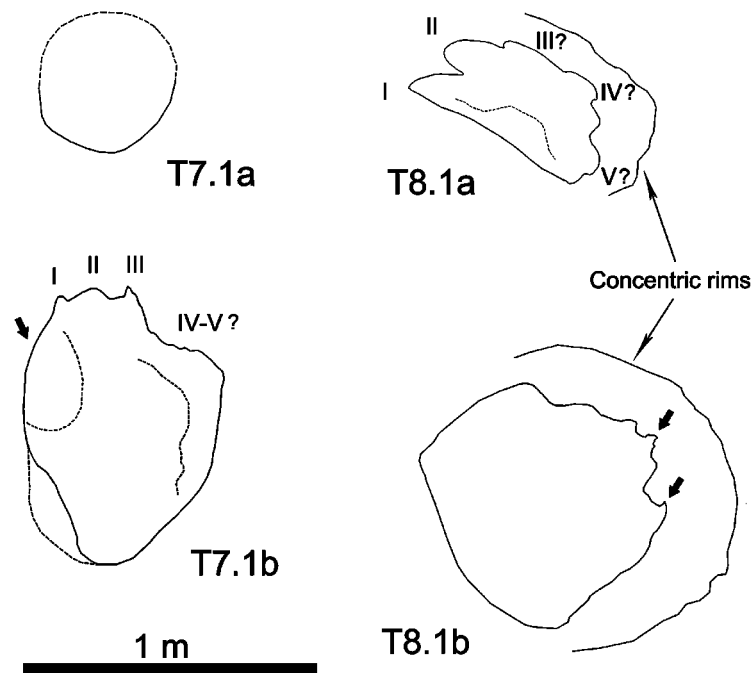


Fig. 4 Outline drawings of Nanguzhai sauropod tracks T7. 1a and T7. 1b from Site I, and T8. 1a and T8. 1b from Site II. Dashed lines within the footprint delineate concavities within each footprint; dashed footprint outlines indicate indistinct footprint borders. Gray areas around T8. 1a and T8. 1b represent raised ridges of sediment preserved around the tracks. Arrow in T7. 1b points to a blunt pad or callosity on the plantar surface of digit I. Arrows in T8. 1b point to possible claw impressions.

Table 2 Measurements (in cm; ° as noted) of sauropod tracks from Sites I—III

Measurement	T2.		T3.		T4.		T7.		T8.	
	1b	6a [†]	8b	1a [†]	1b	1a	1b	1a	1b	
Maximum length	35.7	9.4	35.1	26.4	50	37.8	92.4	30.8	75.9	
Maximum width*	24.3	16.9	24.9	68.6	33.2	49	77.4	66.7	79	

* Distance between the lateral and medial rims; †due to deformation, the specimens likely do not accurately reflect track maker appendage morphology.

Description When they were first discovered in the 1980s, more than ten sauropod tracks were preserved at the site. However, many of them were damaged by road work, farmland reclamation and cultivation on the track site. The distance between the remaining manus impression and pes impression is 41.3 cm. As in other sauropod tracks, the pes impression angles outward with respect to the trackway axis. The manus impression lies slightly anterolateral to the pes impression. On this basis, T7. 1a and T7. 1b are probably right ichnites.

The length : width ratio of T7. 1a is 0.77 : 1;

that of T7. 1b is 1.19 : 1. Only the posterior half of the manus impression is well preserved; the anterior half was damaged by roadwork, but its round border is discernible. A round indentation at the proximomedial end could represent a blunt pad or callosity on the plantar surface of digit I. The pes impression is well-preserved and possesses three indentations at its anteromedial margin, corresponding to the predicted positions of digits I—III. Posterolateral to these indentations, the track margin insets posteriorly; no clear evidence of digits IV or V is visible. A posteriorly directed prominence of sediment within and on the lateral

side of the track could be sediment that infilled a crease on the plantar surface of the pes of the track maker. A complete metatarsophalangeal pad impression has smoothly curved margins.

5.2.2 Site II

Material One complete manus-pes set of a sauropod was preserved as natural molds at Nanguzhai Site II. The tracks are cataloged individually as T8.1a (manus) and T8.1b (pes) (Fig. 4, Table 2). Casts of the specimens are deposited in the HDT, where they are cataloged as HDT.206a and HDT.206b, respectively. The original tracks remain in the field.

Description As at Site I, many previously discovered tracks at site II have been damaged irreparably; today, only a single manus (T8.1a)—pes (T8.1b) print set is preserved. Both impressions are circumscribed by concentric rims, which are more pronounced on the lateral sides of the tracks. The distance between the manus and pes impressions is 66 cm, similar to the tracks at Site I. These footprints also appear to be right footprints.

The length : width ratios of T8.1a and T8.1b are 0.46 : 1 and 0.96 : 1, respectively. The manus impression is well-preserved. A few indentations within the footprint could be delineations of digits I and II and a metacarpophalangeal region. The inferred digit I impression is sharply protruding print, possibly representing a claw; the possible digit II impression is less distinct. Arcs on the lateral side of the footprint may represent digits III—V. Among these, digit III is shallow; the sediment around the possible digit IV is slightly damaged. None of the latter possesses a discernible claw mark. The metacarpophalangeal pad region is slightly concave.

The pes impression (T8.1b) is better preserved, but digit impressions are difficult to distinguish. Two angular marks possibly represent claws. The metatarsophalangeal region is well defined, with smoothly curved margins; it is broader and less acute than that of T7.1b.

5.2.3 Site III

Material Forty-two complete natural molds were found at Nanguzhai Site III. The tracks occur in five sequences that are numbered and cataloged as T2—T6 (Fig. 2); individual tracks within those trackways are numbered sequentially (Figs. 5, 6, 7; Plate I, fig. A, Plate II, figs. A—F, H; Table 2). Three casts of the best footprints (T3.6a, T3.8b, T4.1b) are curated at the HDT, where they are cataloged as HDT.207—209, respectively. The original tracks remain in the field.

Description The tracks at Site III have been known and exposed for a long time but have not yet suffered serious damage and are therefore the best preserved footprints at any of the track sites discussed herein. There are four definite trackways, of which T2 has seven tracks, T3 has 15, T4 has 5, and T5 has 2. T6 has 13 tracks, but the tracks are disordered, representing not only one sauropod trackways. Prints in trackways T2, T3, and T6 are smaller than those in T4 and T5, and possibly represent juveniles. T2 is unusual in that it comprises six pes impressions but only one manus impression.

Length : width ratios of the best preserved pes prints in these trackways are as follows: T2.1b=1.47 : 1 and T3.8b=1.41 : 1. T3.6a, a substantially deformed manus impression, has a length : width ratio of 0.56 : 1.

In trackway T3, the manus impressions are rotated 50°—70° outward from the trackway axis, substantially greater than the outward rotations of the pes impressions (16°—19°). The centers of the pes impressions are somewhat closer to the trackway midline than the centers of the manus impressions. Pace angulations range from 117°—124°. Width between tracks ranges from 9.2—22.9 cm.

Manus print T3.6a is waisted at midlength, dividing the impression into medial and lateral parts (Fig. 5). Two deep concavities at the medial part probably indicate digits I and II. A shallow concavity at the lateral part probably indicates the presence of digit V. Deformation was observed at digit I and cranial part (probably digit III) due to

the influence of mud backfill. A sizable pit occupies the middle part of the impression, which may have been formed by invasive vegetation or wea-

thering. The lateral part of the impression is parabolic and is followed by a relatively long drag impression.

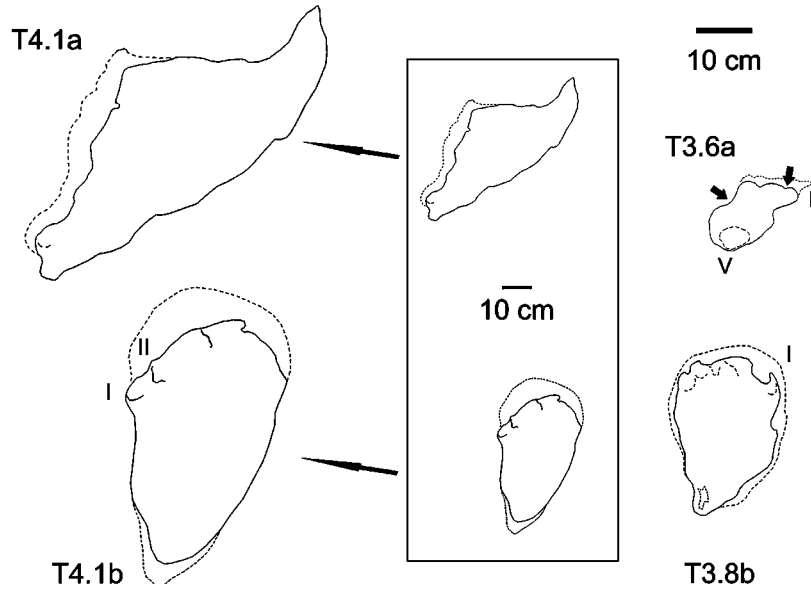


Fig. 5 Outline drawings of Nanguzhai sauropod tracks T3. 6a, T3. 8b and T4. 1a, T4. 1b from Site III

Dashed lines indicate indistinct footprint borders and the maximum extent of sediment deformed by registration of the track. Arrows in T3. 6a indicate the directions of mud backfill.

Well preserved pes print T3. 8b has an especially well-developed digit I impression that is 5.0 cm wide, 3.5 cm deep, and sharp. Several deep concavities (2.5—4.0 cm deep) beside digit I may represent digits II—IV. They have less discernible claw marks than digit I. The metatarsophalangeal pad region is smoothly curved.

The length : width ratios of manus print T4. 1a and pes print T4. 1b are 0.38 : 1 and 1.51 : 1, respectively. These larger tracks may have been made by adults of the smaller track markers of T3. 6a and T3. 8b, but T4. 1a is not only deformed but also heavily weathered. Due to the absence of manus tracks in this sequence, it is difficult to compare with T3. 6a.

Trackway T3 changes along its path from narrow to wider gauge (Fig. 6). One of the probable two trackways in T6 is wide gauge compared to T2. Trackway T4 also appears to be wide gauge. Using the equation to calculate speed (Alexander, 1976), the walking velocity of the track maker decreases along the trackway: track sequence T3. 4b—T3. 6b has a calculated velocity of 0.64 m/s,

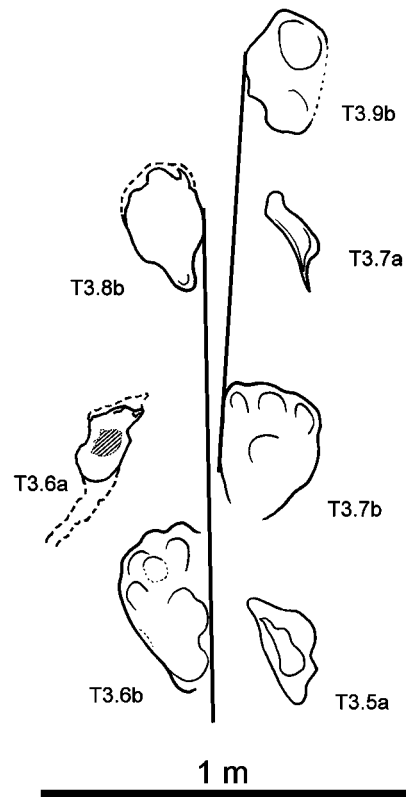


Fig. 6 Portion of Nanguzhai Site III trackway T3 that exhibits a change from narrow to wide gauge

T3. 5b—T3. 7b is 0.54 m/s, T3. 6b—T3. 8b is

0.45 m/s, and T3.7b—T3.9b is 0.5 m/s. This decreasing velocity corresponds to the switch from narrow gauge to wider gauge—the narrow gauge portion was made at higher speed, while wider gauge portions demonstrate slower track maker velocity. A similar change in gauge corresponding to track maker velocity was reported in a Middle Jurassic theropod trackway in England (Day *et al.*, 2002).

Discussion *Brontopodus* (Farlow *et al.*, 1989) is one of the most common and well known Cretaceous track types. Previously, Early Cretaceous sauropod tracks in eastern Asia have been attributed to wide gauge *Brontopodus* (Lockley *et al.*, 2002), not narrow gauge *Parabrontopodus* (Lockley *et al.*, 1994). However trackways T2—T6 can be attributed to *Parabrontopodus* because they have little to no space between the trackway midlines and the inside margins of the pes tracks. Pes footprints are longer than wide, with their long axes rotated outward. Although the manus tracks are not semicircular, they are smaller than their associated pes tracks.

The primary difference between T2—6 and *Parabrontopodus mcintoshi* (Lockley *et al.*, 1994), *Parabrontopodus distercii* (Meijide Fuentes *et al.*, 2001), and *Iguanodonichnus frenki* (Moreno and Benton, 2005) is that the manus impressions lie away from the trackway midline. Other morphological characteristics are difficult to compare due to the comparatively poor preservation of the Mengtuan tracks. Therefore, there is no justification for placing the Mengtuan tracks into a new ichnotaxon; they are best attributed to *Parabrontopodus* isp.

Chronologically, *Parabrontopodus* ranges from Early Jurassic (*P. isp.* (Niedzwiedzki and Pieńkowski, 2004)) through the Late Jurassic (*P. mcintoshi* (Lockley *et al.*, 1994) and “*Iguanodonichnus frenki*” (Moreno and Benton, 2005)) and into the Early Cretaceous (*P. distercii* (Meijide Fuentes *et al.*, 2001)). The discovery of *Parabrontopodus* tracks in China provides new evidence for the distribution of track makers capable

of registering *Parabrontopodus* tracks.

6 INFLUENCE OF SUBSTRATE AT SITE III

The substrate of Site III appears to have been soft and wet at the time the tracks were made, mud cracks developed in a few places suggest that the sediment dried subaerially before being buried. Using trackway T3 as an example, both the track maker mani and pedes left deep impressions. Of these, the pes prints, which are larger and bore more weight, are more complete and less deformed than the manus prints.

Manus print T3.6a (Fig. 7A) was the least influenced by substrate conditions, whereas manus print T3.7a (Fig. 7B) was influenced by the sediment the most; the latter is bounded by at least 2—3 concentric mud impressions both medially and laterally, especially in the central part of the anterior region. The impressions tend to be deepest medially and centrally (the medial part probably constitutes an impression of digit I). That suggests that the tracks were filled to varying degrees with collapsed, unconsolidated sediment after the track maker appendage was extracted (Fig. 8).

The consecutive tracks T.3.3a—T3.7a were influenced by substrate conditions to varying degrees, but their medial parts (impressions of digit I or digits I—II) are the deepest, which suggests that these areas were probably the foci at which force were applied by the track maker mani.

This trend is readily discerned in the theropod tracks (T1.1—1.4); the tracks change from having wider to narrower posterior ends through the sequence, suggesting that the substrate transitioned from drier, easily deformed sediment to wetter and muddier sediment more likely to collapse and, backfill the tracks. For example, T1.4 consists only of two unconnected digit impressions because the remainder was infilled by backfilling sediment. In a similar case, poorly-defined tracks of *Iguanodontipus* isp. and *Megalosauropus* isp., contrasted with well-defined examples, have been considered as indistinct primarily because of sedi-

ment water content (Diedrich, 2004). The “back-filled” tracks of Nanguzhai Site III are the products

of appendage-sediment interactions where the substrate was fluid and behaved plastically.

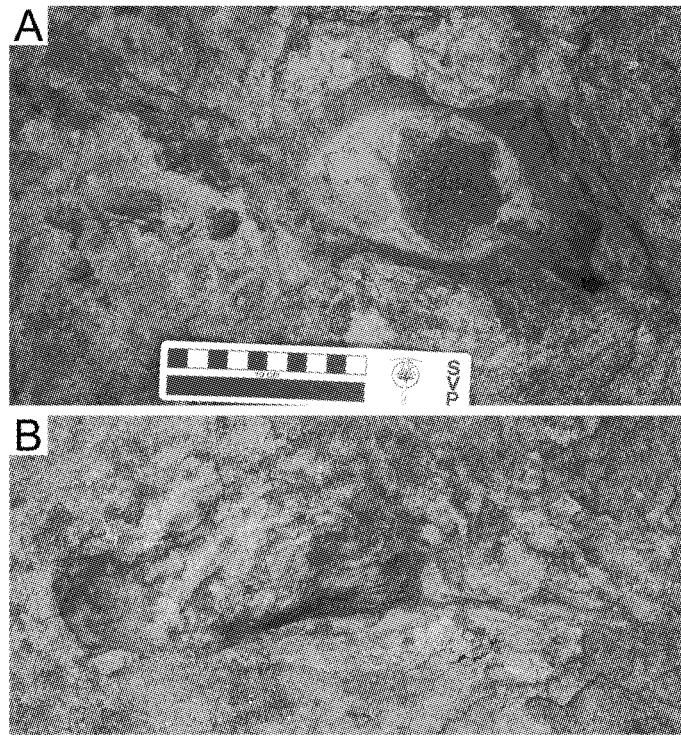


Fig. 7 Photographs of Nanguzhai track Site III sauropod manus tracks T3.6a (A) and T3.7a (B)

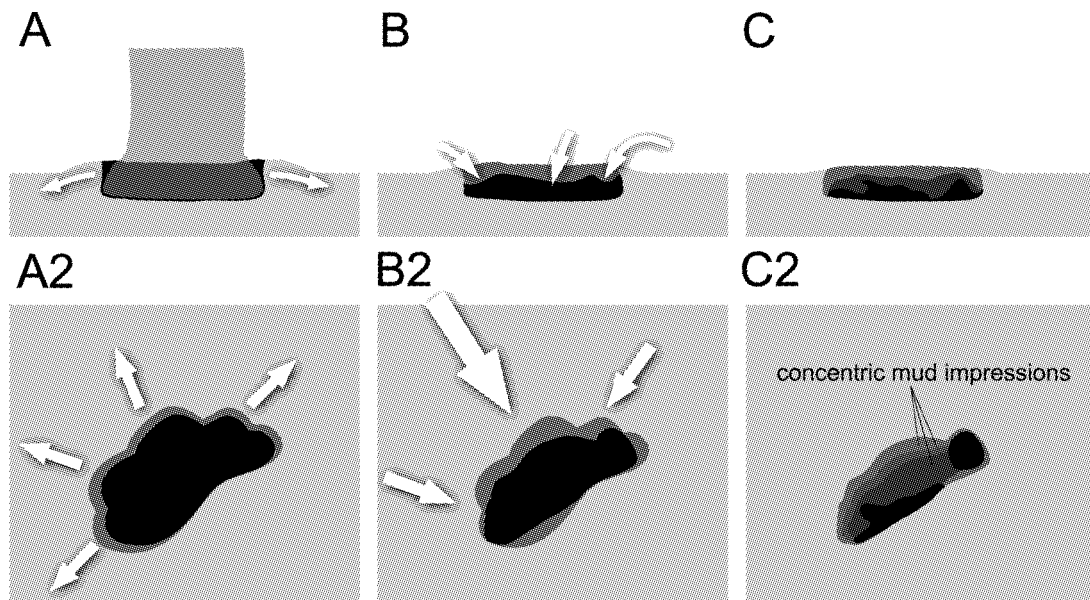


Fig. 8 Track making in loose, muddy, fluidic sediment at the Nanguzhai track site

A. appendage steps in; B. appendage has pulled up; C. mud backfills track. A—C are in medial view; A2—C2 are in dorsal view. The arrows indicated the mud filling in the tracks.

7 MORPHOLOGICAL DIVERSITY OF NANGUZHAI SAUROPOD TRACKS

The Nanguzhai tracksite is unusual in the di-

versity of sauropod track and trackway morphologies preserved within a small area and in the same stratum. The manus print at Site I is clawless and more round than the expected U-shape, likely a function of sediment consistency rather than sub-

stantial differences in forelimb morphology. The manus impression at Site II is similar to that of the unnamed sauropod tracks from the Middle Jurassic of the Galinha tracksite, Portugal (Santos *et al.*, 1994) and may exhibit a discernable digit I claw mark. Partial well-preserved manus impressions at Site III in trackway T3 are similar to those at Site II, but the pes impressions are markedly different.

The manus : pes area ratio of T7. 1 (Site I) is about 1 : 2. 5; that of T8. 1 (Site II) is 1 : 2. 2. Both coincide with wide gauge trackways, as in other Chinese sauropod tracks (Lockley *et al.*, 2002). These values are also similar to manus : pes area ratios from most other Cretaceous sauropod trackways globally (Lockley, 1999, 2001), though in some instances, reported ratios are as high as 1 : 5 (Santos *et al.*, 1994). However, the area ratios of *Parabrontopodus* isp. T3. 6a and T3. 8b at Site III are closer to 1 : 3. 7, and the area ratios of trackway T3 are 1 : 2. 4—1 : 5. 9, both as results of feet dragging through the muddy sediment.

Marty *et al.* (2006) divided sauropod trackways into four groups: quadrupedal trackways (manus and pes present), manus-dominated trackways (quadrupedal trackways with deep manus prints and shallow, barely visible pes prints), pes-dominated trackways (quadrupedal trackways with deep pes prints and shallow, barely visible manus prints), and pes-only trackways. Nanguzhai *Parabrontopodus* trackway T3 is quadrupedal, while T2 is pes-dominant. Similar discoveries include ROLM 26, which consists of unnamed tracks from the Lavini di Marco site (Leonardi and Mietto, 2000), and S5 and S6, consisting of unnamed tracks from Switzerland (Marty *et al.*, 2006). Such trackways have frequently been regarded as made by relatively fast moving sauropods, where the pes overprints the manus (Meyer, 1990); alternatively, slight changes in palaeoenvironment and substrate consistency may have similar effects (Marty *et al.*, 2006). No pedes overprint the manus in T2, for which stride lengths do not differ substantially from T3, in which the velocity is not fast.

Thus, the pes-dominant situation at the Mengtuan sites is probably more the result of paleoenvironmental and substrate consistency differences.

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Explanation of Plates

Plate I

- A. Overview of sauropod tracks at Nanguzhai Site III.
B. Sauropod tracks at Nanguzhai Site II.

Plate II

Theropod and sauropod tracks from the Nanguzhai track site. Scale

bar=10 cm.

- A—D. Theropod tracks (T1. 1.—1. 4, sequentially) from Site III.
E. Sauropod pes track T2. 1b from Site III.
F. Sauropod pes track T3. 8b from site III.
G. Sauropod manus-pes track set from Site I.
H. Sauropod pes track T4. 1b from Site III.

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图版 I

Plate I



