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Research Paper

Dinosaur footprint assemblage from the Lower Cretaceous Khok Kruat Formation, Khorat Group, northeastern Thailand

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ABSTRACT

The Khok Kruat Formation is the upper part of the Khorat Group, which consists of upper Lower Cretaceous non-marine sedimentary rocks in northeastern Thailand. Many dinosaur footprints have been known from the upper Lower Cretaceous (Aptian–Albian) Khok Kruat Formation at the Huai Dam Chum (Tha Uthen) site, northeastern Thailand. Approximately 600 tracks occur in thin mudstone layer of the northern part of the outcrop at the Huai Dam Chum track site. Two types of footprints, small-sized theropod and crocodylomorph are imprinted with mud cracks and ripple marks on the thin mud layer. Most of footprints are referred to cf. *Asianopodus*, and are imprinted by small-sized theropoda, probably ornithomimosauria. Theropod tracks are mainly separated into two groups, Group A and Group B. From ichnological viewpoints, the small-sized theropod track assemblage indicates the herd behaviour and its idiosyncratic group composition. In particular, the histogram of size-frequency measurements of Group A shows the anomalous bimodal distribution. We consider that there are two hypotheses; the first one is due to the male-female difference, and the second is a result of the different growing stage.

1. Introduction

Gregarious behaviour has been suggested for a number of dinosaur taxa, including ceratopsids, ornithopods, theropods, and sauropods (Myers and Fiorillo, 2009). Such behaviour is known from multiple examples of skeletal evidence and from abundant footprint evidence (Gillette and Lockley, 1989; Lockley, 1991). However, at present, most of the firm evidence of gregarious behaviour is provided by the ichnological record, with many tracksites exhibiting signs of group behaviour (Table 1 in García-Ortiz and Pérez-Lorente, 2014). The footprint record provides a great deal of information about the herds of imprint producers that is not available in the bone fossil record, including movement speed, style of gregarious behaviour, herd structure, and the organigram within a group (e.g. Gillette and Lockley, 1989; Lockley, 1991). Gregarious behaviour has been confirmed in sauropod track assemblages (e.g. Lockley et al., 1994, 2012) and ornithopod track assemblages (e.g. Ostrom, 1972; Currie, 1983; Fiorillo et al., 2014). Similarly, gregarious behaviour was common in small bipedal dinosaurs (Lockley and Matsukawa, 1999).

The Upper Triassic to Lower Cretaceous Khorat Group, which consists of non-marine sedimentary rocks, crops out widely in northeastern Thailand (Fig. 1). Many fossils such as dinosaur bones, dinosaur footprints, fish, crocodilians, turtles, bivalves, and palynomorphs have been recovered from the Khorat Group (Fig. 2) (Meesook, 2011; Meesook and Saengsrichan, 2011). At the Huai Dam Chum dinosaur tracksite, which is located on the eastern edge of northeastern Thailand, a number of dinosaur tracks formed by small-sized bipedal dinosaurs are present in outcrop. Dinosaur footprints have previously been reported from this area (Buffetaut et al., 2005; Le Loeuff et al., 2005, 2009; Sato and Tumpeesuwan, 2005; Matsukawa et al., 2006); however, there has been no previous study of the ichnotaxonomic classification or quantitative community analysis of the dinosaur footprint assemblage. In this study, we systematically describe tracks and conduct quantitative analysis of theropod tracks from the upper Lower Cretaceous Khok Kruat Formation of northeastern Thailand.

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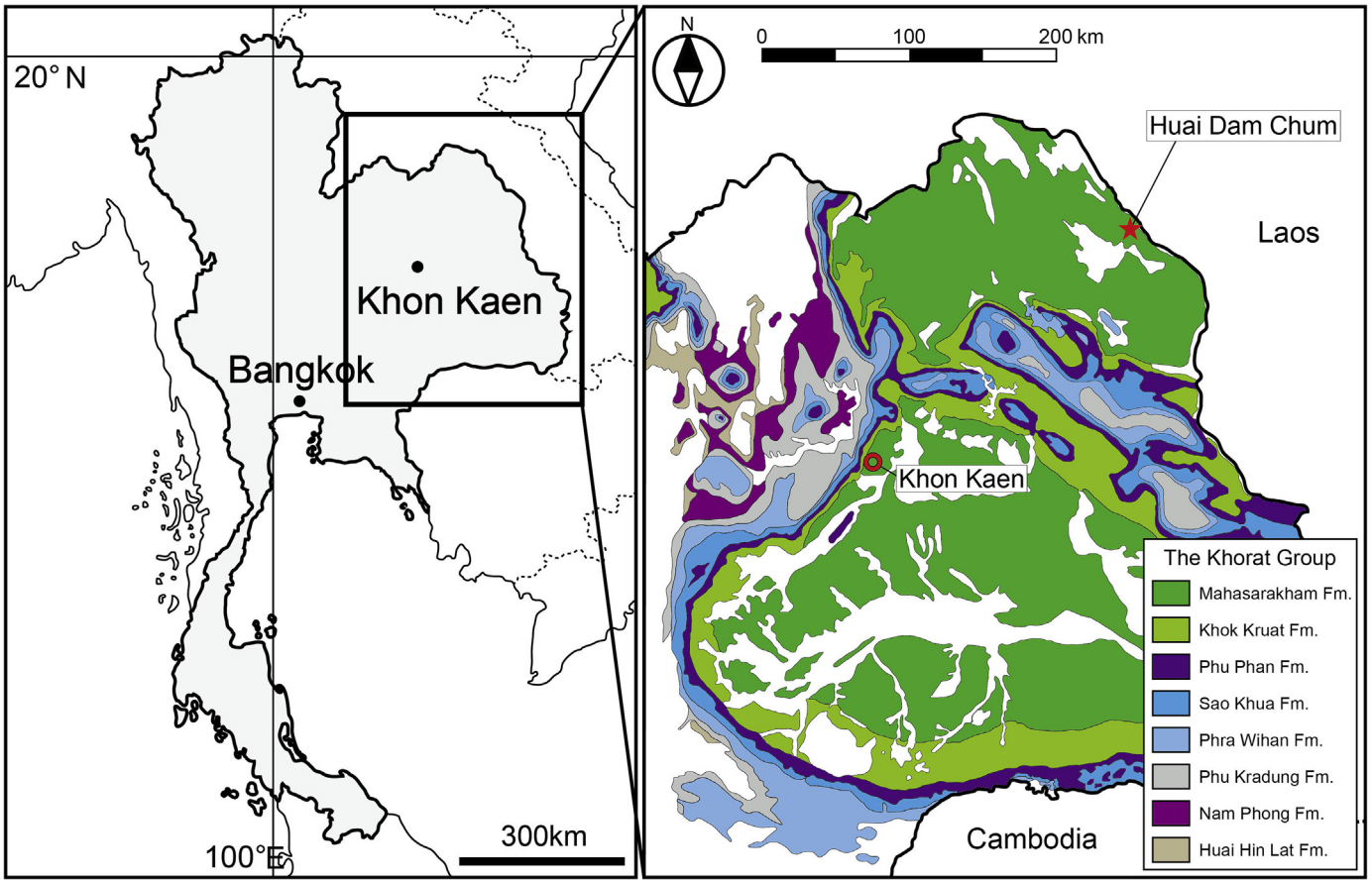

Figure 1. Index map showing the distribution of the Khorat Group and footprint sites (original map is from DMR, 1999; Meesook, 2011).

2. Geological setting

The Upper Triassic to Lower Cretaceous non-marine sedimentary rocks exposed in northeastern Thailand are referred to as the Khorat Group (Ward and Bunnag, 1964). Buffetaut et al. (1993) subdivided this group into eight formations, which are (from oldest to youngest) the Huai Hin Lat, Nam Phong, Phu Kradung, Phra Wihan, Sao Khua, Phu Phan, Khok Kruat, and Maha Sarakham formations (Fig. 2). However, there is still considerable debate about the age, internal stratigraphic relationships, and depositional environment of the group (e.g. Racey et al., 1994).

The Khorat Group has yielded many dinosaur bone fossils; footprints have also been reported from several areas such as Phu Faek and Tha Uthen on the Khorat Plateau (e.g. Le Loeuff et al., 2005, 2009). Knowledge of the East Asian dinosaur fauna has been improved by these studies. Dinosaur footprints at the Phu Luang site were first reported by Buffetaut et al. (1985a); this pioneering work was followed by many studies of dinosaur ichnology in northeastern Thailand (e.g. Buffetaut et al., 1985b, 1997, 2005; Buffetaut and Suteethorn, 1993; Polahan and Daorerk, 1993; Le Loeuff et al., 2002, 2003, 2005, 2007, 2008, 2009; Lockley et al., 2002, 2006b, 2009).

The Khok Kruat Formation, which is one of the upper units of the Khorat Group, is widely distributed in the foothills of the Phu Phan Range. In general, the formation consists of fluvial deposits of mainly reddish-brown fine- to medium-grained sandstone, conglomerate, siltstone, and mudstone (Meesook, 2011). The Khok Kruat Formation is conformably underlain by the Phu Phan Formation and is unconformably overlain by the Maha Sarakham Formation. The fresh-water shark *Thaiodus ruchae* has been recovered from the Khok Kruat Formation and also from the Takena Formation of the Lhasa block of Tibet, the latter having been dated as Aptian–Albian on the basis of foraminiferal fossils (Cappetta et al., 1990). From borehole samples, Sattayarak et al. (1991) suggested an Aptian age for the upper part of the Khok Kruat Formation (Racey and Goodall, 2009).

Meesook (2011) indicated that the depositional environment of these rocks was meandering rivers, although less mature than the rivers that deposited the Sao Khua Formation.

3. Occurrence of tracks

The tracks described herein are preserved at the Huai Dam Chum site (N17°71′30.01″, E104°38′15.76″), Ban Lao Nat, Tha Uthen District, Nakhon Phanom Province, northeastern Thailand (Fig. 1). The Khok Kruat Formation crops out at the Huai Dam Chum site (e.g. Le Loeuff et al., 2003). The outcrop, which consists mainly of very-fine-grained sandstone, is exposed along route 212 (Fig. 3A). Footprints are imprinted on the upper surface of a thin mudstone layer. The succession at this site (Fig. 4) consists of pinkish-brown sandstone with parallel laminations (~25 cm thick) overlying the footprint-bearing thin mudstone layer, which contains mud cracks and ripple marks. Pinkish-brown fine-grained sandstones with cross-laminations (5–15 cm thick) and pinkish-brown fine-grained sandstones with wavy-parallel laminations (15–25 cm thick) are observed in the lower part of the section. Reddish-brown fine-

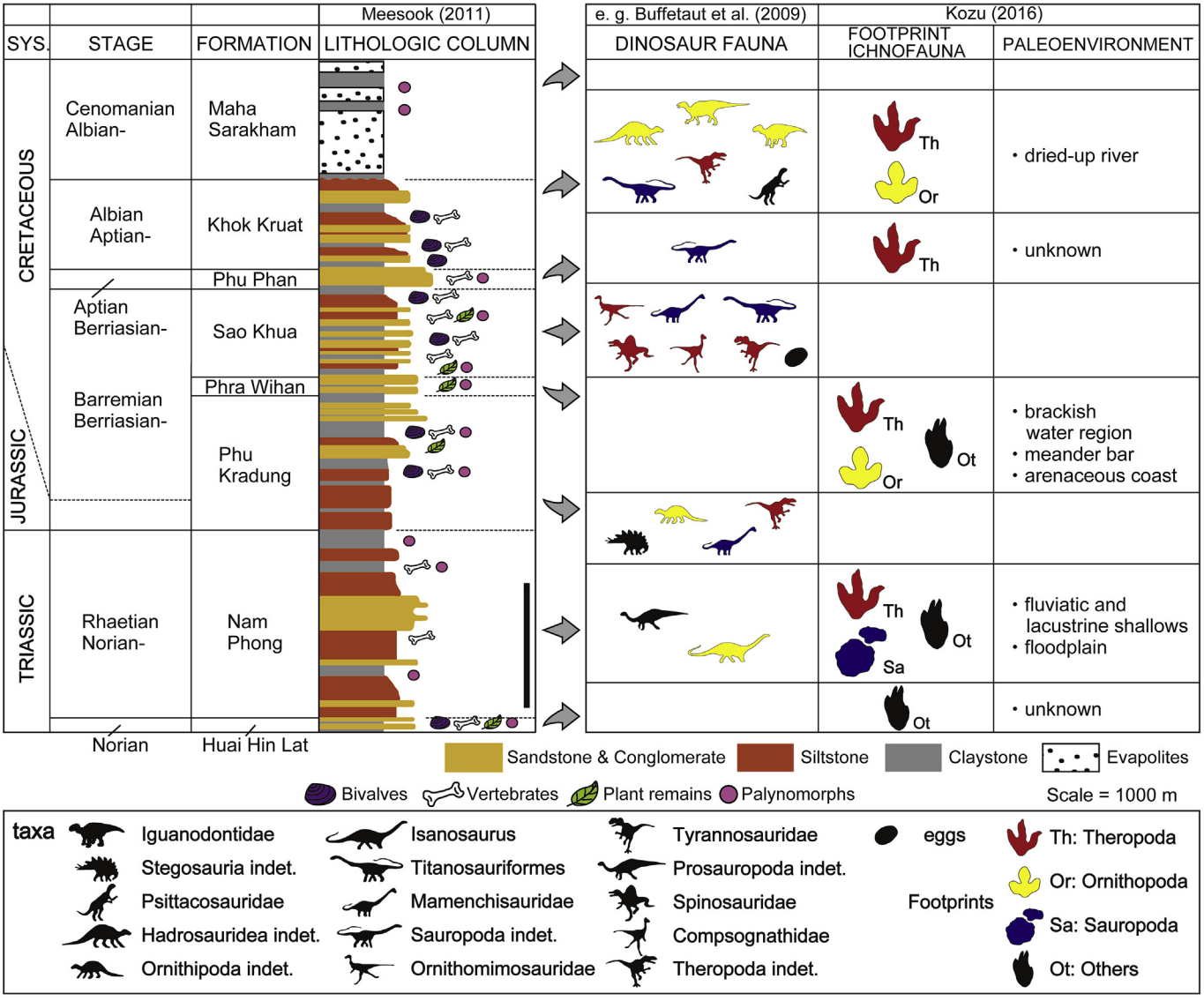

Figure 2. Lithostratigraphic column and dinosaur ichnofauna of the Khorat Group (modified from Buffetaut et al., 2009; Buffetaut and Suteethorn, 2011; Meesook, 2011; Shibata et al., 2011, 2015; Kozu et al., 2016).

grained sandstone, with parallel laminations in its lower part and wavy-parallel laminations in its upper part (~65 cm thick in total), is underlain by pinkish-brown fine-grained sandstone (~30 cm thick) in the middle part of the section. In the upper part of the section, pinkish-brown fine-grained sandstone with wavy-parallel laminations, often discontinuous, is intercalated with white medium-grained sandstone with wavy-parallel laminations (10–15 cm thick). The stratigraphically uppermost part of the section consists of pinkish-brown fine-grained sandstone (~60 cm thick). On the footprint-bearing thin mudstone layer, current-ripple marks that show a NW flow direction and mud cracks are overprinted by footprints (Figs. 5 and 6).

The footprint-bearing outcrops are covered by an artificial roof for their protection and are easily accessed to observe footprints. The outcrop can be roughly separated into southern, middle, and northern parts (Fig. 3B). The area in which abundant footprints were found was originally a quarry; footprints were first reported by Le Loeuff et al. (2003). Subsequently, there have been other reports of footprint in this area (Buffetaut et al., 2005; Le Loeuff et al., 2005, 2009; Sato and Tumpeesuwan, 2005; Matsukawa et al., 2006). Le Loeuff et al. (2003) reported more than 40 small-sized footprints (80 to 135 mm in length) on two large slabs at the Tha Uthen site. They estimated the trackmakers to have been small-sized theropods, and indicated the presence of deinonychosaurs. In 2005, they described a large assemblage of small theropod tracks (Le Loeuff et al., 2005). Sato and Tumpeesuwan (2005) also reported more than 100 footprints of small-sized theropods from the quarry in the same area at Tha Uthen. Those theropod tracks are generally of the same size and morphology as those at the Huai Dam Chum track site. In the northern outcrop, ~600 dinosaur footprints are imprinted in the thin mudstone layer. In this study, we measured dinosaur footprints in the northern part of the outcrop at the Huai Dam Chum track site.

The total area of the outcrop of the track-bearing bedding surface is 72 m^2 in the north part of the Huai Dam Chum site (Fig. 5). Mainly, the tracks of small-sized theropod were recognized on the same bedding plane. On the basis of the track directions, the theropod tracks can be separated into two groups, Group A (tracks indicating a NW movement direction) and Group B

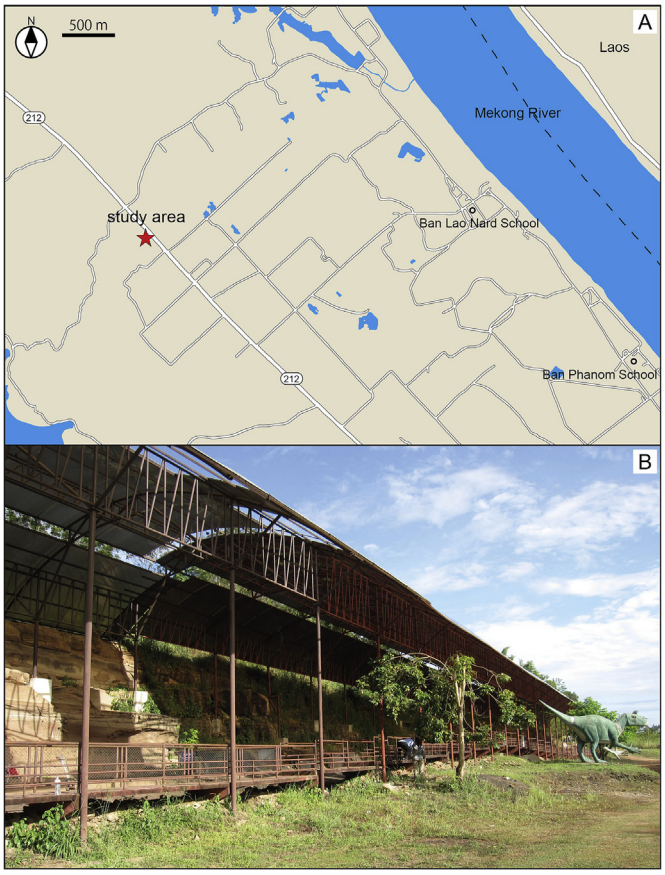

Figure 3. Locality map (A), and outcrop photograph of the Huai Dam Chum site (B). The outcrop is cropping out along the route 212, and footprint-bearing outcrops were covered by artificial roof and easily to access to observe footprints at the site.

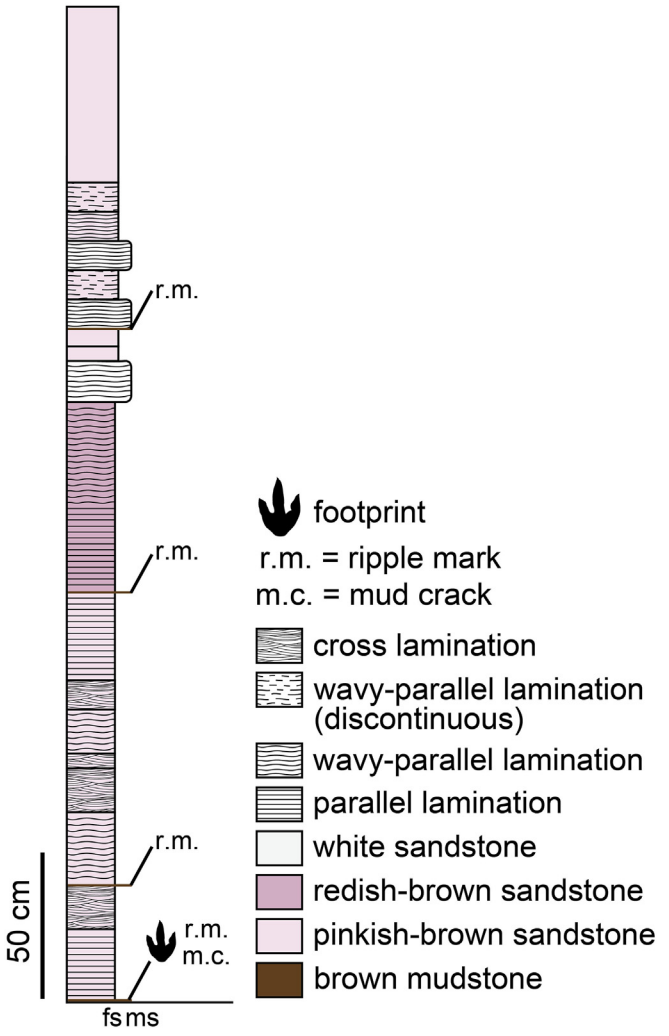

Figure 4. Lithostratigraphic clumn of northern part the outcrop at the Huai Dam Chum site.

(NE movement direction). As shown in Figs. 5 and 6, a total of 584 discrete theropod tracks were mapped, and 79 well-defined trackways (Group A: 66, Group B: 13) consisting of 341 tracks (Group A: 300, Group B: 41) were clearly recognized. The remaining 243 theropod tracks were either isolated or too closely clustered to recognize individual trackways. The ichnological measurement data of the theropod tracks of Groups A and B are similar (Tables 1 and 2). Thus, we consider that the theropod tracks of both groups were formed by the same type of small-sized theropod. On the other hand, two well-defined probably theropod trackways consisting of 8 flattened tracks were also recognized on the same bedding plane, and they shows S to SE movement directions. Many indistinct small-sized tetrapod tracks (length ~4.5 cm) occur on bedding surfaces in the formation, running across or parallel to the theropod trackways at the northern part of the outcrop (Figs. 5 and 6). Le Loeuff et al. (2005, 2009) regarded them as crocodile tracks. In our investigation, we could not capture the ichnological characteristics of the tracks precisely, because of their poor preservation. The manus tracks are smaller than pes tracks. Pes tracks are elongate with indistinct elongated digit impressions directed anteriorly. The length of outer digit impressions is long comparatively. Thus, the tracks are neither lizard-like footprint nor dinosaur footprint. We tentatively refer those as crocodylomorph tracks, although the taxonomic designation of the tracks will be restudied eventually. These observations may suggest that gregarious theropods, a few solitary theropods, and crocodylomorphs travelled along the side of a river, which was probably meandering (Fig. 6).

4. Systematic ichnology

4.1. Theropod tracks

Theropod Marsh, 1881
Asianopodus Matsukawa, Shibata, Koarai and Lockley, 2005

cf. *Asianopodus* isp. (Fig. 7)

Material: At least 79 trackways composed of 341 consecutive tracks in total, as the remaining 243 theropod tracks were isolated. The original tracks and trackway remain in the field (Figs. 5 and 6).

Locality and horizon: Khok Kruat Formation, Lower Cretaceous. Huai Dam Chum site, Ban Lao Nat, Tha Uthen District, Nakhon Phanom Province, Thailand (N17°71′30.01″, E104°38′15.76″).

Description: In the northern part of the outcrop, specimens T8n4, T8n5, T11n3, T14n2, T14n4, T32n5, and T84n3 are well-preserved pes impressions that are sub-symmetrical, tridactyl small-sized tracks with slender digit impressions (Fig. 7; Table 1). In general, the digit III impression is directed anteriorly and is longest, whereas that of digit II is shorter than that of digit IV. Digit II has two phalangeal pad impressions; digits III and IV have three phalangeal pad impressions. There is a distinct claw mark at the tip of each digit. The region and outline of the metatarsophalangeal

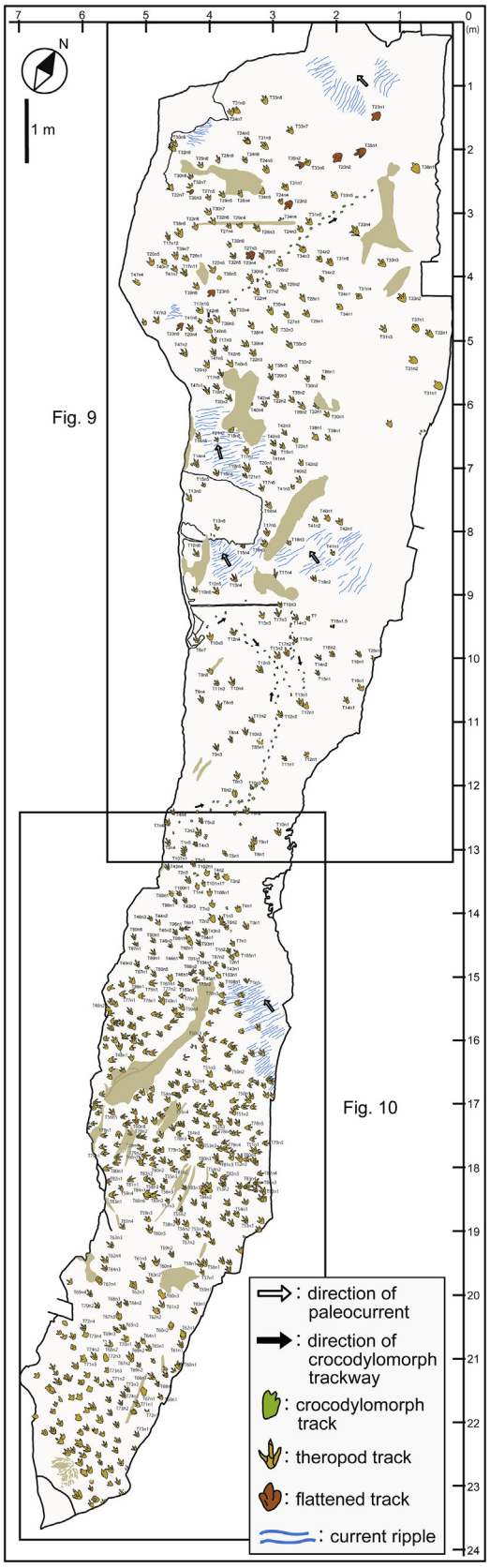

Figure 5. Mesh map of the north part of the outcrop of north part of the Huai Dam Chum site.

pad impression are indistinct. The region also lies nearly in line with the axis of digit III. In well-preserved tracks T1–11, T14, T32 and T84, the interdigital angles between digits II and III are almost equal to those of digits III and IV. The interdigital angle between digits II and IV is 35°–63° (mean 50.7°).

A total of 79 well-defined theropod trackways (T1–18, 20–22, 24, 27–34, and 38–84) were recognized on the northern outcrop (Table 2). Essentially, a "trackway" is composed of more than three consecutive tracks (Thulborn, 1990); in this study, we use "trackway" to mean more than two consecutive tracks for descriptive purposes. The mean footprint length and width are 13.6 cm and 10.1 cm, respectively, and the mean length/width ratio (L/W) is 1.35, indicating moderate mesaxony. The mean step, stride, and pace angulation are 65.6 cm, 131.9 cm, and 172.6°, respectively.

Comparison and discussion: Tridactyl tracks of the type that occur at the Tha Uthen site were typically made by bipedal theropods. Many theropod tracks have been described from the Khorat Group (e.g. Buffetaut et al., 1985a,b, 1997; Le Loeuff et al., 2007, 2008). Lockley et al. (2002, 2006b) described *Siamopodus khaoyaiensis*, which represents small- to medium-sized gracile theropods from the Khao Yai site, from the Lower Cretaceous strata of the Khorat Group. This ichnospecies has a length range of 14–30 cm and a width range of 11–25 cm; in addition, *S. khaoyaiensis* has a sub-symmetric bilobed heel. From an ichnological viewpoint, the Tha Uthen specimens are different from *S. khaoyaiensis*.

In size, the Tha Uthen theropod tracks (mean footprint length 13.6 cm) are similar to *Grallator*, which is a "brontozoid ichnite". However, according to Hitchcock (1858), *Grallator* is characterized as a small (<15 cm) bipedal, functionally tridactyl ichnite, and is also more narrow (length/width ratio near or greater than 2). This difference means that the Tha Uthen specimens are not referred to brontozoid ichnites such as *Grallator* (Fig. 7).

Xing et al. (2011) reported dinosaur footprint assemblage from the Upper Jurassic–Lower Cretaceous Tuchengzi Formation, Hebei Province, China. In the lower part of the track site, small-sized tracks are referred to *Therangospodus* isp. (Fig. 7). The specimens are tridactyl theropod tracks with distinct claw marks, and reveal footprint length/width ration 1.3. In the specimens, discrete borders separate the metatarsophalangeal pad from digit traces II and III, but not digit IV. On the other hand, each proximal end of digit traces II, III and IV is separated from the metatarsophalangeal pad impression in the Tha Uthen specimens. The morphology of the "heel" (metatarsophalangeal pad of digit IV) is an important characteristic in theropod tracks (e.g. Xing et al., 2014b). Thus, the Tha Uthen specimens are not referred to *Therangospodus*.

Azuma et al. (2006) made a report of more than a thousand dinosaur footprints in the Lower Cretaceous of the Ordos Plateau, Inner Mongolia, China. In total six different types of footprints (Footprint Type 1 to 6) are represented in Site I, II, and III. From the Site II, many small-sized tracks labelled as Footprint Type 6 are found. They do not have distinct toe impressions and are teardrop-shaped, however, the trackmaker is estimated as theropod because of the typical gaits such as narrow trackways. The type 6 footprints are similar to the Tha Uthen specimens in size, however it is difficult to identify the internal structure because of its poor preservation of the type 6 footprints.

Zhang et al. (2006) reported the track assemblages from the Lower Cretaceous of Gansu Province, China. In the main site, the unnamed small-sized tracks, Morphotype 2 (footprint length from 15 to 20 cm, narrow digit divarication) are briefly presented (Fig. 9; Zhang et al., 2006). The ichnological characteristics of Morphotype 2 tracks are not in agreement with Tha Uthen specimens. Li et al. (2006) also reported vertebrate track sites, from the Lower Cretaceous, Gansu Province. Three different types of theropod tracks are

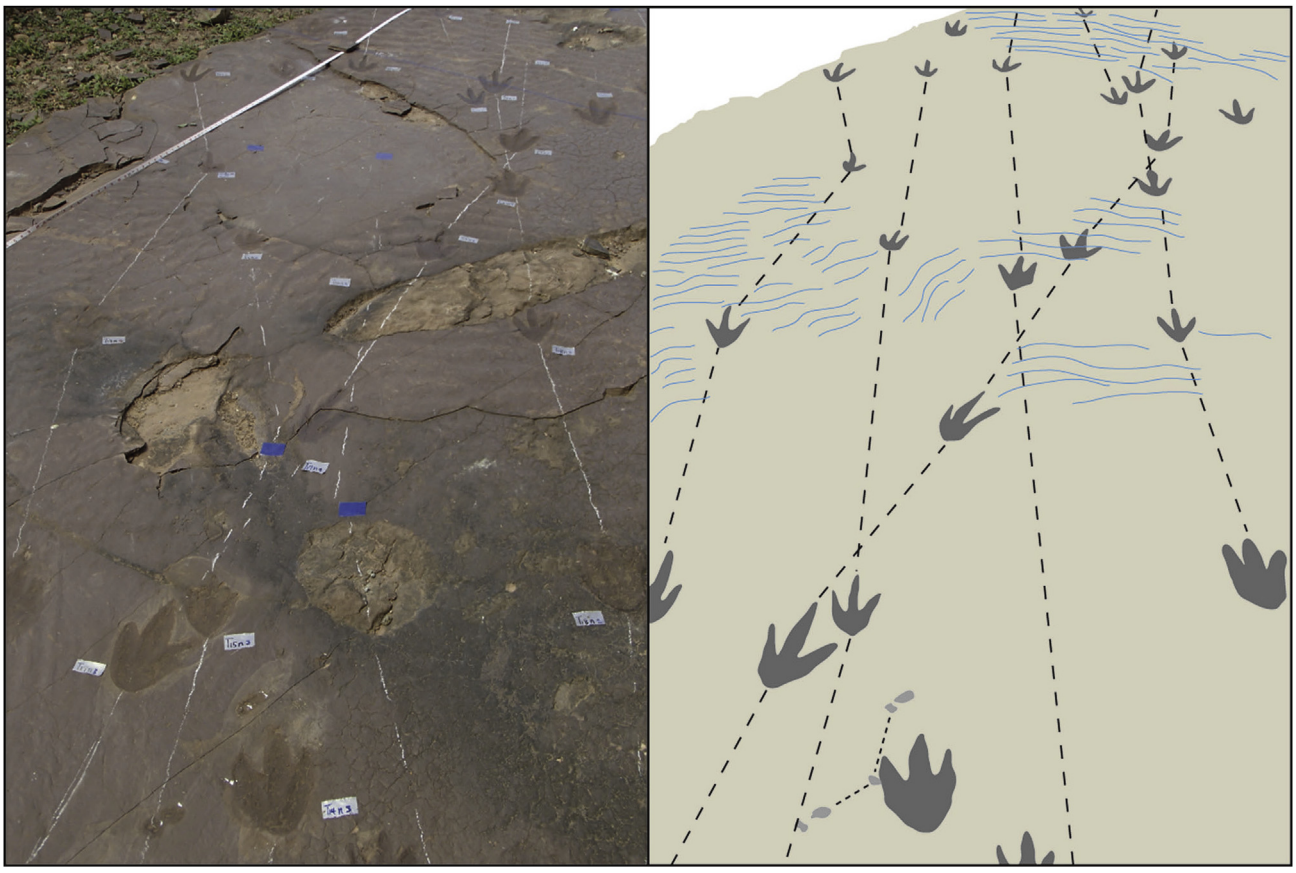

Figure 6. Photographs and sketch of tracks of the Huai Dam Chum site. In the sketch and photograph, many theropod consecutive tracks and a few small-sized crocodylomorph tracks are imprinted with current-ripple marks on the thin mud layer.

Table 1
Measurements of well-preserved tracks of theropod and flattened tracks of possible theropod at the Huai Dam Chum site.

Tw	No.	FP	FL	FW	II-IV	II-III	III-IV	Dir	Step	Stride	PA	TD
T1	n1	R	10.5	9	55	30	25	N65°W	53.5	105	-	
	2	L	11	8.5	45	20	25	N58°W	52.5	111.5	165	
	3	R	11.5	7.5	40	18	22	N62°W	61	121.5	165	
	4	L	12.5	8	42	20	22	N62°W	62	-	170	
	5	R	13	8	40	20	20	N70°W	-	-	-	
Average			**11.7**	**8.2**	**44.4**	**21.6**	**22.8**		**57.3**	**112.7**	**166.7**	**A**
T2	n1	L	13	10	42	20	22	N65°W	66	135.5	-	
	2	R	17	12	59	24	35	N70°W	70	139.5	175	
	3	L	16	12	50	23	27	N68°W	69.5	-	172	
	4	R	15	10.5	48	25	23	N70°W	-	-	-	
Average			**15.3**	**11.1**	**49.8**	**23**	**26.8**		**68.5**	**137.5**	**173.5**	**A**
T3	n1	L	17.5	11.5	48	23	25	N63°W	81	162.5		
	2	R	15.5	12	60	25	35	N70°W	82		170	
	3	L	17	12	56	28	28	N66°W				
Average			**16.7**	**11.8**	**54.7**	**25.3**	**29.3**		**81.5**	**162.5**	**170**	**A**
T4	n1	L	12.5	10	39	19	20	N70°W	60	120		
	2	R	12	9	63	35	28	N73°W	60	122	177	
	3	L	13	9	44	22	22	N65°W	60		176	
	4	R	12	10	61	30	31	N82°W				
Average			**12.4**	**9.5**	**51.8**	**26.5**	**25.3**		**60**	**121**	**176.5**	**A**
T5	n1	L	12.5	7.5	45	20	25	N74°W	63			
	2	R	12.5	8.5	48	28	20	N77°W				
Average			**12.5**	**8**	**46.5**	**24**	**22.5**		**63**			**A**
T6	n1	R	10	9	55	27	28	N40°E	58			
	2	L	12	8.5	43	23	20	N35°E				
Average			**11**	**8.8**	**49**	**25**	**24**		**58**			**B**
T7	n1	R	14	9	50	24	26	N66°W	70	140		
	2	L	13.5	10	54	29	25	N65°W	70	144	175	
	3	R	15	10.5	55	30	25	N75°W	76		169	
	4	L	13	-	61	30	31	N70°W				

Table 1 (*continued*)

Tw	No.	FP	FL	FW	II-IV	II-III	III-IV	Dir	Step	Stride	PA	TD
Average			**13.9**	**9.8**	**55**	**28.3**	**26.8**		**72**	**142**	**172**	**A**
T8	n1	L	16	10.5	63	33	30	N50°W	56.5	111.5		
	2	R	16	10.5	59	29	30	N60°W	55	112.5	170	
	3	L	15	10.5	52	27	25	N55°W	57.5	113	172	
	4	R	14	9.5	49	25	24	N67°W	55.5	111.5	170	
	5	L	14.5	10.5	53	31	22	N68°W	56	109.5	170	
	6	R	14.5	10	57	26	31	N70°W	54		170	
	7	L	15	10	60	33	27	N60°W				
Average			**15**	**10.2**	**56.1**	**29.1**	**27**		**55.8**	**111.6**	**170.4**	**A**
T9	n1	L	16.5	11	52	30	22	N55°W	79	154.5		
	2	R	16	12.5	57	30	27	N53°W	75.5	155	180	
	3	L	15.5	11	53	28	25	N65°W	79.5		174	
	4	R	16	11	50	27	23	N58°W				
Average			**16**	**11.4**	**53**	**28.8**	**24.3**		**78**	**154.8**	**177**	**A**
T10	n1	L	17.5	13	53	28	25	N50°W	82.5	164		
	2	R	16.5	12.5	60	29	31	N70°W	81.5	160.5	177	
	3	L	15.5	12.5	60	33	27	N63°W	79	158	175	
	4	R	16	13	63	30	33	N65°W	80	155.5	170	
	5	L	16.5	13	61	33	28	N62°W	76		175	
	6	R	14.5	11	56	30	26	N60°W				
Average			**16.1**	**12.5**	**58.8**	**30.5**	**28.3**		**79.8**	**159.5**	**174.3**	**A**
T11	n1	L	13.5	10	-	-	-	N84°W	76.5	153.5		
	2	R	13	9	41	19	22	N80°W	77		174	
	3	L	12	10	55	27	28	N78°W				
Average			**12.8**	**9.7**	**48**	**23.0**	**25.0**		**76.8**	**153.5**	**174.0**	**A**
T14	n1	R	16.5	14	-	-	-	N62°W	74	146		
	2	L	15.5	11	47	32	15	N72°W	72.5		170	
	3	R	16	11	48	26	22	N76°W				
	4	R	15	11	44	16	28	N63°W				
Average			**15.8**	**11.8**	**46.3**	**24.7**	**21.7**		**73.3**	**146**	**170**	**A**
T23	n1	R	17.5	14.5	-	-	-	N172°E	90.0	196.0		
	2	L	17.5	15	-	-	-	N177°E	106.0	207.0	172	
	3	R	18.5	14	-	-	-	N183°E	102.0	187.0	171	
	4	L	17	14.5	-	-	-	N175°E	86.0	156.0	175	
	5	R	16.5	13	-	-	-	N190°E	71.0		176	
	6	L	17.5	14	-	-	-	N180°E				
Average			**17.4**	**14.2**	-	-	-		**91.0**	**186.5**	**173.5**	**C**
T32	n1	L	12.5					N74°W	67	134		
	2	R	15	10.5	45	20	25	N68°W	67	134	177	
	3	L	14.5	11	50	26	24	N68°W	67	132	175	
	4	R	15	12	50	29	21	N64°W	65	129.5	172	
	5	L	15	12	47	21	26	N65°W	64.5	134	176	
	6	R	15	11	53	-	-	N70°W	69.5	131	173	
	7	L	13	11	50	30	20	N78°W	62		171	
	8	R	12.5	10	35	16	19	N74°W				
Average			**14.1**	**11.1**	**47.1**	**23.7**	**22.5**		**66.0**	**132.4**	**174**	**A**
T35	n1	L	15.5	11.5	-	-	-	N205°E	96.5			
	2	R	12.5	11.5	-	-	-	N226°E				
	3	R	12.5	11	-	-	-	N208°E				
Average			**13.5**	**11.3**	-	-	-		**96.5**			**C**
T84	n1	L	13.5		-	-	-		87.5	171.5		
	2	R	16.5	11.5	-	-	17		84		175	
	3	L	15.5	12	49	20	29					
Average			**15.2**	**11.8**	**49.0**	**20.0**	**23.0**		**85.8**	**171.5**	**175**	**B**

Tw: trackway number, No.: footprint number, FP: foot part (L or R), FL: footprint length (cm), FW: footprint width (cm), II-IV: interdigital angle between II to IV, II-III: interdigital angle between II to III, III-IV: interdigital angle between III to IV, Dir: direction of digit axis III, Step: pace length (cm), Stride: stride length (cm), PA: pace angulation, TD: trackmaker description; A = theropod Group A, B = theropod Group B, and C = solitary theropod.

represented from the site 1 and 2. In particular, Type 2 and 3 tracks are basically tridactyl with digit impressions II to IV. However, Type 2 and 3 tracks are tentatively referred as ichnogenus *Changpeipus* and *Grallator*, respectively. Some of Type 2 tracks *Changpeipus* show traces of digit I behind the digit II impression. Type 3 tracks *Grallator* show the footprint length/width ratio 0.6 which is lower than that of Tha Uthen specimens. Thus, these Gansu tracks are different from the Tha Uthen specimens in morphology.

Matsukawa et al. (2005, 2006) illustrated track-bearing slabs at a locality near Lao Nat (= Huai Dam Chum site), and mentioned that those specimens are similar to the ichnogenus *Asianopodus*. Unfortunately, the horizon yielding *Asianopodus* type tracks was not indicated in detail. Le Loeuff et al. (2009) also illustrated a sketch of some theropod trackways from the Tha Uthen site and indicated a resemblance to *Asianopodus*. *Asianopodus* is characterized as a small- to medium-sized tridactyl, mesaxonic and subsymmetrical track with a distinct bulbous heel impression (Matsukawa et al., 2005). The interdigital angle between II and IV is 42°–59° and the footprint length/width ratio is 1.38 to 1.63 (mean 1.48; Matsukawa et al., 2005). In the Tha Uthen specimens of the northern outcrop, each track has indistinct metatarsophalangeal pad impressions, but a distinct bulbous heel impression is difficult to recognize because of poor preservation of the posterior part. The ichnological measurements of the Tha Uthen specimens are basically similar to those of *Asianopodus*. Because of these morphological differences, the Tha Uthen specimens at the northern outcrop are assigned tentatively to cf. *Asianopodus* in the present study (Fig. 7).

Table 2
Measurements of trackways of the Huai Dam Chum site.

Tw	FL	FW	FL/FW	h	Step	Stride	PA	S (m/s)	S (km/h)	TD
T1	11.7	8.2	1.427	52.65	57.3	112.7	166.7	2.023	7.28	A
T2	15.25	11.1	1.371	68.63	68.5	137.5	173.5	2.069	7.45	A
T3	16.7	11.8	1.408	75.00	81.5	162.5	170	2.465	8.87	A
T4	12.375	9.5	1.303	55.69	60.0	121	176.5	2.134	7.68	A
T5	12.5	8	1.563	56.25	63.0	-	-	-	-	A
T6	11	8.8	1.257	49.50	58.0	-	-	-	-	B
T7	13.9	9.8	1.411	62.44	72.0	142	172	2.439	8.78	A
T8	15	10.2	1.469	67.50	55.8	111.6	170.4	1.489	5.36	A
T9	16	11.4	1.407	72.00	78.0	154.8	177	2.383	8.58	A
T10	16.1	12.5	1.287	72.38	79.8	159.5	174.3	2.491	8.97	A
T11	12.8	9.7	1.328	57.75	76.8	153.5	174	3.043	10.96	A
T12	14.8	12	1.229	66.38	70.9	142	172	2.271	8.17	A
T13	15.2	11.1	1.368	68.25	73.5	146.5	172.3	2.315	8.33	A
T14	15.8	11.8	1.340	70.88	73.3	146	170	2.203	7.93	A
T15	11.7	8.4	1.393	52.65	61.0	115.8	166	2.119	7.63	A
T16	14.4	11.6	1.241	64.80	69.0	132.5	-	2.080	7.49	A
T17	16	11.7	1.364	72.00	64.1	127.3	171	1.720	6.19	A
T18	15.7	10.5	1.492	70.50	67.7	136	170.8	1.969	7.09	A
T20	16.6	11.9	1.395	74.70	63.3	124.8	166	1.594	5.74	A
T21	12.3	9.3	1.324	55.13	72.0	-	-	-	-	A
T22	15.8	11.6	1.364	71.04	74.1	147.3	169.8	2.230	8.03	A
T23	17.4	14.2	1.229	78.38	-	186.5	173.5	2.947	10.61	C
T24	11.6	9.5	1.218	52.07	53.8	107.5	172.2	1.895	6.82	A
T27	12.8	9.0	1.417	57.38	55.6	110.3	170.3	1.767	6.36	A
T28	14.3	10.2	1.397	64.13	63.9	127.2	176	1.966	7.08	A
T29	12.8	9.5	1.351	57.75	57.6	115.5	174.8	1.893	6.81	A
T30	14	9.7	1.440	63.00	60.9	120.4	173.3	1.831	6.59	A
T31	14.8	10.3	1.438	66.50	66.7	134.6	171.6	2.073	7.46	A
T32	14.1	11.1	1.270	63.28	66.0	132.4	174	2.137	7.69	A
T33	15.5	11.6	1.341	69.75	63.8	126.9	184.5	1.776	6.39	A
T34	12.3	8.6	1.427	55.13	54.5	109.4	174.3	1.825	6.57	A
T35	13.5	11.3	1.191	60.75	-	180.5	-	3.759	13.53	C
T38	15.6	11.9	1.308	70.13	64.9	128.1	165.7	1.793	6.46	A
T39	16.3	11.6	1.407	73.29	62.8	125	168.6	1.634	5.88	A
T40	15	12.6	1.188	67.50	69.7	137.7	173.8	2.115	7.61	A
T41	12.3	9.4	1.303	55.29	65.8	122.5	172.7	2.197	7.91	A
T42	12.7	10.4	1.216	57.00	54.0	108.8	168	1.740	6.26	A
T43	12.8	9.8	1.308	57.38	59.3	117.8	172.5	1.969	7.09	A
T44	13.8	10	1.375	61.88	64.0	-	-	-	-	A
T45	16.3	9.3	1.757	73.13	77.5	-	-	-	-	A
T46	11.3	7.7	1.478	51.00	53.3	106.5	175	1.911	6.88	A
T47	15.3	10.4	1.470	68.63	68.2	134.8	168	2.001	7.20	A
T48	13.5	10.3	1.317	60.75	61.0	-	-	-	-	A
T49	13	10.3	1.268	58.50	70.0	-	-	-	-	A
T50	12.6	8.8	1.438	56.63	61.9	123.6	170	2.169	7.81	A
T51	12.5	10.5	1.190	56.25	68.8	137.5	175	2.611	9.40	A
T52	13.1	9.9	1.329	59.06	65.0	128.8	171	2.210	7.96	A
T53	15.5	11	1.409	69.75	69.0	138.3	176	2.049	7.38	A
T54	12.4	8.6	1.435	55.69	69.2	137.5	176.5	2.642	9.51	A
T55	10.5	7	1.500	47.25	49.3	98	170	1.819	6.55	A
T56	12.7	10.1	1.257	57.15	69.0	137	171.7	2.548	9.17	A
T57	10.7	8.2	1.301	48.00	60.5	124	178	2.646	9.52	A
T58	12.3	9.7	1.271	55.50	73.3	148	178	3.000	10.80	A
T59	11	8.3	1.333	49.50	63.7	129	171.5	2.726	9.81	A
T60	15.7	12.3	1.280	70.59	54.9	104.9	172.5	1.275	4.59	A
T61	12.4	9.8	1.269	55.69	68.5	136.3	178	2.602	9.37	A
T62	16.5	12.2	1.356	74.25	57.7	113.5	171	1.370	4.93	A
T63	13	10.2	1.279	58.50	83.0	166	170	3.416	12.30	A
T64	13.8	10.2	1.361	62.25	64.8	129	170	2.085	7.51	A
T65	11.5	8.75	1.314	51.75	51.5	-	-	-	-	A
T66	15.5	12	1.292	69.75	82.5	-	-	-	-	A
T67	15.3	11.1	1.371	68.63	62.2	126	171	1.788	6.44	A
T68	11	8.7	1.269	49.50	68.8	157	175	3.785	13.62	A
T69	11.6	9.5	1.224	52.31	65.0	131.8	175	2.647	9.53	A
T70	13.3	10.5	1.262	59.63	66.5	-	-	-	-	A
T71	13.2	10.7	1.234	59.25	54.8	109	170	1.667	6.00	A
T72	13.2	10.1	1.300	59.25	56.8	114	176.5	1.797	6.47	A
T73	11	9.1	1.205	49.50	57.3	113.5	171.5	2.201	7.93	A
T74	12.3	10.8	1.140	55.13	75.0	-	-	-	-	A
T75	13.5	10	1.350	60.75	66.5	-	-	-	-	B
T76	11.3	9.7	1.172	51.00	64.0	128.5	175	2.616	9.42	B
T77	14.8	12.3	1.204	66.38	69.5	-	-	-	-	B
T78	12	9.1	1.319	54.00	56.8	114.8	171.7	2.028	7.30	B
T79	14.8	11.2	1.317	66.38	63.8	127.2	171	1.888	6.80	B

Table 2 (*continued*)

Tw	FL	FW	FL/FW	h	Step	Stride	PA	S (m/s)	S (km/h)	TD
T80	13.8	10.3	1.341	61.88	71.5	145.8	175.5	2.575	9.27	B
T81	12.7	10.2	1.252	57.30	70.8	141	174	2.665	9.59	B
T82	11.8	9.6	1.221	52.88	58.0	123	-	2.331	8.39	B
T83	16.1	12.8	1.265	72.56	70.7	144.8	171.5	2.112	7.60	B
T84	15.2	11.8	1.291	68.25	85.8	171.5	175	3.012	10.84	B
T87	10	7.5	1.333	45.00	-	-	-	-	-	B
T88	11.5	8.5	1.353	51.75	-	-	-	-	-	B

Tw: trackway number, FL: mean footprint length (cm), FW: mean footprint width (cm), FL/FW: mean footprint length/width ratio, h: mean hip height (cm), Step: mean pace length (cm), Stride: mean stride length (cm), PA: mean pace angulation, S (m/s): mean speed in s/h, S (km/h): mean speed in km/h, TD: trackmaker description; A = Group A, B = Group B, and C = solitary theropod.

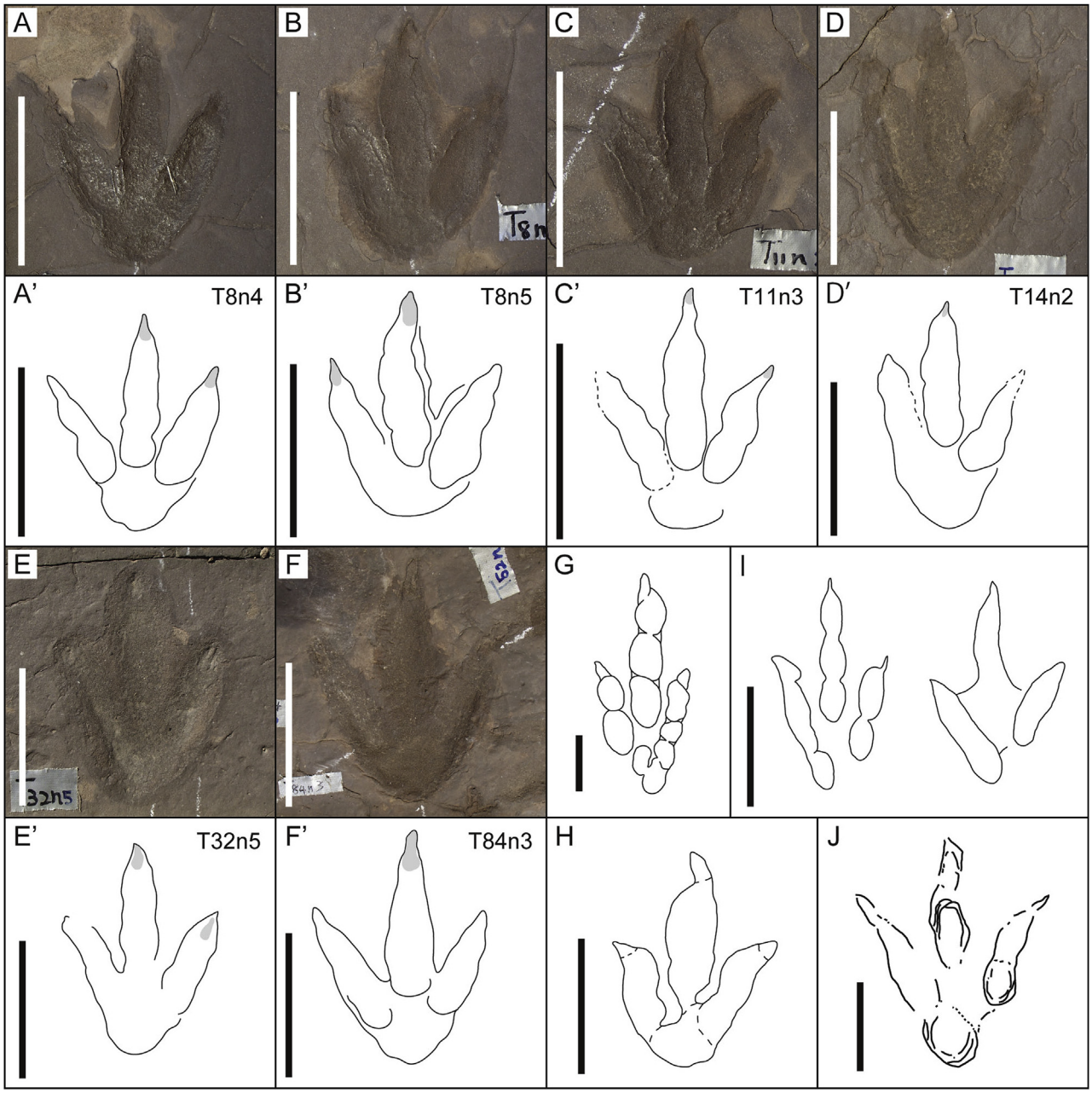

Figure 7. Comparison chart of theropod tracks. (A–F) Photographs of pes tracks of Tha Uthen specimens T8n4, 5, T11n3, T14n2, T32n5, and T84n3; (A'–F') sketches of pes track of Tha Uthen specimens T8n4, 5, T11n3, T14n2, T32n5, and T84n3; (G) sketch of genoholotypic track of *Grallator parallelus* (modified from Olsen et al., 1998); (H) sketch of *Therangospodus* isp. (modified from Xing et al., 2011); (I) sketches of small-sized track morphotype 2 from the Yanguoxia site (modified from Zhang et al., 2006); (J) sketch of *Asianopodus pulvinicalx* (modified from Matsukawa et al., 2005). Scale bars of A to F, A' to F', H, I and J are 10 cm. Scale bar of G is 2 cm.

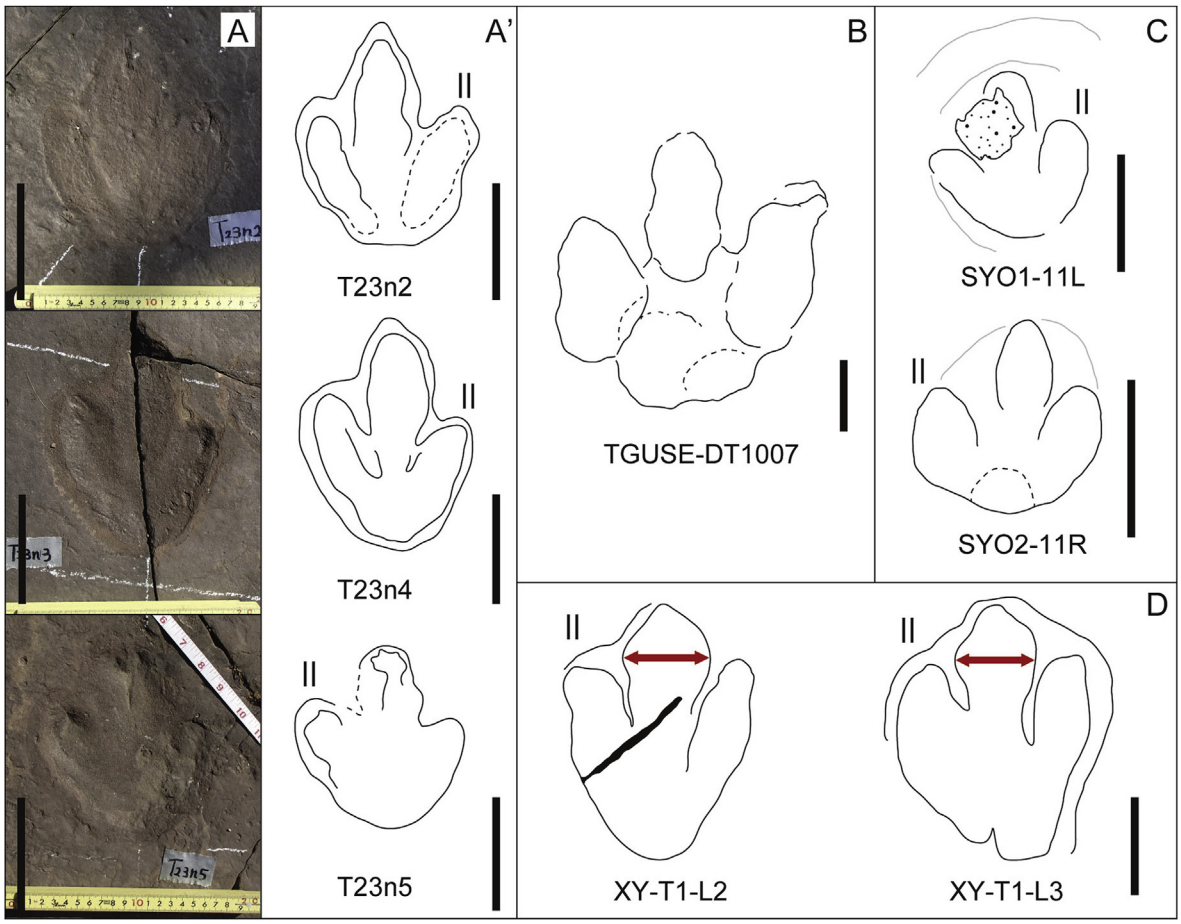

Figure 8. Comparison chart of flattened tracks. (A) Photographs of pes tracks of Tha Uthen tacks T23; (A') sketches of pes track of Tha Uthen tracks T23; (B) sketch of *Caririchnium* sp. TGUSE-DT1007 (modified from Matsukawa et al., 2005); (C) sketch of ornithopod tracks SYO1-11L and SYO2-11R (modified from Xing et al., 2014a); (D) sketch of flattened theropod tracks XY-T1-L2 and XY-T1-L3 (modified from Lockley and Xing, 2015). Arrows mean maximum width of cast of digit III. Scale bar is 10 cm.

4.2. Flattened possible theropod tracks

Theropoda Marsh, 1881

Ichnogen. et sp. indet. (Fig. 8)

Material: Two trackways: T23 composed of 6 consecutive tracks and T35 composed of 3 discontinuous tracks. The original tracks and trackway remain in the field (Figs. 5 and 6).

Locality and horizon: Same as Section 4.1.

Description: The average footprint length and width of Tha Uthen trackway T23 (Fig. 8) are 17.4 and 14.2 cm, respectively (Table 1). The mean step and stride length are 91.0 and 186.5 cm, respectively. The mean pace angulation is 176.5°. Tha Uthen trackway T35 is poorly preserved, mostly as round impressions or incomplete. The average footprint length and width of trackway T35 are 13.5 cm (maximum 15.5 cm) and 11.3 cm (maximum 11.5 cm), respectively. The mean step is 96.5 cm. The well-preserved trackway T23 shows tridactyl impressions and facultative bipedal walking gait. The trackway width of T23 is narrow and each track is inwardly rotated. Most tracks of trackways T23 and T35 are flattened or round impressions with no distinct digital pad traces, and are circular to semicircular in shape with an indistinct border to the three digits. Each digit impression is comparatively elongate. The footprint length/width ratio is 1.23 (maximum 1.28).

Comparison and discussion: Le Loeuff et al. (2009) remarked that the Tha Uthen specimen (T23) is very similar to ornithopod tracks from Japan described by Matsukawa et al. (2006), and they provisionally referred the Tha Uthen specimen to the ichnogenus *Caririchnium*. However, *Caririchnium* has broad and quite blunt digits, and is also characterized by a bilobed heel (Fig. 8); thus, the Tha Uthen specimen cannot be identified as *Caririchnium*.

Ornithopod tracks are rare in the Khorat Group. Lockley et al. (2009) reported *Neoanomoepus* sp., which was formed by a primitive small-sized ornithopod, at the Hin Lat Pa Chad site in the Lower Cretaceous Phra Wihan Formation. However, those tracks show quadrupedal walking with five manual and four pedal digits. Kozu et al. (2014) reported one ornithopod track, a natural cast 19.8 cm long and 15.9 cm wide, from the Khok Kruat Formation, but that specimen is larger than the Tha Uthen specimen and shows robust digit impressions and the metatarsophalangeal pad.

Xing et al. (2014a) reported small-sized possible ornithopod tracks from the Houcheng Formation, Shangyi, China. The Shangyi specimens (Fig. 8: SYO1 and SYO2) are tridactyl pes impressions with no manus impressions, and lack claw marks. The size (length SYO1: 12.1 cm, SYO2: 15.1 cm on average) and narrow trackway width are similar to the Tha Uthen material. However, the Shangyi specimens show round and robust digit impressions, and the maximum length/width ratio (1.00) is smaller than in the Tha Uthen specimen.

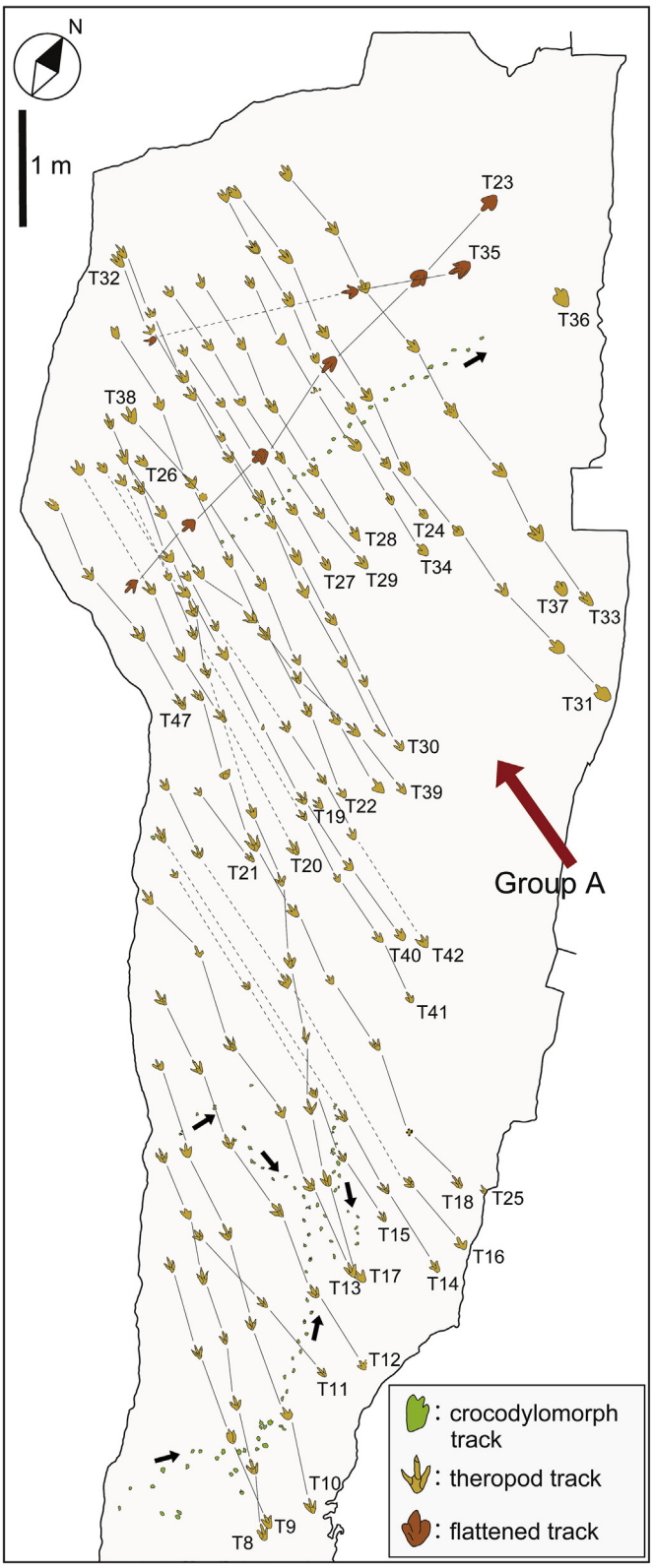

Figure 9. Northern part of the mesh map at the Huai Dam Chum site. Most of theropod trackways of Group A are parallel or sub-parallel to each other, and show small or irregular intertrackway spacing, but some theropod trackways are overlapping each other. Two solitary trackways consisting of flattened tracks intersect at a right angle with theropod trackways of Group A. Black arrows indicate the directions of crocodylomorph trackways. Red arrow indicates the direction of movement of Group A.

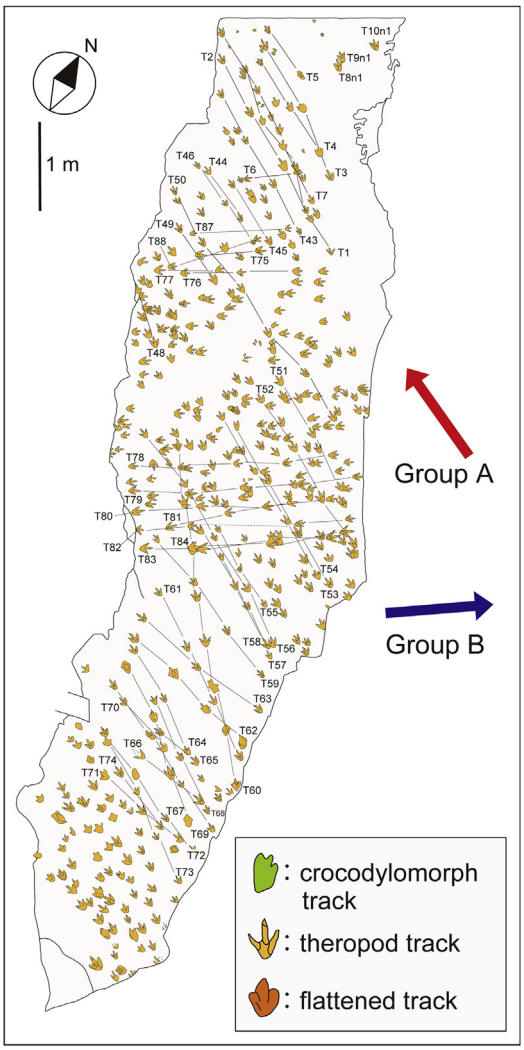

Figure 10. Southern part of the mesh map at the Huai Dam Chum site. Most of theropod trackways of Group A are parallel or sub-parallel to each other, and show NW direction. Some theropod trackways of Group B are identified, but most of tracks are overlapping each other, and intersect at a right angle with tracks of Group A. Each arrow indicates the directions of movement of Group A and B, respectively.

The Tha Uthen trackways T23 and T35 lack manus impressions. From the point of view of the ichnological shape of the specimens, at first glance, it looks like trackway T23 and T35 are imprinted by ornithopod. However we suggest that the Tha Uthen specimens T23 and T35 are tracks of small-sized theropod. Lockley and Xing (2015) made a comparative review of flattened tracks which are imprinted by theropod. According to them, the lack of discrete digital pads and inter-pad creases makes the tracks appear more like those of ornithopods than theropods. However the trackway pattern remains characteristically theropodan. Additionally, flattened tracks of theropod often reveal digit III with distinctive, diamond- or rhomb-shaped outlines (Fig. 8). In the Tha Uthen specimens T23 and T35, the tracks lack digital pads and inter-pad creases. The tracks also show high footprint length/width ratio, narrow trackway width, and the impressions of digit III appear to widen distally (Fig. 8). Thus, the trackmakers of T23 and T35 are estimated to have been a small-sized theropod. It is impossible to give those tracks ichnological names because the tracks are in a poor state of preservation. In comparison with other *Asianopodus* type theropod tracks, the

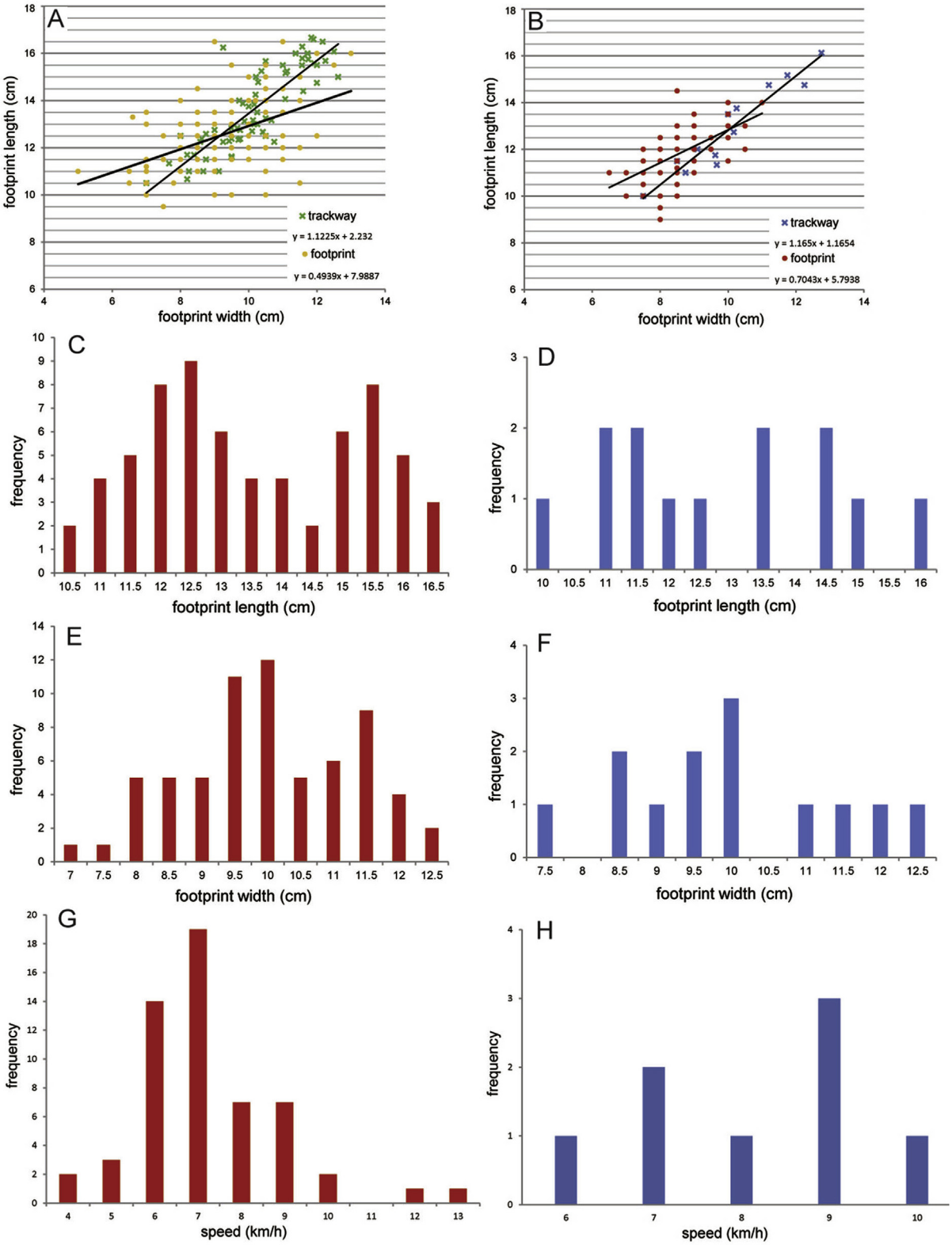

Figure 11. Histograms of the measurement data in the Tha Uthen theropod tracks. (A and B) are bivariate plots of footprint length-width measurements of Group A and B, respectively. (C, E and D, F) are size-frequency histogram for Group A and B, respectively. (G and H) are histograms of estimated speed of the trackmakers of Group A and B, respectively.

tracks of T23 and T35 are relatively large, and shows solitary pattern. Thus, the trackmakers of T23 and T35 are different with those of other *Asianopodus* type tracks.

5. Interpretation of the trackway assemblage

5.1. Trackway and group distribution

A total of 584 theropod tracks referred to cf. *Asianopodus* are recognized in association with unnamed theropod and crocodylomorph tracks in an area of 72.5 m^2 on the northern outcrop surface at the Huai Dam Chum track site (Figs. 5 and 6). This occurrence constitutes an example of high-density dinosaur tracks in the Cretaceous strata of Thailand.

As mentioned above, the *Asianopodus* type theropod tracks are separated into two groups because the tracks show two directions of migration, to the northeast and to the northwest. We define the group aligned NW as Group A and the group aligned NE as Group B (Fig. 5). Table 2 lists the estimated hip height and speed of the cf. *Asianopodus* trackmakers (Thulborn, 1982, 1989). The mean estimated hip heights of Group A and B are 61.7 and 58.3 cm, respectively; the speeds of those groups are estimated as 8.04 and 8.65 km/h, respectively (Table 2). The relative stride length (stride length/hip height = SL/h) is indicative of the use of different gaits such as walking (<2), trotting (2 to 2.9), and running (>2.9; Thulborn, 1990). According to these definitions, the relative stride lengths of Groups A and B are 2.10 and 2.35, respectively, implying that the trackmakers of Group A and B were trotting.

Recent discoveries of multiple trackway sites indicate that many dinosaur groups were habitually gregarious (Lockley, 1991). As shown in Fig. 9, the cf. *Asianopodus* trackways are parallel or subparallel to each other with little overlap, and show small or irregular "intertrackway spacing" (the lateral space between adjacent trackways). Barco et al. (2006) concluded that a dinosaur group moved in a pack comprising at least three waves, on the basis of the closeness of the parallel trackways and their superimpositions on the same substratum. In Fig. 9, we illustrate some well-defined trackways of Group A. The trackways imprinted by individuals of the same size are oriented parallel or sub-parallel to one another with little overlap, and the intertrackway spacings are small and partially irregular. In addition, the estimated travelling speeds are similar to each other. In common with Barco et al. (2006), we follow the hypothesis that Group A moved in a single pack comprising several waves. For Group B, there are low number of well-defined trackways and many isolated tracks because most tracks are overlapping (Fig. 10). Thus, on the basis of the ichnological measurement data, we could not describe those behavioural patterns in detail, but Group B was probably produced by a single group. Thus, the theropod trackways of Groups A and B at the Huai Dam Chum site are considered to record patterns of gregarious behaviour. Two trackways consisting of the flattened possible theropod tracks (labelled C; Tables 1 and 2) show S to SE movement directions meaning solitary behaviour.

5.2. Trackmaker affinity and its herd structure

From the measurements of the track assemblage, Groups A and B are inferred to have been imprinted by the same type of small-sized theropod. Theropod remains are relatively poorly known in the Khok Kruat Formation. On the basis of isolated teeth, Buffetaut et al. (2005) indicated the existence of a small-sized theropod; however, little is known about the affinity of the indeterminate theropod. On the other hand, the ornithomimosaurian *Kinnareemimus khonkaenensis* was described by Buffetaut et al. (2009) from the Lower Cretaceous Sao Khua Formation of the Khorat Group. In general, ornithomimosaurs are the best-known example of gregarious dinosaurs. Although direct evidence is lacking, we consider that the theropod tracks referred to cf. *Asianopodus* in the Huai Dam Chum site were imprinted by ornithomimosaurian dinosaurs.

From the quantitative community analysis, scatterplots of footprint length-width measurements of the tracks of Groups A and B at the Huai Dam Chum site were constructed (Fig. 11). In Group A, the values of trackway are widely scattered (regression line: $y = 0.4939x + 7.9887$); in contrast, the footprint values are clustered around the regression line ($y = 1.1225x + 2.232$). From those results, we constructed a histogram showing frequency-length measurements using the trackway data ($n = 66$). The footprint length is related to the size of the trackmaker. In this case, the histogram exhibits an anomalous bimodal distribution, whereas the herd structure of dinosaur footprint assemblages normally shows a monomodal distribution (e.g. Barco et al., 2006; Lockley et al., 2006a). In this study, we consider two hypotheses as explanations for this pattern: male-female differences and different growth stages. In general, footprint shape and morphology may not reflect diagnostic differences between genera or species, or sexual dimorphism (e.g. Farlow, 2001; Myers and Fiorillo, 2009). There is no direct evidence that the bimodal distribution of the size-frequency histogram of the Tha Uthen theropod tracks reflects sexual dimorphism. Ichnotaxa do not correspond to the taxonomical classification based on bone fossils (Myers and Fiorillo, 2009); thus, it is difficult to describe the trackmaker of the Tha Uthen theropod track at a lower taxonomic level and to estimate the seasonal periodicity of the Tha Uthen site in detail. However, this result indicates the possibility of a pair-bonded lifestyle or reproductive cycles in dinosaurs (Fiorillo et al., 2014). For the second hypothesis, the mean estimated hip height of the trackmakers of Group A is 61.7 cm (Table 2). If all of those theropod producers were juveniles, the size of mature or old individuals would have been comparable to that of large-sized theropods such as Ceratosauria, Megarosauria, and Carcharodontosauria in the Lower Cretaceous (Aptian–Albian). It is highly unlikely that such large-sized theropods were living in a large-scale family. The trackmakers of the cf. *Asianopodus* Group A were probably mainly two distinct ontogenetic age groups without juveniles. If the ichnological interpretations of sexual and age segregation in the Tha Uthen theropod tracks are correct, then small-sized theropods may have possessed a complex herd social construction, as is already known for sauropods and ornithopods. For Group B, the measurement data from the quantitative community analysis are insufficient to describe the herd structure. However, on the basis of the tentative values, we consider that Group B was composed of the same type of small-sized theropods as Group A, and therefore probably had the same herd structure.

6. Conclusions

At the Huai Dam Chum site, ~600 dinosaur footprints are preserved in a thin mud layer in the northern part of the outcrop. We provide the first evidence that the trackmakers of cf. *Asianopodus* were probably gregarious dinosaurs at this site, although the flattened tracks of possible theropod cannot be given an ichnological name. On the basis of the ichnological evidence, the *Asianopodus* type theropod tracks are separated into two gregarious groups, Groups A and B. The tracks in Group A show well-defined characteristics of gregarious behaviour such as parallel or subparallel trackways and small intertrackway spacing with little overlap. On the basis of the sedimentary structures, it is estimated

that the dinosaurs of Group A travelled along the course of a river. From the quantitative community analysis, the histogram of size-frequency measurements of Group A shows an anomalous bimodal distribution. There are two possible hypotheses to explain the distribution: male-female differences and trackmakers of different growth stages. The results of quantitative community analyses demonstrate the presence of small-sized theropod dinosaurs showing gregarious behaviour in Thailand during the Early Cretaceous.

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