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Brief Report

An Unusual Spinosaurid Tooth Morphotype from the Early Cretaceous of Eastern Thailand

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Abstract

At the Lower Cretaceous Phra Prong locality in eastern Thailand, isolated spinosaurid teeth show two distinct morphotypes: one with well-marked apicobasal enamel ribs and one without ribs, with the enamel showing only a subtle wrinkling. The latter morphotype is unusual, since most spinosaurid teeth from Asia show a well-marked ribbing. The occurrence of two tooth morphotypes at Phra Prong is interpreted as corresponding to the presence of two distinct spinosaurid taxa. These two morphotypes probably indicate different feeding habits and niche partitioning. However, the functional significance of enamel ribbing (or its absence) remains poorly understood.

Keywords: Spinosauridae; teeth; Early Cretaceous; Thailand

1. Introduction

Although fossils referrable to this group of dinosaurs had already been reported (but misidentified) from China and Thailand as early as the 1960s (Buffetaut and Tong [1] and references therein), the presence of Spinosauridae in Asia was first revealed in 1986 when teeth from the Lower Cretaceous Sao Khua Formation of north-eastern Thailand were described as *Siamosaurus suteethorni* by Buffetaut and Ingavat [2]. Since then, spinosaurid remains have been reported from other eastern Asian countries, including Japan [3–5], China [6,7], Laos [8], and Malaysia [9]. In Thailand, abundant isolated spinosaurid teeth, plus various skeletal remains, have been found in both the Sao Khua Formation (Early Cretaceous, age uncertain: see below) and the Khok Kruat Formation (Aptian–Albian) of the Khorat Plateau [2,10,11] and Kut Island in the eastern part of the Gulf of Thailand [12]. Although several morphotypes can be distinguished [11], all spinosaurid teeth hitherto reported from Thailand were characterized by the presence of well-marked apicobasal ribbing on both faces of the crown. However, a different type of spinosaurid tooth, with no enamel ribbing, is present, together with ribbed teeth, at the Phra Prong locality in eastern Thailand. The purpose of the present paper is to briefly describe the unusual unribbed tooth morphotype from Phra Prong and to discuss its implications.

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2. Materials and Methods

The spinosaurid teeth from Phra Prong were surface-collected during several visits to the badland-type outcrop. They are part of the collection of the Palaeontological Research and Education Centre (PRC) of Mahasarakham University, Thailand.

Morphotype A (ribbed enamel): PRC 466, 471, 472.

Morphotype B (unribbed enamel): PRC 465, 467, 468, 469, 470.

A comparative study of these morphotypes has been carried out, with reference to spinosaurid tooth morphotypes from other localities.

3. Geographical and Geological Setting

Together with sites on Kut Island in the eastern part of the Gulf of Thailand, the Phra Prong locality, in Sa Kaeo Province, is one of the few Early Cretaceous vertebrate localities currently known in eastern Thailand. It is located south of the Khorat Plateau, and correlations with the fossil-rich non-marine Mesozoic formations of the Khorat Group are not obvious. The geographical location and the geology of the locality were described in some detail by Manitkoon et al. [13]. It has yielded a diverse non-marine vertebrate assemblage comprising sharks, bony fishes, turtles, squamates, crocodiles, pterosaurs, and theropod and sauropod dinosaurs. According to Manitkoon et al. [13], fossils, including freshwater bivalves and hybodont sharks, suggest that the Phra Prong beds may be an equivalent of the Sao Khua Formation of the Khorat Plateau, one of the formations of the Khorat Group. This correlation is supported by the turtle assemblage from Phra Prong. The site has yielded a rich turtle fauna. The turtle remains from Phra Prong are fragmentary, consisting mostly of isolated shell elements and a few limb bones. The assemblage includes Carettochelydae, Adocidae, and a large trionychoid, as well as an unnamed Testudinoidea. It is dominated by trionychoids, like those from the Early Cretaceous of the Khorat Group (top of the Phu Kradung Formation, Sao Khua and Khok Kruat formations), and is distinct from the Late Jurassic turtle fauna (lower part of the Phu Kradung Formation), which is composed of xinjiangchelyids (see Tong et al. [14] for a recent discussion of turtle distribution in the Khorat Group). The vertebrate-bearing strata of the Phra Prong site are likely coeval with the Sao Khua Formation based on the evidence from turtle remains, including a keeled *Kizylkumemys*, the presence of *Protoshachemys*, an adocid with the shell showing a pitted ornamentation, and large trionychoids.

It should also be noted that the absence of ornithischian dinosaurs in the Phra Prong assemblage is reminiscent of that from the Sao Khua Formation; by contrast, ornithischian remains are abundant in the younger Khok Kruat Formation [10].

The age of the Sao Khua Formation has been a matter of discussion. In recent years, it has often been referred to the Barremian on the basis of freshwater molluscs [15,16], but according to Tucker et al. [17], it should be placed in the Valanginian on the basis of zircon radiometric dates. As correctly noted by Tumpeesuwan et al. [16], the zircon-based age is a Maximum Depositional Age, and the true age of the Sao Khua may be younger.

Similarities between the vertebrate assemblage from Phra Prong and that from Kut Island (Ko Kut) in the eastern part of the Gulf of Thailand have been noted [13]. Biostratigraphic correlations between the Ko Kut beds and the Sao Khua Formation are mainly based on sharks [18], turtles [19], and spinosaurid dinosaurs [12]. It should be noted, however, that the lithologies of the fossil-bearing beds at Phra Prong and at Ko Kut are very different. The grey sandstones at Ko Kut are more similar to the fossil-bearing beds of Koh Moul, an island off the Cambodian coast, where turtle remains suggesting an Early Cretaceous age have been found [14]. The Mesozoic rocks on Ko Kut may have been deposited in the same sedimentary basin as those on Koh Moul, which, like the rest of the thick non-marine

series in south-western Cambodia, apparently correspond to a sedimentary basin that was distinct from the Khorat Basin, as shown by a different lithostratigraphic succession [20].

4. Spinosaurid Tooth Morphotypes from Phra Prong

A number of isolated teeth from Phra Prong can be identified as belonging to spinosaurid dinosaurs, on the basis of the following characters (see Hone and Witton [21] for a recent review of spinosaurid dentition):

- they differ from the teeth of most theropod dinosaurs by their weak or absent mediolateral compression;
- they differ from crocodilian teeth by their mesiodistal rather than labiolingual curvature.

An additional frequent character of spinosaurid teeth is a fine wrinkling of the enamel surface [22,23].

Two distinct morphotypes can be distinguished among the spinosaurid teeth from Phra Prong on the basis of enamel ornamentation (in terms of general shape, compression, and curvature, they are otherwise quite similar):

- Morphotype A ('ribbed'):
- Teeth with a strongly ornamented crown (Figure 1), bearing up to 14 well-marked apicobasal ribs on each face, and with a wrinkled enamel between the ribs and at the apex. These teeth are reminiscent of *Siamosaurus suteethorni* from the Sao Khua Formation of the Khorat Plateau; the indistinct carinae are reminiscent of some teeth from the Khok Kruat Formation [11].

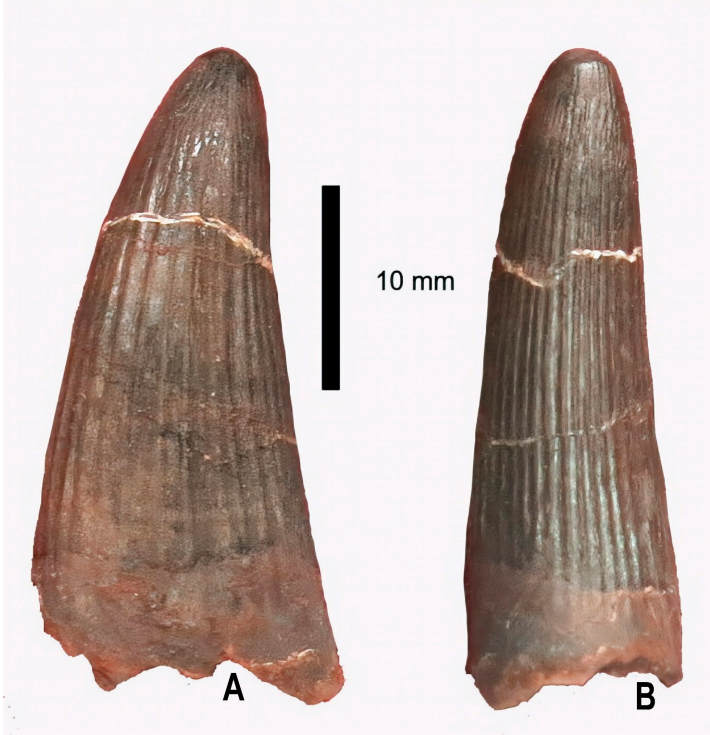

Figure 1. Spinosaurid tooth, PRC 466, morphotype A (apicobasal ribbing), from Phra Prong, Sa Kaeo Province, eastern Thailand, Early Cretaceous: (**A**) labial view; (**B**) distal view.

Tooth PRC 466 is a good example of this morphotype (Figure 1), with the following measurements (as preserved):

- Apicobasal height: 32 mm
- Labiolingual width: 9 mm
- Basal mesiodistal length: 14 mm

– Morphotype B ('unribbed'):
– Teeth with no apicobasal ribs on the crown (Figure 2). The enamel shows the fine wrinkling seen on most spinosaurid teeth (Figure 3). The carinae are well-marked. The mesial carina seems to be unserrated, unless this lack is only apparent and caused by stronger wear mesially. The distal carina bears very small irregular serrations (up to 12 per millimetre) which become indistinct when the tooth is worn (Figure 4). As noted by D'Amore [24], the distal carina of theropod dinosaurs is usually totally serrated while the mesial carina can be only partially denticulated.

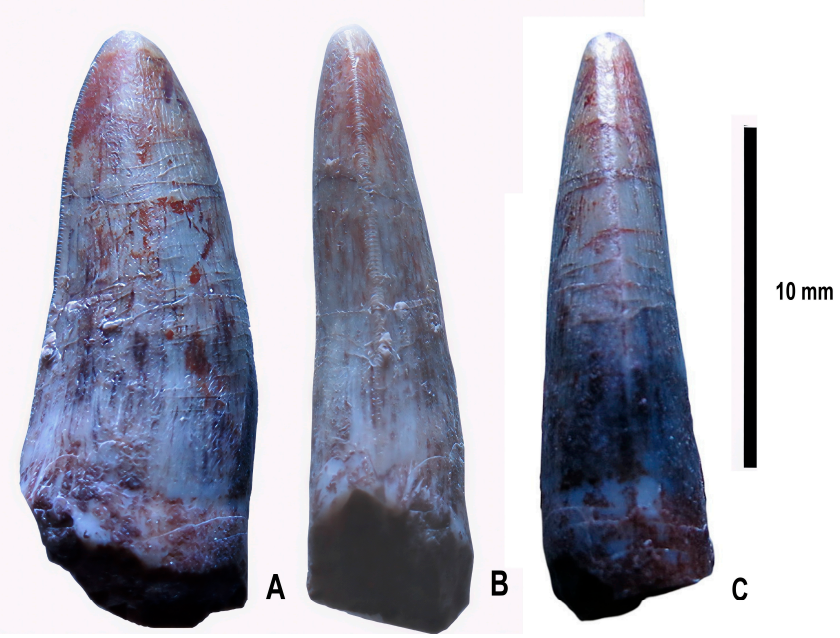

Figure 2. Spinosaurid tooth, PRC 467, morphotype B (unribbed), from Phra Prong, Sa Kaeo Province, eastern Thailand, Early Cretaceous: (**A**) lingual view; (**B**) distal view; (**C**) mesial view.

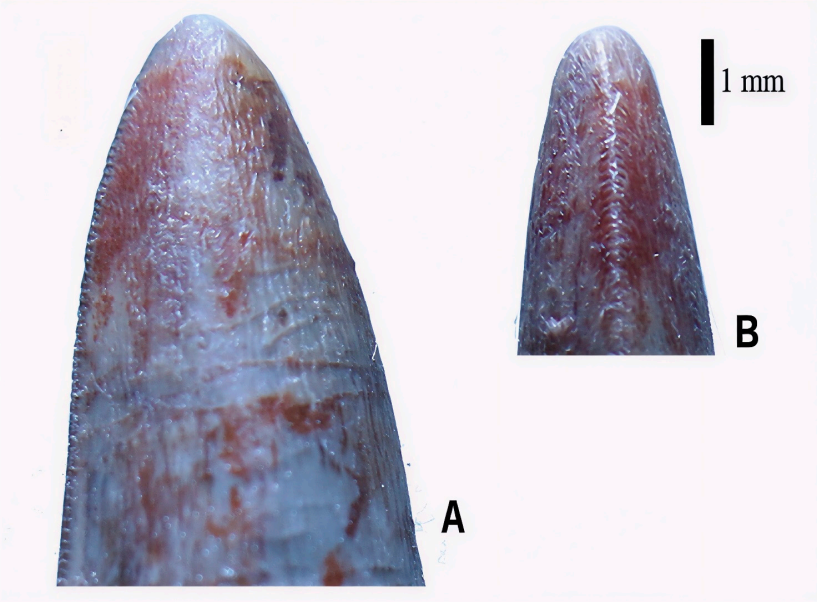

Figure 3. Close-ups of the apical region of tooth PRC 467, morphotype B, showing details of enamel wrinkling (**A**) and denticles on the distal carina (**B**).

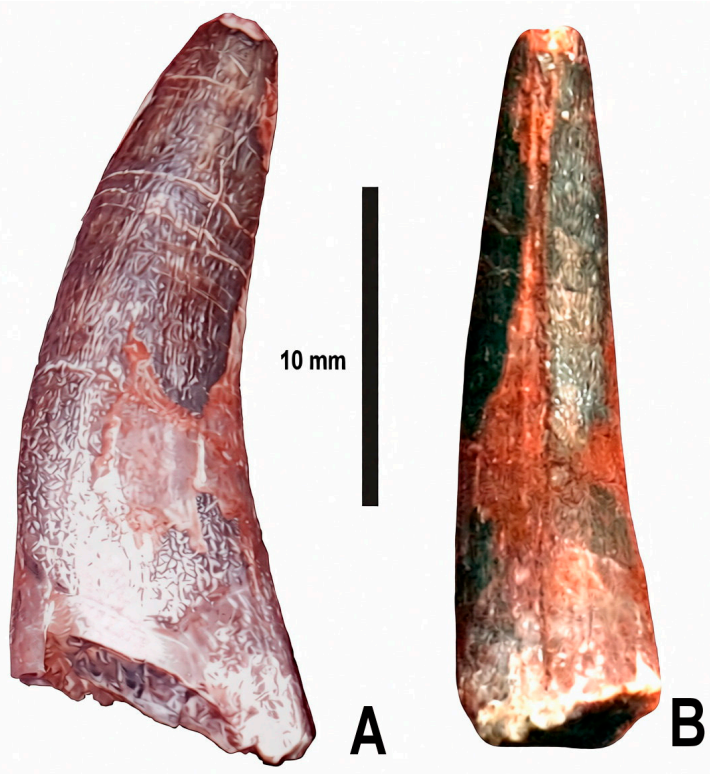

Figure 4. Morphotype B, worn tooth (PRC 465): (**A**) labial view; (**B**) distal view. Enamel wrinkling is still visible but serrations have become indistinct.

The best specimen in the collection is tooth PRC 467, with the following measurements (as preserved):

- Apicobasal height: 18 mm
- Labiolingual width: 5 mm
- Basal mesiodistal length: 7 mm

Interestingly, both types exhibit a blunt rather than pointed apex.

Spinosaurid teeth show a fairly wide range of enamel ornamentation [23], in addition to the fine wrinkling seen on most of them. They frequently display some degree of ribbing (or fluting), with Asian specimens being noticeable for the high number of prominent ribs on both faces of the crown. This is exemplified by *Siamosaurus suteethorni* from the Sao Khua Formation [2] and teeth from the Khok Kruat Formation [11] in Thailand, by the spinosaurid teeth from the Xinlong Formation of Guangxi Zhuang Autonomous Region in southern China [6,7], and by those from Japan [3–5]. Smooth spinosaurid teeth with no ribbing are less common, although the teeth of the holotype of *Spinosaurus aegyptiacus* from the Cenomanian of Egypt, for instance, show no fluting or ribbing [25]; isolated unribbed teeth are fairly common in North African formations from the middle part of the Cretaceous. It should be noted that, according to Stromer [25], the enamel of the teeth of *Spinosaurus aegyptiacus* from Egypt was smooth, with only fine striations near the base of the crown and a very fine wrinkling visible only with a magnifying glass, whereas the unribbed teeth from Phra Prong show a well-marked wrinkling, notably near the apex. Morphotype B from Phra Prong is therefore remarkable for the absence of ribs, which distinguishes it from other spinosaurid teeth from Asia, including morphotype A from Phra Prong. No specimens from Phra Prong show an intermediate morphology between the two morphotypes, with, for instance, a reduction in the number of ribs or fainter ribbing. Wear can also be excluded as an explanation for the unribbed surface of the teeth, since the fine serrations on the distal carina and the delicate wrinkling of the enamel are preserved.

Therefore, it seems likely that the two morphotypes from Phra Prong correspond to two distinct spinosaurid taxa, rather than being the result of intraspecific variation (or even variation within a single tooth row). The co-existence of several spinosaurid taxa in the same geological formation has already been reported on the basis of skeletal and dental evidence from various parts of the world. Stromer [26,27] was the first to hint at such a co-existence in the Baharija Formation of Egypt when he described "*Spinosaurus* B" in addition to *Spinosaurus aegyptiacus*. Since then, although it has sometimes been disputed, the co-occurrence of distinct spinosaurid taxa has been reported in various fossil-bearing formations, notably from Morocco (e.g., [28,29]), the Iberian Peninsula (e.g., [30,31]), England (e.g., [32,33]), and Brazil (e.g., [34,35]), and cannot be considered as surprising. In Thailand itself, spinosaurid teeth from the Khok Kruat Formation exhibit a morphological diversity suggesting the co-occurrence of several taxa [11]. However, the unribbed morphotype present at Phra Prong is uncommon. Apart from Phra Prong, the only other known instance from Thailand consists of poorly preserved teeth from the Sao Khua Formation at Huai Lao Yang, a locality in Nong Bua Lam Phu province, discovered by Paladej Srisuk and now in the collection of the Palaeontological Research and Education Centre, Mahasarakham University. There, both ribbed and unribbed spinosaur teeth occur together (this may be seen as an additional reason to consider the Phra Prong beds and the Sao Khua Formation as coeval). Interestingly, unribbed spinosaurid teeth have so far not been reported from the presumably Aptian–Albian Khok Kruat Formation, where ribbed morphotypes occur [11]. Hone et al. [36] tentatively referred to a baryonychine spinosaurid an isolated tooth from the Late Cretaceous of Henan, China, which shows a smooth, unribbed enamel. However, the tooth in question is strongly compressed mediolaterally, unlike the usual condition in spinosaurids, and it is unlikely to belong to that clade [4,33].

5. Functional Significance

Although a ribbed crown surface is a common feature of the teeth in various reptile groups, including crocodiles, ichthyosaurs and plesiosaurs, the functional significance of this ribbing remains unclear. MacKenzie et al. [37] have shown that apicobasal ridges do not strengthen the teeth, contrary to what had sometimes been suggested. On the basis of a review of apicobasal ribbing in a wide range of mammals and reptiles, McCurry et al. [38] suggested that 'they increase the efficiency of puncture, grip and/or removal'. They noted that ridges are extremely uncommon in terrestrial-feeding taxa, whereas they evolved in various aquatic-feeding taxa. Despite such studies, the exact function of ribbing remains uncertain, although it could be argued that it may make the capture of slippery aquatic prey easier. Because of uncertainty about the function of ribbing, its absence is also difficult to interpret. At first sight, it may be tempting to assume that this absence may be linked to a less aquatic type of food, since the teeth of terrestrial-feeding taxa are usually unribbed. Interestingly, the spinosaurid tooth embedded in a pterosaur vertebra from the Early Cretaceous of Brazil described by Buffetaut et al. [39] shows a smooth enamel. However, as mentioned above, *Spinosaurus aegyptiacus*, which is usually considered as a prime example of an aquatic-feeding spinosaurid, had unribbed teeth. It should also be mentioned that the rather blunt apex of spinosaurid teeth from Phra Prong (and some other Thai localities), reminiscent of Massare's "crunching" type [40], suggests that they may have had a crushing rather than piercing function, possibly as an adaptation to feeding on relatively hard prey, such as fishes with thick ganoid scales, the remains of which are common in Lower Cretaceous non-marine formations in Asia [41]. As noted above, turtle remains are abundant at Phra Prong and it cannot be excluded that turtles were also part of the diet of blunt-toothed spinosaurs. The bluntness of some spinosaurid teeth has seldom been mentioned and the distribution of this character among spinosaurids would be worth

examining; however, this is beyond the scope of the present paper. The functional difference between ribbed and unribbed teeth remains obscure, largely because the function of enamel ribbing is still poorly understood. As far as Asian spinosaurids are concerned, unribbed teeth are the exception rather than the rule, as mentioned above. In the absence of cranial, and especially jaw material, an interpretation of the feeding habits of Asian spinosaurs remains difficult, but the occurrence of several distinct tooth morphotypes, including an unribbed one, does suggest a certain diversity of adaptations, possibly related to different prey types. No attempt is made here at a phylogenetic assessment of the unribbed spinosaur teeth from Phra Prong, given the absence of more complete material

6. Conclusions

Phra Prong is one of the very few localities in Asia where unribbed spinosaurid teeth, with a finely wrinkled enamel but no distinct apicobasal ribs, have been reported. The occurrence of this unusual morphotype together with the much more common ribbed morphotype is interpreted as indicating the co-existence of at least two spinosaurid taxa, which in itself is not surprising, since such a co-existence has often been reported (see Hone and Witton [21] and references therein). The different morphologies observed among the Phra Prong teeth (ribbed vs. unribbed) suggest differences in feeding adaptations, resulting in niche partitioning. However, since the functional significance of enamel ribbing (and absence of ribbing) remains poorly understood, it is difficult to reach a better understanding of this diversity of spinosaurid taxa in the Phra Prong beds. Pending the discovery of more complete specimens (especially jaw material), the functional and dietary implications of dental diversity in Asian spinosaurid dinosaurs will remain uncertain

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Abbreviation

PRC: Palaeontological Research and Education Centre, Mahasarakham University.

References

1. Buffetaut, E.; Tong, H. The First Discovery of Spinosaurid Remains in Asia: Thailand, 1962. *Ann. Paléont.* **2024**, *110*, 102664. [CrossRef]
2. Buffetaut, E.; Ingavat, R. Unusual Theropod Dinosaur Teeth from the Upper Jurassic of Phu Wiang, Northeastern Thailand. *Rev. Paléobiol.* **1986**, *5*, 217–220.
3. Hasegawa, Y.; Eric, B.; Manabe, M. A Possible Spinosaurid Tooth from the Sebayashi Formation (Lower Cretaceous), Gunma, Japan. *Bull. Gunma Mus. Nat. Hist.* **2003**, *7*, 1–5.
4. Kubota, K.; Takakuwa, Y.; Hasegawa, Y. Second Discovery of a Spinosaurid Tooth from the Sebayashi Formation (Lower Cretaceous), Kanna Town, Gunma Prefecture, Japan. *Bull. Gunma Mus. Nat. Hist.* **2017**, *21*, 1–6.
5. Hattori, S.; Azuma, Y. Spinosaurid Teeth from the Lower Cretaceous Kitadani Formation of the Tetori Group, Fukui, Japan. *Mem. Fukui Prefect. Dinosaur. Mus.* **2020**, *19*, 1–9.

6. Buffetaut, E.; Suteethorn, V.; Tong, H.; Amiot, R. An Early Cretaceous Spinosaurid Theropod from Southern China. *Geol. Mag.* **2008**, *145*, 745–748. [CrossRef]
7. Mo, J.; Buffetaut, E.; Tong, H.; Amiot, R.; Cavin, L.; Cuny, G.; Suteethorn, V.; Suteethorn, S.; Jiang, S. Early Cretaceous Vertebrates from the Xinlong Formation of Guangxi (Southern China): A Review. *Geol. Mag.* **2016**, *153*, 143–159. [CrossRef]
8. Allain, R.; Xaisanavong, T.; Richir, P.; Khentavong, B. The First Definitive Asian Spinosaurid (Dinosauria: Theropoda) from the Early Cretaceous of Laos. *Naturwissenschaften* **2012**, *99*, 369–377. [CrossRef] [PubMed]
9. Sone, M.; Hirayama, R.; He, T.Y.; Yoshida, M.; Komatsu, T. First Dinosaur Fossils from Malaysia: Spinosaurid and Ornithischian Teeth. In *Proceedings of the 2nd International Symposium on Asian Dinosaurs (ISAD2015) Program and Abstract, Bangkok, Thailand, 19–20 November 2015*; Nakhorn Ratchasima Rajabhat University and Department of Mineral Resources: Bangkok, Thailand, 2015; p. 18.
10. Buffetaut, E.; Suteethorn, V.; Tong, H. Dinosaur Assemblages from Thailand: A Comparison with Chinese Faunas. In *Proceedings of the Heyuan International Dinosaur Symposium*; Lü, J., Kobayashi, Y., Huang, D., Lee, Y.N., Eds.; Geological Publishing House: Beijing, China, 2006; pp. 19–37.
11. Wongko, K.; Buffetaut, E.; Khamha, S.; Lauprasert, K. Spinosaurid Theropod Teeth from the Red Beds of the Khok Kruat Formation (Early Cretaceous) in Northeastern Thailand. *Trop. Nat. Hist.* **2019**, *19*, 8–20. [CrossRef]
12. Buffetaut, E.; Suteethorn, S.; Suteethorn, V.; Tong, H.; Wongko, K. Spinosaurid Teeth from the Lower Cretaceous of Ko Kut, Eastern Thailand. *Ann. Paléont.* **2019**, *105*, 239–243. [CrossRef]
13. Manitkoon, S.; Pêgas, R.V.; Nonsrirach, T.; Warapeang, P.; Lauprasert, K.; Deesri, U.; Tumpeesuwan, S.; Wongko, K.; Zhou, X. First Gnathosaurine (Pterosauria, Pterodactyloidea) from the Early Cretaceous of Eastern Thailand. *Cret. Res.* **2025**, *173*, 106135. [CrossRef]
14. Tong, H.; Buffetaut, E.; Lim, V.; Philippe, M.; Boonchai, N.; Claude, J. Turtle Remains from Koh Moul (SW Cambodia) and Their Stratigraphical Implications. *Diversity* **2026**, *18*, 249. [CrossRef]
15. Tumpeesuwan, S.; Sato, Y.; Nakhapadungrat, S. A New Species of *Pseudohyria* (*Matsumotoina*) (Bivalvia: Trigonioidoidea) from the Early Cretaceous Sao Khua Formation, Khorat Group, Northeastern Thailand. *Trop. Nat. Hist.* **2010**, *10*, 93–106. [CrossRef]
16. Tumpeesuwan, S.; Udchachon, M.; Lauprasert, K.; Deesri, U.; Suteethorn, S.; Nuley, P.; Bunchalee, P.; Thassanapak, H.; Nahok, B.; Tumpeesuwan, C. The Richest Diversity and Highest Abundance of Freshwater Bivalve Fossils from the New Fossil Locality of the Early Cretaceous Sao Khua Formation at Roi Et Province, Northeastern Thailand. *Trop. Nat. Hist.* **2024**, *24*, 137–152. [CrossRef]
17. Tucker, R.T.; Hyland, E.G.; Gates, T.A.; King, M.R.; Roberts, E.M.; Foley, E.K.; Berndt, D.; Hanta, R.; Khansubha, S.; Aswasereelert, W. Age, Depositional History, and Paleoclimatic Setting of Early Cretaceous Dinosaur Assemblages from the Sao Khua Formation (Khorat Group), Thailand. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **2022**, *601*, 111107. [CrossRef]
18. Cuny, G.; Laojumpon, C.; Lauprasert, K. Fossil Vertebrate Remains from Kut Island (Gulf of Thailand, Early Cretaceous). *Cret. Res.* **2010**, *31*, 415–423. [CrossRef]
19. Tong, H.; Naksri, W.; Buffetaut, E.; Suteethorn, S.; Suteethorn, V.; Deesri, U.; Claude, J. Turtle Remains from the Early Cretaceous of Kut Island, Gulf of Thailand. *Comptes Rendus. Palevol* **2021**, *20*, 345–349. [CrossRef]
20. Buffetaut, E.; Tong, H.; Cavin, L.; Lim, V.; Ly, P.S.; Heng, M. Fossil-Bearing Non-Marine Mesozoic Formations of South-Western Cambodia. In Proceedings of the 18th Regional Geoscience Conference of Southeast Asia: GEOSEA 2024, Khon Kaen, Thailand, 20–23 February 2024; pp. 55–63.
21. Hone, D.; Witton, M. *Spinosaur Tales: The Biology and Ecology of the Spinosaurs*; Bloomsbury Publishing: London, UK, 2025.
22. Hasegawa, Y.; Tanaka, G.; Takakuwa, Y.; Koike, S. Fine Sculptures on a Tooth of *Spinosaurus* (Dinosauria, Theropoda) from Morocco. *Bull.Gunma Mus.Nat. Hist.* **2010**, *14*, 11–20.
23. Buffetaut, E. An Early Spinosaurid Dinosaur from the Late Jurassic of Tendaguru (Tanzania) and the Evolution of the Spinosaurid Dentition. *Oryctos* **2013**, *10*, 1–8.
24. D'Amore, D.C. A Functional Explanation for Denticulation in Theropod Dinosaur Teeth. *Anat. Rec.* **2009**, *292*, 1297–1314. [CrossRef] [PubMed]
25. Stromer, E. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltier-Reste der Baharije-Stufe (Unterstes Cenoman). 3. Das Original des Theropoden *Spinosaurus aegyptiacus*. *Abh. Königl. Bayer. Akad. Wiss. Math. Phys. Kl.* **1915**, *28*, 1–32.
26. Stromer, E. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltierreste der Baharije-Stufe (Unterstes Cenoman) 13. Dinosauria. *Abh. Bayer. Akad. Wiss. Math. Phys. Abt. N.F.* **1934**, *22*, 1–79.
27. Stromer, E. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. VII. Baharije-Kessel und -Stufe mit deren Fauna und Flora. Eine ergänzende Zusammenfassung. *Abh. Bayer. Akad. Wiss. Math. Phys. Abt. N.F.* **1936**, *33*, 1–102.
28. Hendrickx, C.; Mateus, O.; Buffetaut, E. Morphofunctional Analysis of the Quadrate of Spinosauridae (Dinosauria: Theropoda) and the Presence of *Spinosaurus* and a Second Spinosaurine Taxon in the Cenomanian of North Africa. *PLoS ONE* **2016**, *11*, e0144695. [CrossRef]

29. Lakin, R.J.; Longrich, N.R. Juvenile Spinosaurs (Theropoda: Spinosauridae) from the Middle Cretaceous of Morocco and Implications for Spinosaur Ecology. *Cret. Res.* **2019**, *93*, 129–142. [CrossRef]
30. Alonso, A.; Canudo, J.I. On the Spinosaurid Theropod Teeth from the Early Barremian (Early Cretaceous) Blesa Formation (Spain). *Hist. Bio.* **2016**, *28*, 823–834. [CrossRef]
31. Malafaia, E.; Gasulla, J.M.; Escaso, F.; Narvaéz, I.; Ortega, F. An Update of the Spinosaurid (Dinosauria: Theropoda) Fossil Record from the Lower Cretaceous of the Iberian Peninsula: Distribution, Diversity, and Evolutionary History. *J. Iber. Geol.* **2020**, *46*, 431–444. [CrossRef]
32. Barker, C.T.; Hone, D.W.; Naish, D.; Cau, A.; Lockwood, J.A.; Foster, B.; Clarkin, C.E.; Schneider, P.; Gostling, N.J. New Spinosaurids from the Wessex Formation (Early Cretaceous, UK) and the European Origins of Spinosauridae. *Sci. Rep.* **2021**, *11*, 19340. [CrossRef] [PubMed]
33. Barker, C.T.; Naish, D.; Gostling, N.J. Isolated Tooth Reveals Hidden Spinosaurid Dinosaur Diversity in the British Wealden Supergroup (Lower Cretaceous). *PeerJ* **2023**, *11*, e15453. [CrossRef] [PubMed]
34. Sales, M.A.; Schultz, C.L. Spinosaur Taxonomy and Evolution of Craniodental Features: Evidence from Brazil. *PLoS ONE* **2017**, *12*, e0187070. [CrossRef] [PubMed]
35. Lacerda, M.B.S.; Grillo, O.N.; Romano, P.S.R. Rostral Morphology of Spinosauridae (Theropoda, Megalosauroidea): Premaxilla Shape Variation and a New Phylogenetic Inference. *Hist. Biol.* **2022**, *34*, 2089–2109. [CrossRef]
36. Hone, D.W.; Xu, X.; Wang, D. A Probable Baryonychine (Theropoda: Spinosauridae) Tooth from the Upper Cretaceous of Henan Province, China. *Verteb. Palasiat.* **2010**, *48*, 19–26.
37. MacKenzie, A.S.; Brock, G.A.; McCurry, M.R. The Impact of Apicobasal Ridges on Dental Load-Bearing Capacity in Aquatic-Feeding Predatory Amniotes. *Paleobiology* **2024**, *50*, 346–363. [CrossRef]
38. McCurry, M.R.; Evans, A.R.; Fitzgerald, E.M.; McHenry, C.R.; Bevitt, J.; Pyenson, N.D. The Repeated Evolution of Dental Apicobasal Ridges in Aquatic-Feeding Mammals and Reptiles. *Biol. J. Linn. Soc.* **2019**, *127*, 245–259. [CrossRef]
39. Buffetaut, E.; Martill, D.; Escuillié, F. Pterosaurs as Part of a Spinosaur Diet. *Nature* **2004**, *430*, 33. [CrossRef] [PubMed]
40. Massare, J.A. Tooth Morphology and Prey Preference of Mesozoic Marine Reptiles. *J.Vert. Paleont.* **1987**, *7*, 121–137. [CrossRef]
41. Cavin, L.; Deesri, U.; Suteethorn, V. The Jurassic and Cretaceous Bony Fish Record (Actinopterygii, Dipnoi) from Thailand. In *Late Palaeozoic and Mesozoic Continental Ecosystems in SE Asia*; Buffetaut, E., Cuny, G., Le Loeuff, J., Suteethorn, V., Eds.; Geological Society: London, UK; Special Publications: Bath, UK, 2009; Volume 315, pp. 125–139.