

A theropod–sauropod track assemblage from the ?Middle–Upper Jurassic Shedian Formation at Shuangbai, Yunnan Province, China, reflecting different sizes of trackmakers: Review and new observations

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Abstract

A dinosaur tracksite at Hemenkou (Shuangbai County, Yunnan Province) in the ?Middle–Upper Jurassic Shedian Formation that consists mainly of gray–purple feldspathic quartz sandstones was previously reported incorrectly as being in the Lower Cretaceous Puchanghe Formation. The previous assignment is also inconsistent with two regional geological maps. Although mostly yielding poorly preserved tracks, the site nevertheless indicates a diversity of theropod and sauropod trackmakers partly consistent with the Late Jurassic body fossils from the region. Purported ornithopod are re-evaluated here as those of theropods. The theropod tracks and trackways show distinct similarities to those of the *Grallator–Eubrontes* plexus and can be subdivided into three morphotypes that may reflect different pes anatomy and/or substrate conditions. Two sizes of tracks (small, large) indicate the presence of different size classes or species in this area in the Late Jurassic. Similarly, the sauropod trackways document three differently sized trackmakers (small–medium–large) showing a typical wide-gauge (*Brontopodus*) pattern. The track record is the first evidence of theropods in the ?Middle–Late Jurassic of central Yunnan, whereas the sauropod tracks suggest a relation to the coeval basal eusauropods known from this region by skeletal remains.

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1. Introduction

The Lufeng Basin in Yunnan Province is an ideal site for the study of dinosaur evolution in the Jurassic. Abundant skeletal fossils of sauropodomorph and theropod dinosaurs have been found in the Lower and Middle Jurassic deposits of the Lufeng Basin (Young, 1951; Dong, 1992; Upchurch et al., 2007; Xing et al., 2013a). Fang et al. (2004) discovered fragmentary fossils of basal eusauropods (*Mamenchisaurus*) in the Upper Jurassic

Laochangqing–Dajianfeng profile of Chuanjie Town and theorized that a *Mamenchisaurus* fauna, which may have flourished in today's China during the Jurassic, probably also inhabited the Lufeng region in this time interval. However, in contrast with the rich *Mamenchisaurus* fauna in the Sichuan Basin, the dinosaur record from the Jurassic of the Lufeng Basin is still quite poor. It has to be mentioned that the stratigraphic age of the Sichuan *Mamenchisaurus* fauna is controversial. This assemblage has traditionally been regarded as Late Jurassic in age, but K. Li et al. (2011) considered it to be Middle Jurassic.

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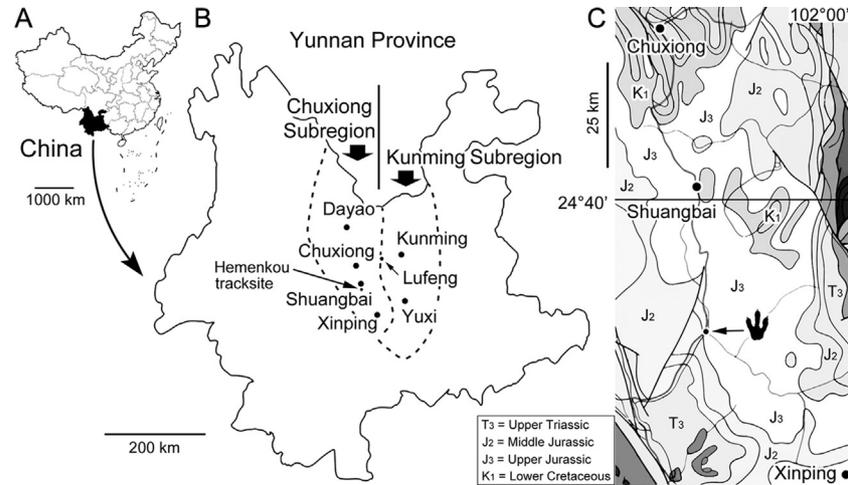


Fig. 1. Geographic (A, B) and geologic (C) maps showing the position of the study area with the Hemenkou dinosaur footprint locality (footprint icon) and distribution of Mesozoic strata.

workers cooperated to explore the Hemenkou tracksite near Shuangbai County, about 78 km southwest of World Dinosaur Valley Park, Chuxiong Yi Autonomous Prefecture, Yunnan Province, China (Fig. 1A). Fujita et al. (2008) preliminarily described the Hemenkou tracksite, assuming that it represented the first dinosaur tracksite from the Lower Cretaceous of Yunnan Province. In the summer of 2013, we (LX, ML, TW, and SK) investigated various dinosaur tracksites in the Lufeng Basin. During re-examination of the Hemenkou tracksite new tracks (Table 1) were discovered at this location ($24^{\circ}22'54.53''\text{N}$, $101^{\circ}40'4.99''\text{E}$). The assemblage indicates that the Hemenkou tracksite represents a characteristic Jurassic ichnofauna and should be assigned to the ?Middle–Upper Jurassic Shedian Formation. These tracks complement the abundance of body fossils from the Upper Jurassic Lufeng Basin.

Institutional abbreviations and acronyms

HMK = Hemenkou tracksite, Yunnan Province, China;
ZLJ = Lufeng Dinosaur Museum of World Dinosaur Valley Park, China.

2. Geological setting

The Jurassic dinosaur fossils of Yunnan Province are mostly found in the central part of the region that consists of a series of basins, the largest of which is the Lufeng Basin (414 km^2 in area and comprising a sequence about 750 m in thickness, Bien, 1941). Outcrops in the Chuxiong and Kunming subregions of central Yunnan can be attributed to two different strata reflecting distinct sedimentary environments and characteristics (Cheng et al., 2004) (Fig. 1B). In the Chuxiong Subregion these are large-area, deep-water lake basin deposits that are divided in ascending order into the Lower Jurassic Yubacun and Fengjiahe formations, the Middle Jurassic Zhanghe Formation, and the ?Middle–Upper Jurassic Shedian and Tuodian formations. The Kunming Subregion is characterized by several small basins scattered around the margin of the Chuxiong Subregion. In this

part deposits are divided in ascending order into the Lower Jurassic Yubacun and Lufeng formations, the Middle Jurassic Chuanjie and Laoluocun formations, and the Upper Jurassic Madishan and Anning formations, of which the Lufeng Formation and the Chuanjie Formation are especially rich in vertebrate fossils (Fang et al., 2000).

The tracks described here were discovered in the ?Middle–Upper Jurassic Shedian Formation, a sandstone–mudstone sequence that in the Shuangbai area is up to 725.5 m thick. Near the tracksite, sediments of the Shedian Formation indicate a shallow lacustrine depositional environment (Chen, 1992). Preliminary rare earth element analyses indicate that the tracksite belongs to the Jurassic (Huang et al., 2009).

The Shedian Formation was originally considered a second layer of the Lufeng Red Beds (Zhang, 1996). In 1961, the Regional Geological Survey Team of the Yunnan Geological Bureau named this unit the Shedian Formation and assigned it to the Jurassic (Regional Geological Survey Team, Yunnan Bureau of Geology, 1961). Sheng et al. (1962) considered a Middle Jurassic age for the Shedian Formation based on the presence of the ostracods *Darwinula* and *Timiriasevia*. At the time, no Upper Jurassic strata were known from the Lufeng Basin. These were identified later by Fang et al. (2000). Niu et al. (2005) considered the age of the Shedian and Tuodian formations to be lower Upper Jurassic in age. This was based on conchostracan (*Eosestheriopsis–Chuanjieestheria*) and ostracod (*Darwinula–Damonella–Djungarica–Prolimnocythere*) assemblages. The record corresponds with the ostracod assemblages from the Tuchengzi (Upper Jurassic–Lower Cretaceous), Datonghe (Upper Jurassic) and Hongshuigou (Upper Jurassic) formations in northern China (Chen and Hudson, 1991; Wang, 2000; Shen et al., 2002). Gastropods also indicate an Upper Jurassic age for the Shedian Formation (Wang et al., 1981). In 1965, the First Regional Geological Survey Team of the Yunnan Bureau of Geology and Mineral Resources assigned the Shedian Formation to the Upper Jurassic, which has since been widely accepted (Zhang, 1996). Nevertheless, considering the

Table 1
The relationship between the newly discovered tracks and the original assemblage reported by Fujita et al. (2008).

Fujita et al. (2008)		This paper	
Number	Trackmaker	Number	Trackmaker
Unrecorded	—	HMK-T1L1–T1L4	Theropod
YT1–YT3	Theropod	HMK-T2L1–T2L2, T2L3	Theropod
YT4, YT5	Theropod	ZLJ-HMK-T1, T2	Theropod
Unrecorded	—	HMK-TI1	Theropod
YO1–YO7	Ornithopod	HMK-T3R1–T3L4	Large theropod
YS4–YS8	Sauropod	HMK-S1RP1–S1RP2	Sauropod
YS12–YS15	Sauropod	HMK-S2RP1–RP2	Sauropod
YS1–YS3, YS9–YS10, S11	Sauropod	Unnumbered isolated footprints	Sauropod
unrecorded	—	HMK-SIM1, SIP1	Small sauropod
Total	27	Total	59

conchostracan and ostracod record as well as the uncertain taxonomic status and stratigraphic age of various “*Mamenchisaurus*” skeletal assemblages from the Sichuan and Lufeng basins, we here give a more tentative ?Middle–Upper Jurassic age for the trackbearing Shedian Formation. Fujita et al. (2008) assumed that the tracks occur in the Lower Cretaceous Puchanghe Formation. However, according to a 1:2 500 000 Geologic Map of Yunnan Province (Compilation Committee of Geological Atlas of China, 2002) cited by Fujita et al. (2008), the Hemenkou tracksite is located within Jurassic, not Cretaceous, strata. Further information (such as a 1:200 000 map; Second Areal Geological Survey Team, Yunnan Bureau of Geology, 1970; Fig. 1C) indicates that the Hemenkou tracksite is in the Jurassic Shedian Formation. Whereas the Puchanghe Formation is dominated by gray-purple or mottled mudstones and calcareous mudstones,

the track-bearing Shedian Formation consists of grey, grayish purple and light purplish red, fine-medium grained feldspathic and quartzose sandstone, interbedded with sandy mudstone, calcareous mudstone, conglomerate, and sandy conglomerate (Zhang, 1996). This basically matches the description of the strata at the Hemenkou tracksite given by Fujita et al. (2008). The Cretaceous strata within the Shuangbai area are restricted to the east and southeast of Shuangbai County, whereas all other parts of this region are Jurassic in age. The Shedian Formation conformably overlies the Middle Jurassic Zhanghe Formation and is conformably overlain by the Upper Jurassic Tuodian Formation.

A detailed stratigraphic section of the Shedian Formation is in preparation elsewhere. Presently we are conducting a more complex investigation of the geological history of the Lufeng and Shuangbai areas.



Fig. 2. Working process at the Hemenkou tracksite. (A) One of the authors (ML) at work on the site; (B) the mountaineering team members making a complete tracing of the site on a plastic sheet.

3. Material and methods

The Hemenkou tracksite is approximately 20 m long and 6 m wide, the surface showing a dip of approximately 50°. The China National Mountaineering Team and Sichuan Mountaineering Association were employed in the investigation. Tracks were accessed with the help of ropes anchored at the top of the outcrop and were individually catalogued and outlined with chalk. The entire tracksite was also traced on transparency film (Fig. 2A, B). Drawings are housed at China University of Geosciences, Beijing. The tracks were scanned, and a digital map with the distribution pattern was made via Adobe PhotoShop CS6 (Fig. 3).

Fujita et al. (2008) also made artificial moulds of partial theropod tracks. They used a non-contact three-dimensional digitizer to scan the site, and superimposed an outline of the tracksite on a topographic map. This partially superimposed outline (Fujita et al., 2008) is referred to in our descriptions. All tracks were re-measured for this study.

For the trackways of quadrupeds, gauge (trackway width) was quantified for pes and manus tracks by using the ratio between the width of the angulation pattern of the pes (WAP) and the pes length (PL) (Marty, 2008; Marty et al., 2010, fig. 4). The (WAP/PL)-ratio was calculated with the Pythagorean Theorem from pace and stride length, assuming that the width of the angulation pattern intersects the stride under a right angle and approximately at the midpoint of the stride (Marty, 2008, p. 37). Although these data are not based on a direct measurement of the width of the angulation pattern in the field, the obtained values are a good approximation of the trackway gauge. If the (WAP/PL)-ratio is less than one (i.e., $PL > WAP$), the pes tracks are likely to intersect the trackway midline, which corresponds to the definition of narrow-gauge (Farlow, 1992). Accordingly, a value of 1.0 is taken to separate narrow-gauge from medium-gauge trackways, whereas the value 1.2 is fixed between medium-gauge and wide-gauge trackways, and trackways with a value higher than 2.0 are considered very wide-gauge (Marty, 2008).

According to Olsen (1980), Weems (1992), and Lockley (2009), theropod tracks can be differentiated based on mesaxony (i.e., the degree to which the central digit (III) protrudes anteriorly beyond the medial (II) and lateral (IV) digits), thereby defining an anterior triangle. There is also, in most cases, a positive correlation between the L/W ratio of the anterior triangle (which is used here as an index of mesaxony) and that of the whole track.

4. Tracks

4.1. Theropod tracks

Materials: Three trackways cataloged as HMK-T1–T3, with 7, 4, and 8 tracks respectively. Five isolated tracks, of which two were collected by the Lufeng Dinosaur Museum of World Dinosaur Valley Park, China and cataloged as ZLJ-HMK-T1 and T2. All other tracks remain *in situ* (Figs. 3–5).

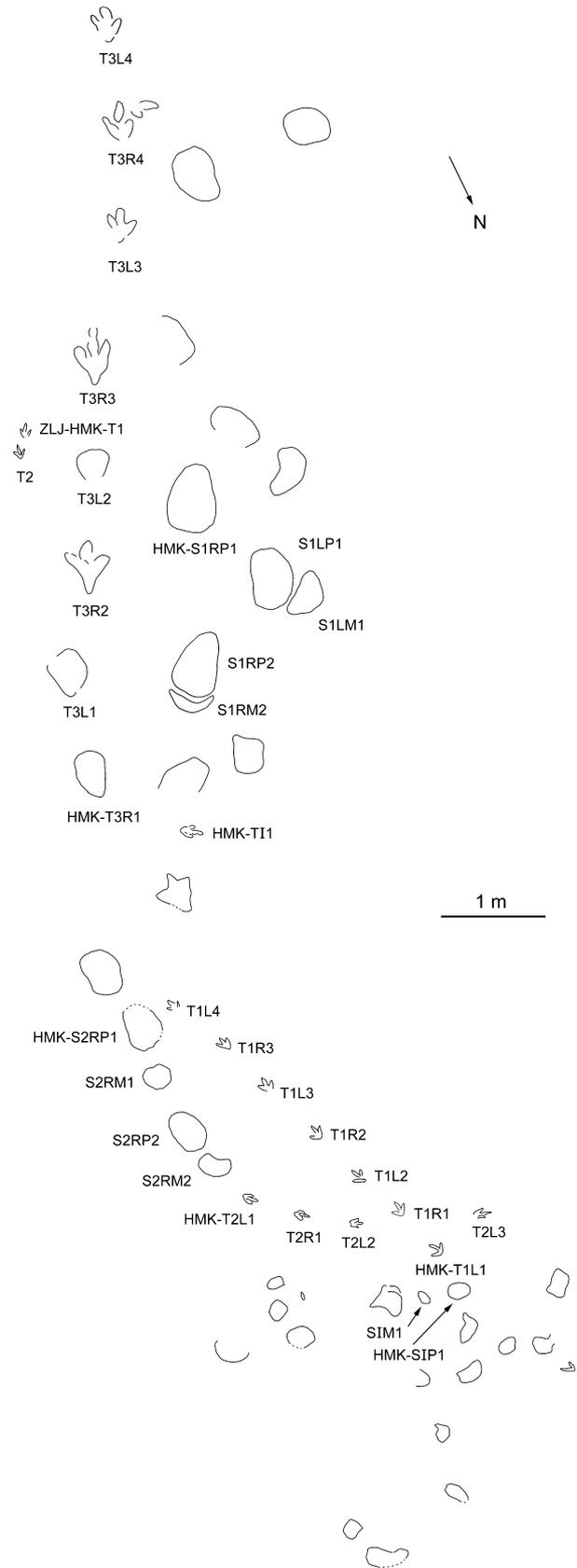


Fig. 3. Map with interpretative outline drawings of track-bearing level at the Hemenkou tracksite.

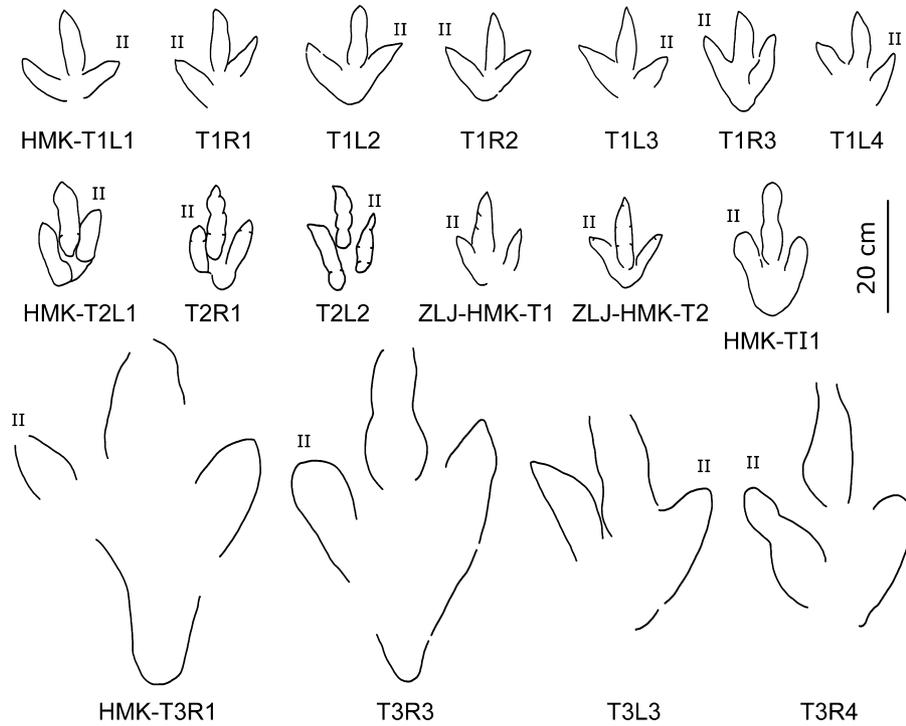


Fig. 4. Outline drawings of theropod tracks from the Hemenkou tracksite. Specimens ZLJ-HMK-T1 and T2 from the Lufeng Dinosaur Museum of World Dinosaur Valley Park correspond to those in Fig. 5.

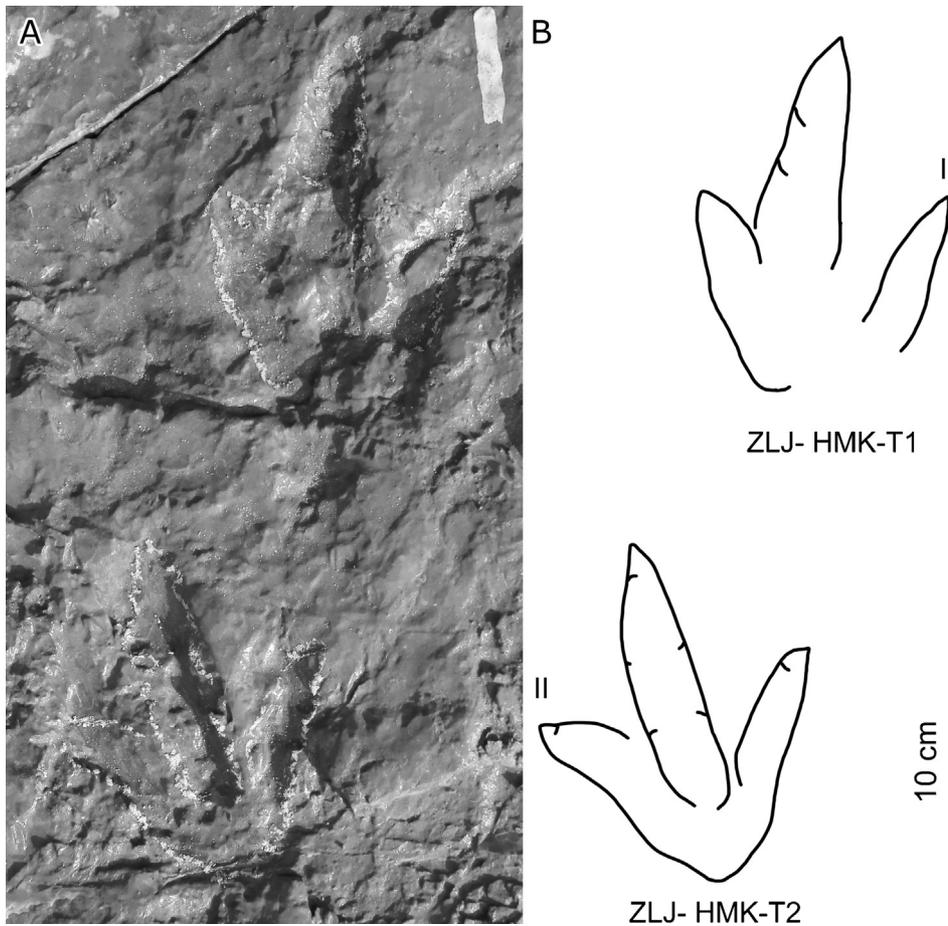


Fig. 5. Photograph (A) and outline drawing (B) of theropod tracks ZLJ-HMK-T1 and T2 from the Hemenkou tracksite, housed at Lufeng Dinosaur Museum of World Dinosaur Valley Park, China.

Locality and horizon: Shedian Formation, ?Middle–Upper Jurassic. Hemenkou tracksite, Shuangbai County, Yunnan Province, China.

Description and comparisons: Except for HMK-T2, the theropod tracks at the Hemenkou tracksite are poorly-preserved. Nevertheless, two different sizes and three morphologies can be observed.

Morphotype A consists of seven natural molds cataloged as HMK-T1L1–T1L4 (Figs. 4, 5, Table 2) and two isolated natural molds (ZLJ-HMK-T1 and T2 (=YT4–5 sensu Fujita et al., 2008)) (Fig. 4). They are small to medium sized (length ~14–15 cm) and tridactyl, with an average length/width ratio of 1.2. They resemble the classic theropod footprint genera *Eubrontes*, *Anchisauripus*, and *Grallator* from the Upper Triassic–Lower Jurassic, but they commonly have a wider divarication of digits II–IV (average 73°) compared with the former (10°–40°; Olsen et al., 1998). The pace angulation of HMK-T1

is 173°. Our measurements of track lengths differ partly from those given by Fujita et al. (2008) due to the different interpretation of purported metatarsophalangeal pad impressions in some specimens (ZLJ-HMK-T1, ZLJ-HMK-T2). We consider these as sedimentary structures and therefore (contrary to Fujita et al., 2008) our values exclude them. HMK-T1 is characterized by weak to moderate mesaxony (average 0.47, range 0.37–0.54, $N=7$), which is typical for footprints of the ichno- or morpho-family Eubrontidae Lull, 1904.

In morphology, Morphotype A is similar to tracks described by Lockley et al. (2011, fig. 8) from the Upper Cretaceous of Colorado. They are characterized by small size and a general theropod (grallatorid) shape, with only faintly separated digit pad traces, giving the overall digit traces an elongate cigar-shaped outline. This morphology is unlike typical *Grallator* tracks, which are slender (high L/W ratios) and elongated with strong mesaxony and digital pad traces (Lockley, 2009).

Table 2

Measurements (in cm) of the dinosaur tracks from the Jishan tracksites. Abbreviations: ML: maximum length; MW: maximum width; II–III: angle between digits II and III; III–IV: angle between digits III and IV; II–IV: angle between digits II and IV; PL: pace length; SL: stride length; PA: pace angulation; L/W: maximum length/maximum width.

Number	ML	MW	II–III	III–IV	II–IV	PL	SL	PA	L/W
HMK-T1L1	15.0	15.0	52°	44°	96°	54.5	103.5	165°	1.0
HMK-T1R1	13.5	—	—	—	—	50.0	107.5	170°	—
HMK-T1L2	17.5	14.0	27°	40°	67°	57.5	—	177°	1.3
HMK-T1R2	15.0	15.5	44°	32°	76°	49.5	106.5	179°	1.0
HMK-T1L3	15.5	15.5	—	—	—	57.5	120.5	173°	1.0
HMK-T1R3	16.0	11.5	27°	26°	53°	62.5	—	—	1.4
HMK-T1L4	14.5	12.5	—	—	—	—	—	—	1.2
Mean	15.3	14.0	38°	36°	73°	55.3	109.5	173°	1.2
HMK-T2L1	15.0	8.5	25°	18°	43°	52.0	102.5	171°	1.8
HMK-T2R1	15.5	9.0	14°	29°	43°	51.0	—	—	1.7
HMK-T2L2	13.5	9.5	31°	26°	57°	—	123.0	—	1.4
HMK-T2L3	16.0	10.0	—	—	—	—	—	—	1.6
Mean	15.0	9.3	23°	24°	48°	51.5	112.8	171°	1.6
HMK-T3R1	47.5	28.0	—	—	—	105.5	213.0	156°	1.7
HMK-T3L1	50.0	34.0	—	—	—	109.5	203.0	171°	1.5
HMK-T3R2	52.5	38.0	29°	30°	59°	93.0	217.5	180°	1.4
HMK-T3L2	33.5	30.5	—	—	—	124.5	—	170°	1.1
HMK-T3R3	59.0	28.0	—	17°	42°	—	—	169°	2.1
HMK-T3L3	36.0	27.5	37°	23°	60°	109.0	—	172°	1.3
HMK-T3R4	36.5	25.0	35°	30°	65°	—	—	—	1.5
HMK-T3L4	36.0	27.5	37°	23°	60°	—	—	—	1.3
Mean	43.9	29.8	35°	25°	57°	108.3	211.2	170°	1.5
HMK-TI1	21.1	9.7	21°	22°	43°	—	—	—	2.2
HMK-ZLJ-T1	14.9	10.1	31°	30°	61°	—	—	—	1.5
HMK-ZLJ-T2	14.4	11.6	35°	35°	70°	—	—	—	1.2
HMK-S1RP1	64.4	46.7	—	—	—	107.6	157.6	89°	1.4
HMK-S1LP1	57.7	39.0	—	—	—	113.4	—	—	1.5
HMK-S1LM1	26.7	45.3	—	—	—	150.4	—	—	0.6
HMK-S1RP2	62.2	41.8	—	—	—	—	—	—	1.5
HMK-S1RM2	14.8	43.4	—	—	—	—	—	—	0.3
HMK-S2RP1	47.0	35.5	—	—	—	117.0	—	—	1.3
HMK-S2RM1	24.5	26.5	—	—	—	109.0	—	—	0.9
HMK-S2RP2	45.0	26.5	—	—	—	—	—	—	1.7
HMK-S2RM2	21.5	30.0	—	—	—	—	—	—	0.7
HMK-SIP1	21.2	15.7	—	—	—	—	—	—	1.4
HMK-SIM1	7.26	15.4	—	—	—	—	—	—	0.5

These tracks are more transverse (lower L/W ratios) with weaker mesaxony and fainter digital pad traces. Similar characteristics can be seen, for example, in the two Early Cretaceous theropod tracks SLZh(08)-03-01 and 02 from the Zhongpu area, Gansu (Xing et al., 2014a). However, theropod tracks show a wide range of morphological variations, not to mention preservational differences, and so, without detailed analysis, no significance can be attached to the similarities between grallatorid tracks from the Jurassic and Cretaceous.

Morphotype B consists of three natural molds cataloged as HMK-T2L1–T2L3 (Figs. 4, 5, Table 2; =YT1–3 sensu Fujita et al. (2008)) and one isolated natural mold HMK-TI1. These tracks are similar to Morphotype A in size (approximately 15–21 cm) but have a greater grallatorid (or *Grallator*) affinity in the sense that they have a higher L/W ratio (1.6–2.2) and stronger mesaxony (0.66–0.85).

The best-preserved is T2L2, a tridactyl left pes, with a L/W ratio of 1.4. Digit II is the shortest and digit IV is the longest. Each digit has a sharp claw mark. Digits II and III have two and three phalangeal pads, respectively. The borders of the digital pads of digit IV are indistinct. However, referring to the superimposed outline (Fujita et al., 2008), there are three digit pads and a relatively large metatarsophalangeal pad. The metatarsophalangeal pad of digit IV is close to the axis of digit III. The divarication between digit II and III is larger than that between digit III and IV.

Morphotype C consists of eight large (average length 43.9 cm) tridactyl tracks (Fig. 4; Table 2) cataloged as HMK-T3R1–T3L4, with weak mesaxony (average 0.56, range between 0.44 and 0.75, $N=3$), which is typical for footprints of the ichno- or morphofamily Eubrontidae. HMK-T3 tracks are poorly-preserved as undertracks, but some characteristics are discernable. Two phalangeal pads are distinct for digit II of T3R4. Partially digits of T3L3, T3R3 preserve relatively sharp claw marks, and partial tracks preserve a metatarsophalangeal area that is elongated posteriorly into a “heel”, such as in T3R1 and T3R3. The latter is probably influenced by the comparatively wet and soft sediments. The divarication of digits II and IV ranges from 42° to 65°.

Fujita et al. (2008) suggested that HMK-T3 might be an ornithopod trackway because of the “zigzag” pattern and the broad rounded shape of digits, but noted that a theropod origin was also possible based on the narrow posterior margin. A “zigzag” pattern and alternating arrangement of imprints is seen in many tetrapod trackways, and the purported broad shape of the digit traces in HMK-T3 cannot be confirmed, except for some extra-morphological (substrate-related) variation of width. These tracks also possess relatively sharp claw marks. Trackways are narrow (pace angulation 170°). All features, including the metatarsophalangeal area, imply a theropod affinity. In addition, given our interpretation of the tracks as Jurassic, there is little ichnological evidence of large ornithopods (average track length about 44 cm) at this time (Lockley et al., 2014a), other than the inferred *Campylosaurus* tracks discussed by Gierliński and Sabath (2008), which are, in any event, gracile and convergent with theropod tracks.

Eubrontes, together with *Grallator*, *Kayentapus*, and *Anomoepus* are typical components of the Lower Jurassic ichno-associations from North America (Lockley and Hunt, 1995; Olsen et al., 1998). However, in China, they occur not only in the Lower Jurassic formations, but also in Middle and even Upper Jurassic strata. Thus, theropod tracks from the Jurassic of China presently cannot be used for more detailed biostratigraphic purposes (Xing et al., 2013b). So far most large theropod tracks in the Jurassic of China are universally assigned to *Eubrontes* (Lockley et al., 2013). Large theropod tracks were also found in the Lower–Middle Jurassic of the Lufeng Basin: *Eubrontes* isp. from the Middle Jurassic of the Beikeshan tracksite (Xing et al., 2014b) and *Eubrontes pareschequier* from the Lower Jurassic of the Lufeng Basin (Xing et al., 2009a; Lockley et al., 2013). Based on the present characteristics, HMK-T3 tracks can be referred tentatively to cf. *Eubrontes*.

4.2. Sauropod tracks

Materials: Approximately 35 oval natural impressions; two trackways cataloged as HMK-S1PR1–PR2 and S2PR1–PR2, with four and two pairs of manus and pes traces, respectively; all other tracks are isolated (Figs. 3, 6). A well-preserved pair is cataloged as HMK-SIP1 and M1. All tracks are *in situ*.

Locality and horizon: Shedian Formation, ?Middle–Upper Jurassic. Hemenkou tracksite, Shuangbai County, Yunnan Province, China.

Description and comparisons: Although the sauropod tracks at the Hemenkou tracksite are weathered, there are clearly three size classes present.

HMK-S1 is the trackway with the largest imprints. The average length and width of the pes is 61.4 cm and 42.5 cm, respectively. The mean L/W ratio is 1.4. Taking the well-preserved S1RP2 (Fig. 6) as an example, the pes trace is sub-oval in shape, the anterior edge is wide, and the metatarsophalangeal region is narrow. No discernable digital or claw marks were observed. The impression of the metatarsophalangeal region is complete with smoothly curved margins. S1RM2, with a concave crescent-shaped posterior edge, is a manus trace, overlapped by S1RP2 at the posterior margin. No significant deformation was observed in another manus trace, S1LM1, which is U-shaped with a L/W ratio of 0.6. Both the manus and pes traces are rotated outward from the trackway axis, the divarication being approximately 15° and 21°, respectively. The pace angulation of HMK-S1 is 89°. The ratio of manus area to pes area is 1:2.1. The (WAP/PL)-ratio is 1.25, a value indicating wide-gauge trackways (Marty, 2008).

HMK-S2RP1–RP2 (Fig. 6) are two pairs of medium-sized sauropod tracks (average length and width of the pes is 46 cm, 31 cm, respectively). The mean L/W ratio is 1.5. The average length and width of the manus are 23 cm and 28.3 cm, respectively. The mean L/W ratio is 0.8. Morphologically, the pes and the manus are basically consistent with HMK-S1RP2 and S1RM2. No left-side tracks were preserved for HMK-S2. Based on the outward rotation, the two pairs of tracks are estimated as right-side footprints. The ratio of manus area to pes area is 1:2.0.

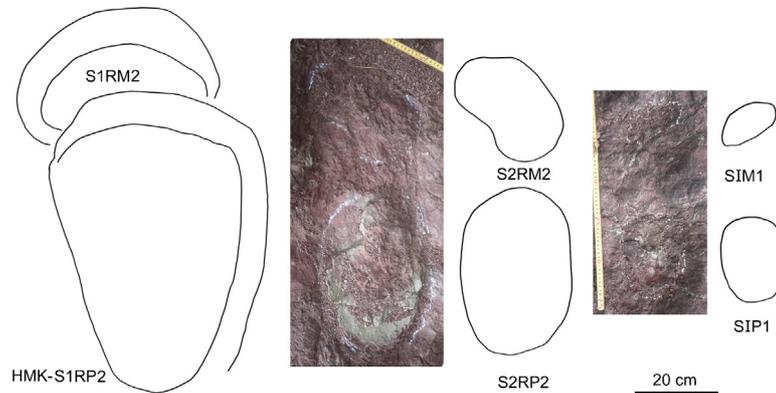


Fig. 6. Outline drawings and photographs of sauropod tracks from the Hemenkou tracksite.

HMK-SIP1 and SIM1 (Fig. 6) appear to be part of a trackway. The length and width of the pes is 21.2 cm and 15.7 cm, respectively, and its L/W ratio is 1.4. The length and width of the manus is 7.3 cm and 15.4 cm, respectively, and its L/W ratio is 0.5. Morphologically, except for the difference in size, HMK-SIP1 and SIM1 are basically consistent with other sauropod tracks at the tracksite. The main difference is the apparently long distance between the anterior edge of the pes and the posterior edge of the manus traces, which is almost as long as the length of the pes trace. Furthermore, the posterior margin of SIM1 is convex whereas, for example in S2RM2, it is concave. The ratio of manus area to pes area in SIM1 is 1:2.8.

Most wide-gauge sauropod trackways from China have been referred to the ichnogenus *Brontopodus* (Lockley et al., 2002). The large HMK-S1 sauropod tracks are congruent in shape with *Brontopodus* and are assigned here to this ichnogenus based on the following combination of features: (1) wide- (or medium-) gauge, (2) ratio of manus area to pes area of 1:2.0–2.8, (3) U-shaped manus tracks, and (4) pes tracks longer than wide (Farlow et al., 1989; Lockley et al., 1994).

5. Discussion

Theropod and sauropod tracks at the Hemenkou tracksite vary in size and quality of preservation. The hip heights of the three differently sized sauropod trackmakers at the Hemenkou tracksite can be calculated at approximately 3.6 m, 2.7 m, and 1.3 m based on the estimates of Thulborn (1990; hip height = $5.9 \times$ foot length). The body length: hip height ratio of *Shunosaurus* (a typical Middle Jurassic Chinese sauropod) is 3.7:1 (based on Farlow, 1992, fig. 3). The body lengths of the Hemenkou sauropod trackmakers are estimated to be approximately 13.4 m, 10.0 m, and 4.6 m (Fig. 7). For the theropod trackmakers of the Hemenkou tracksite, body lengths are estimated at 1.6 m (HMK-T1 and T2) and 4.6 m (HMK-T3), respectively, using the average hip height to body length ratio of 1:2.63 (Xing et al., 2009b) and the formula hip height $\approx 4 \times$ footprint length (Henderson, 2003) (Fig. 7). It has to be noted that body length values may vary due to different relative lengths of the tail (Hone, 2012).

The theropod tracks at the Hemenkou tracksite exhibit an interesting association that includes typical small and medium

grallatorids with low digit divarication angles, a grallatorid with wider divarication angles, and a large morphotype cf. *Eubrontes*. It suggests the presence of at least three different individuals of theropod trackmakers. Some individual tracks exhibit a wider digit divarication, probably due to wet and soft sediments and variation of sediment consistency (Xing et al., 2014c). Interestingly, HMK-T1 tracks generally show a wider divarication of digits II–IV. This suggests that the trackmaker differs from those of typical grallatorid tracks that show a narrow divarication. Theropod tracks with similar sizes but different L/W ratios and mesaxony (moderate to strong mesaxony vs. weak mesaxony) are not rare, as exemplified by Grallatoridae indet. and *Corpulentapus* from the Lower Cretaceous of the Zhucheng area, Shandong Province, China (R.H. Li et al., 2011), and Grallatoridae indet. and *Paracorpulentapus* from the Upper Cretaceous of the Qiyunshan area, Anhui Province, China (Xing et al., 2014d).

The naming of theropod tracks, especially those associated with the *Grallator–Eubrontes* plexus (Olsen et al., 1998), abundantly represented in the Jurassic, has proved difficult for many reasons, including the conservative morphology of the theropod foot. Despite this, too many theropod tracks have been named, especially from the Jurassic of China, without adequate comparative analysis of similar tracks from other regions (Lockley et al., 2013). Thus, even when given ichnotaxonomic labels, theropod tracks are of little biostratigraphic (ichnostratigraphic) use. In recent years it has also become apparent that grallatorid tracks (cf. *Grallator* sensu stricto) are abundant in the Cretaceous of China (Matsukawa et al., 2006; Lockley et al., 2012, 2013, 2014b). Therefore, in this study we refrain from naming the grallatorid tracks unequivocally, and point out that the age determination of the Hemenkou site is based on geological evidence, not on ichnostratigraphy. As noted above, we also argue that there is little evidence for the claim of Fujita et al. (2008) that the large tridactyl tracks represent ornithopod trackmakers.

No sauropod tracks have been reported previously from the Upper Jurassic of China, most having been reported from the Early Cretaceous strata. Most of the Early Cretaceous sauropod tracks in East Asia have been attributed to wide gauge *Brontopodus* (Lockley et al., 2002) and to narrow gauge *Parabrontopodus* (Xing et al., 2013c). Additionally, some tracks were yielded from the Lower Jurassic, such as the Dazu (Lockley and Matsukawa,

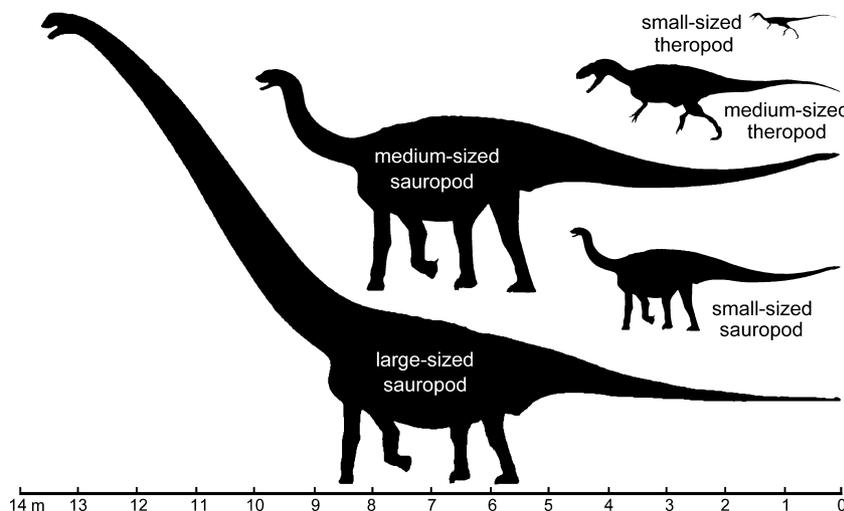


Fig. 7. Different sizes of sauropod and theropod trackmakers from the Hemenkou tracksite.

2009) and the Zigong tracksites (Xing et al., 2014e). An isolated sauropod pes trace was also discovered from the Middle Jurassic at the Beikeshan tracksite, Yunnan (Xing et al., 2014b).

Rare skeletons of basal eusauropods (“mamenchisaurids”) have been discovered in the Jurassic of central Yunnan (Fang et al., 2004). However, a dinosaur fauna also flourished in the nearby Jurassic Sichuan Basin, dominated by *Mamenchisaurus* and *Omeisaurus* (Peng et al., 2005). The large sauropod trackmakers at the Hemenkou tracksite may have had an affinity to basal eusauropods, whereas the medium and small sauropod trackmakers were either adult eusauropods or represented immature individuals of large forms.

Although saurischian (theropod and sauropod) track assemblages are common in the Jurassic of China (Matsukawa et al., 2006), they are nevertheless important in adding to the growing track record. These datasets establish that such assemblages are representative of the faunas of that period, and are supported quite consistently by the skeletal data, even though in places this is sparse. Thus, we argue it is justifiable to compare the track and skeletal record, especially from coeval formations and epochs in the region, to suggest possible correlations. These are presented here with the understanding that they are reasonable inferences, not definitive track–trackmaker correlations. The diversity of theropod and sauropod tracks at the Hemenkou tracksite provides an important addition to the dinosaurian fauna of central Yunnan, which lacks a theropod skeletal record and has yielded only rare sauropod body fossils. These tracks suggest that the dinosaur fauna flourished in the Jurassic in central Yunnan and survived into the Cretaceous: e.g., tyrannosauroid teeth have been found in the Lower Cretaceous strata of western Yunnan (Ye, 1975), whereas the Lower Cretaceous strata at the Baomanjie area of Chuxiong have yielded abundant sauropod trackways and poorly-preserved theropod trackways (Lockley et al., 2002).

6. Conclusions

1) All presently available geological and biostratigraphic evidence indicates that the Hemenkou tracksite is ?Middle–Late

Jurassic rather than Cretaceous in age (contra Fujita et al., 2008).

- 2) The ichnofauna consists of an exclusive saurischian track assemblage with tracks and trackways of theropods and sauropods. Former inferences that ornithopod tracks may be present is not supported.
- 3) Despite the poor preservation of many tracks, the size range of both theropod and sauropod tracks suggests that the track-making ichnofauna was quite diverse.
- 4) The track assemblage is consistent with the known Jurassic skeletal faunas of the region.

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