# Thai Geoscience Journal 6(9), 2025, p. 13-28 Copyright © 2025 by the Department of Mineral Resources of Thailand ISSN-2730-2695 (Print); ISSN-3056-9370 (Online); DOI-10.14456/tgj.2025.2

# The occurrence of Spinosauridae (Dinosauria: Theropoda) during the Cretaceous of Asia: Implications for biogeography and distribution

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Received 26 January 2025; Revised 16 May 2025; Accepted 6 June 2025.

#### **Abstract**

The theropod dinosaur clade Spinosauridae lived on almost all continents during the Cretaceous. It has been suggested that the group originated in Laurasia, likely in Europe. Asian spinosaurid fossils have been discovered in Southeast and East Asia, particularly from Barremian-Aptian deposits of the Early Cretaceous, with some additional evidence from Cenomanian-aged sediments in the Late Cretaceous. The presence of this theropod clade in Asia, including Thailand, Malaysia, Laos, China, and Japan, may have been influenced by the regression of the Uralian seaway, which temporarily connected Europe and Asia via an ephemeral landbridge. This change likely affected the dispersal of spinosaurids from Europe, facilitating their spread across Asia and shaping their evolution through geographic vicariance. This study reviews the Asian fossil record of Spinosauridae to examine their emergence, paleogeographic distribution, and dispersal patterns. The reports of Asian spinosaurids suggested that the distribution of this clade in Asia is complex and dubious due to the incompleteness of materials and uncertainty of the age of several fossil-bearing strata. The spinosaurid ancestors dispersed along the coastal shoreline from Europe by crossing ephemeral landbridge during pre-Barremian. Then, they spread out to Thailand, Malaysia, southern China, and Japan. The presence of Late Cretaceous spinosaurids in China suggests that Asian spinosaurids persisted until the extinction event of this clade, as happened in western Laurasia and Gondwana during the Cenomanian.

Keywords: Asia, dispersal event, Early Cretaceous, Spinosauridae

#### 1. Introduction

Spinosauridae, a clade of large-bodied theropod dinosaurs that lived in the Cretaceous period, are found in almost all continents (except North America, Australia, and Antarctica) and are one of the abundant and cosmopolitan theropods (Sereno et al., 1998; Hone and Holtz, 2017; Poropat et al., 2019). The laterally compressed and narrow elongated skulls, the conical-shaped teeth with size-heterodont (different sizes of teeth along the premaxilla, maxilla, and dentary) (Hendrickx et al., 2019), and neural spine expansion reaching approximately twice the height of the centrum are observed in most spinosaurids (e.g.,

Suchomimus tenerensis), whereas extremely elongated neural spines are observed in some spinosaurines (e.g., Spinosaurus aegyptiacus) (Stromer, 1915; Charig and Milner, 1986, 1997; Sereno et al., 1998; Hone and Holtz, 2017; Ibrahim et al., 2020). Spinosauridae is traditionally classified as a member of Megalosauriodea (Fig. 1) (Benson, 2010), which is divided into two subclades, the Baryonychinae and the Spinosaurinae (Charig and Milner, 1986, 1997; Sereno et al., 1998).

Spinosauridae was distributed in Laurasia and Gondwana (Stromer, 1915; Charig and Milner, 1986, 1997; Sereno et al., 1998; Martill et al., 1996). Laurasia was suggested as the land of spinosaurid

origins, especially Europe, where the early spinosaurids probably evolved and emerged (Milner, 2003; Barker et al., 2021). The probable oldest evidence is the tooth DCM- G95b (?Baryonychinae indet.) from the Purbeck Limestone Group, England (Berriasian age). The specimen, the so-called "Saurian" tooth, exhibits characteristics that point to Baryonychinae. These include granular enamel, which is probably a veined texture, flutes present only on the lingual side, slight lingual curvature, and a crown that is convex mesially, moderately concave distally, and lacks denticles (see Hendrickx et al., 2019). These characteristics have been observed in baryonychines such as Baryonyx walkeri and Suchomimus tenerensis, whereas the non-denticulated teeth are found in spinosaurines such as Irritator challengeri and Spinosaurus aegyptiacus

(Charig and Milner, 1997; Sereno et al., 1998; Sues et al., 2002; Fowler, 2007; Hendrickx et al., 2019). However, some characteristics (e.g., conidont teeth ornamented by the pack of flutes with non--denticulated crowns) are present in both spinosaurids and marine reptiles such as pliosaurids, which are found in the same localities (Fowler, 2007; Solonin et al., 2021). The oldest well-known spinosaurid, NHMUK 36536, originates from the Wadhurst Clay Formation, England (Valanginian age). Initially classified as the crocodilian Suchosaurus cultridens (Owen, 1840-45), it was later reassigned as Baryonyx (Milner, 2003) and may represent Baryonyx walkeri (Mateus et al., 2011). This evidence supports the hypothesis of a Laurasian origin, initially proposed by Milner (2003) and later reinforced by Barker et al. (2021).

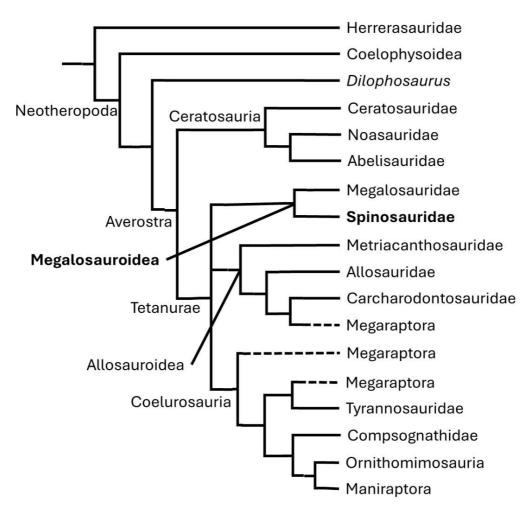


Fig. 1: Simplified cladogram of Spinosauridae among theropods (modified from Samathi et al., 2019a).

#### 2. Institutional abbreviations

FPDM, Fukui Prefectural Dinosaur Museum, Fukui, Japan; GMNH, Gunma Museum of Natural History, Tomioka, Japan; HIII, Henan Geological Museum, Zhengzhou, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; KDC, Kanna Dinosaur Center, Gunma, Japan; MDS, Dinosaur Museum, Savannakhet, Laos; NP, Nanjing Paleontology Museum, China; PM, Phu Wiang Fossil Research Center and Dinosaur Museum, Khon Kaen, Thailand; PRC, Paleontological Research Education Centre, Mahasarakham University, Maha Sarakham, Thailand: SM, Sirindhorn Museum, Kalasin, Thailand; UM, University of Malaya, Kuala Lumpur, Malaysia; XMDFEC, Xixia Museum of Dinosaur Fossil Eggs of China.

# 3. Spinosauridae in Asia

The oldest report of spinosaurids in Asia is from northeastern Thailand. It is a conical tooth collected during the geological survey in the 1960s (Ward and Bunnag, 1964; Buffetaut and Tong, 2024). Initially, this specimen was described as a marine reptile tooth by Kobayashi et al. (1963). Subsequently, Siamosaurus suteethorni was discovered at the Phu Pratu Teema locality and described as a member of the Spinosauridae (Buffetaut and Ingavat, 1986). This discovery led to the recognition that the previously identified teeth also belong to Spinosauridae, and belong to Siamosaurus as well (Buffetaut and Tong, 2024). Before the description of Siamosaurus, 'Sinopliosaurus' fusuiensis was established based on teeth discovered in Guangxi, southern part of China (Hou et al., 1975). These teeth were initially classified as a pliosauroid, dating to the Aptian age (late Early Cretaceous). Subsequently, the specimens were redescribed as being related to, if not the same genus as, Siamosaurus (Buffetaut et al., 2008). Asian spinosaurids were mainly discovered from the early and late Early Cretaceous, with at least one report

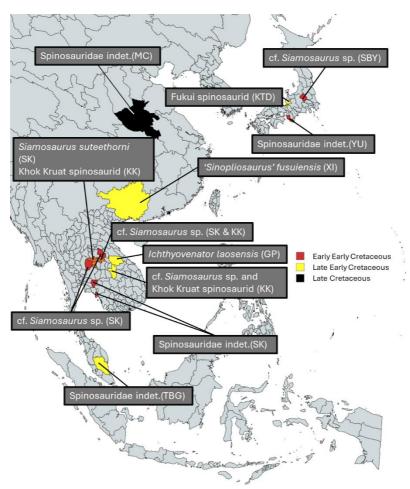
from the Late Cretaceous (Fig. 2, 3; Appendix Table 1).

# 3.1 Early Early Cretaceous

Spinosauridae reported from the early Early Cretaceous can be found in the northeastern part of Thailand (Sao Khua Formation), Wakayama, and Gunma prefectures of Japan (Yuasa and Sebayashi formations, respectively) (Buffetaut et al., 2009; Racey and Goodall, 2009; Tumpeesuwan, 2010; Matsukawa, 1983; Matsukawa and Obata, 1994; Kubota et al., 2017).

#### **Thailand**

Sao Khua Formation: This formation is a member of the non-marine Mesozoic Khorat Group. Based on sedimentology, palynology, and fauna remains, the formation is considered to date from the Late Valanginian to possibly the latest Barremian or the earliest Aptian (Buffetaut and Suteethorn, 1999; Buffetaut et al., 2009; Racey and Goodall, 2009; Tumpeesuwan, 2010; Tucker et al., 2022). Spinosaurid materials discovered in this formation include conical teeth of Siamosaurus suteethorni from Phu Wiang National Park, Khon Kean Province. The Phu Wiang National Park is the main area where most Sao Khua spinosaurid materials have been collected, including Phu Wiang Site 1, Site 5, Site 7, and Site 9 (Buffetaut and Ingavat, 1986; Samathi et al., 2019b). Notably, the Phu Wiang Site 9 locality has yielded teeth and the caudal series of the so-called 'Phuwiang spinosaurid B' (Samathi et al., 2021). Additionally, spinosaurid teeth (referred to cf. Siamosaurus sp.) have been collected from various localities in northeastern Thailand, including Phu Kum Khao locality in Kalasin Province, Huai Huat locality in Sakon Nakhon Province, Non Lhiam locality in Chaiyaphum Province, and Phu Din Dang locality in Nakhon Phanom Province (KP and AS pers. obs.). Furthermore, spinosaurid teeth have been also discovered in Eastern Thailand, including localities such as Ko Kut locality in Trat Province and Phra Prong locality in Sra Keao Province, near the Gulf of Thailand



**Fig. 2:** The regions of Asia (Southeastern Asia + Eastern Asia) from which spinosaurid remains were reported. Abbreviation: (GP), "Grès supérieurs" Formation; (KK), Khok Kruat Formation; (KTD), Kitadani Formation; Mangchuan Formation (MC); (SK), Sao Khua Formation; (TBG), Tembling Group; (XI), Xinlong Formation; Yuasa Formation (YU).



**Fig. 3:** Selected material of Asian spinosaurids. (A) *Siamosaurus suteethorni* (SM-TF2043). (B) Khok Kruat spinosaurid tooth (SM-PNS-2018). (C) A tooth from Nakazato locality, Gunma, Japan (GMNH-PV-999 cast). (D) A tooth from Kanna locality, Gunma, Japan (KDC-PV-0003 cast). (E) *Ichthyovenator laoensis* dorsal vertebra (cast of MDS BK10). (F) Sam Ran spinosaurid dorsal neural spine (SM-KK14, Samathi et al., in prep.). (G) *Ichthyovenator laoensis* caudal vertebra (cast of MDS BK10). (H) Phuwiang spinosaurid B caudal vertebra (SM-PW9B-15). Photographs taken by the authors. Not to scale.

(Suteethorn et al., 2018; Buffetaut et al., 2019).

# Japan

Yuasa Formation: This formation is considered to be approximately Hauterivian in age based on stratigraphic correlation with adjacent formations (Ide and Maejima, 2011). A spinosaurid tooth fragment has been recovered in this formation in Wakayama Prefecture (Kubota, 2023), and it is currently under study (Y. Nakajima pers. comm.).

Sebayashi Formation: This formation was deposited in approximately the latest Barremian to Aptian age (middle to late Early Cretaceous) of Japan, based on ammonites and bivalves collected from the underlying Ishido Formation and overlying Sanyama Formation (Matsukawa, 1983; Matsukawa and Obata, 1994). Spinosaurid material found in this formation includes tooth fragments (GMNH-PV-999 and KDC-PV-0003) from Gunma Prefecture, Japan, which have been referred to as *Siamosaurus* (Hasegawa et al., 2003; Buffetaut et al., 2008; Kubota et al., 2017; AS pers. obs.).

# 3.2 Late Early Cretaceous

Most Asian spinosaurids have been discovered from the late Early Cretaceous (approximately Aptian to Albian age) sediments, indicating that spinosaurids were diverse during this period and likely spread across several regions of Asia, including Thailand, Laos, China, and Japan.

## Thailand

Khok Kruat Formation: This formation is a member of the Khorat Group, which is considered to date to the Aptian age, based on the palynological evidence and other fossil remains (Sattayarak et al., 1991; Racey et al., 1996; Buffetaut et al., 2005a, b; Chokchaloemwong et al., 2019). Furthermore, the diversity of spinosaurids was studied by Wongko et al. (2019), who identified two morphotypes of conidont teeth from the Khok Kruat Formation of Sam Ran, Khok Pha Suam, and Lam Pao

Dam localities: Morphotype I, the 'Khok Kruat' morphotype, and Morphotype II, the 'Siamosaurus' morphotype. This evidence suggests that two spinosaurid taxa were occurring in the Aptian age of Thailand. Additionally, the postcranial skeleton SM-KK14 comprises cervical and dorsal vertebrae, pelvic elements, an elongated neural spine, and a chevron was discovered at the Sam Ram locality, Khon Kaen Province (Buffetaut et al., 2004, 2005b; Samathi et al., 2019b). The Sam Ran postcranial material may belong to the same taxon, if not individual, as the Morphotype I teeth found in the same locality. However, this postcranial material requires further study (Samathi et al., in prep.). Other Khok Kruat localities that yielded spinosaurid material are Ban Pha Nang Sua locality in Chaiyaphum Province (Khansubha et al., 2017) and Ban Wang Mon locality in Nong Bua Lamphu Province (Samathi et al. 2024).

#### Laos

"Grès supérieurs" Formation: The stratigraphy of the "Grès supérieurs" Formation is estimated to date from Aptian to Albian based on the occurrence of freshwater bivalves of the superfamily Trigonioidacea, which are known from the Aptian to Albian (Kobayashi, 1963, 1968). Ichthvovenator laosensis is the only spinosaurid theropod discovered and named in Laos. The holotypic material of Ichthyovenator laosensis comprises a dorsal vertebra, a neural spine, caudal vertebrae, sacral vertebrae, ilia, the right pubis, ischia, and a dorsal rib. The referred material includes a series of cervical vertebrae, the first dorsal vertebra, the left pubis, caudal vertebrae, and teeth (Allain et al., 2012; Allain, 2014; cast of MDS BK10-01 to 15 housed at FPDM and NRRU, KS and AS pers. obs.). This dinosaur has been classified as belonging to the subclade Spinosaurinae (Barker et al., 2021).

## Malavsia

**Tembeling Group:** The depositional environment of the Tembeling Group is

generally accepted to be fluvial-lacustrine (Teng et al., 2019). It was considered to date to the Barremian–early Aptian age (Sone et al., 2022). Spinosaurid teeth (UM10575 and UM10576) were recovered from the state of Pahang, Peninsular Malaysia (Sone et al., 2015). The teeth exhibit sharp vertical ridges, serrated carinae with minute denticles, and a veined enamel texture (Sone et al., 2015; Samathi et al., 2019b).

## China

**Xinlong Formation:** The sediment of the Xinlong (or Napai) Formation of China was deposited during the Early Cretaceous. This formation may be correlated with either the Sao Khua or Khok Kruat formations in Thailand (Buffetaut et al., 2006). Based on the faunal similarities, it is more closely related to the Khok Kruat Formation (approximately Aptian age) (Buffetaut et al., 2008). Hou et al. (1975) identified several conical teeth (IVPP V 4793, which includes five teeth, and the referred material: NP03 and NP07 tooth fragments) from Guangxi, China (Hou et al., 1975; Amiot et al., 2010), as belonging to a pliosauroid and named them 'Sinopliosaurus' fusuiensis. Subsequently, the discovery of Siamosaurus suteethorni from Thailand led to the reassignment of 'Sinopliosaurus' fusuiensis as a spinosaurid related to Siamosaurus (Buffetaut et al., 2008; Samathi et al., 2019b).

#### Japan

Kitadani Formation: This formation in Japan is dated to the Aptian age, based on the co-occurrence of multiple species of charophyte gyrogonites (Sano, 2015). Eighteen spinosaurid teeth were recovered from Kitadani Formation of Fukui, central Japan (Hattori and Azuma, 2020). Interestingly, the Fukui spinosaurid teeth exhibit characteristics of both Baryonychinae and Spinosaurinae and are distinct from those of the Sebayashi spinosaurids, suggesting that the Fukui spinosaurid may represent a basal member of Spinosauridae (Hasegawa et al., 2003; Kubota et al., 2017; Hattori and Azuma, 2020).

#### 3.3 Late Cretaceous

Asian spinosaurids from the Late Cretaceous were reported only from Henan, China.

#### China

Mangchuan Formation: The sediment of the Mangchuan Formation (or Ruyang Basin), Henan, China, has been estimated to be early Late Cretaceous, possibly Cenomanian (Bertin, 2010). A spinosaurid tooth has been briefly reported. It was found with other dinosaurs, including ornithomimosaurs, oviraptorosaurs, and sauropods (Lü et al., 2009). The tooth shows a slightly recurved profile with indistinct flutes on the lingual side (see Lü et al., 2009, fig. 4B). Unfortunately, no other information has been reported.

Majiacun Formation: The Majiacun Formation of Sanlimiao, Xixia County, Henan, China, is estimated to date to the middle Santonian (Hone et al., 2010). A relatively large and complete isolated tooth of a probable baryonychine XMDFEC V0010 was reported (Hone et al., 2010; Hone and Holtz, 2017). The conical tooth shows a slightly recurved profile with denticles on both anterior and posterior carinae, and the enamel texture is smooth, but there are no ridges on the crown (Hone et al., 2010; p. 21).

However, XMDFEC V0010 was later found to be not a spinosaurid (based on dental characters, Kubota et al. 2017), but could belong to Allosauroidea or Abelisauridae (based on discriminant function analyses and cluster analyses, Barker et al. 2023). We follow this suggestion and note that a thorough study of this tooth is needed.

# 4. Distribution and evolution of spinosaurids in Asia

Since the discovery of *Siamosaurus* suteethorni in Thailand, spinosaurid materials have been reported in Laos, Malaysia, China, and Japan. The evidence of spinosaurids in Asia is important in terms of

spinosaurid evolution and distribution in Laurasia (Europe and Asia), which probably migrated due to the lower level of the Uralian seaway (Upchurch and Chiarenza, 2024) and then led to the dinosaur fauna dispersals from Europe to Asia by passing through the ephemeral landbridge during Late Hauterivian to Early Barremian (Upchurch and Chiarenza, 2024). This hypothesis follows the spinosaurid dispersion model by Milner (2003). Milner (2003) suggested that Laurasia was the region of origin for spinosaurids, based on older taxa such as Baryonyx walkeri from the Valanginian of England (Charig and Milner 1986, 1997). These dinosaurs were likely distributed through regional diversification within Laurasia. This hypothesis was later supported by Barker et al. (2023), who proposed that spinosaurids originated in Europe and dispersed throughout Laurasia during the first half of the Early Cretaceous. It is likely that basal spinosaurids dispersed along the coastal shoreline (Sereno et al., 2022) from Europe by crossing ephemeral landbridge during the pre-Barremian (probably Late Hauterivian), reaching parts of Southeast Asia, from where they spread to Thailand, Malaysia, southern China, and Japan (Hou et al., 1975; Buffetaut and Ingavat, 1986; Kubota, 2023) (Fig. 4).

The earliest evidence of spinosaurids in Asia comes from an isolated tooth discovered in the Yuasa Formation of Japan, which likely dates to the Late Hauterivian (Kubota, 2023). This finding suggests that spinosaurids may have dispersed into Asia during the first half of the Early Cretaceous. Additional support for this hypothesis comes from other early Early Cretaceous Asian records, such as Siamosaurus suteethorni from the Sao Khua Formation of Thailand (probably Late Valanginian to Late Barremian) and cf. Siamosaurus sp. from the Sebayashi Formation of Japan (likely Late Barremian to Aptian) (Buffetaut and Ingavat, 1986; Hasegawa et al., 2003; Kubota et al., 2017).

However, the proposed distribution of spinosaurids in Asia during this period remains tentative, as the stratigraphic data are inconsistent, the fossil record is sparse, and the evidence is geographically and temporally discontinuous.

Fossil evidence indicates that spinosaurid remains in Asia were more widely distributed during the late Early Cretaceous than the early Early Cretaceous. During the late Early Cretaceous, spinosaurid fossils have been recovered from several countries across East and Southeast Asia (e.g., Buffetaut et al., 2005a; Allain et al., 2012; Sone et al., 2015; Wongko et al., 2019; Hattori and Azuma, 2020). This interval also marks an important phase of spinosaurid diversity in the region, highlighted by the discovery of at least two different tooth morphotypes-Morphotype I (Khok Kruat morphotype) and Morphotype II (Siamosaurus morphotype)—from the Khok Kruat Formation in Thailand (Wongko et al., 2019). The two tooth morphotypes display several distinct characteristics. For example: (1) Morphotype I has approximately 46-64 apicobasal ridges (flutes) on both the labial and lingual surfaces, whereas Morphotype II has only 22–32 flutes on both sides; (2) the enamel surface of Morphotype I is smooth or irregular, whereas Morphotype II shows a wrinkled or veined enamel texture (see Table 2 in Wongko et al., 2019, p. 17). The numerous packs of flutes irregular enamel texture Morphotype I can be observed in spinosaurines (e.g., Irritator challengeri; Sues et al., 2002; AS pers. obs.). The fewer flutes and veined enamel texture in Morphotype II can be observed in most baryonychines (i.e., Baryonyx walkeri and Suchomimus tenerensis; Charig and Milner, 1997; Hendrickx et al., 2019; AS pers. obs.). However, the non-denticulated carinae on both morphotypes are considered a characteristic of Spinosaurinae, which involves dental evolution for increasing predatory potential (Hendrickx et al., 2019).

The teeth of 'Sinopliosaurus' fusuiensis from the Xinlong Formation of China (Hou et al., 1975) and an isolated spinosaurid tooth from the Sebayashi Formation of Japan (Hasegawa et al., 2003) exhibit characteristics similar to those of Siamosaurus suteethorni from the Sao Khua Formation of Thailand (i.e., the shape of the crown, the same flutes pattern, and wrinkling (veined) of the enamel, with poorly defined serrations), and have been reassigned to Siamosaurus sp. (Buffetaut et al., 2008). These materials are evidence that Siamosaurus sp. roamed Asia during the Early Cretaceous. The Fukui spinosaurid from the Kitadani Formation of Japan exhibits some differences in dental characteristics. which are not found in the Sebayashi Formation tooth—for example, the restricted presence of denticles on the carinae. Due to the combination of Baryonychinae and Spinosaurinae dental features, the Fukui spinosaurid teeth were assigned as basal spinosaurid (Hattori and Azuma, 2020). Nevertheless, the differences in dental characteristics may reflect factors such as position in the jaws, completeness, and ontogeny, and more information is needed for this dinosaur group.

The postcranial skeletons from the Sam Ran locality (Khok Kruat Formation, Khon Kaen, Thailand) and the Tang Vay locality ("Grès supérieurs" Formation, Savannakhet, Laos) exhibit notable differences in the morphology of the posterior dorsal neural spines and pubes (Buffetaut et al., 2005a; Allain et al., 2012; Samathi et al., 2019b). In the Sam Ran spinosaurid, the posterior dorsal neural spine is paddlelike, whereas in Ichthyovenator it has the shape of an upside-down triangle (Allain et al., 2012; pers. obs.). Additionally, the pubis is anteriorly concave in lateral view in the Sam Ran specimen, while it is straight in Ichthvovenator (Samathi et al., 2019b; Samathi et al., in prep.). The differences between spinosaurids from coeval in Southeast Asia provide evidence

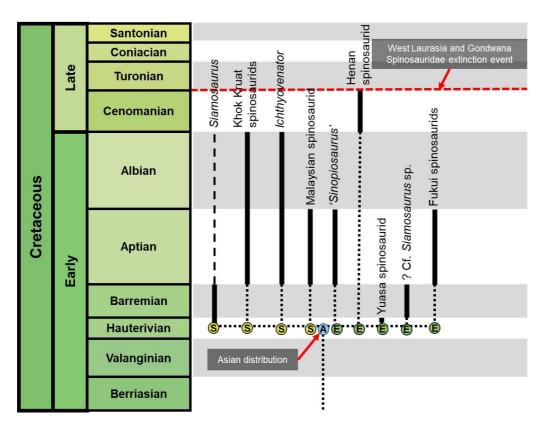
that this clade was diverse and probably at least two or more taxa were present during the Early Cretaceous in this region (Samathi et al., 2021). This is similar to the Barremian to Aptian spinosaurids in Europe, e.g., Baryonyx walkeri (Weald Clay Formation), Ceratosuchops inferodios and Riparovenator milnerae (Wessex Formation) in England (Charig and Milner, 1997; Barker et al., 2021), and the Iberian Peninsula spinosaurids including Camarillasaurus cirugedae (Camarillas Formation), Iberospinus natarioi (Papo Seco Formation), Protathlitis cinctorrensis and Vallibonavenatrix cani (Arcillas de Morella Formation), and Riojavenatrix lacustris (Enciso Group) (Sánchez-Hernández and Benton, 2014; Malafaia et al., 2019; Samathi et al., 2021; Mateus and Estraviz-López, 2022; Santos-Cubedo et al., 2023; Isasmendi et al., 2024).

Spinosaurids appear to have diversified primarily in Laurasia, particularly in western regions such as Europe, where numerous taxa have been discovered. In contrast, fossil evidence from eastern Laurasia (Asia) remains limited. Most Asian specimens consist of isolated or fragmentary teeth, while postcranial material has been reported from only a few localities, such as Phu Wiang site 9 and Sam Ran in Khon Kaen, Thailand (Buffetaut et al. 2004, 2005b; Samathi et al. 2019b, 2021), and Tang Vay in Savannakhet, Laos (Allain et al., 2012; Allain, 2014). This scarcity of comprehensive material hinders the precise identification and classification of Asian spinosaurids. Nevertheless, the discovery of the Sam Ran spinosaurid and Ichthyovenator laosensis supports the presence of at least two distinct spinosaurid taxa in Asia.

The presence of early Late Cretaceous spinosaurids from China (possibly dating to the Cenomanian age) suggests that Asian spinosaurids persisted through the extinction event of this clade, which is hypothesized to have occurred in the



**Fig. 4:** Possible spinosaurid dispersal from Europe to Asia by crossing the ephemeral Landbridge during pre-Barremian (Map modified from PALEOMAP; Christopher Scotese). Red circle = early Early Cretaceous spinosaurids; yellow circle = late Early Cretaceous spinosaurids; black circle = Late Cretaceous spinosaurids.



**Fig. 5:** Asian spinosaurids with simplified time calibration. Blue = Asia distribution; yellow = Southeast Asia distribution; green = East Asia distribution.

western Laurasia and Gondwana during the Cenomanian (Fig. 5) (Lü et al., 2009; Hone et al., 2010; Hone and Holtz, 2017; Candeiro et al., 2017). This is the only report of the Late Cretaceous spinosaurids in Asia (Lü et al., 2009). A tooth from the Santonian of China was once assigned to Spinosauridae (Hone et al., 2010), although a later study suggested that it might belong to Allosauroidea or Abelisauridae (Barker et al., 2023). This suggests a lower diversity of spinosaurids in Asia and the replacement of other theropod clades after the Cenomanian age of China (Hone et al., 2010; Barker et al., 2023). This pattern corroborates the hypothesis of the extinction event of Spinosauridae in the Cenomanian age of western Laurasia and Gondwana (Candeiro et al., 2017). Therefore, the fossil records of spinosaurids in Asia confirm that this dinosaur clade became extinct no earlier than the end of the Cenomanian age globally (Fig. 5). The extinction event of Spinosauridae could possibly involve environmental changes (Candeiro et al., 2017), including loss of flood-plain habitats resulted in the extinction of some aquatic taxa (Eaton et al., 1997). Interestingly, Carnosauria, where Spino-sauridae is nested, is thought to have originated in South-East Asia (Rauhut et al., 2024). Since Megalosauroidea appears to have originated in Asia (Rauhut et al., 2024), the evolution and emergence of spinosaurids among megalosauroids might have appeared in Asia during or prior to the Middle Jurassic (Bertin, 2010; Rauhut et al., 2024).

#### 5. Conclusion

Most Asian spinosaurids are found in the Barremian to Aptian strata (from the early to late Early Cretaceous). Some of these fossils were discovered in the early Early Cretaceous, including the Sao Khua Formation of Thailand and Yuasa and Sebayashi formations of Japan. In contrast, spinosaurids from the late Early Cretaceous have been found in several countries, including the Khok Kruat

Formation of Thailand, the "Grès supérieurs" Formation of Laos, the Tembling Group of Malaysia, the Xinlong Formation of China, and the Kitadani Formation of Japan. The Late Cretaceous spinosaurids have been reported from Mangchuan Formation of China. The presence of spinosaurids in Asia may have been influenced by the retreat of the Uralian Seaway, which affected the dispersal of spinosaurids from Europe. It is believed that the spinosaurid ancestors may have spread along coastal shorelines from Europe, possibly crossing ephemeral landbridge during the pre-Barremian period, before expanding into Southeast Asia, southern China, and eastern Asia. They persisted until the extinction event of this clade during the Cenomanian, as happened in western Laurasia and Gondwana. Recent evidence suggests that the distribution of Asian spinosaurids is both complex and uncertain, as the fossil record of these dinosaurs in Asia appears to be fragmented and discontinuous, indicating the incomplete nature of the fossil evidence.

## 6. Acknowledgment

We are sincere and grateful to Sirindhorn Museum, the Department of Mineral Resources, Kalasin, Thailand for allowing and helping us to collect the spinosaurid data in the present study. Thanks to Varavudh Suteethorn, Suravech Suteethorn, Tanachot Boonjarern, Kongkrapan Chaitongsri, Phanitada Srikampa (Department of Biology, Faculty of Science, Mahasarakham University, Thailand), and Siripat Kaikaew (Synchrotron Light Research Institute, Nakhon Ratchasima, Thailand) for excavation and laboratory supported, exchange information, and advisory. Thanks to Masateru Shibata (Fukui Prefectural Dinosaur Museum, Katsuyama, Japan) and Wilailak Naksri (Nakhon Ratchasima Rajabhat University, Nakhorn Ratchasrima, Thailand) for access to the cast of Ichthyvenator laoensis. The second author thanks Yasuhisa Nakajima (Tokyo City University, Japan) for access to the Japanese

spinosaurid specimens under his care, to Paul Sereno (University of Chicago, USA) for access to the specimens of Suchomimus tenerensis, and to Rainer Schoch (Staatliches Museum für Naturkunde Stuttgart, Germany) for access to the holotypic material of Irritator challengeri. Special thanks go to the editor and two anonymous reviewers that greatly improved the quality of the manuscript. This project is funded by National Research Council of Thailand (NRCT) to the second author (Grant number: N42A660838) and partially supported by Mahasarakham University Postgraduate Grant to the first and second authors (Grant number: 6719007/2567).

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# **Appendix**

**Table 1:** The reports of spinosaurids discovered in Asia (Southeast Asia + East Asia)

Taxa/ specimens	Clades	Materials	Localities	Formations	References
Thailand					
cf. Siamosaurus sp.	Spinosauridae	Teeth fragment	Nong Bua Lamphu – Udon Thani highway, Thailand.	Sao Khua Fm.	Buffetaut and Tong 2024; Personal observation
Siamosaurus suteethorni	Spinosauridae	Holotype: SM-TF2043, tooth	Phu Wiang Site 1 Locality, Khon Kean, Thailand	Sao Khua Fm.	Buffetaut and Ingavat 1986; Personal observation
Spinosauridae indet.	Spinosauridae	SM2017-138 to 141, fragmentary teeth	Phu Wiang Site 5 Locality, Khon Kean, Thailand	Sao Khua Fm.	Personal observation
Spinosauridae indet.	Spinosauridae	SM-PW7, fragmentary tooth	Phu Wiang Site 7 Locality, Khon Kean, Thailand	Sao Khua Fm.	Personal observation
Hin Lat Yao spinosaurid	Spinosauridae	SM-PW9, PW9A-C, fragmentary teeth	Phu Wiang Site 9 Locality, Khon Kean, Thailand.	Sao Khua Fm.	Puntanon et al., in prep.
Phuwiang spinosaurid B	Spinosauridae	Caudal vertebrae SM-PW9-11to17	Phu Wiang Site 9 Locality, Khon Kean, Thailand.	Sao Khua Fm.	Samathi et al. 2019b; 2021; observation
cf. Siamosaurus sp.	Spinosauridae	Referred materials to <i>Siamosaurus</i> sp. SM-K4-395 and 343 teeth.	Phu Kum Khao Locality, Kalasin, Thailand	Sao Khua Fm.	Personal observation
cf. Siamosaurus sp.	Spinosauridae	Referred materials to <i>Siamosaurus</i> sp. TF15-1 and 2 teeth.	Huai Huat Locality, Sakon Nakhon, Thailand	Sao Khua Fm.	Personal observation
Spinosauridae indet.	Spinosauridae	BNL-1 and 2 teeth fragment	Non-Lhiam Locality, Chaiyaphum, Thailand.	Sao Khua Fm.	Personal observation
Spinosauridae indet.	Spinosauridae	NP02-1 tooth fragment	Phu Din Dang Locality, Chaiyaphum, Thailand.	Sao Khua Fm.	Personal observation
Phra Prong spinosaurid	Spinosauridae	Teeth fragment	Phra Prong Locality, Sa Kaeo, Thailand.	Sao Khua Fm.	Suteethorn et al. 2018; KP personal observation
cf. Siamosaurus sp.	Spinosauridae	PRC 32 and 33 teeth fragment	Ko Kut Locality, Trat, Thailand.	Sao Khua Fm.	Buffetaut et al. 2019; KP personal observation
Spinosauridae indet.	Spinosauridae	PM2016-1-001 and 002 teeth fragmentary (Morphotype I 'Khok Kruat' spinosaurid)	Sam Ran Locality, Khon Kean, Thailand.	Khok Kruat Fm.	Wongko et al. 2019
Spinosauridae indet.	Spinosauridae	PM2016-1-003 and 004 teeth fragmentary (Morphotype I 'Khok Kruat' spinosaurid)	Khok Pa Suam Locality, Ubonratchathani, Thailand.	Khok Kruat Fm.	Wongko et al. 2019
Spinosauridae indet.	Spinosauridae	PM2016-1-005 tooth fragmentary (Morphotype II 'Siamosaurus')	Khok Pa Suam Locality, Ubonratchathani, Thailand.	Khok Kruat Fm.	Wongko et al. 2019
Spinosauridae indet.	Spinosauridae	PW2016-1-006 tooth fragmentary (Morphotype II 'Siamosaurus')	Lam Pao Dam Locality, Kalasin, Thailand.	Khok Kruat Fm.	Wongko et al. 2019
Spinosauridae indet.	Spinosauridae	PM2016-1-007 and 008 teeth fragmentary (Morphotype I 'Khok Kruat' spinosaurid)	Lam Pao Dam Locality, Kalasin, Thailand.	Khok Kruat Fm.	Wongko et al. 2019
Spinosauridae indet.	Spinosauridae	PNS-2018-03-05 to 07 teeth fragmentary (Morphotype I 'Khok Kruat' spinosaurid)	Pha Nung Suae Locality, Chaiyaphum, Thailand.	Khok Kruat Fm.	Personal observation
Sam Ran spinosaurid	Spinosauridae	SM-KK14 cervical and dorsal vertebrae, pelvic materials, an elongated neural spine, chevron, and metacarpal	Sam Ran Locality, Khon Kean, Thailand.	Khok Kruat Fm.	Buffetaut et al. 2004,2005b; Samathi et al. 2019b; Personal observation
Laos		•			
Ichthyovenator laosensis	Spinosaurinae	Holotype MDS BK10-01 to 15: dorsal vertebra, the neural spine of the last dorsal vertebra, caudal vertebrae, sacral vertebrae, ilia, the right pubis, ischia, and a dorsal rib  Referred material: series of cervical vertebrae, the first dorsal vertebra, the left pubis, caudal vertebrae, and teeth materials.	Ban Kalum, Tang Vay Locality, Savannakhet, Laos	"Grès supérieurs" Fm.	Allain et al. 2012; Allain 2014; cast Personal observation
Malaysia			·		
Spinosauridae indet.	Spinosauridae	UM10575 and UM10576 teeth fragment	The state of Pahang, Peninsular Malaysia	The Tembeling Group	Sone et al. 2015
China		'			
'Sinopliosaurus' fusuiensis	Spinosauridae	Holotype: IVPP V 4793 five teeth materials Additional material: NP03 and NP07 teeth fragmentary	Fusui Locality, Guangxi, China	Xinlong Fm.	Hou et al. 1975; Amoit et al. 2010
Spinosauridae indet.	Spinosauridae	41HIII-00012 (?Baryonychinae)	Ruyang Basin, Henan, China	Mangchuan Fm.	Lü et al., 2009

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Japan					
Spinosauridae indet.	Spinosauridae	Tooth Fragmentary	Wakayama Prefecture, Japan.	Yuasa Fm.	Kubota et al. 2023; Nakajima personal com- municatuion
cf. Siamosaurus sp.	Spinosauridae	GMNH-PV-999 tooth material	Nakazato Locality, Gunma Prefecture, Japan.	Sebayashi Fm.	Hasegawa et al. 2003; cast AS Personal observation
cf. Siamosaurus sp.	Spinosauridae	KDC-PV-0003 tooth fragment	Kanna Locality, Gunma Prefecture, Japan.	Sebayashi Fm.	Kubota et al. 2017
Fukui spinosaurid	Spinosauridae	FPDM-V-546, 9475, 9999, 10000, 10237–10249, 10251 teeth materials	Katsuyama Locality, Fukui, Japan.	Kitadani Fm.	Hattori and Azuma 2020