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Fossil assemblage from the Khok Pha Suam locality of northeastern, Thailand: an overview of vertebrate diversity from the Early Cretaceous Khok Kruat Formation (Aptian-Albian)

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Abstract

The Khok Pha Suam locality in the province of Ubon Ratchathani, northeastern, Thailand, is known as "the last home of Thai dinosaurs", because it belongs to the Lower Cretaceous Khok Kruat Formation (Aptian-Albian) which is currently the youngest Mesozoic vertebrate fossil producing formation in the Khorat Group. Here, we describe a diverse vertebrate assemblage, including hybodonts, ray-finned fishes, turtles, crocodyliforms, pterosaurs, and dinosaurs from the Khok Pha Suam locality. The updated data on the Khok Kruat fauna provides a better understanding of the variety and distribution of Early Cretaceous continental ecosystems, which are useful for palaeoenvironmental reconstruction. In addition to consolidating unincorporated data on fauna, this study also provides the palaeontological data necessary to illustrate the palaeoecosystem to the general public, as well as improving the academic value of the Pha Chan-Sam Phan Bok Geopark.

Key Words

Aptian-Albian, Khorat Group, Lower Cretaceous, Pha Chan-Sam Phan Bok Geopark, Vertebrates

1. Introduction

The Mesozoic Khorat Group is composed of non-marine sedimentary rocks ranging from the Upper Jurassic to Lower Cretaceous in northeastern Thailand. Three of the formations (Phu Kradung, Sao Khua, and Khok Kruat) have yielded rich vertebrate remains including selachians, actinopterygians, sarcopterygians, temnospondyl amphibians, turtles, crocodyliformes, pterosaurs, non-avian dinosaurs, and birds (Fig. 1) (Buffetaut and Suteethorn 1998; Buffetaut et al. 2003b, 2005, 2006). The Khok Kruat Formation is the youngest Mesozoic vertebrate-bearing formation of Thailand (Buffetaut et al. 2005) named after the Ban Khok Kruat locality in Nakhon Ratchasima Province (commonly known as Khorat Province). The Khok Kruat Formation also crops out in several other areas of northeast Thailand notably in Kalasin, Nakhon Phanom, Khon Kaen, Chaiyaphum, and Ubon Ratchathani Provinces (Buffetaut and Suteethorn 1992; Buffetaut et al. 2005; Shibata et al. 2015; Wongko et al. 2019) The Khok Kruat Formation is well-distributed in the outer rims of the Phu Phan mountain range and separated from the overlying Maha Sarakham Formation by an unconformity forming a sharp contact with basal anhydrite (Sattayarak et al. 1991; Racey et al. 1996; Jin-Geng and Meesook 2013). The Khok Kruat Formation consists mainly of reddish brown, fine- to medium-grained sandstones with minor siltstones, mudstones and conglomerates (Jin-Geng and Meesook

2013). The Khok Kruat Formation is considered the lateral equivalent to the Grès Supérieurs Formation of southern Laos. Both are considered as Aptian-Albian in age based on their vertebrate assemblages, bivalves, and palynomorphs (Cappetta et al. 1990; Buffetaut et al. 2005; Racey 2009; Allain et al. 2012). In contrast to the Barremian Sao Khua Formation, which contains no evidence of ornithischians, three taxa of hadrosauroid iguanodontians and a basal ceratopsian have been described from the Khok Kruat Formation (Buffetaut et al. 2005; Shibata et al. 2015).

Khok Pha Suam is part of the Pha Chan-Sam Phan Bok Geopark. It is the third national geopark that has been created after the Satun Global Geopark (Satun Province) and the Khorat Geopark (Nakhon Ratchasima Province). This geopark has many outstanding geological sites and contains three main spots: 'land of the last Thai dinosaurs' in the Khok Pha Suam locality; unique natural places such as Pha Chan (high cliffs above the Mekong River), the Sam Pan Bok (known as the 'Grand Canyon of Thailand', which consists of extensive bedrock with many potholes outcropping in the Mekong River), Pha Taem (ancient cliff paintings in the Pha Taem National Park); and the two-color river viewpoint where the blue water of the Mun River mixes with the brown water of the Mekong River (Singtuen and Won-in 2019; Department of Mineral Resources 2021). The creation of a geopark will help to promote trade investment and tourism, improve the quality of its inhabitants, strengthen communities, and contribute substantially to both geoconservation and geotourism by promoting a new type of tourism in Thailand (Singtuen and Won-in 2019). This study summarises the palaeontological data that illustrates to the general public what Khok Pha Suam looked like a hundred million years ago, and will also improve the academic interest of the geopark.

2. Institutional abbreviations

PRC Palaeontological Research and Education Centre, Mahasarakham University, Thailand;
SM Sirindhorn Museum, Kalasin Province, Thailand.

3. Geological settings and palaeoenvironment

Khok Pha Suam is located in the Na Kham Subdistrict, Si Muang Mai District, Ubon Ratchathani Province. The outcrop was discovered in 1993 by villagers near the forested area maintained by the Na Kham Subdistrict Administrative Organization. The site has been extensively eroded by water into a badlands-type landscape (Cappetta et al. 2006).

The thickness of the lithostratigraphic section is about 4 meters (Fig. 2c). The exposed deposits are composed of siltstone and very fine sandstone with some carbonate

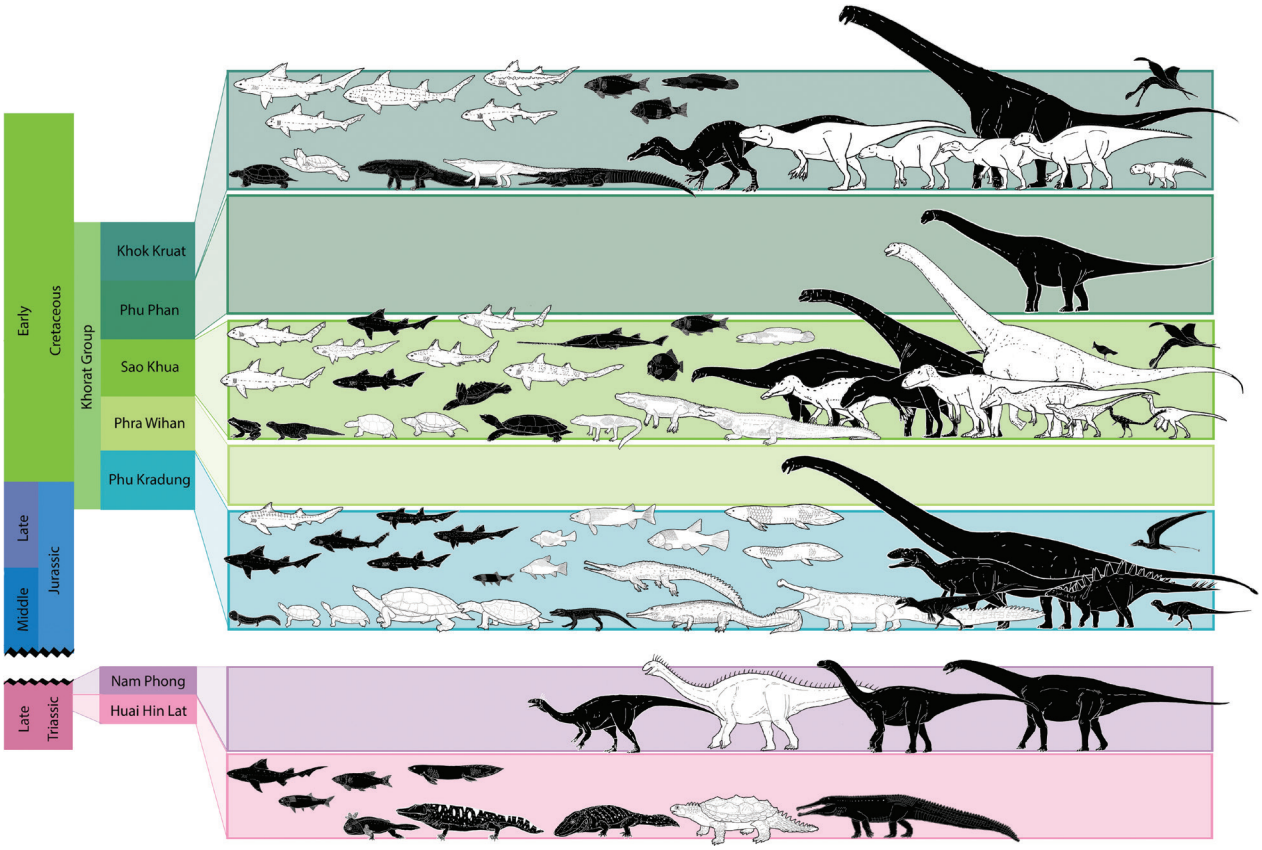

Figure 1. Mesozoic vertebrate fauna from the Indochina Terrane of NE Thailand, species-level identified taxa shown in white silhouettes, tentatively identified taxa in black silhouettes, further details in Suppl. material 1 (Modified from Lionel Cavin: All not to scale).

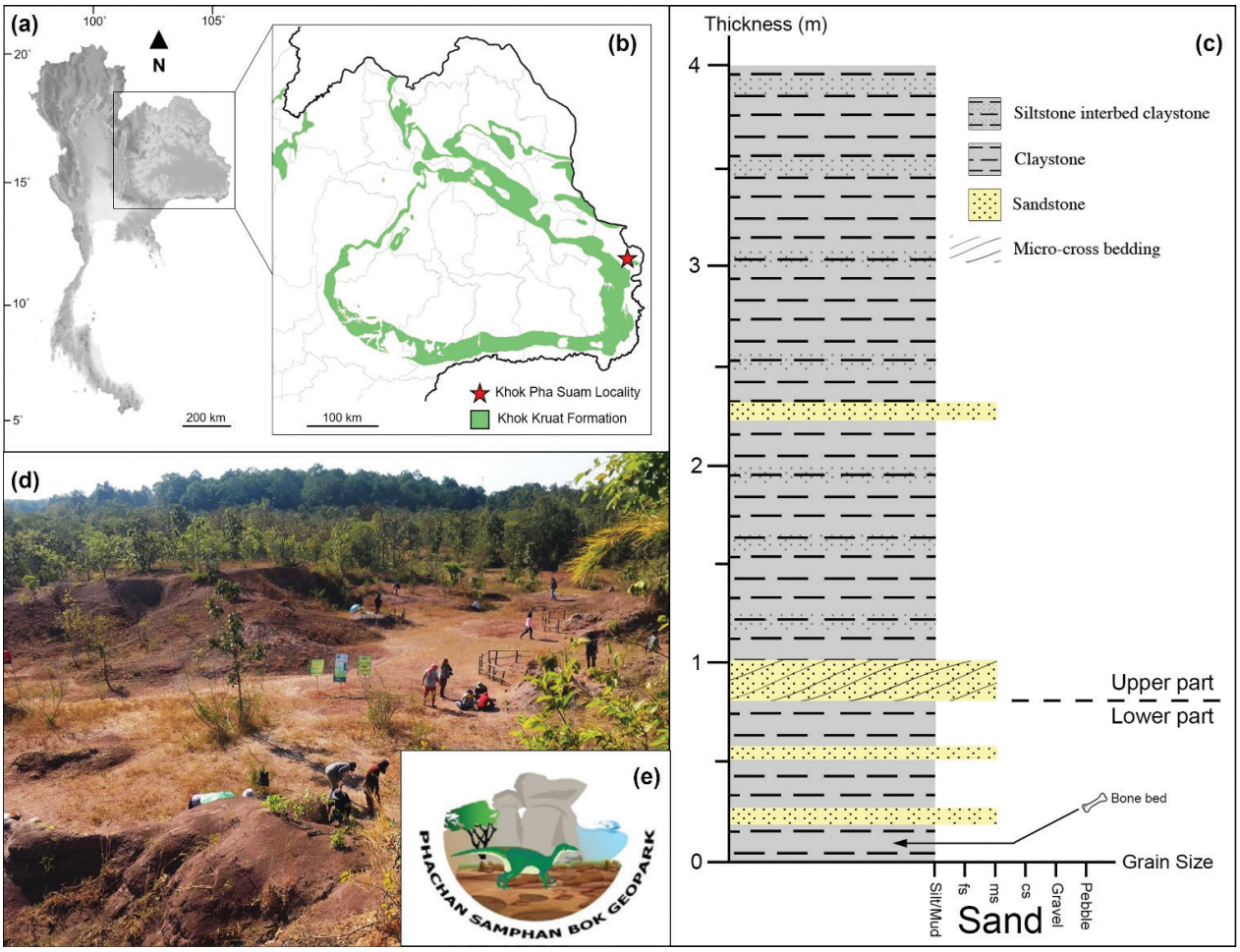

Figure 2. Locality map and Lithostratigraphic section of Khok Pha Suam locality. **a.** Map of Thailand, showing the location of the Khorat Plateau; **b.** Distribution of the Khok Kruat Formation in northeastern Thailand (green color; modified from DMR, 2004), location of Khok Pha Suam locality (red star); **c.** Stratigraphic column of Khok Pha Suam, d, a photograph of the excavation site; **e.** Logo of The Pha Chan-Sam Phan Bok Geopark.

caliche pebble conglomerates. The fining-upward sequence is pale red to grayish-red and reddish brown. The dip of the strata is 10/135 to the south-east. The lower part is 1 meter thick and consists of reddish brown very thin to thin bedded claystone grading up to thin bedded siltstone interbedded with fine-grained sandstone. The fragile vertebrate remains are found on the eroded surface of this layer which can be collected directly. The upper part is 3 meters thick and consists of reddish-brown, thin-to medium bedded, medium-grained sandstones interbedded siltstones, claystones. A calcrete horizon (palaeosol) has been found at the top of the succession (Wongko 2018; Wongko et al. 2019).

The bonebed presents lithostratigraphic and sedimentary structures composed of fining-upward sequences, carbonate caliche horizon, micro cross-bedding, load-cast and rip-up clasts, micaceous fine sand and silt which also form scattered thin lenticular beds and laminated carbonaceous shale in the sequences. These features indicate low-energy current, floodplain deposits. Fossil remains consist of isolated or fragmentary elements indicating transport under high energy conditions and deposition on floodplains. It could correspond to an arid or semi-arid subtropical climate, as indicated by the caliche pebble conglomerate (Fig. 6) (Wongko 2018; Wongko et al. 2019).

4. Material

The specimens were collected from Khok Pha Suam locality, Na Kham Subdistrict, Si Muang Mai District, Ubon Ratchathani Province (Fig. 2) and are now housed in the collections of the Palaeontological Research and Education Centre, Mahasarakham University and Sirindhorn Museum. This work includes a review of published specimens and new records from recent discoveries.

5. Vertebrate palaeontology

The vertebrates found at the Khok Pha Suam locality comprise five taxa of hybodont sharks, at least two taxa of ginglymodians, a sinamiid fish, carettochelyid and adocid turtles, neosuchian crocodyliforms, pterosaurs, dinosaurs (iguanodontians, sauropods, and at least two taxa of theropods). The faunal diversity described in this article

together with additional data from other localities allows us to propose a preliminary reconstruction of the Early Cretaceous Khok Kruat Formation ecosystem (Fig. 6).

5.1 Selachians

Class Chondrichthyes Huxley, 1880
Euselachii Hay, 1902
Hybodontiformes Patterson, 1966
Family Thaiodontidae Cuny, Suteethorn, Khamha & Buffetaut, 2008
***Thaiodus ruchae* Cappetta, Buffetaut, & Suteethorn, 1990 (Fig. 3a)**

T. ruchae possesses asymmetric teeth with an occlusal crest displaced lingually. Its serrated teeth are strongly interlocked, which usually indicates preference in hunting large prey and possibly occasional scavenging via the ability to cut tough meat (Cuny et al. 2008). *T. ruchae* is also found in the Ban Sam Ran locality (Khon Kaen Province), Lam Pao Dam (Kalasin Province), Ban Khok Kruat and Ban Sapan Hin localities (Nakhon Ratchasima Province) (Cuny et al. 2007, 2008; Wongko 2018).

***Khoratodus foreyi* Cuny, Suteethorn, Khamha & Buffetaut, 2008 (Fig. 3b)**

K. foreyi teeth are very elongated, flattened, and rod shaped. *Thaiodus* and *Khoratodus* teeth show common features in addition to their asymmetry, such as the ornamentation restricted to the upper half of the crown and they also show a common vascularization pattern of the root and an interlocking system between the teeth which is unusual among hybodonts. These genera are included in the family Thaiodontidae, which appear to be restricted to Asia (Cuny et al. 2008).

"*Hybodus*" *aequitridentatus* Cuny, Suteethorn, Khamha, and Buffetaut., 2008 (Fig. 3c)

"*H.*" *aequitridentatus* teeth are probably adapted towards an opportunistic feeding method, but the low and blunt cusps indicate some specialization towards hard-shelled preys (Cuny et al. 2008). Based on new material found in the Xinlong Formation (Guangxi Province, southern China), Cuny et al. (2017) proposed that this species does not belong to the genus *Hybodus* but to a new genus of the family Thaiodontidae.

Family incertae sedis
***Heteroptychodus steinmanni* Yabe & Obata, 1930 (Fig. 3d)**

H. steinmanni is quite abundant at Khok Pha Suam. Its teeth are typically broad, with a low crown densely and are strongly ornamented, which indicates specialization towards a durophagous diet (Cuny et al. 2008). *H. steinmanni* occur also in other Khok Kruat Formation outcrops including Ban Sam Ran, Wat Wang Sai (Khon Kaen Province), Lam Pao Dam, and Ban Sapan Hin (Cuny et al. 2007, 2008; Wongko 2018). Moreover, A single tooth of *Heteroptychodus* sp. was discovered in Ban Pha Nang Sua (Chaiyaphum Province) (Department of Mineral Resources Division of Fossil Protection 2016).

Besides the Khok Kruat Formation, *H. steinmanni* was also discovered from various localities of the Sao Khua Formation (Cuny et al. 2007). Another species, *H. kokutensis* have been reported from Ko Kut, Trat Province, which is likely correlated with the Sao Khua Formation (Cuny et al. 2010). *Heteroptychodus* sp. have been reported from the Phu Kradung Formation in Chong Chat, Nong Bua Lamphu Province, and Kham Phok, Mukdahan Province (Cuny et al. 2007).

Family incertae sedis
***Acrorhizodus khoratensis* Cappetta, Buffetaut, Cuny & Suteethorn, 2006 (Fig. 3e)**

A. khoratensis teeth possess a high root with a U-shaped longitudinal crest, except in the posterior teeth. The crown is broadly rectangular in apical view. A blunt cusp is also observed on the labial side that is almost as wide as the crown. The tooth morphology indicates adaptations towards various food source, in a way probably similar to *H. aequitridentatus* (Cuny et al. 2008).

5.2. Actinopterygians

Isolated remains of actinopterygians (ray-finned fishes) preserved in the Khok Pha Suam locality usually consist of vertebral centra, fragments of skull bones, fragments of jaws, isolated teeth, and numerous scales.

Holostei Müller, 1844 sensu Grande, 2010
Ginglymodi Cope, 1872 sensu Grande, 2010
Lepisosteiformes Hay, 1929 sensu López-Arbarello, 2012
Family incertae sedis (Fig. 3f–g)

Two taxa of ginglymodians can be separated by the ornamentation of their ganoid scales (Cavin et al. 2009). Ginglymodi type I (Fig. 3f) is represented by scales with a smooth surface whereas Ginglymodi type II (Fig. 3g) possess slightly larger scales with parallel ridges on the surface.

***Lanxangichthys* sp. Cavin, Deesri, Veran, Khentavong, Jintasakul, Chanthasit & Allain, 2018**

So far, only one genus of ginglymodian, *Lanxangichthys*, has been identified on the basis of fossil material from the Khok Kruat Formation and from the Grès supérieurs Formation in Laos. Isolated skull remains from Ban Sapan Hin and Khok Pha Suam localities present strong

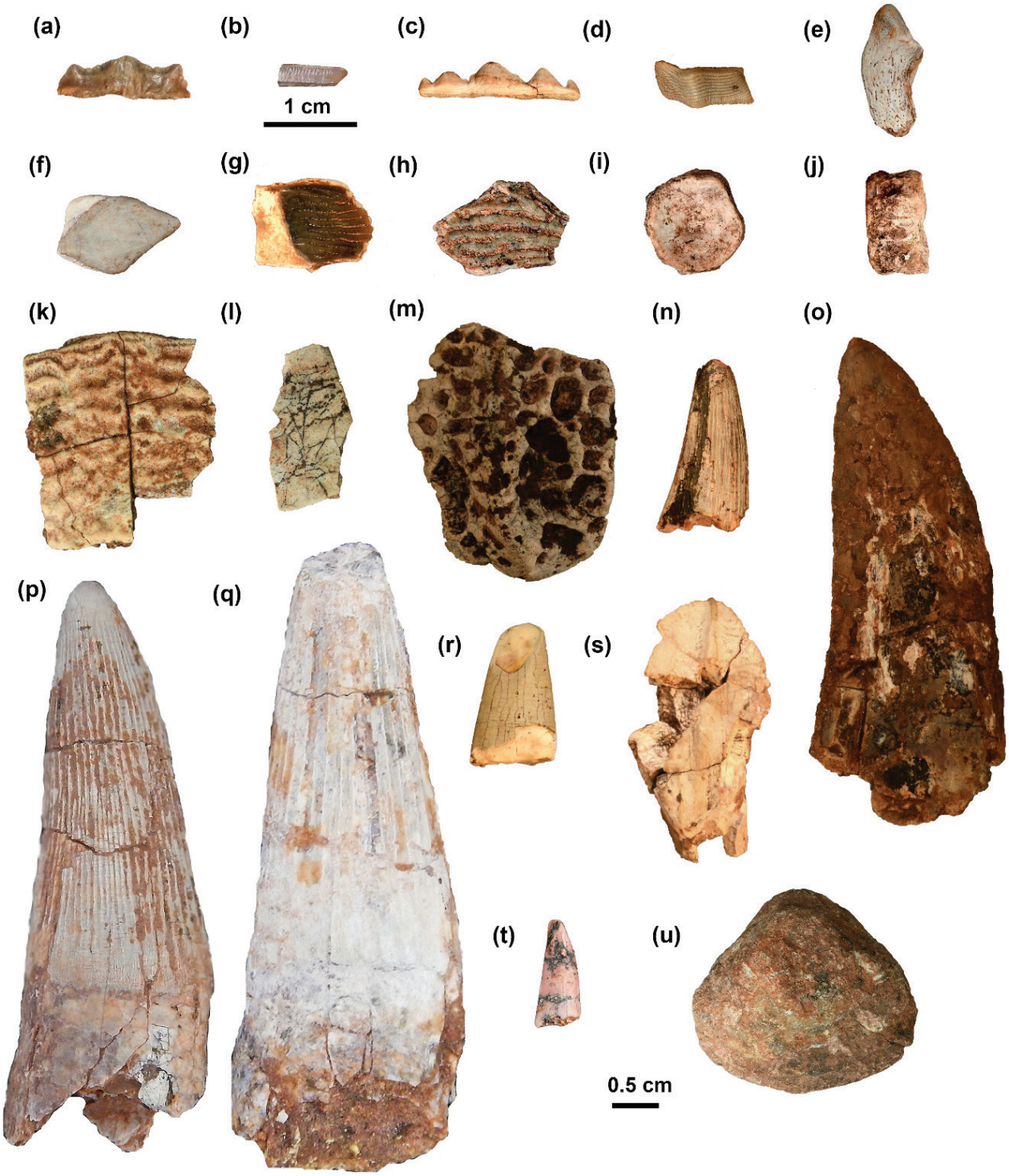

Figure 3. Isolated microremains from Khok Pha Suam locality. *Thaiodus ruchae* tooth (**a.** PRCMR301) in labial view, *Khoratodus foreyi* tooth (**b.** PRCMR302) in lingual view, "*Hybodus*" *aequitridentatus* tooth (**c.** PRCMR303) in labial view, *Heteroptychodus steinmanni* tooth (**d.** PRCMR304) in apical view, *Acrorhizodus khoratensis* tooth (**e.** PRCMR305) in mesio-lingual or disto-lingual view, ginglymodian external side scales with ganoin, uncovered field and bone on the anterior margin (**f–g.** PRCMR305-306) in dorsal view, ginglymodian external side of the dermal bone (**h.** PRCMR307) in dorsal view, sinamiid centrum (**i–j.** PRCMR308) in anterior (**i.**) and dorsal (**j.**) views, carettochelyid shell fragment (**k.** PRCMR309) in dorsal view, adocid shell fragment (**l.** PRCMR310) in ventral view, neosuchian osteoderm (**m.** PRCMR311) in dorsal view, neosuchian tooth (**n.** PRCMR312) in lingual view, theropod tooth (**o.** SM2016-1-155), spinosaurid tooth morphotype I (**p.** PM2016-1-003) in anterior view, spinosaurid tooth morphotype II (**q.** PM2016-1-006) in anterior view, sauropod tooth (**r.** PRCMR315) in lingual view, iguanodontian tooth (**s.** SM2021-1-121), pterosaur tooth (**t.** PRCMR317), and bivalve mold right valve of articulated shell (**u.** PRCMR318) in external view. Scale bars: 0.5 cm (**a, c–s**); 1 cm (**b**).

ornamentation of ganoin forming radiating and tuberculate patterns similar to the ornamentation of non-weathered bones of a single articulated skull of the holotype of *L. alticephalus* from the Savannakhet Basin in Laos. As the Grès supérieurs Formation from the Savannakhet Basin are regarded as an equivalent to the Khok Kruat Formation, the isolated ornamented cranial remains from Khok Kruat Formation are referred, with caution, to *Lanxangichthys* sp. (Cavin et al. 2018). In regard to the body shape of *Lanxangichthys*, the scales type II from the Khok Pha Suam locality probably belongs to the genus *Lanxangichthys* as the scale itself are deep.

Amiiformes sensu Grande & Bemis, 1998
Halecomorphi Cope, 1872
Family Sinamiidae Berg, 1940
cf. *Siamamia* Cavin, Suteethorn, Buffetaut, Claude, Cuny, Le Loeuff & Tong, 2007 (Fig. 3i–j)

Vertebral centra are referred to a sinamiid together with fragments of dentaries, a premaxilla, possible fragments of maxillae and many scale types from the Khok Pha Suam locality. The material shows similarities with *Siamamia naga* from the older Sao Khua Formation (Cavin et al. 2009; Deesri et al. 2017). For instance, the scales are much smaller and thinner than those of the two different ginglymodian scales whereas the isolated fragment of jaws are obviously similar in each. In 2018, another sinamiid specimen was discovered during a Thai-Japan joint excavation in the Ban Krok Duean Ha locality, Nakhon Ratchasima province. This sub-complete and articulated specimen is significantly different from *S. naga*, and possibly represents a new species or even a new genus (Deesri et al. 2021).

5.3. Turtles

Testudines Cope, 1868
Cryptodira Cope, 1868
Trionychoidae Fitzinger, 1826 sensu Gaffney & Meylan, 1988
Family Adocidae Cope, 1870 (Fig. 3k)
Family Carettochelyidae Boulenger, 1887 (Fig. 3l)

Two different families of trionychoids have been collected from the Khok Pha Suam locality, each identified by the ornamentation pattern of their shell fragments: the carettochelyid fragment is covered with strong ornamentation (Fig. 3k), while the adocid fragment is covered with tiny pits (Fig. 3l). Although turtle remains are quite abundant in Khok Pha Suam, they are too fragmentary for in-depth identification. Two genera of trionychoids have been reported from the Khok Kruat Formation, the carettochelyid *Kizylkumemys khoratensis* from Ban Sapan Hin (Nakhon Ratchasima), and the adocids *Shachemys laosiana* from the Grès Supérieurs Formation of southern Laos and *Shachemys* sp. from Ban Sapan Hin (Tong et al. 2005, 2009).

5.4. Crocodyliforms

Crocodylomorpha Walker, 1970
Crocodyliformes Hay, 1929
Neosuchia Benton & Clark, 1988
Family incertae sedis (Fig. 3m–n)

Osteoderms (Fig. 3m) and teeth (Fig. 3n) of neosuchian crocodyliforms have been collected on the outcrop surface and are rather poorly preserved. The teeth sample can be divided into four morphotypes: morphotype I is robust, high and conical; morphotype II is slender and conical; morphotype III is roughly triangular; morphotype IV is relatively short and robust (Lauprasert 2006).

Family Goniopholididae Cope, 1875 (Fig. 4)

A nearly complete left mandible of goniopholidid (SM2021-1-112: Fig. 4), 327 mm in length, consists of a dentary, splenial, surangular and angular. The anterior extremity to the second alveolus of the specimen is lacking. The dentary is elongated and about 285 mm in length. In dorsal view, 23 dentary alveoli, the second to the 24th ones, can be counted. The dentary alveoli are separated by equal interalveolar septum 2 mm long, except between the second and the third, the fourth and the fifth ones, which show slightly wider spaces of about 5 mm. The ventral surface of the specimen is strongly convex transversally. Above this convexity, the base of the root of the second dentary tooth is observed *in situ*, below the level of the third dentary alveolus. The preserved tooth is slightly curved lingually and has an oval cross-section. In dorsal view, the lateral margin of the specimen exhibits three convexities. The first convexity is situated at the level of the fourth dentary alveolus, suggesting the position of the largest tooth on the dentary. The second convexity reaches its maximum at the level of the 16th dentary alveolus while the third convexity is located at the level of the anterodorsal extremity of the surangular. The dentary floor is partly preserved at the medial margin of the fourth to the sixth dentary alveoli. Because the splenial is crushed and distorted, a part of its medial surface is visible in dorsal view only from the sixth to the 17th dentary alveoli. A row of vascular foramina is visible in the medial margin of the tooth row, each about 1–2 mm in diameter. Posteriorly, the 18th to the 24th dentary alveoli are worn but parts of their labial edges remain partially intact. In lateral view, the dorsal margin of the specimen presents two convexities. The first convexity rises to the level of the third and fourth dentary alveoli. The dorsal margin becomes strongly concave and reaches its maximum concavity at the level of the 10th and 11th dentary alveoli. The second convexity reaches the maximum curvature at the level of the 18th dentary alveolus. These convexities are about twice as high as the maximum of the concavity.

This left mandible of SM2021-1-112 cannot be compared with the slender-snouted neosuchian crocodyliform *Khoratosuchus jintasakuli* (Lauprasert et al. 2009), from the Khok Kruat Formation of Nakhon Ratchasima, which is only known by a partial skull without mandible.

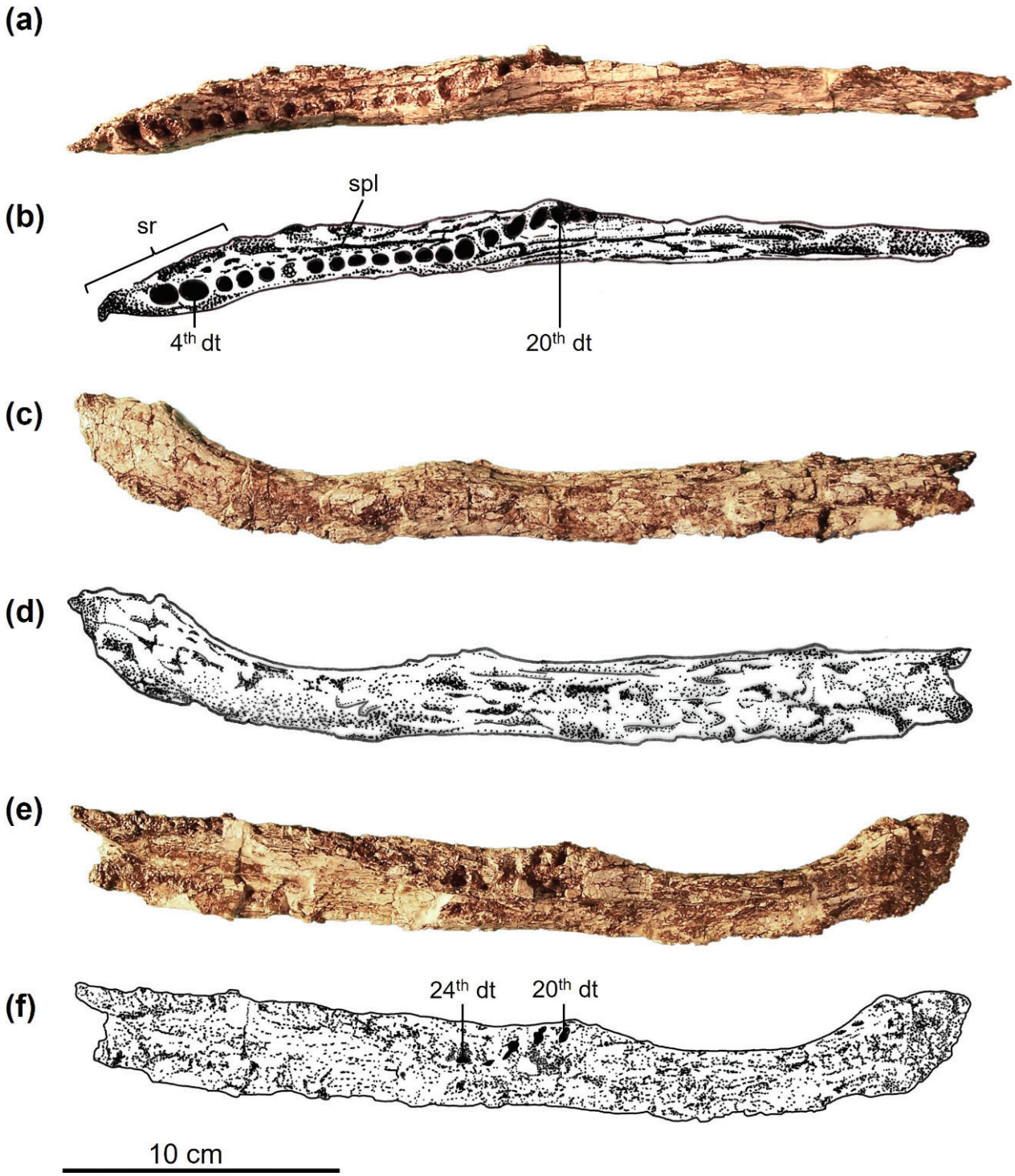

Figure 4. Photos and drawing of a nearly complete left mandible of Goniopholididae indet. from Khok Pha Suam (SM2021-1-112) in dorsal (**a, b**), lateral (**c, d**) and lingual (**e, f**) views. Abbreviation: dt, dentary tooth; spl, splenial; sr, symphyseal region.

However, the presence of a short dentary symphysis and the number of preserved dentary teeth indicate that SM2021-1-112 is also a short-snouted crocodyliform. Moreover, the presence of the enlarged and contiguous third and fourth dentary alveoli reinforces the idea that SM2021-1-112 belongs to the family Goniopholididae (Buffetaut and Ingavat 1983). It is quite difficult to distinguish the goniopholidid genera from only a part of the lower jaw. Short-snouted crocodyliforms have been reported from the older Sao Khua Formation, including "*Goniopholis*" *phuwiangensis* (Buffetaut and Ingavat 1983), which cannot be confidently attributed to the genus *Goniopholis* (Lauprasert 2006; Andrade et al. 2011) and *Siamosuchus phuphokensis* (Lauprasert et al. 2007). The latter taxon is known only from a upper jaw and postcranial material. However, more material is needed in order to confirm the exact taxonomic status of SM2021-1-112.

On the contrary, SM2021-1-112 shows a combination of characters on the dentary that have been described in "*G.*" *phuwiangensis*, which are: 1) anterior portion of the

tooth row with no marked angulation; 2) absence of a strong outward protrusion of the lateral margin at the level of the third and the fourth dentary alveoli and 3) presence of dentary curvatures in both lateral and vertical planes. However, based on the strong undulation of its lateral margin on a vertical plane, SM2021-1-112 can be distinguished from "*G.*" *phuwiangensis*. The first and the second convexities of SM2021-1-112 are about twice as high as its concavity, whereas in "*G.*" *phuwiangensis*, the proportion between the maximum height of convexity and concavity is significantly less than that of SM2021-1-112. Additionally, the ornamentation on the lateral surface of SM2021-1-112 is faintly sculptured whereas that of "*G.*" *phuwiangensis* is heavily sculptured. These two characters, therefore, are sufficient to validate SM2021-1-112 as a species different from "*G.*" *phuwiangensis*.

Based on the obscured relationships of the Thai, European and North American *Goniopholis* as well as the absence of the lower jaw of *Siamosuchus*, it should be suitable for the time being to consider SM2021-1-112 as an uncertain genus in the family Goniopholididae until further studies can accurately evaluate the internal relationships of Thai goniopholidids.

5.5. Sauropods

Dinosauria Owen, 1842
Saurischia Seeley, 1888
Sauropoda Marsh, 1878
Neosauropoda Bonaparte, 1986
Macronaria Wilson & Sereno, 1998 (Fig. 3r)

Sauropod remains are rare in Khok Pha Suam. A small femur approximately 40 cm in length of a probable juvenile sauropod is an exhibit at the local museum under the supervision of Na Kham Subdistrict Administrative Organization. Some isolated teeth have been found but are very fragile. A peg-shaped tooth (PRCMR315, Fig. 3r), missing half its proximal portion shows a nearly cylindrical crown and symmetrical D-shaped cross-section and possesses an apical wear facet on the lingual side, suggesting that it is an upper tooth based on comparisons with *Nemegtosaurus mongoliensis* (Wilson 2005). The ridges on both the mesial and distal edges are notable. The tooth is lingually curved with a smooth grey enamel on the crown surface except for the wear facet. Thai sauropod teeth can be divided into two morphotypes; spoon-shaped teeth were discovered from the Late Jurassic Phu Kradung Formation and the Early Cretaceous Sao Khua Formation whereas peg-shaped teeth were discovered from the Sao Khua and Khok Kruat Formations. Peg-shaped sauropod dentition tend to be associated with Diplodocoidea and Titanosauriformes (Macronaria) (Upchurch 1995, 1998; Wilson and Sereno 1998). The Khok Pha Suam teeth are reminiscent of *Phuwiangosaurus sirindhornae*, a basal titanosauriform from the Sao Khua Formation (Buffetaut et al. 2005; Suteethorn et al. 2009).

5.6. Theropods

Theropoda Marsh, 1881
Superfamily Allosauroidea Marsh, 1878 (Fig. 3o)

Several teeth of theropod dinosaurs differing in size have been collected and can be divided into Allosauroidea and Spinosauridae. The allosauroid teeth (Fig. 3o) resembles the Khok Kruat basal carcharodontosaurian *Siamraptor suwati* (Chokchaloemwong et al. 2019). Teeth are ziphodont (blade-shaped and serrated) with subquadrangular denticles (serration) on both margins, lenticular shaped in crown cross-section, and with arcuate enamel wrinkles that extend across the labial and lingual margins, which is a feature shared with other members of Allosauroidea (Brusatte et al. 2007; Hendrickx et al. 2015).

Family Spinosauridae Stromer, 1915 (Fig. 3p–q)

Spinosaurid teeth exhibit conical crown and extremely reduced serrations, a morphology reminiscent of crocodilian teeth. The teeth of Khok Kruat spinosaurids can be categorized into two sub-morphotypes (Wongko et al. 2019), both found in the Khok Pha Suam locality. Sub-morphotype I (Fig. 3p) presents a smooth enamel surface of the crown and possesses more than 20 fine ridges on each side. Sub-morphotype II (Fig. 3q) shows a wrinkled enamel surface of the crown and no more than 16 coarse ridges on each side, which is similar to *Siamosaurus suteethorni* from the Sao Khua Formation.

The spinosaurid *Ichthyovenator laosensis* (Allain et al. 2012) has been described from Laos on the basis of skeletal remains, and post-cranial elements of an indeterminate spinosaurid have been reported from Ban Sam Ran (Buffetaut et al. 2005), but no bones of spinosaurid have been found so far in the locality of Khok Pha Suam.

5.7. Iguanodontians

Onithischia Seeley, 1888
Neornithischia Cooper, 1985
Ornithopoda Marsh, 1881
Iguanodontia Dollo, 1888 (Fig. 3s and Fig. 5)

Teeth of iguanodontian dinosaurs are common and show a heavy degree of wear. SM2021-1-121 (Fig. 3s) is the largest one collected presently. It resembles the dentary tooth of *Sirindhorna khoratensis* (Shibata et al. 2015), with a leaf-shape and enamel-covering on the lingual surface of the tooth. A strong primary ridge runs along the entire height of the crown. At least two weak secondary ridges are present on the mesial side and one on the distal side. Denticles are present on both mesial and distal crown borders. The lower part of the crown possesses a facet for an adjacent tooth allowing the formation of a complex dental battery.

Although Khok Pha Suam vertebrates are mostly known from microremains and fragmentary larger remains, some

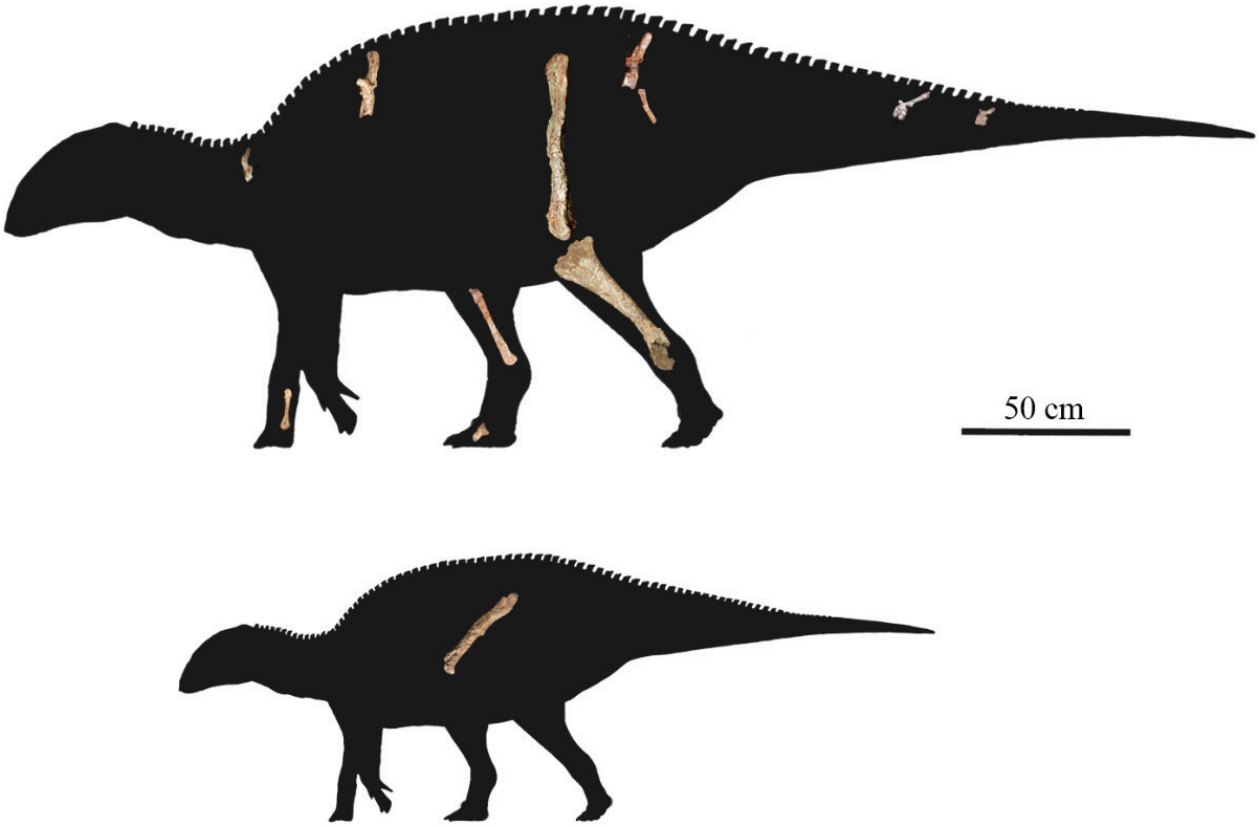

Figure 5. Tentative reconstruction of Khok Pha Suam iguanodontian indet. showing recovered bones in left lateral view

isolated postcranial bones belonging to iguanodontians were discovered (Fig. 5), including vertebrae and limb bones from different individuals. For this reason, these herbivores are outstanding from all the other tetrapods of the Khok Pha Suam locality, becoming therefore an iconic symbol of Pha Chan-Sam Phan Bok Geopark (Fig. 2c).

Three taxa of hadrosauroids have been described from the Khok Kruat Formation in Nakhon Ratchasima Province, including *Siamodon nimngami* (Buffetaut and Suteethorn 2011), *Ratchasimasaurus suranareae* (Shibata et al. 2011), and *Sirindhorna khoratensis* (Shibata et al. 2015). Material of *S. nimngami* and *R. suranareae* encompass only a left maxilla and a left dentary, respectively. However, *S. khoratensis* is the best-preserved iguanodontian ornithopod in Southeast Asia, described from a composite individual including skull and mandible, as well as postcranial elements (Shibata et al. 2018). Therefore it is necessary to compare the postcranial material between Khok Pha Suam taxa and *S. khoratensis* in our further research.

5.8. Pterosaurs

Pterosauria Kaup, 1834
Pterodactyloidea Plieninger, 1901 (Fig. 3t)

Pterosaur teeth in Thailand are very scarce. An isolated Ornithocheirid tooth has been reported from the Sao Kua Formation in northeastern Thailand (Buffetaut et al. 2003a). A well-preserved tooth (Fig. 3t) from Khok Pha Suam presents a slender crown with an oval cross-section, pointed apex and no carinae on both margins. The labial and lingual sides are slightly convex, moderately recurved mesiodistally, and nearly straight labiolingually. The enamel surface is smooth without ridges on the labial and lingual sides. The enamel covering the apex to the base on both surfaces indicates that this specimen is the tip of the crown (Wellnhofer and Buffetaut 1999). The Khok Pha Suam pterosaur is probably related to ornithocheiroids based on the mentioned characters (Alves et al. 2007). Teeth of Khok Kruat pterosaur are also found in Nakhon Ratchasima. They are on exhibit at the Northeastern Research Institute of Petrified Wood & Mineral Resources (In Honor of His Majesty the King) Nakhon Ratchasima Rajabhat University.

6. Overview of other Khok Kruat localities

The sedimentology of Khok Kruat localities shows that the vertebrate fossils were deposited in a fluvial system including flood plains and channels of meandering rivers. At Ban Saphan Hin, Nakhon Ratchasima Province, various vertebrate remains were found scattered and fragmented in a medium to thick-bedded reddish-brown conglomerates. The conglomerates are locally cross-bedded. These elements indicate that the fossils were transported with medium to high energy and deposited in the channel. Carbonate clasts are commonly found and well cemented by calcite. These shreds of evidence

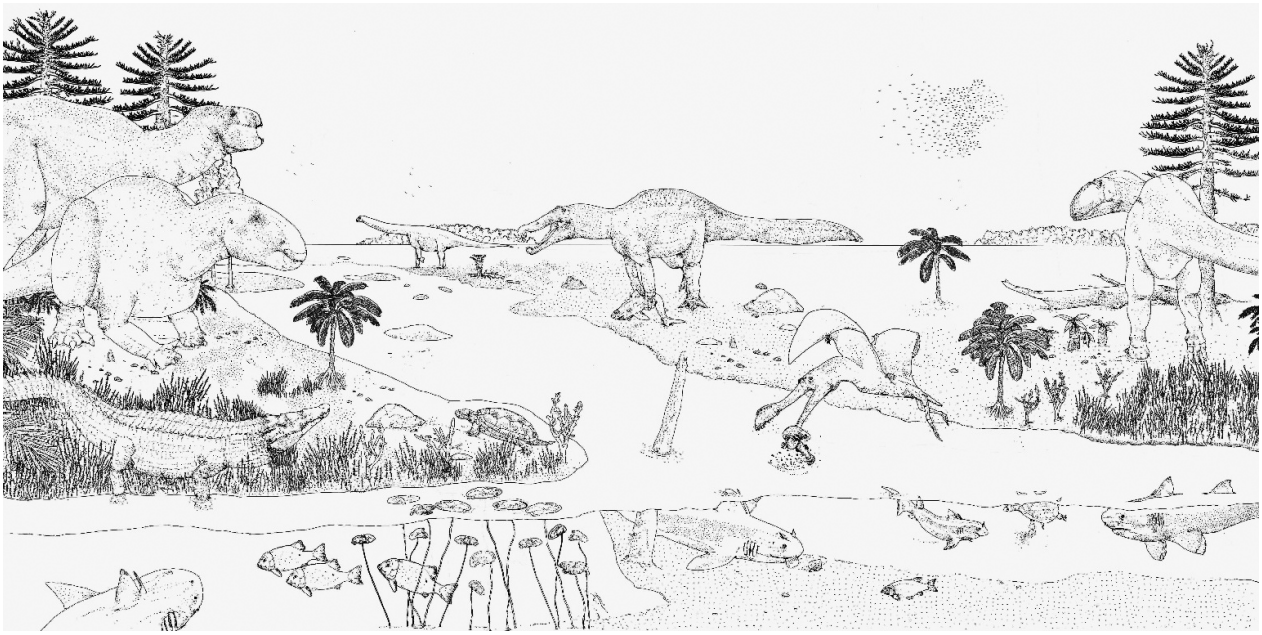

Figure 6. Palaeoenvironmental interpretation of the Early Cretaceous (Aptian-Albian) Khok Pha Suam Locality. Drawing by Sakka Weerataweemat.

suggest a semi-arid environment. This locality has yielded *Thaiodus ruchae*, *Heteroptychodus steinmanni*, *Lanxangichthys* sp., *Shachemys* sp., *Kizylkumemys khoratensis*, *Khoratosuchus jintasakuli*, Eusuchian indet., *Sirindhorna khoratensis*, *Siamraptor suwati* (Tong et al. 2005; Cuny et al. 2008; Lauprasert et al. 2009; Shibata et al. 2015; Cavin et al. 2018; Kubo et al. 2018; Chokchaloemwong et al. 2019).

Many groups of vertebrates have been found in the Sam Ran locality, Khon Kaen Province, including teeth of two hybodont taxa (incl. *H. steinmanni*, and *T. ruchae*), ganoid scales of actinopterygians (Ginglymodi type II), turtle shell fragments, teeth of crocodyliforms, teeth of large theropods and partial postcranial bones of spinosaurid indet. The presence of sedimentary structures such as fining upward, planar cross-bedding, load casted, rip-up clasts indicate meandering channel deposits and crevasse splay sequences. The very good preservation of the vertebrate fossils, notably the partial skeleton of a spinosaurid indet. is likely a result of a low-energy current system. The calcisol with pedogenetic carbonates is an indication of a semi-arid climate (Wongko 2018). Unfortunately, this locality has been transformed due to land use making further excavation attempts more difficult.

Lam Pao Dam locality in Kalasin Province has poor fossil preservation. This locality has yielded the teeth of hybodonts (incl. *H. steinmanni*, *T. ruchae* and possibly *K. foreyi*), teeth and scales of ginglymodians, teeth of crocodyliforms and theropods. Trace fossils, such as theropod footprint, *Lockeia*, *Phycodes*, *Planolites*, and *Skolithos* indicate a moderately to well-drained floodplain. It could have been arid or semi-arid in a subtropical climate, as indicated by the caliche-siltstone granule calcareous sandstone deposits. The presence of lithostratigraphic and sedimentary structures such as stacked fining-upward sequences, small scale cross-bedding, rip-up clasts, and conglomerates at the base of sequences indicate high-energy current, meandering channel conglomerate deposits or point-bar deposits (Wongko 2018).

The fossil remains from Ban Pha Nang Sua locality, Chaiyaphum Province are found in reddish-brown sandstones and siltstones in the lower part of the sequence which is interpreted as a crevasse splay deposit. Most of the specimens belong to a giant titanosauriforms indet., associated with some teeth of hybodonts, crocodyliforms, and theropods (Department of Mineral Resources Division of Fossil Protection 2016).

7. Discussion

The vertebrate fauna from Khok Pha Suam represents the richest assemblage at the generic level within the Khok Kruat Formation (Table 1). Although there are similarities when compared to the Barremian Sao Khua Formation, the existence of ornithischian dinosaurs is an important difference between the two formations.

Hundreds of isolated teeth and many dorsal fin spine fragments of hybodonts representing up to five different genera have been recovered so far. Pattern and form variation of these shark teeth show adaptations towards various diets: cutting (*Thaiodus*), crushing (*Khoratodus*, "*Hybodus*" and *Acrorhizodus*), and grinding (*Heteroptychodus*) (Cuny et al. 2017). Bivalve internal molds (Fig. 3u) which have been found in Khok Pha Suam resemble *Trigonioides trigonus* (Hoffet 1937) from the Grès Supérieurs Formation of southern Laos and *Pseudohyria* (*Matsumotoina*) *somanai* (Tumpeesuwan et al. 2010) from the older Sao Khua Formation based only on comparisons with external shell morphology. Additional

Table 1. List of vertebrate faunas from Khok Pha Suam locality with other taxa from the Khok Kruat Formation (*The Grès Supérieurs Formation of southern Laos is laterally considered an equivalent to the Khok Kruat Formation).

Taxa	Khok Pha Suam	References	Khok Kruat (other localities)	References
Ornithopods	Iguanodontian indet.	(Buffetaut et al. 2003b, 2005)	*Mandschurosaurus laosensis* (Laos*)	(Hoffet 1944)
			Siamodon nimngami (Nakhon Ratchasima)	(Buffetaut and Suteethorn 2011)
			Ratchasimasaurus suranareae (Nakhon Ratchasima)	(Shibata et al. 2011)
			Sirindhorna khoratensis (Nakhon Ratchasima)	(Shibata et al. 2015)
Ceratopsians			*Psittacosaurus sattayaraki* (Chaiyaphum)	(Buffetaut and Suteethorn 1992)
			Psittacosaurid indet. (Khon Kaen & Laos*)	(Buffetaut et al. 2007)
Spinosaurids	Spinosaurid type I	(Wongko et al. 2019)	*Ichthyovenator laosensis* (Laos*)	(Allain et al. 2012)
	Spinosaurid type II	(Wongko et al. 2019)	Spinosaurid indet. (Khon Kaen, Kalasin & Chaiyaphum)	(Buffetaut et al. 2005; Department of Mineral Resources 2016)
Allosauroids	Carcharodontosaurian indet.	(Buffetaut et al. 2005)	*Siamraptor suwati* (Nakhon Ratchasima)	(Chokchaloemwong et al. 2019)
Sauropods	Titanosauriforms indet.	(Buffetaut et al. 2005)	*Tangvayosaurus hoffeti* (Laos*)	(Allain et al. 1999)
			Titanosauriforms indet. (Chaiyaphum & Khon Kaen)	(Khansubha et. al. 2017)
Pterosaurs	Pterodactyloid indet.	In this paper	Pterosaur indet. teeth (Nakhon Ratchasima)	
Crocodyliforms	Goniopholidid indet.	(Lauprasert 2006)	*Khoratosuchus jintasakuli* (Nakhon Ratchasima)	(Lauprasert et al. 2009)
			Eusuchian indet. (Nakhon Ratchasima)	(Kubo et al. 2018)
	Neosuchian indet.		Neosuchian indet. (Khon Kaen, Kalasin & Chaiyaphum)	(Department of Mineral Resources 2016; Wongko 2018)
Turtles	Carettochelyid indet.	(Tong et al. 2009)	*Kizylkumemys khoratensis* (Nakhon Ratchasima)	(Tong et al. 2005)
			Carettochelyid indet. (Kalasin, Khon Kaen)	(Wongko 2018)
	Adocid indet.	(Tong et al. 2009)	*Shachemys laosiana* (Laos*)	(de Lapparent de Broin 2004)
			Shachemys sp. (Nakhon Ratchasima & possibly Khon Kaen)	(Tong et al. 2009; Wongko 2018)
Halecomorphs	cf. *Siamamia* indet.	(Deesri et al. 2017)	Sinamiidae indet. (Nakhon Ratchasima)	(Deesri et al. 2021)
Ginglymodians	*Lanxangichthys* sp.	(Cavin et al. 2018)	*Lanxangichthys alticephalus* (Laos*)	(Cavin et al. 2018)
	Ginglymodi type I	(Wongko 2018)	*Lanxangichthys* sp. (Nakhon Ratchasima)	(Cavin et al. 2018)
	Ginglymodi type II	(Wongko 2018)	Ginglymodi type I (Kalasin)	(Wongko 2018)
			Ginglymodi type II (Kalasin & Khon Kaen)	(Wongko 2018)
Hybodontiforms	*Heteroptychodus steinmanni*	(Cuny et al. 2003)	*Heteroptychodus steinmanni* (Kalasin, Khon Kaen, Nakhon Ratchasima & probably Chaiyaphum)	(Cuny et al. 2007; Department of Mineral Resources 2016; Wongko 2018)
	Thaiodus ruchae	(Cappetta et al. 1990)		
	"*Hybodus*" *aequitridentatus*	(Cuny et al. 2008)		
	Khoratodus foreyi	(Cuny et al. 2008)	*Thaiodus ruchae* (Nakhon Ratchasima,Khon Kaen, & Kalasin)	(Cappetta et al. 1990; Cuny et al. 2003; Cuny et al. 2007)
	Acrorhizodus khoratensis	(Cappetta et al. 2006)		

comparisons of hinge teeth characters are needed to establish more taxonomic precision. These bivalves could potentially have been food for *H. steinmanni*. The five species of hybodonts from the same assemblage have also been found in the Xinlong Formation in southern China (Cuny et al. 2017). They are indeed endemic to Southeast Asia and South China, four of them (*Acrorhizodus*, "*H.*" *aequitridentatus*, *Thaiodus* and *Khoratodus*) are restricted to the Aptian-Albian interval (Cuny 2012). The fifth genus, *Heteroptychodus* is currently restricted to Thailand, Japan, Kyrgyzstan, South China and Mongolia, and is the most common hybodont species found in the Khorat Group (Cuny et al. 2008, 2014), exhibiting a large stratigraphic distribution, from the Upper Phu Kradung Formation to the Khok Kruat Formation (Cuny et al. 2014). Three species are currently recognized including *H. steinmanni*, *H. kokutensis*, and *H. chuvalovi* (Cuny et al. 2008). It is important to note, that Khok Pha Suam has yielded few large teeth compared to the number of small ones, contrary to Ban Saphan Hin, where only large teeth are recovered. If we consider the large teeth as belonging to adult specimens, small ones to juveniles, then Khok Pha Suam may appear as a potential nursery for these sharks.

Among the thousands of dinosaur bones from the Sao Khua Formation that belong to sauropods and theropods, there is so far no evidence of any ornithischians. In the Khok Kruat Formation, the diversity of sauropods appears to be greatly diminished with the appearance of basal ceratopsians and advanced iguanodontians (Buffetaut and Suteethorn 1998; Buffetaut et al. 2005, 2006). The possible palaeobiogeographical reasons for this change are still unclear. The Khok Kruat sauropods are still poorly known although these long-necked plant-eating dinosaurs are very abundant from the older non-marine Mesozoic formations in northeastern Thailand. Khok Pha Suam sauropods are probably closely related to the very large undescribed titanosauriform sauropod (known from a dorsal vertebra, sacral vertebrae, pelvic girdle, humerus, femur, and ribs) from the dinosaur site in the vicinity of Ban Pha Nang Sua, Nong Bua Rawe District, Chaiyaphum Province of Thailand (Khansubha et al. 2017) and from *Tangvayosaurus hoffeti* from the Grès supérieurs Formation of Savannakhet Province in Laos (Allain et al. 1999).

The teeth of Khok Kruat spinosaurids can be categorized into two morphotypes (Wongko et al. 2019) and indicate that two distinct spinosaurid taxa potentially occur in the Albian-Aptian of Thailand. If these morphotypes are not related to differences between taxa, they are due to dimorphism within a single species. However, there are evidences of several spinosaurid taxa in the same area from many formations such as *Spinosaurus aegyptiacus* and *Sigilmassasaurus brevicollis* from the Cenomanian Kem Kem beds of Morocco and *Ceratosuchops inferodios* and *Riparovenator milnerae* from the Barremian Wessex Formation of UK (Richter et al. 2013; Hendrickx et al.

2016; Barker et al. 2021). This suggests the possibility of a co-occurrence of two distinct spinosaurid taxa in the Khok Kruat Formation.

It is worth noting that the material of psittacosaurids seems to be the only group of Khok Kruat animals that have never been discovered in Khok Pha Suam (Table 1). Although psittacosaurids were abundant in the Early Cretaceous of Eastern Asia (especially China, Mongolia, and Siberia), they appear to be scarce in Southeast Asia (Buffetaut and Suteethorn 1992; Buffetaut et al. 2007). Specimens of *Psittacosaurus* are often found in lacustrine deposits (Averianov et al. 2006; Buffetaut et al. 2007). Moreover, an exceptionally well-preserved specimen of *Psittacosaurus* sp. from the Jehol biota of China shows countershade adaptations for closed habitat with an evergreen canopy (Vinther et al. 2016). This differs greatly from the reconstructed palaeoenvironment of the Khok Kruat Formation and the Grès Supérieurs Formation which are fluvial deposits with an arid or -semi-arid subtropical climate (Racey et al. 1996; Wongko 2018). Both factors, depositional environment and palaeoclimate, may provide an explanation for the scarcity of psittacosaurid materials uncovered in Thailand and Laos.

Another noteworthy point is the absence of amphibians from the Khok Kruat Formation (Fig. 1). Mesozoic Thai amphibian remains are assigned to temnospondyls (Cyclotosauridae, Plagiosauridae, and Brachyopoidea) and Anura, which have been discovered from three formations of the Indochina Terrane ranging from the Upper Triassic to the Lower Cretaceous (Nonsrirach et al. 2021). The Upper Triassic Huai Hin Lat Formation, which is mainly formed by fluvio-lacustrine deposits, has yielded the most amphibian specimens so far in terms of generic-level diversity and numerical abundance (including *Cyclotosaurus*, Plagiosauridae, and Stereospondyli indet.) (Ingavat and Janvier 1981; Suteethorn et al. 1988; Racey et al. 1996; Meesook 2000; Nonsrirach et al. 2021). However, the younger formations show a marked decrease in the number of temnospondyls. Brachyopoids have been found in the Upper Jurassic Phu Kradung Formation that was deposited in a lacustrine-dominated alluvial floodplain (Meesook 2000; Racey 2009; Nonsrirach et al. 2021). A few fragments of frogs have been found in the Early Cretaceous Sao Khua Formation that was deposited in an alluvial floodplain and meandering river (Racey et al. 1996; Buffetaut and Suteethorn 1999; Meesook 2000; Nonsrirach et al. 2021). Temnospondyls reached worldwide very high diversity in the Early Triassic, then gradually decreased during the Middle to Late Triassic (Ruta and Benton 2008). With the rise of the crocodyliforms in the middle Triassic that would have competed with them, only Brachyopoidea were able to surive into the Jurassic to Early Cretaceous deposits across Asia and Australia (Ruta and Benton 2008). The giant *Koolasuchus cleelandi* is the youngest known brachyopoid from the Aptian of Australia inhabiting a polar environment too cold in the winter for crocodyliforms to survive (Warren et al. 1991; Rich and Rich 2014). Although no fossils of anura were found in the Khok Kruat Formation, it cannot be concluded that they did not exist -taphonomy of amphibians in a semi-arid meandering river may affect fossilization.

8. Conclusions

The Khok Pha Suam locality has yielded vertebrates from the Aptian-Albian stages. It represents one of the most diverse vertebrate assemblages in the Khok Kruat Formation of Thailand and the laterally equivalent Grès Supérieurs Formation of Laos. The site is characterized by the dominance of hybodont teeth and iguanodont postcranial material. This study underlines the palaeontological value of this site, which is an essential feature of the Pha Chan-Sam Phan Bok Geopark. The locality improves our knowledge of the diversity of Early Cretaceous vertebrate faunas and provides a useful point of comparison with other East and Southeast Asian taxa.

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Supplementary material 1

Mesozoic vertebrate fauna from the Indochina Terrane of Thailand and additional photos

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Data type: Images

Explanation note: Fig. S1. Mesozoic vertebrate fauna from the Indochina Terrane of Thailand. Figs S2–S5. Additional photos were mentioned in the article.

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