

The first sauropod trackways from China



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The first reported sauropod tracks and trackways (ichnogenus *Brontopodus*) from the Lower and Upper Cretaceous of China occur at multiple stratigraphic levels in the Jing Chuan Formation (Lower Cretaceous, Barremian–Aptian) of the Chabu area, near Otago, Inner Mongolia and in the Jiang Di He Formation (Upper Cretaceous, Turonian–Coniacian), near Kunming, Yunnan Province, People's Republic of China. Sauropod tracks at several sites are quite well preserved and reveal distinctive trackway patterns strongly suggestive of gregarious behaviour among small individuals. The trackways at both sites tend towards being slightly wide gauge with relatively large manus impressions (i.e., heteropody is not strongly developed). They are best accommodated in the ichnogenus *Brontopodus*, a senior synonym of the little-known Chinese ichnogenus *Chuxiongpus*. The co-occurrence of sauropod and theropod tracks without evidence of large ornithomimids or other ornithischians supports the suggestion that this 'saurischian' association is characteristic of many inland basins in the Cretaceous of China.

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1. Introduction

The abundance and distribution of dinosaur tracks and other fossil footprints in the Peoples' Republic of China is relatively poorly known. A recent summary (Zhen *et al.*, 1989) reported a total of only 27 sites from the entire country. No sauropod tracks were reported from any of these sites. Since that time there have been relatively few additional reports of dinosaur tracks either in the Chinese or western scientific literature (Chen and Huang, 1993; Matsukawa *et al.*, 1995; Lockley & Matsukawa, 1998). This does not mean that dinosaur tracksites are rare in China in comparison with other large areas of comparable size, for example North America (Lockley & Hunt, 1995). On the contrary, recent studies, such as this one, reveal a high density of interesting sites in relatively localized areas where arid climates produce abundant outcrops, as in Inner Mongolia. Outcrops are much scarcer in tropical southern China.

A joint Sino–Japanese–American expedition visited the Chabu area near Otago, Inner Mongolia (Figure 1), in August 2000 (see Acknowledgements). Seven

tracksites were visited during this time, all in the Lower Cretaceous (Barremian–Aptian) Jing Chuan Formation (Table 1). The majority of tracks at these sites were made by theropod dinosaurs or birds; these are being described elsewhere. The sites described herein are dominated by sauropod tracks, and it is therefore convenient to describe them separately.

We also describe another sauropod tracksite that was reported from the Chuxiong area, Yunnan Province, by Chen and Huang (1993). This site (Figure 2) was also visited by the joint Sino–Japanese–American expedition in 2001 and remapped. The Chuxiong site is important as the first Upper Cretaceous sauropod tracksite reported from China, and as the type locality for the sauropod ichnogenus *Chuxiongpus*.

2. History of discovery and research at Chinese sauropod tracksites

2.1. Chabu sites, Inner Mongolia

The Chabu area tracksites were mentioned by Zhen *et al.* (1989) in their review of Chinese dinosaur

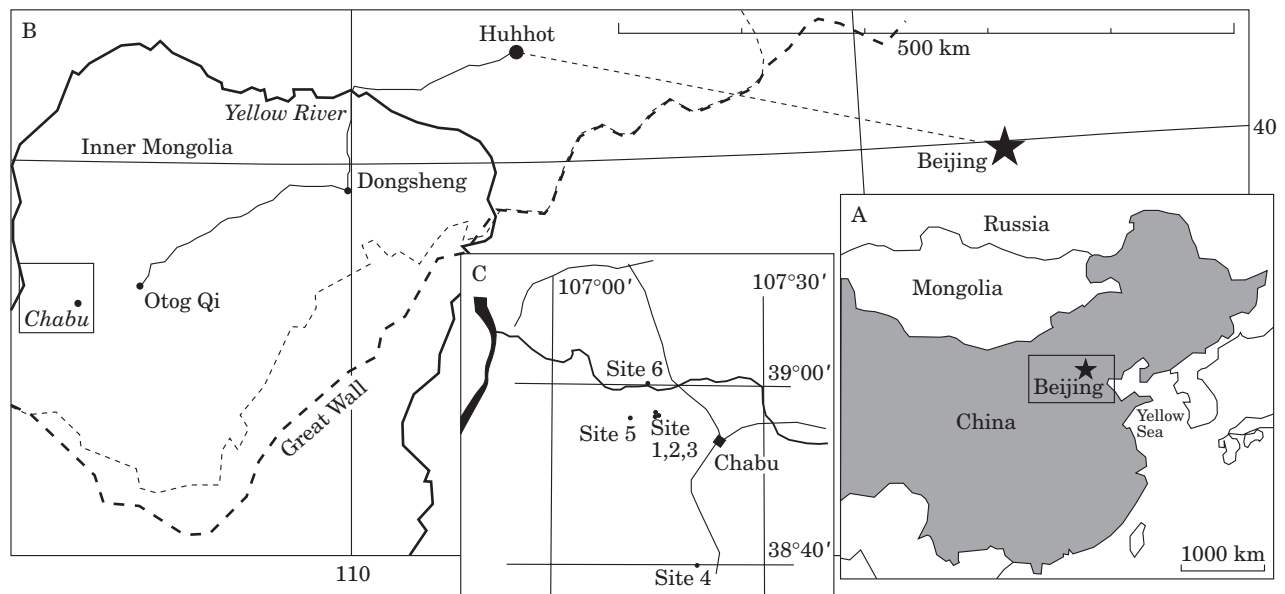


Figure 1. A, B, location of the dinosaur tracksite region in China. C, the tracksites in relation to one another.

tracksites. Only theropod tracks had been reported from the Chabu area at that time. Tracks were first reported from this area in the 1980s with rumors of a tracksite with over a thousand footprints. This site is our Chabu 7, otherwise known as the Li Rong site. There are probably fewer than 1000 dinosaur tracks at this site but many bird tracks are preserved here. The integrity of the site has been compromised by excavation of many tracks by geologists and, to date, no map of the site has been published. A few of the excavated tracks reside in the Inner Mongolia Museum at Huhhot.

In their review of dinosaur tracks from China, Zhen *et al.* (1989) noted that most dinosaur tracks from China had been attributed to theropods. They pointed out the scarcity of ornithopod tracks in Cretaceous rocks where ornithopod tracks are usually abundant, especially in Laurasia, and remarked upon the absence of sauropod tracks. This paper partially redresses the balance by showing that sauropod tracks are more abundant than previously supposed. Incidentally, the local people have known about these footprints for some time. We were taken to site number 6 by a farmer who wanted to show us his 'elephant' tracks.

2.2. Chuxiong sites, Yunnan Prefecture

Sauropod tracks were reported by Chen and Huang (1993, 1994) from the Jiang Di He Formation near the village of Yuan Ji Tun, Changlang town, Chuxiong Prefecture, Yunnan Province (Figure 2). In this paper they presented a map of the main tracksite

(which we refer to as Yuan Ji Tun site 1) in which four more or less discrete trackways were shown in association with a jumbled configuration of footprints. All the tracks were attributed to sauropods and assigned to the ichnospecies *Chuxiongpus changlingensis* and *Chuxiongpus zheni*, which we consider better assigned to the ichnogenus *Brontopodus*. Similar sauropod tracks were recorded at several other sites in the immediate vicinity, and the tracks of a bipedal dinosaur (probably a theropod) from another site, about 1.5 km to the west, were named *Yunnanpus huangcaoensis* by Chen and Huang (1993). This study is not well-known to geologists outside the local region and was unknown to us prior to 2001.

We re-examined the site in September of 2001 in order to determine the validity of the cartography and ichnotaxonomic assignments. The results were the production of a new map for the main site (as described below) and a rubber mould of a representative sauropod manus pes set for the ichnogenus *Chuxiongpus* (CU-MWC 214.28). It is outside the scope of this paper to describe all Chuxiong Prefecture sites in detail. However, a revised description of the main site is presented, and the existence of formal ichnotaxonomic names for Chinese sauropod tracks must be taken into consideration in any description or discussion of Chinese ichnofaunas.

2.3. Other sauropod tracksites

The Sino-Japanese-American expedition also visited a Lower Jurassic sauropod tracksite, with a single

Table 1. List of tracksites in the Chabu area with information on the location, ichnoassemblages and lithological composition at each site.

| Site name | Lat/Long coordinates | Elevation (m) | Stratigraphy | Lithologic description | Colour | Features | Biostratigraphy | Thickness (cm) | Source of description |
|---------------------------------|----------------------------|---------------|---|--|-----------------------------------|--|----------------------------------|----------------|-----------------------|
| Chabu 2 <i>Qi Lao home</i> | 38°54'30"N, 107°16'58"E | 1230 | ash fall in fluvial system | fine-grained light grey ash-embedded sandstone, siliceously altered. 65% quartz content, silt 5%, biotite 3–4%, mafics – angular to subangular mafic clasts. | light grey | moderate wave-length ripple marks; organic root marks; water-escape structures | theropod and sauropod | 268 | strat. column |
| Chabu 4 <i>Anubrage home</i> | 38°41'30"N, 107°20'33"E | 1402 | palaeosol sequence with intercalated erosional based flood sandstones | red–green variegated mudstones with rootlets and burrows. Green medium-grained sandstones | red–green | large water-escape structures, desiccation cracks, rootlet, burrows | theropod, bird-like and sauropod | | strat. column |
| Chabu 5c | 38°54'03"N, 107°14'06"E | 1228 | ash fall in fluvial system | med.-grained buff sandstone; clast supported; subrounded clasts, alternating with red–pale brownish mudstones and coarser-grained grey resistant sandstones | varies from buff to reddish brown | | theropod, sauropod and ostracod | 100 | strat. column |
| Chabu 6 <i>Du Situ River</i> | 38°59'23"N, 107°15'57"E | 1137 | lake-bed and playa deposits | moderately sorted medium-grained sandstone; no ash content found; clast-supported; clay matrix | yellowish grey or buff | ripple marks | theropod and sauropod | | hand sample |

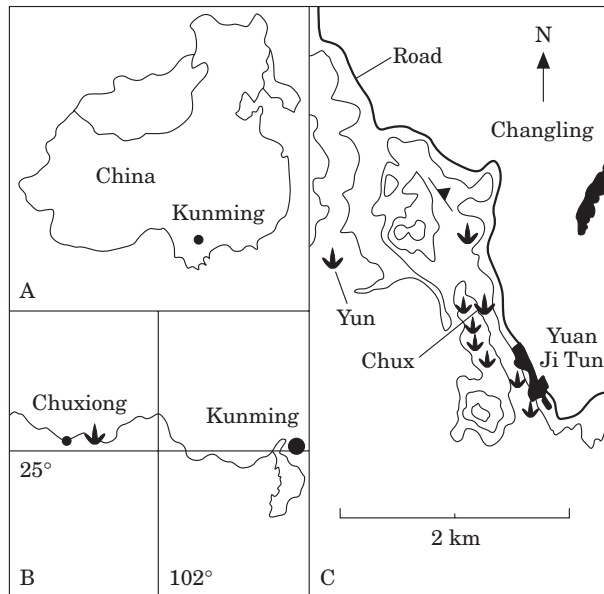


Figure 2. Location of Chuxiong Prefecture dinosaur track-sites, about 100 km west of Kunming City and Tien Chi Lake (A and B), Yunnan Province, China. C, location of *Yunnanpus* (Yun) and *Chuxiongpus* (Chux) type localities, west of Yuan Ji Tun village and Changling town. Small track symbols indicate other tracksites (see Figure 9). Road, just below 1800 m contour, marks base of hills composed of ENE dipping outcrops of the Jiang Di He Formation.

trackway, in the Zhen Zhu Chong Formation, near Dazu in the Chongqing Autonomous Region (Sichuan Basin). Tracks from this site were reported by Yang and Yang (1987) without formally naming the footprints or inferring the affinity of the track-maker. They will be described elsewhere.

This expedition also visited a Cretaceous tracksite in Emei County, Sichuan Province, from which an assemblage of small vertebrate tracks is known (Zhen *et al.*, 1994). One probable small sauropod track was noted on a small outcrop.

Newly discovered sauropod tracks were recently reported from Gansu Province, but they have not yet been described. Pictures of tracks from this site were posted on the internet in 2001 and made available to the authors (Zhang Jianping, pers. comm. 2001). After being exposed the tracks were covered again to protect them from harsh winter weather. The precise age of these tracks is not yet known.

Thus, treating the multiple Chabu and Chuxiong tracksites as representative of two single regions, we are presently aware of five regions from which sauropod tracks are known. However, the Dazu site is evidently much older than the other four, the Emei site yields very limited evidence, and the Gansu site has yet to be investigated thoroughly, or dated with

any accuracy. Thus, we focus our attention on the information available from the Chabu and Chuxiong sites.

3. Geographical and geological setting

3.1. General setting of Chabu sites

The small settlement of Chabu (38°53'41.7"N, 107°23'39.9"E) is situated about 650 km west of Beijing in the western part of the Inner Mongolian Autonomous Region (Figure 1). The elevation ranges from 1100–1400 m and the climate is arid to semi-arid. The topography is low relief and the vegetation steppe-like and subject to overgrazing.

Six dinosaur tracksites in the Chabu region were documented. These preserve bird, theropod and sauropod tracks. Sites were designated Chabu 1 through Chabu 6, and an additional large site, Chabu 7, was visited with a view to further study in the future. Specimens from an eighth site are also known; they were collected some time ago and now are in the Huhhot Museum. The sites all have local names. These are listed in Table 1, which also indicates the track types that are present, and whether single (S) or multiple (M) track-bearing levels were recorded.

All the tracksites are preserved in subhorizontal strata of the Jing Chuan Formation exposed in relatively small outcrops on the tops of hills or in dry river valleys. Rock exposure is frequent and fairly extensive so there is potential for more tracksite discoveries.

The track horizons occur within clastic, fluvio-lacustrine sequences consisting of interbedded light grey and buff coloured sandstones (with volcanoclastic components, i.e., ash) and variegated, red–green siltstones and mudstones with varying degrees of palaeosol development. Wave ripple marks and high concentrations of 'shorebird' or 'shorebird-like' tracks suggest sedimentary regimes with lacustrine or flood-plain deposition. The presence of *Darwinula* ostracods at the top of the stratigraphic section at Chabu 5 indicates an ephemeral lake and semi-arid conditions.

During the Early Cretaceous the southeastern and northwestern regions of China were uplifted, causing a significant reduction in the area of inland basins and the disappearance of some rivers (Chen Peiji, 1986). This uplift was accompanied by volcanic eruptions, which produced the ash found in many of the sedimentary horizons in this area. Deposition at this time was mainly in large ephemeral, shallow, freshwater lakes which were fed by intermittent shifting streams in a semi-arid climate.

All tracksites are preserved in similar lithologic settings: laminated to massive mudstones interbedded

with channel or crevasse-splay sandstones. The dominant lithology is light grey and buff-coloured, moderately sorted sandstone with localized beds of siltstone, mudstone, and channel deposits, often with palaeosol profiles. Sandstones contain calcareous cement and are dominated by ripple marks. Several of the sections contain finely sorted, laminated, ash-flow deposits suggesting nearby volcanic sources that erupted repeated sequences of ash. The ash was then carried by fluvial systems and deposited nearby, helping to preserve the fossil footprints. Varicoloured mudstones, stream channel sandstones, and conglomerates also make up the distinctive lithologies of the sections studied.

Chabu 2. This section consists mainly of red to green/grey mudstones interbedded with several siliciclastic layers which contain the footprint horizons (Figure 3). The sandstones are fine- to coarse-grained, light greyish-green ash-embedded sandstone with silty lenses altered by siliceous diagenesis in a fluvial system. Most of the grains are quartzitic (>65%), 5% biotite, and 3–4% angular to subangular mafic clasts. The overall colour index is leucocratic. Theropod tracks can be seen along the lower portion of the stratigraphic level in coarse buff-coloured sandstone. Reddish-purple palaeosols are present, followed by vertical burrows or roots in an ashy sandstone layer. Towards the top of the section sauropod and theropod tracks are preserved in sandstone with silty-ash lenses, and near the top large theropod tracks are preserved on a surface with moderate-length wave ripple marks (Figure 3).

Chabu 4. The first 4 m of this measured section (where the footprints occur) are very poorly exposed (Figure 3). The upper part of the section is composed of a series of red and green mudstones with burrows and rootlets, intercalated with medium-grained greenish to grey quartzitic sandstones. This is interpreted as a floodplain palaeosol sequence interrupted by occasional sheet flood sandstones. The only exposed lithologies in the lower 4 m are sandstones, and it seems likely that the unexposed portions are palaeosol mudstones. There are two, possibly three, footprint horizons; bird footprints are preserved at the top of a fine-grained sandstone bed, and on the top of the overlying bed, a coarse grained sandstone, theropod footprints are preserved.

Chabu 5. The basal part of this section is the lower footprint horizon with theropod and ‘bird-like’ tracks. River muds covering the bedding plane are overlain by the pale blue-green and purplish-red mudstone

sequences that dominate this section (Figure 3). These mudstones are intercalated with layers of ashy fine-grained fining-upwards sandstones. Channel beds cut through sections of pale brown and blue laminated layers of sandstones. Greenish-grey tinged ashy siltstones also alternate between mudstone layers. Resistant layers of grey sandstone are found toward the top of the section. Sauropod and theropod tracks are preserved near the top of the section in a subrounded clast-supported buff-tan sandstone. Above this track horizon, more alternating layers of red to pale brown and blue-tinged mudstone layers cover the sauropod and theropod track horizon. In close proximity to the top layer, but not found *in situ*, is a coquina of the ostracod *Darwinula simplus*.

Chabu 6. No rocks above the track horizon were exposed in this area. This site was on the banks of the Du Situ River and the section below this surface could not be measured as the bed was falling into the river. Sauropod and theropod tracks are well preserved as natural moulds in moderately-sorted, medium-grained sandstones with subrounded clasts in a clay matrix. This sandstone does not contain any ash. Medium-energy wave ripple marks are preserved in the sandstone bedding plane between the tracks.

In summary, the close similarity of the lithologies, facies types, and fossil footprint assemblages implies that all the Chabu sites are part of the same system, a floodplain sequence containing volcanic ash and with considerable pedogenic development. The sediments and structures indicate subaqueous deposition in a fluvio-lacustrine system with long periods of subaerial exposure.

3.2. Stratigraphy of Chabu sites

The Jing Chuan Formation is part of the Zhidan Group and is late Early Cretaceous in age. Relative dating for the Jing Chuan Formation is based on ostracod zones, which give an age of late Barremian–early Aptian (Qi *et al.*, 1986; Keiichi Hayashi, Konan University, Kobe, Japan, pers. comm. 2001). Fossils found in the Jing Chuan Formation, include the following spores and pollen grains: *Cicatricosisporites*, *Concavissimisporites*, *Cycadopites*, *Densoisporites*, *Klukisporites*, *Piceapollenites* and *Schizaeoisporites*. Among the ostracods encountered are: *Cypridea koskulensis*, *C. (Pseudocypridina) aff. globra*, *Darwinula simplus*, *Lycopteroocypris infantilis* and *Mongolianella palmosa*.

3.3. Context of the Chuxiong sites

The Chuxiong sauropod tracksites are associated with a sequence of red terrigenous clastics of the Jiang Di

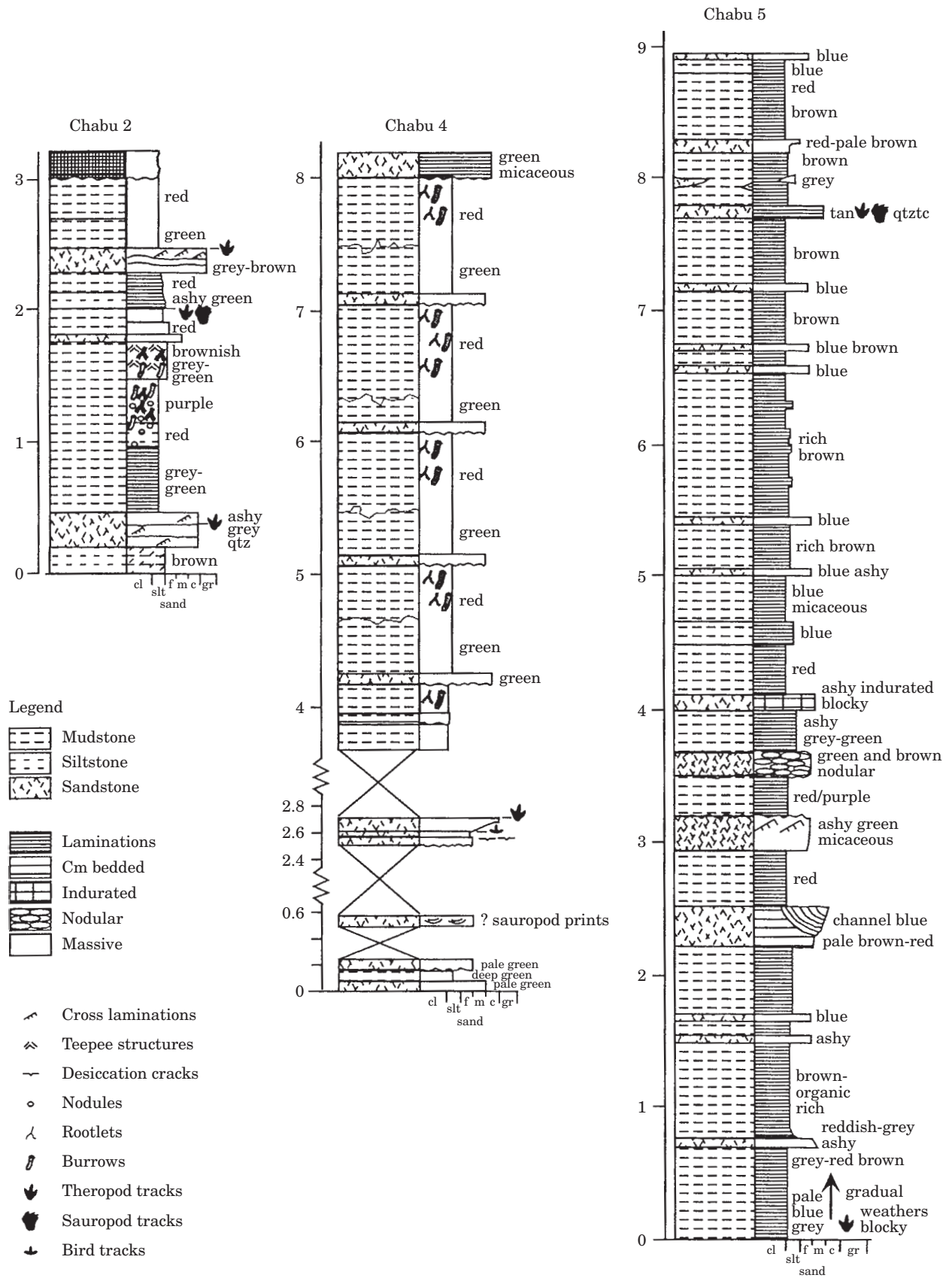


Figure 3. Stratigraphic sections of the Chabu 2, 4 and 5 sauropod tracksites, Inner Mongolia; qtz, quartz; qtztc, quartzitic.

He Formation that form a series of eastward dipping red sandstone outcrops in the hills just west of the village of Yuan Ji Tun, 25° 02' 482"N, 101° 40' 062"E (Figure 2). The terrain is well vegetated and deeply weathered under a humid subtropical climate. Chinese scientists infer that the formation is Upper Cretaceous (Turonian–?Coniacian) based on spores and pollen and invertebrate faunas (ostracods and conchostracans: Chen, 1996). The Jiang Di He Formation conformably overlies the Ma Tou Shan Formation. This contains the conchostracan *Nemesteria*, which is known from the Cenomanian of Texas (Zhou & Chen 1992). In addition, the Chinese dictionary of geological formations (Hao *et al.*, 2000) lists the Jiang Di He Formation as K3 (i.e., Coniacian–Maastrichtian) in their three part division of the Cretaceous (K1–K3). Fossil recovered from the Jiang Di He Formation include the spores and pollen grains: *Cicatricosisporites*, *Echinatisporites*, *Ephedripites*, *Pinuspollenites*, *Psophosphaera*, *Schizaeosporites*, *Tricolpites* and *Triporopollenites*, and the conchostracans *Aglestheria* and *Halyssestheria*.

In addition, during our visit to the site, Dr Keiichi Hayashi obtained the ostracods *Darwinula oblongata*, *D. leguminella*, *Ecypris* cf. *anluensis* and *E.* cf. *debiloides*, indicative of a Late Cretaceous age.

The track-bearing beds consists of a monotonous series of fine-grained sandstones, siltstones and mudstones with small scale wave ripples (wavelength 5–6 cms) and mud cracks. In addition to the main sauropod tracksite (described below), which occurs high stratigraphically in the top of the exposed sequence just west of the village, there are a number of additional tracksites at approximately this same stratigraphic level just south of the main site. These yield only sauropod tracks (ichnogenus *Chuxiongpus*). Further to the west, and lower in the stratigraphic sequence, there are a number of other poorly exposed tracksites, including the type locality for the dinosaur (theropod) ichnospecies *Yunnanpus huangcaoensis* (Chen and Huang, 1993). This trackway is poorly preserved and cannot be used for detailed comparisons with other theropod trackways. The ichnospecies name is, therefore, best regarded as a *nomen dubium*.

4. Methods, specimens and data repository

All sites of any size in the Chabu and Chuxiong regions were mapped using chalk grids laid out with tape and compass. Wherever possible, stratigraphic sections above and below the track horizons were measured (Figure 3).

Representative examples of well-preserved tracks were measured, photographed, and traced, using

acetate film overlays. Latex molds were made of some of these well-preserved tracks. For the Chabu sites, a total of 21 tracings (T 486–506 in the CU Denver catalog) and 19 latex molds were made (CU-MWC 214.1–214.19: abbreviation refers to the joint University of Colorado at Denver-Museum of Western Colorado collection). Only one latex mould (CU-MWC 214.28) and five tracings (T 584–585 and T 589–591) were made at the Chuxiong sites. Copies of representative molds were cast in plaster of Paris and distributed to the Otog Qi Museum, the Inner Mongolia Museum in Huhhot, the Beijing Natural History Museum, and Tokyo Gakugei University, Japan. Tracings were also shared with these institutions.

5. Description of the main sauropod tracksites

5.1. The Chabu sites

The main sauropod tracksites in the Chabu area are sites 5 and 6. Isolated rounded depressions were observed at sites 2 and 4; these may be sauropod tracks or trampling, based on the sizes and shapes of the indentations. The sauropod tracks are associated with large theropod tracks at all sites and with bird tracks at Chabu sites 4 and 5. Multiple track-bearing levels were recorded at all sites except Chabu 6. The sites with the best preserved trackways are described first in the following account.

Chabu 6 (Du Situ River). This preserves at least four discrete sauropod trackways heading in approximately the same direction, towards the NE (Figures 4 and 5). The trackways are associated with large theropod tracks. They are preserved as natural moulds in a light grey, moderately sorted medium to coarse-grained sand, infilled by dark grey, ashy, clast-supported muddy sandstone. All of the tracks are deeply impressed (30–45 mm) and some of the tracks, both theropod and sauropod, show considerable morphological detail.

The site is on the bank of the river, on the outside of a meander and is being undercut and eroded; parts of the tracksite were falling into the river. Most of the site was covered by wind blown and river transported sand. We excavated the 17 × 2 m (34 m²) exposure using shovels, then cleared out the tracks with brooms (Figure 5). Some of the tracks could be seen disappearing beneath the sand cover so more tracks would be uncovered by further excavation.

The sauropod tracks at this site are all very small for sauropods; pes lengths range from 21–34 cm

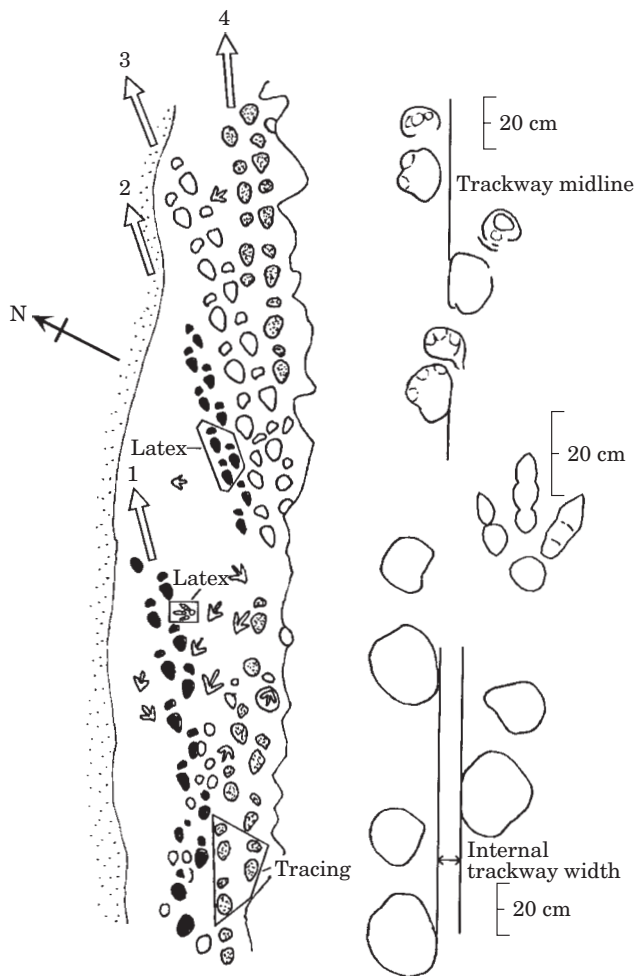


Figure 4. Map of the Du Situ River (Chabu 6) sauropod tracksite; note the preferred orientation of trackways towards the NE.

(Table 2). The manus impressions are relatively large, 14–23 cm wide, up to half the area of the pes impressions. The pes impressions are toed outwards at an angle of 15–30 degrees to the trackway axis. The

manus impressions fall slightly in front of and outside the pes impressions. There is little overstepping (i.e., pes on manus overlap) in these trackways. The trackways are fairly long, up to 25 manus-pes pairs (Figure 4), although the longest consecutive, clearly defined trackway section is nine manus-pes pairs (Table 2). This is because at the centre of the exposed area there is a break in the trackways. It seems likely that Trackway 3 or 4 extends from one end of the tracksite to the other but it curves slightly over the eroded part of the tracksite so that the middle part of this trackway is no longer present.

The best preserved trackway is Trackway 2, which is the only one that seems to show internal morphological detail (Figure 6). Some footprints of trackway 2 (Figures 4, 6A) show indentations within the footprint. The indentations are in the antero-lateral part of the footprints, in both the manus and pes. They correspond to the predicted positions of pes digits I, II, III and maybe IV, and the manus indentations may correspond to manus digits I, II and III or possibly II, III and IV. Indentations associated with the predicted positions of both digits I and II occur in three consecutive footprints in the left-right-left (L-R-L) sequence illustrated in Figures 4 and 5. Footprints on the left side of this sequence appear to be more completely and consistently preserved, showing lateral impressions that evidently correspond to digits III and/or IV. The lack of sharp claw impressions may suggest that all the digits had blunt pads or callosities on their plantar surfaces, and any claws may have been enclosed by flesh or held in such a way that their sharp distal ends did not leave impressions. There are impressions of what may have been sharper, terminal claws on the ungual phalanx of digits I and II in the first, left pes track in this sequence but not in subsequent tracks. They may be extra-morphological features unrelated to the tracks, or the narrow claw impressions may have collapsed in on themselves after



Figure 5. Photograph of the sauropod tracks at Chabu 6 on the banks of the Du Situ River.

Table 2. Sauropod trackway dimensions at Chabu 6 site.

| | Pes Tracks | | | | Manus Tracks | | | |
|------------------------------|------------|------|-------|------|--------------|-------|-------|-----|
| | FL | FW | PL | SL | L | W | PL | SL |
| Chabu 6, sauropod trackway 1 | | | | | | | | |
| 1 | 32 | 25.5 | 61 | 101 | 19 | 20 | 58 | 103 |
| 2 | 31 | 26 | 51 | | 18.5 | 22.5 | 68 | |
| 3 | 30 | 23 | | 101 | 18 | 18 | | 107 |
| 4 | | | | | | | | |
| 5 | 30 | 25 | 63 | 113 | 20 | 22 | 60 | 113 |
| 6 | | | 66 | | | | 63 | 110 |
| 7 | | | 66 | 59 | | | 61.5 | 58 |
| 8 | | | 55 | | | | 44 | |
| 9 | | | 62.5 | | | | | |
| Av | 30.8 | 24.9 | 60.64 | 93.5 | 18.9 | 20.63 | 59.08 | 98 |
| Chabu 6, sauropod trackway 2 | | | | | | | | |
| 1 | 22 | 18 | | 40 | 130 | 175 | | 49 |
| 2 | | | | | | | | |
| 3 | 22 | 18 | | | 100 | 135 | | |
| Av | 22 | 18 | | 40 | 115 | 155 | | 49 |
| Chabu 6, sauropod trackway 3 | | | | | | | | |
| 1 | | | 59 | 104 | | | 59 | 98 |
| 2 | 34 | 29 | 56 | 103 | | | 64.5 | 107 |
| 3 | | | 65 | 100 | | | 69 | 109 |
| 4 | | | 58 | 108 | 13 | 22 | 64 | 108 |
| 5 | 33.5 | 24 | 60 | 102 | 17 | 23 | 63 | 96 |
| 6 | | | 52 | 93 | | | 64.5 | |
| 7 | 33 | 29 | 55 | | | | | |
| Av | 33.5 | 27.3 | 57.86 | 102 | 15 | 22.5 | 64 | 104 |
| Chabu 6, sauropod trackway 4 | | | | | | | | |
| 1 | | | 40 | 75.5 | | | 43 | 74 |
| 2 | | | 46 | 87 | | | 41 | 88 |
| 3 | 30 | 24 | 43 | 83.5 | 183 | 195 | 44 | 82 |
| 4 | | | 42 | | | | 46.5 | |
| 5 | | | 37.5 | | | | 48 | |
| 6 | | | 43 | 75 | | | 48.5 | 76 |
| Av | | | 41.92 | 80.3 | | | 45.17 | 80 |
| Chabu 6, sauropod trackway x | | | | | | | | |
| 1 | | | 56 | 102 | | | 56 | 105 |
| 2 | | | 61 | 108 | | | 68 | 109 |
| 3 | | | 57 | 97 | | | 58 | 96 |
| 4 | 28.5 | 22 | 56 | 103 | 20 | 20.5 | 50 | 107 |
| 5 | 32 | 25 | 59 | 105 | 18 | 20 | 62 | 107 |
| 6 | 34 | 23 | 56 | | 15 | 18 | 53 | |
| Av | 31.5 | 23.3 | 57.5 | 103 | 17.7 | 19.5 | 57.83 | 105 |

the foot was withdrawn, and thus not have left an impression in the other tracks.

The two left manus impressions in this track sequence show three subequal, rounded indentations that may be the impressions of digits II, III and IV. In the first manus in this sequence there is a posteriorly

directed groove or indentation that may be the trace caused by digit I (possibly in forward motion, rather than during a downward or vertical registration). It is notable that this small trackway (2) is essentially narrow gauge. By contrast slightly larger trackways (e.g., 4) are wider gauge (Figure 6). All trackways appear to indicate animals that were walking at similar speeds (i.e., between 1.8 and 2.5 m/sec or 0.5–0.7 km/hr), using the well known formula of Alexander (1976). The size range suggests that all the animals were juveniles or subadults travelling as a gregarious group (see discussion).

The Chabu 6 trackways are among the best preserved sauropod tracks known from China. They are dominated by the tracks of small individuals, the smallest of which has a pes foot length of less than 21 cm and an estimated gleno-acetabular length of about 60 cm. Gleno-acetabular length is most easily estimated by measuring the distance from the mid point between two consecutive hind footprints and the midpoint between the two manus footprints that are in front of the anteriormost of these two hind footprints (Leonardi, 1987). This essentially gives an approximation of the distance between the midpoints of the pelvic and pectoral girdles of the animal.

Apart from their small size these tracks conform very closely to typical sauropod tracks such as *Brontopodus birdi* (Farlow *et al.*, 1989). They have ovoid pes impressions and horseshoe-shaped manus impressions. Comparison of these tracks with the osteological remains of dinosaurs shows that only sauropods could have made such tracks; other quadrupedal dinosaurs have relatively longer toes which leave discrete impressions. Claw impressions have not been preserved in most of the Chinese tracks described herein. The lack of definition of the individual toes of both manus and pes, and the shapes of the tracks, are typical of sauropod tracks. Inner trackway width (the space between the inside of pes tracks; Figure 6) in these trackways is of the wide gauge type, which is again like *Brontopodus birdi*, and has been interpreted as typical of titanosaurid sauropods (Lockley *et al.*, 1994a, 2002; Wilson & Carrano, 1999).

All four sauropod trackways at Chabu 6 trend in the same direction. In the western part of the tracksite, trackway 1 and trackways 2 and 3, or possibly 4, criss-cross one another, and the preservation is such that the order in which all the animals traversed the site could not be determined with confidence. In the eastern half of the site trackways 2, 3, and 4 run parallel to one another, although the apparent absence of the proximal part of trackway 4 may indicate that its trackmaker was in front of the maker of trackway 3. If the small jumbled tracks in the western half of the

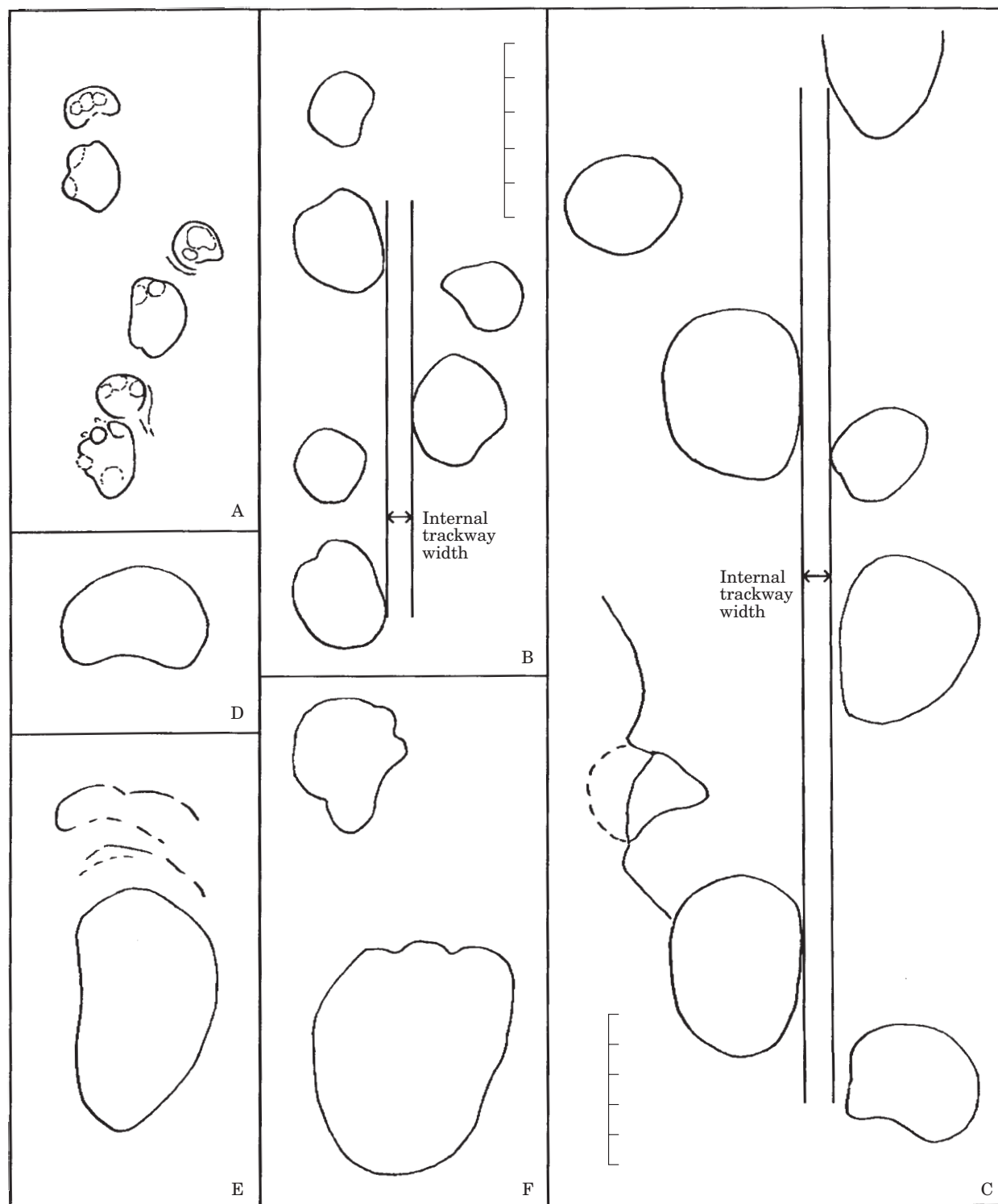


Figure 6. Comparison of sauropod tracks and trackways from the Chabu 5 (A and B) and Chabu 6 (C-F) sites. All drawn from tracings except C; see text for details.

tracksite are the proximal part of trackway 2, and the larger tracks the proximal part of trackway 3, then all the trackways would seem to be turning at about the

same point. In addition, the indistinct nature of the trackways in this part of the site is likely to be a result of subsequent trampling by other animals. This means

that the order of the trackways can be tentatively reconstructed. Trackways 2 and 4 were made before trackway 3, although the relative timing of 2 and 4 cannot be determined as they do not cross. The apparent simultaneous turning of all trackways, with the possible exception of trackway 4, is a strong indication of gregarious behaviour, so it may be assumed that all four trackways were made at almost the same time. The similarity in preservation quality and depth of all the trackways supports this conclusion. The theropod tracks do not show any preferred orientation, so a geographic explanation (e.g., lake shoreline) for the sauropod directional trend seems less likely than gregarious behaviour.

The makers of these trackways would have been fairly small individuals, with hip heights of about 1.5–1.8 m (Thulborn, 1990). This would correspond to a length of 7–9 m depending on whether the trackmakers were camarasaurids, diplodocids or titanosaurids. This is small for sauropods and so the makers of these trackways were probably juveniles. Other sauropod tracksites have shown gregarious tendencies for sauropods (Lockley *et al.*, 1994b; Farlow *et al.*, 1989) and footprint size ranges are not generally very great, i.e., the sizes of individuals within a group is fairly limited. Perhaps the sauropod tracksite with the greatest individual size range is that of Glen Rose in Texas where the estimated length of the footprints ranges from 35–78 cm (Lockley 1987).

Chabu 5. This is a larger site than Chabu 6 and preserves tracks of larger animals. It is beside a dry river gully and the cliff exposes a continuous stratigraphic section. The sauropod track horizon occurs 8 m stratigraphically above a theropod tracksite. At this site there are two track-bearing levels in a measured stratigraphic section of 9 m (Figure 3). In contrast to Chabu 6 all the tracks known from the Chabu 5 site represent large animals (pes length 60 cm or more).

Only one clear trackway was recorded, at the lowest stratigraphic level examined. It is moderately wide gauge (Figure 6C) with a pes foot length of about 60 cm (width about 50 cm) and a manus foot length and width of at least 25–35 cm respectively. Although the outlines of the tracks are clear it is possible that the tracks may have been slightly enlarged by erosion, since the trackway is situated on a bedding plane in the floor of a dry wash.

Other sauropod tracks from the Chabu 5 site are all associated with the upper track-bearing level (Figures 3, 7), where more than 50 more or less randomly-distributed tracks have been identified, 49 of which are shown on a simple sketch map (Figure 7) which

covers an area of approximately 120 m². Two tracings were obtained from this area. The first is of a probable right pes-manus set (Figure 6E) where the pes is about 70 cm long and 38 cm wide, with the probable manus partly obscured by the mud rim at the anterior margin of the pes. The second, a probable left manus-pes set, has a pes about 70 cm long and 50 cm wide with three blunt, rounded indentations associated with the anterior margin. The manus is about 35 cm wide and 30 cm long and is semicircular–slightly crescentic in shape, as also seen in another isolated manus (Figure 6D) that measures about 40 cm wide and 30 cm long. Many of the tracks at this level are quite deep with prominent sediment rims. However no discrete trackways could be identified. Probably the orientation of the tracks (Figures 6E, F) towards the north is reflected in several of the other pes tracks which appear to have their long axes aligned approximately north–south (Figure 7).

5.2. The Chuxiong sites

The main Chuxiong tracksite at Yuan Ji Tun village (Figure 2) is located inside a protective fence (Figure 8). The site was re-mapped during our 2001 study (Figure 9) and reveals the presence of at least ten recognizable trackways (designated A–J). This is in contrast to the illustrations presented by Chen and Huang (1993), which indicate only four clear trackways against a background of footprints that had not been resolved into recognizable trackways. The tracks are all relatively small. With the exception of trackway D all pes-track lengths range from 28 to 39 cm (Table 3). It is also possible to differentiate between hind and front footprints and even, in some cases, discern traces of pes claw impressions (Figure 10A).

It is also clear that at least eight of the ten trackways are associated with a bimodal NNW–SSE trend, i.e., trackways B, C, E, F and H are oriented between azimuth 330–320° while A, D and G have azimuths between 137° and 160°. Only trackways I and J (20–36°) run approximately perpendicular to this trend. Such orientations are suggestive of gregarious behaviour, but may also indicate shore-parallel progression, given that wave ripple crests are typically oriented from 140–320°. Speed estimates for the trackways, using the formula of Alexander (1976) indicate slow progression in the range of 0.7–1.2 m/sec or 2.52–4.32 km/sec.

Based on tracings of trackways from this site (Figure 10A) and adjacent localities (Figure 10B, C) it is possible to infer that the sauropods were wide-gauged, though the internal trackway width is somewhat variable. It is also evident that the manus is

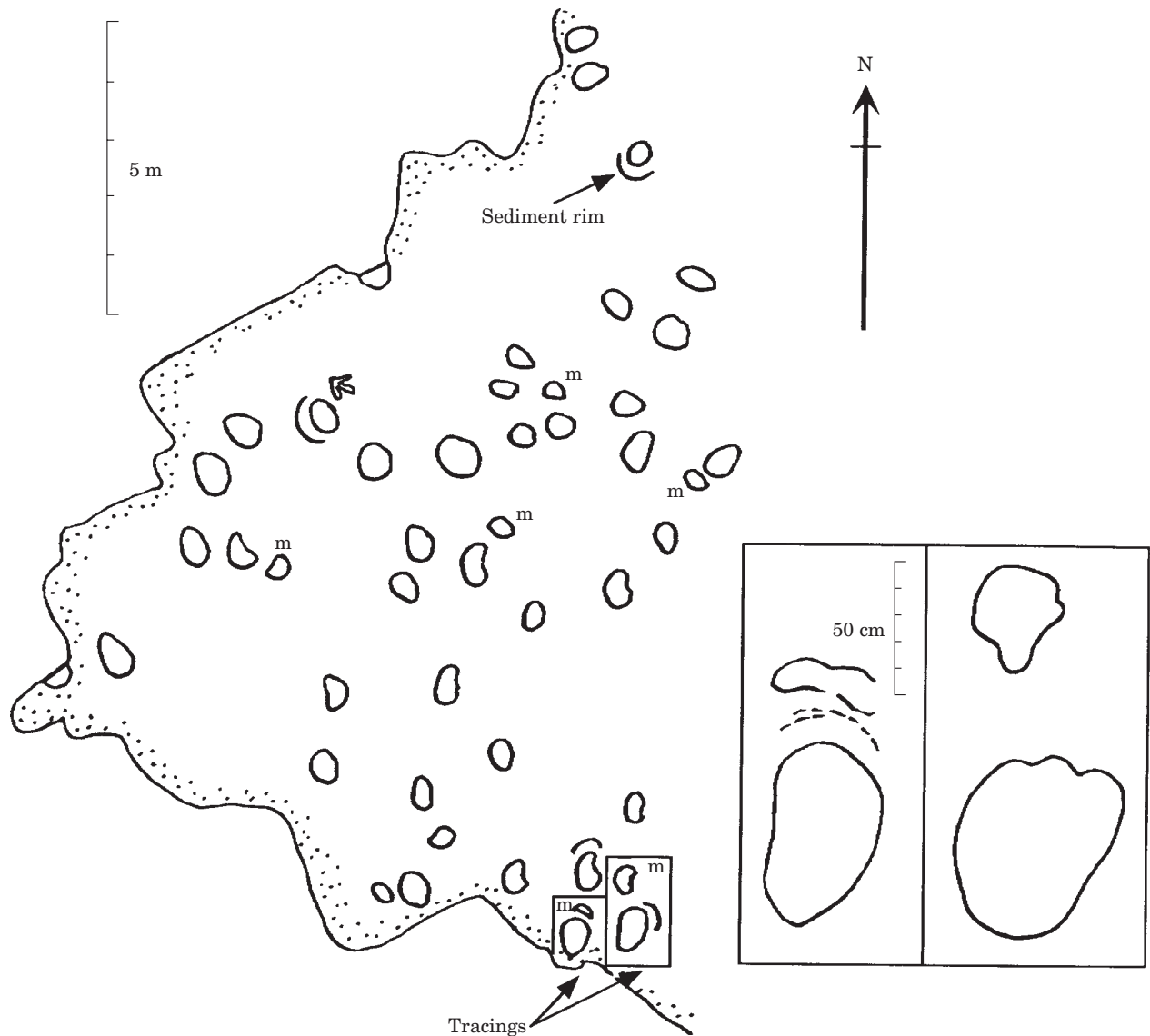


Figure 7. Map of the Chabu 5 sauropod tracksite (upper level); m, probable manus tracks.

relatively large, i.e., up to about half the size of the pes in cases where it is not distorted by the registration of the pes. For example the average manus/pes ratio for trackway B (Figure 8) is 1:2.9 (range 1:2.6–1:3.0). Similarly, the average ratios for two other well-preserved trackways from a nearby site (Figures 10B and C respectively) are 1:2.2 and 1:2.4 (ranges 1:1.9–1:2.3 and 1:2 and 1:2.9 respectively). Thus the average ratio for all three trackways is about 1:2.5.

These important details of manus/pes ratio, or heteropody, are not available from the original descriptions of the two *Chuxiongpus* ichnospecies (Chan and Huang, 1993). However, such information is very important for making comparisons of these sauropod trackways with those found in Chabu and other

regions. Without such observations ichnologists cannot assess the utility of the formal ichnotaxonomic names that have been proposed. This problem is considered in the following section.

6. Ichnotaxonomy

6.1. Ichnotaxonomic background

Chuxiongpus changlingensis and *C. zheni* are the only sauropod tracks from China that have been formally named. As indicated in the previous section, they represent wide-gauge trackways. As such they can be compared with *Brontopodus birdi* from Texas (Farlow *et al.*, 1987), the first-named and best-preserved

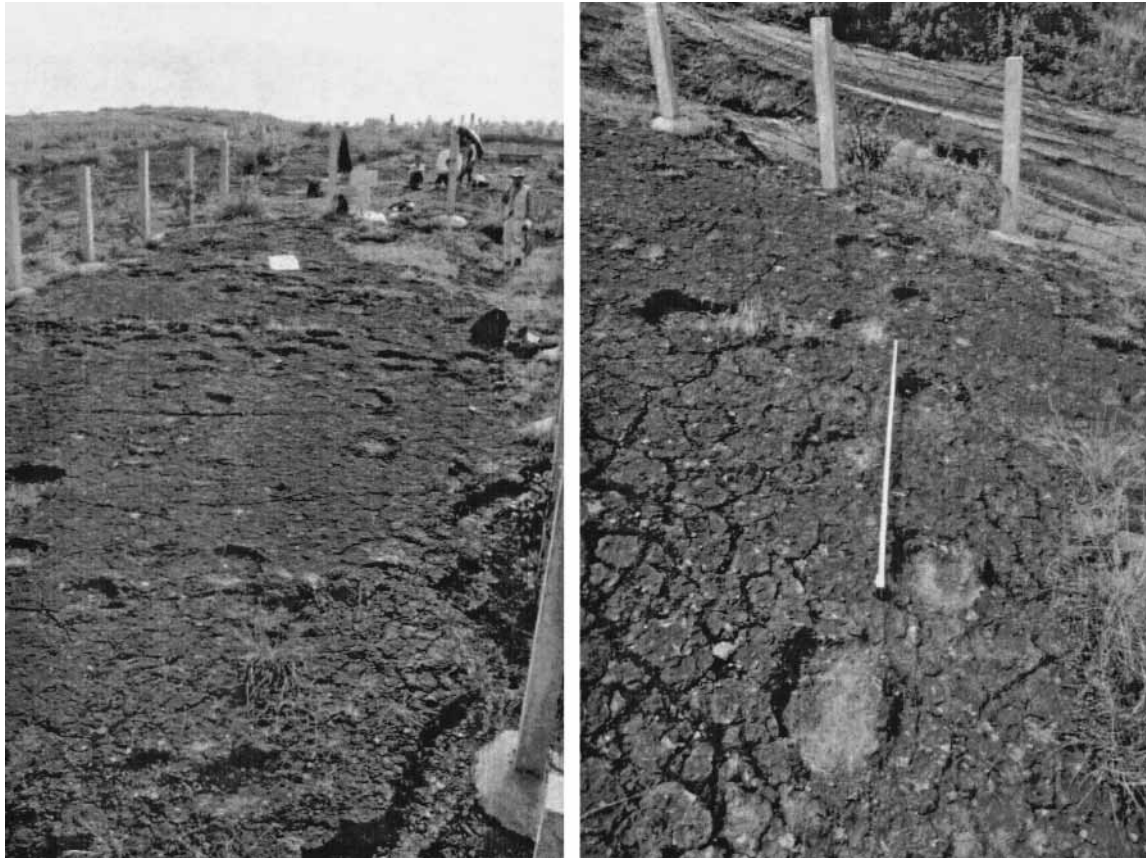


Figure 8. Left, photograph of main ‘*Chuxiongpus*’ tracksite looking west; right, detail of trackway B, direction of progression away from camera. Compare with Figure 9.

example of a diagnostic, wide-gauge, relatively large-manus sauropod trackway from the Cretaceous. Few well-preserved sauropod trackways were named prior to 1987, and among these few, none can be considered adequately described examples of wide-gauge, large-manus Cretaceous sauropod trackways (Lockley *et al.*, 1994a). Indeed many Jurassic sauropod trackways are narrow gauge with a small manus.

Thus the question arises as to whether the *Chuxiongpus* is sufficiently distinct from *Brontopodus* to warrant the erection of a separate ichnogenus. A related issue is whether the Chuxiong Province material warrants the naming of two ichnospecies. In our opinion the differentiation is not warranted in either case. We therefore propose that *Chuxiongpus* is a junior synonym of *Brontopodus* and that the latter named ichnospecies (*C. zheni*) is a junior synonym of the former. Because there are minor morphological differences between the type material of *Chuxiongpus* and *Brontopodus*, we consider it appropriate to differentiate the Chinese and Texan material, but only at the ichnospecies level. The following formal ichnotaxonomic amendment of the Chinese ichnotaxa

under the single ichnospecies *Brontopodus changlingensis* comb. nov. reflects this rationale. Although no new ichnotaxon is erected, the existing ones are combined and defined more carefully in comparison with others. We stress that the previous descriptions of *Chuxiongpus* were inadequate because they were not based on complete trackway descriptions; rather they were based on manus and pes sets that were distorted by overlap (Chen and Huang, 1993, 2–5). Such incomplete descriptions fail to conform to the guidelines recommended for the formal description of new ichnotaxa (Peabody, 1955; Sarjeant, 1989).

6.2. Formal ichnotaxonomy

Class: Reptilia
Order: Saurischia
Suborder: Sauropoda
Ichnogenus *Brontopodus*

Brontopodus changlingensis comb. nov.
Figures 9, 10

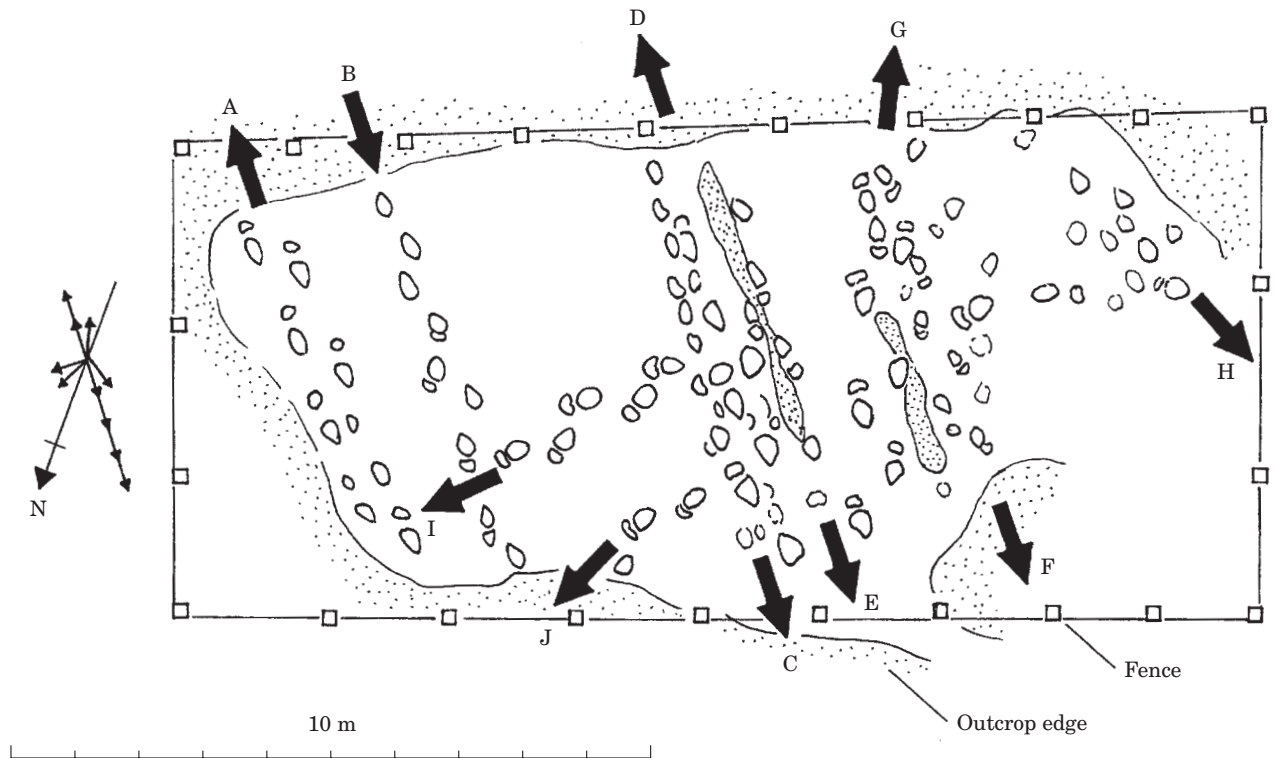


Figure 9. Map of main ‘*Chuxiongpus*’ sauropod tracksite, Yuan Ji Tun village area, Chuxiong Prefecture, Yunnan Province. A–J represent individual trackways, with direction of progression, see rose diagram (left) and Table 3. Protective fence (with square posts) and outcrop edge also shown.

Synonyms. *Chuxiongpus Changlinensis* (Chen & Huang, 1993, 1994); *Chuxiongpus Zheni* (Chen & Huang, 1993, 1994).

Holotype (for *C. changlinensis*). Uncertain; designated by Chen & Huang (1993) as specimen CYCD-09 FP8. CYCD prefix obscure, refers to mapping serial numbers: C, Changling town; Y, Yuanzhen, a local locality name; CD, indicates local Chinese pronunciation. FP8 probably refers to footprint 8. Redesignated here as trackway J (Figure 10A). Manus pes replica CU-MWC 214.28 replica from same trackway.

Paratypes CYCD 04 and undesigned specimens recorded as T. 590–591 (Figures 10 B, C).

Type locality. Main site at Yuan Ji Tun village, near Changling town.

Description. Trackway of sauropod with oval pes about twice as large and long as transverse manus. Long axis of pes rotated outwards at about 30° from trackway axis. Trackway slightly wide gauge with internal trackway width 5–15 cm approx. Pes elongately-oval with heel narrower than anterior part; length varies from c. 28–47 cm in the type sample (Table 3). Indistinct

pes claw impressions preserved in some trackways. Manus semicircular to crescentic, wider than long, varying from 17–24 cm (Table 3). Pes area averaging 2.5 times that of manus.

Discussion. Since *Brontopodus birdi* was named on the basis of well-preserved trackways from Albian carbonates from Texas, ichnologists have generally been cautious in the naming of sauropod trackways. Given that few well-preserved trackways have been discovered that are significantly different morphologically from *Brontopodus*, this caution is justified. For example, the large sample of at least 120 trackways from the Lower Cretaceous of South Korea has so far been accommodated informally under the label *Brontopodus* (Lim *et al.*, 1994). We therefore argue that the naming of two ichnospecies in the ichnogenus *Chuxiongpus* (Chen and Huang, 1993) was unjustified as it created a junior synonym of *Brontopodus* (Farlow *et al.*, 1989). In suppressing *Chuxiongpus* and re-describing the type material in more detail we simplify the previously misleading ichotaxonomy and also emphasize the relationship and potential for careful comparison between Cretaceous sauropod tracks in China, Korea, North America and elsewhere.

Table 3. Sauropod trackway dimensions at Yuan Ji Tun site.

| Trackway | | Pes | | Manus | | Pace | Stride | Internal Trackway width | Direction |
|----------|---|-----|----|-------|----|------|--------|-------------------------|-----------|
| | | L | W | L | W | | | | |
| A | R | 38 | 26 | 17 | 24 | | | 15 | 137 |
| | R | 37 | 28 | 16 | 19 | 93 | 156 | | |
| | L | 36 | 27 | 18 | 18 | 93 | | | |
| | R | 35 | 26 | 12 | 20 | | | | |
| B | L | 32 | 26 | 14 | 20 | 78 | 130 | 10 | 320 |
| | R | 31 | 24 | | | 78 | | | |
| | L | 30 | 23 | | | | | | |
| C | R | 28 | 20 | 15 | 21 | | 117 | | 320 |
| | R | 28 | 20 | | | | | | |
| D | R | 47 | 34 | | | | 145 | 10 | 140 |
| E | L | 32 | 26 | | | | | | |
| | R | 35 | 24 | | | | | | |
| | L | 32 | | 15 | 17 | | 115 | | |
| F | R | 30 | 20 | 13 | 22 | 84 | 143 | 18 | 320 |
| | L | 28 | 20 | 16 | 22 | 84 | | | |
| | R | 28 | 20 | 13 | 20 | | | | |
| G | L | 39 | 28 | 15 | 24 | 97 | 162 | 26 | 160 |
| | R | 39 | 30 | 15 | 23 | 97 | | | |
| | L | 37 | 30 | 18 | 28 | | | | |
| H | R | 32 | 25 | | | 85 | 158 | 10–17 | 300 |
| | L | 33 | 23 | | | 85 | | | |
| | R | 38 | 26 | | | | | | |
| I | R | 38 | 32 | 13 | 27 | 72 | 134 | 10 | 036 |
| | L | 38 | 32 | 16 | 27 | 86 | | | |
| | R | 39 | 32 | 15 | 26 | | | | |
| J | L | 33 | 27 | | | 85 | 155 | 7 | 020 |
| | R | 32 | 26 | | | 80 | | | |
| | L | 35 | 28 | | | | | | |

It is impossible, in our opinion to differentiate *Chuxiongpus changlingensis* from *C. zheni*, since both were based in part on extra-morphological variation (i.e., the manus impression was incomplete owing to overlap by the pes). We therefore see no justification for naming two ichnospecies. Thus we assign all trackways from this region to the former first named ichnospecies *changlingensis* under the existing ichnogenus *Brontopodus*, which adequately describes this general sauropod morphology at the ichogenus level. Further study of the Chuxiong sample may be necessary to determine if ichnospecific differences can be determined.

7. Saurischian trackway variation and morphodynamics

The sauropod tracks described from the Chabu and Chuxiong sites appear to be dominated by the footprints of relatively small individuals, as is the case with the sauropod tracks of Korea (Lim *et al.*, 1994).

However at all three localities one may encounter the tracks of larger individuals; for example, measurements obtained from the Chabu 2 site suggest pes track lengths ranging from about 75–80 cm long and 55–60 cm wide. Similarly a few pes tracks from the Chuxiong assemblages are at least 60 cm long by 45 wide, and one manus track was measured at 38 cm long and 55 cm wide.

As noted above, there is no immediate evidence that the tracks are morphologically distinct from other sauropod tracks of this age (Early Cretaceous). Generally speaking, tracks in the Chinese samples tend to be wide-gauge with relatively large manus:pes area ratios of about 1:2, compared with small manus sauropods where the ratio is 1:5 (Santos *et al.*, 1994). The Chabu tracks give values of about 1:2 (= 1:2–2.75 exactly for trackways 2 and 4 from site 6). Similarly the range of values for the Chuxiong sites (Figure 9) is about 1:1.9–1:29. Such morphologies are consistent with what is known of most Cretaceous sauropod trackways (Lockley 1999, 2001).

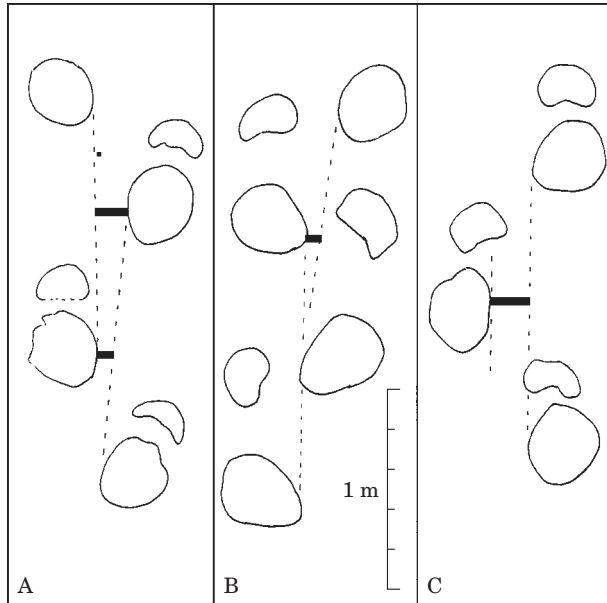


Figure 10. Trackways of *Brontopodus* (*Chuxiongpus*) *changlingensis*, Yuan Ji Tun village area, Chuxiong Prefecture, Yunnan Province. A, tracing of trackway I, main tracksite (Figure 8). B, C, tracings of trackways from southernmost locality (see Figure 2).

The narrow-gauge of the smallest Chabu trackway (Figure 6A) may be a function of size, suggesting that even among wide-gauge sauropods, juveniles may have been narrow gauge. In fact it is now known that all major saurischian groups (theropods, prosauropods and sauropods) produced both narrow and wide-gauge trackways. Nearly all small theropods produced narrow-gauge trackways, with wide-gauge patterns occurring only among large forms (Lockley 1999, 2001), which could switch or ‘change gears’ from slow wide-gauge to fast, narrow-gauge progression in the same trackway (Day *et al.*, 2002). Similarly, prosauropod trackways (ichnogenus *Otozoum*) show switching from narrow to wide-gauge progression, and sauropod trackways are divided ichnotaxonomically into mostly Jurassic, narrow-gauge, small-manus trackways (ichnogenus *Parabrontopodus*) and dominantly Cretaceous, wide-gauge, large-manus trackways (*Brontopodus*; Lockley *et al.*, 1994b; Lockley, 1999, 2001). In this case, however, the narrow–wide-gauge polarity represents a broad division at the level of sauropod families; i.e., the narrow gauge forms are thought to be diplodocids and their relatives whereas the wide gauge forms are probably brachiosaurids and titanosaurids. This does not mean that sauropods from these particular groups did not vary their gait either as adults in response to substrate changes in their speed of progression or at earlier stages in

ontogeny. Generally speaking, however, the weight of evidence suggests that the smaller and more primitive saurischians tended to make narrow-gauge trackways while, larger or derived forms tended to make wide-gauge trackways (Lockley *et al.*, 2001). Such dynamic changes in saurischian trackway-pattern reflect allometric variation during ontogeny, but they are also part of larger evolutionary trends that reflect large scale heterochronic or morphodynamic trends (McNamara, 1997; Lockley 1999, 2001). Simply put, at higher taxonomic levels the polarity in sauropod trackway gauge is no longer merely an ontogenetic phenomenon when it becomes evolutionarily differentiated in discrete sauropod families. This higher taxonomic level differentiation also has a lawful relationship to manus size (heteropody), i.e., small manus correlates with narrow gauge, large manus with wide gauge. This pattern appears to hold true for other Mesozoic reptiles including ornithischian dinosaurs, and Triassic non-dinosaurian archosaurs (Peabody, 1948; Lockley 1999, 2001; Avanzini and Lockley, *in press*).

8. Saurischian ichnofaunas and their palaeoecological implications.

Based on the information obtained from a minimum of seven sites studied in the Chabu area, it appears that theropod, bird and sauropod tracks are all fairly common, and occur at multiple stratigraphic levels at some sites. Thus all elements seem to be an integral part of the ichnofauna in this region. The association of theropod and sauropod tracks is quite common (Lockley *et al.*, 1994b), and it is also well known that sauropod and large ornithopod tracks rarely occur together, though there are rare but notable exceptions, such as in the Korean assemblages (Lim *et al.*, 1994). Thus the ichnological associations in the Chabu dinosaur track assemblages appears to be saurischian dominated to the point that track evidence of ornithischian dinosaurs appears to be completely lacking.

Sauropod tracks are common in low latitude coastal settings where carbonate substrates predominate, i.e., where evaporation tends to exceed precipitation, but they appear to be rare in humid coastal settings where coal-bearing facies are well-developed (Lockley *et al.*, 1994c). Here, at least in the Cretaceous, large ornithopod tracks predominate. However, sauropod tracks are quite common in fluvio-lacustrine facies associated with inland, semi-arid settings. Perhaps the best Jurassic example is the Morrison Formation, where both sauropod body fossils and tracks are common (Dodson *et al.*, 1980; Lockley *et al.*, 1998). Given the similarities in facies and palaeogeographic

setting between the Jing Chuan and Morrison formations, it is tempting to suggest that ichnological comparisons are also fruitful. For example, in the Morrison formation theropod tracks are also abundant and ornithischian tracks are rare. The lack of bird tracks is a function of age and is, therefore, predictable. We might conclude that there is a tendency for saurischian-dominated assemblages to be associated with semi-arid inland basin settings. Evidence from the Chuxiong red bed sites, where sauropod tracks are abundant in association with a few theropod tracks and no ornithopod tracks, suggests a similar pattern. Indeed at almost all Cretaceous sites in China, which represent small red-bed-dominated continental basins (Chen, 1996), similar saurischian or saurischian-bird dominated ichnofaunas dominate. It is only towards the Korean peninsula in the northeast that we find a significant component of ornithopods in the ichnofaunas (Lim *et al.*, 1994, Matsukawa *et al.*, 1995). Ornithopod tracks may also become more common at higher latitudes, i.e., in Mongolia (Ishigaki 1999).

General support for such suggestions come from several sources. Lucas & Hunt (1989, p. 75) explicitly noted that sauropods are absent from western North America where the region is "devoid of inland basin deposits." Similarly, Lockley *et al.* (1994c) noted the association of inland sauropod ichnofaunas with semi-arid climatic regimes such as those which produce carbonate in lacustrine basins. Retallack (1997, p. 355) reported that sauropods are primarily associated with "dry, dusty soils" and "strongly calcareous palaeosols (Aridisols, calcic Alfisols)" typically in "dry tropical uplands." Sauropod tracks also occur in inland basin settings in association with carbonate lake systems in South America (Leonardi, 1994; Lockley *et al.*, in press). They are abundant in Korea, where carbonate lacustrine systems developed in a back arc setting but, as has been pointed out, the presence of ornithopod tracks here is somewhat anomalous since they do not often occur at the same stratigraphic levels as the sauropod tracks (Lim *et al.*, 1994).

In Europe sauropods are abundant in Upper Jurassic carbonate platform settings (Lockley *et al.*, 1994c), but become increasingly rare in the Lower Cretaceous, as the palaeoenvironment became more humid and led to more siliciclastic deposition, notably in the Wealden succession of southern England and northern Europe. Where the track-bearing facies have been studied, for example in England, Germany and Spain (Wright *et al.*, 1998), we see a reduction of sauropod tracks and an increase in ornithopod tracks beginning in earliest Cretaceous times. Although this may reflect dinosaur evolution, sauropods did not die out with the advent of large ornithopods (iguanodon-

tids, and later, hadrosaurs). Instead it seems that they migrated inland. In Spain for example, where the 'Wealden' of the Cameros Basin includes various carbonate units associated with inland lake systems, sauropods remained in the area, and large ornithopods are quite rare. This suggests that ornithopods never became as abundant in Spain as they did in England and Germany. Sauropods also appear to have had a preference for low latitudes, as ornithopods did for higher latitudes, and this factor must also be taken into account in interpreting distribution patterns.

The association of sauropod tracks with bird tracks is interesting. The only area, other than China, where bird and sauropod tracks are commonly associated is in Korea. Based on current evidence, the tracks in China and Korea are about the same age, and occur at a similar palaeolatitude. By contrast, in North America, notably in Colorado, South Dakota, Alberta and British Columbia (Lockley *et al.*, 1992, in press), Cretaceous bird tracks are generally associated with ornithopod and theropod track assemblages associated with siliciclastic coastal plain and coal-bearing facies from higher palaeolatitudes. The distribution of Cretaceous bird tracks in other regions (Europe, Africa and South America) is spotty and insufficient to suggest any obvious large scale patterns of biotic or facies association. Therefore, at first glance the Chinese and Korean occurrence of bird tracks in association with sauropod tracks, in inland basin settings, appears to be more characteristic of ichnofaunas from eastern Asia than those from other regions.

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References

- Alexander, R. McN. 1976. Estimates of speeds of dinosaurs. *Nature*, **261**, 129–130.
- Avanzini, M. & Lockley, M. G. (in press). Middle Triassic archosaur ontogeny and population structure: interpretations based on

- Isochirotherium delicatum* fossil footprints (Southern Alps- Italy). *Palaeogeography, Palaeoclimatology, Palaeogeography*.
- Chen, P. J. 1986. Cretaceous paleogeography in China. *Palaeogeography, Palaeoclimatology, Palaeoecology* **59**, 49–56.
- Chen, P. J. 1996. Freshwater biota, stratigraphic correlation of Late Cretaceous of China. *Geological Society of India, Memoir* **37**, 35–62.
- Chen, S. & Huang, X. 1993. Preliminary study of dinosaur tracks in Changling, Chuxiong Prefecture. *Journal of Yunnan Geology* **12** (3), 266–276.
- Chen, S. & Huang, X. 1994. Changling, Chuxiong dinosaur tracks and related problems. *Journal of Yunnan Geology* **13** (3), 285–289.
- Day, J. J., Norman, D. B., Upchurch, P. & Powell, H. P. 2002. Dinosaur locomotion from a new trackway. *Nature* **415**, 494–495.
- Dodson, P., Berensmeyer, A. K., Bakker, R. T. & McIntosh, J. S. 1980. Taphonomy of the dinosaur beds of the Jurassic Morrison Formation. *Paleobiology* **6**, 208–232.
- Farlow, J. O., Pittman, J. G. & Hawthorne, J. M. 1989. *Brontopodus birdii*, Lower Cretaceous sauropod footprints from the U. S. Gulf Coastal plain. In *Dinosaur tracks and traces* (eds Gillette, D. D. & Lockley, M. G.), pp. 371–394 (Cambridge University Press, Cambridge).
- Hao, Z. C. *et al.* (eds). 2000. Chinese geological formations: Cretaceous, 124 pp. (Chinese Stratigraphy Committee, Geological Publication Co., Beijing).
- Ishigaki, S. 1999. Abundant dinosaur footprints from the Upper Cretaceous of Gobi Desert, Mongolia. *Journal of Vertebrate Paleontology* **19**, 54A.
- Leonardi, G. 1987. Glossary and manual of tetrapod footprint paleoichnology, 75 pp., 20 pls (Ministry of Mines and Energy, Brasilia).
- Leonardi, G. 1994. Annotated atlas of South America tetrapod footprints (Devonian to Holocene), 248 pp., 35 pls (Companhia de Pesquisa de Recursos Minerais, o Servico Geologico do Brasil, Brasilia).
- Lim, S. K., Lockley, M. G., Yang, S.-Y., Fleming, R. F. & Houck, K. A. 1994. Preliminary report on sauropod tracksites from the Cretaceous of Korea. *Gaia: Revista de Geociencias, Museu Nacional de Historia Natural* (Lisbon) **10**, 109–117.
- Lockley, M. G. 1987. Dinosaur trackways. In *Dinosaurs past and present. Volume 1* (eds Czerkas, S. J. & Olsen, E. C.), pp. 80–95 (Los Angeles County Museum Symposium).
- Lockley, M. G. 1999. The eternal trail: a tracker looks at evolution, 334 pp. (Perseus Books, Reading, MA).
- Lockley, M. G. 2001. Trackways–dinosaur locomotion. In *Palaeobiology II* (eds Briggs, D. E. G. & Crowther, P.) pp. 412–416 (Blackwell, Oxford).
- Lockley, M. G. & Hunt, A. P. 1995. *Dinosaur tracks and other fossil footprints of the Western United States*, 338 pp. (Columbia University Press, New York).
- Lockley, M. G. & Matsukawa, M. 1998. Lower Cretaceous vertebrate tracksites of East Asia. In *Lower and Middle Cretaceous terrestrial ecosystems* (eds Lucas, S. G., Kirkland, J. I. & Estep, J. W.), *New Mexico Museum of Natural History and Science Bulletin* **14**, 135–142.
- Lockley, M. G. & Santos, V. F. 1993. A preliminary report on sauropod trackways from the Avelino site, Sesimbra region, Upper Jurassic, Portugal. *Gaia: Revista de Geociencias, Museu Nacional de Historia Natural* (Lisbon) **6**, 38–42.
- Lockley, M. G., Farlow, J. O. & Meyer, C. A. 1994a. *Brontopodus* and *Parabrontopodus* ichnogen. nov. and the significance of wide- and narrow-gauge sauropod trackways. *Gaia: Revista de Geociencias, Museu Nacional de Historia Natural* (Lisbon) **10**, 135–146.
- Lockley, M. G., Foster, J. & Hunt, A. P. 1998. A short summary of dinosaur tracks and other fossil footprints from the Morrison Formation. In *The Upper Jurassic Morrison Formation: an interdisciplinary study* (eds Carpenter, K., Chure, D. & Kirkland, J.), *Modern Geology* **23**, 277–290.
- Lockley, M. G., Hunt, A. P. & Meyer, C. 1994c. Vertebrate tracks and the ichnofacies concept: implications for paleoecology and palichnostratigraphy. In *The palaeobiology of trace fossils* (ed. Donovan, S.), pp. 241–268 (Wiley, Chichester).
- Lockley, M. G., Janke, P. & Theisen, L. 2001. First reports of bird and ornithopod tracks from the Lakota Formation (Early Cretaceous), Black Hills, South Dakota. In *Mesozoic vertebrate life. New research inspired by the paleontology of Philip J. Currie* (eds Carpenter, K. & Tanke, D.), pp. 443–452 (Indiana University Press, Bloomington).
- Lockley, M. G., Meyer, C., Hunt, A. P. & Lucas, S. G. 1994b. The distribution of sauropod tracks and trackmakers. *Gaia: Revista de Geociencias, Museu Nacional de Historia Natural* (Lisbon) **10**, 233–248.
- Lockley, M. G., Schulp, A., Meyer, C. A., Leonardi, G. & Kerumba Mamani, D. 2002. Titanosaurid trackways from the Upper Cretaceous of Bolivia: evidence for large manus, wide-gauge locomotion and gregarious behaviour. *Cretaceous Research* **23**, 383–400.
- Lockley, M. G., Wright, J. L., Lucas, S. G. & Hunt, A. P. 2001. The late Triassic sauropod track record comes into focus. Old legacies and new paradigms. *New Mexico Geological Society, Guidebook, 52nd Field Conference*, pp. 181–190.
- Lockley, M. G., Yang, S.-Y., Matsukawa, M., Fleming, F. & Lim, S.-K. 1992. The track record of Mesozoic birds: evidence and implications. *Philosophical Transactions of the Royal Society of London* **336**, 113–134.
- Lucas, S. G. & Hunt, A. P. 1989. *Alamosaurus* and the sauropod hiatus in the Cretaceous of the North American Western Interior. In *Paleobiology of the dinosaurs* (ed. Farlow, J. O.), *Geological Society of America, Special Paper* **238**, 75–85.
- Matsukawa, M., Futakami, M., Lockley, M. G., Chen Peiji, Jinhua, C., Zenyao, C. & Bolotsky, U. 1995. Dinosaur footprints from the Lower Cretaceous of eastern Manchuria, northeast China: evidence and implications. *Palaios* **10**, 3–15.
- McNamara, K. 1997. *Shapes of time: the evolution of growth and development*, 342 pp. (John's Hopkins University Press, Baltimore).
- Peabody, F. E. 1948. Reptile and amphibian trackways from the Lower Triassic Moenkopi Formation of Arizona and Utah. *Bulletin of the Department of Geological Sciences, University of California* **27**, 295–468.
- Peabody, F. E. 1955. Taxonomy and the footprints of tetrapods. *Journal of Paleontology* **29**, 915–918.
- Qi Hua, Li Yougui, Su Deying, Li Longyun & Ye Liusheng. 1986. Outline of regional stratigraphy: northwestern China region. In *The Cretaceous System of China* (eds Hao Yichun, Su Deying, Yu Jingxian, Li Peixian *et al.*, 10 other authors), pp. 168–172 (Geological Publishing House, Beijing).
- Retallack, G. 1997. Dinosaur and dirt. In *Dinofest International* (eds Wolberg, D. L., Stump, E. & Rosenberg, G. D.), pp. 345–359 (The National Academy of Natural Sciences, Washington DC).
- Santos, V. F., Lockley, M. G., Meyer, C. A., Carvalho, J., Galopim de Carvalho, A. M. & Moratalla, J. J. 1994. A new sauropod tracksite from the Middle Jurassic of Portugal. *Gaia: Revista de Geociencias, Museu Nacional de Historia Natural* (Lisbon) **10**, 5–14.
- Sarjeant, W. A. S. 1989. Ten paleoichnological commandments: a standardized procedure for the description of fossil vertebrate footprints. In *Dinosaur tracks and traces* (eds Gillette, D. D. & Lockley, M. G.) pp. 369–370 (Cambridge University Press, Cambridge).
- Thulborn, R. A. 1990. *Dinosaur tracks*, 410 pp. (Chapman Hall, London).
- Wilson, J. A. & Carrano, M. T. 1999. Titanosaurs and the origin of wide gauge trackways: a biomechanical and systematic perspective on sauropod locomotion. *Paleobiology* **25**, 252–267.
- Wright, J. L., Barrett, P. M., Lockley, M. G. & Cook, E. 1998. A review of Early Cretaceous terrestrial vertebrate track-bearing strata of England and Spain. In *Lower and Middle Cretaceous*

- terrestrial ecosystems* (eds Lucas, S. G., Kirkland, J. I. & Estep, J. W.), *New Mexico Museum of Natural History and Science, Bulletin* **14**, 143–153.
- Yang, X. L. & Yang, D. H. 1987. *Dinosaur footprints from Mesozoic Sichuan Basin*, pp. 1–30, pls 1–14 (Sichuan Science and Technology Publishing House).
- Zhen, S., Li, R., Rao, C., Mateer, N. & Lockley, M. G. 1989. A review of dinosaur footprints in China. In *Dinosaurs past and present* (eds Gillette, D. D. & Lockley, M. G.), pp. 187–197 (Cambridge University Press, Cambridge).
- Zhou, Z. & Chen, P. J. 1992. *Biostratigraphy and geological evolution of Tarim* (Science Press, Beijing).