第47卷 第1期
2009年1月
古 脊 椎 动 物 学 报
VERTEBRATA PALASIATICA
pp.35－52
figs.1－5

记河北省后城组新发现之小型兽脚类足迹1)

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摘要:几十年前人们就已经开始研究中国东北侏罗纪—白垩纪界线附近地层中的小型兽脚类恐龙足迹,虽然这些遗迹化石比辽宁省义县组带羽毛的恐龙及其他实体化石逊色了许多。本文记述了河北省承德南双庙后城组(土城子组)最下部河流相沉积中发现的一组兽脚类恐龙足迹。南双庙足迹具有三趾,趾粗大,其形态与美国下侏罗统经典的"brontozoid"足迹(*Grallator*, *Anchisauripus* 和 *Eubrontes*)相符。虽然许多产自辽宁土城子组中基本同时的 brontozoid 足迹被鉴定为小型的跷脚龙足迹属(*Grallator*),但南双庙足迹更大一些(全长可达28.8 cm),可能应该归入安琪龙足迹属(*Anchisauripus*)。南双庙足迹很可能是一群小型兽脚类行走而产生。在辽宁义县组的兽脚类恐龙中,最可能留下这类足迹的是小型的窃蛋龙类——尾羽龙(*Caudipteryx*)。不过这个解释还很勉强,因为这些足迹缺乏鉴定性特征,而且河北的后城组与辽宁的义县组之间还有一定的时间及地理间隔。

关键词:河北承德,后城组,土城子组,兽脚类,足迹

中图法分类号:Q915.22 **文献标识码**:A **文章编号**:1000-3118(2009)01-0035-18

A NEW OCCURRENCE OF SMALL THEROPOD TRACKS IN THE HOUCHENG (TUCHENGZI) FORMATION OF HEBEI PROVINCE, CHINA

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Abstract Small theropod footprints have been known from the Jurassic-Cretaceous boundary strata of northeastern China for several decades, although these ichnofossils have been overshadowed by the feathered dinosaurs and other body fossils from the Yixian Formation of Liaoning Province. This paper describes a sample of several theropod footprints from a coarse fluvial deposit at Nanshuangmiao, in the lowermost Houcheng (Tuchengzi) Formation of Hebei Province. The Nanshuangmiao tracks exhibit a tridactyl, pachydactylous morphology corresponding to classic "brontozoid" ichnites (*Grallator*, *Anchisauripus* and *Eubrontes*) from the Lower Jurassic of the United States of America. Although many brontozoid tracks from the roughly equivalent Tuchengzi of Liaoning have been previously

1)国家自然科学基金项目(编号:40472018, 40121202)和国家基础科学人才培养基金特殊学科点项目(编号:J0630965)资助。

收稿日期:2008-05-09

assigned to the small ichnogenus *Grallator*, as *G. ssatoi*, the Nanshuangmiao tracks are larger (up to 28.8 cm total length) and are probably referable to *Anchisauripus*. The Nanshuangmiao tracks were most likely produced by small theropods travelling in a group. Of the abundant theropod taxa known from the Yixian Formation of Liaoning, the small oviraptorosaur *Caudipteryx* is the most plausible trackmaker, but this interpretation remains uncertain because of a lack of diagnostic features in the tracks and because of the temporal and geographic gap between the Houcheng of Hebei and the Yixian of Liaoning.

Key words Chengde, Hebei; Houcheng Formation; Tuchengzi Formation; Theropoda; footprints

1 Introduction

In recent years, a steady stream of important dinosaur finds have come from the Yixian Formation of Liaoning Province (summarized by Xu and Norell, 2006). The specimens include feathered and proto-feathered specimens that help to illuminate the transition from non-avian dinosaurs to birds. Approximately half a century before the earliest feathered dinosaur discoveries, however, numerous small dinosaur footprints were reported from a locality near Yangshan, a village in what is now western Liaoning (Yabe et al., 1940; Shikama, 1942). The footprints were discovered by Japanese geologists led by S. Satô in beds of the Tuchengzi Formation, lying stratigraphically just below the Yixian. Yabe et al. (1940) regarded the beds as "presumably Lower Cretaceous" (p. 560), whereas Shikama (1942) suspected they were Rhaeto-Liassic. Recent radiometric dating studies imply that the footprint-bearing Tuchengzi strata are Upper Jurassic, but within several million years of the the Jurassic-Cretaceous boundary (Lockley et al., 2006a; Matsukawa et al., 2006; Fujita et al., 2007). The upper part of the Tuchengzi is probably Lower Cretaceous (Swisher et al., 2002).

The dinosaur tracks discovered by Satô's team were described by Yabe et al. (1940) as a new theropod ichnotaxon, "*Jeholosauripus s-satoi*", which was subsequently reassigned to the widespread and well-established ichnogenus *Grallator* (Zhen et al., 1989). It should be noted in passing that the hyphen in the specific epithet *s-satoi* is unacceptable under the International Code of Zoological Nomenclature, since the species name was formed from the name of S. Satô (Yabe et al., 1940). Under article 32.5.2.4.4 of the Code, the epithet must be emended to *ssatoi*, and the binomen *Grallator ssatoi* is used throughout the remainder of this paper.

Although only four individual tracks of *G. ssatoi* were originally collected, Shikama (1942) subsequently visited the locality and estimated that approximately 1200 tracks were visible at the site. He apparently believed that the exposed track-bearing surface was a remnant of a larger area that had contained approximately 4000 tracks of conspecific animals all travelling in the same direction, perhaps even as a herd. A team from the Institute of Vertebrate Paleontology and Paleoanthropology later collected dozens more tracks from the same area (Young, 1960), and Matsukawa et al. (2006) reported mapping a total of 1170 tracks resembling *G. ssatoi* at two nearby sites at the same stratigraphic level. Other recently discovered footprint localities in the Tuchengzi of western Liaoning (Zhang et al., 2004; Fujita et al., 2007) have yielded non-avian theropod tracks that span a wider range of sizes. The largest tracks reported by Zhang et al. (2004) approach 30 cm in length, compared to a maximum of about 12 cm for *G. ssatoi* (Shikama, 1942). Some of the new tracks appear to be morphometrically distinct from *G. ssatoi*, although to what degree remains uncertain pending detailed comparisons. The Tuchengzi of Liaoning has also yielded a few avian tracks (Lockley et al., 2006a), in addition to body fossils of the basal ceratopsian *Chaoyangsaurus* (Zhao et al., 1999) and of the isolated forefoot of a sauropod (Dong, 2001).

Theropod (including bird) and ornithopod tracks are also known from various other, approximately stratigraphically equivalent sites in northeastern China (Matsukawa et al., 2006). Young (1960) described a few tracks specifically attributable to *G. ssatoi* from near Chengde, in Hebei Province. The exact provenance of these tracks is uncertain, but they are probably from strata roughly equivalent to the Tuchengzi of Liaoning (Young, 1960). The Xiguayuan Formation of Hebei Province, which is younger by at least several million years, has yielded a sample of theropod tracks somewhat larger than those of *G. ssatoi* and apparently of different morphology (You and Azuma, 1995).

The present paper describes newly discovered theropod tracks from the lower part of the Houcheng Formation at Nanshuangmiao, Xinzhangzi Village, Chengde County, Hebei Province. The name Tuchengzi is sometimes applied to the Houcheng Formation of Hebei, especially in the palaeontological literature (e.g., Matsukawa et al., 2006), even though the Houcheng of Hebei and the Tuchengzi of Liaoning may not be strictly contemporaneous. The term Houcheng is preferred in the present paper. However, the stratigraphic separation between the two rock units is probably not large, so that the Nanshuangmiao tracks are close to the age of reported occurrences of *G. ssatoi* (Yabe et al., 1940; Shikama, 1942; Young, 1960) and more recently discovered theropod tracks from western Liaoning (Zhang et al., 2004; Fujita et al., 2007). The Nanshuangmiao tracks show a broad general resemblance to *G. ssatoi*, but are larger than any previously described specimen of this ichnospecies (Yabe et al., 1940; Shikama, 1942; Young, 1960) and also seem to be different in their proportions. Particularly considering the large number of known *G. ssatoi* tracks, the discrepancies in size and morphology strongly imply that the new tracks represent a different ichnotaxon, although one possibly similar or even equivalent to some of the tracks described by Zhang et al. (2004) and Fujita et al. (2007). The present paper describes the structure and considers the ichnotaxonomic position of the new Nanshuangmiao prints, considers their significance in the context of the Late Jurassic and Early Cretaceous record of theropod ichnofossils and body fossils from northeastern China, and briefly considers the identity and behaviour of the trackmakers.

Institutional abbreviations IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; TU, Tohoku University (formerly Tohoku Imperial University), Sendai, Japan.

2 Materials and methods

The Nanshuangmiao tracks occur in convex hyporelief on the underside of a mudstone layer exposed partway up the face of a steep roadside outcrop (Fig. 1). There is no indication of corresponding prints in concave epirelief on the upper surface of the track-bearing layer, so the original tracks were clearly imprinted into the layer underlying the mudstone. The mudstone represents a deposit that infilled the track impressions and formed natural casts of them. Distinct pad impressions and claw marks can be seen on some digits, although they are not always clear. Preservation of these features implies that the tracks are either true tracks or very shallow undertracks, not deep undertracks that would preserve only a vague and distorted reflection of each original print.

A portion of the track-bearing layer was collected in blocks (IVPP V 15816). A further portion, preserving eight individual tracks in an area of about 0.25 m^2, was left intact but moulded in latex in the field. The mould was used to produce a cast replicating the original positive track impressions (Fig. 2). Both the mould and the cast are housed in the IVPP under specimen number IVPP VC 15815. Because 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, detailed study of the tracks was carried out based largely on the cast. The tracks on the cast were assigned the letters A through H for ease of reference. Measurements reported in this paper were tabulated and averaged for these eight tracks only.

Outlines of individual tracks were traced from a photo of the plaster cast. Tracing was carried out with reference to the cast, to the latex mould, and to original photos of the tracks in the field. Following Olsen and Baird (1986) and Olsen et al. (1998), outlines were drawn to re-

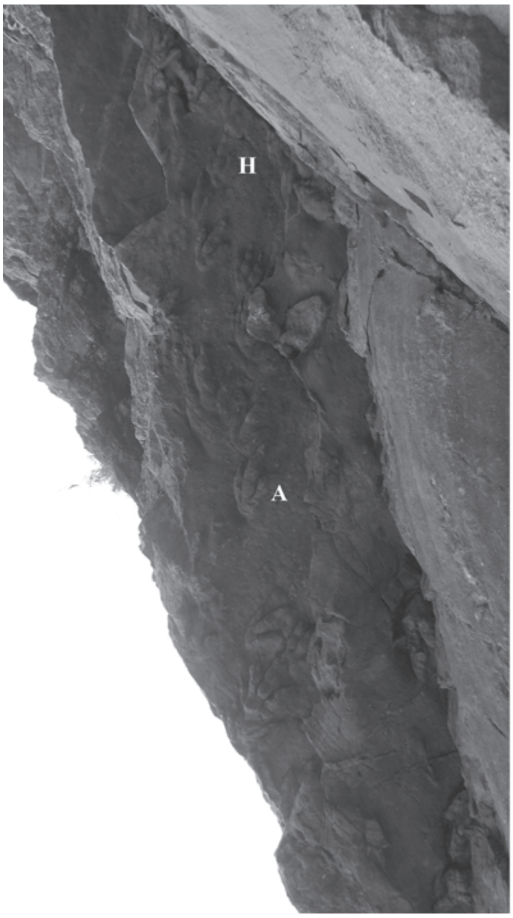

Fig. 1 The Nanshangmiao tracks in situ
The tracks are exposed in convex hyporelief on the underside of a rock stratum, so the photo was taken with the camera directed upwards; the track-bearing stratum dips towards the top of the photo; letters identify the tracks at the beginning and end of the portion of the rock surface that was collected by moulding and subsequently cast in plaster

Preservation of the tracks was sufficiently unclear that it was generally not possible to reliably distinguish between left and right footprints. When reporting divarication angles, digits are identified by their position on the cast of the track (left, right or centre, with the track facing away from the observer) rather than by their anatomical identity. In most cases, individual phalangeal pad impressions along the digits were also indiscernible. For this reason, the osteometric approach to determining digit lengths described by Farlow and Lockley (1993), which relies on measuring flect the topographically steepest part of the track edge. Where possible, morphometric measurements of each track were then taken from the two-dimensional outlines. The maximum length and maximum width of each track was measured, as were the angles of divarication among the three digits. Divarication was defined as the angle between the median lines of a pair of neighbouring digits, each median line being drawn so that the area of the digital imprint falling on either side of the line was approximately equal (Zhen et al., 1996). Only the impression of the digit itself, as opposed to the adjacent part of the "heel" of the track, was taken into account when constructing a median line (Fig. 3). The alignment of the median line of the middle digit was used as proxy for the orientation of the footprint as a whole.

Fig. 2 Outline drawing (left) and photograph (right) of a plaster cast of eight small theropod tracks from the Houcheng Formation of Nanshuangmiao, Hebei Province

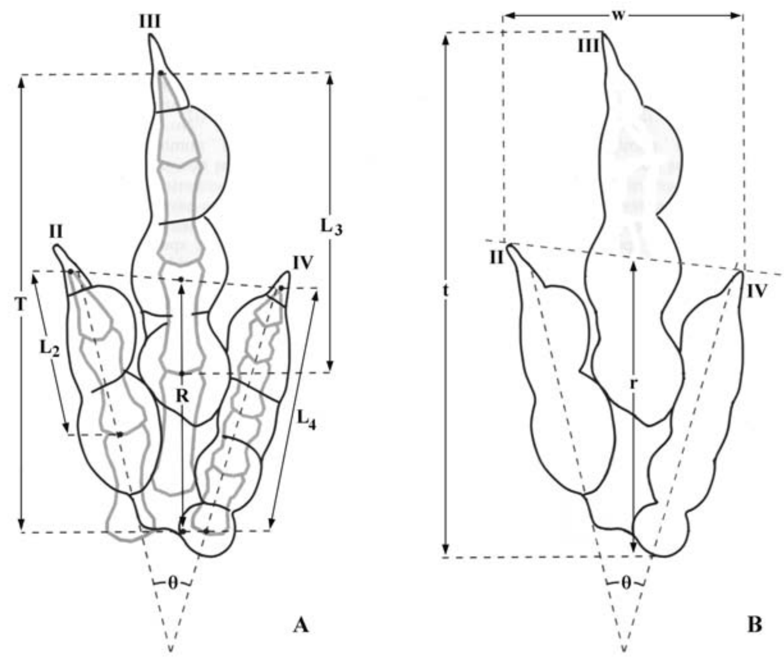

Fig. 3 Measurements used to evaluate theropod tracks (A) by Olsen et al. (1998) and in the present paper (B)
The measurements presented in B are designed to be feasible on tracks with very poorly preserved pad impressions along the digits; note that the median line of the middle digit has been omitted, for clarity, from both illustrations; modified from Olsen et al. (1998)
Abbreviations: Lx. osteometric length of digit x; r. length of rear part of track; R. osteometric length of rear part of track; t. total length of track; T. osteometric length of track; θ. divarication angle between digits II and IV; w. total width of track

distances between the centres of pad impressions, could not be applied. Similarly, Olsen et al. (1998) defined a "projection ratio" (P) that expressed the degree of protrusion of the middle digit of an individual track beyond the two flanking digits. However, P could not be strictly calculated for the tracks described in the present paper, because Olsen et al. (1998) used the centres of pad and claw impressions as reference points for establishing digital lengths (Fig. 3A). However, we devised a roughly comparable metric, the approximate projection ratio (AP), which is calculated using the measurements shown in Fig. 3B.

Olsen et al. (1998) defined P as follows:

$$P = R' / (T - R') \quad (1)$$

where T is the total inferred length of the phalangeal skeleton, from the centre of the proximal pad of digit IV to the centre of the claw impression of digit III (Fig. 3A), and R' is a corrected value of R, the length of the "rear" (proximal) part of the phalangeal skeleton. R is the part of T falling posterior to the intersection between the middle digit and a line drawn between the centres of the claw impressions of the two flanking digits (Fig. 3A). This figure is corrected trigonometrically to account for the angle of divarication (θ) between the second and fourth digits:

$$R' = R / \cos(\theta/2) \quad (2)$$

Because T and R, as defined by Olsen et al. (1998), could not be precisely measured on the tracks in the present sample, the total length of each track (t) was used as an approximation of T (Fig. 3B). In order to approximate R, a transverse line was drawn between the distal tips of the impressions of the second and fourth digits. The distance from the most proximal point on the track to the level at which the transverse line intersected the median line (Fig. 3B: r) was used as an approximation of R.

The formula for the approximate projection ratio AP was therefore

$$AP = r' / (t - r') \quad (3)$$

where

$$r' = r / \cos(\theta/2) \quad (4)$$

Trackmaker size was estimated according to the simple formula recommended by Henderson (2003) for dinosaurs generally, in which the hip height of the trackmaker is taken to be four times the total length of an individual footprint.

3 Geological setting

The Nanshuangmiao tracks were discovered within steeply dipping coarse fluvial deposits of the lower Houcheng Formation of Hebei Province, which represent the distal toe of a large alluvial system that fed into the region from the north (Cope et al., 2007). Evidence for a fluvial facies association includes pervasive cross stratification and the numerous scour surfaces that occur within the coarse sandstone and conglomerate beds surrounding the tracks. Soil horizons present within the upper Houcheng Formation are predominantly calcic, indicating a semiarid to arid climate, whereas coal is present in underlying Jurassic strata. The lower Houcheng Formation at Nanshuangmiao probably represents a period of transition between wet and dry climatic end members. The tracks occur in a layer of mudstone a few centimetres thick that probably represents a mud drape on a fluvial gravel bar.

Tiaojishan Formation volcanic rocks that underlie the lower Houcheng Formation ~100 m beneath the trackway yield a kspar $^{40}Ar/^{39}Ar$ age of 152.57 ± 0.34 Ma (Cope et al., 2007), and gently dipping volcanic strata that unconformably overlie the Houcheng Formation have been U/Pb dated at ca. 135 Ma (Niu et al., 2004). The Late Jurassic-Early Cretaceous age of the Nanshuangmiao locality is therefore constrained by geochronological data. The track-bearing layer is stratigraphically much closer to the underlying volcanics dating to 152 Ma. The tracks are therefore probably Tithonian in age.

The track-bearing layers in the middle of the Tuchengzi Formation of Liaoning Province have been fission-track dated to 145.9 ± 4.8 Ma (Lockley et al., 2006a) and 153 ± 9 Ma (Fujita et al., 2007). By contrast, Swisher et al. (2002) obtained a sanidine $^{40}Ar/^{39}Ar$ age of 139.4 ± 0.19 (1SD) ± 0.05 Ma for the upper part of the Tuchengzi. These results strongly suggest partial overlap between the Houcheng Formation of Hebei Province and the Tuchengzi Formation of western Liaoning, but deposition of the two stratigraphic units was probably diachronous (Davis, 2005). In addition, the Tuchengzi and the Houcheng were deposited in different basins separated by significant Late Jurassic uplifts (Davis, 2005; Cope and Graham, 2007; Cope et al., 2007). The Houcheng Formation strata within which the Nanshuangmiao tracks occur represent the distal portion of a south-flowing braidplain or alluvial fan that was deposited during initial formation of a hydrologically closed basin (the Chengde basin). Approximately 500 m of overlying Houcheng Formation strata were then deposited by northwest-directed alluvial fan systems that advanced over the Nanshuangmiao beds from the southern margin of the Chengde basin (Cope et al., 2007). Northeast of Nanshuangmiao, Houcheng Formation strata equivalent to these northward-flowing alluvial fan deposits consist of lacustrine redbeds.

The Chengde basin was typical of Late Jurassic basins throughout northeast China. Although the Late Jurassic palaeogeography of northeast China is still poorly understood, several authors agree that the Houcheng and Tuchengzi Formations were deposited in numerous separate basins, separated from the overlying Cretaceous by a widespread unconformity (Davis, 2005;

Cope et al., 2007; Liu et al., 2007).

4 Description

The tracks in the present sample are less densely packed than those described by Shikama (1942). The partial cast of the track-bearing surface bears eight individual pedal prints, one of which (Fig. 4: Track D) is superimposed on an additional impression that almost certainly represents an overprinted track. There is no indication of associated manual prints, implying a bipedal trackmaker. The size distribution and spacing of the eight tracks rule out the possibility that they all belong to a single trackway (see below), but they do share a common approximate orientation that establishes a beginning-to-end polarity for the track cluster. The median lines of all eight tracks fall within an arc of 35° (Table 1; Fig. 5), so that each track is within 18° of the average orientation for the cluster as a whole.

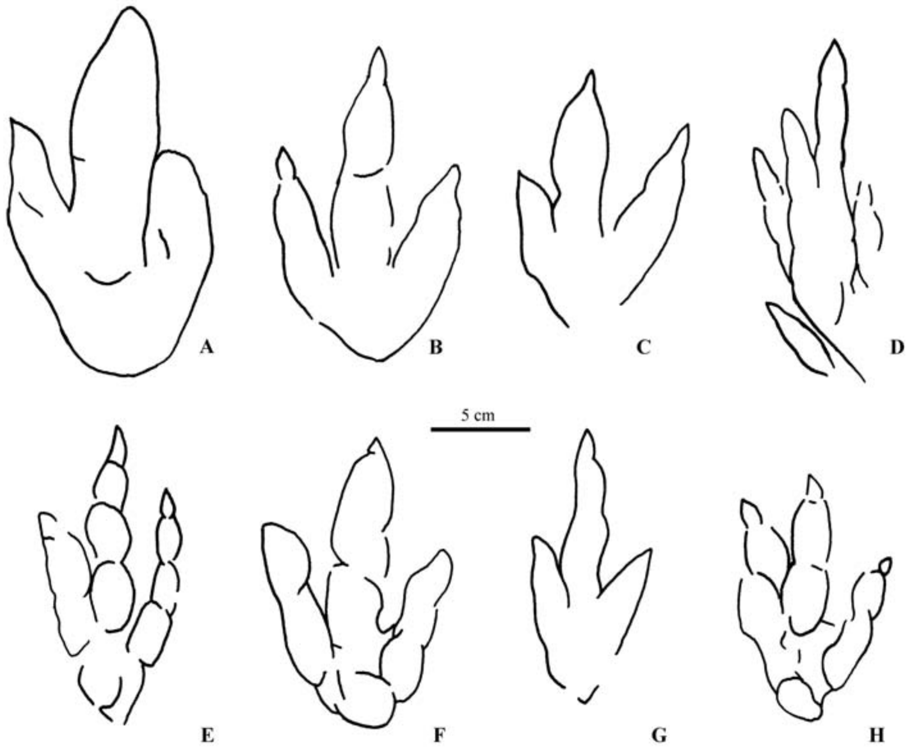

Fig. 4 Outline drawings of the eight tracks from the Nanshuangmiao sample that were collected by casting
All tracks aligned so that their middle digits share a single orientation

The blocks collected directly from the track-bearing layer were taken from near the end of the track cluster, to the left of the tracks preserved on the cast. These blocks contain three more tracks, including one that represents the largest in the sample. The other two are smaller and rather poorly preserved. Field photos show that a fourth track, also poorly preserved, fell between the area of the track-bearing layer that was collected and the area that was cast. Five further tracks lay prior to the beginning of the part of the cluster preserved on the cast, but these five additional tracks were not collected.

Each track is tridactyl, and none shows any trace of a hallux or metatarsal print behind the impressions of the three functional digits. The tracks are pachydactylous, with broad and well-defined digit impressions. Some of the tracks, but not all, show a trenchant claw mark at the end of one or more of the digits. The central digit of each track is invariably longest, and is approximately straight, whereas the two flanking digits are variable in length and curvature. In some cases (Fig 4: Tracks B, F, G) they are subequal in both length and divarication, and approximately straight. In other cases, the lengths of the flanking digits may be obviously unequal (e. g., Track C) and/or the flanking digits may diverge from the central digit at substantially different angles of divarication (e. g., Track E). In the case of Track A, the right digit actually has a slightly negative angle of divarication (−2.7°) because the median lines of the right and central digit converge on each other rather than diverging. This is due to a convex bulge on the right edge of Track A, which presumably is a deformity resulting from the softness of the substrate. Substrate incompetence also probably accounts for the lack of clear phalangeal pad impressions along most of the digits, and for much of the observed variation in the thickness, length and shape of the digital impressions themselves.

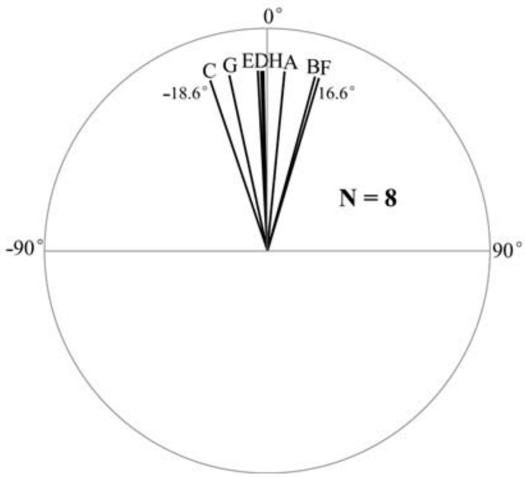

Fig. 5 Rose diagram showing the orientations of the eight tracks from the Nanshuangmiao sample that were collected by casting
Since the compass orientation of the slab was not recorded during collection, the zero degree line corresponds to the average orientation of the eight tracks

The shape of the posterior "heel" of each track, actually formed by the pads of the metatarso-phalangeal (MP) joints (Olsen et al., 1998: fig. 4), also varies. The heel may be broadly rounded (e. g., Track A) or sharply pointed (Track G). In some cases, the heel is asymmetric, in that one side extends further posteriorly than the other. A corresponding asymmetry in small theropod tracks discussed by Olsen et al. (1998) was thought to have resulted from slight elevation of the base of the second digit, so that only the third and fourth MP joints left clear impressions. Applying this explanation to the tracks described in the present paper, the more posteriorly protrusive side of the heel could then be interpreted as lateral. This would permit right and left footprints to be distinguished, but heel shape is so variable (and frequently indistinct) among the preserved tracks that this evidence cannot be considered conclusive.

Table 1 Measurements of eight small theropod tracks from the Houcheng Formation of Nanshuangmiao, Hebei Province (cm)

Track	length (t)	width (w)	t/w	left/centre divarication	centre/right divarication	total divarication (θ)	approximate projection (AP)	orientation
A	18.5	10.2	1.8	19.4°	−2.7°	16.7°	1.8	−5.5°
B	15.7	9.3	1.7	19.0°	16.8°	35.8°	2.3	−15.3°
C	?	8.6	?	9.2°	23.7°	32.9°	?	18.6°
D	?	?	?	?	?	?	?	−2.0°
E	?	7.1	?	12.4°	17.2°	29.6°	?	3.0°
F	14.5	9.5	1.5	21.8°	8.9°	30.7°	2.2	−16.6°
G	13.7	6.0	2.3	15.6°	26.9°	42.5°	1.8	12.2°
H	12.3	7.6	1.6	6.3°	19.2°	25.5°	4.4	1.2°
average	**14.9**	**8.3**	**1.8**	**14.8°**	**15.7°**	**30.5°**	**2.5**	**0°** 1)

1) Orientation of 0° corresponds to average orientation of all tracks.

Table 1 contains simple measurements of size, proportions, and divarication angle for each of the eight tracks that were collected by moulding. Approximated projection ratios for the eight tracks average 2.5, although Track H is a clear outlier in having an AP of 4.4. Removing this track from the sample results in an average AP of 1.9 for the remaining tracks. AP values could not be measured for Tracks C, D and E, because the outline of the heel was unclear in each case, but Track E is similar to Track H in that the flanking digits appear almost as long as the middle digit. The length-width ratios of the tracks have an average value of 1.8, and range from 1.5 to 2.3. Within the sample, there is no obvious correlation between the length of an individual track and its length-width ratio.

It is difficult to be certain how many individual animals were responsible for the tracks in the present sample. The total lengths of the eight footprints preserved on the cast range from 12.3 cm to 18.5 cm (Table 1), so that the longest track is about 150% the length of the shortest, and the best-preserved track on the slabs that were collected directly from the field is even larger (28.8 cm). Furthermore, the spacing of successive tracks on the plaster cast is considerably shorter than the minimum distance that would be expected between tracks of an individual theropod; for example, Lockley et al. (2008) measured the pace length of *Minisauripus* as ranging from 3 to 10 times the length of the foot. The exact number of trackmakers represented in the sample is uncertain, but the spatial distribution of the tracks, the range of variation in track length, and the evident case of overprinting imply that the eight tracks on the plaster cast (nine, counting the overprinted track) were probably produced by at least four, and possibly several more, individuals.

5　Ichnotaxonomic attribution of the tracks

Tridactyl pes prints from the later part of the Mesozoic are attributed to either theropod (including avian) or ornithopod dinosaurs. The two possibilities can be difficult to distinguish, but ornithopod pes prints are more likely to have associated manus prints, and tend to be more symmetric and wider relative to their length (Lockley and Matsukawa, 1999). The relatively high average length-width ratio of the tracks described in the present study (1.8), the lack of manus prints, and the asymmetry of the heel in some individual tracks all support the theropod interpretation. The trenchant claws visible on some of the prints are also more characteristic of theropods than of ornithopods, since ornithopod tracks typically lack claw marks or display only poorly-developed ones (Ferrusquia-Villafranca et al., 2007).

Some recent authors (Olsen and Baird, 1986; Olsen et al., 1988; Carrano and Wilson, 2001) have stressed the importance in trackmaker identification of specific ichnological features that correlate with derived characters of the pedal skeleton, rather than general patterns of resemblance like those presented above. In the present context, the primitive condition of the dinosaur pes may have been relatively theropod-like (Olsen and Baird, 1986) so a broadly theropod-like track might in fact be attributable to a very basal dinosaur. However, neither basal saurischians (Langer, 2004) nor basal ornithischians (Norman et al., 2004) survived into the Late Jurassic. Accordingly, a theropod origin can be assumed for Late Jurassic tridactyl pes prints that do not match the derived pattern of ornithopods, as in the present study.

With a few exceptions, such as didactyl tracks attributed to dromaeosaurs (Li et al., 2008), the footprints of theropods are rather uniform in their gross morphology. Although some qualitative differences certainly exist (Lockley, 1998; Lockley et al., 1998a), diagnoses of theropod ichnotaxa are often based primarily on size and proportions (e.g., Olsen et al., 1998). For example, the tracks of birds have very wide divarication angles that distinguish them from most but not all non-avian theropod tracks (Farlow et al., 2000), and support their assignment to different ichnogenera.

The Nanshuangmiao tracks are notable mainly for their relatively small size (average length 14.9 cm for the eight tracks preserved on the cast, although one 28.8 cm specimen was collected separately) and narrow angles of divarication (averaging 30.5° for the tracks on the cast). Small generalized theropod tracks with low divarication are routinely assigned to the classic ichnogenera *Grallator*, *Anchisauripus*, and *Eubrontes*, all originally described from the Lower Jurassic of the Connecticut Valley in the United States, but the ichnotaxonomy of these genera is contentious (Olsen, 1980; Olsen et al., 1998; Rainforth, 2005; Milner et al., 2006; Lockley et al., 2008). The three ichnogenera are traditionally distinguished in large part by size, *Grallator* being smallest and *Eubrontes* largest (Olsen et al., 1998). However, *Grallator* tracks also tend to be relatively narrow with a low projection ratio (i.e. digit III is long in comparison to the other digits) whereas *Eubrontes* tracks are broad with a higher projection ratio. Olsen (1980) plotted projection ratio against track length and found a positive correlation, suggesting that the three putative ichnogenera formed a continuum of increasing size and concomitantly increasing projection ratio. Milner et al. (2006) retained *Eubrontes* and *Grallator* as distinct genera, but eschewed the use of *Anchisauripus* on the grounds that this ichnogenus was difficult or impossible to distinguish from *Grallator*. Lockley et al. (2008) simply chose to refer to *Grallator*, *Anchisauripus* and *Eubrontes* collectively as "the *GAE* plexus".

Olsen et al. (1998) restudied the Connecticut Valley type material of *Grallator*, *Anchisauripus* and *Eubrontes*, and concluded that valid characters could be found to distinguish among the type specimens of the three ichnogenera. However, this left open the possibility that equally careful study of further material might uphold the earlier interpretation of a continuum (Olsen, 1980). Rainforth (2005) synonymized all three ichnogenera under the name *Eubrontes*, and coined the term "brontozoid" to describe this overall track morphology. Her use of a single ichnogenus was based on an explicit methodological framework in which ichnogenera were defined to include all tracks made by members of a particular clade, whereas ichnospecies were taken to represent variants due to behaviour, substrate consistency, and taphonomy, as well as intraclade differences in pedal anatomy. This methodology amounted to a commitment to lumping ichnogenera and splitting ichnospecies, although Rainforth (2005) did not evaluate the species-level ichnotaxonomy of her concept of *Eubrontes* beyond eliminating objective synonymies. To produce a stable and widely accepted ichnotaxonomy of brontozoid tracks will require extensive further study of large numbers of specimens from the Connecticut Valley and elsewhere around the world, since some previously erected taxa will likely prove to be subjective synonyms.

Olsen et al. (1998: table 2) presented measurements from over 30 individual tracks of *Grallator*, *Anchisauripus* and *Eubrontes*, including type material. These values, and the accompanying diagnoses and descriptions for type specimens of the three ichnogenera, indicate that brontozoid traces are tridactyl pedal prints ranging from approximately 7 to 34 cm in length, with divarication angles ranging from 9° to 40°, length-width ratios ranging from 1.4 to "near or greater than two" (Olsen et al., 1998:595), and projection ratios ranging from 1.0 to 2.7, with the highest projection ratios all belonging to *Eubrontes*. Average values for the new tracks from Nanshuangmiao fall comfortably within these ranges, although it should be noted that lengths and projection ratios were measured slightly differently in the present study than in the study by Olsen et al. (1998). The Nanshuangmiao tracks also agree with brontozoid ichnites in their pachydactylous structure (Rainforth, 2005). The absence of hallux and metatarsal impressions in the Nanshuangmiao tracks is typical of brontozoids, since previous references to hallux impressions in at least some specimens of *Anchisauripus* (e.g., Young, 1960; Zhen et al., 1989) are apparently spurious (Rainforth, 2005). About half of the Nanshuangmiao tracks show an asymmetry of the heel region that is strongly reminiscent of brontozoids, in which the impression of digit IV typically extends further proximally than that of digit II (Olsen et al., 1998). The absence of this asymmetry in the remaining tracks is probably the result of glancing or imprecise contact between the heel and the substrate.

Assignment of the Nanshuangmiao tracks to other established theropod ichnotaxa is precluded by factors such as the small size of the Nanshuangmiao tracks, their narrow angles of divarication (correlated with relatively high length-width ratios), their pachydactylous structure, and the absence of hallux and metatarsal impressions. For example, the widespread Late Jurassic theropod ichnogenus *Megalosauripus* has a minimum track length of about 40 cm (Lockley et al., 1998a), compared to a total length of only 28.8 cm for the largest track in the present sample. A possible alternative assignment for the Nanshuangmiao tracks is to the ichnogenus *Therangospodus*, another Late Jurassic theropod ichnotaxon with a distribution spanning North America and Eurasia (Lockley et al., 1998b). The size range of *Therangospodus* overlaps with the Nanshuangmiao prints, and the range of variation in divarication angles and other taxonomically significant metrics is apparently broad enough to encompass the Nanshuangmiao tracks (Lockley et al., 1998b). However, *Therangospodus* is characterized by fleshy digital impressions that lack any trace of discrete pads (Lockley et al., 1998b), whereas some pad impressions can be seen on the better-preserved tracks in the sample from Nanshuangmiao.

Accordingly, the Nanshuangmiao tracks are best regarded as brontozoid, even though brontozoid footprints were first described from the Lower Jurassic of North America (Hitchcock, 1848; Olsen et al., 1998; Rainforth, 2005) rather than the Upper Jurassic to Lower Cretaceous of Asia. Tracks of similar age from Liaoning (Yabe et al., 1940; Shikama, 1942; Young, 1960; Zhen et al., 1989; Matsukawa et al., 2006) and Hebei (Young, 1960) have been uncontroversially referred to the ichnogenus *Grallator* as *G. ssatoi* (Zhen et al., 1989), and the additional tracks described from the Tuchengzi of Liaoning by Fujita et al. (2007) display a broadly similar morphology. Insisting on the grounds of provenance that these specimens should be excluded from Connecticut Valley ichnogenera would favour the misleading use of what Matsukawa et al. (2006:6) referred to as "provincial ichnotaxonomies".

However, stratigraphic and geographic proximity invites detailed comparison between *G. ssatoi* and the new tracks from Nanshuangmiao. According to the diagnosis presented by Zhen et al. (1989), the track length of *G. ssatoi* ranges from 7.0 ~ 12.0 cm and the track width ranges from 5.0 ~ 8.5 cm. This implies a length to width ratio of about 1.4 in *G. ssatoi*. Shikama (1942) tabulated length and width measurements for several dozen individual tracks of *G. ssatoi*, and on the basis of these data the average length-width ratio is 1.5. Zhen et al. (1989) gave the divarication angle of *G. ssatoi* as 27°, essentially agreeing with Shikama's (1942) statement that the modal value was 30°. However, the accompanying line drawing (Shikama, 1942: fig. 1) shows a track with considerably wider divarication, and photos of the densely packed trackway surfaces (Shikama, 1942: pls. XIV, XV) suggest that angles of divarication are highly variable in *G. ssatoi*.

The *G. ssatoi* material from Hebei and Liaoning described by Young (1960) cannot presently be located. Although the type material of *G. ssatoi* (Yabe et al., 1940) consists of only three complete tracks and one partial one, detailed restudy of these specimens (TU 61677) might help characterize the ichnospecies. However, the average length of the Nanshuangmiao tracks preserved on the cast is 14.9 cm, exceeding the maximum recorded length of *G. ssatoi*, and the longest specimen in the Nanshuangmiao sample (28.8 cm) is more than double the maximum recorded length of *G. ssatoi*. Because of the relatively large sample of tracks measured by Shikama (1942), the maximum length probably does represent a reliable upper bound. Furthermore, the Nanshuangmiao tracks have a higher average length-width ratio (1.8, compared to 1.4 or 1.5 for *G. ssatoi*), although the discrepancy is of small magnitude. Primarily on the basis of size, it seems inappropriate to refer the Nanshuangmiao prints to *G. ssatoi*, and indeed any ichnospecific assignment for the Nanshuangmiao prints is probably unwarranted given the somewhat confused state of brontozoid taxonomy at the ichnospecies level.

At the ichnogenus level, accepting Rainforth's (2005) proposal to sink all brontozoid tracks into *Eubrontes* would entail assigning the Nanshuangmiao tracks to this ichnotaxon. However, Rainforth's (2005) dissertation on brontozoid ichnotaxonomy has not yet been published and evaluated by other workers, and the names *Anchisauripus* and *Grallator* are both familiar and useful for distinguishing among brontozoid tracks with different sizes and proportions (Olsen et al., 1998). Furthermore, Lockley et al. (1998a) described the middle digit impression of *Eubrontes* as spindle-shaped, and extending proximally almost far enough to contact the proximal pad at the base of the digit IV impression. These features are not apparent in the *Anchisauripus* and *Grallator* tracks figured by Olsen et al. (1998), suggesting that significant differences of form may in fact exist among brontozoid ichnites. Accordingly, retention of the names *Grallator* and *Anchisauripus* is probably justified for the present.

The average length of the Nanshuangmiao tracks (14.9 cm) is almost exactly on the size boundary between *Grallator* and *Anchisauripus* given by Olsen et al. (1998), whereas the average divarication angle falls well within the range for *Anchisauripus* and just above the upper bound of the range given for *Grallator*. Olsen et al. (1998) diagnosed *Anchisauripus* tracks as having a length-ratio "near 2", and *Grallator* tracks as having a ratio "near or greater than 2", so the average length-width ratio of 1.8 calculated for the Nanshuangmiao tracks could probably be considered to conform to either ichnogenus. The average adjusted projection ratio of 2.5 is too large for either *Grallator* or *Anchisauripus*, even considering that the adjusted projection ratio calculated in the present study is not precisely comparable to the Olsen et al.'s (1998) projection ratio (see Materials and Methods).

At present, the Nanshuangmiao tracks are probably best assigned to *Anchisauripus* sp., and considered to represent a small species of *Anchisauripus* with a short middle digit (captured by the high projection ratio). On the grounds of size, referral to the ichnogenus *Grallator* would be equally justified, but the divarication angle is much more characteristic of *Anchisauripus* according to the measurements presented by Olsen et al. (1998). Furthermore, even though the validity of *Anchisauripus* as a distinct genus from *Grallator* is questioned by some workers, referral of the Nanshuangmiao tracks to the former genus has the additional advantage of clearly distinguishing them from the smaller *G. ssatoi* from the Tuchengzi of Liaoning. However, we acknowledge that discovery and evaluation of more material from the Houcheng Formation of Hebei, as well as revisions of the ichnotaxonomy of brontozoid tracks in general, might easily provide grounds for changing this ichnotaxonomic assessment. In any case, the primary importance of the specimens is that they establish the existence of medium-sized brontozoid tracks in the Houcheng Formation of Hebei Province, irrespective of their exact ichnotaxonomic position.

6 Discussion

Regional comparisons As noted above, the new tracks from Nanshuangmiao, Hebei are broadly similar to *G. ssatoi* tracks previously described from the Tuchengzi Formation of western Liaoning Province (Yabe et al., 1940; Shikama, 1942; Young, 1960) and the Houcheng Formation of Hebei Province (Young, 1960), the primary difference being the larger size of the new Nanshuangmiao tracks. However, theropod footprints that are substantially larger than *G. ssatoi* have recently been described from localities at Nanbajiazi (Zhang et al., 2004) and Sijiaban (Fujita et al., 2007) in the Tuchengzi of western Liaoning. At Sijiaban, tracks designated by Fujita et al. (2007) as "type B" have an average foot length of 13.4 cm, whereas those of "type C" have an average foot length of 16.7 cm (type A tracks are considerably smaller). Divarication angles for the Sijiaban tracks are rather large, the average values for types B and C being 37° and 46° respectively. Both types have an essentially brontozoid morphology, apart from the rela-tively wide divarication angles. Accordingly, the Sijiaban tracks described by Fujita et al. (2007), combined with the new tracks from Nanshuangmiao, increase the known size range of brontozoid or at least brontozoid-like tracks in the Late Jurassic strata of both Liaoning and Hebei provinces. The Nanbajiazi tracks briefly described by Zhang et al. (2004) may also fit a brontozoid-like pattern, although some of them display divarication angles in excess of 50°, but these tracks require more detailed description and analysis.

Other small avian and non-avian theropod tracks have also been reported from Tuchengzi strata in Liaoning Province. Matsukawa et al. (2006) mapped a total of approximately 1170 tracks, tentatively assignable to *Grallator*, at two Tuchengzi sites that were stratigraphically and geographically close to the original *G. ssatoi* locality in western Liaoning. The tracks at each site shared a common approximate orientation, as in the Nanshuangmiao tracks, and were densely packed (Matsukawa et al., 2006). Dense packing and common alignment were also characteristic of the large sample of *G. ssatoi* tracks described by Shikama (1942). Lockley et al. (2006a) described three extensive trackways of small shorebird-like avians from a Tuchengzi site at Kangjiatun in western Liaoning, and noted that small bird tracks are also known from the Houcheng of Hebei.

However, we are aware of no reports of large theropod tracks from the Houcheng of Hebei; in fact, the 28.8 cm track from the Nanshuangmiao locality is apparently the longest theropod track ever discovered in this formation. Considerably larger theropod tracks are known from the Tongfosi Formation of Jilin Province (Matsukawa et al., 1995) and the Fuxin Formation of Liaoning Province (Young, 1960). However, both of these formations are high in the Lower Cretaceous, and are therefore substantially younger than the Tuchengzi and Houcheng (Chen et al., 2006). Theropod tracks are also known from the Xiguayuan Formation of Luanping County, Hebei Province, another Lower Cretaceous unit postdating the Houcheng (You and Azuma, 1995). These tracks include a morphotype (You and Azuma, 1995: "Track B") that broadly resembles the Nanshuangmiao tracks apart from its larger size and wider divarication, in addition to a morphotype ("Track A") that is closer to the larger Nanshuangmiao tracks in size and divarication but apparently differs from them in consistently lacking a heel impression.

Elsewhere in China, theropod tracks have recently been discovered in the Middle Jurassic Sanjianfang Formation of the Turpan Basin, Xinjiang Province (Wings et al., 2007). Some of these tracks ("Morphotype B") were regarded by Wings et al. (2007) as comparable to *Grallator*, *Anchisauripus* and *Eubrontes*, although the reported angles of divarication are anomalously high for brontozoid tracks. However, this discovery shows that tracks with many brontozoid features were present in the Middle Jurassic of Xinjiang, as well as the Late Jurassic of Liaoning and Hebei provinces. Particularly because the Houcheng and Tuchengzi have yielded so few dinosaur body fossils, the recent ichnological discoveries at Nanshuangmiao and in western Liaoning provide critical clues to the nature of the dinosaurs that inhabited northeastern China in the Late Jurassic, predating the Early Cretaceous fauna known from the abundant and spectacular body fossils of the Yixian Formation.

Trackmaker behaviour Ichnology can often provide the strongest evidence for the behaviour of extinct animals, though this evidence must be interpreted with caution. The Nanshuangmiao tracks are of a reasonably uniform size (although the largest is approximately twice the size of the smallest) and orientation. Their proportions and spacing indicate that they represent at least four, and probably more, individuals. In fact, no two tracks can be confidently assigned to a single individual, preventing any analysis of gait-related parameters such as stride length. The obvious conclusion is that several animals were travelling as a group, and indeed many trackways have been used to infer sociality in various dinosaurs (e.g., see Roach and Brinkman, 2007, and references therein).

The track-bearing layer at Nanshuangmiao was probably deposited on a fluvial gravel bar, implying that the trackmakers were walking in the vicinity of a river channel. It is likely that the terrain would have restricted the animals to a limited set of paths, opening up the possibility that the Nanshuangmiao tracks represent an incidental collection of footprints produced by individuals that traversed the same route at different times. However, such an assemblage would be expected to include traces from a wider variety of taxa, and it is reasonable to attribute the Nanshuangmiao tracks to a small social group travelling as a unit. If the landscape was in fact relatively open, the inference that the trackmakers formed a cohesive group would be even stronger, since the clustering of the tracks could not then be explained as an artefact of the terrain.

The large range of body sizes that can be inferred from the tracks is perhaps unusual, but a recent paper supports the possibility of similar size discrepancies within social groups of at least one taxon (*Psittacosaurus* – Zhao et al., 2007) and other dinosaur social groups are known that include both adults and subadults (e. g. *Albertosaurus* – Currie, 1998). However, the Nanshuangmiao tracks cover a rather greater range of sizes than in these examples. It remains a possibility that the single large track was laid down by an individual of a second taxon, though the relatively conservative morphology of the prints might argue against this. Despite the theropod nature of the prints, the existence of a social group would suggest that these animals were herbivores (since in extant taxa sociality in herbivores is far more common than in carnivores) and indeed several theropod groups include taxa that are considered to be either omnivorous or herbivorous (e. g., see Barrett and Rayfield, 2006). Therefore, these prints are most likely attributable to a small group of social, herbivorous or omnivorous theropods.

Possible trackmaker identity Identifying likely or even possible trackmakers for any fossil tracks is difficult, particularly given that the trackmaking species may be unknown in the osteological fossil record. As detailed above, the animals that produced the Nanshuangmiao tracks were relatively small theropod dinosaurs from the Late Jurassic (probably the Tithonian) of China. Based on the lengths of the eight tracks that were collected by casting, and the scaling formula suggested by Henderson (2003), the average hip height of the animals was 60 cm. No precise scaling factor is available for calculating total body length as a function of either foot length or hip height. However, estimates based on published illustrations of theropods (e. g. Holtz et al., 2004) suggest that a hip height of 60 cm should correspond to a total length of approximately 2 m. Considering the total sample of tracks, including the large (28.8 cm) track collected separately, implies that the hip heights of the track makers ranged from 50 to 115 cm and that their body lengths ranged from perhaps 1.7 to 3.7 m (note that oviraptorsaurids have reduced tails).

Detailed comparisons between the Nanshuangmiao tracks and the osteological features of potential trackmakers are impractical because of the mediocre preservation of the tracks and the fact that footprints never perfectly capture pedal anatomy in any case. Fleshy pads on the foot do not necessarily display a direct or consistent relationship with the underlying bones or joints (Smith and Farlow, 2003, Milan, 2006) and apparent pads in prints may not even fully correspond to the fleshy pads (Milan, 2006). Furthermore, the prints of a single individual can vary considerably even from stride to stride.

Nevertheless, basic information about the sizes and provenances of postulated theropod trackmakers can be used to narrow the field considerably. Large theropods (e. g. spinosaurids and carcharodontosaurids) and very small theropods (e. g. compsognathids—even the largest known compsognathids, *Huaxiagnathus* (Hwang et al., 2004) and *Sinocalliopteryx* (Ji et al., 2007) from the Yixian Formation, are too small to have produced the largest of the Nanshuangmiao tracks) can therefore be excluded as possible trackmakers due to the gross incompatibility of sizes. Coelophysids were long extinct at this point, and need not be considered further. Theropods of certain other clades can be eliminated as possible trackmakers on morphological grounds-dromaeosaurs leave characteristic didactyl pes prints (Li et al., 2008), therizinosaurs have tetradactyl feet (Clark et al., 2004) and ornithomimid footprints are thought to display very high angles of digital divarication (Lockley et al., 2006b).

All of these features are incompatible with the form of the Nanshuangmiao tracks. Eliminating these various clades as candidates leaves small tyrannosaurs and oviraptorosaurs as possible trackmakers, plus a residue of less derived theropods such as ceratosaurs and basal tetanurans that retain a generalised foot morphology. No ceratosaurs have so far been described from China, but basal tetanurans, tyrannosaurs and oviraptorosaurs are all plausible on the grounds of provenance. Several relatively basal tetanurans are known from the Middle and Late Jurassic of China, and the taxa *Gasosaurus* (Dong and Tang, 1985) and *Kaijiangosaurus* (He, 1984) from the Middle Jurassic Lower Shaxiamiao Formation of Sichuan Province are only slightly too large to have left the largest of the Nanshuangmiao tracks. It is possible that the tracks were produced by unknown, smaller relatives of these basal tetanurans that survived into the Late Jurassic.

The small tyrannosaurs *Guanlong* (Xu et al., 2006) and *Dilong* (Xu et al., 2004) are respectively known from the Late Jurassic of Xinjiang Province and the Early Cretaceous dinosaur beds of the Yixian Formation. *Guanlong* is close in size to *Gasosaurus* and *Kaijiangosaurus*, whereas *Dilong* is represented by four specimens that are all apparently subadult. The holotype specimen (IVPP V 14243) probably stood about 1 m at the hip, implying that an adult would have somewhat exceeded the size of the Nanshuangmiao trackmaker. However, the existence of near-contemporary Chinese tyrannosaurs that were only slightly too large to have made the tracks suggests that a small unknown tyrannosaur would be a highly plausible candidate.

The oviraptorosaur *Caudipteryx* from the Yixian Formation (Osmólska et al., 2004), whose limb proportions suggest a hip height of approximately 60 cm (pers. obs. DWEH), is also close to the inferred size of the Nanshuangmiao trackmaker. Although no oviraptorosaur body fossils are presently known from the Jurassic, the fact that *Archaeopteryx* is a Jurassic taxon implies that Jurassic oviraptorosaurs existed as a ghost lineage and hence remain to be discovered. A Late Jurassic oviraptorosaur the size of *Caudipteryx* could have produced most of the Nanshuangmiao footprints, although possibly not the largest track on the cast (Track A). Only an exceptionally large individual of a species equal in average size to *Caudipteryx* could have produced the separate track measuring 28.8 cm. However, a mixed adult and subadult group of a slightly larger oviraptorosaur could have produced the entire sample of tracks from Nanshuangmiao.

The average longevity of a dinosaur genus has been estimated as 7.7 Ma (Dodson, 1990), and the Nanshuangmiao tracks are probably separated from both the Early Cretaceous Yixian Formation and the Middle Jurassic Lower Shaximiao by temporal gaps approaching or exceeding 15 Ma. Because of this temporal separation and the slight incompatibilities in body size, it is highly unlikely that the Nanshuangmiao trackmaker belonged to any of the genera mentioned above. However, these genera are close enough to the Nanshuangmiao trackmaker in space, time and morphology (inferred, of course, in the case of the trackmaker) to suggest that a relatively small Jurassic tyrannosaur, oviraptorosaur or basal tetanuran is a highly plausible candidate trackmaker.

Among these possibilities, an oviraptorosaur is particularly likely. There is some evidence for herbivory in oviraptorosaurs in general (Osmólska et al., 2004), and the presence of undoubted gastroliths associated with specimens of *Caudipteryx* strongly suggests a herbivorous diet. Herbivores are more likely than carnivores to travel in groups, as the Nanshuangmiao trackmakers probably were doing. It is also suggestive that *Caudipteryx* is slightly too small to have produced the Nanshuangmiao tracks, whereas other known oviraptorosaurs are generally too large. Oviraptorosaurs thus bracket the likely size range of the Nanshuangmiao trackmaker, in contrast to tyrannosaurs and Chinese basal tetanurans.

Accordingly, we suggest that the Nanshuangmiao tracks were quite likely produced by a group of subadult and adult oviraptorosaurs belonging to an undiscovered Late Jurassic taxon slightly exceeding *Caudipteryx* in size. We acknowledge that the evidence for this interpretation is circumstantial, although we believe it represents the most reasonable inference that can be made from the limited data available. Nevertheless, it remains possible that the tracks were produced by a species from an entirely different theropod clade.

Acknowledgements We are grateful to ZHOU Zhonghe for supporting this study, LI Yan and LUO Zhigang for collecting and moulding samples of the Nanshuangmiao tracks, and JIN Fan for lending us his personal copy of a volume of papers by Tokio SHIKAMA. CS and DWEH are supported by the Chinese Academy of Sciences. Fieldwork by TDC was supported by the DePauw University Science Research Fellows program, a DePauw University grant for faculty development, and a DePauw University Mellon award for faculty career enhancement. Other fieldwork associated with this project was supported by a grant from the Major Basic Research Projects (2006CB806400) of MST of China.

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