

Spinosaurid theropod teeth from the Red Beds of the Khok Kruat Formation (Early Cretaceous) in Northeastern Thailand

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ABSTRACT.— Teeth from the Aptian – Albian Khok Kruat Formation of the Khorat Group in Northeastern Thailand, are described as belonging to spinosaurine dinosaurs. They consist of two morphotypes, i.e., the Khok Kruat morphotype and *Siamosaurus* morphotype. The Khok Kruat morphotype shows fine ridges and a smooth enamel surface of the crown while the *Siamosaurus* morphotype shows coarse ridges and a wrinkled enamel surface. Comparisons of the Thai material with the teeth of Asian and other spinosaurids indicate that the Khok Kruat morphotype is similar to other Asian spinosaurid teeth and more closely to those of *Siamosaurus suteethorni* or *Siamosaurus* morphotype from the older Sao Khua Formation of Northeastern Thailand. The differences in their morphology indicate a greater diversity of spinosaurids in Thailand and Asia.

KEY WORDS: Spinosauridae, Early Cretaceous, Northeastern Thailand, Khorat Group, Asia

INTRODUCTION

The first Thai spinosaurid dinosaur, *Siamosaurus suteethorni* Buffetaut and Ingavat, 1986, was described on the basis of isolated teeth without bone material (Buffetaut & Ingavat, 1986). It is only known by the peculiar isolated teeth which have tall and slightly compressed crowns with a ribbed enamel and very faint or non-existent serrations. Based on the isolated teeth, this dinosaur strongly evoked a spinosaurid theropod (Buffetaut et al., 2003). It came from the Sao Khua Formation, which is referred to the Barremian age based on pollen, molluscs and vertebrate microremains (Racey, 2009; Tumpeesuwan, 2010; Khamha, 2017). In 2003, Buffetaut and his colleagues reviewed

the dinosaurs from Thailand, including isolated teeth similar to those of *Siamosaurus* found in the Khok Kruat Formation, which is younger than the Sao Khua Formation. Two years later, in 2005, Buffetaut and his colleagues also insist the existence of spinosaurid in the Khok Kruat Formation by discovery of the teeth with a number of blade-like teeth and serrations on both margins at Khok Pha Suam, Ubon Ratchathani Province, as well as cervical and dorsal vertebrae of a spinosaurid from Khon Kaen Province which had been found by staff of the Department of Mineral Resources. However, these Khok Kruat teeth have not yet been described in detail and differences in their size and morphology strongly suggest that there are several spinosaur taxa in Thailand. Asian

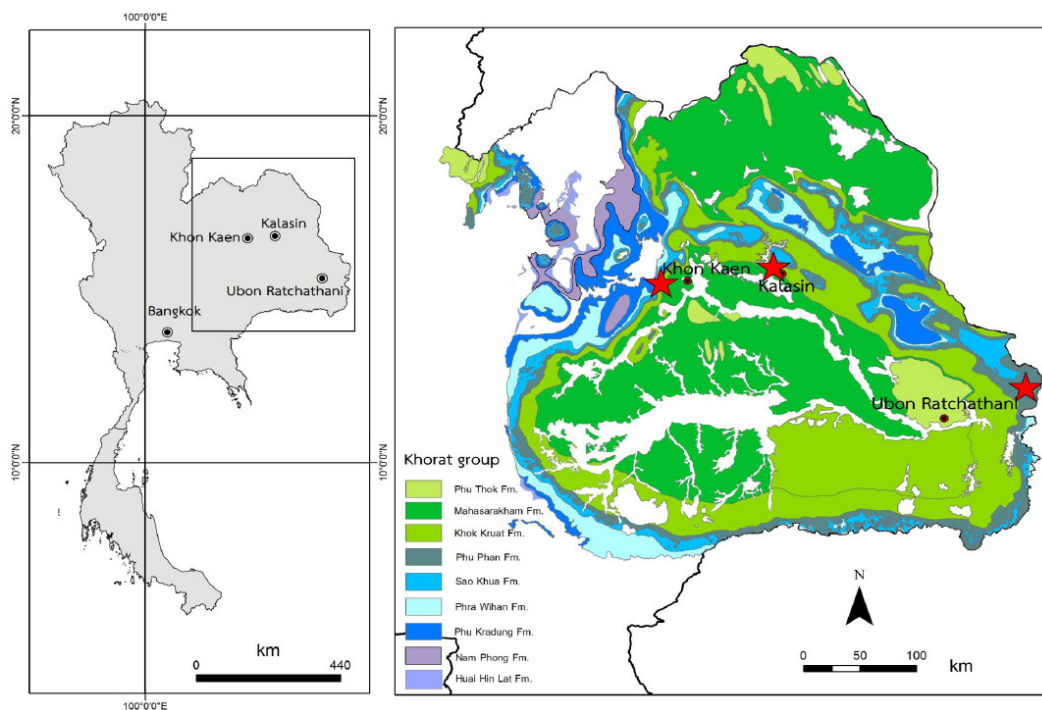


FIGURE 1. Geological map of the Khorat Plateau showing the three studied localities (red stars)

spinosaurid dinosaurs was revealed when the teeth have been found from Sao Khua Formation (Buffetaut et al., 2018). Since then, fieldwork in northeastern Thailand as part of Thai–French research projects on the Mesozoic vertebrates of Thailand during 2003–2008 has also yielded more teeth from many localities in the Khok Kruat Formation including the Sam Ran, Khok Pha Suam and Lam Pao Dam sites. These spinosaurid specimens can be separated by the number of ridges and the enamel surface of a crown. Here, we compare Khok Kruat tooth material with other spinosaurid teeth from Asia, Europe and South America in order to allow us understand the diversity and geographical distribution of the Spinosauridae as well as the biogeography of Thai Spinosaurid which can help to

address the presence of spinosaurid taxa in Southeast Asia.

Geological setting

The Khok Kruat Formation is well distributed in the outer parts of the Phu Phan Range along the outer rims of the Phu Phan Formation with conformable contacts. The sharp contact with the basal anhydrite of the overlying Maha Sarakham Formation was observed (Hite 1974; Hite and Jappakasetr, 1979) and was reported on seismic profiles (Sattayarak et al., 1991). Generally, the Khok Kruat Formation consists of reddish brown, fine- to medium-grained sandstones; siltstones, mudstones and conglomerates are also present. Its distribution on the Khorat Plateau is shown in Figure 1.

Three significant fossil assemblages of the Khok Kruat Formation in northeastern Thailand i.e., Sam Ran, Khok Pha Suam and Lam Pao Dam, are discussed in the present paper. The geological settings of these localities are described below:

- The deposits exposed at Sam Ran locality consist of reddish brown siltstone interbedded with fine- to medium- grained sandstone. The beds of sandstone show load-casts, rip-up casts and large-scale horizontal cross-bedding.

- The deposits exposed at Khok Pha Suam locality are of reddish brown color, very thin to thin bedded claystone grading up to thin bedded siltstone interbedded with fine- to medium- grained sandstone. Sandstone beds are micro-crossbedded. A calcrete horizon (paleosol) has been found at the top of the succession.

- The Lam Pao Dam sedimentary sequence consists of fining-upward sequences of channelized conglomerates grading up to reddish brown, thin to medium bedded, medium- to coarse-grained sandstone interbedded with greenish gray, thin bedded siltstone.

The lithology and sedimentary structures of these three localities suggest that they were formed in a meandering system deposit. The Sam Ran Unit is composed of sandstone and siltstone channel deposits corresponding to a crevasse splay sequence. The Khok Pha Suam Unit consists of siltstone and claystone channel deposits classical of flood plain sequences (Einsele, 1992). The Lam Pao Dam Unit shows conglomerate channel deposits, characterizing a point bar sequence (Einsele, 1992). It seems that the Lam Pao Dam Unit was deposited in a high energy river current. The Sam Ran Unit was deposited in a low energy current, an even lower energy

current being observed in the Khok Pha Suam Unit.

MATERIAL AND METHODS

Almost sixty spinosaurid teeth were collected by Staffs of the Department of Mineral Resources during the last decade from 3 localities of the Khok Kruat Formation, i.e., Sam Ran site, Khon Kaen Province; Khok Pa Suam site, Ubonratchathani Province and Lam Pao Dam site Kalasin Province. All the material is housed in the Phu Wiang Fossil Research Center and Dinosaur Museum, Khon Kaen Province where tooth material was subsequently prepared with scalpel (blades number 10 and 11) and pneumatic air pen. Only eight specimens, with completely preserved base and crown of the teeth, were described and compared with spinosaurid teeth from Asia including *Siamosaurus suteethorni*, GMNH – PV –999 from Japan, Chinese spinosaurid from Guangxi IVPP–4793 from China, spinosaurids from the Kem Kem Beds of Morocco, spinosaurine *Irritator* from Brazil, baryonychines *Suchomimus* from Niger and *Baryonyx* from England. Characters of the teeth were studied using the technical terms of Smith *et al* (2005) as follows: the crown base length (CBL) is the mesiodistal length of the crown at the level of the cervix; the crown base width (CBW) is the labiolingual width of the crown at the cervix level, perpendicular to CBL; the crown base ratio (CBR) is the ratio of CBW to CBL and shows the labiolingual compression; crown height (CH) is the basoapical extent of the distal margin of the crown, from the most distal point of the cervix to the most apical point of the apex; the crown height ratio (CHR) is the ratio of CH to CBL and shows the

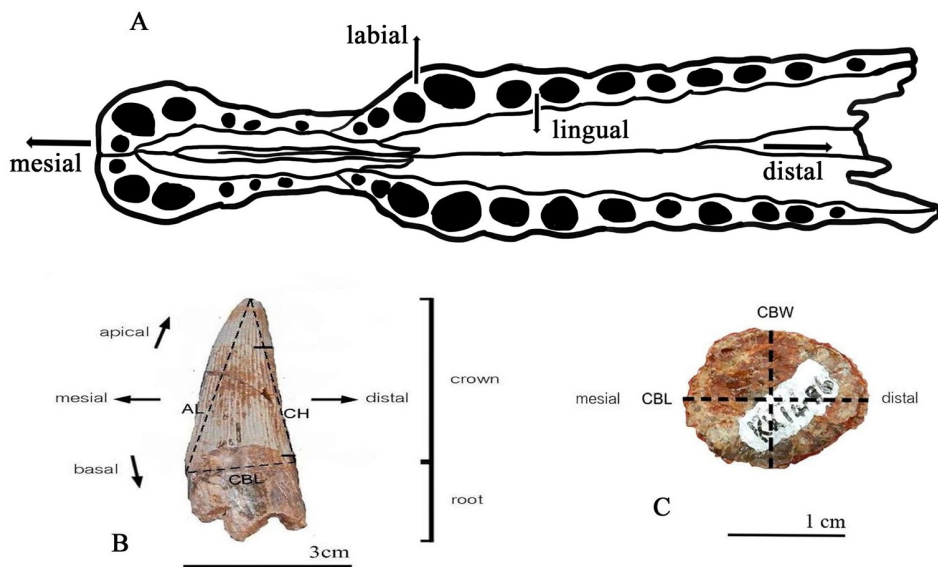


FIGURE 2. Dorsal view of an upper jaw of spinosaurid skull (modified from Smith et al., 2005) in A, technical terms of spinosaurid tooth in B (lateral view) and C (cross-section) (photo by Ployphan Chittarach, 2017)

crown elongation; the apical length (AL) is the basoapical extent of the mesial margin of the crown; the mesial serration density is the number of denticles per mm on the mesial margin; initials change according to the position of the denticles (MA refers to mesioapical denticles per mm, MC refers to mesiocentral denticles per mm, MB refers to mesio basal denticles per mm); the distal serration density is the number of denticles per mm on the distal margin (DA refers to distoapical denticles per mm, DC refers to distocentral denticles per mm, DB refers to distobasal denticles per mm); the average mesial serration density (MAVG) is the arithmetic mean of denticles per mm along the mesial carina ($MA+MC+MB/3$); the average distal serration density (DAVG) is the arithmetic mean of denticles per mm along the distal carina ($DA+DC+DB/3$) (Figure 2).

Institutional Abbreviations: PM stands for Phu Wiang fossil research center and Dinosaur Museum; GMNH stands for the Gunma Museum of Natural History, Tomioka, Gunma, Japan; IVPP stand for Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China

RESULTS

Systematic palaeontology

Dinosauria Owen, 1842
 Theropoda Marsh, 1881
 Tetanurae Gauthier, 1986
 Spinosauridae Stromer, 1915
 Spinosaurinae Stromer, 1915
 Spinosaurinae *indet.*

The described material in this paper belongs to the collections of the Department of Mineral Resources. In this study, there are 8 specimens (Figure 3) from 3 localities, i.e., Sam Ran site (n=2), Khon Kaen Province, Khok Pa Suam site (n=3), Ubonratchathani Province and Lam Pao Dam site (n= 3), Kalasin Province. Descriptions and morphological measurements of spinosaurid teeth from the studied sites are provided below and in Table 1, respectively.

Sam Ran site, Khon Kaen Province

Material: PM2016-1-001 and PM2016-1-002

From numerous material found in this site, only two specimens can be used to describe, i.e., PM2016-1-001 and PM2016-1-002. The tip of PM2016-1-002 is broken while PM2016-1-001 preserves only part of the crown, up to the tip. The cross-sections of these teeth are oval in shape. The teeth show well-pronounced carinae and ridges. The carinae are present on the mesial and distal margins of the teeth. They are slightly serrated. The ridges are slightly undulating and flutes can be observed. The enamel surface of the crown is smooth, while the base of the crown in PM2016-1-002 shows a wrinkling, similar to the tip of the apex. The number of ridges on each side is 21 and 22.

Khok Pa Suam site, Ubonratchathani Province

Material: PM2016-1-003, PM2016-1-004, and PM2016-1-005

The specimens, only PM2016-1-003 and PM2016-1-004, are complete showing well preserved their crowns and roots. The teeth are oval in cross-section with well-pronounced carinae. The carinae are present on the mesial and distal margins of the teeth

and slightly serrated. The crown surface is covered with distinctive striations. Each striation runs almost along the entire length of the crown. The enamel surface of the crown of PM2016-1-003 and PM2016-1-004 is smooth while the base of the crown enamel surface show wrinkles. The crowns show a mesiodistal curvature. The number of ridges on each side of PM2016-1-003 and PM2016-1-004 is about 25 and 22 respectively. Their ridges are finer than on PM2016-1-005 which has a wrinkled enamel surface of the crown and its base. This crown shows a slightly mesiodistal curvature. The number of ridges on each side is about 16.

Lam Pao Dam site, Kalasin Province

Material: PM2016-1-006, PM2016-1-007, and PM2016-1-008

All the teeth are incomplete and have no root. PM2016-1-007 and PM2016-1-008 show finer ridges than PM2016-1-006. The ridges and the enamel surface of the crown show some differences. The cross-section is oval in outline. The carinae are well-pronounced and clearly extend from the base of the crown to its apex. The teeth present distinct ridges. The serrations of the carinae are unclear. They have an irregular morphology similar to an undulating rope. On the crown, the enamel surface of PM2016-1-007 and PM2016-1-008 is smooth while the base of the crown shows a wrinkled enamel surface. The crowns show a mesiodistal curvature. The number of ridges on each side of PM2016-1-007 and PM2016-1-008 is about 32 and 36 respectively. Their ridges are finer than on PM2016-1-006 which has a wrinkled enamel surface on the crown and its base. Its crown shows a mesiodistal curvature. The number of ridges on each side is about 11.

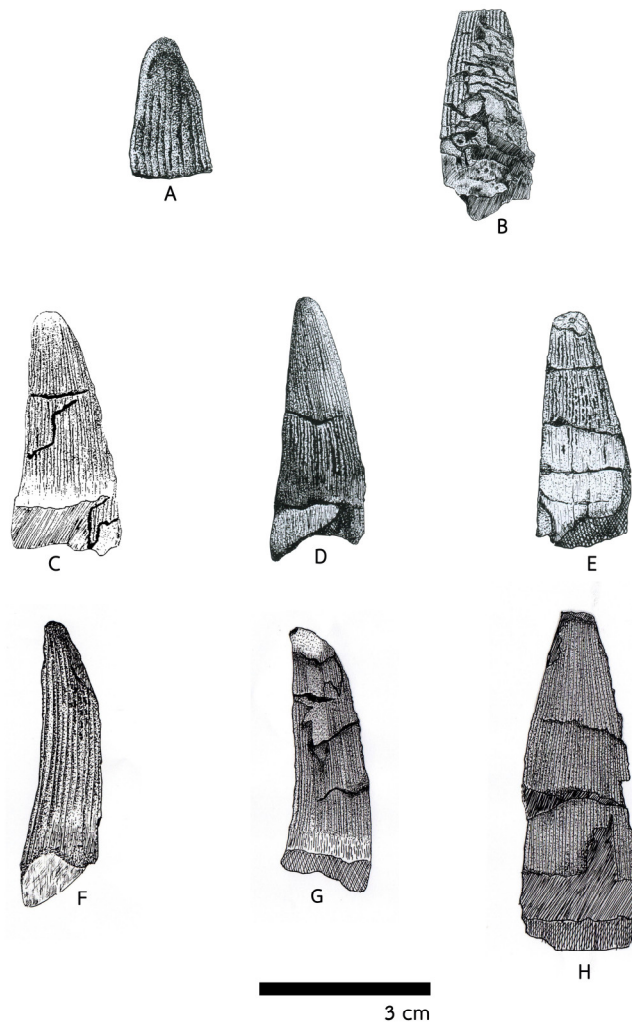


FIGURE 3. A-H, Spinosaurid tooth material studied in this paper A; PM2016-1-001 in labial view and B; PM2016-1-002 in lingual view from Sam Ran site, Khon Kaen Province C; PM2016-1-003 in labial view, D; PM2016-1-004 in labial view and E; PM2016-1-005 in labial view from Khok Pa Suam site, Ubonratchathani Province F; PM2016-1-006 in labial view G; PM2016-1-007 in labial view and H; PM2016-1-008 in lingual view from Lam Pao Dam site, Kalasin Province.

Comparisons

Comparison among Thai materials

The Khok Kruat Formation has yielded abundant conical teeth with an oval cross-section and distinct ridges and flutes, which resemble both crocodiles and spinosaurid

dinosaurs. However, there are differences in their teeth morphology. Spinosaurid teeth are bigger and longer than crocodile teeth. This might suggest that Spinosaurid was feeding on larger prey than crocodiles. Additionally, teeth of Spinosaurid are

TABLE 1. Morphological measurements of Thai spinosaurid specimens (PM2016-1-001 to 008) from 3 localities of the Khok Kruat Formation

Characters	PM2016-1-001	PM2016-1-002	PM2016-1-003	PM2016-1-004	PM2016-1-007	PM2016-1-008	PM2016-1-005	PM2016-1-006
	I						II	
Morphotype	I						II	
CBL (mm)	12.8	15.4	16.7	16.9	32.6	16.0	19.6	15.0
CBW (mm)	9.50	14.3	13.1	13.1	22.7	11.0	14.7	14.6
CBR (mm)	0.74	0.93	0.78	0.77	0.69	0.69	0.75	0.97
CH (mm)	20.0	33.6	44.3	43.3	75.1	46.3	39.8	56.8
CHR (mm)	1.56	2.18	2.65	2.56	2.30	2.89	2.03	3.78
AL (mm)	21.7	35.2	46.2	45.1	77.6	52.3	42.6	59.9
Tooth crown sub-oval to sub-circular in cross-section	yes	yes	yes	yes	yes	yes	yes	yes
Presence of flutes	yes	yes	yes	yes	yes	yes	yes	yes
Carinae bearing 6 or more denticles per mm	no	no	no	no	no	no	no	no
Enamel surface of the crown	s	s	s	s	s	s	w	w
Base of the crown enamel surface	n/a	w	w	w	w	w	w	w
Number of ridges on s each side	21	22	25	22	36	32	16	11
45 degree orientation of enamel sculpture near interdenticle sulci	no	no	no	no	no	no	no	no
Well-pronounced carinae	yes	yes	yes	yes	yes	yes	yes	yes
Curvature of the crown	n/a	n/a	yes	yes	yes	n/a	yes	yes

Note: n/a stand for not available; s stand for smooth; w stand for wrinkled.

slightly curved posteriorly while crocodile teeth are curved lingually. PM2016-1-001 to PM2016-1-008 possess labiolingual compression and anteroposterior curvature, teeth crown sub-oval to sub-circular in cross-section, well-pronounced carinae. All of these characters indicate that all studied specimens here belong to spinosaurid dinosaurs (Naksri, 2007), reminiscent of *Siamosaurus suteethorni* Buffetaut and Ingavat, 1986, from the Sao Khua Formation. However, based on the differences in number of ridges, striation

and enamel surface of the crown, two spinosaurid morphotypes (Figure 4) are recognized as follows:

Morphotype I or Khok Kruat morphotype

The average total length of this morphotype is 46.35 mm (n= 6). The average of mesiodistal length of the crown at the level of the cervix (CBL) is 18.40 mm. The average of crown base width (CBW) is 13.5 mm and the ratio of the crown base width to the crown base length (CBR) is 0.77. The average height of the

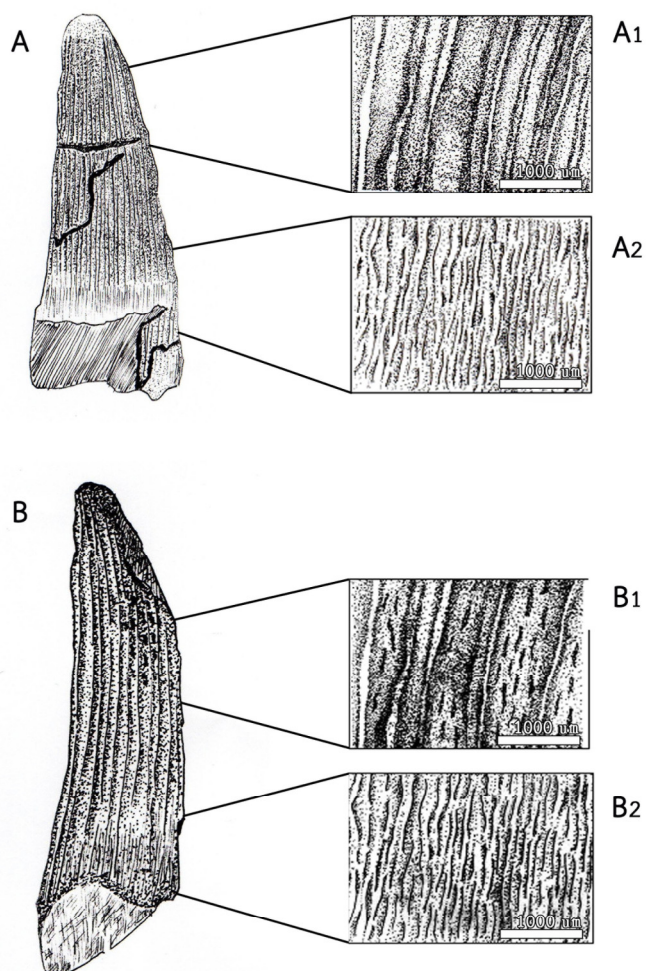


FIGURE 4. A-B Drawing of spinosaurid teeth in labial view (A) morphotype I: PM2016-1-003; (A1) smooth surface of crown; (A2) wrinkled of enamel surface of the crown and in (B) morphotype II: PM2016-1-006; (B1) ridges and the enamel surface of the crown; (B2) wrinkled of enamel surface at its base.

crown (CH) is 43.77 mm and the ratio of the crown height to the crown base length (CHR) is 2.36. The basoapical extent of the mesial margin of the crown is 38.16 mm. Teeth of morphotype I show an oval shape in cross-section with well-pronounced carinae as well as fine and sharp ridges. The

crown surface is covered with distinct striations. Each striation runs along almost the entire length of the crown. The enamel surface of the crown is smooth while the crown base shows a wrinkled enamel. The ridge numbers on each side of morphotype I are about 21 to 32.

Morphotype II or *Siamosaurus* morphotype

The average total length of this morphotype is 51.25 mm ($n=2$). The average of mesiodistal length of the crown at the level of the cervix (CBL) is 17.30 mm. The average of crown base width (CBW) is 14.65 mm and the ratio of the crown base width to the crown base length (CBR) is 0.86. The average height of the crown (CH) is 48.30 mm and the ratio of the crown height to the crown base length (CHR) is 2.90. The basoapical extent of the mesial margin of the crown is 43.00 mm. Teeth of morphotype II also show an oval shape in cross-section with well-pronounced carinae but present distinct ridges. The enamel surface of the crown and crown base are wrinkled. The ridge numbers on each side of morphotype II are about 11 to 16.

Comparison with other spinosaurids

All Khok Kruat specimens were compared with spinosaurid teeth from Asia including *Siamosaurus suteethorni*, GMNH-PV-999 from Japan, Chinese *Siamosaurus* IVPP-4793 from the Xinlong Formation of Guangxi, China, spinosaurids from the Kem Kem Beds of Morocco, spinosaurine *Irritator challenger* from Brazil, baryonychines *Suchomimus tenerensis* from Niger, and *Baryonyx walker* from England (Table 2).

Comparison of Thai material with the Baryonychinae, i.e., *Baryonyx walker* and *Suchomimus tenerensis* shows that Baryonychinae are different in having long and slender tooth roots, a sculptured (vertical striation) enamel surface of the crown base, 0–10 ridges on each side, a marked 45° degree orientation of enamel sculpture near the interdentine sulci, and no well pronounced carinae (see details in Table 1). For these reasons, the teeth from the Khok Kruat Formation should be excluded from the Baryonychinae. The

results also indicated that the Khok Kruat teeth belong to Spinosaurinae in having the follow combination characters: an oval to sub-circular outline in cross-section, bearing flutes on the crown, presence distinctive anterior and posterior carinae, the surface of the crown is covered by distinctive striations, presence a finely granular on the enamel surface, smooth or wrinkled enamel surface, irregular denticle size and the base of the crown enamel surface are wrinkled (Yoshikazu et al., 2003; Mateus et al., 2011, Smith et al., 2005).

In addition, the Khok Kruat specimens also share common spinosaurinae characters with *Irritator challenger*, *Spinosaurus* from the Kem Kem Beds of Morocco, GMNH-PV-999, *Siamosaurus suteethorni*, and Chinese *Siamosaurus* IVPP-4793 as follows: sub-oval to sub-circular cross-section, presence of flutes on the crown, and well-pronounced carinae. However, the enamel surface of the crown and crown base of *Irritator challenger* and *Spinosaurus* from the Kem Kem Beds of Morocco is smooth while the others Asian spinosaurinae, including the Khok Kruat specimens, commonly show wrinkled enamel surface of the crown and crown base. In addition, Asian spinosaurinae, except GMNH-PV-999, shows more laterally compressed teeth than *Irritator challenger* and *Spinosaurus*.

Siamosaurus teeth morphotype II share common characters with *Siamosaurus suteethorni*, GMNH-PV-999 and Chinese *Siamosaurus* IVPP-4793 as follows: wrinkled enamel surface of the crown and a number of ridges on each side, viz. between 12 to 15 ridges. In contrary, Khok Kruat teeth morphotype I show smooth enamel surface of the crown and higher ridge number on each side, viz. between 21 to 32 ridges.

TABLE 2. Comparison of dental characters between Thai specimens and other spinosaurid dinosaurs. Shaded columns are Thai spinosaurids.

	Spino- sauridae	Baryonychinae		Spinosaurinae		Asian Spinosaurinae				
	<i>Ostafrikasaurus</i> (Buffetaut, 2012)	<i>Baryonyx walker</i> Claring & Milne (1997) and Mateus <i>et al.</i> (2011)	<i>Suchomomus</i> <i>tenerensis</i> (Sereeno <i>et al.</i> , 1998)	<i>Irritator challenger</i> (Sues <i>et al.</i> , 2002)	<i>Spinosaurus</i> (Kem Kem Bed, Morocco (1*))	GMNH-PV-999 (Hasegawa <i>et al.</i> , 2003)	<i>Siamosaurus suteehorni</i> (Buffetaut and Ingavat, 1986)	Chinese <i>Siamosaurus</i> IVPP 4793 (Buffetaut <i>et al.</i> , 2008)	Khok Kruat teeth MORPHOTYPE I	<i>Siamosaurus</i> teeth MORPHOTYPE II
Tooth crown sub-oval to sub-circular in cross-section	no	yes	yes	yes	yes	yes	yes	yes	yes	yes
Carinae bearing 6 or more denticles per mm	no	yes	yes	n/a	n/a	n/a	no	n/a	n/a	n/a
Enamel surface of the crown	wrinkled	wrinkled (vertical striation)	wrinkled (vertical striation)	smooth	smooth	wrinkled	wrinkled	wrinkled	smooth	wrinkled
Base of the crown enamel surface	n/a	sculptured (vertical striation)	Smooth or poorly sculptured	smooth	smooth	n/a	wrinkled	n/a	wrinkled	wrinkled
Generally more laterally compressed	yes	yes	yes	n/a	no	no	yes	yes	yes	yes
Number of ridges on both sides	14	6 – 8	0 – 10	7	10-40	24	30	24	42-64	22-32
45 degree orientation of enamel sculpture near interdenticle sulci	no	yes	yes	no	no	yes	no	n/a	no	no
Well-pronounced carinae	yes	no	no	yes	yes	yes	yes	yes	yes	yes
Curvature of the crown	no	yes	yes	no	no	no	no	no	yes	yes
Age	Late Kimmeridgian	Barremian	Aptian	Albian	Early Cenomanian	Barremian - Aptian	Barremian - Aptian	Aptian	Aptian - Albian	Barremian - Albian

DISCUSSION AND CONCLUSION

The spinosaurid tooth specimens from the Khok Kruat Formation were collected from 3 localities, i.e., Sam Ran site, Khon Kaen Province, Khok Pa Suam site,

Ubonratchathani Province and Lam Pao Dam site Kalasin Province. They are all clearly identified as belonging to the Family Spinosauridae on the basis of their sub-oval to oval cross-section in shape of the crown and well-pronounced carinae.

The Khok Kruat teeth can be categorized into 2 types. The first is morphotype I or Khok Kruat morphotype. This type presents a smooth enamel surface of the crown and possesses more than 20 fine ridges on each side (Table 2). Another type is morphotype II or *Siamosaurus* morphotype. This type shows a wrinkled enamel surface of the crown and as far as we know not more than 16 coarse ridges on each side (Table 2). Its shape is similar to *Siamosaurus suteethorni*, from the Sao Khua Formation of Khon Kaen province, as well as *Siamosaurus* sp., from the Xinlong Formation, China. In conclusion, we, at this time, separate the Thai spinosaurid teeth into two morphotypes (I and II) on the basis of tooth characters. Morphotype II is widely distributed throughout the Sao Khua and Khok Kruat Formations whereas morphotype I can be found only in the Khok Kruat Formation. The result of this study indicates that several spinosaurid taxa potentially occurred in the Early Cretaceous of Thailand. It is likely that the specimens from the Sao Khua and Khok Kruat Formation do not belong to the same taxon because of the age difference (Barremian vs Aptian), although *Siamosaurus*-like teeth occur in both formations. The morphological differences between spinosaurid teeth from the Khok Kruat Formation allow us to distinguish two distinct morphotypes, but what these differences actually reflect is uncertain. It should be noted that we have not observed “transitional” types between the two morphotypes, so that continuous variation from one to the other can apparently be dismissed. If the two morphotypes do not correspond to different taxa, one must postulate the existence of a dimorphism within a single spinosaurid species, possibly of a sexual nature. In the absence of more

complete material (associated with dental material) that could support the hypothesis of a sexual dimorphism, it is difficult to support this idea. It should be noted that in other parts of the world, notably Morocco, it has been possible to demonstrate the coexistence in the same formation of several spinosaurid taxa on the basis of skeletal evidence (Hendrickx et al., 2016). This suggests that the hypothesis of the co-occurrence of two distinct spinosaurid taxa in the Khok Kruat Formation is more likely than that of a sexual dimorphism within a single species (which would probably involve subtle sexual differences in diet since the differences in tooth morphology possibly reflect differences in the kind of prey that was taken and consumed). Nevertheless, it should be admitted that several explanations can be provided for the existence of two tooth morphotypes and that a final solution can only be provided by the discovery of more complete material. In addition, the discovery of spinosaurids in Laos (*Ichthyovenator laosensis* without teeth associated), Japan (*Siamosaurus*-like teeth), China (*Siamosaurus*-like teeth) and Thailand (*Siamosaurus suteethorni* and Khok Kruat spinosaurine teeth) also highlights the diversity of spinosaurids and the wide distribution of these dinosaurs in Asia. Unfortunately, the Asian spinosaurid teeth are not associated with skull material. A more precise taxonomic identification of Thai spinosaurs will have to await the discovery of complete skull material including teeth associated with the jaw.

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