The First Occurrence of a Basal Tyrannosauroid in Southeast Asia: Dental Evidence from the Upper Jurassic of Northeastern Thailand

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ABSTRACT. – Isolated theropod teeth are one of the most common vertebrate fossils that have been found in the Khorat Group of Thailand. Furthermore, several isolated teeth have been discovered from the Upper Jurassic Phu Kradung Formation, located in Phu Noi locality of Kalasin Province, Northeastern Thailand. Three of those theropod teeth from the Phu Noi locality show unique dental features that can be distinguished from previous discovered metriacanthosaurid theropod, including the lateral teeth with mesiolingual twisted mesial carinae extending above the cervix line and braided enamel surface texture. Morphological examination with cladistics and morphometric analyses show that these isolated teeth exhibit the synapomorphies of basal tyrannosauroids, closely related to *Guanlong wucaii* and *Proceratosaurus bradleyi* from the Jurassic Period. This paper notes the first report of a basal tyrannosauroid in Southeast Asia as well as significantly contributes to our understanding of paleoecology of the Upper Jurassic Phu Kradung Formation and paleobiogeography of Tyrannosauroidea during the Jurassic Period.

KEYWORDS: Dinosauria, Theropod, isolated teeth, Phu Kradung Formation, Mesozoic Era

INTRODUCTION

Tyrannosauroidea is a clade of theropods, including well-known carnivorous dinosaurs such as Tyrannosaurus rex from Late Cretaceous North America (Osborn, 1905). They primarily inhabited in the Laurasian supercontinent throughout the Middle Jurassic to Late Cretaceous (Brusatte et al., 2016). The earliest-known members of tyrannosauroids have been discovered in the Middle Jurassic of Europe and Russia (Woodward, 1910; Averianov et al., 2010), suggesting the origin of this theropod group within Eurasia (Delcourt and Grillo, 2018). Tyrannosauroids were distributed from the Late Jurassic to the Late Cretaceous of Asia, with most Asian tyrannosaurs found in China and Mongolia, including Guanlong wucaii (Xu et al., 2006), Yutyrannus huali (Xu et al., 2012), Sinotyrannus kazuoensis (Ji et al., 2009), Dilong paradoxus (Xu et al., 2004), Xiongguanlong baimoensis (Li et al., 2009), Timurlengia euotica (Brusatte et al. 2016), Alectrosaurus olseni (Gilmore, 1933), Oianzhousaurus sinensis (Lü et al., 2014), Alioramus remotus and A. altai (Kuzanov, 1976; Brusatte et al., 2009), Zhuchengtyrannus magnus (Hone et al., 2011), and Tarbosaurus bataar (Marleev, 1955).

Tyrannosauroids have also been reported in Southeast Asia. Post-cranial elements of *Siamotyrannus isanensis* were found in the Early Cretaceous Sao Khua Formation in the Phu Wiang locality, Khon Kaen Province, Northeastern Thailand (Buffetaut et al., 1996). Initially, *Siamotyrannus* was described as the earliest known tyrannosaurid based on pelvic features (Buffetaut et al., 1996). However, lacking distinct tyrannosauroid synapomorphies, it has been considered to belong to other theropod groups, such as an allosauroid (Rauhut, 2003), a metriacanthosaurid (Carrano et al., 2012), or possibly a basal coelurosaur (Samathi et al., 2019). Hence, the presence of tyrannosauroids in Southeast Asia remains ambiguous.

Isolated theropod teeth are frequently reported in the fossil records of Thailand. Many reports of these findings come from different locations within the Khorat Plateau. These discoveries are spread across three geological formations within the Khorat Group, including the Phu Kradung, Sao Khua, and Khok Kruat Formations (Buffetaut et al. 2005a; Tong et al. 2019; Manitkoon et al. 2022; Samathi et al. 2023). Due to the abundance of the dental evidence, isolated teeth are often used for taxonomic identification to reveal the paleoecological diversity of vertebrates when the complete elements of fossil are insufficient (Hendrickx et al. 2015; Barker et al. 2023; Yin et al. 2023).

This contribution presents the first distinct record of a tyrannosauroid from the Upper Jurassic Phu Kradung Formation based on dental evidence from the Phu Noi locality of Kalasin Province, northeastern Thailand. This discovery not only confirms the presence of tyrannosaurs in Thailand but also sheds light on the paleogeographic distribution of this dinosaur clade and provides valuable information regarding the diversity



FIGURE 1. Geological map and stratigraphy of the Phu Noi locality. (A) Map of Thailand; (B) Distribution of the Khorat Group within the Khorat Plateau, Northeastern Thailand (modified from Manitkoon et al., 2023a); (C) Chronostratigraphic column of six geological formations of the Khorat Group based on subsurface data (modified from Booth and Sattayarak, 2011); (D). Photograph of the excavation site in the Phu Noi locality.

of theropod dinosaurs during the Late Jurassic of Southeast Asia.

Geological setting and paleontological context

The Phu Kradung Formation distributes along the western rim of the Khorat Plateau and the Phu Phan Mountain range in northeastern Thailand (Fig. 1A, B). It is underlain unconformably by the Upper Nam Phong Formation and overlain conformably by Phra Wihan Formation of the Mesozoic Khorat Group (Booth and Sattayarak, 2011) (Fig. 1C). The lithological features and palynological evidence in this formation indicate fluvial depositional environment and a subtropical paleoclimate (Racey and Goodall, 2009). The Phu Kradung Formation was initially classified as Late Jurassic in age based on the vertebrate fauna discovered in its lower part, which bears similarities to the Middle to Late Jurassic fauna of China (Buffetaut et al., 2005b; Tong et al, 2019; Manitkoon al., 2023b). However, et further investigations involving detrital zircon analysis and palynology have suggested an Early Cretaceous age for the upper part of this formation (Carter and Bristow, 2003; Racey and Goodall, 2009). The theropod teeth examined in this work were recovered from the Phu

Noi locality, Kham Muang District of Kalasin Province, northeastern Thailand. This locality's outcrop is considered the lowest part of the Phu Kradung Formation (Buffetaut et al., 2001; Cuny et al., 2014) based on the differences in faunal composition such as hybodont shark, turtle and crocodylomorph compared to the upper part of the Phu Kradung Formation (Manitkoon et al., 2023a) (Fig. 1B, D).

The lithology of the Phu Noi locality is composed of conglomerate, grevish green medium to very finegrained sandstone, and grey siltstone (Ditbanjong and Chanthasit, 2019), which the stratigraphical succession can be divided into three parts. The lower part is characterized by conglomerate and sandstone in the lowest unit, while the upper unit consits of grey siltstone with bioturbations, calcretes, and conglomeratic limestone lenses. Isolated teeth of shark and crocodile, fish scales, and turtle shell fragments are found in conglomerate layers of the lowest unit. The middle part is mainly characterized by grey ripple siltstone with the main bone bed is in thin-bedded maroon micaceous very fine-grained sandstone. The upper unit of the middle part shares similar lithology with the lowest unit of the lower part. The upper part of the Phu Noi succesion comprises of medium to finegrained sandstone with planar and cross beddings (Fig. 2)



FIGURE 2. Lithostratigraphic column and fossil record of the Phu Noi locality (modified from Boonchai et al., 2019; Ditbanjong and Chanthasit, 2019; Manitkoon et al. 2023b). Silhouettes by Wongwech Chowchuvech and Chatcharin Somboon. All silhouettes are not to scale.

The Phu Noi locality is renowned as one of the most prolific Mesozoic vertebrate deposits in Southeast Asia. Numerous taxa have been unearthed from this site, including freshwater sharks (Cuny et al., 2014), ray-finned fishes (Deesri et al., 2014), lungfishes (Cavin et al., 2020), amphibians (Nonsrirach et al., 2023), turtles (Tong et al., 2015; 2019), crocodyliforms (Martin et al., 2019; Johnson et al., 2020), pterosaurs (Buffetaut et al., 2015), and dinosaurs (Chanthasit et al., 2015). Within the Phu Noi locality, three dinosaur taxa have been identified, comprising metriacanthosaurid theropods (Samathi et al., 2019), mamenchisaurid sauropods, and a basal neornithischians *Minimocursor phunoiensis* (Manitkoon et al., 2023b) (Fig 2).

MATERIALS AND METHODS

The isolated teeth of tyrannosauroid were recovered alongside isolated teeth of metriacanthosaurid, mamenchisaurid, and neornithischian from the Phu Noi locality. These specimens were excavated by teams from the Palaeontological Research and Education Centre at Mahasarakham University and the Sirindhorn Museum, Department of Mineral Resources. The materials examined in this paper, SM2021-1-009, -048, and -050 are housed at the Sirindhorn Museum in Kalasin Province. Digital vernier caliper (Mitutoyo's Digimatic Caliper CD-6"ASX: 150 mm with an accuracy of 0.01 mm) was applied for morphometric measurements and a stereomicroscope (GEMAX Pro Digital Microscope MRS009P) for the morphological observation of dental features smaller than 1 cm such as denticles and crown ornamentations. The specimen description of the specimens follows the theropod teeth terminology protocol proposed by Hendrickx et al. (2015). Additionally, the positional nomenclature of the teeth followed the dental orientation proposed by Smith and Dodson (2003) and Hendrickx et al. (2015).

Taxonomic identification based on dental features of the studied specimens was performed using cladistics analysis. The analysis used a dental data matrix originally created by Hendrickx et al. (2015), with the most recent version of the data matrix published by Meso et al. (2022) and considered a dentition-based data matrix comprising 146 dental characters of 108 non-avian theropod taxa. The positive constraints were included in the analysis to recover a backbone topology, aligning with the results of previous phylogenetic studies. These constraints encompassed non-neotheropod saurischians (Müller et al., 2018), non-averostran neotheropods (Ezcurra, 2017), Ceratosauria (Rauhut and Carrano, 2016; Wang et al., 2017), non-coelurosaurian tetanurans (Carrano et al., 2012; Rauhut et al., 2012; 2016), Tyrannosauroidea (Brusatte and Carr, 2016), Megaraptora (Aranciaga Rolando et al., 2019), and neocoelurosaurs (Cau et al., 2017). All dental material were analyzed together, treating each tooth as a separate operational taxonomic unit (OTU), following the protocol of cladistic analysis established in previous works (Young et al., 2019; Hendrickx et al., 2020; Meso et al., 2021; Berrocal-Casero et al., 2022). All three analyses were conducted using TNT 1.6 (Goloboff and Morales, 2023), employing a combination of tree-search algorithms, including Wagner Trees, TBR branch swapping, sectorial searches, ratchet (perturbation phase stopped after 20), and tree fusing (5 rounds). The analysis continued until 100 hits of the same minimum tree length were obtained, followed by a final round of TBR branch swapping.

Furthermore, in order to determine the taxonomic position of three isolated teeth in family-level based on quantitative data, discriminant analysis was used in this study. We include three teeth into a morphometric dataset originally created by Hendrickx et al. (2015) and updated by Meso et al. (2022), which comprises 15 measurements (CBL, CBW, CH, AL, CBR, CHR, MCL, MCW, MCR, MSL, LAF, LIF, CA, MDL, DCL) obtained from 1373 teeth representing 91 non-avian theropod taxa (including 21 monophyletic or paraphyletic groups). The analysis was conducted using the linear discriminant analysis function (LDA) in Past version 4.11 (Hammer et al. 2001), treating all dental specimens under investigation as unidentified taxa.

RESULTS

Systematics Paleontology

Dinosauria Owen, 1842 Theropoda Marsh, 1881 Coelurosauria von Huene, 1914 Tyrannosauroidea Osborn, 1905 Tyrannosauroidea indet.

Description

Three isolated teeth consist of crowns and proximal parts of the root (Fig. 3). Several mesiodistal fractures are evident on the crowns. All crowns exhibit a ziphodont morphology, featuring distal curvatures and labiolingual compressions (Fig. 3A–C). Notably, the crown of SM2021-1-008 exhibits a less distinct distal curvature compared to the other two teeth (Fig. 3A). The cross-sections of the crowns are lenticular to elliptical (Fig. 3D–E). The three teeth measure between 15 to 24 mm in height, with a crown base ranging from

4.5 to 6.5 mm and a length of 9 to 11 mm. The crown base ratio varies from 0.5 to 0.6. The mesial carinae are not extended to the cervix in all specimens, with the mesial carina of SM2021-1-009 is terminating at approximately one-third of the crown height (Fig. 3F), whereas the mesial carinae of SM2021-1-048 and -050 are restricted to approximately two-thirds of the crown height (Fig. 3G). Distal carinae reach to the cervix in all teeth. Both the mesial and distal carinae of SM2021-1-009 shows a slight mesial carina of SM2021-1-048 and -050 show a strong twist (Fig. 3G). The distal carinae exhibit straight to slight distolabial twist in distal view (Fig. 3H–I).

Four to five denticles per mm can be observed in mesial carinae of isolated teeth (Fig. 3J-K), while the distal carinae contain three to five denticles per mm (Fig. 3L–N). The denticle size density index (DSDI) is varied from 1.00 to 1.34. Both the mesial and distal denticles are perpendicular to their respective carinae, which are subrectangular (Fig. 3J-K) and proximodistally subrectangular (Fig. 3L-N), respectively. Interdenticular sulci are absent on all crowns of the isolated teeth. The interdenticular space of SM2021-1-009 is shallow and narrow (Fig. 3J), while those of SM2021-1-048 and -050 are shallow and narrow interdenticular spaces (Fig. 3L). The external margins of both mesial and distal denticles exhibit symmetrical convex shapes with semicircular surfaces. Braided enamel texture is present on both labial and lingual surfaces of the teeth (Fig. 3O). The morphometric measurements of three isolated teeth are shown in Table 1.

Cladistics and Discriminant analyses

The results of cladistics analysis using a dentitionbased data matrix with fully constrained tree topology recovered two most parsimonious trees (CI=0.198; RI=0.461; L=1319 steps). All three isolated teeth were found within the Tyrannosauroidea clade and nested within the Proceratosauridae family, closely related to Guanlong and Proceratosaurus. SM2021-1-048 and -050 are found as the sister taxon, while SM2021-1-009 positioned basally (Fig. 4). The discriminant analysis classified isolated teeth among three theropod groups. At the clade level, SM2021-1-009 was identified as belonging to Neovenatoridae, while SM2021-1-048 was placed in Non-megalosauran Megalosauroidea, SM2021-1-048 was categorized as Nonand tyrannosaurid Tyrannosauroidea. PC 1 and PC 2 contributed 48.18% and 19.82% to the variance, respectively, with a reclassification rate of 58.7% (Fig. 5).



FIGURE 3. Isolated teeth of basal tyrannosauroid from the Phu Noi locality. SM2021-1-009 (A, F, and J–K), -048 (B, D, G–H, and O), and -050 (C, E, I, and L–N). in labial (A), lingual (B, C), basal (D, E), mesial (F, G), distal (H, I) views. mesioapical (J), mesiocentral (K), distoapical (L), distocentral (M), distobasal (N) denticles and enamel surface texture (O) in labial view. Abbreviations: dc, distal carina; idsp; interdenticular space; mc, mesial carina. Scale bars: A-I = 1 cm; J-N = 1 mm; O = 0.1 mm.

DISCUSSION

Taxonomic identification

Results of the cladistics and discriminant analyses both support the non-tyrannosaurid tyrannosauroid affinity for the three isolated teeth in term of qualitative and quantitative data. All three isolated teeth exhibit the typical dental features associated with theropod dinosaurs, including ziphodont teeth and serrated carinae (Hendrickx et al., 2019). The mesiodistal orientation of the carinae allows us to classify these teeth as lateral teeth (Hendrickx et al., 2015). Twisted mesial carinae in the lateral teeth is the dental feature that can be found among the coelurosaurian theropod groups, namely tyrannosauroids,

Specimens	Crown height (mm)	Crown base width (mm)	Crown base length (mm)	Crown base ratio	Denticle size density index	Denticl Mesial denticle	e per mm Distal denticle
SM2021-1-009	21.82	6.48	9.87	0.66	1.34	4	3
SM2021-1-048	24.38	5.65	11.09	0.51	1.25	5	4
SM2021-1-050	15.33	4.49	9.07	0.50	1.00	5	5

TABLE 1. Morphometric measurement of isolated teeth from the Phu Noi locality.

therizinosaurs and dromaeosaurids (Hendrickx et al., 2019). The braided enamel surface texture is distributed among various theropod group, including non-abelisaurrid ceratosaurs, non-spinosaurid megalocarcharodontosaurs, sauroids. non-neocoelurosaur coelurosaurs, eudromaeosaurs and most non-averostran theropods (Hendrickx et al., 2019). However, twisted mesial carinae that do not extend to the cervix and a braided enamel surface texture in the lateral teeth are the combination of dental features that can be found in Pianitzkysauridae and non-tyrannosaurid tyrannosauroids (Hendrickx et al., 2019). For Piatnitzkysauridae, numerous transverse undulations on the crown surface of the lateral dentition are considered as an unambigous dental synapomorphy (Hendrickx et al., 2019), whereas these are not present in the studied dental materials. Furthermore, Piatnitzkysauridae is known to be restricted to North and South America (Madsen, 1976; Bonaparte, 1979; Rauhut, 2005), with no fossil records of piatnitzkysaurids discovered in Asia. Therefore, three isolated teeth from the Phu Noi locality should be attributed to non-tyrannosaurid tyrannosauroids.

All three isolated teeth in this study possess dental features that align with the characteristics of Tyrannosauroidea. These features include mesial carinae that extend above the cervix and a braided enamel surface texture on the lateral teeth, which are recognized synapomorphies of non-tyrannosaurid Tyrannosauroidea (Hendrickx et al., 2019). Two of three isolated lateral teeth (SM2021-1-009 and -048) exhibit distal denticles that are larger than mesial denticles (DSDI > 1.25), while only SM2021-1-050 shows equal-sized mesial and distal denticles (DSDI = 1.00). This dental feature is common to most basal tyrannosauroids, especially proceratosaurids such as Guanlong and Proceratosaurus, in which most lateral teeth have distal denticles larger than their mesial denticles (Xu et al., 2006; Rauhut et al., 2010). In addition, the high to normal labiolingual compression of the crown (CBR < 0.75) observed in these three isolated teeth bears a resemblance to the lateral dentition of the non-tyrannosaurid tyrannosauroid

Guanlong, which has a CBR value of 0.5 (Han et al., 2011) (Table 2.). However, due to the absence of nondental elements, these teeth should be regarded as basal tyrannosauroid indet., pending more morphological and phylogenetic details in future studies.

Paleoecology of the Upper Jurassic Phu Kradung Formation

The presence of basal tyrannosauroid in this contribution marks the reconstruction of paleoecology of the Upper Jurassic Phu Kradung Formation. The coexistence of tyrannosauroids and metriacanthosaurids in the Phu Noi locality also appears in the Upper Jurassic Shishugou Formation of China, where a basal tyrannosauroid Guanlong wucaii (Xu et al., 2006) and a metriacanthosaurid Sinraptor dongi (Currie and Zhao, 1993) are found together in the upper part of the formation. Additionally, the cooccurrence between large-bodied allosauroids and small-bodied tyrannosauroids is commonly found throughout Laurasia during the Late Jurassic to early Late Cretaceous, such as in the Late Jurassic Morrison Formation of North America (Allosaurus fragilis; Marsh, 1877 and Stokesosaurus clevelandi; Madsen, 1974), the Early Cretaceous Wessex Formation of southern England (Neovenator salerii; Hutt et al., 1996 and Eotyrannus lengi; Hutt et al., 2001), and the early Late Cretaceous Bissekty Formation of Uzbekistan (Ulughbegsaurus uzbekistanensis; Tanaka et al., 2021 and Timurlengia euotica; Brusatte et al., 2016). It can be suggested that the large allosauroids were probably predator rather than the smaller the apex tyrannosauroids in the Late Jurassic to early Late Cretaceous ecosystems of Laurasia (Tanaka et al., 2021). Hence, the ecosystem of the Upper Jurassic Phu Kradung Formation should share the same pattern with other ecosystems of Laurasia during Late Jurassic based on the same carnivorous dinosaur faunal composition.

Moreover, beyond theropod dinosaurs, the herbivorous dinosaur fauna of the Upper Jurassic Phu Kradung Formation and the Upper Jurassic Shishugou Formation also share similarities with each other. Each



FIGURE 4. A strict consensus tree from the cladistics analysis of three isolated theropod teeth of the Phu Noi locality.

formation contains large-bodied herbivorous dinosaurs such as mamenchisaurids (Phu Noi mamenchisaurid; Manitkoon et al., 2023b and *Mamenchisaurus* sinocanadorum; Russell and Zheng, 1993) or



FIGURE 5. Result of the discriminant analysis performed at clade-level from the whole dataset with three isolated theropod teeth of the Phu Noi locality.

	Crown	Crown	Mesial carina not reaching the cervix	Spiraled mesial carina	Enamel surface texture	Denticle per mm			
Taxon	height (mm)	base length (mm)				Mesial denticle	Distal denticle	References	
Guanlong wucaii	8.9	4.54–9.34	Present	Present	Braided	-	-	Hendrickx et al. (2015)	
Proceratosaurus bradleyi	4–12.8	2.6-6.9	Present	Present	Braided	6–7.5	4.5–7.5	Rauhut et al. (2010)	
Kilekus aristotocus	-	11.5	-	-	-	-	-	Averianov et al. (2010)	
SM2021-1-009	21.82	9.87	Present	Present	Braided	4	3		
SM2021-1-048	24.38	11.09	Present	Present	Braided	5	4	This study	
SM2021-1-050	15.33	9.07	Present	Present	Braided	5	5		

TABLE 2. Morphological and morphometric comparisons of lateral teeth in Jurassic basal tyrannosauroids.

stegosaurids (Khok Sanam stegosaurid; Buffetaut et al., 2001 and *Jiangjunosaurus junggarensis*; Jia et al., 2007), and small-bodied herbivorous dinosaur fauna, including basal ornithischians (*Minimocursor phunoiensis*; Manitkoon et al., 2023b and *Gongbusaurus wucaiwanensis*; Dong 1989). These similarities of both carnivorous and herbivorous dinosaur fauna can be implying niche-partitioning between large- and small-bodied carnivorous theropod dinosaur during the Late Jurassic of Laurasia. Since the differences of body size are among the factors that affect the dinosaur

community structure and contribute to niche partitioning within the ecosystem (Schroeder et al., 2021; Wyenberg-Henzler, 2021), it is conceivable that the large theropod, such as metriacanthosaurids possibly herbivorous hunting large dinosaurs such as mamenchisaurids or stegosaurids, while the smaller herbivorous dinosaur like basal ornithischians may have been hunted by small-bodied tyrannosauroids (Fig. 6). Nevertheless, direct evidence of niche partitioning within the ecosystem of the Phu Kradung Formation should be investigated in future studies.



FIGURE 6. Paleoenvironmental reconstruction of the Late Jurassic Phu Kradung Formation of Northeastern Thailand. Illustrated by Chatcharin Somboon.

Paleobiogeography of Tyrannosauroidea

The discovery of tyrannosauroids in the Upper Jurassic Phu Kradung Formation of Northeastern Thailand, as reported in this study, marks the first substantial evidence of this theropod clade in Southeast Asia. It represents a remarkable extension of their known paleobiogeographical distribution. The fossil record of tyrannosauroids in Asia extends from the Middle Jurassic to the Late Cretaceous. However, there is a noticeable gap in the latest stage of the Jurassic Period (Tithonian Age) (Brusatte and Carr, 2016). The discovery of tyrannosauroids in the lower part of the Phu Kradung Formation, potentially from the Tithonian Age (Racey and Goodall, 2009), serves as crucial evidence to bridge this gap. It suggests that Asian tyrannosauroids were widespread from the Middle to the end of the Jurassic Period. This statement is supported by the discovery of Kileskus in the Middle Jurassic Itat Formation (Bajocian-Bathonian) of Sharypovsky, Southwestern Russia (Averianov et al., 2010), Guanlong in the Late Jurassic Shishugou Formation (Oxfordian) of Xinjiang, Northwestern China (Xu et al., 2006), and Thai basal tyrannosauroid. Furthermore, the occurrence of tyrannosauroids in the

latest stage of the Jurassic Period is not limited to Asia. Tyrannosauroid *Stokesosaurus* was found in the Tithonian Morrison Formation of Utah, North America (Madsen, 1974), and *Juratyrant* in the Tithonian Kimmeridge Clay of Dorset, southwestern England (Benson, 2008; Brusatte and Benson, 2013). These findings collectively suggest that tyrannosauroids were widely distributed in the northern hemisphere during the Late Jurassic.

CONCLUSION

The results of morphological investigation with cladistics and discriminant analyses show that the isolated theropod teeth from the Phu Noi locality are classified as non-tyrannosaurid tyrannosauroids, which phylogenetically related to basal tyrannosauroids *Guanlong* and *Proceratosaurus* from the Jurassic of Asia and Europe, respectively. Three isolated teeth exhibit the twisted mesial carinae that do not reach the cervix and the braided enamel surface texture that are the dental synapomorphies of basal tyrannosauroids. This discovery notes the first report of Tyrannosauroidea in the Jurassic of Southeast Asia and

contributes to the knowledge paleoecology of the lower Phu Kradung Formation, as well as paleobiogeographical distribution of tyrannosauroids during the Late Jurassic. Furthermore, this report sheds light on the possibility to finding new Thai dinosaur taxa in future excavations and studies.

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LITERATURE CITED

- Averianov, A.O., Krasnolutskii, S.A. and Ivantsov, S.V. 2010. A new basal coelurosaur (Dinosauria: Theropoda) from the Middle Jurassic of Siberia. Proceedings of the Zoological Institute, 314(1): 42–57.
- Aranciaga Rolando, A.M., Novas, F.E. and Agnolín, F.L. 2019. A reanalysis of *Murusraptor barrosaensis* Coria and Currie (2016) affords new evidence about the phylogenetical relationships of Megaraptora. Cretaceous Research, 99: 104–127.
- Barker, C.T., Naish, D. and Gostling, N.J. 2023. Isolated tooth reveals hidden spinosaurid dinosaur diversity in the British Wealden Supergroup (Lower Cretaceous). PeerJ, 11: e15453.
- Benson, R.B.J. 2008. New information on *Stokesosaurus*, a tyrannosauroid (Dinosauria: Theropoda) from North America and the United Kingdom. Journal of Vertebrate Paleontology, 28(3): 732–750.
- Berrocal-Casero, M., Alcalde-Fuentes, M. R., Audije-Gil, J. and Sevilla, P. 2022. Theropod teeth from the upper Barremian (Lower Cretaceous) of Vadillos-1, Spain. Cretaceous Research, 142: 105392.
- Bonaparte, J.F. 1979. Dinosaurs: a Jurassic assemblage from Patagonia. Science, 205(4413): 1377–1379.

- Boonchai, N., Suteethorn, S., Sereeprasirt, W., Suriyonghanphong, C., Romain, A., Cuny, G., Legrand, J., Thévenard, F. and Philippe, M. 2019. *Xenoxylon*, a boreal fossil wood in the Mesozoic red beds of Southeast Asia: potential for the stratigraphy of the Khorat Group and the palinspastic reconstruction of Southeast Asia. Journal Asian Earth Science, 189: 104153.
- Booth, J. and Sattayarak, N. 2011. Subsurface Carboniferous-Cretaceous geology of NE Thailand. In: Ridd, M.F., Barber, A.J. and Crow, M.J. (Eds). The Geology of Thailand, Geology Society of London, 185–222.
- Brusatte, S.L. and Benson, R.B.J. 2013. The systematics of Late Jurassic tyrannosauroids (Dinosauria: Theropoda) from Europe and North America. Acta Palaeontologica Polonica, 58(1): 47–54.
- Brusatte, S.L. and Carr, T.D. 2016. The phylogeny and evolutionary history of tyrannosauroid dinosaurs. Scientific Reports, 6: 20252.
- Brusatte, S.L., Carr, T.D., Erickson, G.M., Bever, G.S. and Norell, M.A. 2009. A long-snouted, multihorned tyrannosaurid from the Late Cretaceous of Mongolia. Proceedings of the National Academy of Sciences of the United States of America, 106(41): 17261–17266.
- Brusatte, S.L., Averianov, A., Sues, H.-D., Muir, A. and Butler, I.B. 2016. New tyrannosaur from the mid-Cretaceous of Uzbekistan clarifies evolution of giant body sizes and advanced senses in tyrant dinosaurs. Proceedings of the National Academy of Sciences, 113: 3447–3452.
- Buffetaut, E., Suteethorn, V. and Tong, H. 1996. The earliest known tyrannosaur from the Lower Cretaceous of Thailand, Nature 381(6584): 689–691.
- Buffetaut, E., Suteethorn, V. and Tong, H. 2001. The first thyreophoran dinosaur from Southeast Asia: a stegosaur vertebra from the Late Jurassic Phu Kradung Formation of Thailand. Nues Jahrbuch Fur Geologie Und Palaontologie-Monayshefte, 95–102.
- Buffetaut, E., Suteethorn, V., Le Loeff, J., Khansubha, S., Tong, H. and Wongko, K. 2005a. The dinosaur fauna from the Khok Kruat Formation (Early Cretaceous) of Thailand. In: Wannakao, L., Youngme, W., Buaphan, C., Srisuk, K. and Lertsirivorakul, R. (Eds.). Proceedings of the International Conference on Geology, Geotechnology and Mineral Resources of Indochina, 575–581.
- Buffetaut, E., Suteethorn, V. and Tong, H. 2005b. Dinosaur assemblages from Thailand: a comparison with Chinese faunas. In: J. Lū, Y., Kobayashi, D. Huang, and Y. Lee (Eds.). Papers from the 2005 Heyuan International Dinosaur Symposium, Beijing, 19–37.
- Buffetaut, E., Suteethorn, V., Suteethorn, S., Deesri, U. and Tong, H. 2015. An azhdarchoid pterosaur humerus from the Latest Jurassic (Phu Kradung Formation) of Phu Noi, North-Eastern Thailand. Research & Knowledge, 1:43–47.
- Cavin, L., Deesri, U. and Chanthasit, P. 2020. A new lungfish from the Jurassic of Thailand. Journal of Vertebrate Paleontology, 40: e1791895.
- Carrano, M.T., Benson, R.B.J. and Sampson, S.D. 2012. The phylogeny of Tetanurae (Dinosauria: Theropoda). Journal of Systematic Palaeontology, 10: 211–300.
- Carter, A. and Bristow, C.S. 2004. Linking hinterland evolution and continental basal sedimentation by using detrital zircon thermochronology: a study of the Khorat Plateau Basin, Eastern Thailand. American Museum Novitates, 3438: 1–20.
- Cau, A., Beyrand, V., Voeten, D.F.A.E., Fernandez, V., Tafforeau, P., Stein, K., Barsbold, R., Tsogtbaatar, K., Currie, P.J. and Godefroit, P. 2017. Synchrotron scanning reveals amphibious ecomorphology in a new clade of bird-like dinosaurs. Nature, 552: 395–399.

- Chanthasit, P., Suteethorn, S. and Suteethorn, V. 2015. Dinosaur assemblage from Phu Noi Fossil Sited in Kalasin Province, Northeastern Thailand. In: Proceedings of the 2nd International Symposium on Asian Dinosaurs, Thailand, 22–29.
- Cuny, G., Liard, R., Deesri, U., Liard, T., Khamha, S. and Suteethorn, V. 2014. Shark faunas from the Late Jurassic–Early Cretaceous of Northeastern Thailand. Paläontologische Zeitschrift, 88: 309–328.
- Deesri, U., Lauprasert, K., Suteethorn, V., Wongko, K. and Cavin, L. 2014. A new species of the ginglymodian fish *Isanichthys* (Actinopterygii, Holostei) from the Late Jurassic Phu Kradung Formation, Northeastern Thailand. Acta Palaeontologica Polonica, 59: 313–331.
- Delcourt, R. and Grillo, O.N. 2018. Tyrannosauroid from the Southern Hemisphere: implications for biogeography, evolution, and taxonomy. Palaeogeography, Palaeoclimatology, Palaeoecology, 511: 379–387.
- Ditbanjong, P. and Chanthasit, P. 2019. Sedimentary facies and depositional environment of Phu Noi Site from the Late Jurassic Phu Kradung Formation, Khorat Group, Kalasin Province, Northeastern Thailand. In: Proceedings of the 4th International Symposium on Asian Dinosaurs, Mongolia, 50–51.
- Dong, Z. 1989. On a small ornithopod (*Gongbusaurus wucaiwanensis*) from Kelamaili, Jungar Basin, Xinjiang, China. Vertebrata PalAsiatica, 27: 140–146.
- Ezcurra, M. 2017. A new early coelophysoid neotheropod from the Late Triassic of Northwestern Argentina. Ameghiniana, 54: 506–538.
- Gilmore, C.W. 1933. On the dinosaurian fauna of the Iren Dabasu Formation. Bulletin of the American Museum of Natural History, 67(2): 23–78.
- Goloboff, P.A. and Morales, M.E. 2023. TNT version 1.6, with a graphical interface for MacOS and Linux, including new routines in parallel. Cladistics, 39(2):144–153.
- Hammer, Ø., Harper, D.A.T. and Ryan, P.D. 2001. Past: Paleontological Statistics Software Package for education and data analysis. Palaeontologia Electronica, 4: 1–9.
- Han, F.L., Clark, J.M., Xu, X., Sullivan, C., Choiniere, J. and Hone, D.W.E. 2011. Theropod teeth from the Middle-Upper Jurassic Shishugou Formation of Northwest Xinjiang, China. Journal of Vertebrate Paleontology, 31(1): 111–126.
- Hendrickx, C., Mateus, O. and Araújo, R. 2015. A proposed terminology of theropod teeth (Dinosauria, Saurischia). Journal of Vertebrate Paleontology, 35(5): e982797.
- Hendrickx, C., Mateus, O., Araújo, R. and Choiniere, J. 2019. The distribution of dental features in non-avian theropod dinosaurs: taxonomic potential, degree of homoplasy, and major evolutionary trends. Palaeontologia Electronica, 22(3): 1–110.
- Hendrickx, C., Tschopp, E. and Ezcurra, M. 2020. Taxonomic identification of isolated theropod teeth: the case of the shed tooth crown associated with Aerosteon (Theropoda: Megaraptora) and the dentition of Abelisauridae. Cretaceous Research, 108: 104312.
- Hone, D.W.E., Wang, K., Sullivan, C., Zhao, X., Chen, S., Li, D., Ji, S., Ji, Q. and Xu, X. 2011. A new, large tyrannosaurine theropod from the Upper Cretaceous of China. Cretaceous Research, 32(4): 495–503.
- von Huene, F. 1914. Saurischia et Ornithischia Triadica ("Dinosauria" Triadica). Animalia Fossilium Catalogus, 4: 1–21.
- Hutt, S., Martill, D.M. and Barker, M.J. 1996. The first European allosauroid dinosaur (Lower Cretaceous, Wealden Group, England). Neues Jahrbuch für Geologie und Paläontologie – Monatshefte, 10: 635–644.
- Hutt, S., Naish, D., Martill, D.M., Barker, M.J and Newbery, P. 2001. A preliminary account of a new tyrannosauroid theropod

from the Wessex Formation (Cretaceous) of southern England. Cretaceous Research, 22: 227–242.

- Ji, Q., Ji, S. and Zhang, L. 2009. First large tyrannosauroid theropod from the Early Cretaceous Jehol Biota in northeastern China. Geological Bulletin of China, 28(10): 1369–1374.
- Jia, C., Foster, C.A., Xing, X., and Clark, J.M. 2007. The first stegosaur (Dinosauria, Ornithischia) from the Upper Jurassic Shishugou Formation of Xinjiang, China. Acta Geologica Sinica (English Edition), 81: 351–356.
- Johnson, M.M., Young, M.T. and Brusatte, S.L. 2020. The phylogenetics of Teleosauroidea (Crocodylomorpha, Thalattosuchia) and implications for their ecology and evolution. PeerJ, 8: e9808.
- Kurzanov, S.M. 1976. A new carnosaur from the Late Cretaceous of Nogon-Tsav, Mongolia. The Joint Soviet-Mongolian Paleontological Expedition Transactions, 3: 93–104.
- Li, D., Norell, M.A., Gao, K.-Q., Smith, N.D. and Makovicky, P.J. 2009. A longirostrine tyrannosauroid from the Early Cretaceous of China. Proceedings of the Royal Society B: Biological Sciences, 277(1679): 183–190.
- Lü, J., Yi, L., Brusatte, S. L., Yang, L. and Chen, L. 2014. A new clade of Asian Late Cretaceous long-snouted tyrannosaurids. Nature Communications, 5(3788): 3788.
- Madsen, J.H. 1974. A new theropod dinosaur from the Upper Jurassic of Utah. Journal of Paleontology, 48: 27–31.
- Madsen, J.H. 1976. A second new theropod dinosaur from the Late Jurassic of east central Utah. Utah Geology, 3(1): 51–60.
- Maleev, E.A. 1955. Giant carnivorous dinosaurs of Mongolia. Doklady Akademii Nauk SSSR, 104(4): 634–637.
- Manitkoon, S., Deesri, U., Lauprasert, K., Warapeang, P., Nonsrirach, T., Nilpanapan, A., Wongko, K., and Chanthasit, P. 2022. 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). Fossil Record, 25: 83–98.
- Manitkoon, S., Deesri, U., Warapeang, P., Nonsrirach, T. and Chanthasit, P. 2023a. Ornithischian dinosaurs in Southeast Asia: a review with palaeobiogeographic implications. Fossil Record, 26(1): 1–25.
- Manitkoon, S., Deesri, U., Khalloufi, B., Nonsrirach, T., Suteethorn, V., Chanthasit, P., Boonla, W. and Buffetaut, E. 2023b. A new basal neornithischian dinosaur from the Phu Kradung Formation (Upper Jurassic) of Northeastern Thailand. Diversity, 15: 851.
- Marsh, O. 1877. Notice of new dinosaurian reptiles from the Jurassic formation. American Journal of Science and Arts, 14(84): 514–516.
- Marsh, O. 1881. Principal characters of American Jurassic dinosaurs. Part V. American Journal of Science, 3(21): 417–423.
- Martin, J.E., Suteethorn, S., Lauprasert, K., Tong, H., Buffetaut, E., Liard, R., Salaviale, C., Deesri, U. and Claude, J. 2019. A new Freshwater teleosaurid from the Jurassic of Northeastern Thailand. Journal of Vertebrate Paleontology, 38: 1–28.
- Meso, J.G., Hendrickx, C., Baiano, M.A., Canale, J.I., Salgado, L. and Martinez, I.D. 2021. Isolated theropod teeth associated with a sauropod skeleton from the Late Cretaceous Allen Formation of Río Negro, Patagonia, Argentina. Acta Palaeontologica Polonica, 66(2): 409–423.
- Meso, J.G., Gianechini, R.D. Juárez Valieri, S. and Apesteguía, S.A.S. 2022. Theropods from the La Bonita site, Bajo de la Carpa Formation (Neuquén Group, Santonian), Río Negro, Argentina: analysis of dental evidence. Cretaceous Research, 137: 105250.
- Müller, R.T., Langer, M.C., Bronzati, M., Pacheco, C.P., Cabreira, S.F. and Dias-Da-Silva, S. 2018. Early evolution of sauropodomorphs: anatomy and phylogenetic relationships of a

remarkably well-preserved dinosaur from the Upper Triassic of southern Brazil. Zoological Journal of the Linnean Society, 184: 1187–1248.

- Nonsrirach, T., Manitkoon, S. and Lauprasert, K. 2021. First occurrence of brachyopid temnospondyls in Southeast Asia and review of the Mesozoic amphibians from Thailand. Fossil Record, 24: 33–47.
- Owen, R. 1842. Report on British fossil reptiles, part 2, reptile. In: 11th Meeting of the British Association for the Advancement of Science, Plymouth, 60–204.
- Osborn, H.F. 1905. *Tyrannosaurus* and other Cretaceous carnivorous dinosaurs. Bulletin of the American Museum of Natural History, 21: 259–265.
- Racey, A. and Goodall, J.G.S. 2009. Palynology and stratigraphy of the Mesozoic Khorat Group red bed sequences from Thailand. In: E. Buffetaut, G. Cuny, J. Le Loeff, and V. Suteethorn (eds.), Late Paleozoic and Mesozoic Ecosystems in SE Asia. Geological Society of London Special Publication, 315: 41–68.
- Rauhut, O.W.M. 2003. The interrelationships and evolution of basal theropod dinosaurs. Special Papers in Palaeontology, 69: 1–213.
- Rauhut, O.W.M. 2005. Osteology and relationships of a new theropod dinosaur from the Middle Jurassic of Patagonia. Palaeontology, 48(1): 87–110.
- Rauhut, O.W.M. and Carrano, M.T. 2016. The theropod dinosaur *Elaphrosaurus bambergi* Janensch, 1920, from the Late Jurassic of Tendaguru, Tanzania. Zoological Journal of the Linnean Society, 178: 546–610.
- Rauhut, O.W.M., Milner, A.C. and Moore-Fay, S. 2010. Cranial osteology and phylogenetic position of the theropod dinosaur *Proceratosaurus bradleyi* (Woodward, 1910) from the Middle Jurassic of England. Zoological Journal of the Linnean Society, 158: 155–195.
- Rauhut, O.W.M., Foth, C., Tischlinger, H. and Norell, M.A. 2012. Exceptionally preserved juvenile megalosauroid theropod dinosaur with filamentous integument from the Late Jurassic of Germany. Proceedings of the National Academy of Sciences of the United States of America, 109: 11746–11751.
- Rauhut, O.W.M., Hübner, T.R. and Lanser, K.-P. 2016. A new megalosaurid theropod dinosaur from the late Middle Jurassic (Callovian) of north-western Germany: implications for theropod evolution and faunal turnover in the Jurassic. Palaeontologia Electronica, 19(2): 1–65.
- Russell, D.A and Zheng, Z. 1993. A large mamenchisaurid from the Junggar Basin, Xinjiang, People's Republic of China, Canadian Journal of Earth Sciences, 30(10): 2082-2095.
- Samathi, A., Chanthasit, P. and Sander, P. 2019. A review of theropod dinosaurs from the Late Jurassic to mid-Cretaceous of Southeast Asia. Annales de Paléontologie, 105: 201–215.
- Samathi, A., Suteethorn, S., Boonjarern, T., Sutcha, K., and Suteethorn, V. 2024. Dinosaur fauna from the Lower

Cretaceous of Phu Kao-Phu Phan Kham, northeastern Thailand: A review and update. Palaeoworld, 33(2): 420-438.

- Schroeder, K., Lyons, S.K. and Smith, F.A. 2021. The influence of juvenile dinosaurs on. Community structure and diversity. Science, 371(6532): 941–944.
- Smith, N.D. and Dodson, P. 2003. A proposal for a standard terminology of anatomical notation and orientation in fossil vertebrate dentitions. Journal of Vertebrate Paleontology, 23: 1–2.
- Tanaka, K., Anvarov, O.U.O., Zelenitsky, D.K., Ahmedshaev, A.S. and Kobayashi, Y., 2021. A new carcharodontosaurian theropod dinosaur occupies apex predator niche. In the early Late Cretaceous of Uzbekistan. Royal Society Open Science, 8: 210923.
- Tong, H., Naksri, W., Buffetaut, E., Suteethorn, V., Suteethorn, S., Deesri, U., Sila, S., Chanthasit, P. and Claude, J. 2015. A new primitive eucryptodiran turtle from the Upper Jurassic Phu Kradung Formation of the Khorat Plateau, NE Thailand. Geology Magazine, 152: 166–175.
- Tong, H., Naksri, W., Bu, E., Suteethorn, S., Suteethorn, V., Chanthasit, P. and Claude, J. 2019. *Kalasinemys*, a new xinjiangchelyid turtle from the Late Jurassic of NE Thailand. Geology Magazine, 156: 1645–1656.
- Wang, S., Stiegler, J., Amiot, R., Wang, X., Du, G., Clark, J.M. and Xu, X. 2017. Extreme ontogenetic changes in a ceratosaurian theropod. Current Biology, 27: 144–148.
- Woodward, A.S. 1910. On a skull of *Megalosaurus* from the Great Oolite of Minchinhampton (Gloucestershire). Quarterly Journal of the Geological Society, 66: 1–4.
- Wyenberg-Henzler, T., Patterson, R.T. and Mallon, J.C. 2021. Sizemediated competition and community structure in a Late Cretaceous herbivorous dinosaur assemblage. Historical Biology, 34(1370): 1–11.
- Xu, X., Norell, M.A., Kuang, X., Wang, X., Zhao, Q. and Jia, C. 2004. Basal tyrannosauroids from China and evidence for protofeathers in tyrannosauroids. Nature, 431(7009): 680–684.
- Xu, X., Clark, J.M., Forster, C.A., Norell, M.A., Erickson, G.M., Eberth, D.A., Jia, C. and Zhao, Q. 2006. A basal tyrannosauroid dinosaur from the Late Jurassic of China, Nature 439: 715–718.
- Xu, X., Wang, K., Zhang, K., Ma, Q., Xing, L., Sullivan, C., Hu, D., Cheng, S. and Wang, S. 2012. A gigantic feathered dinosaur from the Lower Cretaceous of China. Nature, 484: 92–95.
- Yin, Y.L., Xie, F., Zhou, C.F. and Pei, R. 2024. Dinosaur teeth from the mid-Cretaceous Sunjiawan Formation of western Liaoning Province, China. Historical Biology, 36(3): 631–637.
- Young, C.M., Hendrickx, C., Challands, T.J., Foffa, D., Ross, D.A., Butler, I.B. and Brusatte, S.L. 2019. New theropod dinosaur teeth from the Middle Jurassic of the Isle of Skye, Scotland. Scottish Journal of Geology, 55(1): 7–19.