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Multiple parallel deinonychosaurian trackways from a diverse dinosaur track assemblage of the Lower Cretaceous Dasheng Group of Shandong Province, China

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ABSTRACT

Many newly-discovered dinosaur tracksites have recently been reported from the Lower Cretaceous Dasheng Group of Shandong Province. These are proving valuable as tools for characterizing the fauna in deposits almost devoid of body fossils. Here we report on a new Cretaceous site, the 14th documented in recent years, with multiple track-bearing levels, that adds ~300 tracks to a growing database. At least two morphotypes tentatively labelled as cf. *Menglongpus* isp., representing a deinonychosaur, and cf. *Tatarornipes* isp., representing an avian theropod, add to the list of at least seven named ichnogenera attributed to avian and non-avian theropods reported from the Dasheng Group in Shandong Province. Combined with two sauropodomorph and two ornithopod ichnogenera, and unnamed turtle tracks, the genus-level ichnodiversity (~14) is one of the highest reported for any Cretaceous unit either regionally in China or globally.

The tracks identified as cf. *Menglongpus* isp. occur in four parallel trackways indicating a group of small didactyl bipeds of inferred deinonychosaurian affinity. Despite the lack of body fossils from the Dasheng Group in Shandong Province, a high diversity of deinonychosaur body fossils is known from the contemporary Jehol Biota from northeastern China. This similarity underscores the importance of the Shandong track assemblage as indicators of regional, tetrapod biodiversity during the Cretaceous.

1. Introduction

Chinese Cretaceous dinosaur tracks are best known and most abundantly reported in Inner Mongolia (Lockley et al., 2002), Sichuan Basin (Jiaguan Formation) (Xing and Lockley, 2016) and the Yishu fault zone in Shandong Province (Xing et al., 2013a; Li et al., 2015). The latter region, the subject of this report, boasts a remarkable concentration and diversity of tracksites, currently numbering 13 with multiple track-bearing levels each representing a separate sample. These track records are important substitutes of local Early Cretaceous skeletons which are absent.

The Yishu fault zone, aligned from Zhucheng to Junan, Linshu and Tancheng, between Shandong Province and northern Jiangsu Province, is part of the famous Tanlu (=Tan-Lu) fault zone in northeastern China (Zhang et al., 2003). The Yishu fault zone area has extensive outcrops of Jurassic–Cretaceous strata, bearing abundant dinosaur tracks. Xing et al. (2015a) summarized data on thirteen dinosaur tracksites, which are all Lower Cretaceous sties except for the Yangzhuang site, which is from the Middle–Upper Jurassic Zibo Group (Li et al., 2002). Recently, a large-scale track site from Nanquan has been reported by Xing et al. (2018a), with a

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diverse sauropod-theropod-dominated track assemblage. The former 13 tracksites can be further divided into five sites from the Laiyang Group and eight sites from the Dasheng Group. The Huanglonggou site is the most important of the Laiyang Group (Valanginian–Barremian) sites and thought to be China's largest dinosaur tracksite with more than 2200 dinosaur footprints, including diverse theropod (*Grallator yangi* and *Corpulentapus lilasia*), sauropod and turtle tracks (Li et al., 2011; Lockley et al., 2015). Among the Dasheng Group (Barremian–Aptian) sites, the most important are the Houzuoshan site with diverse theropod, ornithopod and bird tracks (Lockley et al., 2007, 2008; Li et al., 2015), and the Jishan site with diverse small- and large-sized sauropod, theropod and possible psittacosaur tracks (Xing et al., 2013a).

Diverse didactyl tracks from the Dasheng Group indicate relatively abundant deinonychosaurian trackmakers in this area during the Early Cretaceous. Abundant psittacosaurian (ceratopsian) remains were found in nearby Early Cretaceous deposits in Shandong Province. Young (1958) described these specimens and named them *Psittacosaurus sinensis*. These records correspond to possible psittacosaur tracks from the Jishan site (Xing et al., 2013a). The Jehol Biota has equally abundant deinonychosaurian and psittacosaur records.

In spring of 2015, one of the authors (TY) found a group of tracks near a man-made pond in Houmotuan (GPS: 34°51′33.14N, 118°26′4.84E) (Fig. 1), 3.6 km southeast of Lizhuang Town, Tancheng County. The tracksites described here are located in the Yishu fault zone. In April 2017, a field team (XL, TY, JZ, YW, YG, and XW) investigated these sites and conducted a detailed study of didactyl tracks and other theropod tracks and sauropod tracks from the Houmotuan site.

Institutional abbreviations

HMT = Houmotuan site, Shandong Province, China

Ichnological abbreviations

ML = maximum length, MW = maximum width, II–IV = divarication angle between digits II and IV, PL = pace length, SL = Stride length, h = hip height, SL/h = relative stride length, PA = pace angulation, R = rotation of footprints relative to the midline.

2. Geological setting

The most prominent geologic feature in East China is a regional fault zonethe Tanlu fault zone, which has experienced a prolonged and complex structural geological history involving strike-slip, compression or extension, and controlled development of a series of Mesozoic and Cenozoic sedimentary basins along its route. The part of this zone passing through Shandong Province is the Yishu fault zone, which is about 20–60 km wide, stretches from north to east for about 300 km and comprises four faults aligned in the same direction including, from east to west, the Changyi–Dadian, Aanqiu–Juxian, Yishui–Tangtou and Tangwu–Gegou faults (Xu et al., 1982). The Shuhe rift valley, to the east of the Yishu fault zone, is a linear valley controlled by the Changyi–Dadian and Aanqiu–Juxian faults. Cretaceous strata in this area are divided into the Lower Cretaceous Laiyang Group, the Qingshan Group and the Dasheng Group and the Upper Cretaceous Wangshi Group (Tan, 1923).

The Lower Cretaceous Dasheng Group in Shandong represents a set of alluvial fan–fluvial–lacustrine facies of detrital rocks mixed with muddy limestone (Xing et al., 2015a). The Houmotuan site, described here, belong to the Lower Cretaceous Tianjialou Formation of the Dasheng Group (Fig. 2). The Tianjialou and Mengtuan formations form the majority of the Jiaolai Basin deposits, which are a set of >500 m-thick lacustrine facies deposits dominated by dark gray, yellow green, purple detrital rocks, occasionally mixed with dolomitic mudstones and micrite dolomite (dolomicrite). The dinosaur tracks are from siltstone and sandstone layers, some of

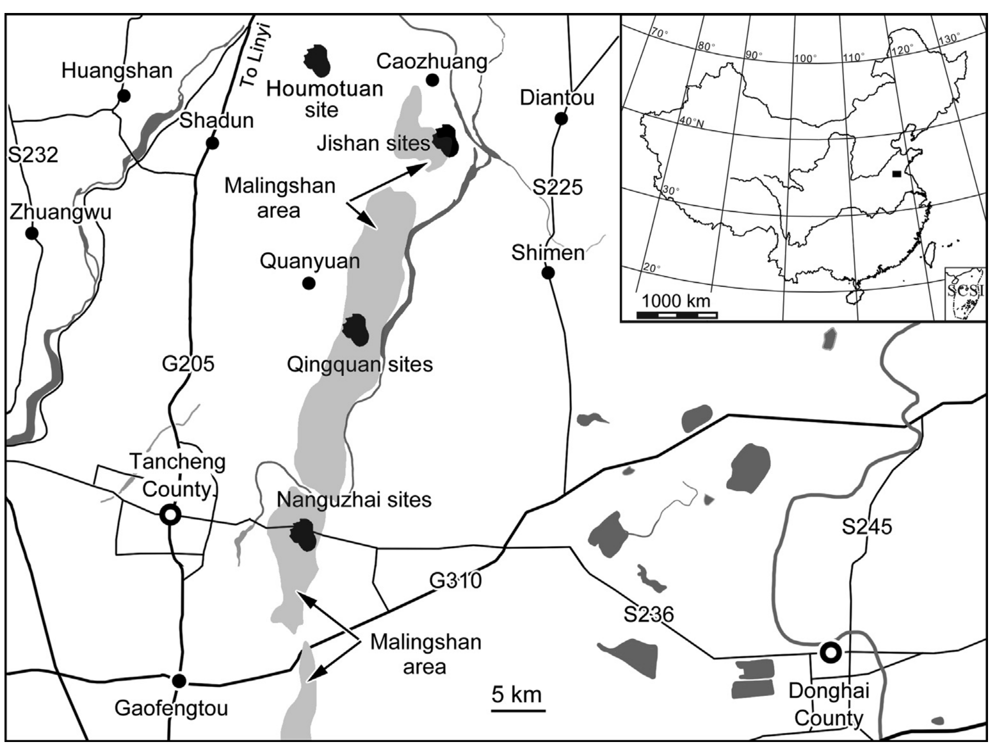

Fig. 1. Location of the Houmotuan, Qingquan, and the Jishan and Nanguzhai tracksites (indicated by sauropod pes track icons) in Shandong Province, China.

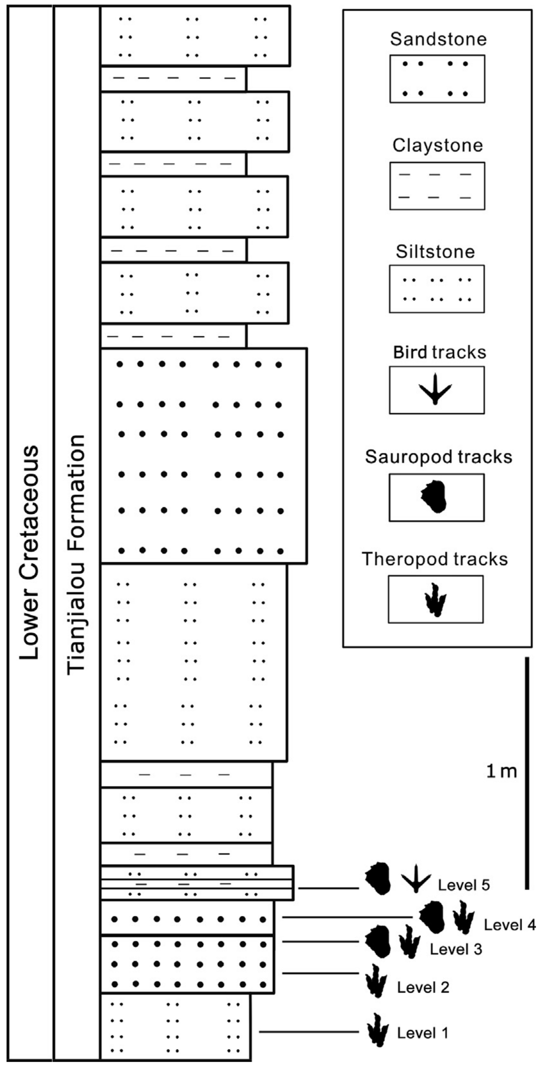

Fig. 2. Stratigraphic section of Lower Cretaceous strata as logged at the Houmotuan tracksite with the position of the track-bearing levels.

which have ripple marks. The sediments suggest a shallow lake environment with calcareous concretions horizons developed in the Tianjialou/Mengtuan formations (Kuang et al., 2013).

3. Methods and materials

The dinosaur tracks from HMT are preserved on an outcrop in farmland (Fig. 3). Most of the outcrop is covered by a pond, and various round sauropod tracks can be seen submerged below the waterline. There are at least 5–6 track-bearing layers. The flat rock surface had been used for refuse disposal and required extensive cleaning by hand to see and study the tracks adequately. The material is distributed as follows:

1) Level 1, which spreads over Area 1, preserves dense theropod tracks, including 20 trackways and 20 isolated tracks, and also reveals ripple marks.
2) Level 2, which spreads over Area 2, preserves five theropod tracks, including two trackways and one isolated track, and also reveals ripple marks.
3) Level 3 spreads over Area 3 and Area 4. The part in Area 3 reveals poorly preserved sauropod tracks and a few theropod tracks. The tracks in Area 4 lie alongside a pond and yield badly weathered saurischian tracks, dominantly sauropod tracks.
4) Level 4, extends over Area 5 and Area 6. Area 5 well preserves sauropod tracks and less theropod tracks and Area 6 preserves a few sauropod tracks and theropod tracks.
5) Level 5, which spreads over Area 7, preserves sauropod tracks and bird tracks.

It is unclear to which level Area 8 belongs. It revealed an isolated theropod track from a pile of rock which may have originated from a higher level.

After extensive cleaning of the site surfaces, all tracks were examined, outlined with chalk, and finally photographed by the field team (XL, TY, JZ, YW, YG, and XW). All trackways and track assemblages were traced with transparent plastic and acetate sheets. Maps of the more important surfaces and trackway segments were produced using a combination of photographs and tracings.

Measurements were taken at the site from original tracks, using standard procedures established by Leonardi (1987) and Lockley and Hunt (1995). Alexander's (1976) formula was employed to estimate trackmaker speeds from trackways whereas the methods proposed by Alexander (1976) and Thulborn (1990) were applied to estimate the hip heights. Relative stride length (SL/h) was calculated using the method of Thulborn (1990) to determine whether the trackmaker was walking, trotting or running. For a small theropod (P'ML < 25 cm), Thulborn (1990) suggests that hip height $h = 4.5*ML$. The relative stride length (SL/h) may be used to determine whether the animal is walking ($SL/h \leq 2.0$), trotting ($2 < SL/h < 2.9$), or running ($SL/h \geq 2.9$) (Alexander, 1976; Thulborn, 1990).

Using the ratio between the width of the angulation pattern of the pes (WAP) and the pes length (PL), gauge (trackway width) was quantified for pes and manus tracks in the trackways of quadrupeds (Marty, 2008; Marty et al., 2010). The pes tracks are likely to intersect the trackway midline if the (WAP/PL)-ratio is less than 1.0, which meets the definition of narrow-gauge (Farlow, 1992). Therefore, 1.0 is considered a threshold separating narrow-gauge from medium-gauge trackways, whereas 1.2 is considered the boundary between medium-gauge and wide-gauge trackways, with the boundary for defining very wide-gauge trackways set at values higher than 2.0 (Marty, 2008).

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) according to Olsen (1980), Weems (1992), and Lockley (2009), thereby defining an anterior triangle. In most cases, there is also a positive correlation between the L/W ratio of the anterior triangle (an index of mesaxony) and that of the whole track.

Measurements from deinonychosaur skeletons of Jehol Biota were taken in order to calculate potential track dimensions. Track lengths were calculated based on the length of digit III and the lengths of the claw corneum and metatarsal bone sections. In some cases, body lengths were estimated based on the tracks, using the track-to-length formula.

4. Description of tracks and trackways

4.1. Didactyl theropod tracks

4.1.1. General observations

We mapped four almost completely continuous trackway segments (HMT-T22 to T25), oriented N to NNE, each with between 15 and 18 recognizable tracks (Figs. 4 and 5; Table 1). The trackways all represent small trackmakers (footprint lengths ~7.0 cm). Although

Fig. 3. Locality map, based in part on modified Google satellite image showing Houmotuan main outcrops.

the tracks have suboptimal preservation, close inspection of individual tracks suggests that the trackmakers were functionally didactyl, thus probably of deinonychosurian affinity like others from the Lower Cretaceous of Shandong. However, unlike the tracks of most previously described deinonchosaurian ichnotaxa, it is difficult to determine the relative length of the trace of digit IV, which generally appears to be short, but shows considerable large variation in length, due to different substrate conditions and the dynamics of the foot. Likewise traces of the proximal digit II pad are generally lacking or ambiguous. This is not an unusual preservational pattern in small deinoychosurian tracks, as for example in *Menglongipus* isp. (Xing et al., 2009a).

The superficial impression given by the tracks in these four trackways is that they are monodactyl. Monodactyl tracks, or tracks that appear to have been made by monodactyl trackmakers are rare in the fossil record, but have been described by Casamiquela (1964) from the mid Jurassic of Argentina as *Sarmientichnus scagliai*. This track type also represented a small trackmaker (footprint length 13 cm, width 3.9 cm) with a very narrow trackway. The type material is represented only by an isolated track and a single trackway.

Although monodactyl theropod dinosaurs are not known from the skeletal record, and no extant avian is monodactyl, functionally-didactyl, deinonychosaurian trackmakers are well-known (e.g., the extant ostrich (*Struthio* sp.)). Thus, it is more parsimonious to conclude that the Houmotuan tracks likely represent a didactyl trackmaker than an unknown monodactyl species.

We must also consider track preservation. It is known that modern birds (theropods) vary the divarication of their digits considerably during the step cycle, thus potentially widening or narrowing the divarication of digit traces in footprints (e.g., Gatesy et al., 1999). If a slender-toed didactyl or tridactyl theropod was to register its footprint with toes held closely together, it could leave what appears to be a monodactyl track. In this case individual digit traces are unseparated or undifferentiated, falsely pretending a monodactyl pes. This could be true, for example, in *Sarmentichnus scagliai*. The ichnotaxon could reflect a repeated behavioural peculiarity that could be of ichnotaxonomic significance for other footprints, such as those decribed from the Dasheng Group. In future, the following questions should be discussed: 1) Why are ostensibly theropod tracks, superficially monodactyl in appearance, reported so rarely among the vast majority that are clearly tridactyl or didactyl? 2) Is the monodactyl appearance related to trackmaker pes anatomy/behaviour, an unusual preservation and extramor-

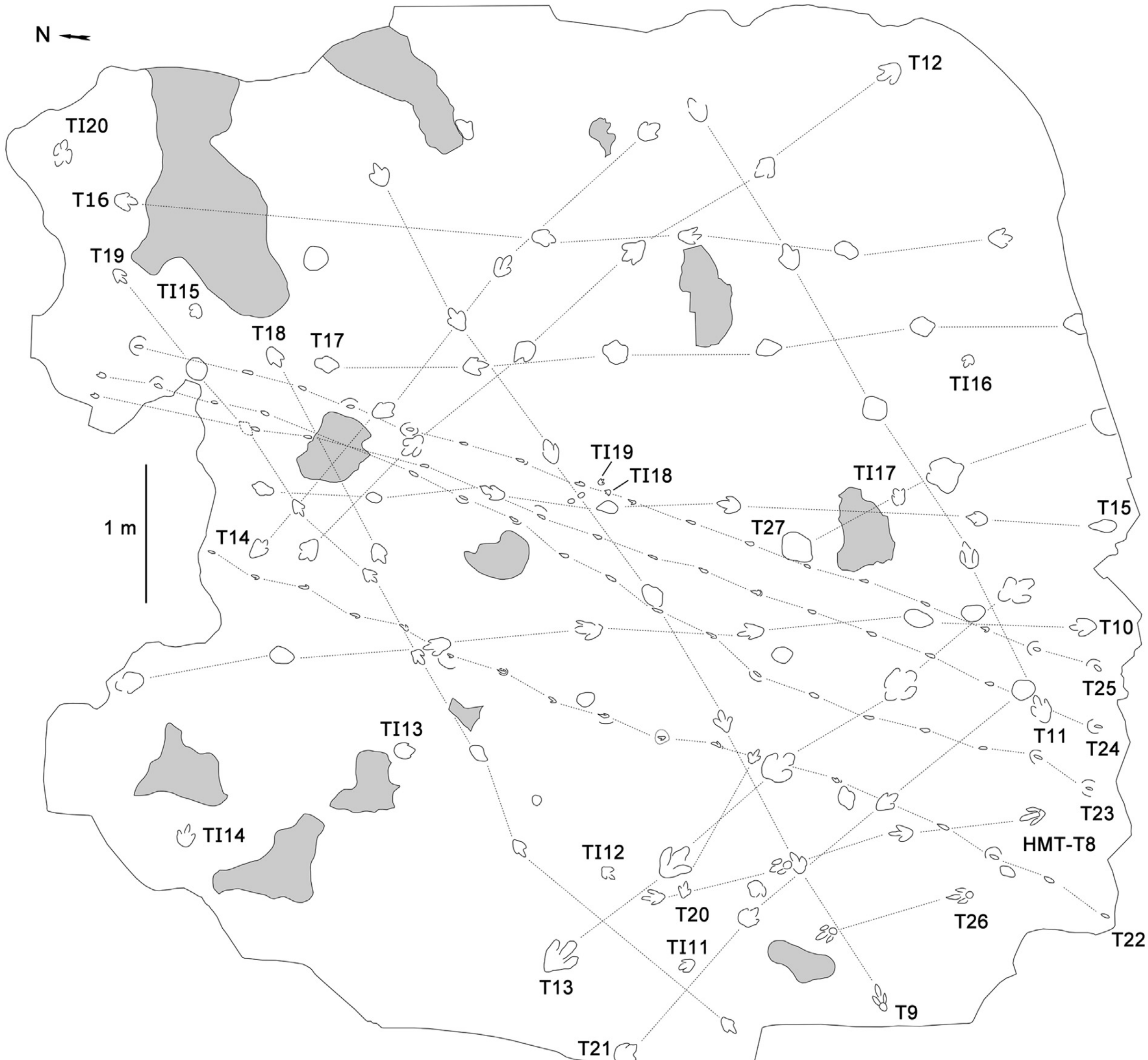

Fig. 4. Interpretative outline drawing at Houmotuan Tracksite Area 1 with theropod trackways.

phological effect, or a combination of both ? Other possibilities, such as the presence of pathological features, for example an injury of the foot, can be excluded, because the phenomenon of "monodactyly" occurs repeatedly in different trackways.

Working on the cardinal assumption that ichnotaxonomy should be based on footprint morphology that reliably reflects trackmaker morphology, rather than extra-morphological, preservation-related factors, digit divarication must be considered. Digit divarication is a diagnostic factor often used in differentiating between ichnotaxa, or at least ichnno-morphotypes, as for example in the typical distinction between narrowly divaricated *Grallator* isp. tracks, made by theropods, and more widely divaricated *Anomoepus* tracks of presumed ornithischian affinity (Hitchcock, 1858 and many subsequent references). These ichnotaxonomic differences may also be emphasized by differences in mesaxony. Thus, many grallatorid morphotypes show pronounced, or 'strong' mesaxony as in the small ichnospecies *Neograllator emeiensis* (Zhen et al., 1994; Lockley, 2009) from the Lower Cretaceous of Sichuan. The Houmotuan tracks are also strongly mesaxonic: i.e., with digit III much longer than IV.

Given all these considerations we conclude that HMT-T22 to T25 were made by small theropods, with strongly mesaxonic feet that created narrow trackways. The presence of a long digit III trace, easily differentiated from that of digit IV in many tracks, rules out a monodactyl trackmaker. There is little obvious support for the inference that the trackmaker was a typical functionally-tridactyl species because all other theropod trackways at the site are clearly tridactyl, and there is no evidence to suggest that conditions of preservation where markedly different when these were made. We therefore regard the trackmaker as functionally didactyl and provisionally assign it to cf. *Menglongpus* isp. (Xing et al., 2009a).

4.1.2. Description

The HMT-T22 trackway exhibits a narrow stance with a pace angulation of 172°. These tracks average 7.4 cm long and 4.3 cm wide. The length: width ratio of HMT-T22 is 1.8. Discernible claw marks were observed on digits III and IV, with digit III as the most distinct. Compared with digits III and IV, the impression of digit II is either lacking or too indistinct to interpret with confidence. A digit II impression may be cautiously inferred for track HMT-T22-R6, as

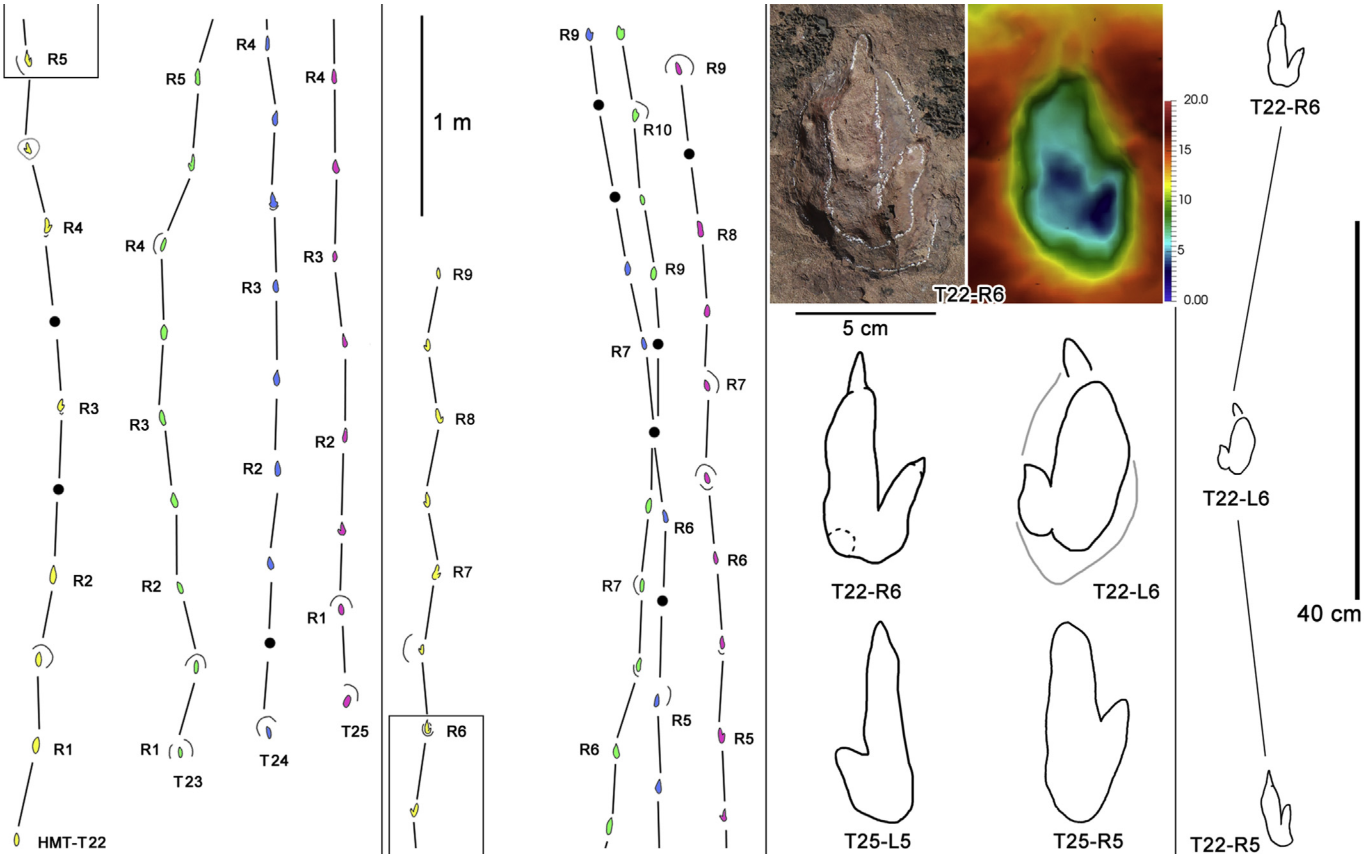

Fig. 5. Photograph, 3D image and interpretative outline drawing of didactyl theropod trackways at Houmotuan Tracksite Area 1.

partially embedded within the impression of digit III at its proximomedial edge. Digital pads are indistinct, but based on the photogrammetric image (Fig. 5) of this same track, some pad differentiation is visible in the traces of digits III and IV. The divarication angle between digits III and IV averages 32°. The metatarsophalangeal region is small; no distinct border demarcating a pad divides this region from either digit III or IV. For the trackway, the step lengths are 40.8 cm, 5.5 times longer than the track length. The tracks slightly rotate to the midline of the trackway (~7°).

HMT-23, 24 and 25 are morphologically similar to HMT-T22. Trackways HMT-23 and HMT-24 crossed over towards their ends. Intertrackway spacing (sensu Lockley, 1989) ranges from 30 to 88 cm, and total intertrackway spacing between HMT-22 and HMT-25 which are almost parallel, is 160 cm, giving an average spacing of ~53 cm.

4.1.3. Ichnotaxonomy and trackmaker identification

As noted above, the two digit impressions are interpreted as traces of digits III and IV, suggesting deinonychosaurian affinity. There have been a growing number of formally named ichnotaxa attributed to deinonychosaurian trackmakers, especially from Asia (Lockley et al., 2016a). These include relatively small (foot length ~10 cm) *Velociraptorichnus sichuanensis* (Zhen et al., 1994; Xing et al., 2009a), *Velociraptorichnus* isp. (Li et al., 2015) and *Menglongipus sinensis* (Xing et al., 2009a), medium sized (foot length 10–20 cm) *Dromaeosauripus hamanensis* (Kim et al., 2008), *Dromaeosauripus jinjuensis* (Kim et al., 2012), *Dromaeosauripus yongjingensis* (Xing et al., 2013b), *Velociraptorichnus zhangi* (Xing et al., 2015b) and *Dromaeosauripus* isp. from Utah (Lockley et al., 2016b), and large-sized tracks (mean pes length up to ~28 cm) such as *Dromaeopodus shandongensis* (Li et al., 2007) and *Dromaeopodus* isp.(Xing et al., 2016a).

The lengths of HMT didactyl tracks are <10 cm and fall into the small-sized deinonychosaurian tracks category. The distinctly short digit IV of HMT didactyl tracks is also atypical of *Velociraptorichnus* isp. and *Dromaeosauripus* isp., in which digit IV is almost as long as digit III. However, the HMT didactyl tracks are similar to *Menglongipus* isp., but there are some apparent differences. In the HMT didactyl tracks, the digit length ratio of III/IV is 2.3, whereas it is 1.8 in *Menglongipus* isp.. In the HMT-T22 tracks the trace of digit III is about twice as wide as digit IV, whereas these are more similar in width in *Menglongipus* isp., and the divarication angle between digits III and IV ranges from 16° to 38° (less than 40°–44° in *Menglongipus* isp.). These latter features (greater digit width and lower divarication angle) could provide some support for the interpretation that the trackmaker was strongly mesaxonic.

Step length in HMT-T22 is 5.5 times longer than track length (range 5.4–6.3, mean 5.8) for all 4 trackways, whereas the value is 7.6 in *Menglongipus* isp. There is also an age difference with *Menglongipus* isp. found in the Upper Jurassic–Lower Cretaceous Tuchengzi Formation (Tithonian–Valanginian) which is earlier than Lower Cretaceous Tianjialou Formation (Barremian–Albian).

Unnamed didactyl tracks with a relatively short digit IV were reported from the Early Cretaceous (Berriasian) of Obernkirchen, northern Germany (van der Lubbe et al., 2009, 2012; Lockley et al., 2016a). These trackways are narrow with a low pace angulation (170–180°). Track sizes range from a total track length 13.0 cm to a maximum of 23.3 cm. The angles of divarication between digit III and IV impressions range from 21 to 36° (average ~28°), and the

Table 1
Measurements (in cm and °) of theropod and bird tracks from Houmotuan tracksite, Shandong Province, China.

Number	ML	MW	II-IV	PL	SL	PA	L/W
HMT-T1-L1	–	13.5	–	85.5	–	–	–
HMT-T1-R1	–	–	–	–	118.0	–	–
HMT-T1-L2	–	–	–	–	–	–	–
HMT-T1-R2	17.5	11.5	60	74.0	–	–	1.5
HMT-T1-L3	17.0	12.0	50	–	–	–	1.4
Mean	17.3	12.3	55	79.8	118.0	–	1.5
HMT-T2-L1	17.5	13.0	66	105	–	–	1.3
HMT-T2-R1	18.0	11.0	55	–	–	–	1.6
Mean	17.8	12.0	61	105.0	–	–	1.5
HMT-T3-R1	24.0	14.0	51	94	–	–	1.7
HMT-T3-L1	24.0	17.0	–	–	–	–	1.4
Mean	24.0	15.5	51	94.0	–	–	1.6
HMT-T4-L1	21.0	16.0	51	86.5	180.0	155	1.3
HMT-T4-R1	24.0	17.0	50	97.7	–	–	1.4
HMT-T4-L2	19.5	16.7	61	–	–	–	1.2
Mean	21.5	16.6	54	92.1	180.0	155	1.3
HMT-T5-L1	15.8	11.3	64	89.0	–	–	1.4
HMT-T5-R1	14.2	10.8	66	–	–	–	1.3
Mean	15.0	11.1	65	89.0	–	–	1.4
HMT-T6-R1	27.5	23	69	121	–	–	1.2
HMT-T6-L1	31.0	22	61	–	–	–	1.4
Mean	29.3	22.5	65.0	121.0	–	–	1.3
HMT-T7-R1	32.5	31	63	105	–	–	1.0
HMT-T7-L1	–	–	–	–	–	–	–
Mean	32.5	31	63	105	–	–	1.0
HMT-T8-L1	19.5	12.0	49	98.0	189.0	168	1.6
HMT-T8-R1	18.0	11.5	52	92.0	187.5	180	1.6
HMT-T8-L2	18.0	10.0	35	95.5	–	–	1.8
HMT-T8-R2	17.5	10.5	48	–	–	–	1.7
Mean	18.3	11.0	46	95.2	188.3	174	1.7
HMT-T9-R1	21.5	10.0	40	118.0	234.5	180	2.2
HMT-T9-L1	18.0	–	–	116.0	219.0	180	–
HMT-T9-R2	17.5	12.5	63	103.0	229.5	169	1.4
HMT-T9-L2	19.0	13.5	–	127.5	245.0	180	1.4
HMT-T9-R3	18.5	11.0	47	116.5	229.0	162	1.7
HMT-T9-L3	19.5	12.0	50	115.5	–	–	1.6
HMT-T9-R4	18.5	12.5	53	–	–	–	1.5
Mean	18.9	11.9	51	116.1	231.4	174	1.6
HMT-T10-R1	19.5	12.0	48	121.5	244.0	180	1.6
HMT-T10-L1	21.0	12.0		122.0	241.0	180	1.8
HMT-T10-R2	20.5	14.0	46	118.5	230.0	167	1.5
HMT-T10-L2	21.0	13.0	47	113.0	227.0	172	1.6
HMT-T10-R3	21.0	11.5	39	114.5	225.5	180	1.8
HMT-T10-L3	19.0	12.0	–	110.5	–	–	1.6
HMT-T10-R4	20.5	14.0	–	–	–	–	1.5
Mean	20.4	12.6	45	116.7	233.5	176	1.6
HMT-T11-R1	21.5	12.0	40	125.0	248.0	170	1.8
HMT-T11-L1	20.0	10.5	38	124.0	247.5	180	1.9
HMT-T11-R2	20.0	15.0	–	123.5	–	–	1.3
HMT-T11-L2	19.5	13.5	66	–	–	–	1.4
HMT-T11-R3	20.0	12.5	–	–	–	–	1.6
Mean	20.2	12.7	48	124.2	247.8	175	1.6
HMT-T12-R1	19.5	15.0	60	113.5	227.5	180	1.3
HMT-T12-L1	19.0	13.5	–	113.7	221.0	168	1.4
HMT-T12-R2	21.0	15.0	47	108.5	215.0	180	1.4
HMT-T12-L2	19.0	12.5	–	105.0	213.0	180	1.5
HMT-T12-R3	20.0	12.5	44	108.0	–	–	1.6
HMT-T12-L3	19.5	13.0	52	–	–	–	1.5
Mean	19.7	13.6	51	109.7	219.1	177	1.5
HMT-T13-L1	31.5	20.5	45	110.0	213.0	180	1.5
HMT-T13-R1	29.0	21.0	59	103.0	206.5	172	1.4
HMT-T13-L2	27.5	18.0	52	104.0	212.0	180	1.5
HMT-T13-R2	29.0	20.0	46	108.0	–	–	1.5
HMT-T13-L3	28.0	17.5	60	–	–	–	1.6
Mean	29.0	19.4	52	106.3	210.5	177	1.5

Table 1 (*continued*)

Number	ML	MW	II-IV	PL	SL	PA	L/W
HMT-T14-L1	17.5	11.0	42	137.0	271.0	173	1.6
HMT-T14-R1	18.0	11.5	53	134.5	–	–	1.6
HMT-T14-L2	18.0	11.5	53	–	–	–	1.6
HMT-T14-R2	18.5	12.0	58	–	–	–	1.5
Mean	18.0	11.5	52	135.8	271.0	173	1.6
HMT-T15-R1	19.0	8.5	–	91.0	–	–	2.2
HMT-T15-L1	16.0	10.0	49	–	178.5	–	1.6
HMT-T15-R2	–	–	–	–	–	–	–
HMT-T15-L2	17.5	10.0	50	90.0	173.5	168	1.8
HMT-T15-R3	16.0	9.5	–	84.5	174.5	171	1.7
HMT-T15-L3	20.0	9.0	45	90.5	171.0	–	2.2
HMT-T15-R4	12.0	7.5	–	80.0	–	–	1.6
HMT-T15-L4	17.0	9.0	–	–	–	–	1.9
Mean	16.8	9.1	48	87.2	174.4	170	1.9
HMT-T16-R1	18.0	11.5	55	–	–	–	1.6
HMT-T16-L1	–	–	–	–	–	–	–
HMT-T16-R2	–	–	–	–	–	–	–
HMT-T16-L2	18.0	11.0	46	108.0	222.0	180	1.6
HMT-T16-R3	18.0	11.5	50	114.0	225.0	180	1.6
HMT-T16-L3	18.5	11.0	–	111.0	–	–	1.7
HMT-T16-R4	16.5	12.0	47	–	–	–	1.4
Mean	17.8	11.4	50	111.0	223.5	180	1.6
HMT-T17-R1	18.5	11.0	–	110.5	213.5	169	1.7
HMT-T17-L1	20.0	12.5	53	104.0	216.0	172	1.6
HMT-T17-R2	19.0	15.0	–	112.5	224.0	167	1.3
HMT-T17-L2	19.0	11.0	–	113.0	222.0	167	1.7
HMT-T17-R3	18.0	12.5	60	110.5	–	–	1.4
HMT-T17-L3	–	13.0	–	–	–	–	–
Mean	18.9	12.5	57	110.1	218.9	169	1.5
HMT-T18-L1	17.0	11.0	46	–	162.5	–	1.5
HMT-T18-R1	–	–	–	–	–	–	–
HMT-T18-L2	16.5	11.0	51	–	–	–	1.5
Mean	16.8	11.0	49	–	162.5	–	1.5
HMT-T19-R1	13.5	8.5	52	–	138.5	–	1.6
HMT-T19-L1	–	–	–	–	–	–	–
HMT-T19-R2	13.5	–	–	–	–	–	–
HMT-T19-L2	14.0	8.0	48	72.0	138.0	158	1.8
HMT-T19-R3	14.0	9.0	51	68.5	148.0	171	1.6
HMT-T19-L3	13.0	8.5	57	80.0	154.0	167	1.5
HMT-T19-R4	15.5	9.0	49	75.0	–	–	1.7
HMT-T19-L4	15.0	9.0	48	–	–	–	1.7
HMT-T19-R5	–	–	–	–	–	–	–
HMT-T19-L5	15.5	9.0	49	–	201.5	–	1.7
Mean	14.3	8.7	51	73.9	156.0	165	1.7
HMT-T20-L1	13.0	9.0	63	109.5	–	–	1.4
HMT-T20-R1	13.0	9.0	63	–	–	–	1.4
Mean	13.0	9.0	63	109.5	–	–	1.4
HMT-T21-L1	19.0	15.0	48	133.0	261.0	166	1.3
HMT-T21-R1	17.0	12.0	58	130.0	258.0	173	1.4
HMT-T21-L2	18.5	11.0	46	128.5	–	–	1.7
HMT-T21-R2	17.5	14.0	–	–	–	–	1.3
Mean	18.0	13.0	51	130.5	259.5	170	1.4
HMT-T22-L1	5.5	–	–	46.0	90.0	180	–
HMT-T22-R1	8.5	–	–	43.0	86.5	180	–
HMT-T22-L2	8.0	–	–	42.5	88.5	–	–
HMT-T22-R2	9.0	–	–	–	–	–	–
HMT-T22-L3	–	–	–	–	–	–	–
HMT-T22-R3	7.0	3.5	26		90.0		2.0
HMT-T22-L4	–	–	–	–	–	–	–
HMT-T22-R4	8.0	4.0	38	41.0	84.5	168	2.0
HMT-T22-L5	6.0	3.5	36	44.0	84.5	180	1.7
HMT-T22-R5	9.0	4.0	16	40.5	83.0	167	2.3
HMT-T22-L6	7.5	4.0	38	43.0	81.5	180	1.9
HMT-T22-R6	7.5	4.5	32	38.5	77.0	167	1.7
HMT-T22-L7	6.0	4.0	32	39.0	75.0	180	1.5
HMT-T22-R7	8.0	5.0	33	35.5	78.0	167	1.6
HMT-T22-L8	8.5	5.0	32	43.0	79.5	158	1.7
HMT-T22-R8	8.0	5.0	34	38.0	73.0	161	1.6
HMT-T22-L9	6.5	4.5	33	36.0	–	–	1.4
HMT-T22-R9	6.0	–	–	–	–	–	–
Mean	7.4	4.3	32	40.8	82.4	172	1.8

Table 1 (*continued*)

Number	ML	MW	II-IV	PL	SL	PA	L/W
HMT-T23-R1	6.0	–	–	43.0	84.5	168	–
HMT-T23-L1	7.0	–	–	42.0	85.5	168	–
HMT-T23-R2	6.5	–	–	44.0	86.0	180	–
HMT-T23-L2	7.5	–	–	41.5	85.0	180	–
HMT-T23-R3	9.0	–	–	43.5	87.5	163	–
HMT-T23-L3	8.0	–	–	45.0	86.0	159	–
HMT-T23-R4	7.5	–	–	42.5	85.0	180	–
HMT-T23-L4	9.0	5.0	22	42.5	83.0	167	1.8
HMT-T23-R5	9.0	–	–	41.0	78.5	158	–
HMT-T23-L5	9.0	–	–	39.0	83.0	167	–
HMT-T23-R6	8.0	–	–	44.5	84.5	180	–
HMT-T23-L6	7.5	–	–	40.0	80.0	180	–
HMT-T23-R7	7.5	–	–	40.0	–	–	–
HMT-T23-L7	8.0	–	–	–	–	–	–
HMT-T23-R8	–	–	–	–	–	–	–
HMT-T23-L8	–	–	–	–	–	–	–
HMT-T23-R9	6.5	–	–	41.5	–	–	–
HMT-T23-L9	8.5	–	–	–	–	–	–
Mean	7.8	5.0	22	42.1	84.0	171	1.8
HMT-T24-L1	7.0	–	–	–	85.5	–	–
HMT-T24-R1	–	–	–	–	–	–	–
HMT-T24-L2	6.5	–	–	47.5	93.5	168	–
HMT-T24-R2	8.0	–	–	46.5	93.0	151	–
HMT-T24-L3	9.0	–	–	49.5	90.0	156	–
HMT-T24-R3	7.0	–	–	42.5	83.5	180	–
HMT-T24-L4	7.0	–	–	41.0	79.5	180	–
HMT-T24-R4	7.5	–	–	38.5	82.0	167	–
HMT-T24-L5	7.5	–	–	44.0	86.5	163	–
HMT-T24-R5	7.5	–	–	43.5	–	–	–
HMT-T24-L6	7.0	–	–	–	94.0	–	–
HMT-T24-R6	–	–	–	–	–	–	–
HMT-T24-L7	6.5	–	–	–	88.0	–	–
HMT-T24-R7	–	–	–	–	–	–	–
HMT-T24-L8	6.5	–	–	36.5	75.0	167	–
HMT-T24-R8	7.0	–	–	39.0	82.0	180	–
HMT-T24-L9	5.5	–	–	42.5	86.0	180	–
HMT-T24-R9	6.5	–	–	43.0	–	–	–
HMT-T24-L10	7.0	–	–	–	–	–	–
Mean	7.1	–	–	42.8	86.0	169	–
HMT-T25-L1	7.0	–	–	47.0	88.0	180	–
HMT-T25-R1	6.0	–	–	41.5	89.5	180	–
HMT-T25-L2	7.5	5.0	38	48.5	95.0	180	1.5
HMT-T25-R2	7.5	–	–	46.5	89.5	180	–
HMT-T25-L3	7.5	–	–	43.0	87.5	180	–
HMT-T25-R3	6.0	–	–	44.0	88.5	180	–
HMT-T25-L4	7.5	–	–	45.5	89.0	180	–
HMT-T25-R4	7.5	–	–	46.0	86.0	180	–
HMT-T25-L5	7.0	4.5	35	40.0	87.0	180	1.6
HMT-T25-R5	8.0	4.0	24	48.0	91.0	180	2.0
HMT-T25-L6	7.5	–	–	43.5	84.5	180	–
HMT-T25-R6	7.0	–	–	42.5	89.5	180	–
HMT-T25-L7	6.5	–	–	47.0	–	–	–
HMT-T25-R7	6.5	–	–	–	–	–	–
Mean	7.1	4.5	32	44.8	88.8	180	1.7
HMT-T26-R1	18.0	10.0	44	103.0	–	–	1.8
HMT-T26-L1	16.5	11.0	54	–	–	–	1.5
Mean	17.3	10.5	49	103.0	–	–	1.7
HMT-TI1	19.0	14.0	52	–	–	–	1.4
HMT-TI2	27.5	19.0	59	–	–	–	1.4
HMT-TI3	18.0	11.0	54	–	–	–	1.6
HMT-TI4	21.5	15.0	56	–	–	–	1.4
HMT-TI5	18.0	10.0	49	–	–	–	1.8
HMT-TI6	20.0	16.0	60	–	–	–	1.3
HMT-TI7	20.5	15.0	61	–	–	–	1.4
HMT-TI10	30.0	23.5	61	–	–	–	1.3
HMT-TI11	13.0	9.0	46	–	–	–	1.4
HMT-TI12	13.5	9.0	63	–	–	–	1.5
HMT-TI13	16.5	9.5	48	–	–	–	1.7
HMT-TI14	17.0	12.0	60	–	–	–	1.4
HMT-TI15	10.5	9.0	58	–	–	–	1.2
HMT-TI16	10.5	8.5	65	–	–	–	1.2
HMT-TI17	12.5	9.5	55	–	–	–	1.3
HMT-TI18	4.5	4.0	67	–	–	–	1.1

Table 1 (*continued*)

Number	ML	MW	II-IV	PL	SL	PA	L/W
HMT-TI19	5.5	4.5	58	–	–	–	1.2
HMT-TI20	20.0	12.0	43	–	–	–	1.7
HMT-TI21	19.2	13.5	55	–	–	–	1.4
HMT-TI22	19.0	10.0	40	–	–	–	1.9
HMT-TI23	18.5	6.6	30	–	–	–	2.8
HMT-TI24	21.0	13.0	45	–	–	–	1.6
HMT-B1-L1	4.4	7.0	128	9.8	20.7	155	0.6
HMT-B1-R1	4.6	6.6	133	11.4	–	–	0.7
HMT-B1-L2	3.7	5.8	146	–	–	–	0.6
Mean	4.2	6.5	136	10.6	20.7	155	0.6
HMT-B2-R1	4.9	7.0	147	16.0	–	–	0.7
HMT-B2-L1	5.5	5.3	120	–	–	–	1.0
Mean	5.2	6.2	134	16.0	–	–	0.9
HMT-BI1	5.0	7.0	137	–	–	–	0.7
HMT-BI2	8.0	4.5	142	–	–	–	1.8
HMT-BI3	4.9	7.3	150	–	–	–	0.7
HMT-BI4	4.2	5.6	124	–	–	–	0.8
HMT-BI5	4.9	6.3	153	–	–	–	0.8
HMT-BI6	5.6	7.1	145	–	–	–	0.8
HMT-BI7	4.2	6.7	152	–	–	–	0.6
HMT-BI8	4.9	7.2	142	–	–	–	0.7

Abbreviations: ML: Maximum length; MW: Maximum width (measured as the distance between the tips of digits II and IV); II-IV: angle between digits II and IV; PL: Pace length; SL: Stride length; PA: Pace angulation.; L/W is dimensionless of ML/MW.

digit traces appear straighter than the aforementioned named didactyl ichnogenera. Lockley et al. (2016a, p. 195) stated that "the digit IV impression are markedly shorter than those of digit III."

In Obernkirchen didactyl tracks, the average ratio of digit III to IV impression length is 1.25 (Lockley et al., 2016a). A study of paravian pedal morphology with a focus on characters (such as digit lengths) that are potentially relevant for ichnology (Mudroch et al., 2011; Sullivan et al., 2012) may show whether or not the hypothesis briefly presented here can be further elaborated. Lockley et al. (2016a) inferred that the didactyl tracks from Obernkirchen differed from all other published didactyl tracks (except *Menglongipus* isp.) in the length (and straightness) of digit IV, and suggested that this is best explained in relation to pedal morphology. They concluded that with in the Deinonychosauria these tracks are probably of troodontid rather than dromaeosaurid origin. Thus, the HMT didactyl tracks could be consistent with troodontid trackmakers.

The SL/h ratios of the HMT didactyl trackways 2.5, 2.4, 2.7, and 2.8 (HMT-T22–T25) and accordingly suggest a trotting gait or close running. Using the formula of Alexander (1976), the speed of these six trackways ranges between an estimated 7.16–8.64 km/s.

4.2. Tridactyl theropod tracks

4.2.1. Description

The HMT tracksites show at least 23 tridactyl trackways (Figs. 4, 6 and 7; Table 1), cataloged as HMT-T1–21, and HMT-26–27; and at least 24 more isolated theropod tracks cataloged as HMT-TI1–24 (where 'I' indicates 'isolated'). The tracks can be divided into four morphotypes.

Morphotype A. Medium-sized theropod tracks with weak or moderate mesaxony and without heel impressions. They are primarily distributed over Areas 1 and 2 (Fig. 3) with HMT-TI10 as the best preserved representative. TI10 is 30.0 cm long, with a length/width ratio of 1.3, anterior triangle ratio is 0.38. Digit III projects the farthest anteriorly, followed by digits II and IV. One distinct metatarsophalangeal pad trace of digit IV is round and blunt and positioned near the axis of digit III. The digits have relatively wide

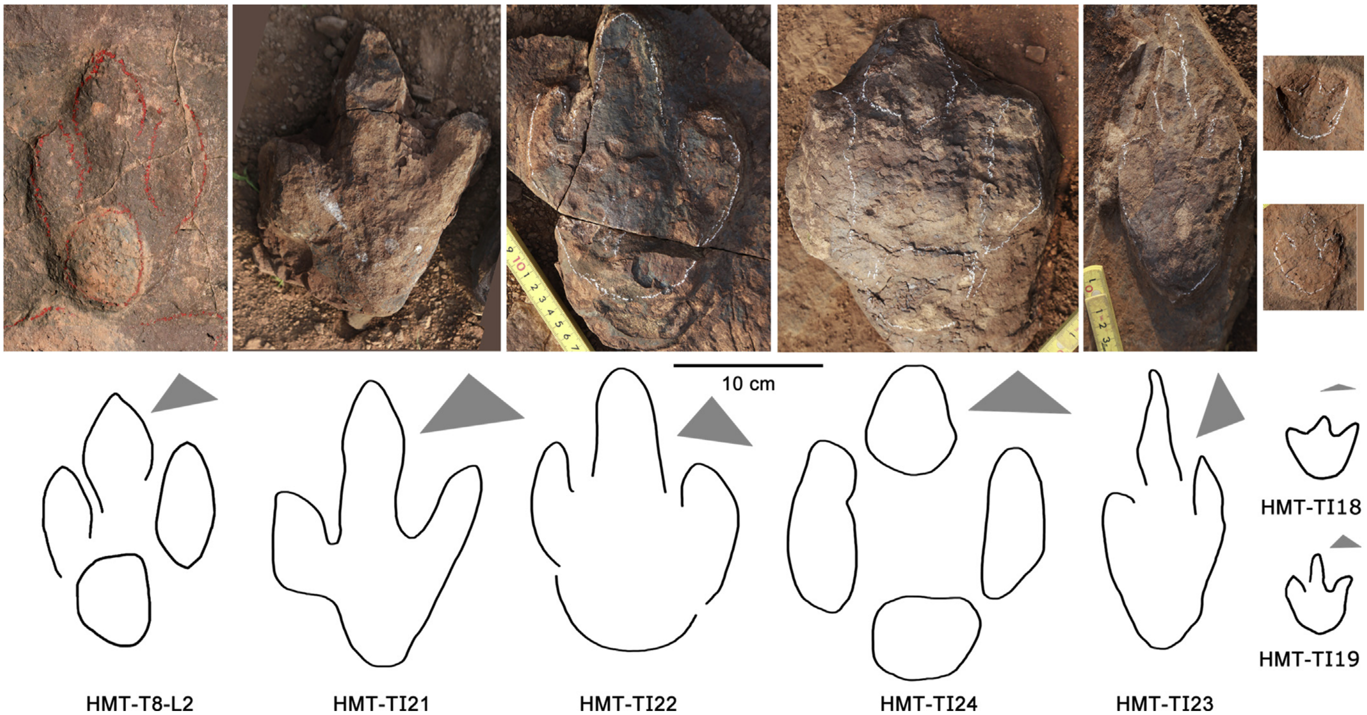

Fig. 6. Photograph, and interpretative outline drawing of tridactyl theropod trackways at Houmotuan Tracksites.

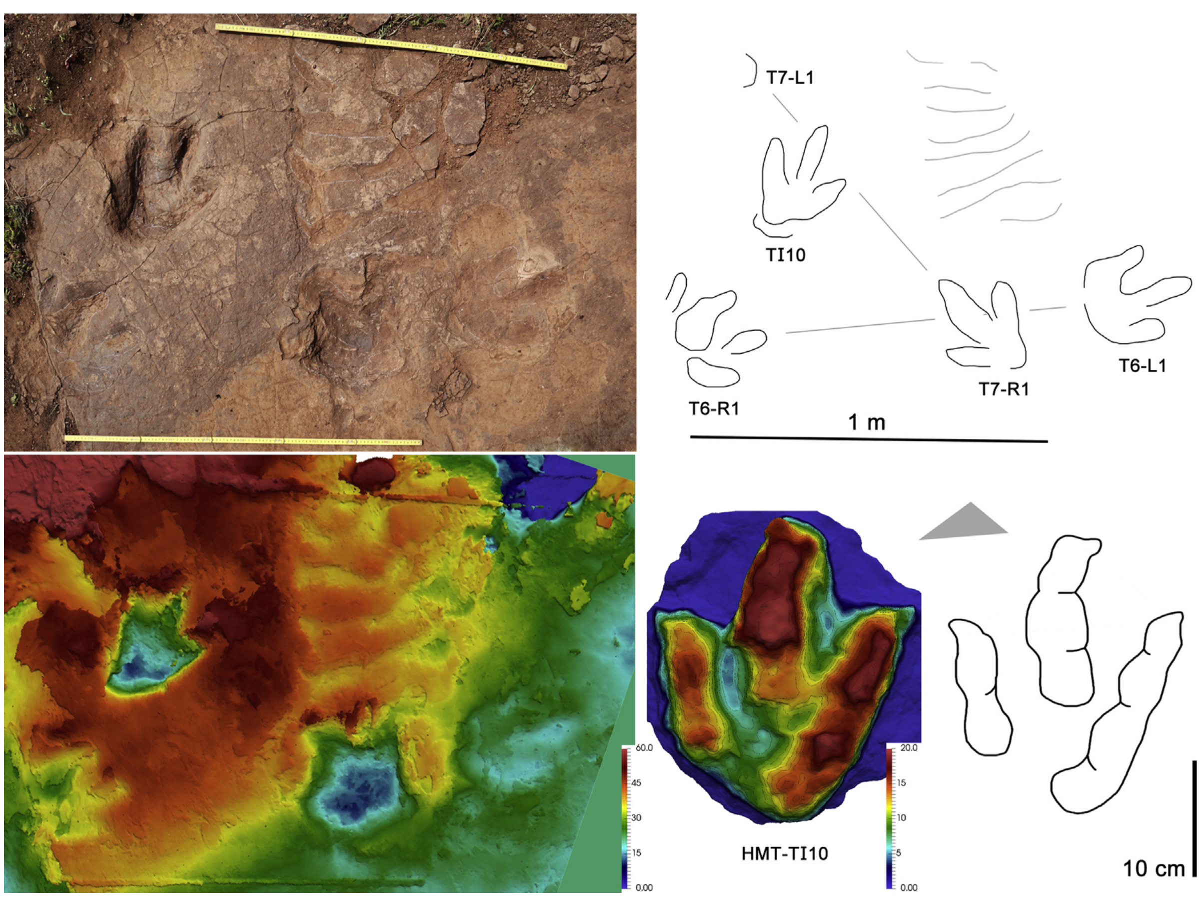

Fig. 7. Photograph, 3D image and interpretative outline drawing of theropod tracks at Houmotuan Tracksite Area 2.

divarication angles between digits II and IV (61°). Digits II-III-IV has a clear phalangeal pad 2-3-4 configuration. Each digit impression ends in a sharp claw mark.

Morphotype B. Small theropod tracks with weak or moderate mesaxony and large heel impressions. They are primarily spread over Areas 1, 3, 4 and 5 (Fig. 3) with HMT-T8-L2 as the best preserved representative. HMT-T8-L2 is 18 cm long, with a length/width ratio of 1.8, anterior triangle ratio is 0.47. Digit III projects the farthest anteriorly, followed by digits II and IV. Digit pads are mostly indistinct. A round and blunt metatarsophalangeal pad trace in axis of digit III. The digits have narrow—wide divarication angles between digits II and IV (35°). Each digit impression ends in a sharp claw mark, so as HMT-TI21 and TI22. In the latter, the divarication angles between digits II and IV are 55° and 40° and the anterior triangle ratios are 0.50 and 0.57, respectively.

TI24 is located in Area 8 (Fig. 3) and is 21 cm in length, with a length/width ratio of 1.6 (from the tip of digit II to IV, or 1.2 from the most lateral sides of digit II to IV), and an anterior triangle ratio of 0.41. Due to its quadripartite morphology including three digits with blunt claw or ungual marks, and triangular heels, TI24 has an affinity to ornithopod tracks, but the anterior triangle ratio may relate to Morphotype B theropod tracks more closely than ornithopod tracks (eg. Xing et al., 2016b).

Morphotype C. Small theropod tracks with high mesaxony. Only one track has been found in Area 6 (Fig. 3) and is catalogued as HMT-TI23. HMT-TI23 is 18.5 cm long, with a length/width ratio of 2.8, and anterior triangle ratio of 1.04. Digit III projects the farthest anteriorly. All digits are slender, and digit pads are mostly indistinct. A round and blunt metatarsophalangeal pad trace in axis of digit III. The digits have relatively narrow divarication angles between digits II and IV (30°). Each digit impression ends in a sharp claw mark.

Morphotype D. Tiny theropod tracks with weak or moderate mesaxony. It includes only two tracks in Area 1 (Fig. 3), which are catalogued as HMT-TI18 and TI19 and 4.5 and 5.5 cm long with length/width ratios of 1.1 and 1.2, respectively. Their anterior triangle ratios are 0.16 and 0.41. The divarication angles between digits II and IV are 67° and 58°, relatively wide. Other morphological features are similar to these of Morphotype B.

4.2.2. Comparison and discussion

Morphotype A tracks are characterized by weak to moderate mesaxony, which is typical for footprints of the ichno- or morphofamily Eubrontidae Lull, 1904. However, Morphotype A tracks do not have distinct metatarsophalangeal pad traces posterior to digit II. This character is common in *Eubrontes* tracks, such as the type specimen of *Eubrontes* (AC 15/3 (Olsen et al., 1998)). Well preserved TI10 is similar to the newly named Late Jurassic tridactyl tracks *Jurabrontes curtedulensis* from Jura Canton, northwest Switzerland (Marty et al., 2017). Both have 2-3-4 phalangeal pads, weak mesaxony, asymmetrical heel region, broad and massive digits with a blunt aspect, and the first digit pad of digit III is shallow. However, TI10 (30 cm) is much shorter than *Jurabrontes curtedulensis* (50 cm) and lacks clear trackway. Therefore, TI10 is temporarily referred to cf. *Jurabrontes* isp. of Eubrontid.

Morphotype B tracks are similar to eubrontid tracks commonly seen in China's Early Cretaceous formations (Lockley et al., 2013; Xing et al., 2015c). In both, lengths are larger than widths and length/width ratios of the anterior triangle are reflected by weak or moderate mesaxony, which are hallmarks of the Eubrontidae (Lull, 1904). These materials which are common in Lower Jurassic North American formations have been frequently found from China's Early Cretaceous sedimentations. But generally, China's Early Cretaceous Eubrontes morphotype is smaller, usually shorter than 25 cm, and has wide divarication angles and highly developed heels reminiscent of *Asianopodus* isp. (Matsukawa et al., 2005). *Asianopodus* isp. has been found in Early Cretaceous sedimentations in Japan, Inner Mongolia, Shandong Province and Gansu Province.

For Morphotype C tracks, the length/width ratios and high mesaxony are similar to the Early Cretaceous *Grallator* morphotype (Lockley et al., 2013; Xing et al., 2014; Li et al., 2015). HMT-TI23 has a well-developed metatarsophalangeal area, resembling *Jialingpus* isp. (Xing et al., 2014), and can be tentatively referred to *Jialingpus* isp.

Morphotype D tracks represent the smallest track in HMT. The anterior triangle ratio of HMT-TI18 is 0.16, which is a very low value. This may result from extramorphological (substrate-related) factors rather than foot morphology of the trackmaker. The anterior triangle ratio of HMT-TI19 is 0.41, similar to that of Morphotype B, and may reflect a minor trackmaker of Morphotype B.

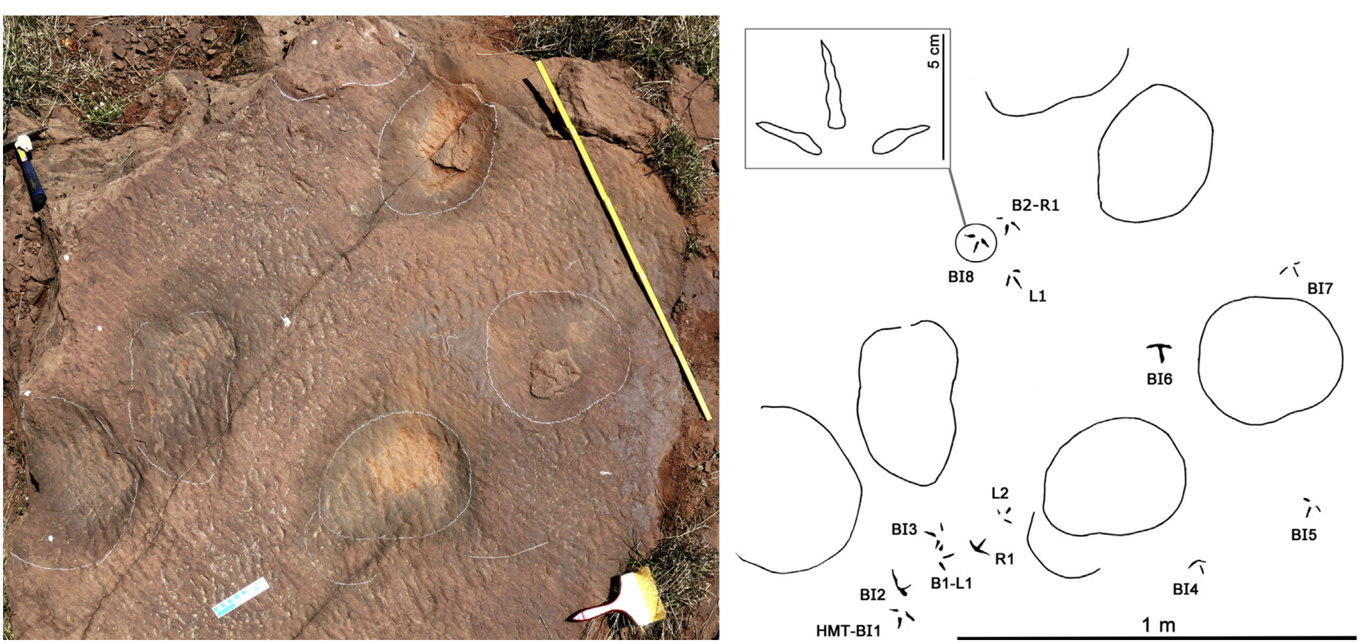

Fig. 8. Photograph, and interpretative outline drawing of sauropod and bird trackways at Houmotuan Tracksites Area 7.

4.3. Bird tracks

4.3.1. Description

Thirteen complete natural molds of small tridactyl tracks in Area 7 (Fig. 3) are cataloged individually as HMT-B1-L1–L2 ('B' indicates 'bird'), B2-R1–L1, and five among them form two trackways (Fig. 8; Table 1). Other tracks are isolated. The original tracks were not collected and are still in the field.

These HMT bird tracks are medium-sized, tridactyl bird tracks lacking hallux impressions, with slender digit impressions typically separated from one another. The average maximum length of HMT bird tracks is 5 cm (range 3.7–8 cm), the average maximum width is 6.4 cm (range 4.5–7.3), and the average length/width ratio is 0.8 (range 0.6–1.8). HMT-BI8 is the best preserved and 4.9 cm long and 7.0 cm wide (length/width ratio of 0.7). Digit III is the longest digit, and broader than digits II and IV that are sub equal in length. Digital pad in impressions digit II and IV are absent. Digit III has 3 digit pads and a sharp claw mark. Divarication angles between digits II and IV average 142°. The divarication angles between digits II and III are larger than those between digits III and IV. HMT-B1 is basically the same with BI8 in morphology, and the average pace length (10.6 cm) is half the size of the stride length (20.7 cm). The pace angulation is 155°. HMT-BI2 is 8 cm long with a length/width ratio of 1.8, resulting in a shape similar to pterosaur manus tracks. This probably resulted from extra-morphological factors attributable to soft, wet sediment.

4.3.2. Discussion

Most of the morphological characteristics of HMT bird tracks match those of Koreanaornipodidae (Kim, 1969; Lockley et al., 1992, 2006): small (2.5–3.0 cm) – medium (~5 cm) size, wide divarication between digits II and IV (>100°), sub-symmetric, functionally tridactyl tracks with slender digit impressions. Koreanaornipodid trackways also exhibit a positive (inward) rotation (Lockley et al., 2006). The pace length:stride length ratio of the HMT bird trackway (0.51) matches that of *Koreanaornis* isp. trackway (0.49) from Dasheng Group Qingquan tracksites (Xing et al., 2017) and *Koreanaornis* isp. trackway (0.49) from the Jindong Formation of Donghae-myeon, Korea (Kim et al., 2013). However, to date all tracks positively identified as ichnogenus *Koreanaornis*, including examples from the Tianjialou formation in Shandong (Li et al., 2015; Xing et al., 2017) are smaller than the HMT tracks described here. Whereas size is not an absolute or reliable criterion for ichnotaxonomy it is well known that extant shorebird tracks of different species are often morphologically similar in all features except size, and that tracks that do differ markedly in size cannot be attributed to a single species (Lockley et al., 1992). Tracks in ichnofamily Koreanaornipodidae are distinguished from those in ichnofamily Jindongornipodidae by the presence of a large hallux in the latter ichnofamily, and from tracks in ichnofamily Ignotornidae (including *Ignotornis* and *Goseongornipes*) which exhibit semi-palmate web traces.

Aquatilavipes (Currie, 1981) and *Tatarornipes* (Lockley et al., 2012) are the only well-defined Cretaceous bird ichnotaxa, larger than *Koreanaornis*, that share Koreanaornipodidae characteristcs (i.e. lacking web traces or large hallux). Based on these size and morphological distinctions, as well as the wide digit divarication the HMT tracks are closer to *Tatarornipes* than any other avian ichnotaxon known from China, and we herein use the label cf. *Tatarornipes*. Moreover, *Tatarornipes* is known from the Lower Cretaceous of Shandong Province.

At least seven sauropod tracks are preserved at the same level with the HMT bird tracks. However, all tracks are shallow (about 1.5 cm depth) without any identifiable digit impression or clear trackway and are likely undertracks from an overlying upper level. Coexistence of sauropod tracks and bird tracks is uncommon. The best example is probably the report of *Koreanaornis hamanensis* on the same surface as the sauropod tracks *Brontopodus pentadactylus* from the Early Cretaceous Haman Formation of Jinju Area, Korea (Kim and Lockley, 2012).

4.4. Sauropod tracks

4.4.1. Description

Area 5 (Fig. 3) yields well preserved sauropod tracks and six large quadruped trackways: HMT-S1–S6, as well as many isolated

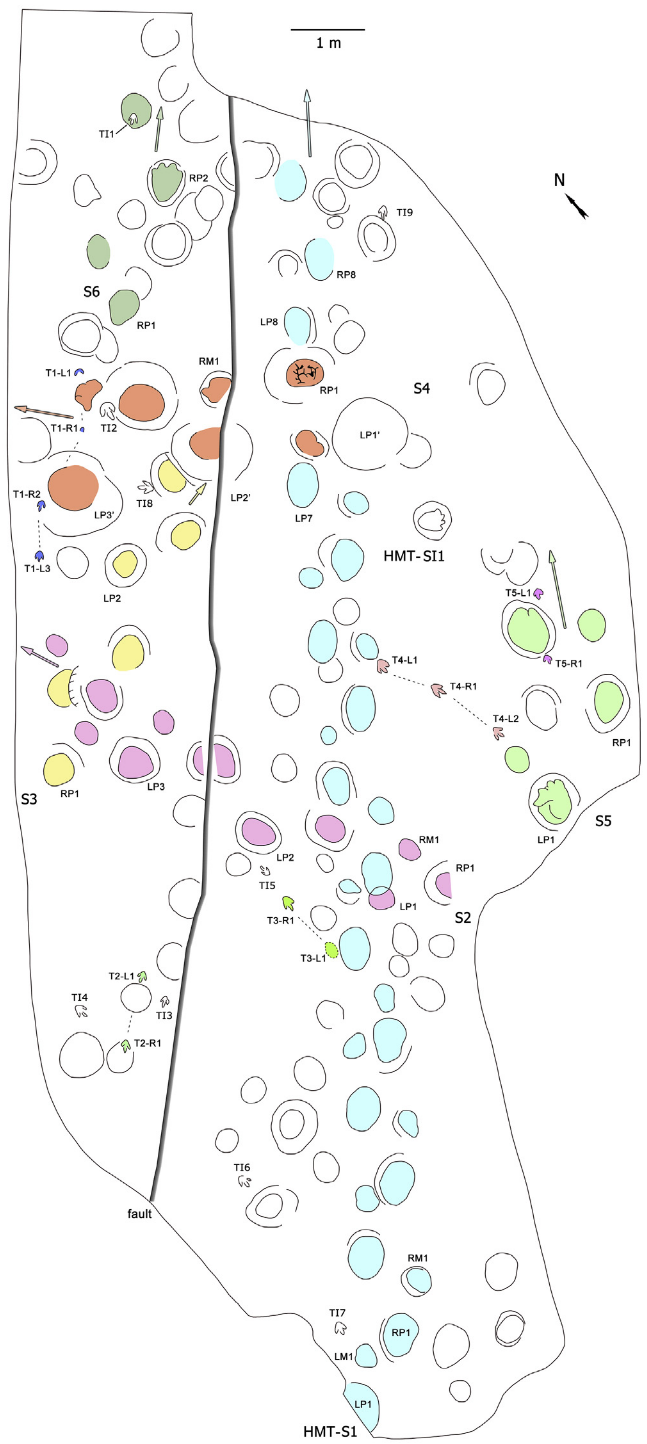

Fig. 9. Interpretative outline drawing at Houmotuan Tracksite Area 5 with sauropod and theropod trackways.

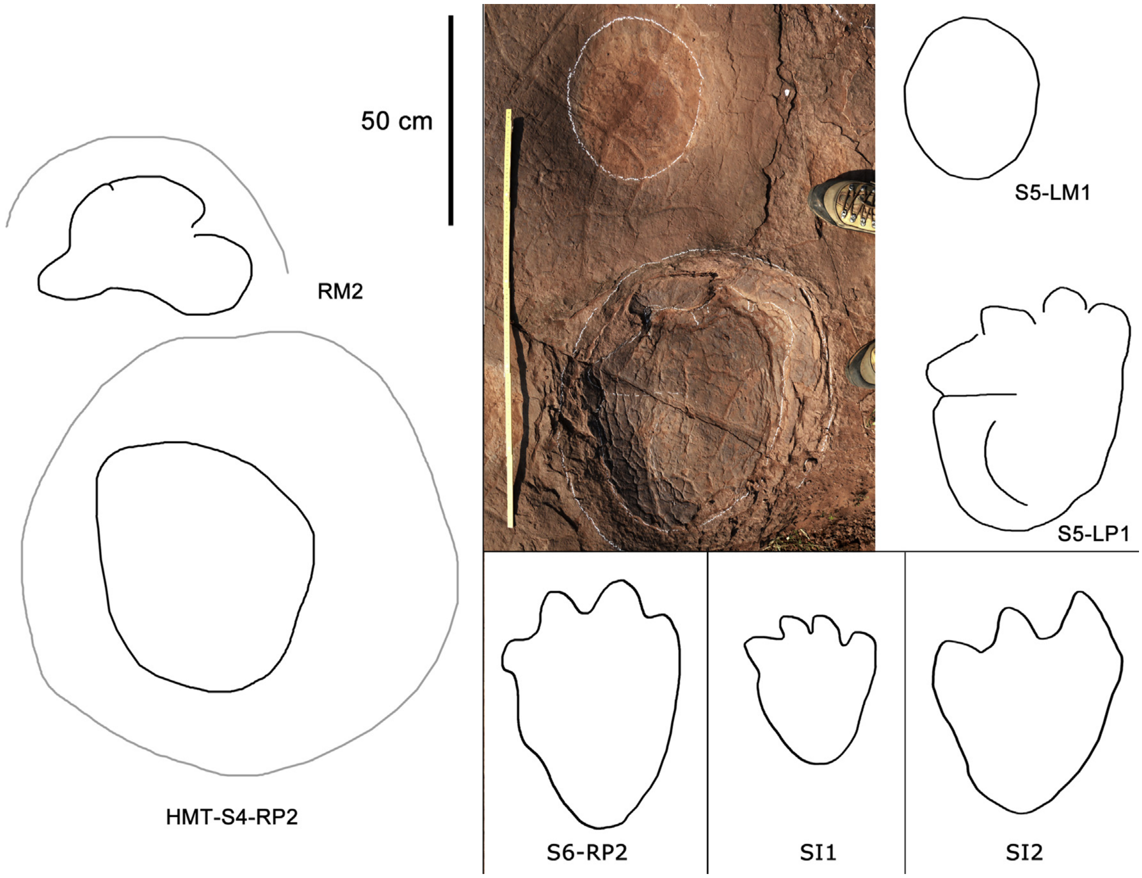

Fig. 10. Photograph, and interpretative outline drawing of sauropod trackways at Houmotuan Tracksites.

ambiguous tracks (Figs. 8–10; Table 2). All the tracks and trackways remain in situ and fall into two morphological categories:

Morphotype A. Trackway HMT-S1 is narrow-gauge with a WAP/P'ML ratio of 0.8 (Marty, 2008). The manus impressions of HMT-S1 lie anteromedially to the pes impressions. The average length/width ratios of the manus and pes impressions are 0.8 and 1.4 respectively. All tracks are poorly preserved without clear digit impression. The manus and pes impression are oval. The heteropody (ratio of manus to pes size) of HMT-S1 is about 1:2.5–3. The manus impression is rotated approximately 39° outward from the trackway axis, which is smaller than the outward rotation of the pes impressions (approximately 14°). The average manus pace angulation is 122°, whereas the average pes pace angulation is 139°.

Morphotype B. Trackway HMT-S2–S6 falls between medium-gauge and wide-gauge trackways, with a WAP/P'ML ratio of 1.3–1.7 (Marty, 2008). Taking the best-preserved manus-pes association HMT-S5-LP1–LM1, the manus imprints show oval digit impressions, whereas the claws and the metacarpo-phalangeal region are indistinct. The pes impression is oval, pes prints are longer than wide, with preserving large, outwardly directed claw marks of digits I–III, the small claw mark of digit IV, and a small callosity or pad mark of digit V, and the metatarso-phalangeal region is smoothly curved. The heteropody of HMT-S5-LP1–LM1 is 1:2.2. The pes impression is rotated approximately 14° outward from the trackway axis. The average pes pace angulation is 97°.

HMT-S6-RP2, SI1 and SI2 all have unambiguous claw marks. With the exception of SI2, which only has 3 digit impressions, both of the other two have four digit impressions, reflecting digits I to IV. Such difference may be caused by extramorphological (substrate-related) factors rather than the anatomy of the pes. Sauropod digits are very short and occasionally fail to leave an impression. SI2 is more than 30 cm deep, whereas the other two are only 10 cm deep. Inner side of SI2 digit may be mixed with digit III and IV.

The pes impressions of HMT-S4 are oval. The manus traces are usually oval or U-shaped, partial well-preserved manus traces with rounded marks of digits I and V. Of note, HMT-S4 tracks have unusually large diameters. This may be a soft substrate effect, giving them a much larger appearance, if compared to the original pes anatomy. The heteropody of the well-preserved HMT- S4-RP2–RM2 is 1:2.3.

4.4.2. Comparisons and discussion

In HMT large quadruped trackways, the pes and manus morphology and trackway configuration are typical of sauropods (Lockley and Hunt, 1995; Lockley, 1999, 2001). China's sauropod trackways are mostly wide- (or medium-) gauge and are, therefore, referred to the ichnogenus *Brontopodus* (Lockley et al., 2002). In the HMT, Morphotype B trackways are between medium-gauge and wide-gauge.

Sauropod trackway configurations from the Zhaojue site share characteristics with *Brontopodus* type tracks from the Upper Jurassic of Portugal and Switzerland (Meyer and Pittman, 1994; Santos et al., 2009) and from the Lower Cretaceous of the USA (Farlow et al., 1989; Lockley et al., 1994). These features include: 1) U-shaped manus prints; 2) large and outwardly directed pes tracks in which length exceeds width; 3) wide-gauge; and 4) low heteropody. The well-preserved HMT sauropod tracks show heteropody of 1:2.2–3, similar to that of *Brontopodus birdi* (1:3) but far less than in the narrow-gauge ichnotaxa *Breviparopus* (1:3.6) or *Parabrontopodus* (1:4 or 1:5) (Lockley et al., 1994). The wide-gauge of the

Table 2
Measurements (in cm) of the sauropod trackways from Houmotuan tracksite, Shandong Province, China.

Number	ML	MW	R	PL	SL	PA	ML /MW	WAP	WAP /P'ML
HMT-S1-LP1	74.0	–	41	118.0	212.0	127	–	64.7	0.9
HMT-S1-LM1	33.0	31.0	13	130.0	224.0	115	1.1	–	–
HMT-S1-RP1	63.0	45.0	18	119.0	213.0	134	1.4	56.6	0.9
HMT-S1-RM1	28.0	38.0	40	135.0	221.0	119	0.7	–	–
HMT-S1-LP2	61.0	49.0	7	112.0	210.0	135	1.2	56.4	0.9
HMT-S1-LM2	29.0	38.0	15	122.0	217.0	120	0.8	–	–
HMT-S1-RP2	64.0	44.0	20	115.0	200.0	131	1.5	48.5	0.8
HMT-S1-RM2	29.5	34.5	68	128.0	179.0	114	0.9	–	–
HMT-S1-LP3	62.0	49.0	2	105.0	228.0	140	1.3	47.0	0.8
HMT-S1-LM3	29.5	39.5	38	84.0	226.0	130	0.7	–	–
HMT-S1-RP3	63.0	46.0	16	137.0	232.0	145	1.4	45.2	0.7
HMT-S1-RM3	37.5	41.0	73	163.0	265.0	138	0.9	–	–
HMT-S1-LP4	61.5	43.5	8	106.0	233.0	159	1.4	48.9	0.8
HMT-S1-LM4	20.5	32.0	18	120.0	215.0	123	0.6	–	–
HMT-S1-RP4	61.5	42.0	8	131.0	236.0	143	1.5	48.2	0.8
HMT-S1-RM4	33.5	40.5	53	125.0	235.0	128	0.8	–	–
HMT-S1-LP5	53.5	37.5	15	118.0	205.0	132	1.4	47.1	0.9
HMT-S1-LM5	22.5	25.0	11	136.0	229.0	121	0.9	–	–
HMT-S1-RP5	65.0	40.5	9	106.0	210.0	139	1.6	48.4	0.7
HMT-S1-RM5	27.0	40.0	62	127.0	207.0	109	0.7	–	–
HMT-S1-LP6	62.0	40.0	6	118.0	226.0	141	1.6	53.7	0.9
HMT-S1-LM6	28.0	33.5	–	127.0	–	–	0.8	–	–
HMT-S1-RP6	60.0	44.0	–	122.0	–	–	1.4	–	–
HMT-S1-RM6	30.0	38.0	–	–	–	–	0.8	–	–
HMT-S1-LP7	64.0	42.5	–	–	–	–	1.5	–	–
Mean(M)	29.0	35.9	39	127.0	221.8	122	0.8	–	–
Mean(P)	62.7	43.6	14	117.3	218.6	139	1.4	51.3	0.8
HMT-S2-RP1	–	–	11	95.0	182.0	115	–	63.2	–
HMT-S2-RM1	33.5	28.5	–	–	–	–	1.2	–	–
HMT-S2-LP1	36.0	33.5	36	120.0	190.0	120	1.1	55.8	1.6
HMT-S2-LM1	–	–	–	–	–	–	–	–	–
HMT-S2-RP2	44.0	34.5	3	99.0	171.0	111	1.3	55.6	1.3
HMT-S2-RM2	–	–	–	–	–	–	–	–	–
HMT-S2-LP2	45.5	35.0	13	109.0	182.0	124	1.3	55.4	1.2
HMT-S2-LM2	–	–	–	–	–	–	–	–	–
HMT-S2-RP3	45.0	37.0	12	97.0	168.0	116	1.2	61.5	1.4
HMT-S2-RM3	27.0	34.0	126	111.0	182.0	–	0.8	–	–
HMT-S2-LP3	49.5	45.5	–	101.0	–	–	1.1	–	–
HMT-S2-LM3	29.5	36.0	–	133.0	–	96	0.8	–	–
HMT-S2-RP4	49.5	38.5	–	–	–	–	1.3	–	–
HMT-S2-RM4	27.0	34.0	–	–	–	–	0.8	–	–
Mean(M)	29.3	33.1	126	122.0	182.0	96	0.9	–	–
Mean(P)	44.9	37.3	15	103.5	178.6	117	1.2	58.3	1.4
HMT-S3-RP1	48.5	42.0	34	117.0	193.0	126	1.2	62.9	1.3
HMT-S3-LP1	53.5	36.5	32	99.0	196.0	115	1.5	70.7	1.3
HMT-S3-RP2	54.5	43.5	17	132.0	196.0	115	1.3	69.9	1.3
HMT-S3-LP2	37.5	31.0	35	99.0	151.0	105	1.2	67.6	1.8
HMT-S3-RP3	46.0	35.5	–	91.0	–	–	1.3	–	–
HMT-S3-LP3	50.0	36.5	–	–	–	–	1.4	–	–
Mean(P)	48.3	37.5	30	107.6	184.0	115	1.3	67.8	1.4
HMT-S4-LP1	–	–	34	–	–	–	–	–	–
HMT-S4-LP1′	103.0	98.0	–	123.0	213.0	93	1.1	89.0	1.2
HMT-S4-LM1	30.0	41.5	81	–	–	–	0.7	–	–
HMT-S4-RP1	51.5	39.0	9	167.0	231.0	110	1.3	–	–
HMT-S4-RP1′	97.5	83.0	–	–	–	–	1.2	77.4	1.3
HMT-S4-RM1	32.0	43.0	45	–	–	–	0.7	–	–
HMT-S4-LP2	–	–	–	–	–	–	–	–	–
HMT-S4-LP2′	115.0	88.0	5	113.0	203.0	95	1.3	89.2	1.3
HMT-S4-RM2	31.0	46.5	–	–	–	–	0.7	–	–
HMT-S4-RP2	63.0	52.0	–	–	–	–	1.2	–	–
HMT-S4-RP2′	106.0	100.0	–	160.0	–	–	1.1	–	–
HMT-S4-LP3	64.0	67.5	–	–	–	–	0.9	–	–
HMT-S4-LP3′	114.0	124.0	–	–	–	–	0.9	–	–
Mean(M)	31.0	43.7	63	–	–	–	0.7	–	–
Mean(P)	59.5	52.8	22	167.0	231.0	110	1.1	–	–
Mean(P′)	107.1	98.6	5	132.0	208.0	94	1.1	85.2	1.3
HMT-S5-LP1	62.9	50.8	14	171.5	247.0	97	1.2	108.9	1.7
HMT-S5-LM1	39.8	32.6	–	220.3	–	–	1.2	–	–
HMT-S5-RP1	58.3	40.7	–	157.7	–	–	1.4	–	–
HMT-S5-RM1	45.5	38.2	–	–	–	–	1.2	–	–
HMT-S5-LP2	71.2	54.3	–	–	–	–	1.3	–	–
Mean(M)	42.7	35.4	–	220.3	–	–	1.2	–	–
Mean(P)	64.1	48.6	14	164.6	247.0	97	1.3	108.9	1.7
HMT-S6-RP2	36.5	32.0	–	–	–	–	1.1	–	–
HMT-SI1	59.0	44.0	–	–	–	–	1.3	–	–

Abbreviations: ML: Maximum length; MW: Maximum; R: Rotation; PL: Pace length; SL: Stride length; PA: Pace angulation; WAP: Width of the angulation pattern of the pes (calculated value); ML/MW, WAP/P'ML and are dimensionless.

Brontopodus-type trackways suggests titanosaurian sauropods as trackmakers (Wilson and Carrano, 1999; Lockley et al., 2002).

5. Dinosaur fauna from Dasheng Group

To date, 13 tracksites have been found in Dasheng Group, whereas body fossils are scarce, making the ichnofossils the overwhelmingly dominant evidence of the local ancient fauna. There are 706 trackmakers (based on trackway and isolated tracks) reported from these 13 tracksites, reflecting a diverse dinosaur fauna from Dasheng Group (Table 3). All sites are dominated by saurischians: theropods (including birds) for three sites and sauropods for the remainder.

Theropods were highly diverse. The Houzuoshan site alone, with 21 different track bearing levels, has yielded small grallatorid, *Asianopodus*, *Minisauripus*, *Velociraptorichnus*, and *Dromaeopodus* (Li et al., 2015). Theropod tracks from the Houmotuan site, with 5 track-bearing levels, include small grallatorids, a eubrontid, cf. *Jurabrontes* isp., and cf. *Menglongpus*. Bird tracks include *Shandongornipes*, *Koreanaornis* (Li et al., 2015) and *Goseongornipes* (Xing et al., 2018b). *Shandongornipes* was reported only from the Houzuoshan site where *Koreanaornis* also occurs. To this record we can add cf. *Tatarornipes* based on the present study.

Sauropods are less diverse and include large *Brontopodus* trackways, cf. *Parabrontopodus* trackways, and small-sized *Parabrontopodus* trackways. The small-sized *Parabrontopodus* trackways have been found in 5 sites in Dasheng Group and are quite similar to the records from Gansu Province, Beijing and South Korea (Xing et al., 2015a).

Ornithopod tracks are rare, but well preserved *Ornithopodichnus* and *Caririchnium* (Li et al., 2015) are similar to the records from the Sichuan Basin, Gansu Province and South Korea (Xing et al., 2015d).

Generally, dinosaur fauna in Dasheng Group are reminiscent of track assemblage from Jiaguan Formation in the Sichuan Basin, but the western Sichuan Basin preserves more evidence of ornithopod

Table 3
Composition of dinosaur-dominated ichnofaunas in the Dasheng Group of Shandong Province, China.

Gr	Sites	Tm	The	Bi	Sa	Or
Dasheng	Houzuoshan	133	90%	2%	–	8%
	Zhangzhuhewang	4	–	25%	50%	25%
	Tangdigezhuang	9	–	–	100%	–
	Jishan	57	5%	–	90%	5%
	Qingquansi I	1	–	–	100%	–
	Qingquansi II–IV	72	21%	1%	78%	–
	Beilin	8	–	–	100%	–
	Nanguzhai I	9	11%	–	89%	–
	Nanguzhai II	26	–	100%	–	–
	Nanquan	302	8%	–	86%	6%
	Houmotun	85	60%	12%	28%	–
	All sites	706	–	–	–	–

Abbreviation: Gr, Group; Tm, estimated number of trackmakers; The, non-avian theropod; Bi, Bird; Sa, Sauropod; Or, Ornithopod.

Table 4
Comparison between deinonychosaurian tracks from Dasheng Group and Jehol Fauna.

	ML	BL
Deinonychosaurian tracks		
Dromaeopodus	28.0	361.0
	26.0	335.0
	24.0	309.0
	26.0	335.0
	26.5	342.0
	28.5	367.0
Velociraptorichnus	9.0	107.0
cf. *Dromaeosauripus*	19.5	231.0
cf. Menglongpus	7.4	88.0
	7.8	92.0
	7.1	84.0
Dromaeosaurid		
Sinornithosaurus millenii	9.5	112.0[a]
Changyuraptor yangi	8.5	132.0
Microraptor zhaoianus	3.0	36.0[a]
Microraptor gui	6.0	74.5
Zhenyuanlong suni	15.7	165.0
Johel troodontid		
Mei long	5.7	53.0
Sinusonasus magnodens	8.2	97.0[a]

ML, Maximum length of the foot/footprint; BL, Body length.
[a] Body length inferred from the maximum length of the footprint.

activity with at least two tracksites dominated by ornithopods. Again, this indicates that similar dinosaur faunas existed in Southwest China and East China in Early Cretaceous.

Deinonychosaurian tracks are relatively diverse in Dasheng Group and include *Dromaeopodus*, *Velociraptorichnus*, cf. *Dromaeosauripus* and cf. *Menlongpus* (the latter inferred in this study). The small theropod (P'ML < 25 cm) has a hip height 4.5 times longer than track length. The large theropod (P'ML > 25 cm) has a hip height 4.9 times longer than track length (Thulborn, 1990). For Theropods, their body length is about 2.63 times long than the hip height (Xing et al., 2009b). Body length of deinonychosaurians are estimiated acocridng to the tracks based on this formula (Table 4).

The Early Cretaceous Jehol fauna (Yixian Formation and Jiufotang Formation) is famous for diverse feathered dinosaurs, including high deinonychosaurian diversity. Various authors have summarized the evidence for Jehol fauna dromaeosaurids and troodontids with complete feet. The former group includes *Sinornithosaurus millenii* (Xu et al., 1999), *Changyuraptor yangi* (Han et al., 2014), *Microraptor zhaoianus* (Xu et al., 2000), *Microraptor gui* (Xu et al., 2003; Xing et al., 2013c), *Zhenyuanlong suni* (Lü and Brusatte., 2015), and the latter comprises *Mei long* (Xu and Norell, 2004) and *Sinusonasus magnodens* (Xu and Wang, 2004). Based on available data, all Jehol deinonychosaurians seem to have had body lengths less than 2 m (Fig. 11; Table 4). Comparison of track lengths and body lengths between deinonychosaurians from Dasheng Group and Jehol fauna suggests that the trackmakers of small *Velociraptorichnus* and cf. *Menglongpus* fall into the same size range and morphological class as Jehol deinonychosaurians.

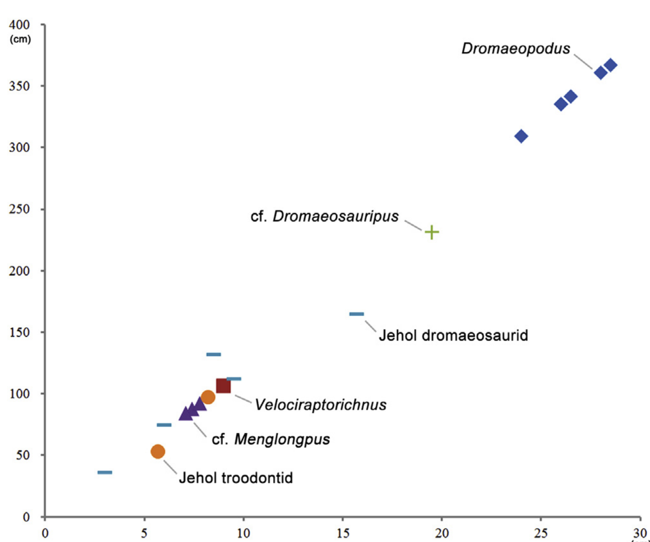

Fig. 11. Bivariate analysis plotting the body length vs. track length of deinonychosaurian tracks and skeleton records.

6. Conclusions

The Houmotuan site adds to the growing list of dinosaur-dominated tracksites reported from the Dasheng Group in Shandong Province. Including the new site described here, the current count is 14 sites, many with tracks at multiple stratigraphic levels. The Houmotuan site yields a saurischian (avian and non avian theropod and sauropod) dominated ichnofauna preserved on five different track-bearing levels. This is typical of the composition of other ichnnofaunas from the Dasheng Group in the region. Four parallel trackways of small didactyl theropod dinosaurs, here referred to cf. *Menglongpus*, are differentiated from larger tridactyl (grallatorid) tracks by size, morphology and direction of travel, which suggests passage of a social group. Bird (avian theropod) tracks are referred to cf. *Tatarornipes*, representing only the second report from Shandong and indicating a possible social behavior.

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