

**Dinosaur Footprints from the Khorat Group,
Northeastern Thailand**

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**Dinosaur Footprints from the Khorat Group,
Northeastern Thailand**

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Contents

	Page
Contents	i
Abstract	iii
List of Figures and Tables	vi
1. Introduction	1
1.1 The History of Dinosaur Footprint Ichnology	1
1.2 The History of Dinosaur Footprint Ichnology in Thailand	2
2. Geological Setting of the Khorat Group	5
2.1 The Khorat Group	5
2.2 Dinosaurs from Thailand	5
3. Methodology; how to study dinosaur footprints	7
3.1 Measuring Methods of Footprints, and Estimation Methods of Hip Height and Moving Speed of Trackmaker	7
3.2 Replica Producing Methods	9
4. Results; description of dinosaur footprints at each location	11
4.1 Huai Hin Lat Formation	11
4.1.1 Site Nam Nao	12
4.2 Nam Phong Formation	15
4.2.1 Site Tha Song Khong	16
4.2.2 Site Non Tum	19
4.3 Phra Wihan Formation	30
4.3.1 Site Phu Kao	31
4.3.2 Site Phu Faek	32
4.3.3 Site Hin Lat Pa Chad (Phu Wiang)	35
4.4 Phu Pan Formation	43
4.4.1 Site Phu Luang	44

4.5 Khok Kruat Formation	47
4.5.1 Site Huai Dam Chum (Tha Uthen)	47
5. Discussions	57
5.1 Reconstruction of the dinosaur ichnofauna in the Khorat Group and its significance	57
5.2 Comparison of the dinosaur ichnofauna in the Khorat Group with East Asia	58
5.3 Footprint assemblage and its quantitative analysis	63
6. Conclusion	69
Acknowledgements	71
References	72
Figures 1 - 59	95
Tables 1 - 13	161

Abstract

Late Triassic to Early Cretaceous terrigenous sedimentary rocks, traditionally called the Khorat Group, are widely distributed in northeastern Thailand. This Group is subdivided into eight formations, in the following stratigraphic order; the Huai Hin Lat, Nam Phong, Phu Kradung, Phra Wihan, Sao Khua, Phu Phan, Khok Kruat, and Maha Sarakham formations. Many fossils such as dinosaurs, fishes, crocodylians, turtles, bivalves and palynomorphs have been reported from the Khorat Group. In particular, abundant dinosaur fossils including footprints, teeth and bones have been known from the northeastern part of Thailand. To date, many tetrapod footprints including dinosaurs have been reported from the Huai Hin Lat, Nam Phong, Phra Wihan, Phu Phan and Khok Kruat formations. On the other hand, only two ichnogenera and one ichnospecies have been described in systematic ichnology in Thailand. During my field works for my Doctoral Course study, I visited eight footprint sites in northeastern Thailand, including Nam Nao, Tha Song Khon, Non Tum, Phu Kao, Hin Lat Pa Chad (Phu Wiang), Phu Luang and Huai Dam Chum (Tha Uthen). In this thesis, on the basis of the detailed measurement data, I describe the dinosaur footprints in ichnological taxonomy, and also reconstruct the dinosaur ichnofauna in Thailand. Additionally, I discuss the paleontological significance of Thai dinosaur footprints in East and Southeast Asia.

In this study, I have identified 877 tetrapod tracks including 151 trackways in a total of eight tracksites from the Khorat Group, northeastern Thailand. I have also classified some kind of tracks of theropoda, ornithopoda, sauropoda, crocodylian, non-dinosauriform archosauromorpha, and didactyl tracks of tetrapoda from the Khorat Group. The ratio of the occurrence of theropod tracks in dinosaur footprint

proportion exceeds more than 90 % and the ratio of each geologic age is so high. Additionally, I newly described five ichnogenera of dinosaur footprints, *Eubrontes* isp., *Gigandipus* isp., *Carmelopodus* isp., *Irenesauripus* isp., and cf. *Asianopodus* isp., and one ichnogenus of archosauromorpha, cf. *Apatopus* isp. in ichnotaxonomy.

As a result of the comparison between dinosaur fauna based on the bone fossils and dinosaur ichnofauna, both of them do not show the “true dinosaur fauna” in Thailand. However, dinosaur ichnofauna compensates for lack of dinosaur fauna based on the bone fossils will lead to reconstruct more precise dinosaur fauna, and it shows the paleontological significance of dinosaur footprint ichnology. As a result of comparison with the Early Cretaceous dinosaur faunas in East and Southeast Asia, there is a possibility that the origins of ornithopoda and allosauria is in the region of Southeast Asia from the ichnological point of view. As a result of comparison between the Khorat ichnofauna and Chinese and Korean ichnofaunas in East Asia, there is partial common point between the Early Cretaceous Khorat Ichnofauna and the ichnofauna of the region C3 (Inner Mongolia) in China. However, the tracksites are few in number in the Khorat Group, and there is few report describing dromaeosaurids tracks, large sauropod and ornithopod tracks, pterosaur, turtle, bird tracks in Thailand compared with East Asian tracksites. The Khorat Group has a little different ichnofauna with East Asia while sharing the partial ichnofauna which is characterized as non-avian theropod track (like *Asianopodus*) rich. FI described the dinosaur footprint assemblage in ichnotaxonomy for the first time in Thailand. As a result of the quantitative analysis of dinosaur footprint assemblage in the site Huai Dam Chum, the footprint assemblage of the theropod tracks referred to cf. *Asianopodus* isp. is estimated to be imprinted by probably gregarious

ornithomimosaur. The tracks are mainly separated into two groups, Group A and Group B, and indicate the accurate herd behaviour and its idiosyncratic group composition. In particular, the histogram of size-frequency measurements of Group A shows the anomalous bimodal distribution. I 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.

Key words: dinosaur, footprint, the Khorat group, Mesozoic, northeastern Thailand

List of Figures and Tables

Figures	Page
Figure 1. Index map showing the distribution of the Khorat Group and footprint sites.	95
Figure 2. Lithostratigraphic column and dinosaur ichnofauna of the Khorat Group.	96
Figure 3. Diagrams of footprints and trackways, showing measurement methods.	97
Figure 4. Photograph of making silicon mold (process 3).	98
Figure 5. Photograph of making silicon mold (process 4).	99
Figure 6. Photograph of making silicon mold (process 7).	100
Figure 7. Photograph of making plaster mold (process 2).	101
Figure 8. Photograph of making plaster cast (process 5).	102
Figure 9. Photograph of the outcrop and sketch of a trackway at the site Nam Nao.	103
Figure 10. Sketch of the trackway of archosauromorpha phytosaur at the site Nam Nao.	104
Figure 11. Photograph and sketch of left manus and pes impressions at the site Nam Nao.	105
Figure 12. Size comparison of a human and an archosauromorph, possible phytosaur at the site Nam Nao.	106
Figure 13. Comparison chart of archosauromorpha tracks.	107
Figure 14. Photograph of the outcrop at the site Tha Song Khon. Each arrow shows footprints.	108

Figure 15.	Sketch of the trackway at the site Tha Song Khon.	109
Figure 16.	Photographs of footprints at the site Tha Song Khon.	110
Figure 17.	Size comparison of a human and a theropod at the site Tha Song Khon.	111
Figure 18.	Comparison chart of theropod tracks.	112
Figure 19.	Locality map and outcrop photograph of the site Non Tum.	113
Figure 20.	Lithostratigraphic column at the site Non Tum.	114
Figure 21.	Photographs and sketch of tracks at the site Non Tum.	115
Figure 22.	Mesh maps at the Non Tum site.	116
Figure 23.	The trackway and photographs of didactyl tracks.	117
Figure 24.	Comparison chart of didactyl tracks.	118
Figure 25.	Meshmap of the Trackway T1 in the northern part of the outcrop at the site Non Tum.	119
Figure 26.	Photographs and sketches of theropod tracks T1 which consist of T1n1 to T1n6.	120
Figure 27.	Size comparison of a human, a theropod, and a sauropod at the site Non Tum.	121
Figure 28.	Photograph of possible sauropod pes and manus impressions. Scale bar is 10 cm.	122
Figure 29.	Comparison chart of the trackway, <i>Eosauropus</i> , <i>Brontopodus</i> and Non Tum specimen T4.	123
Figure 30.	Photograph of the outcrop at the site Phu Kao.	124
Figure 31.	Sketch of the outcrop and a photograph and a sketch of the track T7n1.	125

Figure 32.	Lithostratigraphic column at the site Phu Faek.	126
Figure 33.	Sedimentary structures in the sandstone, including parallel and trough cross-laminations (in the upper part of the study section).	127
Figure 34.	Photograph of the outcrop at the site Phu Faek. Red arrow shows T1n1, and blue arrow shows T3n4.	128
Figure 35.	Sketch of the tracks T1 to T4 at the site Phu Faek.	129
Figure 36.	Size comparison of a human and a theropod.	130
Figure 37.	Photograph of the track T2n2.	131
Figure 38.	Photograph of the trace fossils <i>Thalassinoides</i> sp. which imprinted on the same upper surface with dinosaur tracks.	132
Figure 39.	Meshmap of the outcrop at the site Hin Lat Pa Chad.	133
Figure 40.	Photograph of the trackway T4 <i>Neoanomoepus</i> isp., showing detail of the region outlined by the square in Fig. 39.	134
Figure 41.	Size comparison of a human, a small-sized ornithopod, and a small-sized theropod at the site Hin Lat Pa Chad	135
Figure 42.	Photographs of the outcrop and the trackways T1 and T2.	136
Figure 43.	Photograph of the trackway T10 <i>Carmelopodus</i> isp. at the site Hin Lat Pa Chad.	137
Figure 44.	Photographs of the well preserved tracks T10n2 and T10n3 at the site Hin Lat Pa Chad. Scales are 5 cm.	138
Figure 45.	Comparison chart of the small sized theropod tracks.	139
Figure 46.	Photograph of the outcrop at the site Phu Luang.	140
Figure 47.	Sketch of the tracks at the site Phu Luang (after Buffetaut <i>et</i>	141

al., 1985b).

Figure 48.	Sketch of the tracks <i>Irenesauripus</i> isp. at the site Phu Luang.	142
Figure 49.	Photographs of the tracks T1n1 (upper) and T2n2 (lower).	143
Figure 50.	Size comparison of a human and a theropod at the site Phu Luang.	144
Figure 51.	Locality map (a), and a photograph of the outcrop at the site Huai Dam Chum (b).	145
Figure 52.	Lithostratigraphic column of northern part the outcrop at the site Huai Dam Chum.	146
Figure 53.	Mesh map of the north part of the outcrop of north part of the site Huai Dam Chum.	147
Figure 54.	Photograph and sketch of tracks of the site Huai Dam Chum.	148
Figure 55.	Comparison chart of theropod tracks at the site Huai Dam Chum (after Kozu <i>et al.</i> , in press).	149
Figure 56.	Size comparison of a human and a theropod at the site Huai Dam Chum.	150
Figure 57.	Comparison chart of ornithopod tracks at the site Huai Dam Chum (after Kozu <i>et al.</i> , in press).	151
Figure 58.	Lithostratigraphic column and new reconstructed dinosaur ichnofauna of the Khorat Group.	152
Figure 59.	The Early Cretaceous paleogeography and dinosaur fauna in East and Southeastern Asia (after Shibata <i>et al.</i> , 2017).	153
Figure 60.	Taxonomic and ichnotaxonomic group of dinosaurs in the Khorat group.	154

Figure 61.	Proportion of track producers on the Khorat Group.	155
Figure 62.	Distribution of the Mesozoic tracksites in China (after Lockley <i>et al.</i> , 2014).	156
Figure 63.	Distribution of the Mesozoic tracksites in Goseon County, Southern Korea (after Lee <i>et al.</i> , 2000).	157
Figure 64.	Northern part of the mesh map at the site Huai Dam Chum (after Kozu <i>et al.</i> , in press).	158
Figure 65.	Southern part of the mesh map at the site Huai Dam Chum (after Kozu <i>et al.</i> , in press).	159
Figure 66.	Histograms of the measurement data in the Tha Uthen theropod tracks	160

Tables		Page
Table 1.	Measurements of the trackway T1 at the site Nam Nao.	161
Table 2.	Measurements of the trackway T1 at the site Tha Song Khon.	162
Table 3.	Measurements of the pes of the trackway T3 at the northern part of site the Non Tum.	163
Table 4.	Measurements of the manu of the trackway T3 at the northern part of the site Non Tum.	164
Table 5.	Measurements of the theropod tracks at the site Non Tum.	165
Table 6.	Measurements of the sauropod tracks at the site Non Tum.	167
Table 7.	Measurements of the tracks at the site Phu Kao.	168
Table 8.	Measurements of the theropod tracks at the site Phu Faek.	169
Table 9.	Measurements of the ornithopod trackway T4 at the site Hin Lat Pa Chad (Phu Wiang).	170
Table 10.	Measurements of the ornithopod trackways T1, T2, and T11, and theropod trackway T10 at the site Hin Lat Pa Chad (Phu Wiang).	172
Table 11.	Measurements of the tracks at the site Phu Luang.	174
Table 12.	Measurements of well-preserved tracks of theropod at the Huai Dam Chum site.	175
Table 13.	Measurements of trackways of the Huai Dam Chum site.	177

1. Introduction

1.1 The History of Dinosaur Footprint Ichnology

Since the first scientific report on the dinosaur bone fossils was published by Buckland (1824), many descriptive works on dinosaur bone fossils have been reported and our knowledge of the origin and evolution of dinosaurs was accumulated (e.g., Fastovsky and Weishampel, 1996, 2012). Likewise, the study of dinosaur footprint ichnology began in the early 1800s. The ichnological study of dinosaur footprint began from such the scientific reports of dinosaur footprint assemblage by Hitchcock (1836) and *Iguanodon* tracks by Tagart (1846), however, these footprints had been recognized as large-sized bird tracks at the time. After that, until the mid-20th century, footprint ichnology developed slowly focusing around the discovery and report of footprint fossils. As “ethological paleontology” advocated by Louis Dollo (1857~1931) shows, we can infer such as the trackmaker’s behavior, living environments, and pattern of activity on the basis of the state of preservation and morphology of footprint (e.g. Gillette and Lockley, 1989). Therefore, the footprint fossil is a “live trace” that was made by trackmakers when they were living. Not only the research of describing, but also the research progress of paleoecological ichnology got much attention, and in 1960s, footprint fossils were attracted lots of attention as a tool for reproducing the paleobiology of extinct species (e.g. Langston, 1960). In 1980s, as typified by Thulborn (1982) and Gillette and Lockley (1989), the results of biomechanical study on footprint fossils that

estimating speed, body weight and size of trackmaker dinosaurs were reported little by little. In 1986, the First International Conference on Dinosaur Tracks and Traces had been held in New Mexico, and after that, footprint ichnology has come to be recognized as a main branch of dinosaur research. Leonardi (1987) marshaled the method of tetrapod ichnology, which were inconsistent among researchers and illustrated it in detail. As a result of this achievement, he provided the basis for the classification of modern footprint ichnology. In the aftermath, the researchers adopted not only the morphological description of each footprint but also the ethological approach that focuses on the population of trackmaker as the methods of footprint ichnology. Today, the 3D analytical method based on the newest technology such as Digital 3D modeling by photogrammetry and laser scanning techniques are adopted for the observational footprint and conservation of the outcrop itself. Footprint ichnology is still at a development stage with improvements of ichnological research method.

1.2 The History of Dinosaur Footprint Ichnology in Thailand

In 1960s, the first dinosaur bone fossils have been found from the Khorat group which is distributed in northeastern Thailand (Fig. 1), and abundant bone fossils have been corrected from the area (e.g. Buffetaut *et al.*, 2009a). On the other hand, dinosaur footprint fossils in the Khorat Group were first reported in 1985. Buffetaut *et al.* (1985a) reported the first Early Cretaceous dinosaur footprints from

South-East Asia in the site Phu Luang, northeastern Thailand (“First dinosaur footprints from South-East Asia: Carnosaur tracks from the lower Cretaceous of Thailand”). After that, dinosaur footprints have been found from the sites such as Hin Lat Pa Chad (Buffetaut and Suteethorn, 1993), Khao Yai (Polahan and Daorerk, 1993), and Phu Faek (Buffetaut et al., 1997), however, these descriptions of footprints were mainly subordinate tasks of the scientific reports of dinosaur bone fossils. Since 2000, the results and methods of footprint ichnology were introduced into Thailand from various parts of the world. In particular, Thai, French, and Japanese national team successively conducted the study of footprint fossils in Thailand. Among these, the taxonomic investigations and reports of footprints such as, Le Loeuff *et al.* (2002, 2003, 2007, 2008), Lockley *et al.* (2002, 2006d, 2009), Buffetaut *et al.* (2005), Sato and Tumpeesuwan (2005), Matsukawa *et al.* (2006), Saenyamoon (2006MS), Suraprasit (2008MS) have been published, and until now, footprints are known from in total 12 tracksites including non-reported sites in northeastern Thailand. As new ichnogenera and ichnospecies, there are two specimens, small-sized track of theropod *Siamopodus khaoyaiensis* from the site Khao Yai (Lockley *et al.*, 2006d) and small-sized track of primitive ornithischian, ornithopod *Neoanomoepus* sp. from the site Hin Lat Pa Chad (Lockley *et al.*, 2009). Matsukawa *et al.* (2006) and Le Loeuff *et al.* (2005, 2009) gave an outline of the dinosaur footprints from the Khorat Group. They indicated that the dinosaur ichnofauna corresponds with dinosaur fauna in Thailand, and the ichnofauna shows

the transition of dinosaur fauna accurately. They also indicated that there is a possibility of finding new footprints including small-sized theropod from the Khorat Group in the near future.

Since 2000, some international meetings focused on dinosaur footprints, such as International Conference on Geology of Thailand (GEOTHAI) in 2007, were held in Thailand, and it shows that footprint ichnology became popular gradually. Many footprints and tracksites have been known from the Khorat Group, on the other hand, there has been no previous study of the ichnotaxonomic classification and comparative discussion with other specimens in detail. To this day, only two types of dinosaur footprint, *Siamopodus khaoyaiensis* and *Neoanomoepus* sp., have been described in ichnotaxonomy from Thailand. In this thesis, I summarize the existing dinosaur tracksites in Thailand. On the basis of new ichnological measurement data getting from my investigations in old and new tracksites, I aim to reconstruct the dinosaur ichnofauna from the Upper Triassic to upper Late Cretaceous Khorat Group. In addition to those descriptions in ichnotaxonomy, I also aim to infer the paleoecological and behavioral reactions of trackmakers.

2. Geological Setting of the Khorat Group

2.1 The Khorat Group

The Upper Triassic to Lower Cretaceous non-marine sedimentary rocks, which crops out widely in northeastern Thailand, are referred to as the Khorat Group (Ward and Bunnag, 1964). The Khorat Group is subdivided into eight formations (Buffetaut *et al.*, 1993) in ascending order, the Huai Hin Lat (Late Triassic, Norian), Nam Phong (Norian to Rhaetian), Phu Kradung, Phra Wihan, Sao Khua (Early Cretaceous, Berriasian to Barremian), Phu Phan (Berriasian to Aptian), Khok Kruat (Aptian to Albian) and Maha Sarakham (Albian to Cenomanian) formations (Fig. 2). The group is famous for the occurrence of various types of vertebrate fossils, such as dinosaur, tortoise, crocodile, fish, and plant, bivalve, and pollen fossils. On the basis of those fossils, each age of the formations of the Khorat Group is estimated (Meesook, 2011). However, there is still considerable debate about the age, internal stratigraphic relationship, and depositional environment of the group (e.g. Racey *et al.*, 1994).

2.2 Dinosaurs from Thailand

Many fossils such as dinosaur bones, dinosaur footprints, fish, crocodylians, turtles, bivalves, and palynomorphs have been recovered from the Khorat Group (Fig. 2) (Meesook, 2011; Meesook and Saengsrichan, 2011). In particular, the Khorat Group has yielded many dinosaur bone fossils; footprints have also been reported from

several areas such as Phu Faek, Hin Lat Pa Chad, and Huai Dam Chum on the Khorat Plateau (e.g. Le Loeuff *et al.*, 2005, 2009). New nine genera and nine species in the Khorat Group are described as dinosaur bone fossils, such as spinosaurid *Siamosaurus suteethorni* (Buffetaut and Ingavat, 1986), psittacosaurid *Psittacosaurus sattayaraki* (Buffetaut and Suteethorn, 1992), Thai endemic titanosauria *Phuwiangosaurus sirindhornae* (Martin, V., Buffetaut, E. and Suteethorn, V., 1994), tyrannosaurid *Siamotyrannus isanensis* (Buffetaut, E., Suteethorn, V. and Tong, H., 1996), the earliest known Asian sauropoda *Isanosaurus attavipachi* (Buffetaut, E., Suteethorn, V., Cuny, G., Tong, H., Le Loeuff, J., Khansubha, S. and Jongautchariyakul, S., 2000), ornithomimosaur *Kinnareemimus khonkaensis* (Buffetaut, E., Suteethorn, V. and Tong, H., 2009b), iguanodontian *Siamodon nimngami* (Buffetaut and Suththorn, 2011), *Ratchasimasaurus suranareae* (Shibata, M., Jintasakul, P. and Azuma, Y., 2011), and *Sirindhorna khoratensis* (Shibata, M., Jintasakul, P., Azuma, Y. and You, H. L., 2015). As dinosaur footprints, small-sized tridactyl track of theropod *Siamopodus khaoyaiensis* (Lockley *et al.*, 2006d) and small-sized quadrupedal trackway of primitive ornithopod *Neoanomoepus* sp. (Lockley *et al.*, 2009) have been known from the Khorat Group. Therefore, Thailand is becoming one of the foremost important “dinosaur-producing country” in Asia.

3. Methodology; how to study dinosaur footprints

3.1 Measuring Methods of Footprints, and Estimation methods of Hip Height and Moving Speed of Trackmaker

The measuring method of footprints differs among ichnologists. In this thesis, I refer Ishigaki (1988) who precisely formulated the morphology of the footprints (Fig. 3). I use “footprint” as one track, and “trackway” as consecutive tracks, which consist of more than three tracks (see Thulborn, 1990). I assign a number to each trackway and to each footprint (e.g., T1n1). Then, I construct a mesh map to record the precise positions of the footprints relative to each other. I show the measuring method of footprints in detail in the upper of Fig. 3. On the basis of the longitudinal axis and transvers axis, the length and width measurements of each footprint are called the footprint length and footprint width, respectively. Each digit impression is counted from within (digit I, II, III...). On the basis of each digit axis, the angle between each digit is assumed to be interdigital angle (or divarication angle). Additionally, the axis of digit III and the depth of footprint are important values. I show the measuring method of trackway in the lower of Fig. 3. For bipedal and quadrupedal locomotion, the relevant trackway terminologies are shown in the left and right side of bottom of Fig. 3 respectively. In this figure, on the basis of the midline, a single linear movement from left (right) to right (left) is called “step”, and the distance from the left (right) footprint to the next left (right) footprint is called the “stride”. Mainly, the width between the exterior of left and right feet is known as “trackway width”. The

pace angulation is the angle made by the line drawn from first left (right) foot to the right (left) foot and the line drawn from the right (left) foot to the second left (right) foot. In the quadrupedal case, the trackmaker possesses two manus and two pes, therefore, I must measure each step, stride, and pace angulation individually, and also measure the distance between manus and pes. It is useful for estimating the trackmaker observing the gait and “outward or inward rotation” in the angle of rotation from the midline which is called the “Divarication of foot from midline.”

In this study, the calculation for estimating the moving speed of trackmaker was based on Thulborn (1982). Regardless of the gaits such as walking or running, Thulborn (1982) indicated that the relative stride has a direct relationship with the moving speed. On the basis of Alexander (1976), Thulborn (1982) also showed the following calculation formula to estimate the moving speed of trackmaker;

$$\text{Locomotor velocity} = 0.25 (\text{gravitational acceleration})^{0.5} \times (\text{estimated stride length})^{1.67} \times (\text{hip height})^{-1.17}$$

The hip height (h) is generally the quadruple of the footprint length, however, the value differs according to the type of trackmaker such as “small”-sized “theropod” and “large”-sized “ornithopod” and others (e.g. Thulborn, 1989). In this study, the calculation was based on Thulborn (1989), as follows;

small-sized theropod (FL < 25 cm): $h = 4.5 \text{ FL}$

large-sized theropod (FL > 25 cm): $h = 4.9 \text{ FL}$

small-sized ornithopod (FL < 25 cm): $h = 4.8 \text{ FL}$

large-sized ornithopod (FL > 25 cm): $h = 5.9 \text{ FL}$

The reconstructions of trackmakers in this study were based on above hip height values. In regard to the quadrupedal trackway, I estimated the size of trackmaker (gleno-acetabular length) from the positions of manus and pes impressions.

3.2 Replica Producing Methods

In the present study, I made some replicas of trackways and footprints by using silicon and plaster. The following is the process to make replicas of trackway:

- 1) Select the place of making replica and clean up the bedding plane on which some footprints are preserved.
- 2) Paint mold release materials on the place, and dry them for a day.
- 3) Paint silicon and dry it for a day (Fig. 4).
- 4) Spread fine clothe like gauze to cover the place for the reinforcement (Fig. 5).
- 5) Paint silicon on the gauze, and dry for a day again.
- 6) Repeat the same procedure of above 1) to 5) two or three times a day.
- 7) Finally, peel dried silicon (Fig. 6).

To make replica of footprints, I used plaster and the replica of trackways which

were made in advance. Concerning plaster, it is better to use plaster of low rate of shrinkage for the observation and measurements. The following is the procedure to make replica:

- 1) Make cast by plaster for the reinforcement to maintain the shape of unevenness.
- 2) Turn over the replica of trackways (silicon sheet), and encircle the circumference of footprint by using soil or clay (Fig. 7).
- 3) Pour plaster to cover the mound of the footprint.
- 4) Take out plaster after dried.
- 5) Dry plaster completely by leaving out waters (Fig. 8).

4. Results; description of footprints at each tracksite

I show the lithostratigraphic column, dinosaur fauna and ichnofauna of the Khorat Group in Fig. 2. Vertebrate footprint fossils have been known from the Huai Hin Lat, Nam Phong, Phra Wihan, Phu Phan, and Khok Kruat Formations of the Khorat Group. In this thesis, I mention the results of total eight tracksites including the existing seven tracksites and a new tracksite (Fig. 1; ①Nam Nao, ②Tha Song Khon, ③Non Tum, ④Phu Kao, ⑤Phu Faek, ⑥Hin Lat Pa Chad [Phu Wiang], ⑦Phu Luang, and ⑧Huai Dam Chum [Tha Uthen]). I present below the footprint-fossiliferous strata and each tracksite, and describe the footprints in ichnotaxonomy, from the stratigraphically ascending order.

4.1 Huai Hin Lat Formation

The Huai Hin Lat Formation crops out at the NW margin of the Khorat Plateau where is up to about 400 m thick. It is overlain unconformably by the Nam Phong Formation. In ascending order, the formation is subdivided into the Pho Hai, Sam Khaen Conglomerate, Dat Fa, Phu Hi and I Mo Members. The Pho Hai Member mainly consists of tuff, agglomerate, rhyolite and andesite with some intercalations of sandstone, mudstone and conglomerate. The Sam Khaen Conglomerate Member mainly consists of conglomerate with some intercalations of finer sediments. The Dat Fa Member consists of gray to black carbonaceous, calcareous, well-bedded shale and argillaceous limestone. The Phu Hi Member consists of gray sandstone, shale and argillaceous limestone with some intercalations of conglomerate beds. The I Mo Member consists of gray sandstone, shale and limestone with associated intermediate volcanic rocks.

The Huai Hin Lat Formation was considered to be of Late Triassic (Norian) age on the basis of its plant remains, pollen, spores, and conchostracans (e.g. Chonglakmani, 2011). Haile (1973) assigned a Carnian-Norian age to the palynomorphs from the Nam Phong Formation which can be correlated to the Huai Hin Lat Formation. Racey *et al.* (1996) also considered that the Huai Hin Lat Formation was Carnian-Norian age because of the lack of Rhaetian marker taxa in the pollen assemblage. Additionally, from the Huai Hin Lat Formation, the phytosaur *Mystriosuchus* sp., that was originally described from the Norian Stubensandstein of Germany and subsequently found in the Norian sediments of Austria and Italy (Buffetaut *et al.*, 1993).

Based on the diverse and abundant fauna and flora, the Huai Hin Lat Formation is considered to be of Early-Middle Norian age.

4.1.1 Site Nam Nao

The site Nam Nao is located at about 27 km east of Phetchabun where is famous for the summer resort for local people (N16° 44'12.3", E101° 40'06.1"). The Huai Hin Lat Formation is the lowest stratigraphic unit of the Khorat Group and is cropping out at Nam Nao. The calcareous sandstone of a few tens centimeters thick which strikes N75°E and dips to the south 40° is cropping out extensively (Fig. 9). On the bedding plane, three vertebrate trackways are imprinted, and two of those are traced for 100 meters or more continuously. It is difficult to measure all of those trackways because the formation bearing footprints have a steep slant. Among these, Le Loeuff *et al.* (2005, 2007, 2008, 2009) reported about one of the most clear and measurable trackway.

Systematic Ichnology

Archosauria Cope, 1869

Ichnogenus cf. *Apatopus* isp. Baird, 1957 (Figs. 10, 11 and 12, Table 1)

Material: Three trackways are traced at least 100 m long from the upper to lower part on the bedding plane of calcareous sandstone in this outcrop. In this thesis, I measured clear part of one of the most clear trackway.

Locality: Huai Hin Lat Formation, Huai Yai area, Mueang Phetchabun District, Phetchabun province, Thailand.

Description: This partial specimen consists of consecutive seven pes and seven manus impressions which are externally rotated (Fig. 10). The trackway represents a probably primitive archosauromorph reptile, precisely phytosaur which are known from bone fossils in the Huai Hin Lat Formation. Pes tracks consist of four to five digit impressions and large metatarsal impression, and manus tracks consist of three to four digit impressions (Fig. 11). I measured pes as T1P1 to T1P7 and manus as T1M1 to T1M7 (Table 1). Elongate pes tracks are on average 32.0 cm long and 19.5 cm wide and are composed of impressions of digit I to V. Most of pes tracks have clear impressions of digit V postero-laterally, which digit axis is directed anteriorly. Short pes tracks also reveal an average step of 66.3 cm and average stride of 101.8 cm, and pace angulation is an average of 100° . Footprint length, width, step, stride and pace angulation of manus track average 13.3 cm, 15.3 cm, 63.7 cm, 91 cm and 105.6° respectively. The manus and pes impressions are less everted relative to the

midline respectively. The trackway, using an asymmetrical gait, is nearly straight and show high pace angulation, and trackway width average 64.3 cm. Estimated body length (gleno-acetabulat length) is about 120 cm (Fig. 12).

Remarks: Le Loeuff *et al.* (2005, 2007, 2008, 2009) reported about one of the most clear and measurable trackway. They estimated that the trackmakers of Nam Nao are wide-gauge plantigrade, quadrupedal animals, probably primitive archosauromorph reptiles. Le Loeuff *et al.* (2008, 2009) suggested the possibility that the trackmakers of Nam Nao are phytosaurs because the body length estimated from the partial skull of phytosaur which were found from the same formation is in agreement with the inferred size of the trackmakers of Nam Nao. On the other hand, he also mentioned that the footprints from Nam Nao are strongly morphologically-different from *Apatopus*, which is considered by many authors as a phytosaur track.

In this study, I observed clear impressions of digit V postero-laterally in pes tracks with large metatarsal impression (Fig. 13) in addition to the described morphology by Le Loeuff *et al.* (2008, 2009). Generally, ichnofamily Chirotheriidae including such as ichnogenera *Chirotherium* and *Isochirotherium* is known as a footprint of archosauromorph (e.g. King *et al.*, 2005). However the specimen of Nam Nao is different from ichnofamily Chirotheriidae in morphology in that Chirotheriidae shows very high pace angulation, narrow trackway width and very small-sized manus tracks. The trackmaker of *Apatopus* is estimated as archosauromorpha phytosaur (e.g. Hunt and Lucas, 2007; Padian et al., 2010; Klein and Lucas, 2013). The Diagnosis of *Apatopus* (emended after Baird, 1957) is: Quadrupedal trackways with pace angulation of the pes ranging from 108° to 120°. Pes, but not manus,

toed-out. Pes long and narrow, semiplantigrade to plantigrade, pentadactyl with slender digits increasing in length from I to V. Digit IV often very faintly impressed or missing; digit V straight, antero-laterally oriented and with posteriorly-elongated “heel.” Digits with well-developed articular swellings and sharp claws. Manus pentadactyl, semiplantigrade, short, rounded and symmetrical around digit III, which is longest; position in the trackway anterior or slightly medial to the pes. Although the specimen of Nam Nao is larger than *Apatopus* and show the inner poor preservation, the morphological characters of the specimen, such as the number of digit, pes track digits increasing in length from I to IV with sole part, resembles the morphological characters of *Apatopus*. In terms of these facts, the specimen of Nam Nao is identified as cf. ichnogenus *Apatopus*. And it is difficult to observe inner morphology of the specimen of Nam Nao because of the inner poor preservation. Therefore, I can’t identify the type of ichnospecies to the specimen. In this study, the tracks of Nam Nao are identified cf. ichnogenus *Apatopus* sp. attributed to archosauromorpha, particularly phytosaur.

4.2 Nam Phong Formation

The Nam Phong Formation unconformably overlies the Huai Hin Lat Formation. According to Ward and Bunnag (1964), the total thickness of the formation is 1,465 m, and it consists of resistant red-brown micaceous sandstones, conglomerates, siltstones and mudstones of mainly fluvial origin.

The Nam Phong Formation is generally considered to be of Rhaetian age based on the occurrence in the overlying Phu Kradung Formation of supposed Early Jurassic bivalves and vertebrates, and on the occurrence of Norian palynomorphs in the

underlying Huai Hin Lat Formation (Chonglakmani and Sattayarak, 1978; Buffetaut *et al.*, 2006). Based on the palynological evidence, Racey *et al.* (1996) considered the Nam Phong Formation to be Late Norian or Rhaetian in age.

Buffetaut *et al.* (1995) recorded a large and robustly built prosauropod dinosaur from the Nam Phong Formation. Additionally, the remains of *Isanosaurus attavipachi*, the first sauropod from Thailand to have been found in the Triassic, were described from the Nam Phong Formation of Chaiyaphum Province (Buffetaut *et al.*, 2000).

4.2.1 Site Tha Song Khon

The site Tha Song Khon is located at the region “Phu Kradung” about 75 km south of Loei along the route 201 (N16°90'10", E101°86'10"). The Nam Phong Formation is cropping out at the site. Some footprints were found at the site of Nam Phong River near the village in 2007, and were studied by Le Loeuff *et al.* (2007, 2008, 2009). At the site of Nam Phong River, the calcareous mudstones of 20 to 30 cm thick are cropping out, and strike N10°E and dip to the north 10°.

The trackway consists of six consecutive large pes impressions and were discovered in 2007 (Le Loeuff *et al.*, 2008). In this study, I measured four footprints because other two pes tracks were covered by soil. The trackway is traced on the bedding plane of the lowest calcareous mudstone, likewise mud-cracks are present in this outcrop.

Systematic Ichnology

Theropoda Marsh, 1881

Ichnofamily Gigandipodidae Lull, 1904

Ichnogenus *Gigandipus* E. Hitchcock, 1855

Gigandipus isp. (Figs. 15, 16 and 16, Table 2)

Material: A trackway which composed of 4 large-sized pes impressions are traced on the bedding plane of calcareous mudstone in this outcrop (Fig. 14).

Locality: Nam Phong Formation, Phu Kradung District, Loei province, Thailand.

Description: This specimen (T1n1 to T1n4) consists of four consecutive pes impressions, and it is nearly straight in west-southwest direction (Fig. 15). The trackway represents a medium-sized bipedal trackmaker with a tetradactyl foot. Pes tracks are on average 41.5 cm long and 16.8 cm wide, and are composed of impressions of digits I to IV. There are claw marks in the tip of each digit. Digit I impressions preserved postero-medially are 10.0 to 16.0 cm long (mean 13.6 cm), Digit II impressions are 23.5 to 28.0 cm long (mean 25.6 cm), Digit III impressions are 25.0 to 31.0 cm long (mean 29.8 cm), and Digit IV impressions are 17.0 to 29.0 cm long (mean 26.3 cm). Two tracks T1n3 and T1n4 are in a poor state of preservation, however Digits III of these footprints, which average 30 cm long, are longer than others (Fig. 16, Table 2). Interdigital angles of II to III and III to IV value of between 35.0° and 30.3° respectively, and I to II is wide, means 75.8°. The tracks are fuzzy, but, they show sole impressions which length and width are on average 9.3 cm and 12.0 cm respectively. There is a sand mount around each track. The trackway is nearly straight, and the pace angulation of the pes is 150.0 to 160.0°. The trackway

width is 68.0 cm. The trackway also indicates that the step and stride of the pes are on average 126.7 cm and 260.0 cm. The estimated height at the hip (h) is >200 cm (Fig. 17). The relative stride length (SL/h = 1.3) represents a walking gait. The walking speed is estimated to be about 5.0 km/h.

Remarks: Tracks show narrow interdigital angle, and have slender digit impressions and claw marks. These facts mean that the trackmaker of Tha Song Khon specimen is large theropod. The specimen of Tha Song Khon resembles *Eubrontes* (Hitchcock, 1845) and *Gigandipus* (Hitchcock, 1855) (Fig. 18). The diagnosis of *Eubrontes* redefined by Olsen *et al.*, (1998) reads: Large (>25 cm in length) bipedal, functionally tridactyl ichnite with a relatively short digit III, a broad pes, and a hallux which is rarely, if ever, impressed. Divarication of outer digits averaging 25-40° (Olsen *et al.*, 1998). The specimen of Tha Song Khon resembles *Eubrontes*, but it reveal clear digit I impression, wide interdigital angle, and sole impressions. Therefore, the tracks of this site are not identified *Eubrontes*. On the other hand, the specimen resembles *Gigandipus* in morphology, and Le Loeuff *et al.* (2008, 2009) also mentioned the possibility that this track belongs to *Gigandipus*. *Gigandipus* has the small hallux which lies at right angles to digit II. The tail trace when present is sinuous and continuous. The size of *G. caudatus* (E. Hitchcock, 1855) is same with the specimen of Tha Song Khon, but its Interdigital angles, I to II: 98°, II to III: 22° and III to IV: 33° respectively, are narrower than the specimen of Tha Song Khon. And length of digit I, 80 mm, is shorter than Tha Song Khon track. *Gigandipus hei* (Yang and Yang, 1987; Lockley *et al.*, 2003) is larger than the specimen of Tha Song Khon, and show narrower interdigital angle, and the digit axis of hallax is directed anteriorly more. Therefore, I consider that the specimen of Tha Song Khon is identified as ichnogenus

Gigandipus. Based on the ichnological structure of the specimen, it does not belong to existing ichnospecies. The specimen is in a poor state of preservation, but there is a possibility of the type of new ichnospecies. In this thesis, I consider that the specimen of Tha Song Khon is *Gigandipus* isp. tentatively.

Gigandipus seems to be a semiplantigrade footprint of large crouching theropod (Hitchcock, 1855). Le Loeuff *et al.* (2008) also showed the slight possibility that the trackmaker is a bipedal prosauropod with a reduced digit I, although there is no direct evidence. As a result, he suggested that these tracks had been formed by large theropod. Anyway, the tracks of Tha Song Khon are important to show the occurrence of large theropod in Late Triassic at northeastern Thailand because the bone fossils of theropod have not been known from the Nam Phong Formation.

4.2.2 Site Non Tum

Phu Khieo Wild Sanctuary is located at about 100 km west-southwest of Khon Kaen, northeastern Thailand, and in south site of this sanctuary, “Nong Bua Daeng” is located. The site Non Tum is located at the site of Chi River about 1 km north of Ban Non Toom school in this area (Fig. 19; N 16°11'68.63", E101°66'17.30"). In 2008, many footprints were found by Northeastern Research Institute of Petrified Wood and Mineral Resources and Fukui Prefectural Dinosaur Museum, and the direction board was placed here.

In this site, very-fine-grained sandstone crops out for 45 m along the Chi River, and footprints are imprinted on the upper surface of this sandstone, and fish teeth and bivalve fossils have been found in some layers. The formation strikes N10°W and generally dips to the east at <5°. The stratigraphy at this site (Fig. 20) consists

of (from oldest to youngest) purple mudstone (~60 cm thick) and very-fine-grained sandstone (~40 cm thick). Sandy mudstone (~40 cm thick) overlies the footprint-bearing layer. Parallel and cross-lamination are observed in the lower part of this formation. Red mudstone (>2 m thick) is overlain by purple mudstone. The purple mudstone is overlain by siltstone and silty mudstone. In the upper part of this section, mudstone and siltstone are intercalated with caliche layers. The stratigraphically highest part of the section contains lenticular limestone. I got many freshwater bivalves *Sphaerium* sp. and fish teeth (probably *Lepidotes* sp.) from the mudstone and limestone. On the basis of these facts such as sedimentary structure and the occurrence of freshwater bivalves and fish teeth and dominated mudstone, the paleoenvironment of this site is estimated as the side of slow river. In particular, fine-grained sandstone on which dinosaur footprints are present is estimated to be sand sheet, namely, crevasse spray due to heavy rain or flood at floodplain.

In this site, an enigmatic trackway T3 is imprinted on the fine grained sandstone. The trackway consists of large-sized impressions and small-sized impressions shows quadrupedal gait. Tentatively, I distribute large-sized impressions as pes tracks, and small-sized impressions as manus tracks. Additionally, several theropod and sauropod trackways occur on the same bedding surface in the formation, running across or parallel to the didactyl trackway (Fig. 21).

Systematic Ichnology

Possible didactyl and quadruple trackways

Ichnogen. et sp. indet. (Figs. 22, 23 and 24, Tables 3 and 4)

Material: One trackway T3 composed of 86 consecutive tracks. In this study, I give an explanation of the trackway T3 from north part of the outcrop (Fig. 22a) because the north part of the trackway T3 is well preserved in continuity. Partial replicas of this trackway are stored in the Graduate School of Life and Environmental Sciences, University of Tsukuba, and the Department of Mineral Resources of Thailand (Fig. 22). The original tracks and trackway remain in the field.

Locality: Nam Phong Formation, Non Tum area, Nong Bua Daeng District, Chaiyaphum province, Thailand.

Description: This trackway consists of consecutive 45 pes and 41 manus impressions separated into northern and southern parts (Fig. 22). In this study, I distribute large-sized track as pes impressions, and small-sized track as manus impression. The trackway represents a probably medium-sized quadrupedal trackmaker with a didactyl foot. Each track consists of two slender digit impressions; medium-sized didactyl pes tracks with oval-shaped digit impressions and small-sized didactyl manus tracks with round-shaped digit impressions preserved in a parallel fashion. Digit impressions are directed cranially and nearly parallel to the trackway axis (Fig. 23). Measurements were obtained from the northern outcrop, on which well-preserved tracks were observed (Tables 3 and 4). Pes tracks are on average 17.3 cm long and 22.3 cm wide, and are composed of impressions of digits II and III or III and IV. Inner digit impressions are 7.0 to 22.0 cm long (mean 16.7 cm) and 10.0 cm wide; exterior digit impressions are 10.0 to 23.0 cm long (mean 15.5 cm) and 10.1 cm wide. These are preserved in parallel, and are not united proximally. There is a sand

mount in front of each track. The deepest point of the pes track is the anterior part. The manus tracks are on average 10.0 cm long and 17.3 cm wide, and are composed of impressions of digits II and III or III and IV. Inner digit impressions are 4.0 to 17.0 cm long (mean 9.5 cm) and 8.9 cm wide; exterior digit impressions are 3.0 to 15.5 cm long (mean 9.5 cm) and 9.4 cm wide. The trackway is nearly straight, and the pace angulation of the pes is nearly 60° (mean 58.9°); that of the manus is 60.2° on average. The trackway also indicates that the step and stride of the pes are on average 153.0 cm and 151.0 cm, and for the manus are 148.3 cm and 154.3 cm on average, respectively. The estimated height at the hip (h) is >90 cm. The relative stride length (SL/h = 1.76) represents a walking gait. The walking speed is estimated to be 6.7 km/h.

Comparisons and discussions: Until now, there have been no reports of didactyl and quadrupedal vertebrate bone fossils and related footprint fossils from Upper Triassic to Lower Jurassic continental deposits globally. Non Tum didactyl tracks are in a poor state of preservation, and are under tracks. Therefore, I conclude that it is impossible to assign an ichnogenus name to the Non Tum didactyl tracks, and the trackmaker of the specimen described herein was a medium- to large-sized quadrupedal vertebrate animal.

The didactyl track, *Varanopus didactylus*, was first reported from the Permian Clear Fork Formation by Moodie (1930). Sarjeant (1971) redescribed this ichnological species as *Moodieichnus didactylus* (Fig. 24a). *Moodieichnus didactylus* is a small-sized track with a length of 4 to 8 cm and two digit impressions, of digits III and IV, connected with each other in the proximal portion. Furthermore, *M. didactylus* is thought to be a morphological heteromorphy of a tetradactyl or

pentadactyl “lacertiform” similar to *Dromopus* (Haubold *et al.*, 1995), given the poor preservation. Therefore, the Non Tum specimen differs morphologically from *M. didactylus*. Lockley and Lucas (2013) named a new ichnospecies, *Evazoum gatewayensis*, from the upper part of the Chinle Group (Upper Triassic) from the Gateway area of western Colorado, USA (Fig. 24b). *E. gatewayensis* appears to have been produced with most of the weight on digits II and III. However, the trace of digit II is characterized by a well-developed oval proximal pad at the proximal end of digit II, and a claw trace is present distally in some specimens (Lockley and Lucas, 2013). Therefore, *E. gatewayensis* is functionally didactyl but is tridactyl in ichnotaxonomic terms, and *E. gatewayensis* differs from the Non Tum specimen. The trackmakers of ichnogenera such as *Dromaeosauripus* (Kim *et al.*, 2008), *Dromaeopodus* (Li *et al.*, 2008), and *Velociraptorichnus* (Zhen *et al.*, 1995) have been regarded as deinonychosaurs (dromaeosaurs or troodontids). There are no morphological similarities between deinonychosaurian tracks and the Non Tum specimen (Fig. 24c). Furthermore, the gait of deinonychosaurs involved bipedal walking, whereas the gait of the producer of Non Tum trackway was four-footed walking. The occurrence of Non Tum specimen is geochronologically older than the footprints of dromaeosaurid theropods.

Xing *et al.* (2014c) reported the occurrence of a peculiar trackway of a possibly bipedal archosaur from the Upper Triassic Xujiahe Formation of the Sichuan Basin, China. The large and single trackway consists of 19 deeply impressed pes tracks (Fig. 24d). It is uncertain whether this trackway was made by a bipedal animal or whether the manus tracks were simply destroyed or overprinted by the pes track. Clear longitudinal grooves are observed on several tracks, which were estimated to

be nail marks. Long and narrow oval tracks are morphologically similar to the ichnogenus *Eosauropus*, produced by an archosaurian with a bipedal walking gait; however, comprehensive classification of this track has not yet been performed. This track is characterized by two digit traces, an oval-shaped deep depression at the rear part of each track, and a facultative bipedal walking gait. In addition, the outer digit length is longer than that of the inner digit. In contrast, in the tracks from the Non Tum site the inner digit length is longer or equal to the outer digit length, and the measurement data, such as trackway width, step, stride and pace angulation, are clearly different from those of the track from Sichuan. These lines of evidence suggest that the specimen of Non Tum differs morphologically, ichnotaxonomically from the Sichuanese material (Fig. 24e).

Recently, some dinosaur swimming tracks have been reported from China, Australia, Europe, and other countries (e.g. Ezquerro *et al.*, 2007). According to these studies, swimming tracks have the following characteristics; the digit impressions are scratch marks, the impressions are arranged in parallel, and riverbed sedimentary structures such as ripple marks are preserved (Ezquerro *et al.*, 2007). At the Non Tum site, the digit impressions of the didactyl tracks are arranged in parallel. In general, the manus track is preserved at the front part of the pes of a quadrupedal animal; however, the present material has a long distance between pes and manus tracks, which may indicate that the animal had an unusual walking pattern or was exhibiting swimming behaviour. However, sedimentary structures formed at the bottom of a river are not observed on the bedding plane that contains the tracks. These findings mean that the footprints described herein are not analogous to those made by swimming behaviour. Many brackish-water bivalves,

and fish teeth and scales have been obtained from the Non Tum site. The present didactyl tracks occur on a bedding plane in a very-fine-grained sandstone from which fossil fish teeth have also been identified. Furthermore, the strata underlying and overlying this very-fine-grained sandstone consist of shale-rich alternations of sandstone and shale, indicating the didactyl track-bearing sandstone is a floodplain sediment. The trackmaker of the didactyl tracks walked on sand deposited after a river flood. The trackmaker had to use all four legs to walk effectively on the very soft sediment.

Theropod tracks

In total, there are 43 tridactyl footprints including at least 4 trackways at the site Non Tum. In this thesis, I give an explanation of the trackway Ts1 from southern part (Fig. 22) and trackway Tn1 from northern part (Figs. 22 and 25) in this site.

Theropoda Marsh, 1881

Ichnofamily Eubrontidae Lull, 1904

Ichnogenus *Eubrontes* Hitchcock, 1845

Eubrontes isp. (Figs. 22, 25 and 26, Table 5)

Material: Trackway Ts1 composed of 10 consecutive tracks from southern part, and trackway Tn1 composed of six tracks from northern part in the site Non Tum. Partial replicas of these tracks are stored in the Graduate School of Life and Environmental Sciences, University of Tsukuba, and the Department of Mineral

Resources of Thailand (Fig. 22). The original tracks and trackway remain in the field.

Locality: Nam Phong Formation, Non Tum area, Nong Bua Daeng District, Chaiyaphum province, Thailand.

Descriptive remarks: In the southern part of the outcrop, trackway Ts1 consists of well-preserved pes impressions that are sub-symmetrical, tridactyl large-sized tracks with relatively robust digit impressions (Fig. 22; Table 5). There is a distinct claw mark at the tip of each digit. These facts mean that the trackmaker of those Non Tum specimen is large theropod. The mean footprint length and width are 39.6 cm and 32.0 cm, respectively, and the mean length/width ratio (L/W) is 1.24, indicating moderate mesaxony. Each digit III impression is directed anteriorly and is longest, whereas that of digit II is same as or shorter than that of digit IV. The outline of the metatarsophalangeal pad impression is indistinct. The interdigital angle between digits II and III are almost equal to those of digits III and IV. The interdigital angle between digits II and IV is 44°–75° (mean 58.4°). The trackway is nearly straight. The mean step, stride, and pace angulation are 89.2 cm, 167.5 cm, and 151.3°, respectively. The estimated height at the hip (h) is 194.4 cm (Fig. 27). The relative stride length ($SL/h = 0.86$) represents a walking gait. The walking speed is estimated to be about 3.07 km/h.

In the northern part of the outcrop, the trackway Tn1 consists of tridactyl large-sized tracks which resemble the trackway Ts1 from southern part (Figs. 25 and 26; Table 5). The mean footprint length and width are 33.8 cm and 25.2 cm, respectively, and the mean length/width ratio (L/W) is 1.34. The interdigital angle between digits II and IV is 51°–71° (mean 59.2°). The mean step, stride, and pace

angulation are 114.6 cm, 208.8 cm, and 170.3°, respectively. The estimated height at the hip (h) is 165.6 cm (Fig. 27). The relative stride length (SL/h = 1.26) represents a walking gait. The walking speed is estimated to be about 5.3 km/h. I also observed “running tracks” of theropods which means 15~18km/h (Fig. 22).

The main morphological characteristics of Non Tum specimens Ts1 and Tn1 correspond to ichnogenus *Eubrontes*. In general, ichnogenus *Eubrontes* has been known from Late Triassic to Early Jurassic. The diagnosis of *Eubrontes* (emended by Olsen *et al.*, 1998) reads: Large (>25 cm long) bipedal, functionally tridactyl ichnite with a relatively short digit III, a broad pes, and a hallux which is rarely, if ever, impressed. Divarication of outer digits averaging 25°-40°. Because of the poor state of inner preservation in Non Tum tridactyl specimens, it is difficult to observe clear and discrete digital pad impressions (possible 2-3-3 or 4?). On the other hand, in the northern part of the outcrop, the track Tn1n2 is similar to ichnogenus *Seakatrisauropus*, and the track Tn1n3 resembles ichnogenus *Deiteratrisauropus*. The trackway Tn1 shows a variety of features in morphology which indicate some ichnogenera. However, in general, most of the tridactyl specimens are identified as *Eubrontes* type tracks. Therefore, I classify those tridactyl theropod tracks as *Eubrontes* isp. in this thesis.

Possible sauropod tracks

In this site, one quadrupedal trackway of possible sauropod and some indistinct large-sized isolated impressions are imprinted on the same bedding plane with other footprints.

Sauropoda Marsh, 1878

Ichnogen. et sp. indet. (Figs. 22, 28 and 29, Table 6)

Material: One trackway T4 composed of 16 consecutive tracks, and some possible isolated manus and pes impressions. Partial replicas of this trackway are stored in the Graduate School of Life and Environmental Sciences, University of Tsukuba, and the Department of Mineral Resources of Thailand (Fig. 22). The original tracks and trackway remain in the field. I described the trackway T4 in detail based on the measurement data.

Locality: Nam Phong Formation, Non Tum area, Nong Bua Daeng District, Chaiyaphum province, Thailand.

Descriptive remarks: The specimen T4 in the northern part of Non Tum is large-sized, heteropody, quadrupedal trackway. This trackway consists of consecutive 9 pes and 7 manus impressions (Figs. 22 and 28). Pes large, quarry to round shape, tetradactyl to pentadactyl, slightly outwardly rotated. Pes length averages 46.9 cm long and 52.2 cm wide in the trackway T4 (Table 6). Manus transverse, tetradactyl to pentadactyl?, with slightly outwardly rotated and concave posterior margins. Manus averages 26.6 cm long and 36.0 cm wide in trackway T4. Step and stride short, averaging 147.2 and 214.7 cm, respectively, for pes, and 211.7 and 234.6 cm for manus in the trackway T4. Pace angulation 100.9 and 68.5°, respectively, for manus and pes in the trackway T4 (Table 6). Estimated body length (gleno-acetabulat length) is about 250 cm (Fig. 27). Each sand-mound is present around the most pes tracks.

The Non Tum specimen T4 indicates a large-sized quadrupedal trackmaker having heteropody foot part. Large and round shape pes and transverse and heteromorphic manus are identical to typical sauropod track. However, there is no claw marks in the tip of each digit, and those outline are indistinct. One of the most dominant ichnotaxon of Triassic track, ichnogenus *Eosauropus*, has been known from only North America and Europe. *Eosauropus* is an unusual ichnogenus that appears to be of sauropodmorph, or, more specifically, a small sauropod trackway affinity (e.g. Lockley and Meyer, 2000; Lockley *et al.*, 2001, 2006b). Lockley *et al.* (2011) concluded that *Eosauropus* likely represents a prosauropod, which was a facultative biped. According to Lockley *et al.* (2011), in *Eosauropus*, the trace of pes digit I is relatively short in comparison with a typical sauropod, and it suggests a sauropodmorph, possible prosauropod affinity, consistent with the skeletal foot of general prosauropods (e. g., *Plateosaurus*). Furthermore, they noted that *Eosauropus* also appears to represent a biped in many cases, or at least a facultative biped that left manus impressions intermittently, likewise *Pseudotetrasauropus* and *Otozoum* both of which have been attributed to prosauropods. However, they also noted that it is difficult to determine whether the lack of manus impression reflects poor preservation, overlapping, actual bipedal progression on the part of the trackmaker or a combination of these factors.

Fig. 29 shows a comparison chart of Triassic sauropodmorph tracks. In the case of Non Tum specimen T4, a point worthy of special mention is its relatively wide-gauge trackway. *Eosauropus* has narrow trackway width, and its breadth between tracks shows negative values. This is attributable to the attitude of its trackmaker prosauropod (functionally bipedal or quadrupedal walking). On the other hand, the

trackways of derivative sauropod in Cretaceous, such as *Brontopodus*, show wide-gauge trackway, and are characterized the consummate quadruoedal walking style (Fig. 29e). The Non Tum specimen T4 is a consummate quadrupedal trackway, and its ichnological characteristics in footprint morphology and its pattern of trackway suggest clearly that the trackwaker of T4 is a sauropod dinosaur, not prosauropod. Additionally, as the Triassic sauropod, *Isanosaurus attavipachi* has described from the Nam Phong Formation (Buffetaut *et al.*, 2000, 2002). On the basis of the positive ichnological characteristics of the Non Tum specimen T4 and the occurrence of *Isanosaurus* from the same formation, it is concluded that the specimen is an absolute trackway of Triassic sauropod in Late Triassic, possibly *Isanosaurus*.

4.3 Phra Wihan Formation

The Phra Wihan Formation, 100-250 m in thickness, is conformably underlain by the Phu Kradung Formation and overlain by the Sao Khua Formation. Generally, the formation consists of light buff to gray, fine- to coarse-grained quartzitic sandstones and rarer siltstones and mudstones with occasional conglomerates (Meesook, 2011).

The age of the Phra Wihan Formation was estimated as Middle Jurassic by Heggemann *et al.* (1990) on the basis of plant fossils and arthropods. However this conclusion does not share “the Cretaceous age” attributed to the overlying Sao Khua Formation. On the basis of palynomorphs collected from the Phra Wihan Formation, the formation is dated as Lower Cretaceous (Berriasian to Barremian) age (Racey *et al.*, 1994, 1996; Racey and Goodall, 2009).

4.3.1 Site Phu Kao

The site Phu Kao is located at Nong Bua Lam Phu Province about 40 km northwest of Khon Kaen (N16°55'55.0", E102°29'29.1"). The Phra Wihan Formation is cropping out at this area, and medium-grained sandstone of this formation is cropping out at the side of the river which is formed in rainy season (Fig. 30).

In 2000, Le Loeuff's team visited the site, and found five trackways which consist of 25 footprints. They concluded that those tracks are made by small-sized dinosaurs with three digits (Le Loeuff *et al.*, 2009). However they did not show concrete photos, figs and measurement data of footprints at all. In this study, I recognized 20 depressions including true footprints on the bedding plane. This section explains footprints T7n1.

Systematic Ichnology

Possible theropod tracks

Theropod Marsh, 1881

Gen. et sp. indet. (Fig. 31)

Material: 20 depressions including some true footprints are present on upper surface of medium-grained sandstone (Fig. 31). These tracks are in a poor state of preservation, due to the erosion and deformation.

Locality and horizon: Phra Wihan Formation, Phu Kao-Phu Phan Kham National Park, Non Sang District, Nong Bua Lam Phu province, Thailand.

Descriptive remarks: 20 depressions are present with three digit impressions, which show different directions (longitudinal axis). I show the measurement of some tracks (Table 7). Most of tracks are present with three digit impressions, however each outline is not sharply-defined. These tracks mean 22 to 33 cm in length and 18 to 30 cm in width. It is difficult to distribute each trackway because tracks show different directions (longitudinal axis). These tracks show few claw marks and also mean different values of digit length and digit width. A track is present with distinct digit impressions, and means wide interdigital angle 60°. Each digit is also slender and sharply at the end of it. Therefore there is a possibility that the trackmaker is theropod (Fig. 31). Concerning to footprints of Phu Kao, Le Loeuff *et al.* (2005) suggested that the most remarkable are small footprints of a slender quadripedal ornithischian, and most probably an ornithomimid. However I could not observe those in morphology. Anyway, there is still a lot of uncertainty about trackmaker of tracks Phu Kao.

4.3.2 Site Phu Faek

The site Phu Faek is located at Phu Faek Forest Park 100 km east of Khon Kaen (Kalasin Province, N16°46'17.2", E102°16'34.2"). The Phra Wihan Formation is cropping out at this site (e.g. Le Loeuff *et al.*, 2002). The dinosaur footprints were discovered in 1996 by two schoolgirls in a dry riverbed, and then, a preliminary report of this discovery were given by Buffetaut *et al.* (1997). After that, some Thai and French researchers investigated those footprints at this tracksite (e.g., Le Loeuff *et al.*, 2002, 2009).

I show the lithostratigraphic column in Fig. 32. The lowest lithologic unit is

medium-grained gray sandstone, on which upper surface dinosaur footprints are present. The overlying units are fine-grained sandstone and mudstone of about 20 to 30 cm thick respectively, which are repeatedly overlapping. The upper lithologic units mainly consist of mudstone including thin sandstone layers. I also recognized parallel lamination and trough cross-lamination with climbing ripple in fine-grained sandstone of the middle lithologic unit, which means paleocurrent E-W (Fig. 33). On the basis of these sedimentary structures, I estimated that the paleoenvironment is the riverside such as point-bar.

Le Loeuff *et al.* (2002, 2009) indicated that seven trackways consist of 25 footprints, and estimated the trackmakers as large- and small-sized theropods and sauropod in the site Phu Faek. Matsukawa *et al.* (2006) asserted that there is no clear evidence to describe the tracks as those of sauropod. In this study, I could not recognize the tracks of “sauropod” which Le Loeuff *et al.* reported, however, the footprint-bearing sandstone are widely distributed in this area. Therefore, there is probably high chance of the hard sauropod tracks being found in the near future. In this study, I explain the observed tracks of theropod in this site.

Systematic Ichnology

Theropod tracks

Theropoda Marsh, 1881

Gen. et sp. indet. (Figs. 35 and 37)

Material: Three trackways T1 to T3 composed of 13 consecutive tracks and one

footprint T4 are imprinted on the bedding plane of middle-grained sandstone in this outcrop (Fig. 34). The original tracks and trackway remain in the field.

Locality and horizon: Phra Wihan Formation, Lower Cretaceous. Phu Faek site, Nikhom Huai Phueng, Huai Phueng District, Kalasin province, Thailand (N16°41'44.5", E103°56'19.7").

Descriptive remarks: The average footprint length and width of Phu Faek trackway T1 (Fig. 35) are 46.6 and 39.7 cm, respectively (Table 8). The mean step and stride length are 112.2 and 217.0 cm, respectively. The mean pace angulation is 156.0°. The average footprint length and width of consecutive tracks T2 (Fig. 35) are 43.0 and 38.5 cm, respectively (Table 8). The mean step is 115.0 cm. The average footprint length and width of trackway T3 (Fig. 35) are 41.0 and 35.0 cm, respectively (Table 8). The mean step and stride length are 113.3 and 214.5 cm, respectively. The mean pace angulation is 149.0°. Phu Faek isolated footprint T4 is poorly preserved, mostly incomplete. The average footprint length and width of footprint T4 are 18.0 cm and 27.0 cm, respectively. The well-preserved trackway and tracks T1 to T3 shows tridactyl impressions and facultative bipedal walking gait. The footprint length/width ratio (T1 to T3) ranges from 1.12 to 1.17. As shown in Fig. 36, in general, the digit III impression is directed anteriorly and is longest, and that of digit II is same as that of digit IV. Each digit impression is comparatively elongate. The around-shaped indentation along the medial edge of the digit II impression is observed. There are claw marks at the tip of each digit. The interdigital angle between digits II and IV is 43°–80° (mean 58.6°). Each trackway width is narrow and each track is slightly outwardly rotated. The trackway also indicates that the step and stride of the pes are on average 113.5 cm and 215.8 cm. The estimated height at

the hip (h) is >200 cm (Fig. 37). The relative stride length of specimens T1 and T3 (SL/h = 0.95 to 1.07) represent a walking gait. The walking speeds of specimens T1 and T3 are estimated to be 3.92 and 4.46 km/h, respectively.

Some ichnogenera have been known as the track of large-sized theropod. The Phu Faek specimens are similar to *Megalosauripus glenrosensis* (amended by Lockley *et al.*, 1996). Ichnogenus *Megalosauripus* has been known from Late Jurassic and Early Cretaceous (Lockley *et al.*, 1996, 1998b). The diagnosis of *Megalosauripus* (amended by Lockley *et al.*, 1998b) are as follows; Medium to large, elongate tridactyl tracks with phalangeal pad formula of 2, 3 and 4 corresponding to digits II, III and IV. Elongate heel, relative to length of digit III impression. Trackway very variable ranging narrow to moderately wide, with pace angulation values as low as 120°. On the other hand, the Phu Faek specimens show moderate mesaxony (ratio FL/FW: 1.12~1.17), and those pad impressions are indistinct. There is a tendency for larger and more robust trackmakers to lack well defined digital pads and also to have had more fleshy feet (e.g. Lockley and Meyer, 2000). From the Sao Khua Formation, some body fossils of large-sized theropod such as *Siamosaurus suteethorni* (Buffetaut and Ingavat, 1986) and *Siamotyrannus isanensis* (Buffetaut *et al.*, 1996) have been reported. Any dinosaur bone fossils have not been reported from the Phra Wihan Formation. However, estimated trackmakers of the Phu Faek specimens are large-sized theropods like Carnosauria and Megalosauria.

4.3.3 Site Hin Lat Pa Chad (Phu Wiang)

The site Hin Lat Pa Chad (Phu Wiang) is located at about 50 km west of Khon Kaen (Khon Kaen Province, N16°46'17.2", E102°16'34.2"), and Phu Wiang Dinosaur

Museum is located near place. The Phra Wihan Formation is cropping out at this site (e.g. Lockley *et al.*, 2009). Fine-grained sandstone crops out horizontally on a small scale in grass field. Some dinosaur footprints are present on the upper surface of sandstone with abundant trace fossils. These trace fossils are probably identified *Thalassinoides* (Fig. 38), based on their distinctive structure which are tubular in a vertical and horizontal direction. Current-ripple is also present on the same bedding plane. Based on these trace fossils and sedimentary structure, the paleoenvironment is estimated brackish water region or fluvial shallow.

Since the first report on the Phu Wiang dinosaur footprints was published by Buffetaut and Suteethorn (1993), some works on footprint fossils have been reported (e.g., Le Loeuff *et al.*, 2002, 2005; Matsukawa *et al.*, 2006). I show the mesh map of the outcrop in Fig. 39. At the moment, a part of footprint-bearing outcrop is covered with the deposition substance and the vegetation, and the remaining footprints are measurable. The numbers of trackways in Fig. 39 are corresponding to Fig. 10 in Matsukawa *et al.* (2006) and Fig. 3 in Lockley *et al.* (2009). Most of the Phu Wiang specimens are adjudged as the trackways of small-sized dinosaurs, and Le Loeuff *et al.* (2002) identified those as ornithopod tracks. Matsukawa *et al.* (2006) noted a similarity of Phu Wiang specimens to ichnogenus *Anomoepus*. Subsequently, Lockley *et al.* (2009) classified Phu Wiang specimens as a new ichnogenus *Neoanomoepus* isp. which are smaller than *Anomoepus* and its trackmaker is estimated as small-sized ornithopod on the basis of ichnological morphological characters. Additionally, in this site, there are an isolated tetradactyl track of crocodylian and a trackway consisting of only three pes tracks of small-sized theropod, however there is no report describing those tracks in ichnotaxonomy (e.g. Lockley *et al.*, 2009).

Systematic Ichnology

In this thesis, I give an explanation of the Phu Wiang specimens (T1, 2, 4, 7, and T11) using example from Lockley *et al.* (2009), and also describe a trackway T10 of small-sized theropod for the first time.

Ornithopod tracks

Ornithopoda Marsh, 1881

Ichnofamily Anomoepodidae Lull, 1953

Emended Gierlinski, 1991

Ichnogenus *Neoanomoepus* Lockley, McCrea and Matsukawa, 2009

Neoanomoepus isp. (Figs. 40 and 42)

Material: Five trackways (T1, 2, 4, 7 and 11) composed of consecutive tracks in total are imprinted on the bedding plane of fine-grained sandstone in this outcrop. The original tracks and trackway remain in the field.

Locality and horizon: Phra Wihan Formation, Lower Cretaceous. Hin Lat Pa Chad site, Nai Mueang, Wiang Kao District, Khon Kaen province, Thailand (N17°71'30.01", E104°38'15.76").

Description: Specimens T1, 2, 4, 7, and T11 are small trackways of bipedal or quadrupedal with tetradactyl, slightly elongate pes larger than pentadactyl manus (Fig. 40; Tables 9 and 10). The mean footprint length and width of manus and pes in the specimen T4 are 10.8 cm, 9.6 cm, 5.9 cm, and 4.7 cm, respectively. Pes

impressions slightly inwardly rotated from midline of trackway. Manus impressions slightly outwardly rotated and located lateral to pes impressions, and the distance between manus and pes is short. In the specimen T4, the mean step, stride, and pace angulation of manus are 35.4 cm, 54.2 cm and 121.0° (range 95°–150°), respectively. The mean step, stride, and pace angulation of pes are also 29.2 cm, 55.5 cm, and 148.0° (range 130°–155°), respectively. In the specimen T4, the trackway width of manus (mean 29.5 cm) is greater than those of pes (mean 20.5 cm). In the specimens T1, T2, T4, and T11, the mean footprint length and width of pes are 10.9 cm, and 8.9 cm, respectively. The mean step, stride, and pace angulation of pes are also 27.2 cm, 52.0 cm, and 151.8° (range 130°–170°), respectively. The estimated height at the hip (h) is ranging from 46.6 to 58.1 cm (Fig. 41). The relative stride length (SL/h = 0.9~1.07) represents a walking gait. The walking speed is estimated to be from 1.62 to 2.28 km/h.

Remarks: Buffetaut and Suteethorn (1993) noted that some trackways sometimes show a small, apparently tridactyl, manus impression lateral to the pes impression, and they may have been left by ornithischians. Matsukawa *et al.* (2006) infer that the pes is tetradactyl in some cases (based on two trackways; Fig. 10 in Matsukawa *et al.*, 2006) and that the manus may be pentadactyl. Matsukawa *et al.* (2006) also noted that the trackways resembles the Lower Jurassic ichnogenus *Anomoepus* with Le Loeuff *et al.* (2002). Lockley *et al.* (2009) noted that the pes tracks sometimes show faint impressions of the hallux and are therefore tetradactyl, and that at least one manus track is also tetradactyl, and may be interpreted as pentadactyl. They also noted that the hallux of pes is directed more anteriomedially and may also be more anteriorly situated than in the primitive type (*Anomoepus*). On the basis of

these facts, they proposed a new ichnogenus *Neoanomoepus*, accommodated in the ichnofamily Anomoepodidae.

In the investigation of this study, I observed the trackways T1, 2, 4, 7, and T11 (Fig. 42). I measured T1, 2, 4, and T11 (Tables 9 and 10), and made mesh map including T1, 2, 4, 7, and T11 (Fig. 39). I did not measure T7, however, the trackway shows the ichnological characteristics corresponding with other trackways. There are many faint and indistinctive manus impressions, and some distinctive manus are imprinted with the pes in T4. Pes impressions show tridactyl or tetradactyl, whereas manus are in a poor state of preservation due to erosion, thus I infer the manus is tetradactyl or pentadactyl impressions. The trackway width of *Anomoepus* is about twice as wide as footprint width (Lull, 1953), whereas, in the Phu Wiang specimens, the trackway width is four times as wide as footprint width. The trackway of the Phu Wiang specimens is wider than *Anomoepus*. On the basis of ichnological characteristics in Lockley *et al.* (2009) and this study, the Phu Wiang specimens clearly differ from *Anomoepus* in morphology. *Neoanomoepus* is monospecific ichnogenus, and has ichnospecies *N. perigrinatus*. The Phu Wiang specimens are smaller than *N. perigrinatus* (~81% in length), and its pace angulation is also smaller (about 20% smaller). The Phu Wiang specimens totally resemble *N. perigrinatus*, however, the Phu Wiang specimens are slender than *N. perigrinatus*. On the basis of the poor preservation of the Phu Wiang specimens, I classify it as *Neoanomoepus* isp. as with Lockley *et al.* (2009).

Lockley *et al.* (2009) noted that “heteropody” is usually attributed to basal ornithischians and ornithopods, thus *Neoanomoepus* seems to be of ornithopod affinity because basal ornithischians are not recorded in the Cretaceous, whereas

ornithopod are present and diverse. In the Khorat Group, ornithopod tracks are rare (Kozu et al., 2014) whereas ornithopod body fossils have been known and described from the Lower Cretaceous Khok Kruat Formation (see Buffetaut and Suteethorn, 2011; Shibata *et al.*, 2011, 2015). The appearance of ornithopod track in the site Hin Lat Pa Chad will become an important indicator of radiation and diversity of ornithopod in the Lower Cretaceous, northeastern Thailand.

Theropod tracks

Theropoda Marsh, 1881

Ichnogenus *Carmelopodus* Lockley, Hunt, Paquette, Bilbey and Hamblin, 1998

Carmelopodus isp. (Figs. 43, 44 and 45)

Material: One trackway T10 composed of 3 consecutive tracks is imprinted on the bedding plane of fine-grained sandstone in this outcrop. The original tracks and trackway remain in the field.

Locality and horizon: Phra Wihan Formation, Lower Cretaceous. Hin Lat Pa Chad site, Nai Mueang, Wiang Kao District, Khon Kaen province, Thailand (N17°71'30.01", E104°38'15.76").

Description: The specimens T10n1, 2, and 3 are well-preserved pes impressions that are symmetrical, tridactyl small-sized tracks with slender digit impressions, and no metatarsophalangeal pad (Figs. 43 and 44). Footprint length and width are 12.7 cm and 9.8 cm on average, respectively, and the mean length/width ratio (L/W) is 1.30, indicating moderate mesaxony. Each digit III impression is directed anteriorly and is

longest, and that of digit II nearly equal to that of digit IV. Digit II has two phalangeal pad impressions; digits III and IV have three or four phalangeal pad impressions. There is a distinct claw mark at the tip of each digit. There is no metatarsophalangeal pad impression in the specimen T10. Each interdigital angle between digits II and III is almost equal to those of digits III and IV. The interdigital angle between digits II and IV is 54°–62° (mean 59.0°). The trackway width is narrow, and the axis of digit III slightly outwardly rotated to the axis of trackway. The mean step, stride, and pace angulation are 33.0 cm, 55.0 cm, and 163.0°, respectively. The estimated height at the hip (h) is 57.2 cm (Fig. 41). The relative stride length (SL/h = 1.14) represents a walking gait. The walking speed is estimated to be about 2.64 km/h.

Comparison and discussion: In the Khorat Group, *Siamopodus khaoyaiensis* was described as an endemic track of small-sized theropod by Lockley *et al.* (2006d). They noted the diagnosis of *S. khaoyaiensis* as follows: small- to medium-sized tridactyl theropod track with slender toes and sub-symmetric bilobed heel. Inner hypex between digits II and III situated posterior to outer hypex between digits III and IV. These ichnological characteristics, “the bilobed heel” and “the situation of hypex”, differ from those of the Phu Wiang specimen in obvious (Fig. 45). Therefore, the Phu Wiang specimen is not classified as *S. khaoyaiensis* in taxonomy.

From the Lower Cretaceous Khok Kruat Formation, Khorat Group, small-sized theropod tracks have been known at the site Huai Dam Chum (Tha Uthen) (e.g. Buffetaut *et al.*, 2005; Le Loeuff *et al.*, 2003, 2005; Sato and Tumpeesuwan, 2005; Matsukawa *et al.*, 2006; Suraprasit, 2008MS). Kozu *et al.* (in press) described the Tha Uthen specimens as cf. *Asianopodus* isp. (Fig. 7 in Kozu *et al.*, in press). The

Tha Uthen specimens are sub-symmetrical, tridactyl small-sized tracks with slender digit impressions, and show with indistinct metatarsophalangeal pad impressions. The difference of “heel shape” between the Tha Uthen and Phu Wiang specimens means the ichnological distinction between two specimens.

Lockley *et al.* (1998a) described ichnogenus *Carmelopodus*, small-sized theropod track with no metatarsophalangeal pad. *Carmelopodus* has been reported from the Bajocian-Bathonian of North America, Middle Jurassic of Tunisia, and Upper Jurassic of Morocco (Lockley *et al.*, 1998a; Meyer and Monbaron, 2002; Gierliński *et al.*, 2009; Belvedere *et al.*, 2010; Niedźwiedzka *et al.*, 2017). Both of the Phu Wiang specimens and *Carmelopodus* are characterized by digit impressions that lack a fourth (proximal) pad impression on digit IV, and show narrow trackway width. Monospecific *Carmelopodus untermannorum* is characterized as the following features (Lockley *et al.*, 1998a): High width/length ratio (as wide as long), owing to widely divergent digit II; Digit II also wider and shorter than digit IV; Distal phalangeal pad of digit III is tapered; Larger digit divarication angle between digit II and III than between III and IV; the trackway (holotype CU-MWC184.12) with a short first step (about 24 cm) followed by three more or less equal steps of about 50 cm. Compared with *C. untermannorum*, the Phu Wiang specimens are as long as *C. untermannorum*, but rather elongate. The digits III are tapering at the end of digits. The interdigital angle between digit II and IV is comparable with the angle between III to IV, and the interdigital angle between II to IV is relatively narrower than *C. untermannorum*. The step is short, and the axis of digit III outwardly rotated. The Phu Wiang specimens are different from *C. untermannorum* in morphology, however the specimens show strong similarity with ichnogenus *Carmelopodus*. In particular,

the Phu Wiang specimens are quite similar to the specimen Morphotype 2A assigned as *Carmelopodus* sp. from the Iouaridène Formation, Morocco (Belvedere *et al.*, 2010). Therefore, I identify the Phu Wiang specimens as ichnogenus *Carmelopodus* isp. (Fig. 45).

According to Makovicky *et al.* (2004) and Padian (2004), in general, markedly shorter lateral metatarsals (mt. II and IV) occur in bird, alvarezsauroid and ornithomimosaurid feet. Niedźwiedzka *et al.* (2017) noted the most proximal pad is the metarsophalangeal pad of the middle toe (digit III), as seen for instance in the bird and ornithomimosaurid tracks classed in the ichnofamily of Ornithomimipodidae by Lockley *et al.* (2011). *Carmelopodus* lacks a proximal pad like bird and ornithomimosaurid, thus, Niedźwiedzka *et al.* (2017) indicated that alvarezsauroids seem to be the best candidates for *Carmelopodus* tracks. Although dinosaur bone fossils have not been reported from the Phra Wihan Formation, a small theropod coelurosauria such as alvarezsauroid is estimated as a trackmaker of *Carmelopodus* from the site Phu Wiang.

4.4 Phu Pan Formation

The Phu Phan Formation is well exposed along the Mae Khong River banks and in most parts of the Phu Phan Range. Generally, the formation consists of grayish-white medium- to coarse-grained cross-bedded sandstones and thin lenses of gray siltstone and mudstone with subordinate conglomerate (Meesook, 2011).

Very few plant and vertebrate fossils have been yielded from the Phu Pan Formation, but some palynomorphs from the formation are recorded (Racey *et al.*, 1994, 1996; Racey and Goodall, 2009). On the basis of these pollens, the age of this

formation is estimated to be in the range Berriasian to Aptian. The depositional environment is interpreted to have been predominantly braided, high-energy, low-sinuosity rivers with subordinate floodplains in a warm, humid palaeoclimate (Meesook, 2011).

4.4.1 Site Phu Luang

The site Phu Luang is located at Phu Luang Wild Sanctuary in Loei northwest of Khon Kaen (N17°40'70", E101°63'05"). The Phu Phan Formation is cropping out at this site (Buffetaut *et al.*, 1985b). Near this area, the upper part of Sao Khua Formation (mudstone) is exposed, therefore the section of site Phu Luang is thought to be the lower part of Phu Phan Formation. Some footprints were found by staff of this sanctuary in 1984, after that, Buffetaut and others reported these as first dinosaur footprints from Thailand (Buffetaut *et al.*, 1985a, b). Because of extensive weathering, most of footprints are indistinct, however, Buffetaut *et al.* (1985b) described the Phu Luang footprints on the basis of a comparatively distinct footprint.

According to Buffetaut *et al.* (1985b), the Phu Luang dinosaur footprints are imprinted on uneven fine-grained sandstone surface, which is subdivided into several blocks by deep and wide cracks (Fig. 46). Some of the footprints are partly destroyed by these cracks. Some footprints also overlap, which sometimes makes them difficult to interpret. On the other hand, a few footprints are well preserved and show important morphological details. In this study, I report about the Phu Luang dinosaur footprints on the basis of Buffetaut *et al.* (1985b) and new measurement data in my investigation.

Systematic Ichnology

In this thesis, I give an explanation of the Phu Luang specimens (T1, 2, 4, 7, and T11) using example from Buffetaut *et al.* (1985b) and my measurement data.

Theropod tracks

Theropoda Marsh, 1881

Ichnogenus *Irenosauripus* Sternberg, 1932

Irenosauripus isp. (Figs. 47, 48 and 49)

Material: In total 15 tracks (T1 to T12) are imprinted on the bedding plane of fine-grained sandstone in this outcrop. The original tracks remain in the field.

Locality and horizon: Phu Phan Formation, Lower Cretaceous. Phu Luang site, Khao Luang, Wang Saphung District, Loei province, Thailand (N17°40'70", E101°63'05").

Descriptive remarks: The specimens T1 to T7, and T12n1 are comparatively well-preserved pes impressions that are sub-symmetrical, tridactyl large-sized tracks with slender digit impressions (Figs. 47 and 48). In general, the digit III impression is directed anteriorly and is longest, whereas that of digit II is shorter than that of digit IV. There is a claw mark at the tip of each digit. The region of the metatarsophalangeal pad impression are indistinct. In T1 to T7, the mean footprint length and width are 34.3 cm and 30.0 cm, respectively, and the mean length/width ratio (L/W) is 1.14, indicating moderate mesaxony (Table 11). In well-preserved

tracks T1n1 and T2n2 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 also 57° on average (Fig. 49).

Some of the footprints show morphologically slightly differences, because of the overlapping, individual variation and different degrees of weathering. However, it is clear that the trackmaker of Phu Luang specimen is estimated as theropod because each track has slender digits and claw marks, and indicates moderate mesaxony. Buffetaut *et al.* (1985b) concluded that all the Phu Luang footprints have been produced by the same kind of dinosaur. They also concluded that the Phu Luang trackmakers are large theropod carnosaurs, whereas a more accurate identification is more difficult. Excluding some exceptions (e.g. primitive tyrannosauroida *Yutyranus huali*, Early Cretaceous, China), Carnosauria is typical large-sized theropod in Early Cretaceous, Asia. Additionally, primitive carnosaur *Siamotyrannus isanensis* have been known from the Sao Khua Formation underlying the Phu Phan Formation in Thailand. Therefore, I also infer that the Phu Luang trackmaker is carnosaur. Buffetaut *et al.* (1985b) noted the similarities between the Phu Luang specimens and ichnogenus *Irenesauripus*. However, the Phu Luang specimen seems to be a little smaller than some ichnospecies of the ichnogenus *Irenesauripus*, such as *I. acutus*, *I. mclearnii*, and *I. occidentalis*. Therefore, they described the Phu Luang tracks as *Irenesauripus*. In this thesis, the estimated hip height of Phu Luang trackmaker ranges from 1.57 to 1.91 m (mean 1.71 m). Buffetaut *et al.* (1985b) deduced that the hip height of Phu Luang footprint no. 4 is 1.78 m (Fig. 50). They also assumed that the distance between footprint no. 4 and no. 13 (2.80 m) corresponds to stride length, and gave an estimated speed of

about 8 km/h. An estimated relative stride length 1.57 means walking gait.

4.5 Khok Kruat Formation

The Khok Kruat Formation is widely distributed in the outer parts of the Phu Phan Range, and the formation conformably overlies the Phu Phan Formation. Generally, the formation consists of reddish-brown fine- to medium-grained sandstone, siltstone and mudstone, with some conglomerate beds (Meesook, 2011).

Until now, abundant plant remains, bivalves and vertebrate fragments have been found. In particular, dinosaur remains have been known from the formation since Buffetaut and Ingavat (1983) described teeth and bone fragments. As a new species, the small ceratopsian *Psittacosaurus sattayarakii* (Buffetaut and Suteethorn, 1992), the iguanodontia *Siamodon nimngami* (Buffetaut and Suteethorn, 2011), *Ratchasimasaurus suranareae* (Shibata *et al.*, 2011), *Sirindhorna khoratensis* (Shibata *et al.*, 2015), were described.

Compared with the Takena Formation of Tibet which dated as Aptian-Albian age on the basis of foraminifera, the age of the Khok Kruat Formation also dated as Aptian-Albian (Cappetta *et al.*, 1990). Sattayarakii *et al.* (1991) suggests an Aptian age for the upper part of the formation based on borehole samples.

4.5.1 Site Huai Dam Chum (Tha Uthen)

The tracksite is located at 50 km north of Nakhon Phanom along the route 212, where is near the border between Thailand and Laos (N17°71'30.01", E104°38'15.76"). The Khok Kruat Formation is cropping out at this site (e.g. Le Loeuff *et al.*, 2003). The tracksite was the quarry originally, and the outcrop, which

consists mainly of very-fine-grained sandstone, is exposed along route 212 (Fig. 51a). 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. 51b). Dinosaur footprints in this tracksite were first reported by Le Loeuff *et al.* (2003). Subsequently, there have been other reports of footprint fossils in this area (Buffetaut *et al.*, 2005; Le Loeuff *et al.*, 2005, 2009; Sato and Tumpeesuwan, 2005; Matsukawa *et al.*, 2006; Suraprasit, 2008MS).

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 also described a large assemblage of small theropods 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 this study, I measured dinosaur footprint fossils in the northern part of the outcrop at the Huai Dam Chum track site. In the northern outcrop, ~600 dinosaur footprints are imprinted in the thin mudstone layer. The succession at this site (Fig. 52) 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-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. 53 and 54).

Two types of dinosaur tracks, small-sized theropod tracks and small-sized, flattened possible theropod tracks, were recognized on the same bedding plane of a thin mud layer at the northern part of the outcrop. Many indistinct small-sized crocodylomorph tracks also occur on the same bedding plane in the formation, running across or parallel to the theropod trackways (Figs. 53 and 54). The pes and manus tracks are ~4.5 cm long and ~3.5 cm wide, and are identical to typical crocodylomorph tracks. Le Loeuff *et al.* (2010) have already described the crocodile tracks as batrachopodidae *Batrachopus* sp. and possible crocodilian track gen. et sp. indet. in this site. These observations may suggest that a lot of theropods, a few ornithopods, and small-sized crocodylomorphs travelled along the side of a river, which was probably meandering (Fig. 54).

Systematic Ichnology

In this thesis, I give an explanation of the Tha Uthen specimens using example

from Kozu *et al.* (in press).

Theropod tracks

Theropoda Marsh, 1881

Asianopodus Matsukawa, Shibata, Koarai and Lockley, 2005

cf. *Asianopodus* *isp.* (Fig. 55)

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. 53 and 54).

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. 55; Table 12). 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 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 13). Essentially, a “trackway” is composed of more than three consecutive tracks (Thulborn, 1990); in this study, I 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 (Fig. 56). 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.* (2002a, 2006d) 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. 55).

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. 55). 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 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 ichnogenera *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. 55).

Flattened possible theropod tracks

Theropoda Marsh, 1881

Ichnogen. et sp. indet. (Fig. 57)

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. 53 and 54).

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: The average footprint length and width of Tha Uthen trackway T23 (Fig. 57) are 17.4 and 14.2 cm, respectively (Table 12). 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. 57); 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. 57: 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.

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 I suggest that the Tha Uthen

specimens T23 and T35 are tracks of small-sized theropod (Fig. 56). 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. 57). 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. 57). 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 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. Discussion

5.1 Reconstruction of the dinosaur ichnofauna in the Khorat Group and its significance

I show the new reconstructed dinosaur ichnofauna in the Khorat Group in Fig. 58. In this study, I have identified tracks of theropoda, ornithopoda, sauropoda, crocodylian, non-dinosauriform archosauromorpha, and didactyl tracks of tetrapoda in a total of eight tracksites from the Khorat Group, northeastern Thailand. Compared with the dinosaur fauna and dinosaur ichnofauna in the Khorat Group, many dinosaur footprints have been known from the Phra Wihan Formation from where we have no report on the occurrence of the dinosaur bone fossils. For example, sauropodmiorpha bone fossils have been found from the Nam Phong and Phu Pan Formations, however, the ichnofauna indicate that theropod dinosaurs and other tetrapoda are present in the formations. On the other hand, there is no report of dinosaur footprint from the Phu Kradung and Sao Khua Formations which yields dinosaur bone fossils abundantly. As a result of this comparison, dinosaur fauna based on the bone fossils and dinosaur ichnofauna do not show the true faunal succession of dinosaurs in Thailand. However, dinosaur ichnofauna compensates for lack of dinosaur fauna based on the bone fossils will lead to reconstruct more precise dinosaur fauna, and it shows the paleontological significance of dinosaur footprint ichnology.

Compared with the dinosaur fauna of the Khorat Group and the dinosaur footprint fauna conducted by the present study, we know that there were diversified dinosaur faunas in the Early Cretaceous time in northeastern Thailand. Furthermore, I described Late Triassic dinosaur footprints from the site Non Tum, in

addition to the well know footprint site of the Tha Song Khon. This finding is very important to consider the origin of dinosaur in East Asia because we do not have enough knowledge on the Late Triassic dinosaur footprint fossils from East Asia. Shibata *et al.* (2017) compared and discussed Early Cretaceous dinosaur fauna in East and Southeast Asia (Fig. 59). They indicated that ornithopod dinosaurs appeared for the first time in the Early Cretaceous dinosaur fauna of the Khorat Group, and the records of Early Cretaceous hadrosauroid are restricted to Asia while iguanodontia dinosaurs have some similarities to European species. Therefore, they also introduced the possibility that hadrosauroid dinosaurs have its roots in Early Cretaceous East and Southeast Asia, and extended its habitats there. On the other hand, as shown in Fig. 58, it is obvious from the dinosaur ichnofauna in the Khorat Group that the first occurrence of ornithopod dinosaurs is recorded in the Phra Wihan Formation, Early Cretaceous Berriasian to Barremian. Therefore, although there is no report describing the tracks of hadrosauroidea from the Khorat Group, the origins of ornithopoda are estimated to be in Southeast Asia on the basis the report of primitive small ornithopoda tracks. Shibata *et al.* (2017) also suggested that the origins of allosauroidea are estimated to be in the region of Southeast Asia. From the Khorat Group, there are some reports of the tracks of carnosauria including allosauroidea (e.g. Buffetaut *et al.*, 1985a, b). Therefore, from the ichnological point of view, there is a possibility that the origins of allosauria is in the region of South Asia.

5.2 Comparison of the dinosaur ichnofauna in the Khorat Group with East Asia

Taxonomic Group of dinosaur bone fossils and ichnotaxonomic Group of footprint

from the Khorat Group are shown in Fig. 60. To this day, only two ichnogenera and one ichnospecies of dinosaur footprint, theropod track *Siamopodus khaoyaiensis* (Lockley *et al.*, 2006d) and primitive ornithopod track *Neoanomoepus* sp. (Lockley *et al.*, 2009), have been described in ichnotaxonomy from the Khorat Group. In this study, I newly described five ichnogenera of dinosaur footprints, *Eubrontes* isp., *Gigandipus* isp., *Carmelopodus* isp., *Irenesauripus* isp., and cf. *Asianopodus* isp., and one ichnogenus of archosauromorpha, cf. *Apatopus* isp. in ichnotaxonomy. Fig. 61 shows the ratio of occurrence of dinosaur trackmarkers from the data obtained in this study. I have identified 893 footprints including 151 trackways. I considered that one trackway was made by one trackmaker, and if I cannot discriminate footprint as trackway, I counted one footprint as one trackmaker. The ratio of the occurrence of theropod footprint exceeds more than 90 % and the ratio of each geologic age is almost the same. Concerning the paleoenvironments, footprints were made at the riverside area such as meandering river bar, fluvial shallow, floodplains, rarely brackish water region, and others, based on the analysis of sedimentary structure and trace fossils and also bivalve fossils (Fig. 58). These lines of evidence indicate that the riverside environments are the suitable ones for the group of theropod dinosaur and as their living areas.

The number of tetrapod tracksites reported from China has increased rapidly in recent years and is now in excess of 100, with about 70 being known from the Cretaceous (e.g. Zhen *et al.*, 1989; Chen *et al.*, 2006; Matsukawa *et al.*, 2006; Lockley *et al.*, 2014). The precise age of many formations is uncertain (e.g. Lockley *et al.*, 2014). Lockley *et al.* (2014) focused attention on the more important tracksite regions (C1-C6) in the Early Cretaceous Ichnofaunas in China, and summarized

each ichnofauna (Fig. 62) as follows: Abundant small theropod tracks *Grallator ssatoi* (e.g. Matsukawa *et al.*, 2006), bird tracks (Lockley *et al.*, 2006c), and sauropod tracks (Zhang *et al.*, 2012) have been known from the region C1 (Northeastern China). Because of those oldest type tracks, the units of this area are considered to present the Jurassic-Cretaceous transition. From the region C2 (Shandong Province), abundant small theropod tracks such as *Grallator*, *Paragrallator*, distinctive theropod tracks (*Corpulentapus*), sauropod tracks, turtle tracks, and pterosaur tracks have been reported to date (Li *et al.*, 2011b; Lockley *et al.*, 2012c, d; Xing *et al.*, 2012). Additionally, distinctive tracks such as, dromaeosaur tracks *Dromaeopodus* and *Velociraptorichnus* (Li *et al.*, 2008, 2014), small theropod tracks *Minisauripus* (Lockley *et al.*, 2008), have also been reported from the Barremian-Aptian in age. In the region C3 (Inner Mongolia), saurischian tracks including the theropod tracks *Chapus* and *Asianopodus*, the sauropod tracks *Brontopodus*, and the bird tracks *Tatarornipes* have been described from the Jianchuan Formation (Li *et al.*, 2006, 2011a; Lockley *et al.*, 2002b, 2012b). Many tracksites have been reported from the Hekou Group in the region C4 (Gansu Province). In the area, the first reported *Dromaeosauripus* from China (Xing *et al.*, 2013a), large sauropod tracks, ornithopod tracks, pterosaur tracks, and bird tracks have been reported, respectively (Peng *et al.*, 2004; Zhang *et al.*, 2006). In the region C5 (Sichuan Province and Chongqing City), there are some famous tracksite, the sites Xingfu Cliff, Lotus, and Sanbiluoga. These sites show the high diversity ichnofauna including the old type tracks *Grallator*, small theropod tracks *Minisauripus*, didactyl tracks *Velociraptorichnus*, sauropod tracks, ornithopod tracks *Caririchnium*, a few pterosaur tracks, and bird tracks (Xing *et al.*, 2007, 2013d; Zhen *et al.*, 1995). Finally, from the region C6

(Xinjiang Autonomous Region), two tetrapod tracksites have been described in recent years. The site Wuerhe has yielded theropod tracks, thyreophoran tracks (*Deltapodus*), pterosaur tracks, and turtle tracks (e.g. Xing *et al.*, 2013c). The site Asphaltite also yields theropod tracks and pterosaur tracks (He *et al.*, 2013; Xing *et al.*, 2013b).

Since the discovery of Cretaceous dinosaur tracks in Korea in the early 1980s (Yang, 1982) the rate of report of diverse tetrapod ichnofaunas has increased rapidly (Lockley *et al.*, 2014). Many tracksites at localities along the southern coast of Korea has led to the concept of the “Korea Cretaceous Dinosaur Coast (KCDC)” (e.g. Huh *et al.*, 2003). The majority of tracksites have been known from the Gyeongsang Supergroup of the Gyeongsang Basin which are widely distributed in southeastern part of the Korean peninsula (Fig. 63, after Lee *et al.*, 2000). The Gyeongsang Supergroup is subdivided into three groups, in ascending order: the predominantly sedimentary lower and middle groups, Singdong and Hayang Groups, and the predominantly volcanic Yucheon Group (e.g. Lockley *et al.*, 2006a, 2014). The ages of the Sindong and Hayang Groups are inferred as Hauterivian to Aptian (Houck and Lockley, 2006) or as slightly younger, Aptian to Campanian (Paik *et al.*, 2012). Lockley *et al.* (2014) summarized the dinosaur ichnofaunas in the Sindong and Hayang Groups in Korea. They said that there have been relatively few important tracksites reported from the older Sindong Group. However there are some significant reports including the pterosaur tracks (*Pteraichnus*, Lee *et al.*, 2008) from the Hasandong Formation and the oldest *Dromaeosauripus* (Kim *et al.*, 2012a) from the Jinju Formation. On the other hand, many significant tracksites have been known from the overlying Hayang Group consists of track-rich Haman and Jindong

Formations. Lockley *et al.* (2014) introduced the tracks as follows: The Haman Formation yielded six tetrapod track holotypes assigned to the avian ichnogenera *Koreanaornis* (Kim, 1969), *Ignotornis* (Kim *et al.*, 2006, 2012b), dromaeosaurids (*Dromaeosauripus* Kim *et al.*, 2008), sauropods (*Brontopodus* Kim and Lockley, 2012), pterosaurs (*Haenamichnus* Kim *et al.*, 2012c) and small theropod tracks *Minisauripus* (e.g. Lockley *et al.*, 2008; Kim *et al.*, 2012d), which is only known from the Cretaceous of China and Korea. The Jindong Formation yielded more tracks than the Haman Formation. According to Lockley *et al.* (2014), there are several avian theropod track holotypes assigned to the ichnogenera *Jindongornipes* (Lockley *et al.*, 1992), *Goseongornipes* (Lockley *et al.*, 2006a) and *Gyeongsangornipes* (Kim *et al.*, 2013), the ornithopod ichnogenus *Ornithopodichnus* (Kim *et al.*, 2009).

As concerns the Early Cretaceous tetrapod ichnofauna in China, the regions C1, C2, and C5 are characterized as the theropod track *Grallator* - rich ichnofauna including typical dromaeosaurids tracks, pterosaur tracks and others. The region C4 also shows a remarkable diversity of the dromaeosaurids tracks (*Dromaeosauripus*), and large sauropod, pterosaur, and bird tracks. On the other hand, the ichnofauna in the region C3 and the Khorat ichnofauna partially coincide with each other in showing abundant theropod tracks *Asianopodus*. Although the region C6 has only two cretaceous tracksites, it shows comparatively high diversity of track types including non-avian and avian theropod, tyreophoran (*Deltapodus*), pterosaur and turtle tracks which is inconsistent ichnofauna with the Khorat ichnofauna. As concerns the Early Cretaceous tetrapod ichnofauna in Korea, it is totally characterized high diversity of track types such as, avian and non-avian theropods, sauropods, pterosaurs. In particular, the ratio of the occurrence of ornithopod tracks

(e.g. *Caririchnium* and *Ornithopodichnus*) in the Jindong Formation attains more than those of theropod and sauropod in total (table 2 in Lockley *et al.*, 2014). As the reason why ornithopod footprints were reported so many in this area, the seasonal migration may be the best appropriate answer. However, the detailed cause is not clarified yet (e.g., Lim *et al.*, 1994). As mentioned above, abundant theropod tracks have been reported from East Asia including the Khorat Group, except for a part of Korean tracksites. The ichnofaunas of China and Korea are also characterized typical dromaeosaurids tracks and the smallest theropod tracks *Minisauripus*. As a result of the comparisons between the Early Cretaceous Khorat Ichnofauna and East Asian Ichnofauna, the ichnofauna of the region C3 (Inner Mongolia) in China shares partial ichnological characteristics with the Khorat Ichnofauna. However, the tracksites are few in number in the Khorat Group, and there is few report describing dromaeosaurids tracks, large sauropod and ornithopod tracks, pterosaur, turtle, bird tracks in Thailand compared with East Asian tracksites. The Khorat Group has a little different ichnofauna with East Asia while sharing the partial ichnofauna which is non-avian theropod track (like *Asianopodus*) rich.

5.3 Footprint assemblage and its quantitative analysis

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 herd of trackmakers 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, 2012a) 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).

In the most tracksites known from the Khorat Group, it is difficult to discuss gregarious behaviour of the trackmakers. Because most tracks and trackways in each tracksite show “amblegait” which means various directions of tracks and trackways. Buffetaut *et al.* (1985b) attempted to discuss group behaviour of theropod tracks in the site Phu Luang. There is no trackway in the tracksite, however, some footprints have orientations which fall within 50° sector. By way of conclusion, they suggested that the preferential orientation of the Phu Luang tracks is not due to physical obstructions, and the tracks have been made by a small group of theropod moving together in the same direction. They also said that it is impossible to know what exactly those dinosaurs were doing when they made these footprints. In my investigation at the site Phu Luang, some footprints show in roughly the same direction of digit axis III, however it is impossible to identify “trackway”. There is no direct evidence to show that the trackmaker theropods participated in group behaviour.

Kozu *et al.* (in press) conducted quantitative analysis of theropod tracks at the site Huai Dam Chum. In this thesis, I give an explanation of its gregarious behaviour

using example from Kozu et al. (in press). 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 m² on the northern outcrop surface at the Huai Dam Chum track site (Figs. 64 and 65). This occurrence constitutes an example of high-density dinosaur tracks in the Cretaceous strata of Thailand.

As mentioned in Figs. 64 and 65, the *Asianopodus* type theropod tracks are subdivided into two groups because the tracks show two directions of migration, to the northeast and to the northwest. I define the group aligned NW as Group A and the group aligned NE as Group B (Figs. 64 and 65). Table 13 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 13). 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. 64, the cf. *Asianopodus* trackways are parallel or sub-parallel 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. 64, I 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. 65). Thus, on the basis of the ichnological measurement data, I 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; Table 12 and 13) show S to SE movement directions meaning solitary behaviour.

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.* (2009b) from the Lower Cretaceous Sao Khua Formation of the Khorat Group. In general, ornithomimosaurians are the best-known example of gregarious dinosaurs. Although direct evidence is lacking, I 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 Group A and B at the Huai Dam Chum site were constructed (Fig. 66). 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, I 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, I 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 13). 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 to 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, I 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

- 1) In this study, I have identified 877 tetrapod tracks including 151 trackways in a total of eight tracksites from the Khorat Group, northeastern Thailand. I have also classified some kind of tracks of theropoda, ornithopoda, sauropoda, crocodylian, non-dinosauriform archosauromorpha, and didactyl tracks of tetrapoda from the Khorat Group. The ratio of the occurrence of theropod footprint exceeds more than 90 % and the ratio of each geologic age is almost the same.
- 2) To this day, only two ichnogenera and one ichnospecies of dinosaur footprint, theropod track *Siamopodus khaoyaiensis* (Lockley *et al.*, 2006d) and primitive ornithopod track *Neoanomoepus* sp. (Lockley *et al.*, 2009), have been described in ichnotaxonomy from the Khorat Group. In this study, I newly described five ichnogenera of dinosaur footprints, *Eubrontes* isp., *Gigandipus* isp., *Carmelopodus* isp., *Irenosauripus* isp., and cf. *Asianopodus* isp., and one ichnogenus of archosauromorpha, cf. *Apatopus* isp. in ichnotaxonomy.
- 3) As a result of the comparison between dinosaur fauna based on the bone fossils and dinosaur ichnofauna, both of them do not show the “true dinosaur fauna” in Thailand. However, dinosaur ichnofauna compensates for lack of dinosaur fauna based on the bone fossils will lead to reconstruct more precise dinosaur fauna, and it shows the paleontological significance of dinosaur footprint ichnology.
- 4) As a result of comparison with the Early Cretaceous dinosaur faunas in East and Southeast Asia (Shibata *et al.*, 2017), there is a possibility that the origins of ornithopoda and allosauria is in the region of Southeast Asia from the ichnological point of view.
- 5) As a result of comparison between the Khorat ichnofauna and Chinese and

Korean ichnofaunas in East Asia, there is partial common point between the Early Cretaceous Khorat Ichnofauna and the ichnofauna of the region C3 (Inner Mongolia) in China. However, the tracksites are few in number in the Khorat Group, and there is few report describing dromaeosaurids tracks, large sauropod and ornithopod tracks, pterosaur, turtle, bird tracks in Thailand compared with East Asian tracksites. The Khorat Group has a little different ichnofauna with East Asia while sharing the partial ichnofauna which is characterized as non-avian theropod track (like *Asianopodus*) rich.

6) I described the dinosaur footprint assemblage in ichnotaxonomy for the first time in Thailand. As a result of the quantitative analysis of dinosaur footprint assemblage in the site Huai Dam Chum, the footprint assemblage of the theropod tracks referred to cf. *Asianopodus* isp. is estimated to be imprinted by probably gregarious ornithomimosaur. The tracks are mainly separated into two groups, Group A and Group B, and indicate the accurate herd behaviour and its idiosyncratic group composition. In particular, the histogram of size-frequency measurements of Group A shows the anomalous bimodal distribution. I 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.

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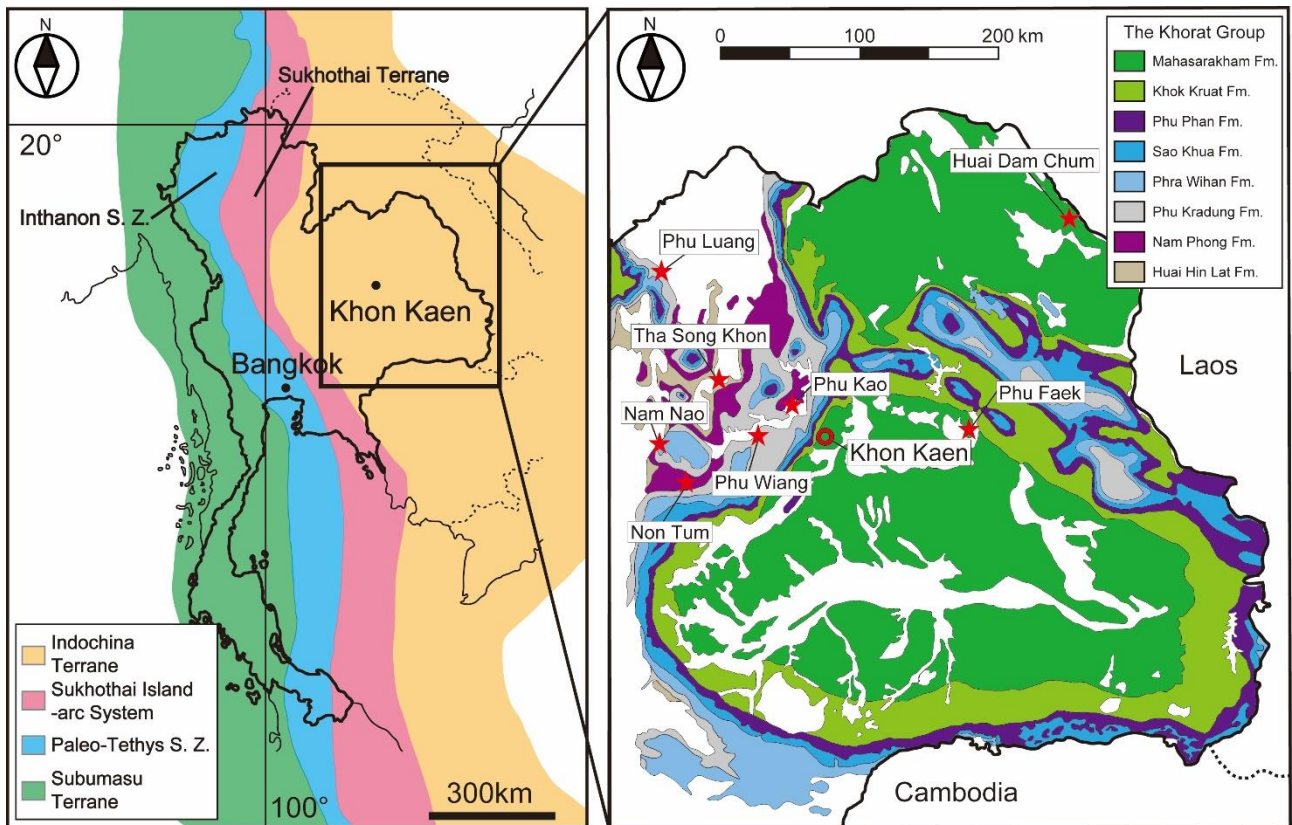


Figure 1 Index map showing the distribution of the Khorat Group and footprint sites (original map is from DMR, 1999; Meesook, 2011; Metcalfe, 2013).

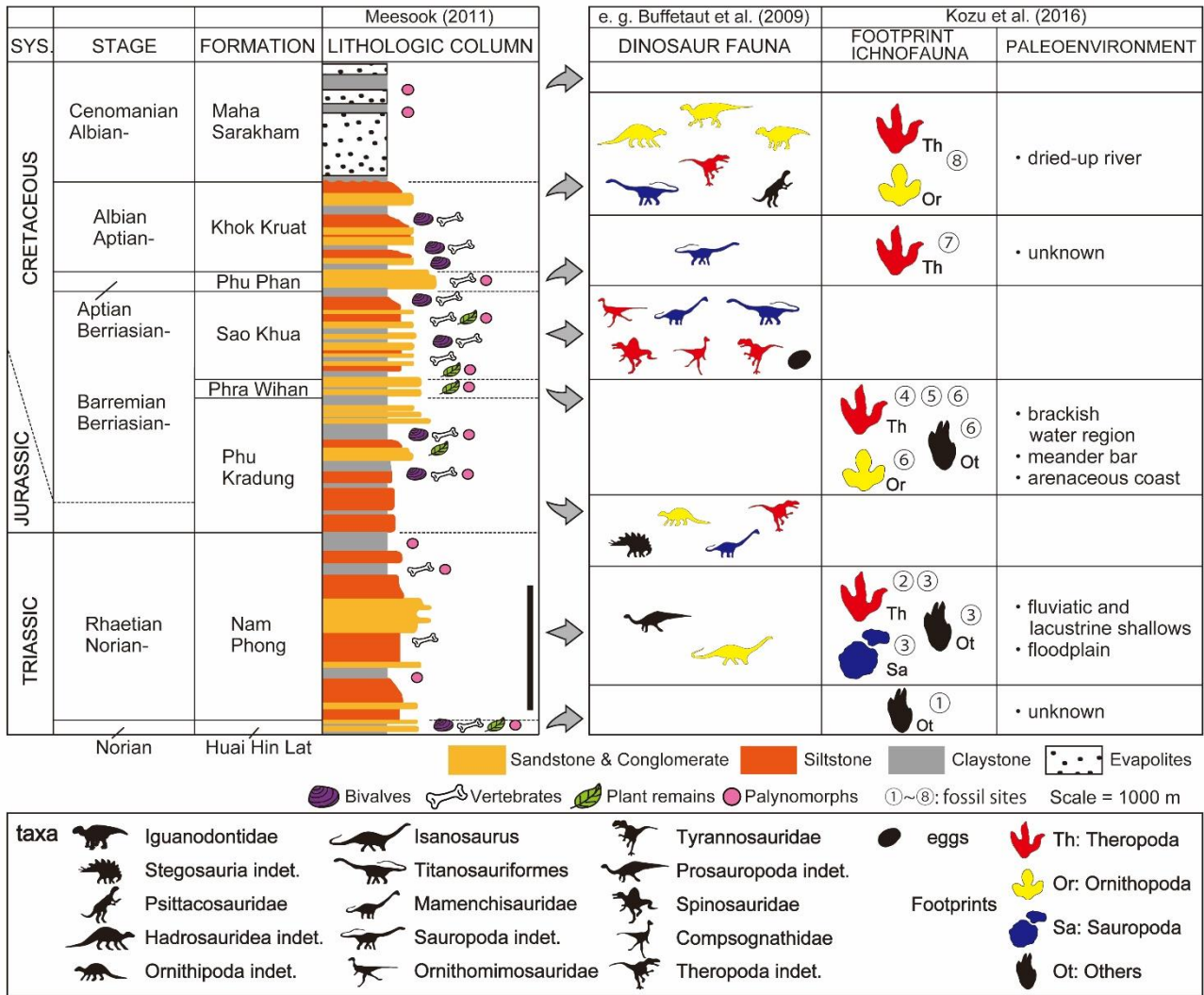


Figure 2 Lithostratigraphic column and dinosaur ichnofauna of the Khorat Group (modified from Buffetaut *et al.*, 2009a; Buffetaut and Suteethorn, 2011; Meesook, 2011; Shibata *et al.*, 2011, 2015; Kozu *et al.*, 2016, 2017).

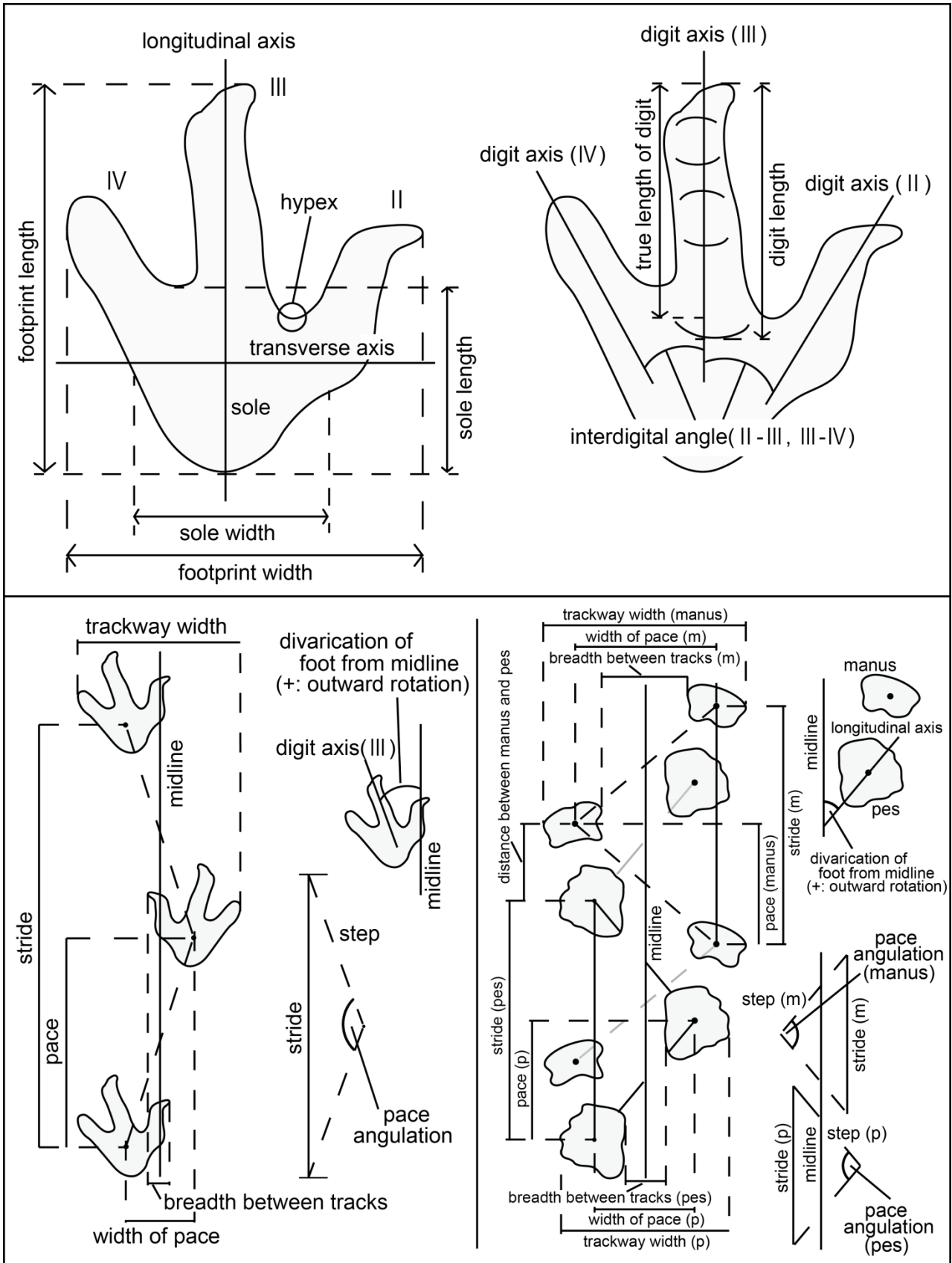


Figure 3 Diagrams of footprints and trackways, showing measurement methods (modified from Ishigaki, 1988).



Figure 4 Photograph of making silicon replica (process 3).



Figure 5 Photograph of making silicon replica (process 4).

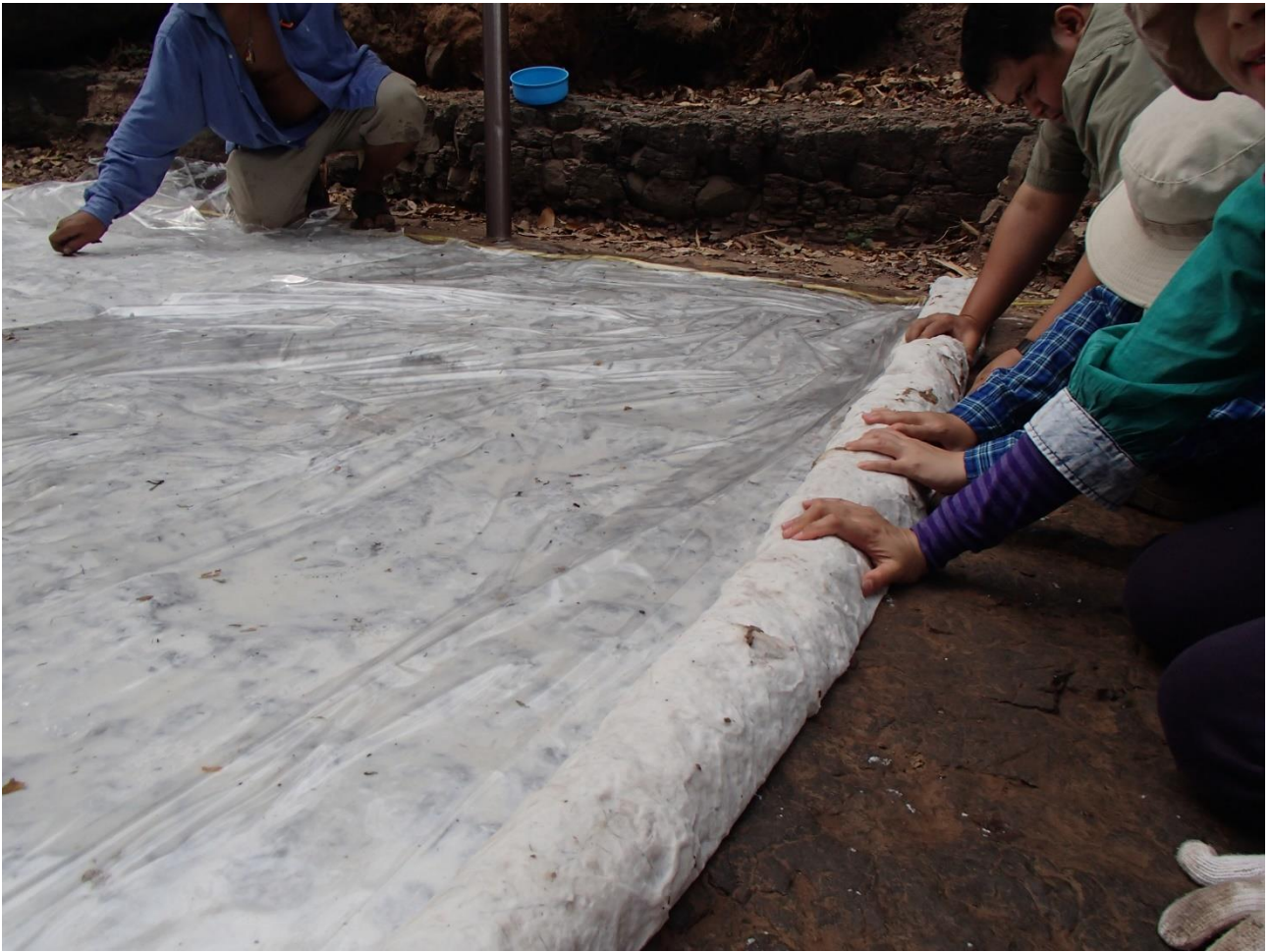


Figure 6 Photograph of making silicon replica (process 7).



Figure 7 Photograph of making plaster replica (process 2).



Figure 8 Photograph of making plaster replica (process 5).

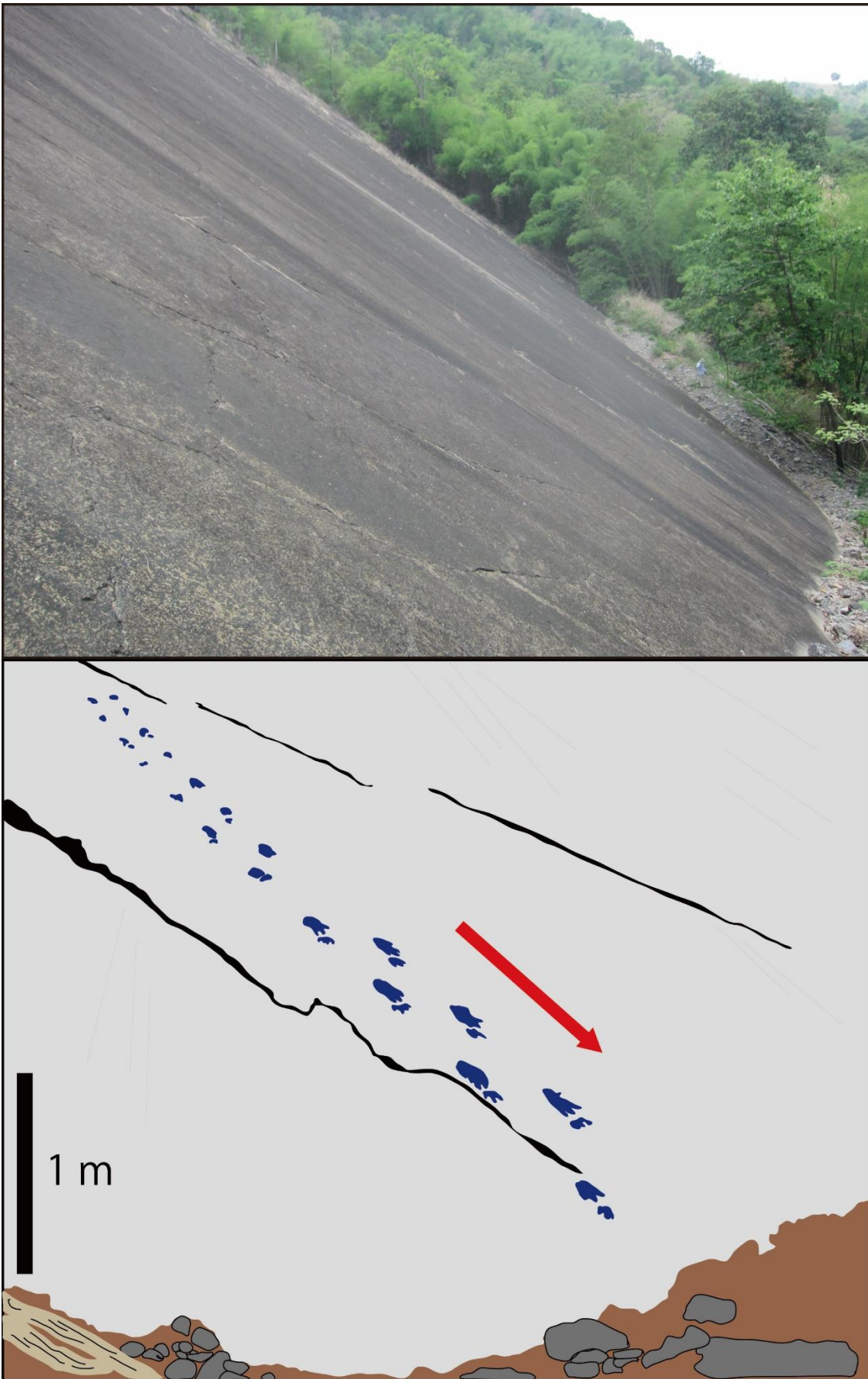


Figure 9 Photograph of the outcrop and sketch of a trackway at the site Nam Nao.

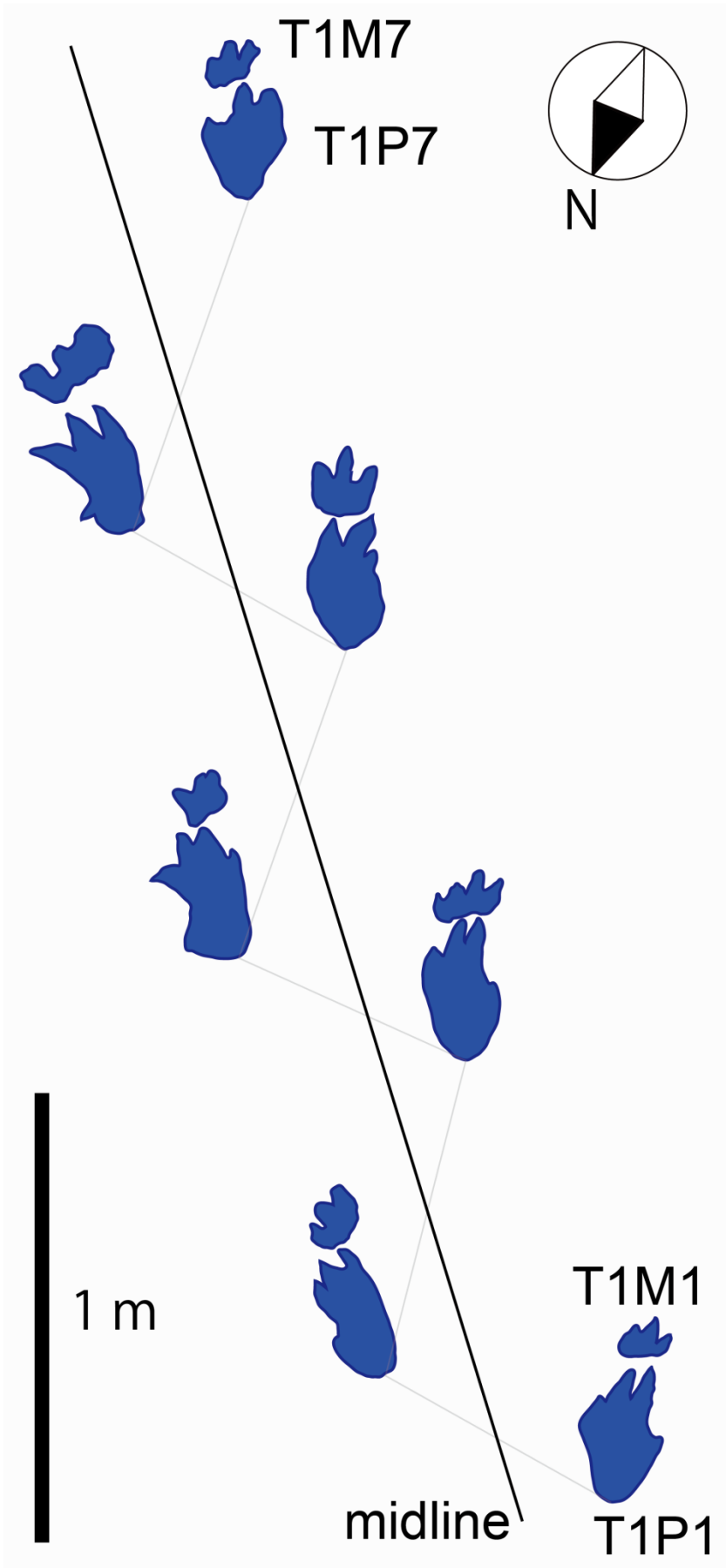


Figure 10 Sketch of the trackway of archosauromorpha phytosaur at the site Nam Nao.

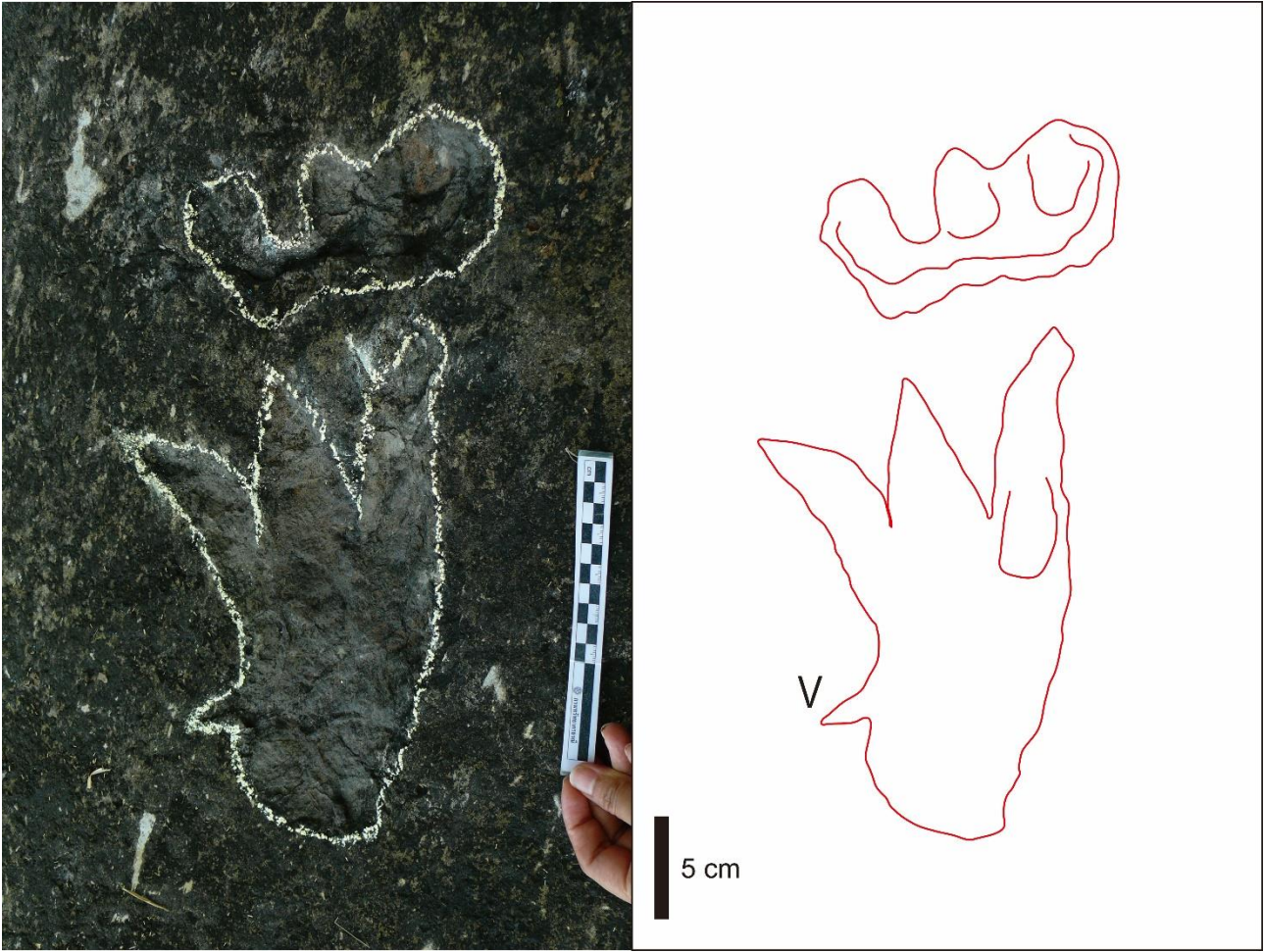


Figure 11 Photograph and sketch of left manus and pes impressions at the site Nam Nao.

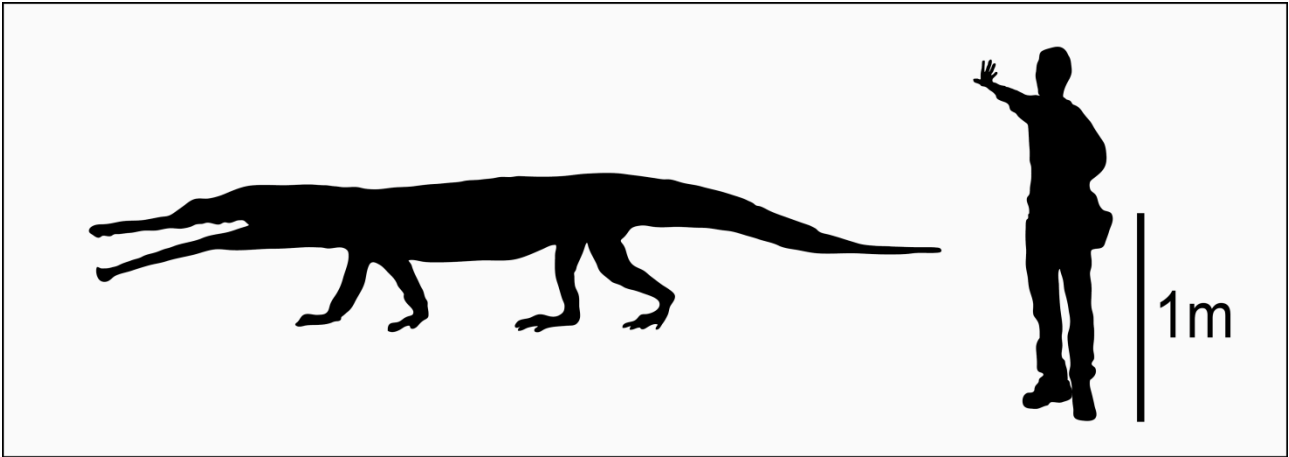


Figure 12 Size comparison of a human and a archosauromorph, possible phytosaur at the site Nam Nao.

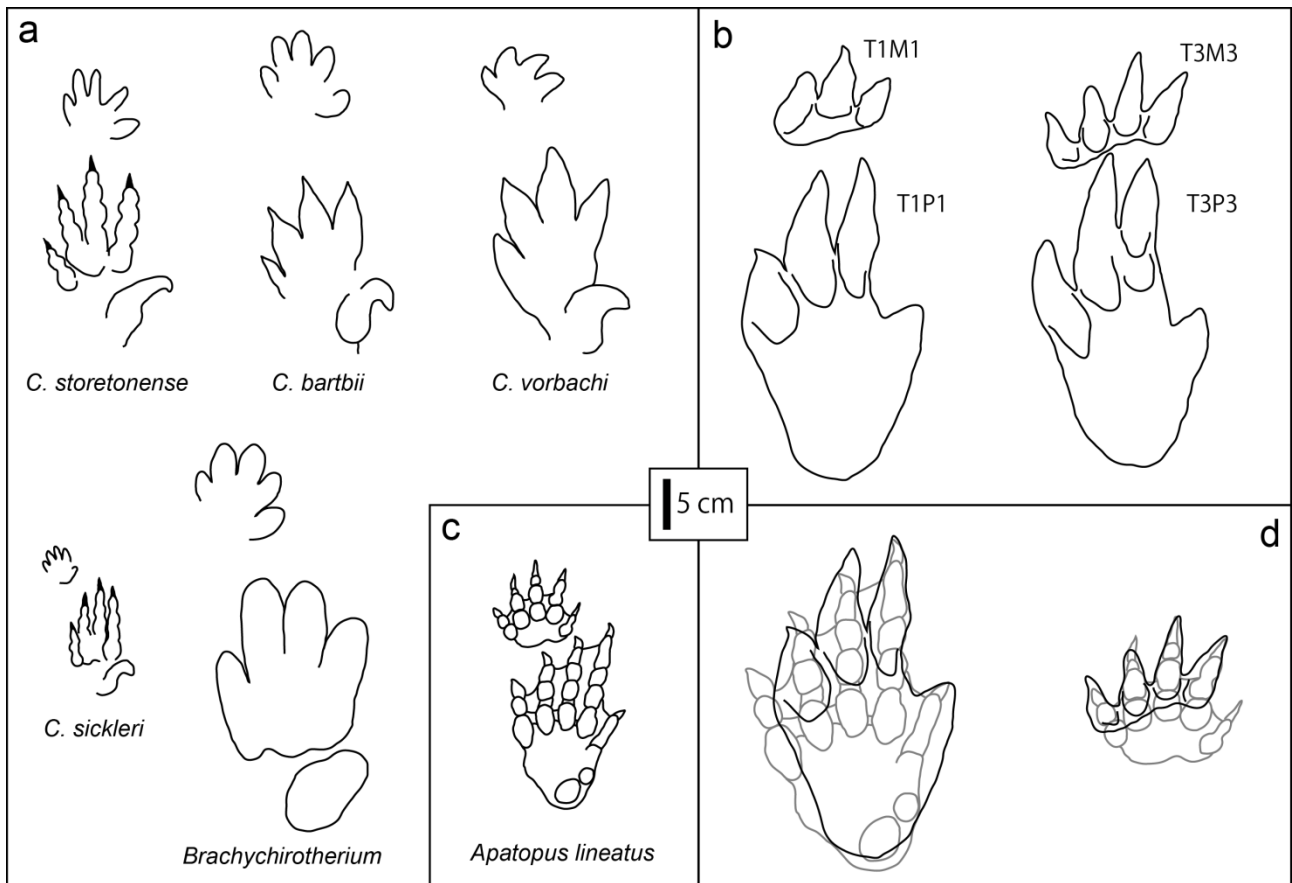


Figure 13 Comparison chart of archosauromorpha tracks.

a: tracks of chirotheriidae (King *et al.*, 2005), b: Nam Nao specimens, c: *Apatopus lineatus* (modified Padian *et al.*, 2010), d: manus and pes impressions of Nam Nao specimen, superimposed over *Apatopus lineatus*.



Figure 14 Photograph of the outcrop at the site Tha Song Khon. Each arrow shows footprints.

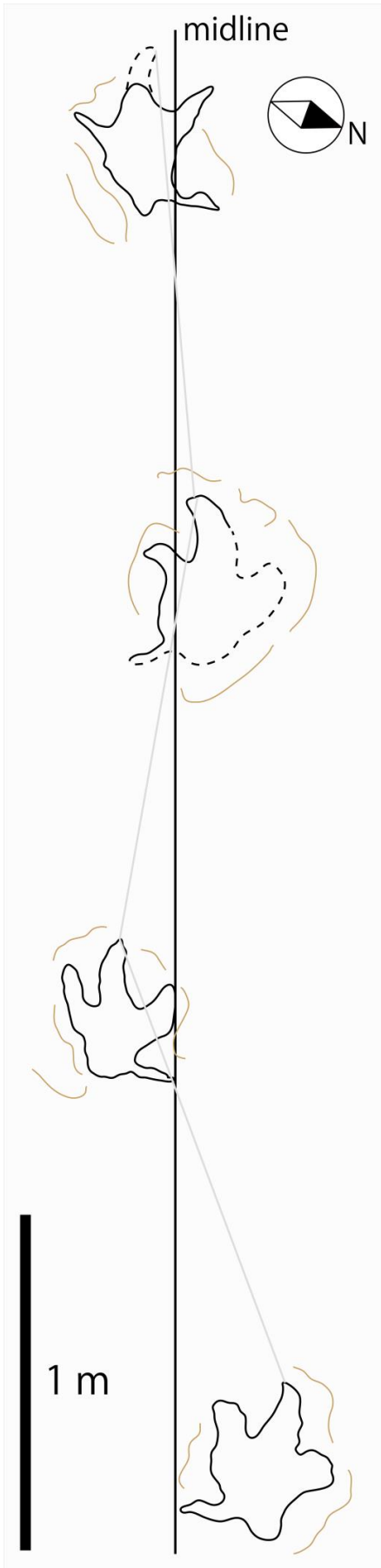


Figure 15. Sketch of the trackway at the site Tha Song Khon.

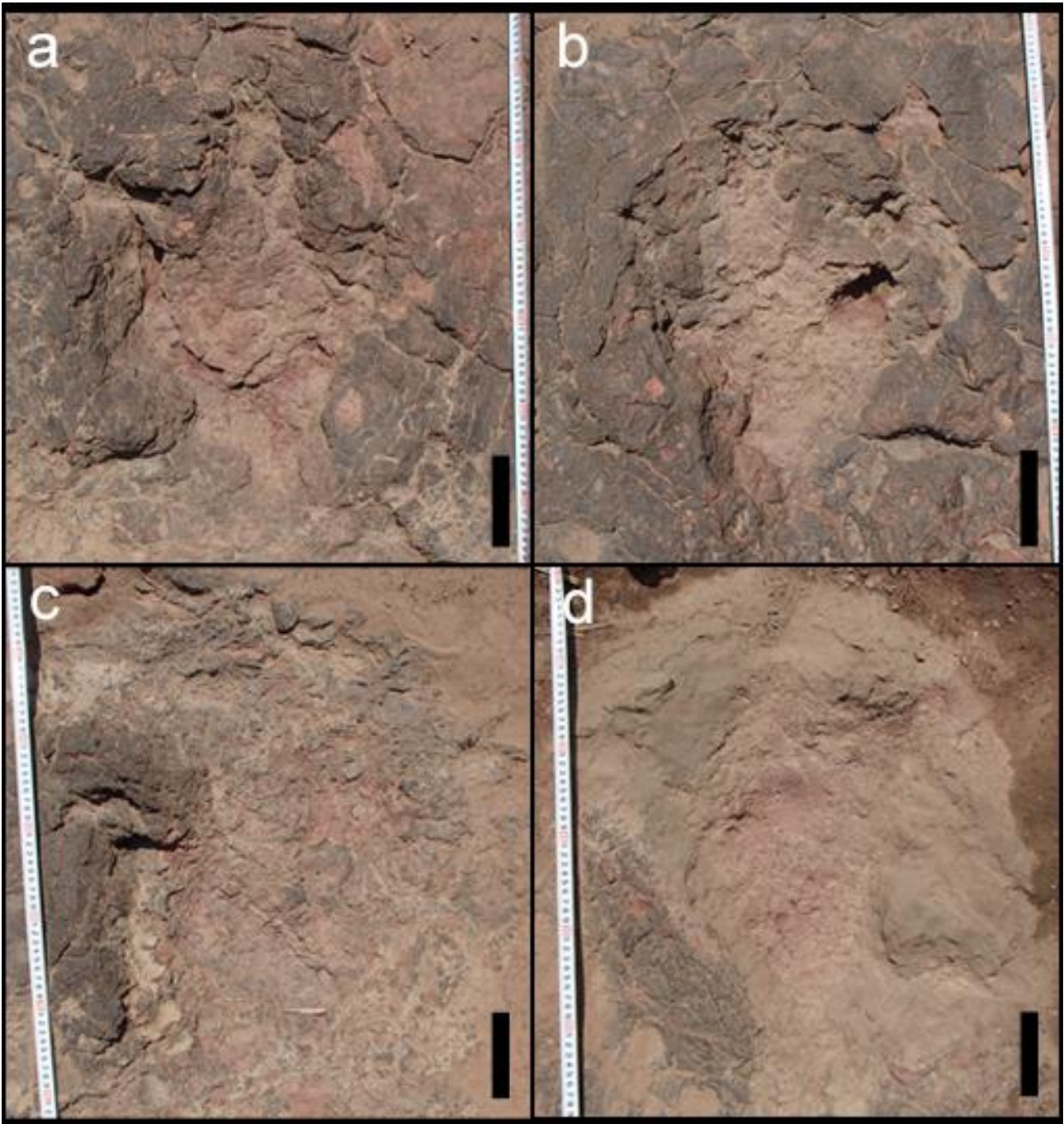


Figure 16 Photographs of footprints at the site Tha Song Khon.

a: T1n1, b: T1n2, c: T1n3, d: T1n4. Scale bars are 10 cm.

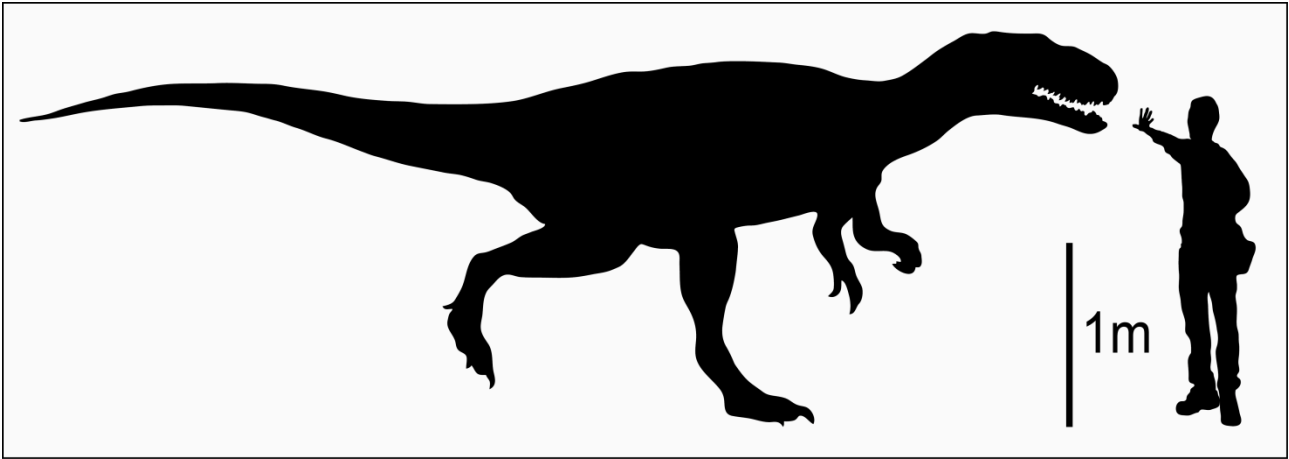


Figure. 17 Size comparison of a human and a theropod at the site Tha Song Khon.

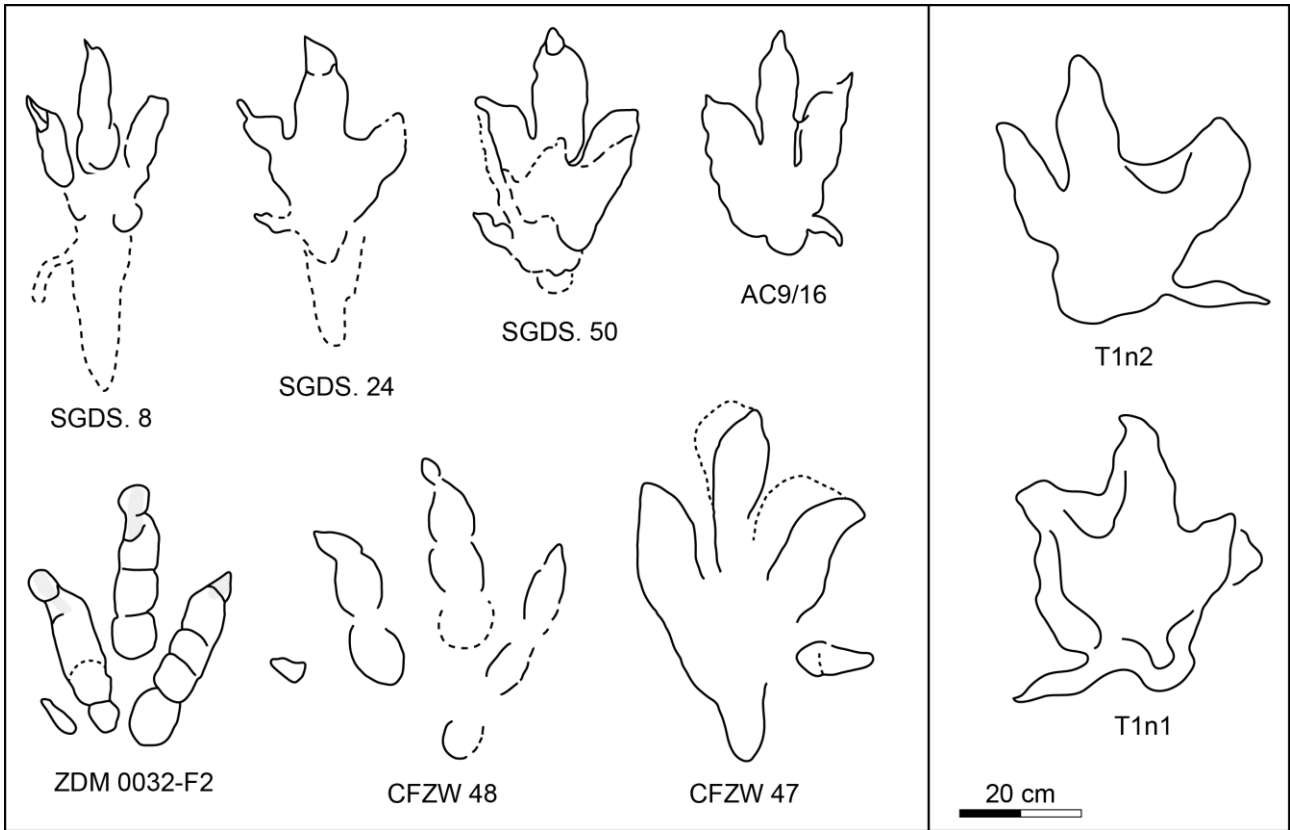


Figure 18 Comparison chart of theropod tracks, *Eubrontes* and *Gigandipus* (modified from Lockley *et al.*, 2003; Lull, 1953; Milner *et al.*, 2006; Xing *et al.*, 2014d).



Figure 19 Locality map and outcrop photograph of the site Non Tum.

Very-fine-grained sandstone crops out for 45 m along the Chi River, and footprints are imprinted on the upper surface of this sandstone.

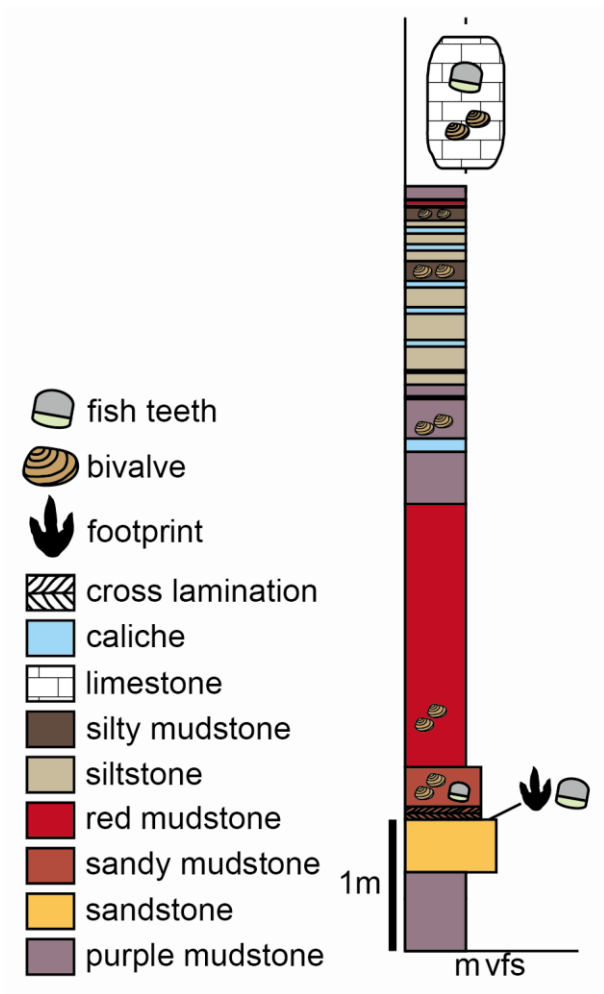


Figure 20 Lithostratigraphic column at the site Non Tum.

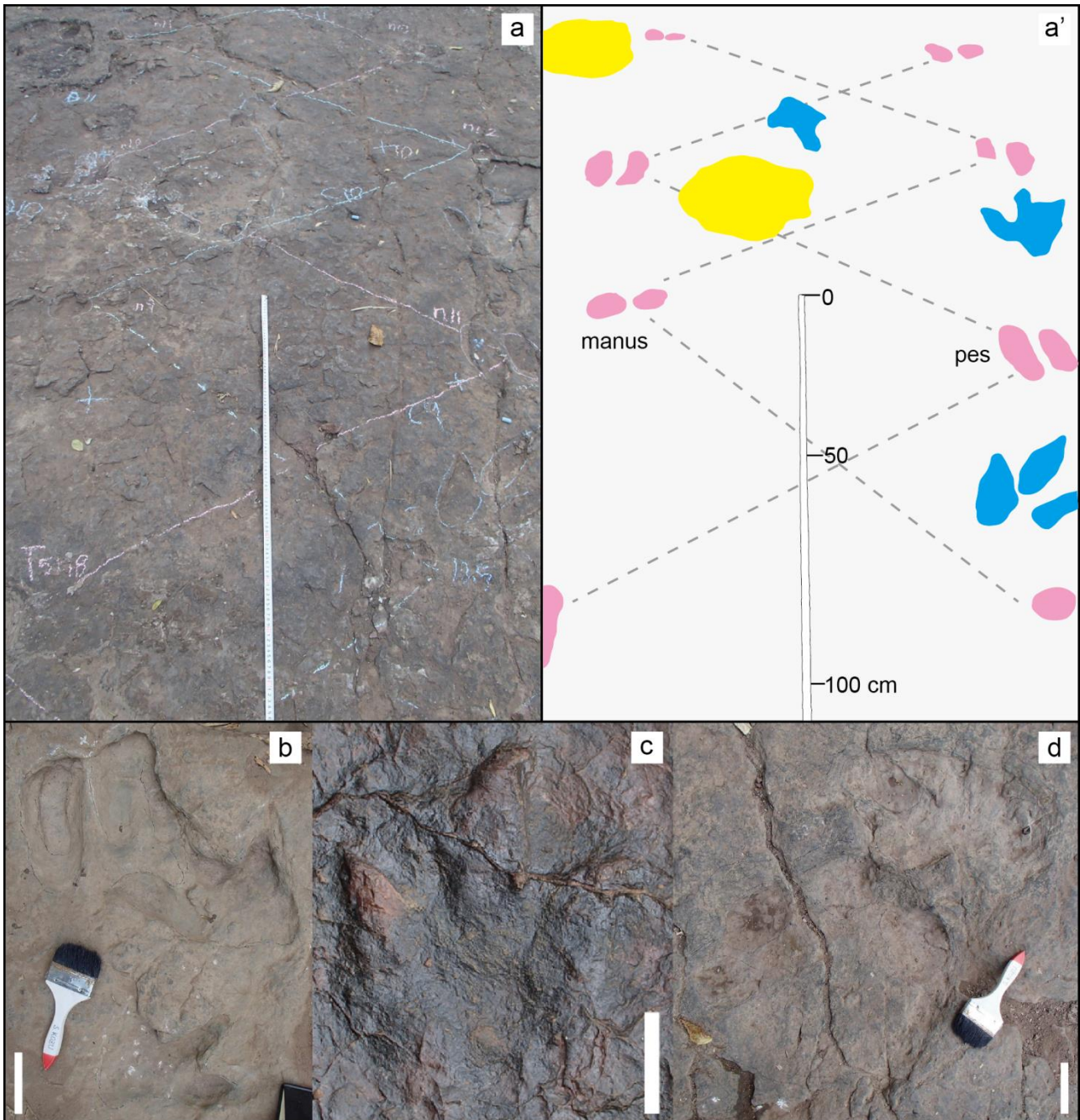


Figure 21 Photographs and sketch of tracks at the site Non Tum.

a: photograph of tracks of northern part of the outcrop, a': sketch of photograph a which showing pink-colored didactyl tracks, blue-colored theropod tracks and yellow-colored sauropod tracks, b: photograph of didactyl track with some theropod tracks on the same bedding plane at southern part of the outcrop, c: photograph of theropod track similar to *Eubrontes*, d: photograph of sauropod right pes and manus tracks. Scale bars are 10 cm.

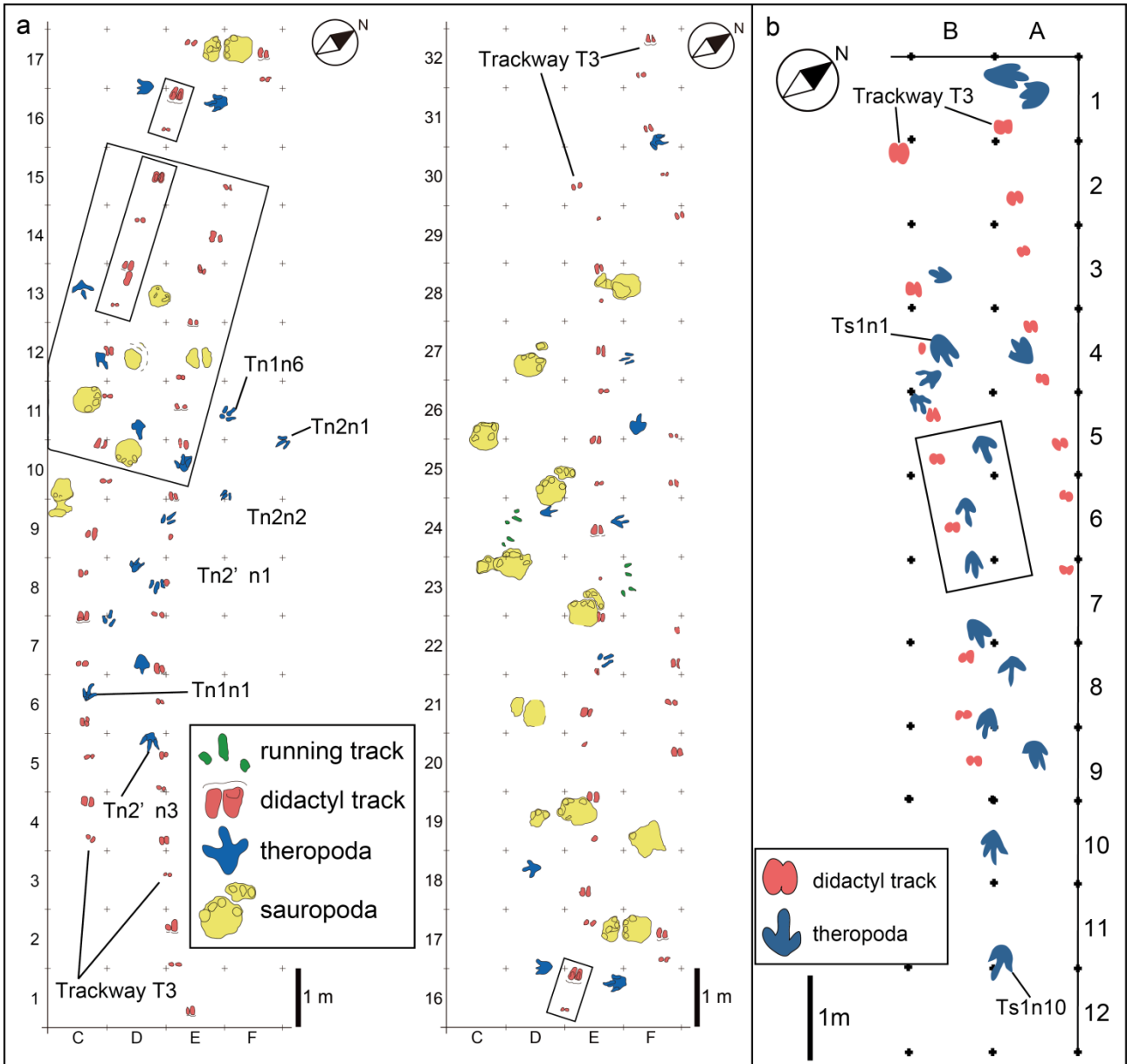


Figure 22 Mesh maps at the Non Tum site.

a: mesh map of northern part of the outcrop, b: mesh map of southern part of the outcrop. Squares indicate partial replicas of tracks stored in the Department of Mineral Resources of Thailand and the Graduate School of Life and Environmental Sciences, University of Tsukuba.

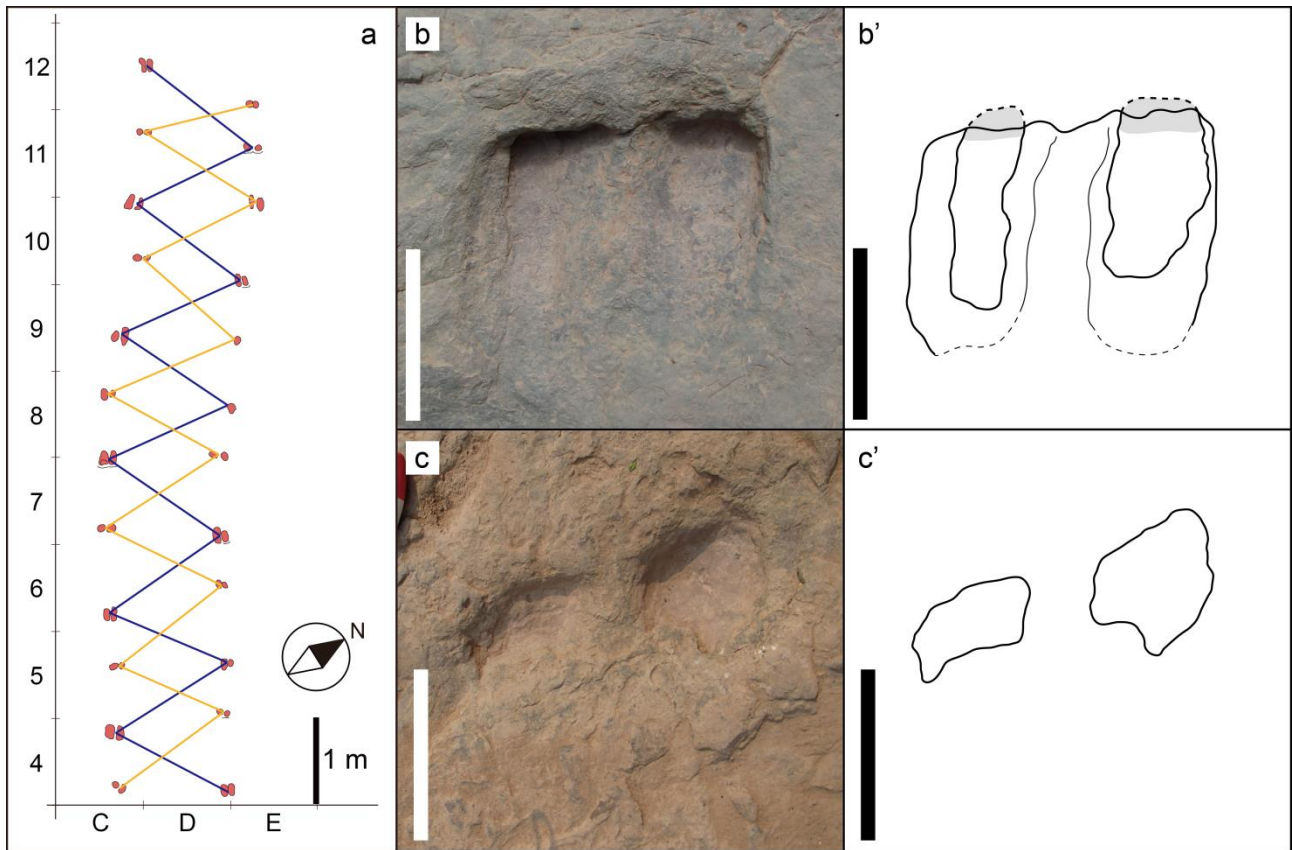


Figure 23 The trackway and photographs of didactyl tracks.

a: Partial sketch of the trackway consists of consecutive pes impressions (blue-lined) and manus impressions (orange-lined), b: photograph of left pes impression, b': sketch of left pes impression, c: photograph of left manus impression, c': sketch of left manus impression. Scale bars are 10 cm. Gray parts mean the deepest point.

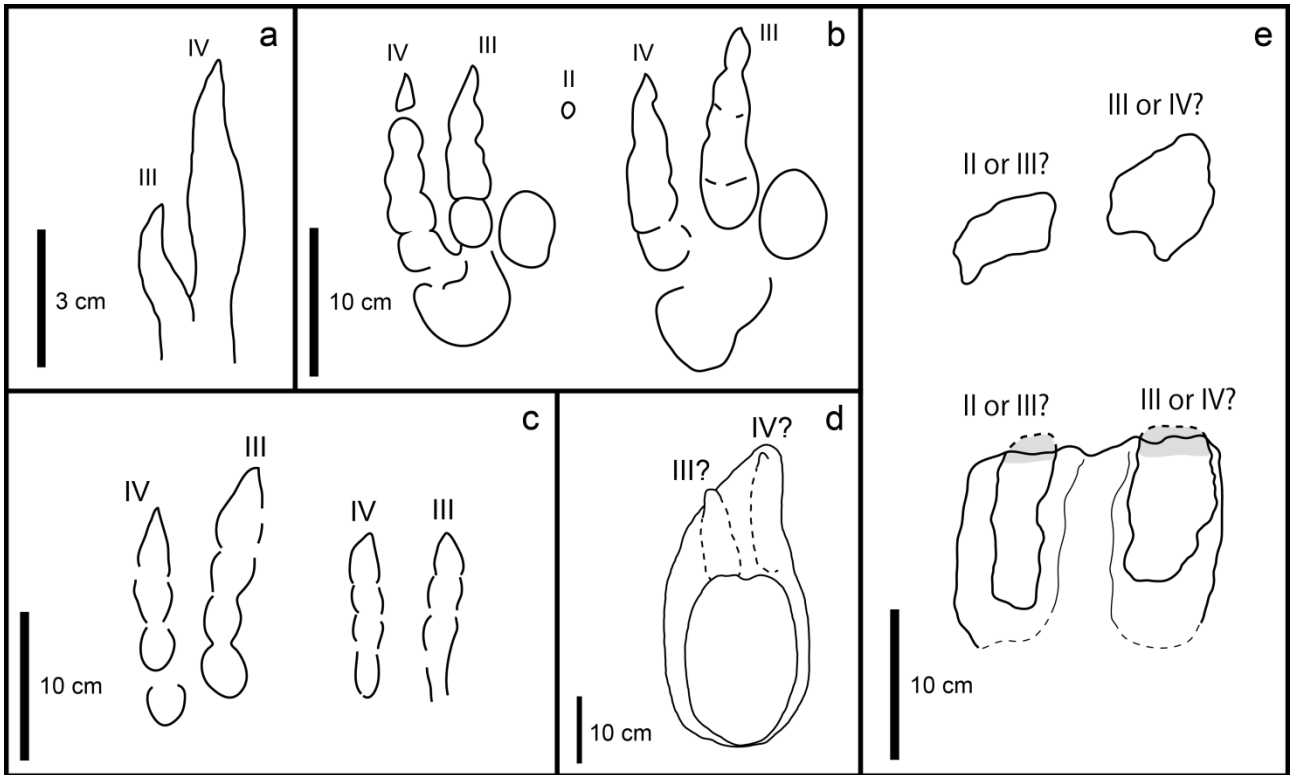


Figure 24 Comparison chart of didactyl tracks.

a: right pes track of *Moodieichnus didactylus* (Moodie, 1930), b: left pes tracks of *Evazoum gatewayensis* (Lockley and Lucas, 2013), c: **left**, left pes track of *Dromaeosauripus hamanensis* (Kim *et al.*, 2008), **right**, left pes track of *Dromaeosauripus jinjuensis* (Kim *et al.*, 2012), d: right pes track of large-sized archosaur (Xing *et al.*, 2014c), e: didactyl left pes and manus tracks in this study. Gray parts mean the deepest point.

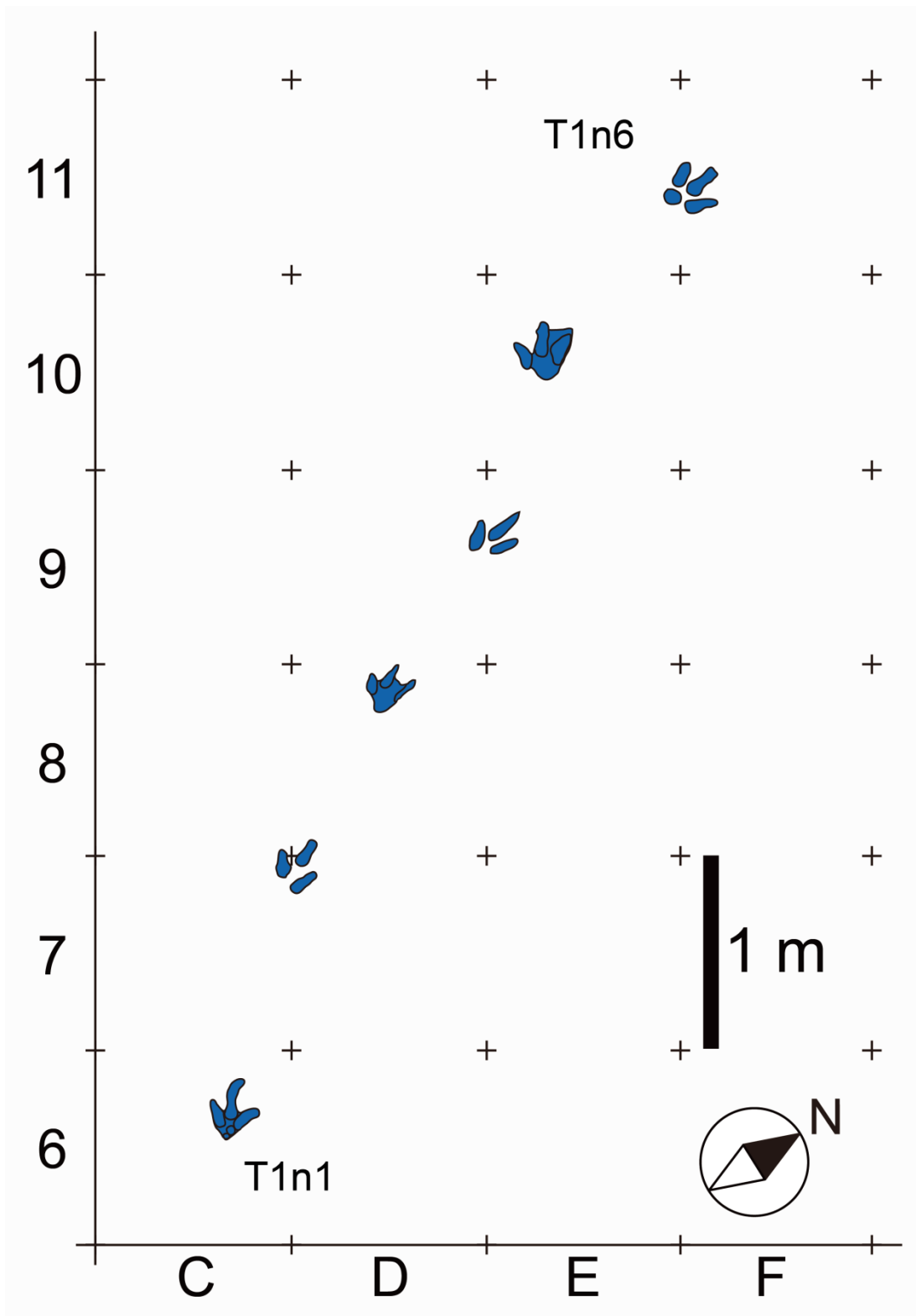


Figure 25 Meshmap of the Trackway T1 in the northern part of the outcrop at the site Non Tum.

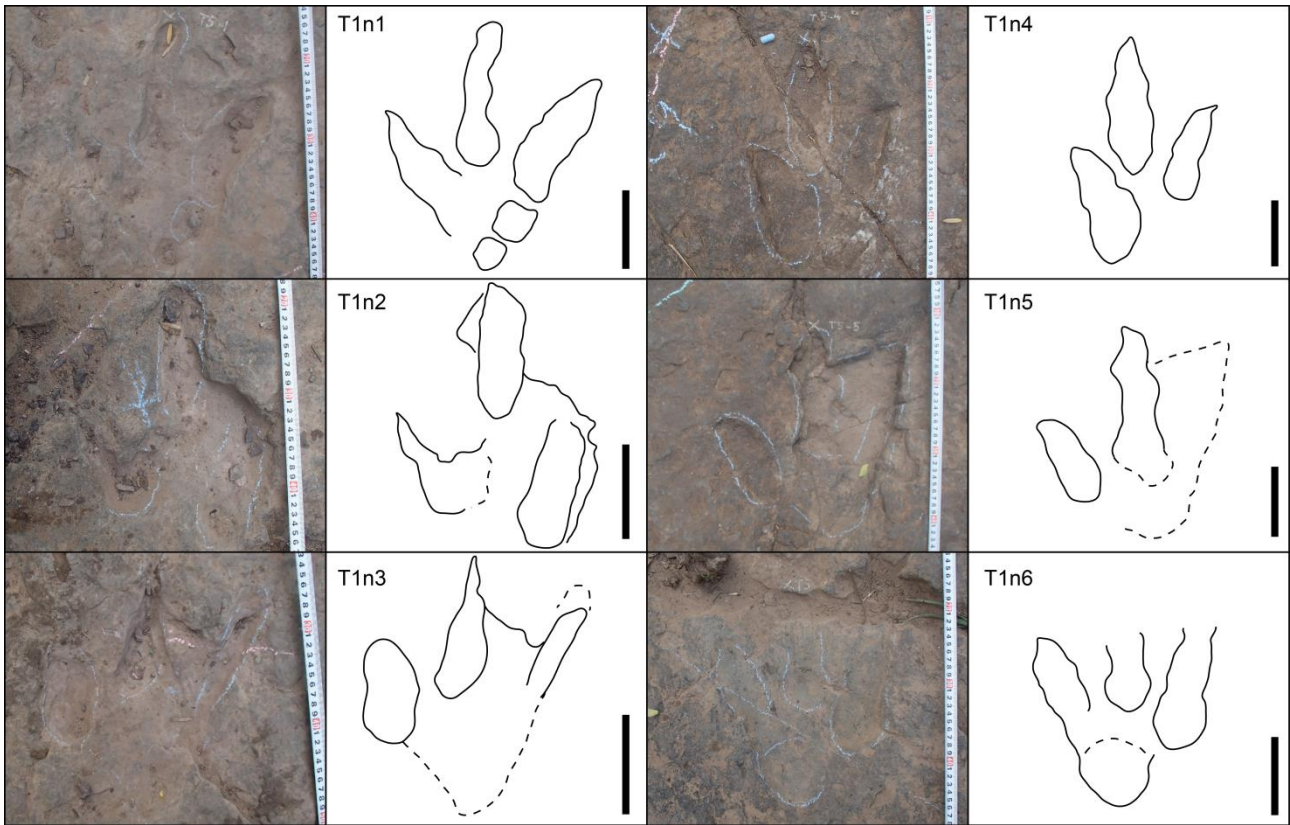


Figure 26 Photographs and sketches of theropod tracks T1 which consist of T1n1 to T1n6.

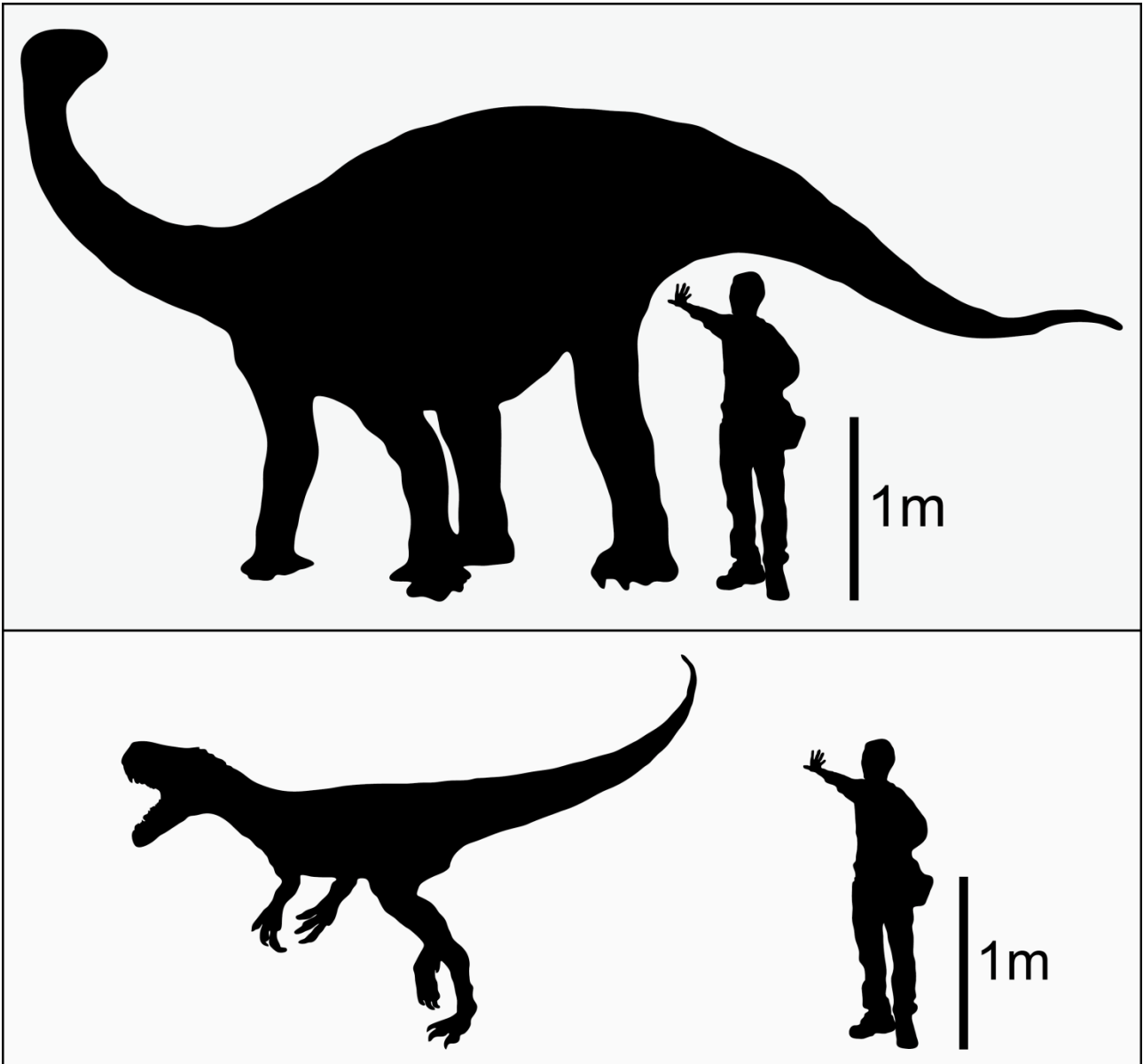


Figure 27 Size comparison of a human, a theropod, and a sauropod at the site Non Tum.



Figure 28 Photograph of possible sauropod pes and manus impressions. Scale bar is 10 cm.

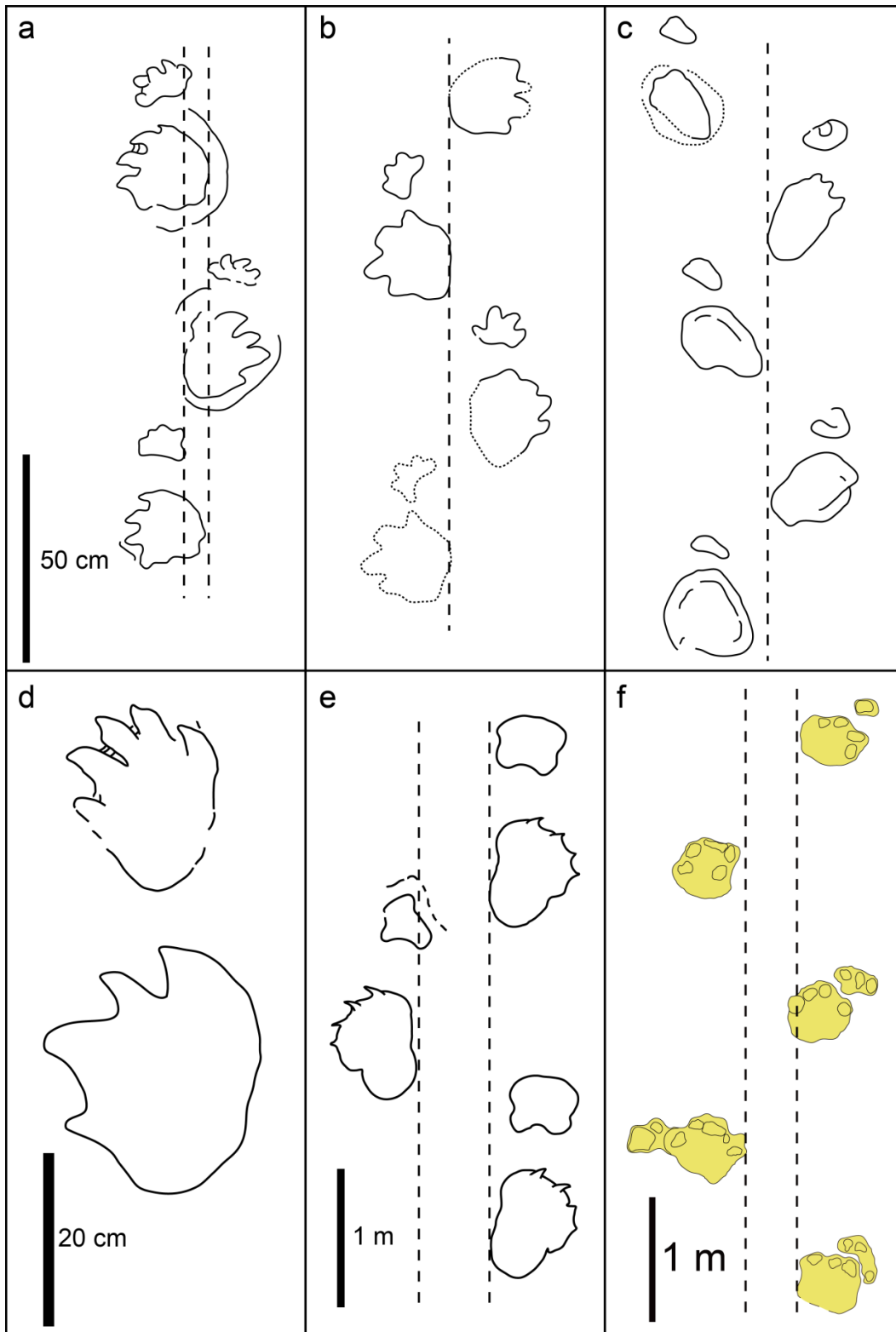


Figure 29 Comparison chart of the trackway, *Eosauropus*, *Brontopodus* and Non Tum specimen T4. a: sketch of the trackway *Eosauropus cimarronensis* (after Lockley *et al.*, 2006b), b: sketch of the trackway *E. cimarronensis* (after Lockley and Hunt, 1995), c: sketch of the trackway *E. cimarronensis* (after Lockley *et al.*, 2001), d: sketch of the tracks *E. cimarronensis* (after Lockley *et al.*, 2006b), e: sketch of the trackway *Brontopodus birdi* (after Farlow *et al.*, 1989; Lockley and Hunt, 1995), f: sketch of the trackway T4 in this study.



Figure 30 Photograph of the outcrop at the site Phu Kao.

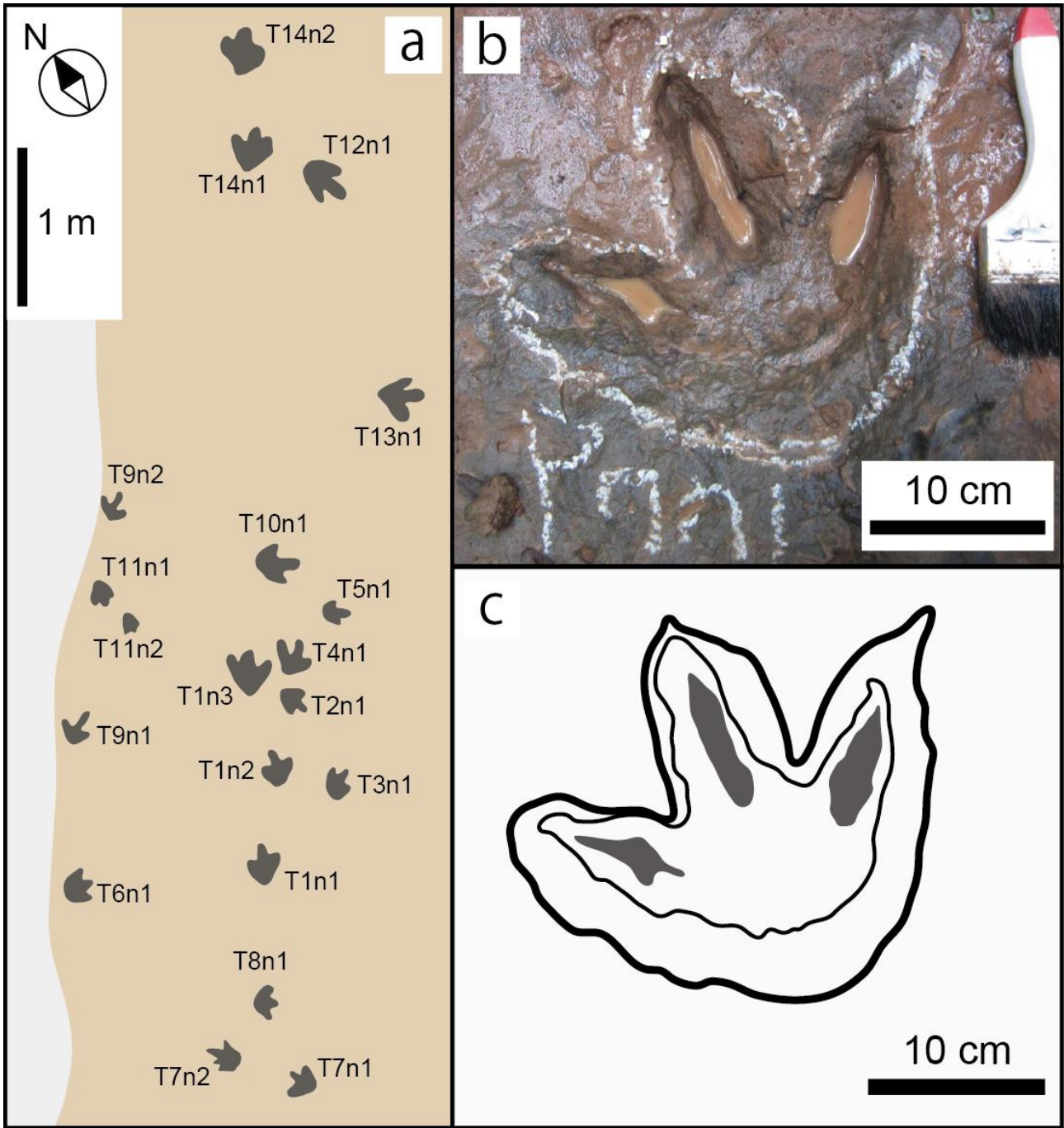


Figure 31 Sketch of the outcrop and a photograph and a sketch of the track T7n1.



Figure 33 Sedimentary structures in the sandstone, including parallel and trough cross-laminations (in the upper part of the study section).



Figure 34 Photograph of the outcrop at the site Phu Faek. Red arrow shows T1n1, and blue arrow shows T3n4.

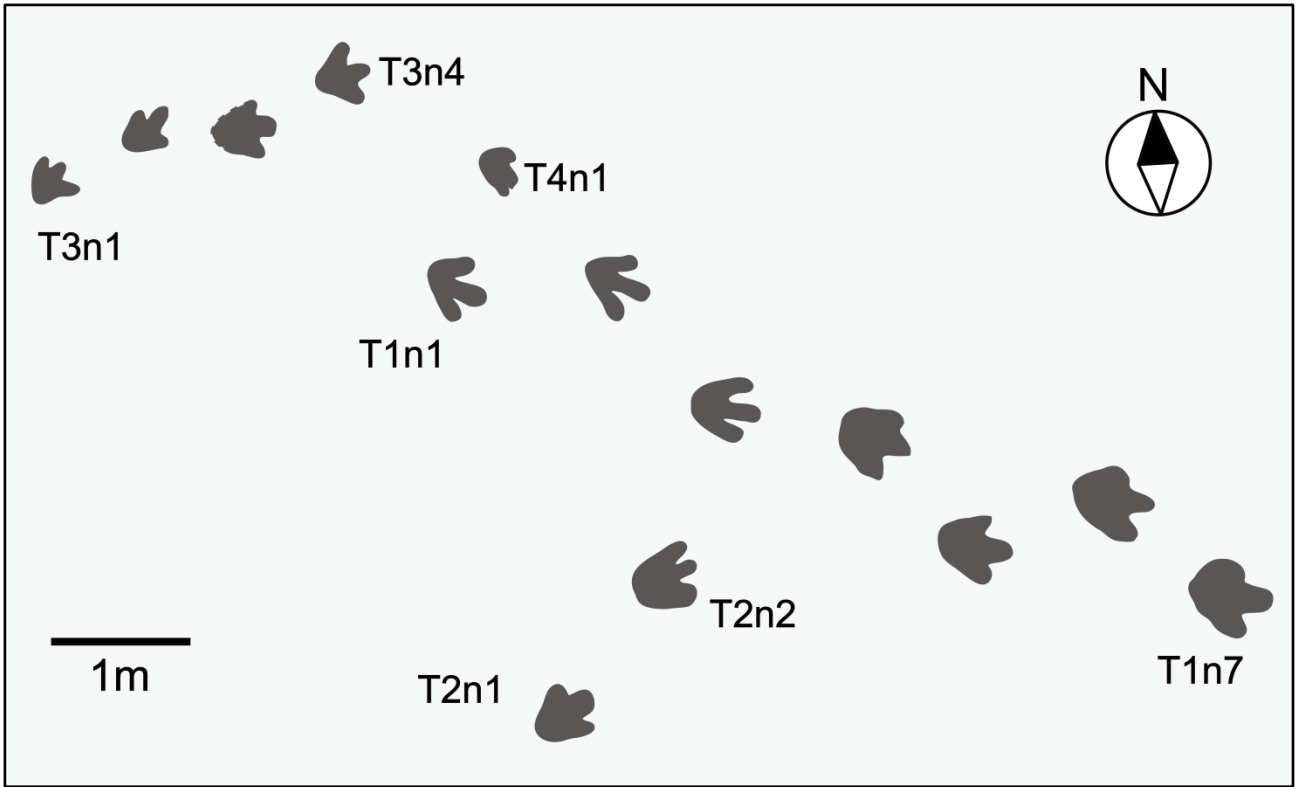


Figure 35 Sketch of the tracks T1 to T4 at the site Phu Faek.

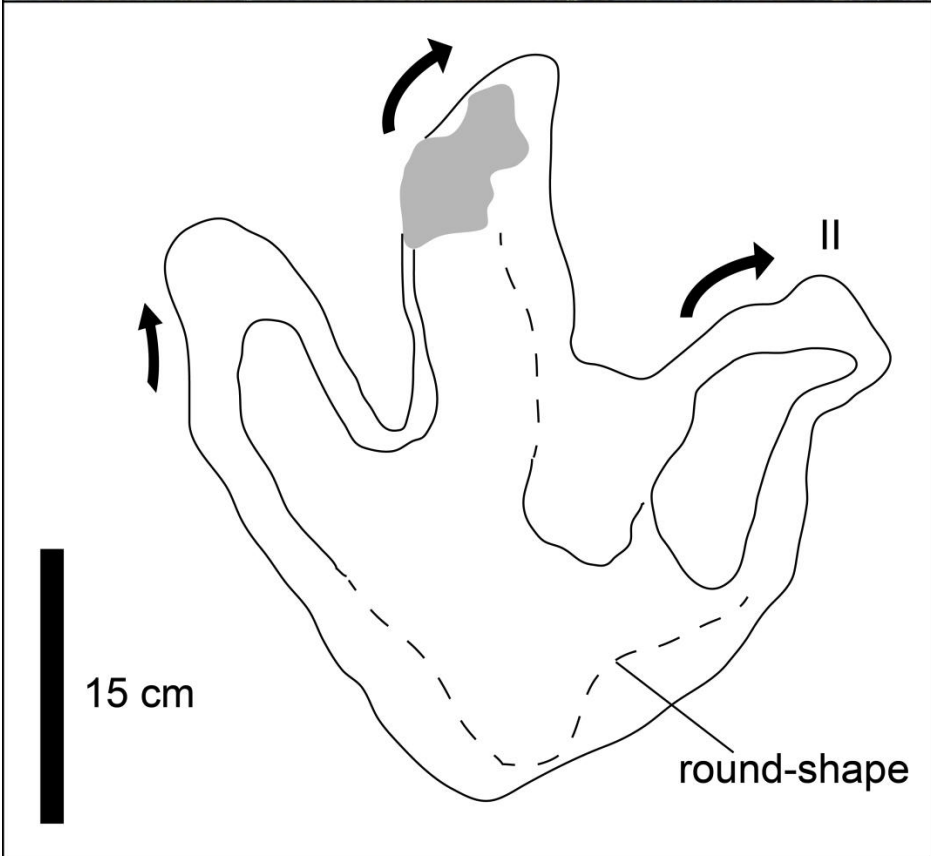


Figure 36 Photograph and sketch of the track T2n2.

Black arrows show the orientation of each digit impression which is typical characteristics of theropod track.

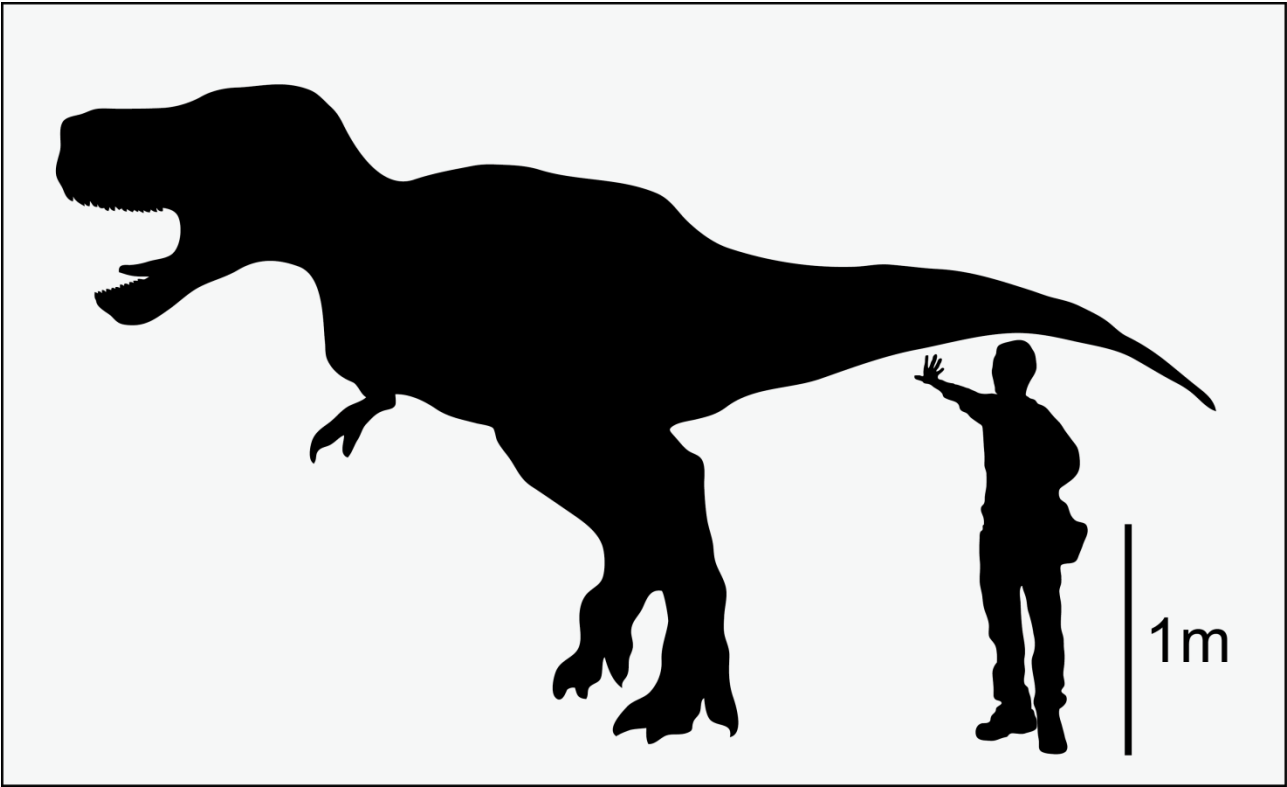


Figure 37 Size comparison of a human and a theropod at the site Phu Faek.



Figure 38 Photograph of the trace fossils *Thalassinoides* sp. which imprinted on the same upper surface with dinosaur tracks.

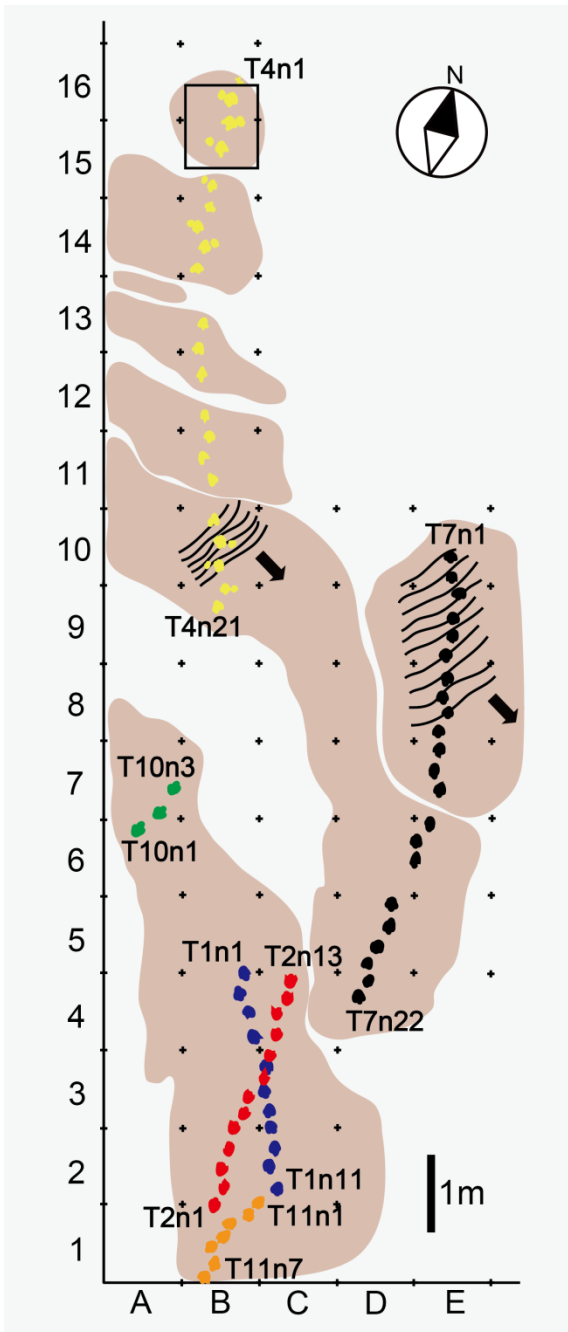


Figure 39 Meshmap of the outcrop at the site Hin Lat Pa Chad.

Arrows indicate paleocurrent directions estimated by ripple-marks. Square equals Fig. 39.

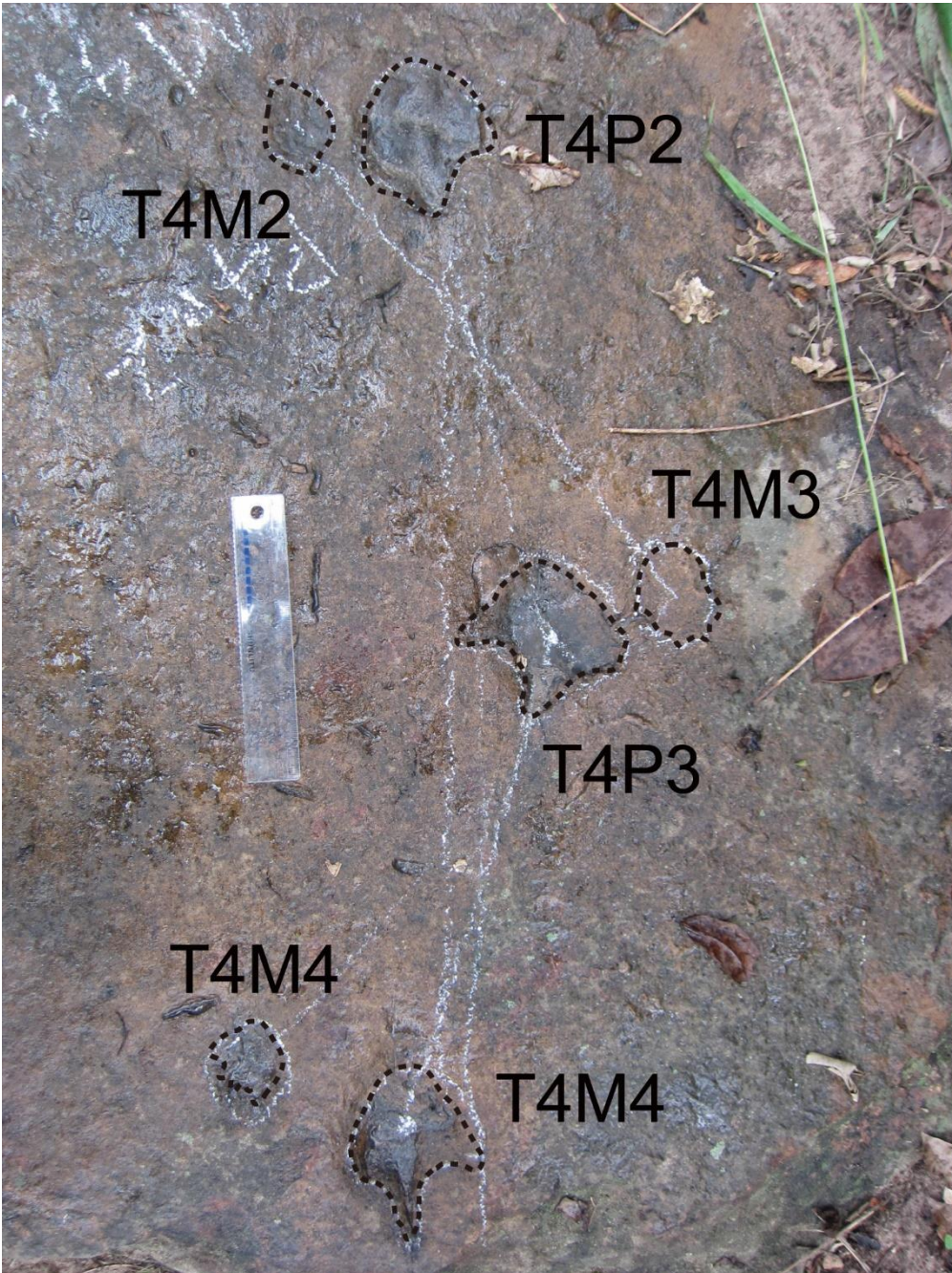


Figure 40 Photograph of the trackway T4 *Neoanomoepus* isp., showing detail of the region outlined by the square in Fig. 37.

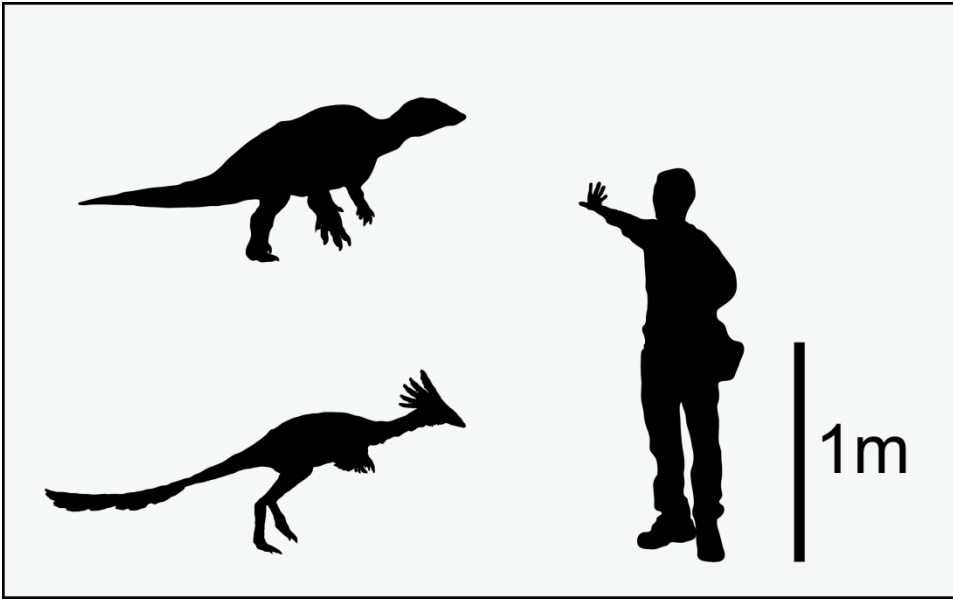


Figure. 41 Size comparison of a human, a small-sized ornithopod, and a small-sized theropod at the site Hin Lat Pa Chad.



Figure 42 Photographs of the outcrop and the trackways T1 and T2. Arrows show each directions of the trackways T1 and T2.



Figure 43 Photograph of the trackway T10 *Carmelopodus* isp. at the site Hin Lat Pa Chad.



Figure 44 Photographs of the well preserved tracks T10n2 and T10n3 at the site Hin Lat Pa Chad. Scales are 5 cm.

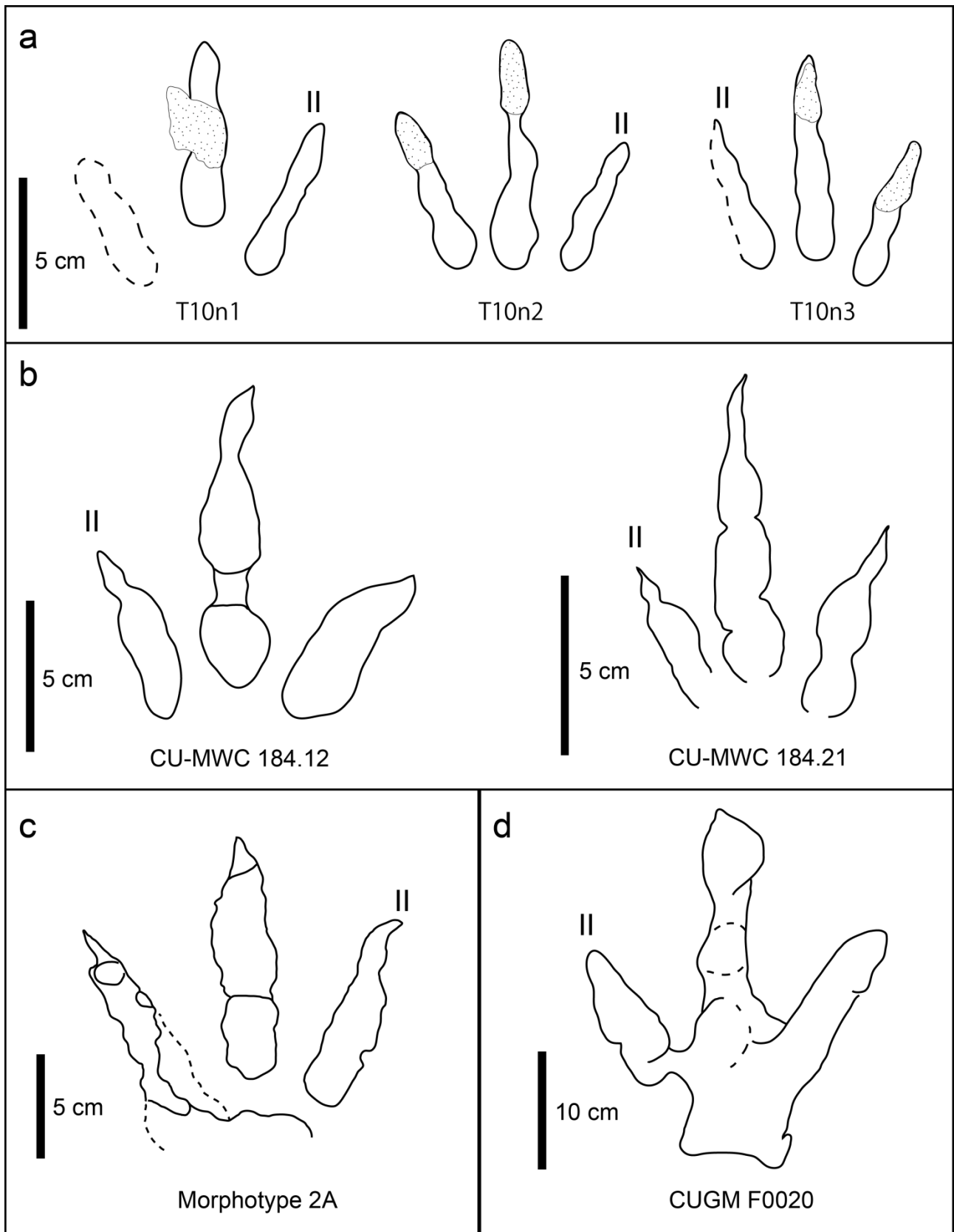


Figure 45 Comparison chart of the small sized theropod tracks.

a: Hin Lat Pa Chad speimens T10n1 to T10 n3, b: *Carmelopodus untermannorum* (after Lockley *et al.*, 1998), c: *Carmelopodus* sp. (after Belvedere *et al.*, 2010), d: *Siamopodus khaoyaiensis* (after Lockley *et al.*, 2006d).



Figure 46 Photograph of the outcrop at the site Phu Luang.

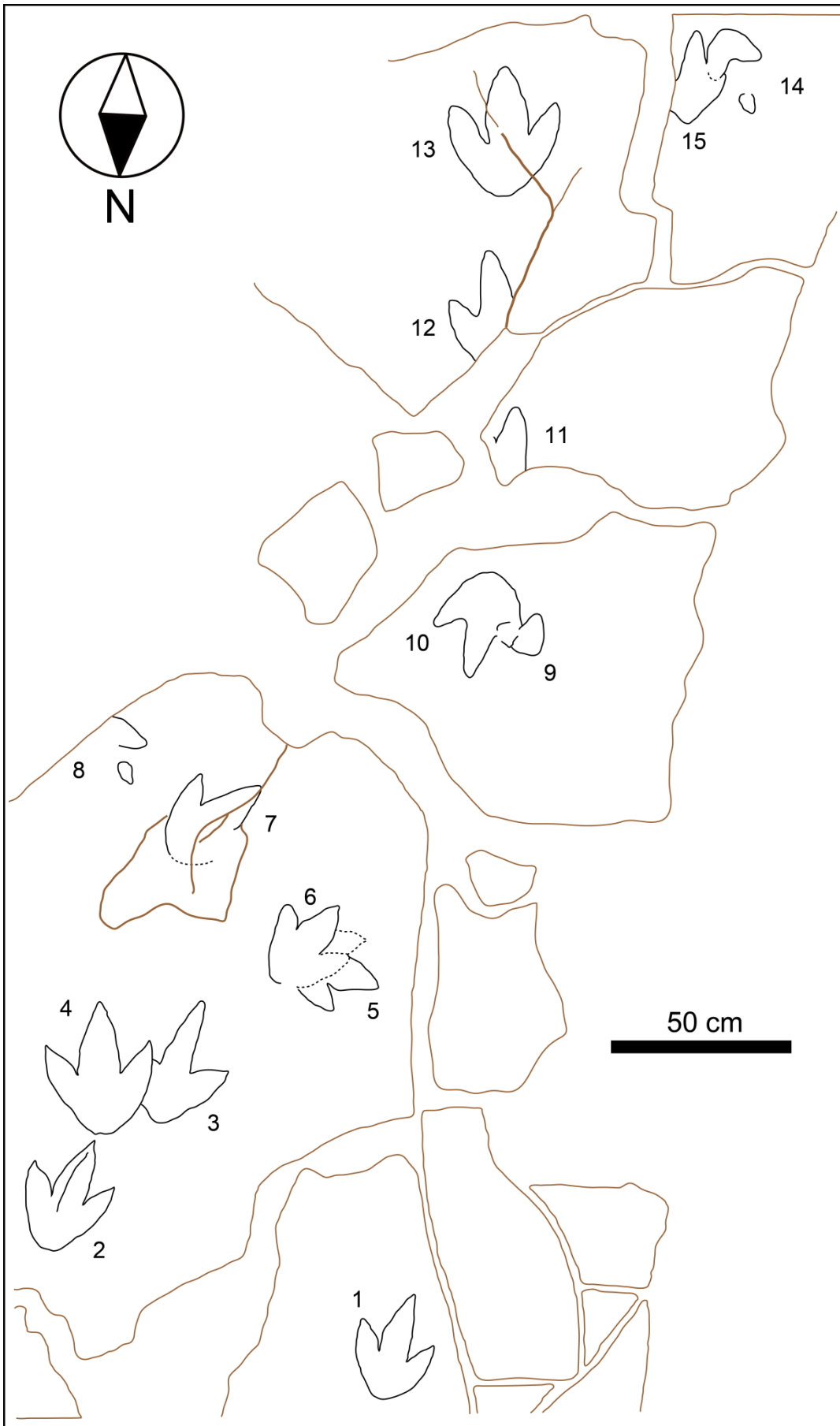


Figure 47 Sketch of the tracks at the site Phu Luang (after Buffetaut *et al.*, 1985b).

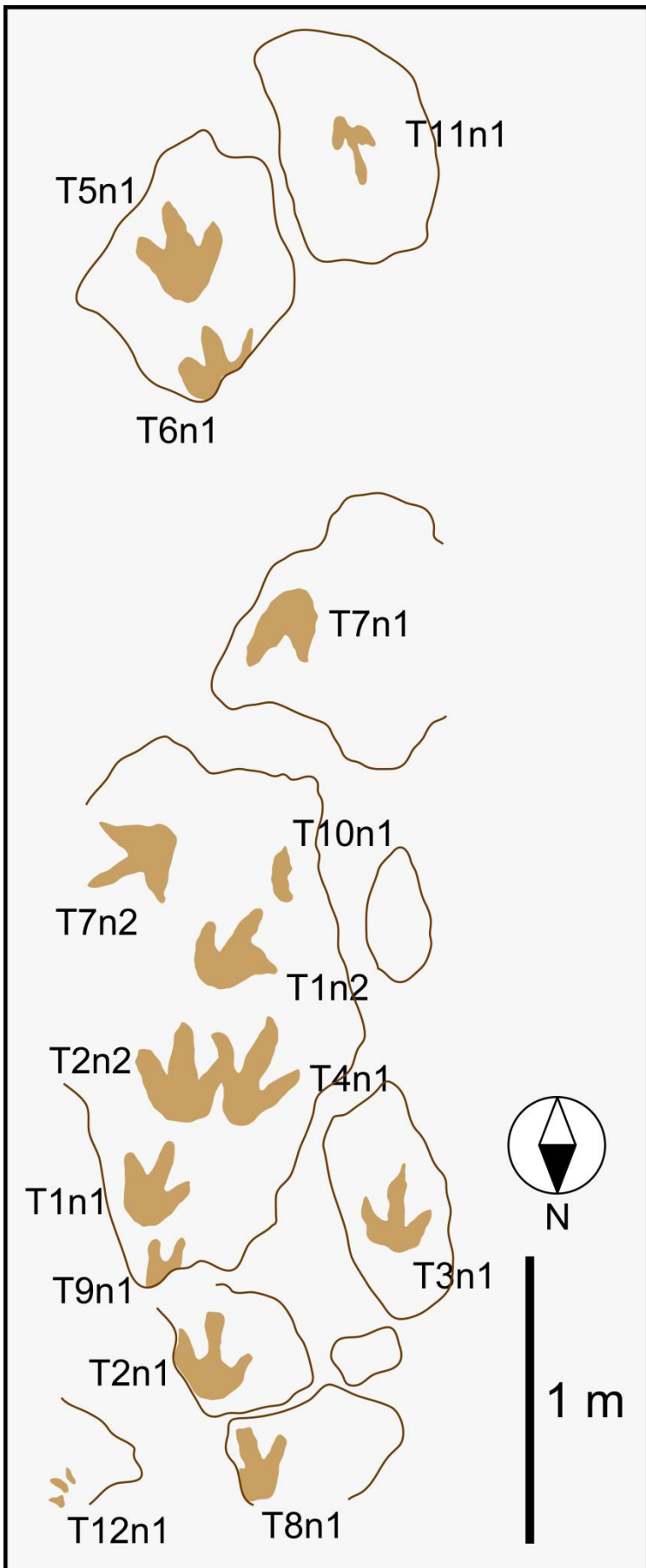


Figure 48 Sketch of the tracks *Irenesauripus* isp. at the site Phu Luang.



Figure 49 Photographs of the tracks T1n1 (upper) and T2n2 (lower).

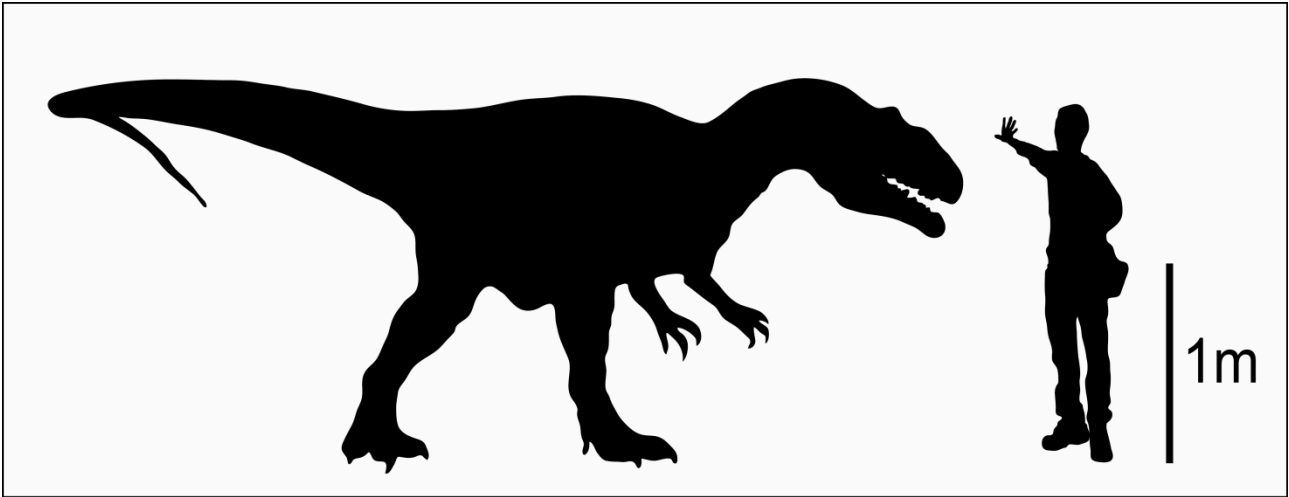


Figure 50 Size comparison of a human and a theropod at the site Phu Luang.

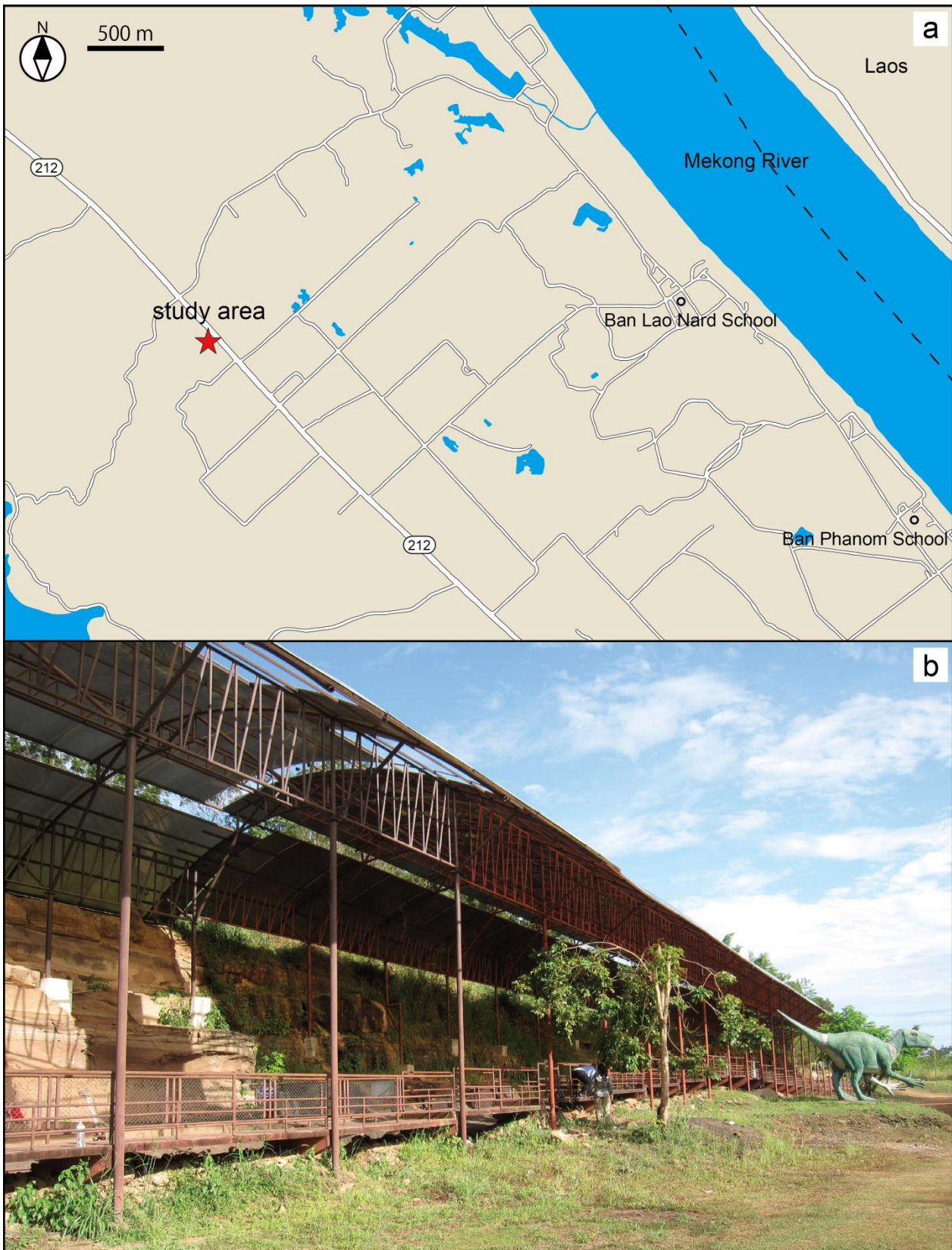


Figure 51 Locality map (a), and a photograph of the outcrop at the site Huai Dam Chum (b) (after Kozu *et al.* in press). The outcrop is cropping out along the route 212, and footprint-bearing outcrops were covered by artificial roof and easily to access to observe footprints at the site.

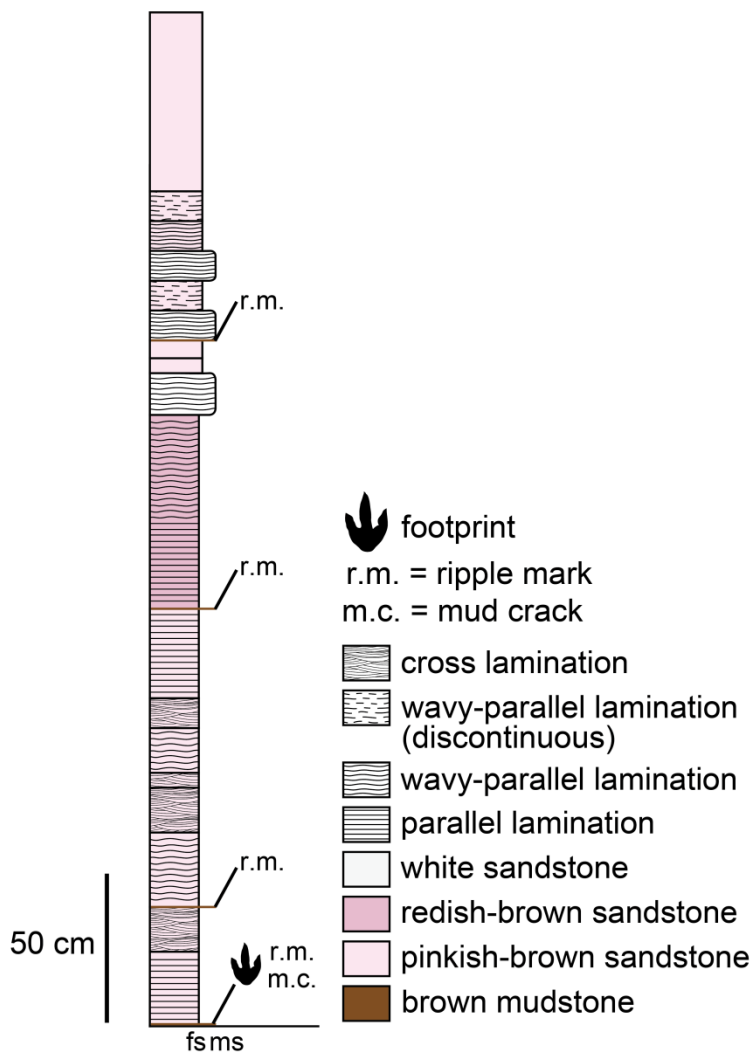


Figure 52 Lithostratigraphic clumn of northern part the outcrop at the site Huai Dam Chum.

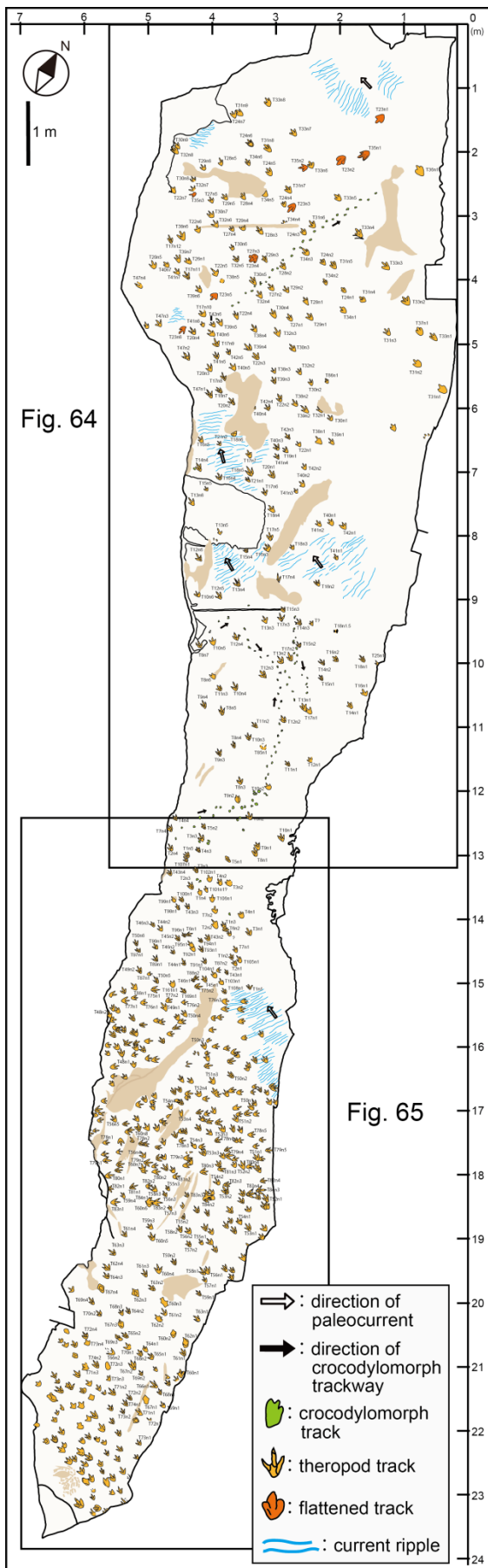


Figure 53 Mesh map of the north part of the outcrop of north part of the site Huai Dam Chum.

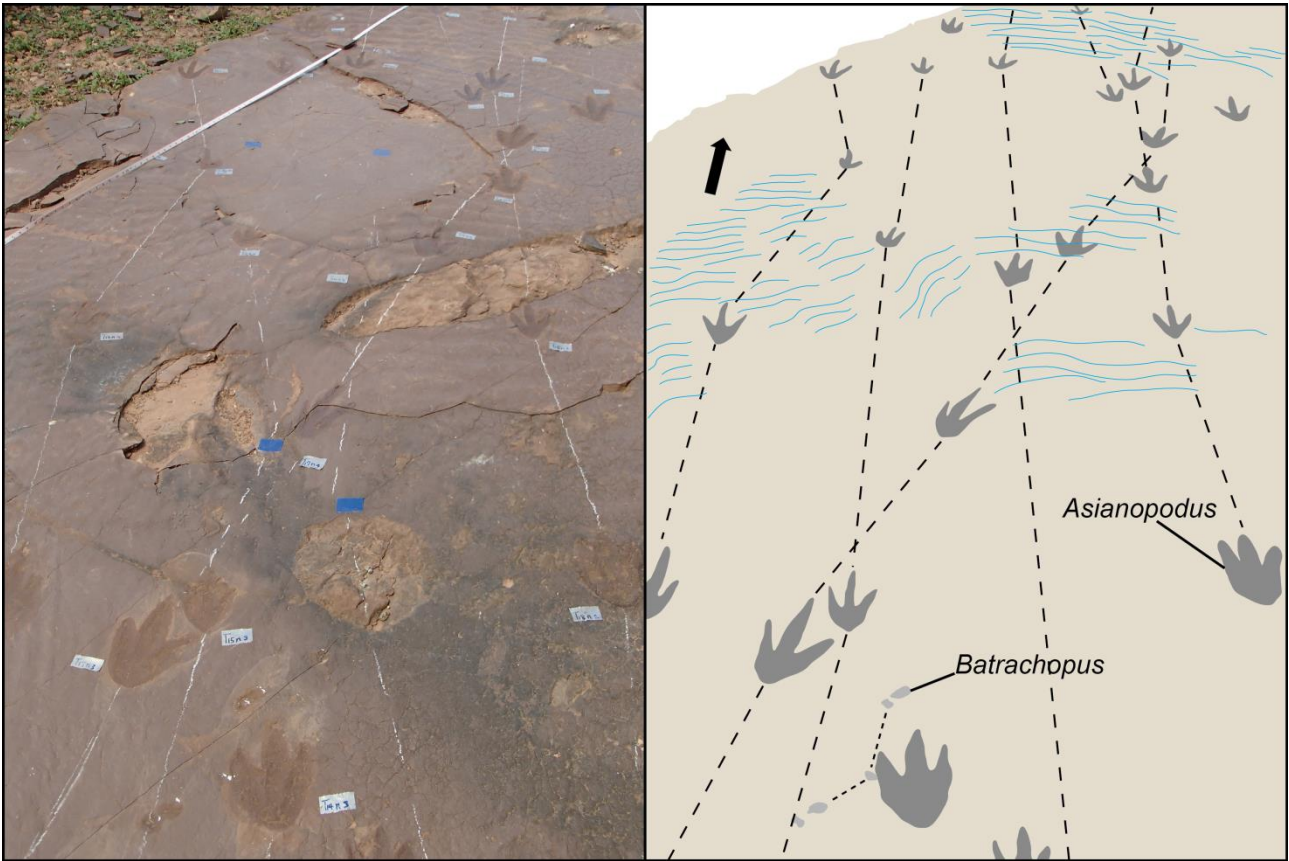


Figure 54 Photograph and sketch of tracks of the site Huai Dam Chum.

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.

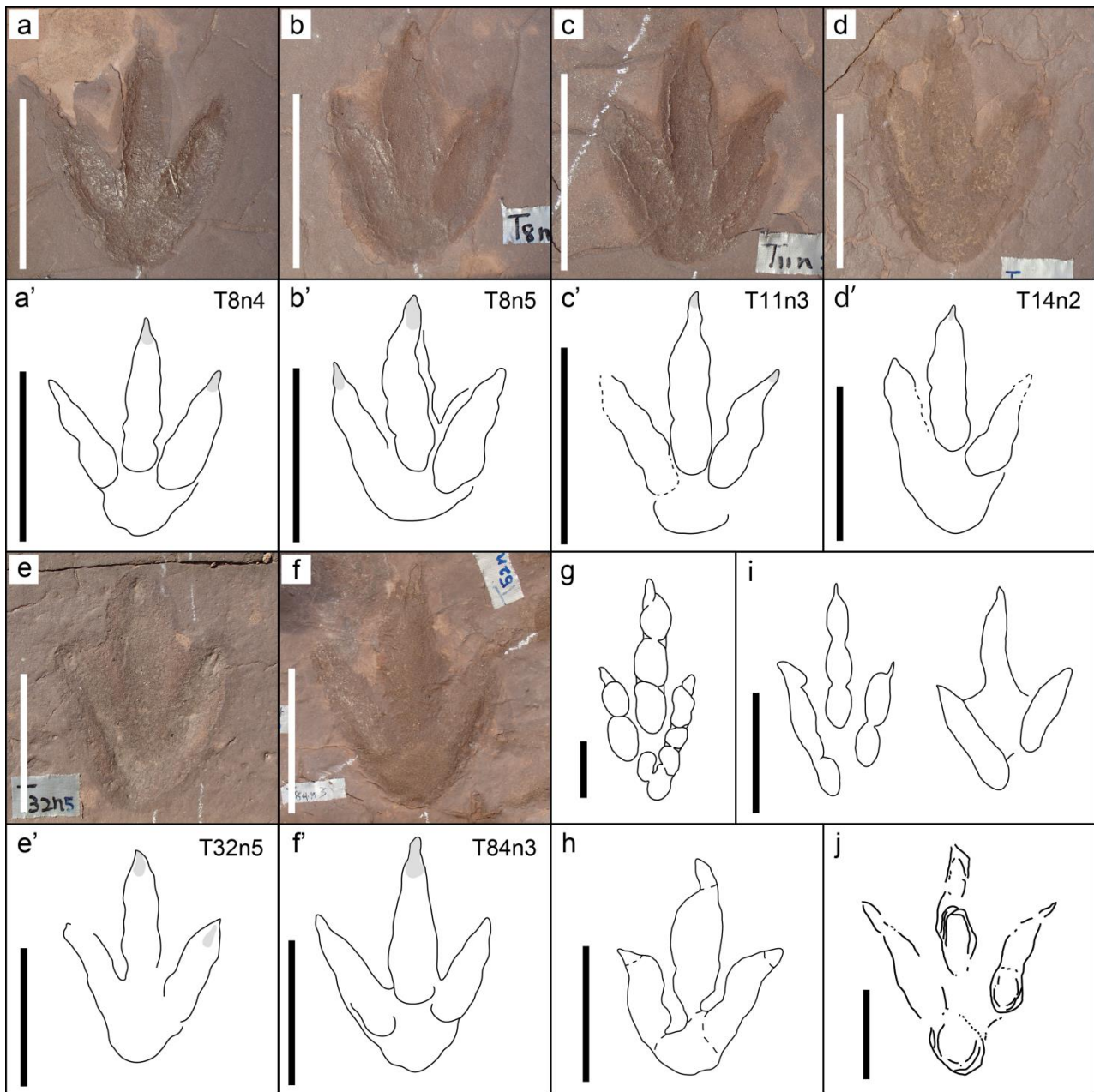


Figure 55 Comparison chart of theropod tracks *Asianopodus* at the site Huai Dam Chum (after Koizu *et al.*, in press).

a~g: photographs of pes tracks of Tha Uthen specimens T8n4, 5, T11n3, T14n2, 4, T32n5, and T84n3, a'~g': sketches of pes track of Tha Uthen specimens T8n4, 5, T11n3, T14n2, 4, T32n5, and T84n3, h: sketch of *Asianopodus pulvinicalx* (modified from Matsukawa *et al.*, 2005), i: sketch of genoholotypic track of *Grallator parallelus* (modified from Olsen *et al.*, 1998). Scale bars of a to g, a' to g', and h are 10 cm. Scale bar of i is 2 cm.

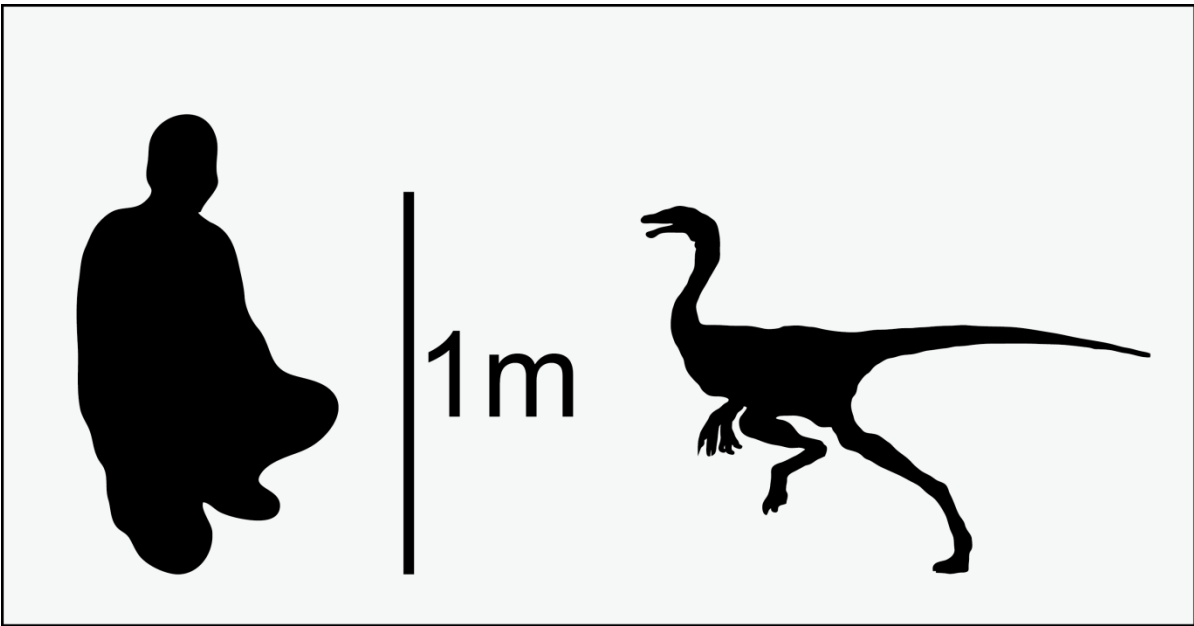


Figure 56 Size comparison of a human and a theropod at the site Huai Dam Chum.

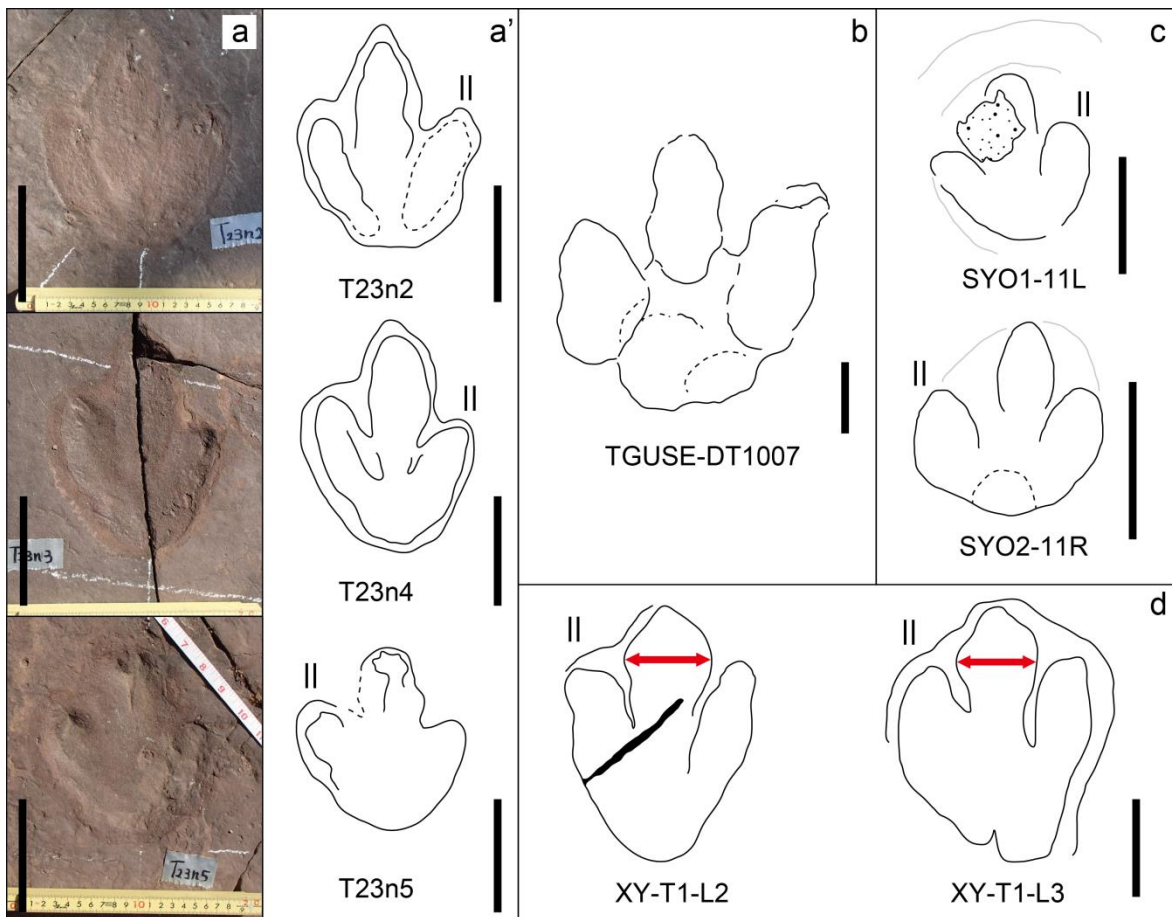


Figure 57 Comparison chart of ornithopod tracks at the site Huai Dam Chum (after Kozu *et al.*, in press).

a: photographs of pes tracks of Tha Uthen tracks T23, a': sketches of pes track of Tha Uthen tracks T23, b: sketch of ornithopod tracks SYO1-11L and SYO2-11R (modified from Xing *et al.*, 2014), c: sketch of *Ornithopodichnus* track ZJ-IIN-O1.6 (modified from Xing and Lockley, 2014), d: sketch of *Caririchnium* sp. TGUSE-DT1007 (modified from Matsukawa *et al.*, 2005), e: sketches of *Dinehichnus socialis* Lockley, dos Santos, Meyer and Hunt, 1998 (modified from Gierliński *et al.*, 2009). Scale bar is 10 cm.

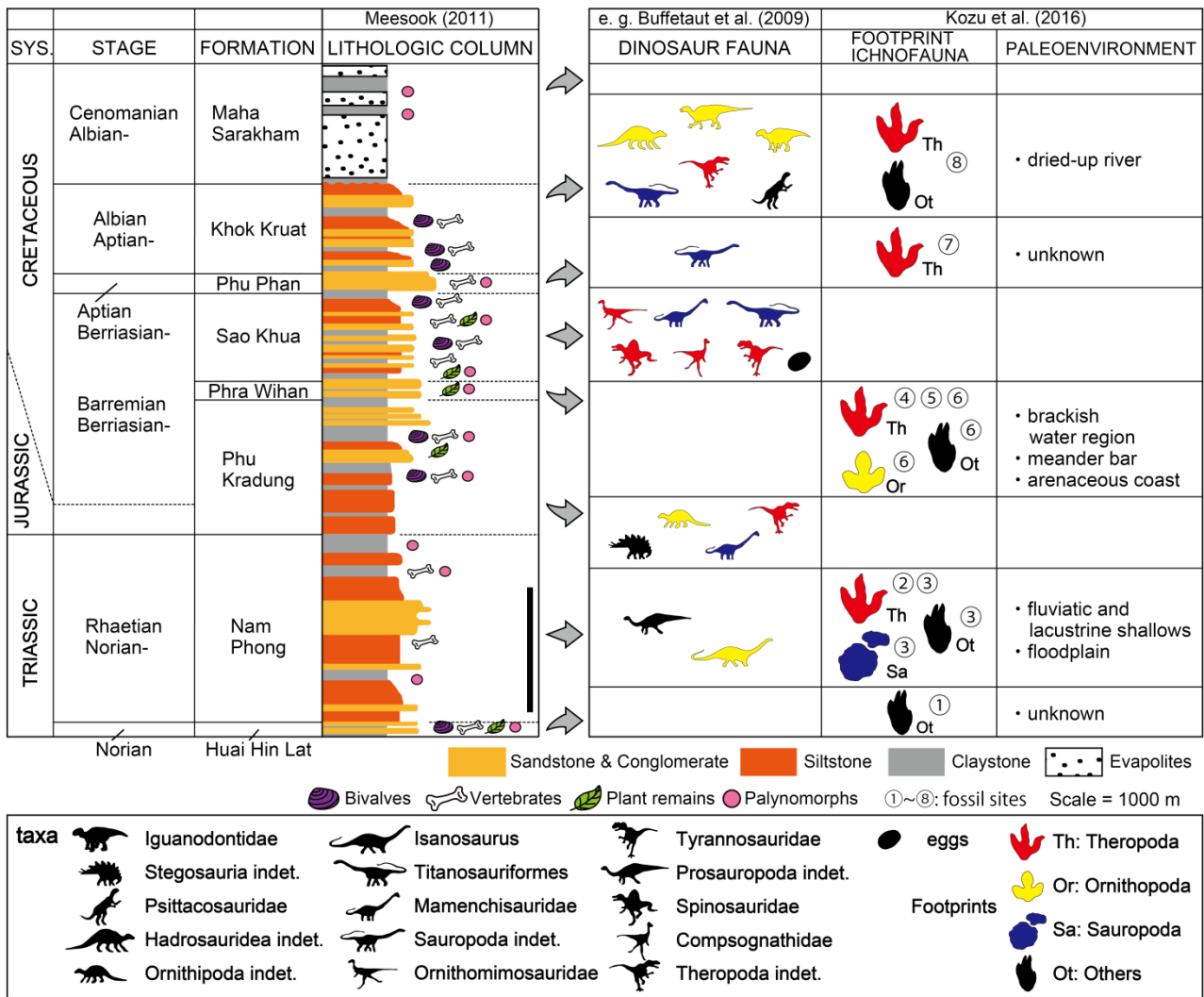


Figure 58 Lithostratigraphic column and new reconstructed dinosaur ichnofauna of the Khorat Group (modified from Buffetaut *et al.*, 2009a; Buffetaut and Suteethorn, 2011; Meesook, 2011; Shibata *et al.*, 2011, 2015; Kozu *et al.*, 2016, 2017).

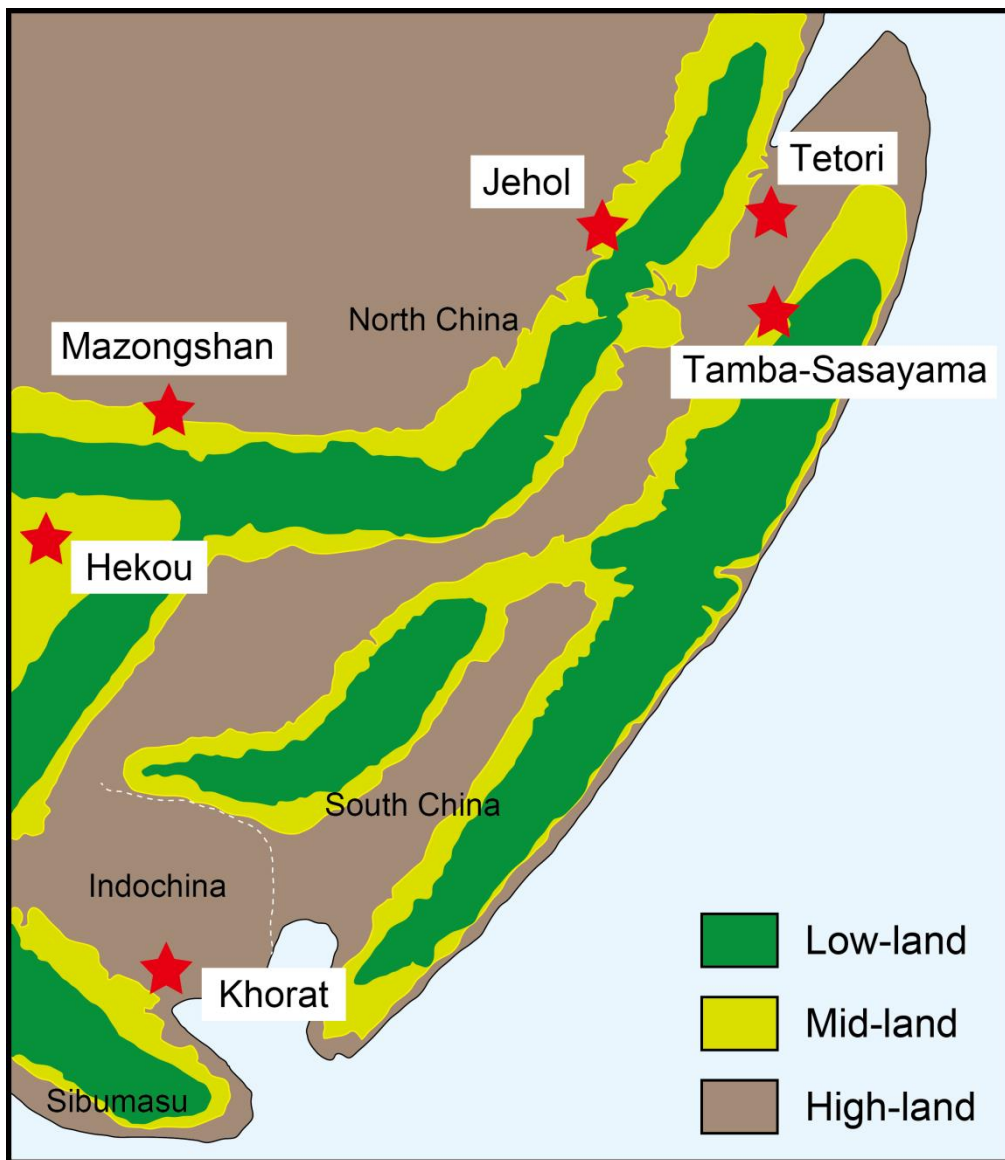


Figure 59 The Early Cretaceous paleogeography and dinosaur fauna in East and Southeastern Asia (after Shibata *et al.*, 2017).

Formation	Taxonomic group	Ichnotaxonomic group
Khok Kruat	Ornithopoda <i>Sirindhorna khoratensis</i> <i>Ratchasimasaurus suranareae</i> <i>Siamodon nimngami</i> Ceratopsia <i>Psittacosaurus sattayarakii</i> Theropoda indet. Sauropoda Titanosauriformes	Theropoda cf. <i>Asianopodus</i> isp. Theropoda indet. Crocodylia <i>Batrachopus</i> sp. Crocodylia indet.
Phu Phan	Sauropoda Titanosauriformes Sauropoda indet.	Theropoda <i>Irenesauripus</i> isp. <i>Siamopodus khaoyaiensis</i>
Sao Khua	Theropoda <i>Siamosaurus suteethorni</i> <i>Siamotyrannus isanensis</i> <i>Kinnareemimus khonkaensis</i> Compsognathidae Sauropoda <i>Phuwiangosaurus sirindhornae</i> Mamenchisauridae	Theropoda <i>Siamopodus khaoyaiensis</i> (Lockley <i>et al.</i> , 2006) ※
Phra Wihan		Ornithopoda <i>Neoanomoepus</i> isp. Theropoda <i>Carmelopodus</i> isp. Theropoda indet. Crocodylia indet.
Phu Kradung	Theropoda indet. Sauropoda Mamenchisauridae Ornithopoda indet. Stegosauria indet.	
Nam Phong	Sauropoda <i>Isanosaurus attavipachi</i> Prosauropoda indet.	Theropoda <i>Gigandipus</i> isp. <i>Eubrontes</i> isp. Sauropoda indet. Tetrapoda indet.
Huai Hin Lat	Archosauromorpha	Archosauromorpha cf. <i>Apatopus</i> isp.

Figure 60 Taxonomic and ichnotaxonomic group of dinosaurs in the Khorat group.

Some footprints *Siamopodus khaoyaiensis* preserved as natural casts on a loose block. Lockley *et al.* (2006) suggested it “probably” originated from either the Sao Khua or the Phu Pan Formations.

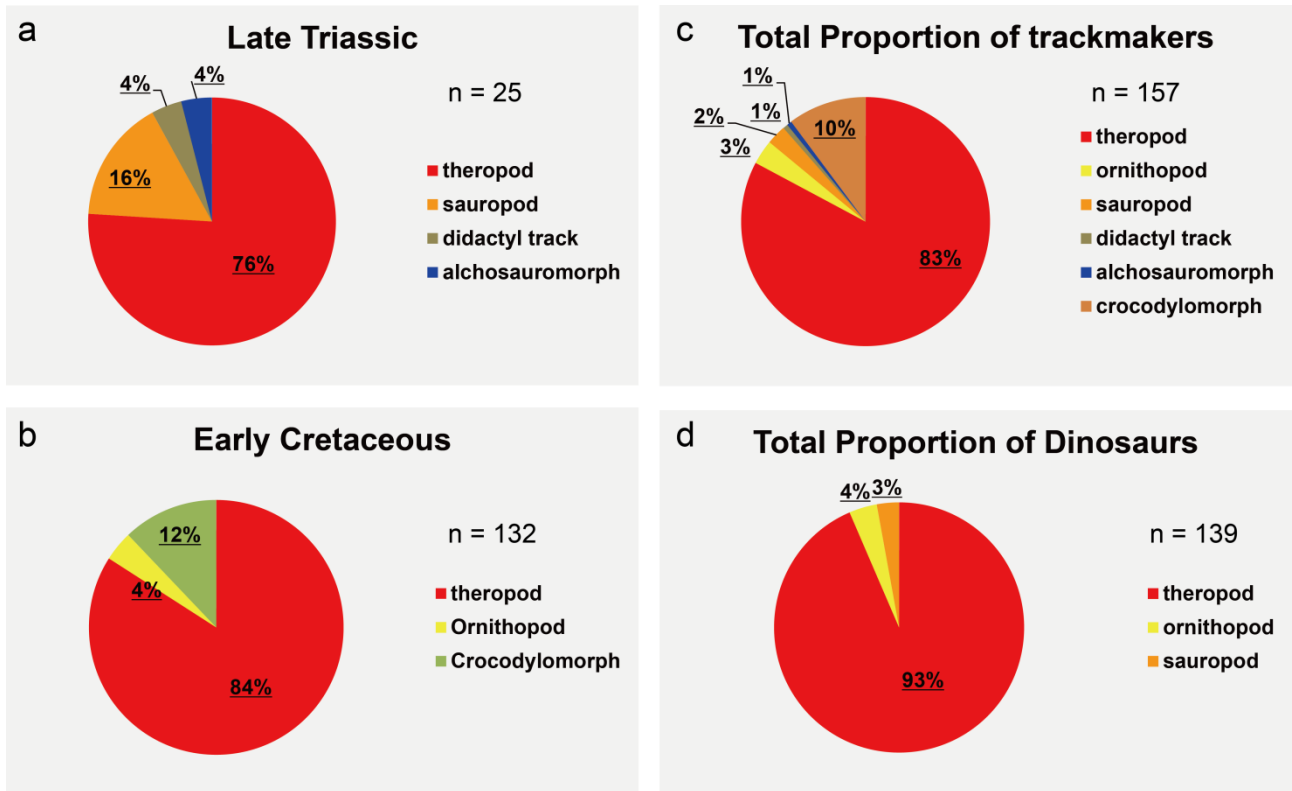


Figure 61 Proportion of track producers on the Khorat Group. a: Late Triassic. b: Early Cretaceous. c: total proportion of trackmaker, d: Total proportion in dinosaurs.

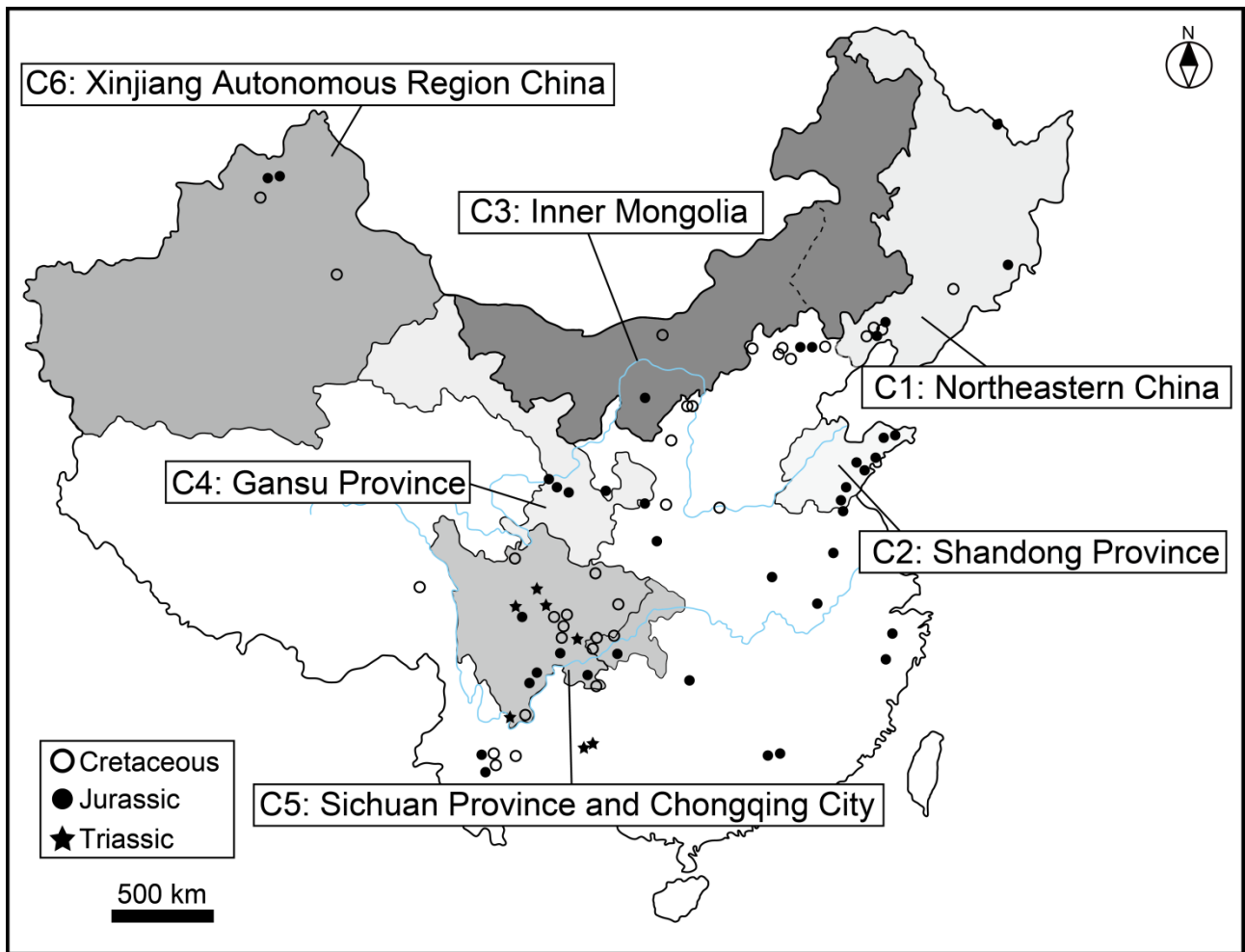


Figure 62 Distribution of the Mesozoic tracksites in China (after Lockley *et al.*, 2014).

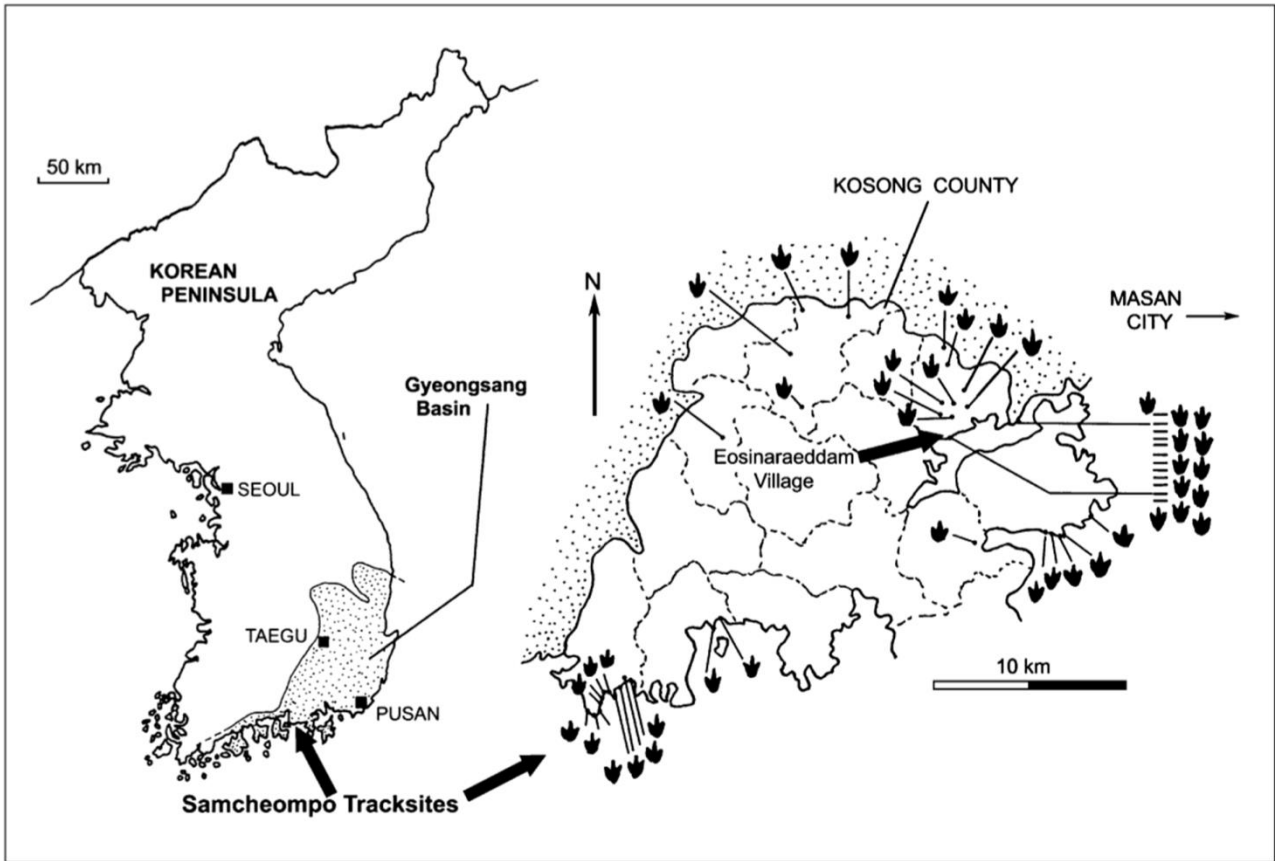


Figure 63 Distribution of the Mesozoic tracksites in Goseon County, Southern Korea (after Lee *et al.*, 2000).

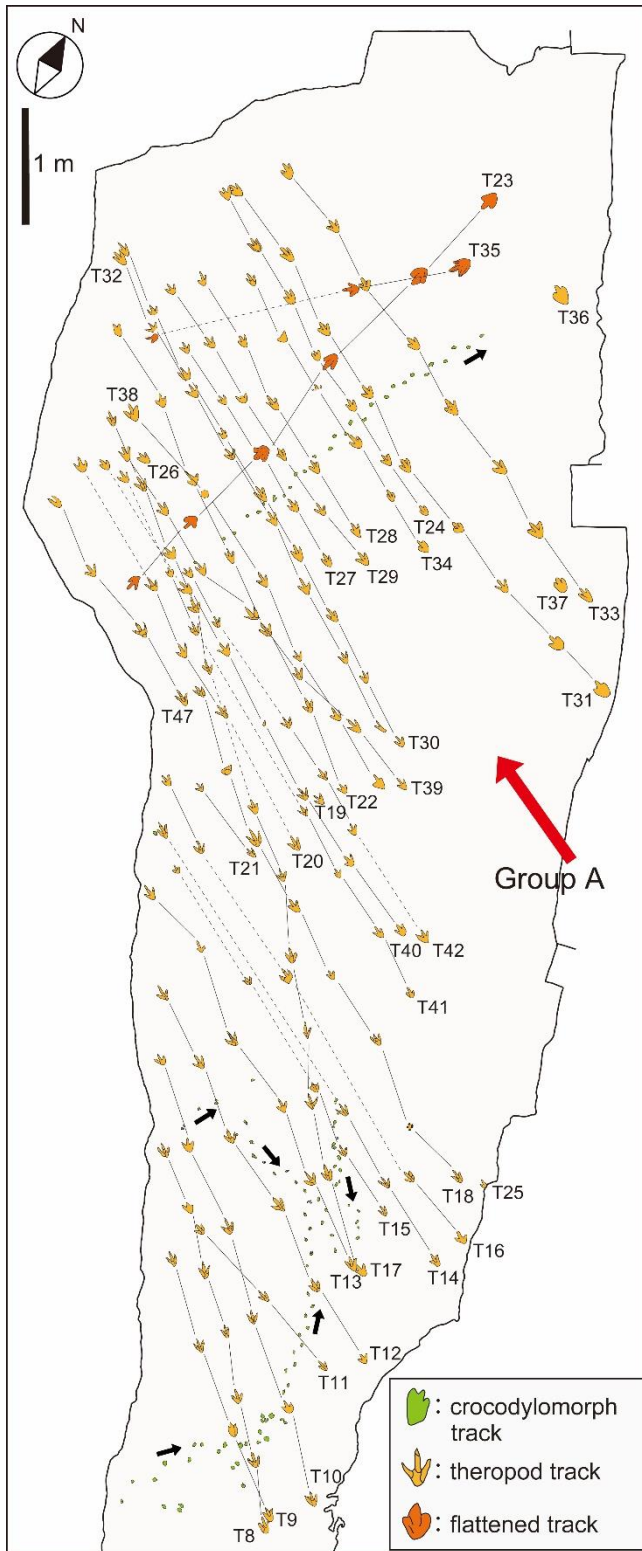


Figure 64 Northern part of the mesh map at the site Huai Dam Chum (after Kozu *et al.*, in press). Most of theropod trackways of Group A are parallel or sub-parallel to each other, and show small or irregular intertrackway spacing, but some theropod trackways are overlapping each other. Two flattened theropod trackways T23 and T35 intersect at a right angle with theropod trackways. Black arrows indicate the directions of crocodylomorph trackways *Batrachopus* (see). Red arrow indicates the direction of movement of Group A.

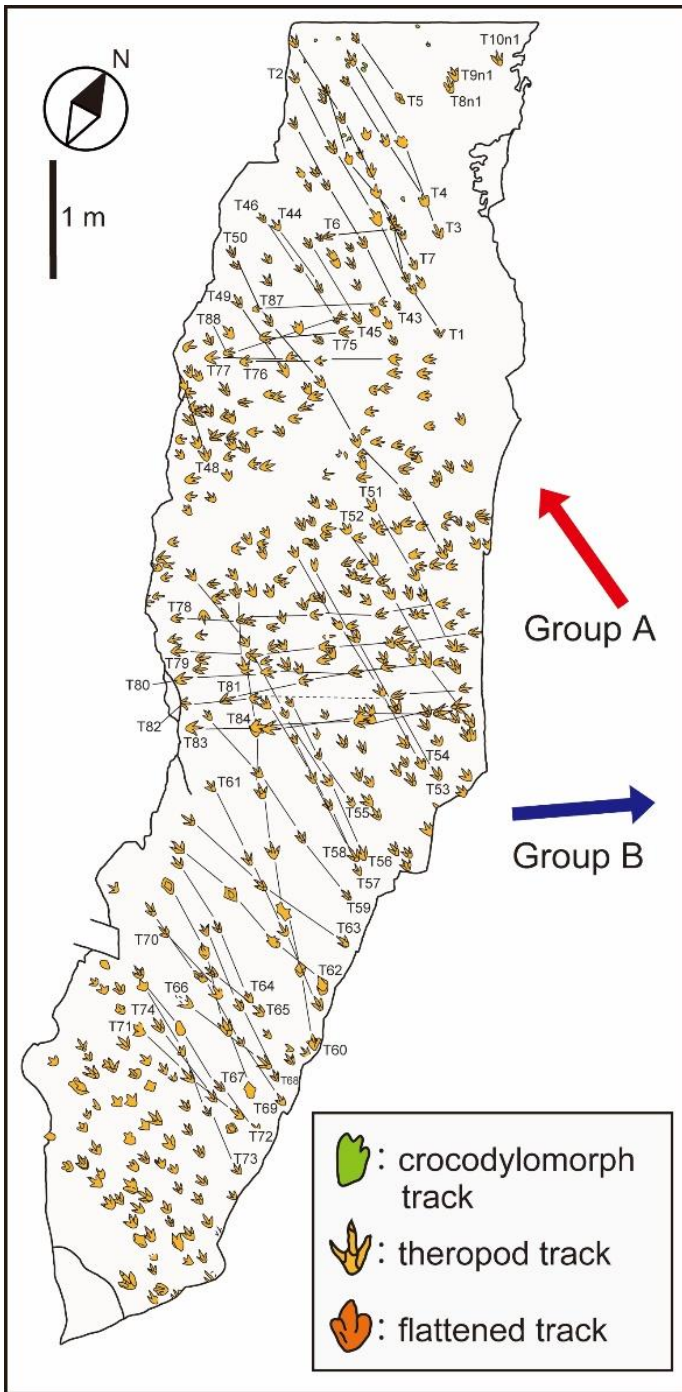


Figure 65 Southern part of the mesh map at the site Huai Dam Chum (after Kozu *et al.*, in press). Most of theropod trackways of Group A are parallel or sub-parallel to each other, and show NW direction. Some theropod trackways of Group B are identified, but most of tracks are overlapping each other, and intersect at a right angle with tracks of Group A. Each arrow indicates the directions of movement of Group A and B, respectively.

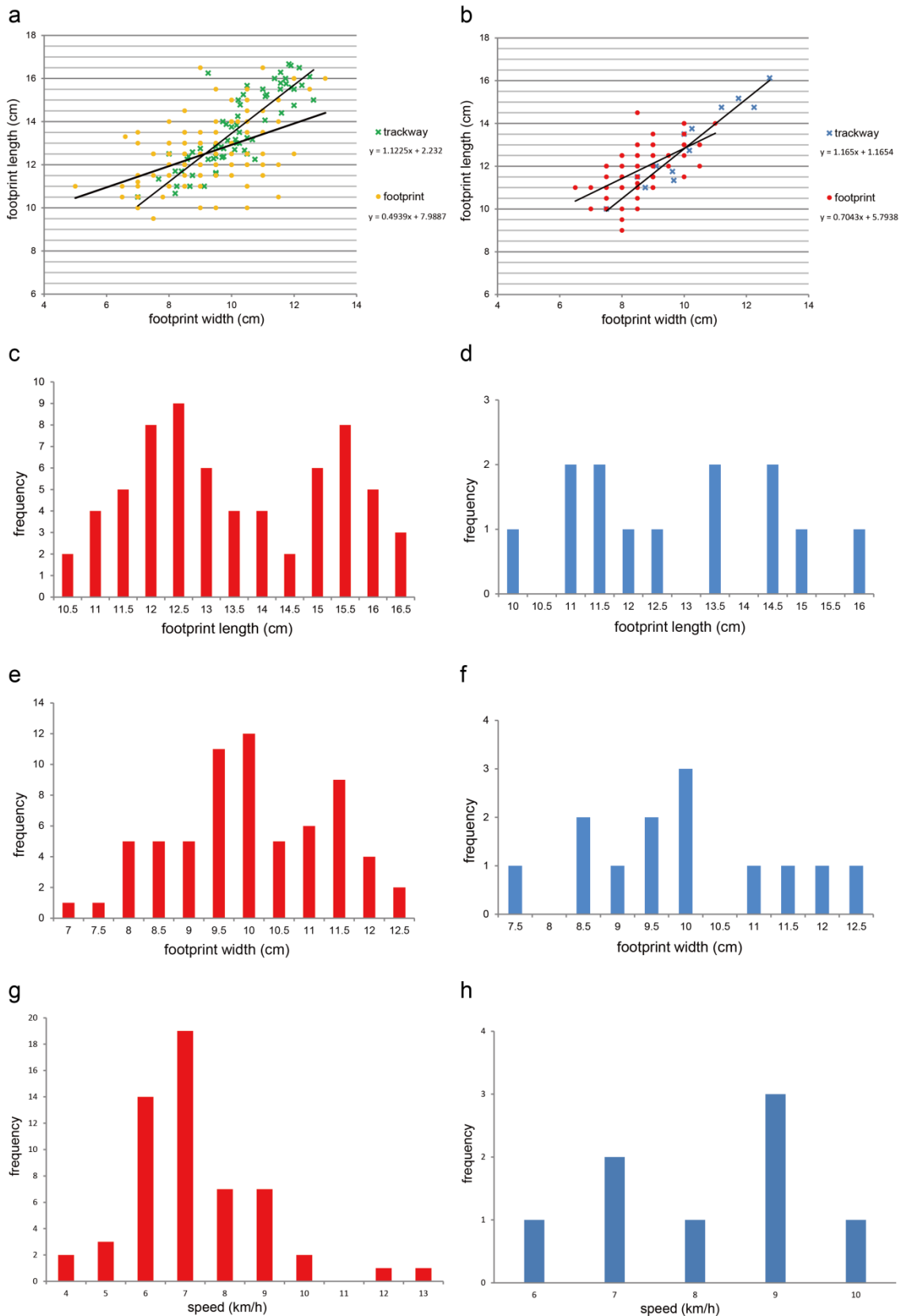


Figure 66 Histograms of the measurement data in the Tha Uthen theropod tracks. a and b are bivariate plots of footprint length-width measurements of Group A and B, respectively. c, e and d, f are Size-frequency histogram for Group A and B, respectively. g and h are histograms of estimated speed of the trackmakers of Group A and B, respectively.

Table 1 Measurements of the trackway T1 at the site Nam Nao.

Position	Footprint No.	Strides(heel to heel)		Strides(finger tip to tip)		Trackway width	Footprint Length			Footprint Width			Stride average	Paces		Angles	
		Left Rear	Right Rear	L.R	R.R		L.F	R.F	L.R	R.R	L.F	R.F		Rear	Front	Rear	Front
1	T1P1		102	102	103	64		33			21		102.5	58		105	
2	T1P2	102		102		63	31			17			102	73		100	
3	T1P3		100		99	65		34			19		99.5	56		95	
4	T1P4	100		101		66	32			21			100.5	77		100	
5	T1P5		105		100	62		32			19		102.5	55		100	
6	T1P6	108		99		66	31			20			103.5	79			
7	average	103.3		102.3		64.3	31.3			19.3			101.8	66.3		100.0	
8																	
9	T1M1									13				15		105	
10	T1M2												15		74	110	
11	T1M3				72					15				18	52	108	
12	T1M4									14				14	71	105	
13	T1M5									12				12	54	100	
14	T1M6									10				18	76		
15	average				83.5					13.0				15.7	63.7	105.6	
16																	

Table 2 Measurements of the trackway T1 at the site Tha Song Khon

No.	track number	fossil description	footprint number	foot part (L or R)	foot length (cm)	foot width (cm)	sole length (cm)	sole width (cm)	depth of footprint (cm)	digit length (true length of digit) (cm)				interdigital angle (degree)
										digit I	digit II	digit III	digit IV	
1	T1	theropod	T1n1	R	49.0	32.0	10.0	9.0	10.0	16.0	23.5	31.0	24.0	I – II – III – IV 81.0 28.0 33.0
2														
3			T1n2	L	40.0	34.0	7.0	12.0	6.0	15.0	24.0	31.0	29.0	71.0 44.0 26.0
4														
5			T1n3	R	38.0	(40.0)	7.0	12.0	7.0	10.0	28.0	(32.0)	(17.0)	88.0 — —
6														
7			T1n4	L	39.0	41.0	13.0	15.0	6.0	13.5	27.0	25.0	26.0	63.0 33.0 32.0
8														
9	average				41.5	16.8	9.3	12.0	7.3	13.6	25.6	29.8	26.3	75.8 35.0 30.3
10														

longitudinal axis (digit axis III) (degree)	pace (cm)	step (cm)	stride (cm)	trackway width (cm)	width of pace (cm)	breadth between tracks (cm)	pace angulation (R-L-R)	pace angulation (L-R-L)	divarication of foot from midline (degree) (+ or -)
	140.0	135.0	260.0	68.0	33.5	12.5(-)	150.0		18.0(+)
	N242E	130.0	120.0	260.0					160.0 9.0(-)
	N240E	136.0	125.0						9.0(+)
	N250E								0
	N230-250E	135.3	126.7	260.0	68.0	33.5	150.0	160.0	

Table 3 Measurements of the pes of the trackway T3 at the northern part of site the Non Tum.

footprint number	foot part (L or R)	foot length (cm)	foot width (cm)	digit length (cm)		digit width (cm)		step (cm)	stride (cm)	pace angulation
				inner digit	outer digit	inner digit	outer digit			
T3P1	R	15	21	14	15	9	10	—	—	—
T3P2	L	—	—	—	—	—	—	—	—	—
T3P3	R	14	22	11	14	9.5	10	—	145	—
T3P4	L	—	—	—	—	—	—	—	—	—
T3P5	R	18	22.5	18.0	17.0	11.0	12.0	—	148	—
T3P6	L	19.5	27	19.5	18	12	13	151	—	—
T3P7	R	18	23	18	13.5	10	11.5	154	148	57
T3P8	L	20	22	20	15	10	9	150	144	46
T3P9	R	19	23	19	13	11	10	154	150	64
T3P10	L	15	23	15	15	11	10	155	169	62
T3P11	R	15	10	—	15	—	10	155	142	56
T3P12	L	22	24	22	15	11	11	153	158	51
T3P13	R	20	23	20	17	11	11	152	154	63
T3P14	L	17	21	17	17	9	8	150	150	55
T3P15	R	15	23	15	13	9	10	150	154	59
T3P16	L	18.0	20.0	18.0	16.0	9.0	8.0	149	159	67
T3P17	R	12.0	22.0	12.0	11.0	7.0	8.0	151	145	61
T3P18	L	—	—	—	—	—	—	147	154	57
T3P19	R	20	26	20	17	12	8	150	149	60
T3P20	L	21	22	21	19	10	11	145	158	62
T3P21	R	—	—	—	—	—	—	—	—	—
T3P22	L	22	23	22	23	11	10	—	147	63
T3P23	R	18	23	18	17	13	9	160	—	—
T3P24	L	16	27	16	16	7	12.5	150	143	58
T3P25	R	—	—	—	—	—	—	—	—	—
T3P26	L	19	24	19	18	11	11	—	151	54
T3P27	R	14	24	14	14	12.5	11	164	—	—
T3P28	L	17	20	17	12	8.5	10	159	151	58
T3P29	R	17.5	17	7	17.5	9.5	6.5	162	151	50
T3P30	L	17	18	14	17	9	5.5	150	163	68
T3P31	R	—	—	—	—	—	—	—	—	—
T3P32	L	15	24	15	15	11	11	—	151	61
T3P33	R	12.5	28.5	12.5	12	10.5	16	154	—	—
T3P34	L	17	24	17	17	10	12	148	148	55
T3P35	R	—	—	—	—	—	—	—	—	—
T3P36	L	20	17.5	20	16.5	6.5	9	—	152	61
T3P37	R	—	—	—	—	—	—	—	—	—
T3P38	L	18	22	17	18	8	10	—	147	65
T3P39	R	16	21	16	10	10	10	150	—	65
T3P40	L	18	26	18	14	11	11	161	150	58
T3P41	R	20	22	16	20	11	10	155	146	53
T3P42	L	—	—	—	—	—	—	—	—	—
T3P43	R	13	21	13	11	9	10	—	152	—
average		17.3	22.3	16.7	15.5	10.0	10.1	153.0	151.0	58.9

Table 4 Measurements of the manus of the trackway T3 at the northern part of the site Non Tum.

footprint number	foot part (L or R)	foot length (cm)	foot width (cm)	digit length (cm)		digit width (cm)		step (cm)	stride (cm)	pace angulation (R-L-R)
				inner digit	outer digit	inner digit	outer digit			
T3M1	L	—	—	—	—	—	—	—	—	—
T3M2	R	—	—	—	—	—	—	—	—	—
T3M3	L	—	—	—	—	—	—	—	—	—
T3M4	R	8	19	8	7.5	8	8	—	—	—
T3M5	L	14	28	14	8	11	15	144	—	—
T3M6	R	9.5	21.5	9	11	9.5	9	147	146	64
T3M7	L	12.0	24.0	10	12	12	11	144	148	60
T3M8	R	9.5	22	9.5	12.0	9.5	11.0	150	151	62
T3M9	L	11	22	9	11	11	9	143	152	64
T3M10	R	10	21	10	10	8	9	150	149	60
T3M11	L	10.5	22	10.5	15.5	9	11	147	156	66
T3M12	R	4.5	3	4.5	3	—	—	144	—	60?
T3M13	L	10	23	10	10	9	10	121	162	73?
T3M14	R	17	—	17	—	—	—	145	11?	67
T3M15	L	10	20	7	6	10	8	152	144	57
T3M16	R	7	16.5	7	8	7	8	130	119	42
T3M17	L	11.5	24	11	11	11.5	10.5	163	159	64
T3M18	R	17	18	13	15	17	9	154	184	70
T3M19	L	11.0	21.5	11.0	8.0	10.0	9.0	138	150	63
T3M20	R	11.0	20.0	11.0	9.5	10.0	10.5	162	154	57
T3M21	L	9	19	7	8	9	8	144	161	65
T3M22	R	—	—	—	—	—	—	178	190	72
T3M23	L	9	23	9	12	9	10	133	159	55
T3M24	R	—	—	—	—	—	—	—	—	—
T3M25	L	6.5	9	—	6.5	—	9	—	136	58
T3M26	R	—	—	—	—	—	—	—	—	—
T3M27	L	10	8	—	10	—	8	—	151	66
T3M28	R	11	20	11	9.5	8	9	160	—	—
T3M29	L	11	3.7	11	—	3.7	—	—	—	58
T3M30	R	—	—	—	—	—	—	184	126?	46
T3M31	L	4	3	4	—	3	—	—	—	49
T3M32	R	—	—	—	—	—	—	—	—	—
T3M33	L	12	19.5	12	10	11	8.5	—	162	54
T3M34	R	7.5	17	7.5	5	4.5	6.5	155	—	—
T3M35	L	10	22	9	11	10	10.5	143	164	67
T3M36	R	—	—	—	—	—	—	—	—	—
T3M37	L	6	5	6	—	5	—	—	151	66
T3M38	R	—	—	—	—	—	—	—	—	—
T3M39	L	11	10	11	—	10	—	—	147	53
T3M40	R	8	17	8	8.5	5	8	127	—	—
T3M41	L	—	—	—	—	—	—	—	—	—
T3M42	R	—	—	—	—	—	—	—	—	—
T3M43	L	—	—	—	—	—	—	—	—	—
average		10.0	17.3	9.5	9.5	8.9	9.4	148.3	154.3	60.2

Table 5 Measurements of the theropod tracks at the site Non Tum.

	No.	track number	fossil description	footprint number	foot part (L or R)	foot length (cm)	foot width (cm)	sole length (cm)	sole width (cm)	depth of footprint (cm)	digit length (true length of digit) (cm)				
											digit I	digit II	digit III	digit IV	
South part	1	Ts1	theropod	Ts1n1	R	44	36					22	23	18	
	2			Ts1n2	L	35	31					17	26	18	
	3			Ts1n3	R	38	26					10	19	14	
	4			Ts1n4	L	39	29					20	23	16	
	5			Ts1n5	R	39	30					13	19	18	
	6			Ts1n6	L	40	32					17	24	20	
	7			Ts1n7	R	45	27					15	23	18	
	8			Ts1n8	L	42	40					20	24	15	
	9			Ts1n9	R	47	34					18	24	17	
	10			Ts1n10	L	27	35					16	28	20	
	11	average					39.6	32.0					16.8	23.3	17.4
	12														
	13	Ts2	theropod	Ts2n1	(L)	39	30						15	22	18
	14			Ts2n2	(R)	35	27						10	22	19
	15	average					37.0	28.5					12.5	22.0	18.5
	16														
	17	Ts5	theropod	Ts5n1	(R)	50	40						22	25	23
	18	Ts6	theropod	Ts6n1	(L)	37	28						18	19	20
	22	Ts7	theropod	Ts7n1	L	25.0	22.0							9	12.5
	23	Ts8	theropod	Ts8n1	R	32.5	30.0						17.5	23	23.5
	24		average				38.41	31.06							
	North part	1	Tn1	theropod	Tn1n1	L	34.0	27.0	14.0	12.5			17.0	19.0	12.5
		2			Tn1n2	R	35.0	22.0	9.0	11.0			12.0	17.0	13.0
		3			Tn1n3	L	36.5	22.0	9.0	13.0			13.5	23.0	11.0
4				Tn1n4	R	36.0	24.0	10.0	10.0			20.0	22.5	16.0	
5				Tn1n5	L	31.0	30.0	11.0	12.0			19.5	19.5	15.0	
6				Tn1n6	R	30.0	26.0	9.5	10.0			12.0	17.0	17.5	
7		average				33.8	25.2	10.4	11.4	2~3		15.7	19.7	14.2	
8															
9		Tn2	theropod	Tn2n1	R	33.0	26.0	10.0	12.0			12.5	20.0	16.0	
10				Tn2n2	L	28.0	24.0	8.5	12.5			11.5	15.0	14.0	
11		average				30.5	25.0	9.3	12.3	3		12.0	17.5	15.0	
12															
13		Tn2'	theropod	Tn2'n1	L	35.0	26.0	11.0	10.0			17.0	23.5	17.0	
14				Tn2'n2	R	30.0	27.0	10.5	15.0			14.0	20.0	15.0	
15				Tn2'n3	L	35.0	29.0	10.5	10.0			13.5	22.5	18.0	
16		average				33.3	27.3	10.7	11.7	2~3		14.8	22.0	16.7	

Table 7 Measurements of the tracks at the site Phu Kao.

Record Number	Track Number	Fossil Description	Footprint Number	Foot Part (L or R)	Foot Length (cm)	Foot Width (cm)	Depth of Footprint (cm)	Length of digits (cm)				Side digit divarication (degree)				Direction of digit III (degree)	Pace direction (degree)	Pace (Step) (cm)	Stride (cm)	Stride angle (R-L-R)	Stride angle (L-R-L)
								digit I	digit II	digit III	digit IV	I - II	II - III	III - IV							
1	T1	theropod	T1n1	L	27	26	7														
2			T1n2	R	25	27	9.5	14	14	16	12	12	40	45	N180	N150	82	195		150	
3			T1n3	L	30	29	5	13	13	12	13	30	40	N350	N130	117					
4	average				27.3	27.3	7.2	13.7	14.0	12.5		38.3	38.3			99.5	195.0				
5																					
6	T4	theropod	T4n1		25	27	7	14	15	12		40	45	N50							
7																					
8	T10	theropod	T10n1		30	37	8	30	10	13		45	30	N110							
9																					
10	T12	theropod	T12n1		22.5	26	5	9	12	8		50	40	N155							
11																					
12	T13	theropod	T13n1		29	26.5	5	16	19	5		35	30	N130							
13																					
14	T14	theropod	T14n1	R	30	26	2	15	15	12		35	30	N40	N20	58.5					
15			T14n2	L	25	18.5	1.8		13	13			35	N45							
16	average				27.5	22.3	1.9	15.0	14.0	12.5		35.0	32.5			58.5					
17																					

Table 8 Measurements of the theropod tracks at the site Phu Faek.

Record Number	Track Number	Fossil Description	Footprint Number	Foot Part (L or R)	Foot Length (cm)	Foot Width (cm)	Depth of Footprint (cm)	Length of digits (cm)				Side digit divarication (degree)				Direction of digit III (degree)	Pace direction (degree)	Pace (Step) (cm)	Stride (cm)	Stride angle (R-L-R)	Stride angle (L-R-L)
								digit I	digit II	digitIII	digitIV	I - II	III - IV								
1	T1	Theropod	T1n1	R	44	46	4		23	24	24	24		35	30	130	100	122	235	155	
2			T1n2	L	47	43	5		21	23	23	21		40	40	120	120	116	215	165	
3			T1n3	R	47	35	6		21	26	26	20		30	23	105	104	104	212	155	
4			T1n4	L	47	37	5		21	27	27	20		35	20	115	115	111	212	150	
5			T1n5	R	44	39	4		24	30	30	20		30	40	108	85	110	211	155	
6			T1n6	L	47	37	4		24	30	30	22		33	24	100	105	110			
7			T1n7	R	50	41	4		24	33	33	21									
8	average				46.6	39.7	4.6		22.6	27.6	27.6	21.1		33.8	29.5			112.2	217.0	156.0	
9																					
10	T2	Theropod	T2n1	L	48	38	5		21	31	31	20		30	30	55	65	115			
11			T2n1	R	38	39	4		20	29	29	21		30	28	40					
12	average				43.0	38.5	4.5		20.5	30.0	30.0	20.5		30.0	29.0						
13																					
14	T3	Theropod	T3n1	R	37	30	5		17	24	24	17		25	25	35	43	117	209	145	
15			T3n2	L	38	31	4		16	23	23	15		20	30	20	70	100	220	153	
16			T3n3	R	47	34	4.5		19	25	25	19		25	18	55	50	123			
17			T3n4	L	42	45	5		18	25	25	17		33	23	60					
18	average				41.0	35.0	4.6		17.5	24.3	24.3	17.0		25.8	24.0			113.3	214.5	149.0	
19																					
20	T4	Theropod	T4n1	(R)	18?	27	2.5		14	17	17	17		40	25	125					

Table 9 Measurements of the ornithopod trackway T4 at the site Hin Lat Pa Chad (Phu Wiang).

Position	Footprint No.	Strides(center to center)				Trackway width	Footprint Length			
		L.Rear	R.Rear	L.Front	R.Front		L.Rear	R.Rear	L.Front	R.Front
1	T4P1									
2	T4P2		58			22		10		
3	T4P3					15	10			
4	T4P4							10.5		
5	T4P5		60			21		11		
6	T4P6	60				15	12.5			
7	T4P7		55			21		12		
8	T4P8					22	12.5			
9	T4P9							7		
10	T4P10	54				15	10			
11	T4P11					27		10.5		
12	T4P12						10.5			
13	T4P13		61			19		10.5		
14	T4P14	52.5				18	10			
15	T4P15					26		10.5		
16	T4P16						10			
17	T4P17		54			24		11		
18	T4P18	53				13.5	11			
19	T4P19		49			23.5		11		
20	T4P20					26	12.5			
21	T4P21							11.5		
22	average	54.9	56.2			20.5	11.0	10.5		
23		55.5					10.8			
24	T4M2				54	30				6
25	T4M3					28.5			6	
26	T4M4									6
27	T4M5				59	30				6
28	T4M6			53		24			5.5	
29	T4M7					29				4.5
30	T4M8								7	
31	T4M17				51	34.5				6
32	T4M18			54.5		23			5.5	
33	T4M19					37				6.5
34	T4M20								6	
35	average			53.8	54.7	29.5			6.0	5.8
36				54.2					5.9	

Table 9 Measurements of the ornithopod trackway T4 at the site Hin Lat Pa Chad (Phu Wiang) (continued).

Footprint Width				Length of digits			Side digit divarication		depth		Paces		Angles			
L.Rear	R.Rear	L.Front	R.Front	II	III	IV	II - III - IV	Rear	Front	Rear	Front	Rear		Front		
												midline	pace	midline	pace	
	8			5	6	5	40	30	0.5		30		20	150		
9.5				5	6	6	45	43	0.5		29.5		20			
	8.5			6	8	6	48	25	1							
	8			6	8	6	30	23	1		30.5		10	155		
11				7	8	6	35	23	1		32		10	155		
	10			6	7	6	35	23	1		29		20	150		
10				7	8	6	30	35	0.5		30		20			
	7								0.5							
											26.5		10	155		
	10.5			6	7	6	30	45	0.5		29		10			
9				6	7	5	35	30	0.5							
	9			7	9	7	35	30	0.5		29		10	150		
10											35		20	130		
	9			5	6	4	45	45	0.8		26		40			
10				5	6	5	25	30	0.3							
	6?				7				0.5		27.5		15	150		
10				5	7	5	35	30	0.5		30		20	150		
	10			6	7	5	35	35	0.5		27		20	135		
11.5				6	8	6	35	40	0.3		27		25			
	10			6	8	6	35	30	0.3							
10.1	9.0			5.9	7.2	5.6			0.6		29.2					
	9.6															
			4.5							0.3		34		45	150	
		5								0.1		36		30		
			5							0.5						
			4.5							1		38.5		25	150	
		4								0.5		31.5		30	110	
			4.5							0.5		36		35		
		5								0.5						
			4.5							0.5		32.5		40	95	
		5								0.5		37		50	100	
			5							0.5		38		50		
		6								0.5						
		4.8	4.7							0.5		35.4				
			4.7													

Table 10 Measurements of the ornithopod trackways T1, T2, and T11, and theropod trackway T10 at the site Hin Lat Pa Chad (Phu Wiang).

Record Number	Track Number	Fossil Description	Footprint Number	Foot Part (L or R)	Foot Length (cm)	Foot Width (cm)	Depth of Footprint (cm)	Length of digits (cm)			
								digit I	digit II	digit III	digit IV
1	T1	ornithopod	T1n1	L	14	10	0.5		5	9	7
2			T1n2	R	13	10	1		5	8	7
3			T1n3	L	11	9	1		6	8	7
4			T1n4	R	12	10	1		6	9	8
5			T1n5	L	12	9	0.5		6	9	6
6			T1n6	R	12	10	1		6	9	8
7			T1n7	L	12	12	1.5		8	10	9
8			T1n8	R	13	10	1		7	10	8
9			T1n9	L	12	8	0.3		7	9	5
10			T1n10	R	12	10	0.5		7	8	6
11			T1n11	L	10	8	1		7	8	6
12	average				12.1	9.6	0.8		6.4	8.8	7.0
13											
14	T2	ornithopod	T2n1	L	12	8	1		7	9	7
15			T2n2	R	12	8	0.3		6	9	8
16			T2n3	L	10	9	1		6	8	7
17			T2n4	R	11	8	0.5		6	7	6
18			T2n5	L	13	9	1		7	9	7
19			T2n6	R	11	8	0.3		6	8	7
20			T2n7	L	10	8	0.5		6	7	7
21			T2n8	R	12	8	0.3		5	8	5
22			T2n9	L	10	8	1		5	7	5
23			T2n10	R	10	8	0.3		5	8	7
24			T2n11	L	11	9	0.2		6	8	7
25			T2n12	R	10	8	0.5		6	8	5
26			T2n13	L	10	8	0.5		6	8	6
27	average				10.9	8.2	0.6		5.9	8.0	6.5
28											
34	T11	ornithopod	T11n1	R	10	8	0.3		6	7	7
35			T11n2	L	8	8	0.3		4	5	5
36			T11n3	R	9	8	1		5	7	6
37			T11n4	L	11	8	0.3		7	8	6
38			T11n5	R	9	7	0.5		4	6	5
39			T11n6	L	10	9	0.5		5	7	6
40			T11n7	R	11	10	0.5		7	8	6
41	average				9.7	8.3	0.5		5.4	6.9	5.9
29	T10	therpod	T10n1	L	14	10	0.5		6	8	5
30			T10n2	R	12	10	0.7		6	8	5.5
31			T10n3	L	12	9.5	0.7		6	8	5
32	average				12.7	9.8	0.6		6.0	8.0	5.2

Table 10 Measurements of the ornithopod trackways T1, T2, and T11, and theropod trackway T10 at the site Hin Lat Pa Chad (Phu Wiang). (continued)

Side digit divarication (degree)			Direction of digit III (degree)	Pace direction (degree)	Pace (Step) (cm)	Stride (cm)	Stride angle (R- L-R)	Stride angle (L-R-L)
I	II	III - IV						
	23	30	155	180	29	59		150
	33	25	145	145	32	62	160	
	32	27	180	170	31	62		160
	34	26	140	145	32	60	150	
	35	27	165	175	30	50		150
	35	30	130	130	25	54	150	
	30	35	170	170	32	62		160
	30	23	135	145	32	57	155	
	40	26	160	175	28	57		155
	30	24	142	150	32			
	34	20	175					
	32.4	26.6			30.3	58.1	154.0	155.0
	26	23	20	20	29	55		145
	24	25	0	345	29	54	155	
	30	29	20	20	27	52		155
	25	21	345	355	27	52	160	
	24	26	20	15	28	50		155
	27	23	10	355	23	47	150	
	25	30	20	30	26	51		145
	23	36	355	355	28	52	155	
	35	30	25	15	25	50		155
	26	30	350	350	26	57	170	
	30	24	10	355	31	55		158
	26	30	350	350	24			
	31	23	10					
	27.1	26.9			26.9	52.3	158.0	152.2
	28	20	215	195	25	44	150	
	35	31	210	230	21	39		140
	30	27	215	190	22	43	155	
	27	22	210	210	22	42		155
	37	25	225	180	22	42	150	
	35	21	205	210	22			
	22	40	195					
	30.6	26.6			22.3	42.0	151.7	147.5
	22	32	24	38	31	65		163
	28	33	35	20	35			
	33	29	15					
	27.7	31.3			33.0	65.0		

Table 11 Measurements of the tracks at the site Phu Luang.

No.	track number	fossil description	footprint number	foot part (L or R)	foot length (cm)	foot width (cm)	sole length (cm)	sole width (cm)	depth of footprint (cm)	digit length (true length of digit) (cm)				interdigital angle (degree)		longitudinal axis (digit axis III) (degree)
										digit I	digit II	digit III	digit IV	I – II – III – IV		
1	T1	theropod	T1n1	(R)	33.0	28.0	9.0	10.0	4.0		16.0	25.0	21.0	26.0	29.0	N210E
2			T1n2	(L)	34.0	31.0	4.0	10.0	3.5		20.0	24.0	21.0	50.0	21.0	N221E
3	average				33.5	29.5	6.5	10.0	3.8		18.0	24.5	21.0			
4																
5	T2	theropod	T2n1	R	33.0	31.0	—	8.0	4.5		(16.0)	(19.0)	(19.0)	21.0	24.0	N190E
6			T2n2	L	35.5	32.0	5.0	6.0	5.0		14.0	20.5	25.5	30.0	29.0	N185E
7	average				34.3	31.5	5.0	7.0	4.8		15.0	19.8	22.3			
8																
9	T3	theropod	T3n1	L	32.0	26.0	9.0	11.0	2.5		15.5	24.0	19.5	41.0	40.0	N190E
10																
11	T4	theropod	T4n1	L?	39.0	34.0	7.0	13.0	6.0		19.0	32.0	24.0	27.0	37.0	N203E
12																
13	T5	theropod	T5n1	L?	37.0	31.0	12.0	13.0	3.0		18.5	25.0	22.0	45.0	29.0	N170E
14																
15	T6	theropod	T6n1		(33.0)	30.0	—	—	2.0		(19.0)	(23.0)	—	28.0	—	N170E
16																
17	T7	theropod	T7n1		33.0	(24.0)	15.0	13.0	3.0		13.0	17.0	—	50.0	—	N40E
18			T7n2		33.0	32.5	—	—	7.0		—	—	—	52.0	40.0	N60E
19	average				33.0	4.3	15.0	13.0	5.0		13.0	17.0	—			
20																
21																
22	T12	theropod	T12n1		(9.0)	14.0	—	—	1.0		7.0	9.0	7.0	(40.0)	(40.0)	N130E

Table 12 Measurements of well-preserved tracks of theropod and tracks of ornithopod at the Huai Dam Chum site.

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 O = solitary theropod.

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	N65W	53.5	105	-	
	2	L	11	8.5	45	20	25	N58W	52.5	111.5	165	
	3	R	11.5	7.5	40	18	22	N62W	61	121.5	165	
	4	L	12.5	8	42	20	22	N62W	62	-	170	
	5	R	13	8	40	20	20	N70W	-	-	-	
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	N65W	66	135.5	-	
	2	R	17	12	59	24	35	N70W	70	139.5	175	
	3	L	16	12	50	23	27	N68W	69.5	-	172	
	4	R	15	10.5	48	25	23	N70W	-	-	-	
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	N63W	81	162.5		
	2	R	15.5	12	60	25	35	N70W	82		170	
	3	L	17	12	56	28	28	N66W				
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	N70W	60	120		
	2	R	12	9	63	35	28	N73W	60	122	177	
	3	L	13	9	44	22	22	N65W	60		176	
	4	R	12	10	61	30	31	N82W				
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	N74W	63			
	2	R	12.5	8.5	48	28	20	N77W				
average			12.5	8	46.5	24	22.5		63			A
T6	n1	R	10	9	55	27	28	N40E	58			
	2	L	12	8.5	43	23	20	N35E				
average			11	8.8	49	25	24		58			B
T7	n1	R	14	9	50	24	26	N66W	70	140		
	2	L	13.5	10	54	29	25	N65W	70	144	175	
	3	R	15	10.5	55	30	25	N75W	76		169	
	4	L	13	-	61	30	31	N70W				
average			13.9	9.8	55	28.3	26.8		72	142	172	A
T8	n1	L	16	10.5	63	33	30	N50W	56.5	111.5		
	2	R	16	10.5	59	29	30	N60W	55	112.5	170	
	3	L	15	10.5	52	27	25	N55W	57.5	113	172	
	4	R	14	9.5	49	25	24	N67W	55.5	111.5	170	
	5	L	14.5	10.5	53	31	22	N68W	56	109.5	170	
	6	R	14.5	10	57	26	31	N70W	54		170	
	7	L	15	10	60	33	27	N60W				
average			15	10.2	56.1	29.1	27		55.8	111.6	170.4	A

Table 12 Measurements of well-preserved tracks of theropod and tracks of ornithopod at the Huai Dam Chum site. (continued)

T9	n1	L	16.5	11	52	30	22	N55W	79	154.5		
	2	R	16	12.5	57	30	27	N53W	75.5	155	180	
	3	L	15.5	11	53	28	25	N65W	79.5		174	
	4	R	16	11	50	27	23	N58W				
average			16	11.4	53	28.8	24.3		78	154.8	177	A
T10	n1	L	17.5	13	53	28	25	N50W	82.5	164		
	2	R	16.5	12.5	60	29	31	N70W	81.5	160.5	177	
	3	L	15.5	12.5	60	33	27	N63W	79	158	175	
	4	R	16	13	63	30	33	N65W	80	155.5	170	
	5	L	16.5	13	61	33	28	N62W	76		175	
	6	R	14.5	11	56	30	26	N60W				
average			16.1	12.5	58.8	30.5	28.3		79.8	159.5	174.3	A
T11	n1	L	13.5	10	-	-	-	N84W	76.5	153.5		
	2	R	13	9	41	19	22	N80W	77		174	
	3	L	12	10	55	27	28	N78W				
average			12.8	9.7	48	23.0	25.0		76.8	153.5	174.0	A
T14	n1	R	16.5	14	-	-	-	N62W	74	146		
	2	L	15.5	11	47	32	15	N72W	72.5		170	
	3	R	16	11	48	26	22	N76W				
	4	R	15	11	44	16	28	N63W				
average			15.8	11.8	46.3	24.7	21.7		73.3	146	170	A
T23	n1	R	17.5	14.5	-	-	-	N172E	90.0	196.0		
	2	L	17.5	15	-	-	-	N177E	106.0	207.0	172	
	3	R	18.5	14	-	-	-	N183E	102.0	187.0	171	
	4	L	17	14.5	-	-	-	N175E	86.0	156.0	175	
	5	R	16.5	13	-	-	-	N190E	71.0		176	
	6	L	17.5	14	-	-	-	N180E				
average			17.4	14.2	-	-	-		91.0	186.5	173.5	C
T32	n1	L	12.5					N74W	67	134		
	2	R	15	10.5	45	20	25	N68W	67	134	177	
	3	L	14.5	11	50	26	24	N68W	67	132	175	
	4	R	15	12	50	29	21	N64W	65	129.5	172	
	5	L	15	12	47	21	26	N65W	64.5	134	176	
	6	R	15	11	53	-	-	N70W	69.5	131	173	
	7	L	13	11	50	30	20	N78W	62		171	
	8	R	12.5	10	35	16	19	N74W				
average			14.1	11.1	47.1	23.7	22.5		66.0	132.4	174	A
T35	n1	L	15.5	11.5	-	-	-	N205E	96.5			
	2	R	12.5	11.5	-	-	-	N226E				
	3	R	12.5	11	-	-	-	N208E				
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

Table 13 Measurements of trackways of the Huai Dam Chum site.

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 O = solitary theropod.

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

Table 13 Measurements of trackways of the Huai Dam Chum site. (continued)

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
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