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Ornithischian dinosaurs in Southeast Asia: a review with palaeobiogeographic implications

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https://zoobank.org/F8C273F5-D7C5-4A5C-BF0A-56C7C3085D55

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Academic editor: Torsten Scheyer + Received 13 August 2022 + Accepted 16 December 2022 + Published 10 January 2023

Abstract

Ornithischian dinosaurs have been discovered in Thailand, Laos, and Malaysia. These bird-hipped herbivores remain relatively rare by comparison with saurischian dinosaurs. In the Late Jurassic, stegosaurs and basal neornithischians from Thailand showed similarities to Middle-Late Jurassic taxa from China. Ornithischians appeared in the fossil record again during the late Early Cretaceous (Aptian-Albian) of Thailand and Laos. They are represented by non-hadrosaurid iguanodontians and basal ceratopsians. A few specimens have been reported from poorly dated Early Cretaceous rocks of Malaysia. Here, we illustrate the diversity of ornithischian assemblages in Southeast Asia and discuss their palaeobiogeographical implications.

Key Words

Cretaceous, Jurassic, Ornithischia, palaeobiogeography, Southeast Asia

Introduction

Southeast Asia consists of a mosaic of microcontinents derived from the northern margin of eastern Gondwana which, after drifting northwards, collided with each other and with South China in the late Palaeozoic and Mesozoic (Metcalfe 1998). Numerous vertebrate fossils have been discovered from the non-marine Mesozoic formations of the Indochina block, from the Khorat Plateau of north-eastern Thailand, as well as from southern Laos (Buffetaut 1991; Buffetaut and Suteethorn 1998a). However, the record of non-marine Mesozoic vertebrates from other SE Asian terranes is far less well known (Buffetaut et al. 2005a). Southeast Asian dinosaur fossils have been discovered in Thailand, Laos, Myanmar, Malaysia, and Cambodia (Buffetaut et al. 1995, 2003, 2021; Allain et al. 1999; Sone et al. 2015; Xing et al. 2016). They are dominated by sauropods and theropods, based on the number of bones and diversity, whereas ornithischians have fewer fossil remains (Buffetaut et al. 2015). The temporal distribution of Southeast Asian non-avian dinosaurs ranges from the Late Triassic/Early Jurassic to the late Early Cretaceous (Buffetaut et al. 2000; Laojumpon et al. 2017; Manitkoon et al. 2022). However, body fossils of ornithischians reported from Southeast Asia have been limited to the Late Jurassic and the late Early Cretaceous (Aptian-Albian) formations (Fig. 1; Table 1).

Josué-Heilmann Hoffet was the first to describe dinosaur fossils from Southeast Asia (Brett-Surman et al. 2012). Various postcranial ornithischian remains were reported from the Grès Supérieurs Formation of Muong Phalane, near Savannakhet in southern Laos (Buffetaut 1991). Hoffet described the material as a new species of hadrosaurid (duck-billed dinosaur) "*Mandschurosaurus laosensis*" (Hoffet 1944). However, some palaeontologists consider "*M. laosensis*" a *nomen dubium* (Buffetaut 1991; Horner et al. 2004).

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Figure 1. Southeast Asia map showing the distribution of Jurassic–Cretaceous non-marine sediments in Southeast Asia (modified from CCOP's 1:2 million Geologic map of East and Southeast Asia), Number in circles = rock formations: 1, Lower Phu Kradung; 2, Upper Phu Kradung; 3, Phra Wihan; 4, ?Tembling Group; 5, Gagau Group; 6, Khok Kruat; 7, Grès Supérieurs; 8, Xinlong (Thanh and Khuc 2006; Department of Mineral Resources 2014; Uchida et al. 2017; Teng et al. 2019; Yan et al. 2019).

Most ornithischians in Southeast Asia are known from the Khorat Group of Thailand. After the first discovery of a dinosaur bone in 1976 from Khon Kaen Province, north-eastern Thailand, a Thai-French team began excavations in 1981, and more dinosaur remains were found (Grote et al. 2009). Ornithischian bones were found in two formations, including the lowest Phu Kradung Formation and the top-most Khok Kruat Formation (Buffetaut et al. 2015). Although the exact genus or species has not yet been identified from the Late Jurassic Phu Kradung Formation, material of stegosaurids and basal neornithischians were excavated (Buffetaut et al. 2001, 2014; Manitkoon et al. 2019). By contrast, the late Early Cretaceous Khok Kruat Formation (Aptian-Albian) yields abundant neornithischian dinosaurs comprising three taxa of iguanodontians, Siamodon nimngami (Buffetaut and Suteethorn 2011), Ratchasimasaurus suranareae (Shibata et al. 2011), and Sirindhorna khoratensis (Shibata et al. 2015), plus one taxon of basal ceratopsian, Psittacosaurus sattavaraki (Buffetaut and Suteethorn 1992). The Khok Kruat Formation of Thailand is considered the lateral equivalent to the Grès Supérieurs Formation of southern Laos (Cappetta et al. 1990; Buffetaut et al. 2005b; Racey 2009; Allain et al. 2012).

The faunal assemblage from the Aptian Xinlong Formation of southern China shows many similarities to the Khok Kruat Formation of the Khorat Group of Thailand, especially the presence of the four endemic genera of hybodont sharks restricted to Southeast Asia and South China (Cuny 2012; Cuny et al. 2017). The Xinlong ornithischians include iguanodontian (*Napaisaurus guangxiensis*) and a possibly basal ceratopsian (Mo et al. 2016; Ji and Zhang 2022).

In Peninsular Malaysia, the Jurassic-Cretaceous rocks are mostly continental deposits, but the record of dinosaurs remains scanty (Rahman 2019). The first discovery was made by the University of Malaya's palaeontological team in 2014 from the State of Pahang, Malay Peninsula (Sone et al. 2015). This included teeth of spinosaurids and an indeterminate ornithischian, together with a fish assemblage that has strong affinities with the Early Cretaceous Sao Khua Formation of Thailand (Teng et al. 2019). Teeth of iguanodontians were found in the inland district of Terengganu in 2014 by a team from the Mineral and Geoscience Department Malaysia and the Malaysian Geological Heritage Group (Akhir et al. 2015).

The principal purpose of this study is to illustrate the diversity of ornithischian assemblages in Southeast Asia and southern China, focusing on Thailand where the majority of material has been reported, and to discuss their evolution and palaeobiogeography.

Institutional abbreviations

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

- NRRU Northeastern Research Institute of Petrified Wood and Mineral Resources (In Honor of His Majesty the King) Nakhon Ratchasima Rajabhat University.
- **WNM** Wittaya Nimngam Museum, Surin Province, Thailand.

Thailand

Thailand comprises two major tectonic terranes: the Shan-Thai (or Sibumasu) block in the western part and the Indochina block in the eastern part that is separated by the Nan-Uttaradit suture (Department of Mineral Resources 2014). The Mesozoic Khorat Group is a Thai stratigraphic group of non-marine rocks ranging from Late Jurassic to Early Cretaceous in north-eastern Thailand and consists of five formations: Phu Kradung, Phra Wihan, Sao Khua, Phu Phan, and Khok Kruat (Racey 2009) (Fig. 2). Three of the formations (Phu Kradung, Sao Khua, and Khok Kruat) have yielded rich deposits with vertebrate remains including selachians, actinopterygians, sarcopterygians, amphibians, turtles, crocodyliformes, pterosaurs, non-avian dinosaurs, and birds (Buffetaut and Suteethorn 1998a; Buffetaut et al. 2003, 2005b, 2006).

Phu Kradung Formation

The formation is considered as forming the base the Khorat Group which outcrops mostly on the Khorat Plateau in north-eastern Thailand (Racey 2009). The age of the Phu Kradung Formation is still uncertain, with contradictory signals coming from vertebrate palaeontology and palynology and it is conventionally considered as either Late

Table 1	I. Ornithischian	taxa in Sout	heast Asia pl	lus southern	China
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Jurassic or Early Cretaceous in age (Racey et al. 1996). The presence of *Dicheiropollis etruscus* in the Phu Kradung Formation seems to confirm an Early Cretaceous age, although some of the lower part of the Phu Kradung Formation could still be Late Jurassic (?Tithonian) (Racey and Goodall 2009). The rich vertebrate site Phu Noi and the nearby Ban Khok Sanam localities, which are in the lower part of the Phu Kradung Formation have yielded fossil assemblages similar to those found in the Middle-Late Jurassic of China (Buffetaut et al. 2003; Cuny et al. 2014; Chanthasit et al. 2019). Currently, no named ornithischian taxa have not been reported from the Phu Kradung Formation.

Stegosauridae indet. Buffetaut et al. 2001

Material. SM2011-1-001 (renumbered from KPS2-1 in Buffetaut et al. (2001)), a single posterior dorsal vertebra (Fig. 3A).

Locality and age. Ban Khok Sanam locality, Kham Muang District, Kalasin Province; the lower Phu Kradung Formation, Late Jurassic.

Previous study. This the first evidence of a thyreophoran dinosaur in Southeast Asia. The specimen is identified as belonging to the family Stegosauridae, which is more advanced than primitive taxa, such as huayangosaurid *Huayangosaurus* from the Middle Jurassic of China (Buffetaut et al. 2001). The specimen has a much higher neural arch and more upright transverse processes, indicating that it should be referred to the Stegosauridae (Buffetaut et al. 2001).

Comments. The anterior part of the centrum and the neural arch of SM2011-1-001 has been destroyed, but likely to possess centra of the dorsal vertebrae longer than wide as most stegosaurians, except for *Miragaia longicollum* (Maidment et al. 2008; Mateus et al. 2009).

Formation	Age	Taxa	Country	References
Xinlong	late Early Cretaceous	Napaisaurus guangxiensis	China	Ji and Zhang (2022)
	(Aptian-Albian)	Iguanodontian indet.		Mo et al. (2016)
		?Psittacosaurid		Mo et al. (2016); Cuny et al. (2017)
Grès Supérieurs	late Early Cretaceous	"Mandschurosaurus laosensis"	Laos	Hoffet (1944)
	(Aptian-Albian)	Iguanodontian indet.		Hoffet (1944); Buffetaut (1991)
		?Psittacosaurid		Allain et al. (1999)
Khok Kruat	late Early Cretaceous	Siamodon nimngami	Thailand	Buffetaut and Suteethorn (2011)
	(Aptian-Albian)	Ratchasimasaurus suranareae		Shibata et al. (2011)
		Sirindhorna khoratensis		Shibata et al. (2015)
		Iguanodontian indet.		Manitkoon et al. (2022)
		Psittacosaurus sattayaraki		Buffetaut and Suteethorn (1992)
		Psittacosaurus sp.		Buffetaut et al. (2007)
Gagau Group	?Early Cretaceous (?Aptian)	Iguanodontian indet.	Malaysia	Akhir et al. (2015)
?Tembeling Group	Early Cretaceous	Ornithischian indet.	Malaysia	Sone et al. (2015, 2022)
	(?late Valanginian			
	-early Hauterivian)			
Phra Wihan	?Berriasian-Valanginian	Neoanomoepus isp. (footprint)	Thailand	Lockley et al. (2009)
Upper Phu Kradung	Early Cretaceous	Basal neornithischian indet.	Thailand	Buffetaut et al. (2001);
	(?Berriasian)			Buffetaut et al. (2014)
Lower Phu Kradung	Late Jurassic	Stegosaurid indet.	Thailand	Buffetaut et al. (2001)
		Basal neornithischian indet.		Buffetaut et al. (2014);
				Manitkoon et al. (2019)



Figure 2. Stratigraphy of Khorat Group (modified from Tucker et al. (2022)) A. Location map showing the formations of the Khorat Group on the Khorat Plateau of north-eastern Thailand (B).

Basal neornithischian indet. ('Phu Noi neornithischian')

References. Buffetaut et al. 2014; Manitkoon et al. 2019.

Material. PRC 149 (renumbered from PN 13-09 in Buffetaut et al. (2014)), a lower jaw (Figs 3B, 4A, B); PRC 150, an articulated postcranial skeleton (Manitkoon et al. 2019) (Fig. 3C).

Locality and age. Phu Noi locality, Kham Muang District, Kalasin Province; the lower Phu Kradung Formation, Late Jurassic.

Previous study. Buffetaut and his team reported a lower jaw (PRC 149) from the Phu Noi locality. The fanshaped teeth with a strongly ridged crown and an asymmetric enamel distribution suggests that the specimen belongs to a small ornithopod dinosaur (Buffetaut et al. 2014). A well-preserved articulated small ornithischian skeleton without skull (PRC 150) was reported from the same locality (Manitkoon et al. 2019). The pre-acetabular process of the ilium is narrow, long with a perfectly rounded termination and slightly ventrally curved. The post-acetabular process is short and high. A combination of characters resembles those Jurassic basal neornithischians from China, such as *Agilisaurus louderbacki* and *Hexinlusaurus multidens* (Manitkoon et al. 2019).

Comments. Many taxa of basal neornithischians, once considered as early members of ornithopods, have been reclassified as the basal neornithischians (Boyd 2015; Madzia et al. 2018, 2021; Dieudonné et al. 2020). The similarities to the Chinese taxa, for example, the axial skeleton, is composed of 15 dorsal and five sacrals; the Brevis shelf of the ilium is visible in lateral view along the entire length; a distinct supra-acetabular flange on the pubic peduncle of

the ilium; prepubis tip extends beyond the distal end of the pre-acetabular process of ilium, suggesting PRC 149 is a basal neornithischian outside the clade Ornithopoda. Numerous limb bones of various sizes from basal neornithischians were also found at the Phu Noi site, indicating that these dinosaurs were abundant in this area. It is the oldest neornithischian known, so far, from southeast Asia. Agilisaurus louderbacki and Hexinlusaurus multidens exhibit symmetrically distributed enamel (Peng 1992; Barrett et al. 2005), but the dentary teeth of PRC 149 and other isolated teeth from Phu Noi are different in having asymmetrically distributed enamel on the teeth as in Yandusaurus hongheensis from the upper Shaximiao Formation, Nanosaurus agilis (= Drinker, Othnielia, Othnielosaurus) from the Late Jurassic Morrison Formation, and a variety of more derived neornithischians (Barrett et al. 2005; Butler et al. 2008; Galton 2009; Carpenter and Galton 2018). Preliminary comparisons seem to indicate that it is a new taxon (Buffetaut et al. 2014; Manitkoon et al. 2019).

Basal neornithischian indet. ('Khok Sanam neornithischian')

Material. WNM-Ks-001, an isolated tooth (Fig. 4C-E).

Locality and age. Khok Sanam locality, Kham Muang District, Kalasin Province; the lower Phu Kradung Formation, Late Jurassic.

Comments. A dentary tooth shows the fan-shaped crown, and has the characters of the posterior teeth present in the dentary teeth of PRC 149 (Buffetaut et al. 2014) and of *Nanosaurus agilis* (Carpenter and Galton 2018). Although



Figure 3. Exceptional specimen of ornithischian dinosaurs from Thailand. Stegosaurid vertebra (A. SM2011-1-001), Phu Noi neornithischian left dentary (B. PRC149), Phu Noi neornithischian articulated skeleton (C. PRC150), Dan Luang neornithischian left femur (D. SM2016-1-081), *Psitacosaurus* indet. Right femur (E. SM2016-1-080), *Psitacosaurus sattayaraki* right dentary (F. SM2016-1-163), Khok Pha Suam iguanodontian dorsal vertebra (G. SM2021-1-113), Khok Pha Suam iguanodontian left femur (H. SM2021-1-118), *Siamodon nimngami* left maxilla (I. PRC-4), *Ratchasimasaurus suranareae* left dentary (J. NRRU-A2064), *Sirindhorna khoratensis* right dentary (L. NRRU3001-167); A and G in anterior view; B–D, and H–J in lateral view; E, F and L in medial view. Scale bars: 10 cm (A, C–E, G–L); 5 cm (B, F).

the enamelled surface is thin, a well-developed ornamentation of ridges is still noticeable on the lingual side as the enamel is asymmetrically distributed. The margin of the laterally compressed crowns bears distinct denticles. The labial side of the tooth bears no enamel and shows worn facets. The ornamented lingual side does not show a prominent median ridge, contrasting with the European Early Cretaceous *Hypsilophodon foxii* (Galton 2009) and other derived neornithischians. There is moderately developed labiolingual expansion ('cingulum') at the base of the crown, as seen in basal neornithischians (Barrett et al. 2005). The cylindrical root has been preserved and curves to the labial side.

Basal neornithischian indet. ('Dan Luang neornithischian')

Material. SM2016-1-081, a left femur (Buffetaut et al. 2003, 2006, 2014) (Fig. 5).

Locality and age. Dan Luang locality, Kamcha-I District, Mukdahan Province; upper Phu Kradung Formation, ?Early Cretaceous.

Previous study. This is the first basal neornithischian specimen to have been discovered in Thailand, excavated in 1996, but it has not yet been described (Buffetaut and Suteethorn 1998a; Buffetaut et al. 2001, 2002, 2003, 2006). Buffetaut and Suteethorn considered that it is generally similar to *Yandusaurus* (= *Hexinlusaurus multi-dens*) from China (Buffetaut and Suteethorn 1998a).

Description. The left femur is robust and almost complete, except the distal end is eroded. It is 12.08 cm in length, and has a transverse mid-shaft diameter of 1.57 cm. The shaft of the femur is bowed in the lateral view resembling that of those early ornithopods and basal neornithischians, such as *Hexinlusaurus multidens* (He and Cai 1984), *Agilisaurus louderbacki* (Peng 1992), *Hypsilophodon foxii* (Galton 2009) and the Phu Noi neornithischian (Manitkoon et al. 2019). The femoral



Figure 4. Basal neornithischian specimens from the lower Phu Kradung Formation. (left) Left dentary (PRC 149) from Phu Noi locality, in lateral (**A**) and medial (**B**) views; (right) isolated tooth (WNM-Ks-001) from Khok Sanam locality, in labial (if dentary) (**C**), lingual (**D**) and mesial/distal (**E**) views. Scale bars: 5 cm (**A**, **B**); 1 cm (**C**–**E**).

head is mostly intact, but the finished, articular surface is unpreserved. The anterior end of the greater trochanter is slightly convex, while the posterior end is strongly convex. The greater trochanter lies upon the same plane as the femoral head. The lesser trochanter is distinguished from the greater trochanter by a deep groove. The fourth trochanter, located on the medial margin, is incomplete, its position being in the proximal half of the femur as in PRC 150. An oval fossa occurs between the base of the fourth trochanter and the femoral shaft for muscle insertion. The distal portion of the femoral shaft shows mediolaterally expansion towards the distal condyles and, although it was damaged, posteriorly the distal condyles are separated by a caudal intercondylar groove.

Comments. The Dan Luang locality has yielded mamenchisaurid teeth (Suteethorn et al. 2013), a possible mamenchisaurid rib, theropod teeth, crocodyliform osteoderms and large teeth resembling the pholidosaurid Chalawan thailandicus (Buffetaut and Ingavat 1980; Martin et al. 2014), shell fragments of the basal trionychoid turtle Basilochelys macrobios (Tong et al. 2009), petrified wood, and amber. The site belongs to the upper part of the Phu Kradung Formation (?basal Cretaceous), based on the appearance of large pholidosaurid crocodylomorphs and large trionychoid turtles. This contrasts with the semi-aquatic fauna, such as the small xinjiangchelyid turtles Phunoichelys thirakhupti, and Kalasinemys prasarttongosothi (Tong et al. 2015, 2019b), and teleosaurid Indosinosuchus potamosiamensis (Martin et al. 2019), from the lower Phu Kradung localities, such as Phu Noi. We suggest that SM2016-1-081 belongs in a basal position in Neornithischia, as with the older Phu

Noi taxon, but more specimens are needed to increase our understanding of the basal neornithischians from the upper Phu Kradung Formation.

Phra Wihan Formation

The Phra Wihan Formation underlies the Sao Khua Formation, is underlain by the Phu Kradung Formation and is dated as Early Cretaceous (Berriasian to early Barremian) by a rich palynological assemblage (Racey 2009; Racey and Goodall 2009). Lithology and stratigraphy indicate a depositional environment of braided streams and occasional meandering rivers in a humid climate. The formation has not yielded skeletal material, but the biodiversity of dinosaurs can be assessed by study of its footprint faunas. The site of Hin Lat Pa Chad is located at Phu Wiang, Khon Kaen Province. Dinosaur footprints are present on the upper surface of the Phra Wihan Formation's sandstone (Buffetaut and Suteethorn 1993) and the palaeoenvironment is thought to be brackish water or fluvial shallow (Kozu 2017). At least one trackway was made by a small-sized theropod. Others belonged to a small quadrupedal or bipedal ornithischian (Fig. 6), as the pes tracks are tetradactyl, and that at least one manus track is also tetradactyl, and may be interpreted as pentadactyl (Lockley et al. 2009; Kozu 2017). The pes axis is inwardly rotated and the pes digit I is short and anteromedially directed, while manus is outwardly rotated and situated lateral to pes digit III or IV (Lockley et al. 2009). It was classified in the ichnogenus Neoanomoepus isp. on the basis of the type material from Canada, and heteropody



Figure 5. Left femur of the 'Dan Luang neornithischian' (SM2016-1-081) in anterior (**A**), posterior (**B**), lateral (**C**) medial (**D**) proximal (**E**) and distal (**F**) views; Reconstruction showing the bone in left lateral view (**G**); Abbreviations: fh, femoral head; ft, fourth trochanter; gt, greater trochanter; mc, medial condyle; lc, lateral condyle; lt, lesser trochanter; pg, posterior intercondyle groove. Scale bar: 5 cm.

was noted (pes much larger than manus). *Neoanomoepus* is attributed to basal ornithischians and ornithopods, suggesting that these hitherto unknown earliest Cretaceous ichnofaunas may represent a radiation of ornithopods (Le Loeuff et al. 2002; Lockley et al. 2009; Kozu 2017).

Khok Kruat Formation

The formation is composed of reddish-brown, reddish-purple sandstone, siltstone and mudstone, with some conglomerate beds (Department of Mineral Resources 2014). The Khok Kruat Formation conformably overlies the Phu Phan Formation and is widespread in the outer parts of the Phu Phan Range. The Khok Kruat Formation of Thailand is equivalent to the upper part of the Grès Supérieurs Formation of southern Laos (Weishampel et al. 2004) and is considered as Aptian-Albian in age on the basis of its vertebrate fauna and palynology (Cappetta et al. 1990; Buffetaut et al. 2005b; Racey and Goodall 2009). By contrast with other formations in the Khorat Group, the ornithischian dinosaur remains are fairly abundant at various localities in north-eastern Thailand. An ornithopod track was previously mentioned in the



Figure 6. The trackway Neoanomoepus isp. from the Hin Lat Pra Chad locality, Scale bar: 10 cm (Photograph by Krishna Sutcha).

Khok Kruat Formation at Huai Dan Chum (Tha Uthen) track-site, Nakhon Phanom Province (Buffetaut et al. 2005a). From hundreds of footprints and dozens of trails on reddish-brown sandstone, it is assumed that there were dinosaurs similar to ornithomimosaurs and small-sized crocodylomorphs (Buffetaut et al. 2005a; Le Loeuff et al. 2009). Le Loeuff et al. (2009) remarked that the Tha Uthen specimen (T23) is remarkably similar to ornithopod tracks. However, Kozu and his team suggested that it belongs to a small-sized theropod (Kozu et al. 2017).

Ratchasimasaurus suranareae Shibata et al., 2011

Material. holotype NRRU-A2064, a left dentary (Fig. 3J).

Locality and age. Ban Pong Malaengwan, Khok Kruat Subdistrict, Nakhon Ratchasima Province; late Early Cretaceous Khok Kruat Formation (Aptian).

Previous study. *R. suranareae* is a hadrosauroid (Madzia et al. 2020; Shibata et al. 2015) and the material comprises a complete toothless left dentary with 18 alveoli (Shibata et al. 2011). One autapomorphy of *R. suranareae* is its elongated and dorsoventrally shallow dentary ramus, with a ratio of length (from the rostral to the caudal margin)/height (at the middle of the dentary) of 6.9 (Shibata et al. 2011). It shows both primitive and derived characters for iguanodontians, such as a caudally inclined coronoid process and alveolar trough with a primitive crown impression, and a derived buccal shelf between the tooth row and the coronoid process (Shibata et al. 2011).

Comment. The length of R. suranareae dentary is 19.81 cm, which is relatively small when compared to other skull material of iguanodontians from Thailand. It is not possible to determine if it is an immature or mature individual (Shibata et al. 2011). This compares with the nearly complete right dentary of Sirindhorna khoratensis (NRRU3001-167), which is about 38 cm in length with 20 alveoli (Shibata et al. 2015). In iguanodontians, tooth number increases during growth and single teeth also becoming relatively wider, as in Dysalotosaurus lettowvorbecki and Zalmoxes robustus, and there is a slight ontogenetic increase of dentary tooth positions from 10 to 13 and 8 to 10, respectively (Weishampel et al. 2003; Hübner and Rauhut 2010). In hadrosauroids, there are many ontogenetic changes occurring in the skull and mandible, and the dentary experiences an elongation of the mandibular ramus during growth (Bell 2011; Campione and Evans 2011; Prieto-Marquez and Guenther 2018). However, the ratio of length/height of the dentary of R. suranareae is 6.9, and approximately 5 in S. khoratensis (NRRU3001-167), contradicting the ontogenetic tend of hadrosauroids mentioned above, if R. suranareae is a younger stage of S. khoratensis.

Siamodon nimngami Buffetaut & Suteethorn, 2011

Material. holotype PRC-4, a left maxilla (Fig. 3I) and the referred materials, an isolated maxillary tooth (PRC-5) and a braincase (PRC-6).

Locality and age. Ban Saphan Hin, Khok Kruat Subdistrict, Nakhon Ratchasima Province; late Early Cretaceous Khok Kruat Formation (Aptian) (Buffetaut and Suteethorn 2011).

Previous study. S. nimngami shows a combination of iguanodontian features: maxilla shaped like an isosceles triangle, with the dorsal process located at about mid-length of the bone; a strong longitudinal bulge on the medial surface of the maxilla; maxillary teeth bear a strong median primary ridge, one short weak subsidiary ridge or no subsidiary ridge; and mamillated denticles on the crown margins similar to Gongpoquansaurus mazongshanensis and Probactrosaurus mongoliensis from China (Buffetaut and Suteethorn 2011). There may have been as many as 25 tooth positions in the maxilla (Buffetaut and Suteethorn 2011). It differs from hadrosaurids in the jugal, which forms a tab-like process, whereas in hadrosaurids, the expanded anterior end of the jugal contacts and overlaps a large sutural area on the maxilla (Buffetaut and Suteethorn 2011). S. nimngami and R. suranareae were mentioned as members of hadrosauroids (Shibata et al. 2015), but the phylogenetic analysis recovered S. nimngami at the base of Hadrosauriformes (Madzia et al. 2020).

Additional material and description. WNM-Sp-001 (Fig. 8I, J), an isolated dentary tooth from the same locality is referred to S. nimngami. It is well preserved and apparently from a right dentary. It generally resembles a previously reported S. khoratensis dentary tooth (Shibata et al. 2015). The crown of the tooth is leaf-shaped with enamel covering only the lingual surface. The ratio of apicobasal length / mesiodistal width: 1.87. One prominent primary ridge situated slightly distal to the mid-line makes the crown asymmetric. The secondary ridge is positioned mesial and it is less prominent. In contrast to S. khoratensis dentary teeth, where the crowns appear to be apicobasally erect, whereas in S. nimngami, the dentary teeth appear to be curved apicobasally. Shibata et al. (2015) noted that there were no other accessory ridges on the crown of S. khoratensis, but WNM-KS-001 shows at least one very faint accessory ridge on the mesial side. Small denticles are present on the mesial and distal margins of the upper half of the crown.

Comment. Some palaeontologists consider *S. nimn-gami* a *nomen dubium* as its material does not show any autapomorphic characters, and it might be referable to some of the other taxa from the same area (Norman 2014). However, Shibata et al. (2015) showed the possibility of three iguanodontians in the Khok Kruat Formation. The holotype specimen of *S. nimngami* and *S. khoratensis* maxilla (NRRU-A2048) are similar in size. They likely to belong to same growth stage, but have distinct physical characteristics suggesting that they represent different animals, while comparisons to *R. suranareae* are not feasible as overlapping material has not been discovered.

There has been some disagreement about the type locality of *S. nimngami* given by Shibata and his team, and Buffetaut and Suteethorn; however, we would like to confirm that, after corroboration from the holotype collector, Mr. Witaya Nimngam, we now know that the type locality of *S. nimngami* is at Ban Saphan Hin. This is far from the type locality of *S. khoratensis* and definitely not from Ban Nong Rangka as previously suggested (Fig. 7).



Figure 7. Locality map of Nakhon Ratchasima Province, showing localities of Siamodon, Ratchasimasaurus and Sirindhorna.

Sirindhorna khoratensis Shibata et al., 2015

Material. holotype NRRU3001-166, an articulated braincase including referred skull elements: a braincase articulating with a left postorbital (NRRU-A2035), dorsal half of a braincase (NRRU3001-65), caudal portion of a braincase (NRRU3001-179), a right premaxilla (NRRU-A3623), a left maxilla (NRRU-A2048) (Fig. 3K), a right maxilla (NRRU-A2047), a right jugal (NRRU3001-7), a right quadrate (NRRU3001-175), a predentary (NRRU3001-169), a left dentary (NRRU3001-14), a right dentary (NRRU3001-167) (Fig. 3L), a right surangular (NRRU3001-137), isolated maxillary teeth (NRRU-A1956, A3630, A3649, NRRU3001-157, 163), an isolated dentary tooth (NRRU3001-28).

Locality and age. Ban Saphan Hin (a different site from the *S. nimngami* was found), Suranaree Subdistrict,

Nakhon Ratchasima Province; late Early Cretaceous Khok Kruat Formation (Aptian).

Previous study. It is known from the presence of several braincases and dentaries that at least four individuals are known. The holotype material, a braincase, shows an autapomorphy: a sagittal crest extending along the entire dorsal surface of the parietal and reaching the frontoparietal suture (Shibata et al. 2015). Referred materials display a unique combination of characters, such as antorbital fossa of the maxilla not visible, a slightly rostrally deepening dentary ramus, and dentary teeth with primary and secondary ridges, but no accessory ridges (Shibata et al. 2015). It was recovered in the basal position of non-hadrosaurid hadrosauroids (Shibata et al. 2015). However, later analysis recovered it near the base of Hadrosauromorpha, more advanced than R. suranareae (Madzia et al. 2020). The S. khoratensis maxilla (NRRU-A2048) has a low-angled triangular shape and the caudally positioned lacrimal



Figure 8. Isolated Thai iguanodontian teeth; *Sirindhorna khoratensis* maxillary tooth (**A**, **B**. NRRU-A1959) and dentary tooth (**G**, **H**. NRRU3001-28); *Siamodon nomngami* maxillary tooth (**C**, **D**. PRC-5) and dentary tooth (**I**, **J**. WNM-Sp-001); Khok Pha Suam iguanodontian maxillary tooth (**E**, **F**. SM2021-1-122) and dentary tooth (**K**, **L**. SM2021-1-121). In labial (**A**, **C**, **E**), mesial (**B**, **D**, **F**), lingual (**G**, **I**, **K**), and distal (**H**, **J**, **L**) views. Abbreviations: ar; accessory ridges, pr; primary ridge, sr; secondary ridge. Scale bars: 0.5 cm (Modified from Buffetaut and Suteethorn (2011); Shibata et al. (2015); Manitkoon et al. (2022)).

process, and its 24 alveoli are rostrocaudally arranged and slightly curved caudolaterally. It is different from the isosceles triangular shape with a dorsal process positioned at the middle of the maxilla in *S. nimngami* (Shibata et al. 2015). *R. suranareae* has a low and elongated dentary ramus and a robust coronoid process that differs from the robust and straight dentary ramus with a subvertical coronoid process seen in *S. khoratensis* (Shibata et al. 2015).

Comment. *S. khoratensis* is considered to be the best-preserved iguanodontian ornithopod in Southeast Asia (Shibata et al. 2015). In addition to the published cranial material, the Ban Saphan Hin locality has also yielded a postcranial skeleton that is assumed to belong to *S. khoratensis* because the five discovered braincases show no features to imply the presence of different taxa (Shibata et al. 2018). CT-scanning revealed the brain morphology of *S. khoratensis*, which has general endocast features resembling those of non-hadrosaurid hadrosauroids (Shibata et al. 2018).

Iguanodontian indet. ('Khok Pha Suam iguanodontian')

Material. Isolated teeth and postcranial material including: cervical vertebra (PRC 155); dorsal vertebra (SM2021-1-113) (Fig. 3G); proximal caudal vertebra (SM2021-1-114); distal caudal vertebrae (PRC 156 and SM2021-1-115); chevron (PRC 157); metacarpal (SM2021-1-116); left femur (SM2021-1-117) (Fig. 3H); right femur (SM2021-1-118); tibia (SM2021-1-119); fibula (PRC 158); and phalanx (SM2021-1-120).

Locality and age. Khok Pha Suam, Na Kham Subdistrict, Si Muang Mai District, Ubon Ratchathani Province; late Early Cretaceous Khok Kruat Formation (Aptian-Albian).

Previous study. Teeth of iguanodontians are common at Khok Pha Suam, but fragmentary (Manitkoon et al. 2022). Some isolated postcranial bones belonging to iguanodontians were discovered, including vertebrae and limb bones from different individuals, based on the great discrepancy in size of the left and right femur (Manitkoon et al. 2022; Samathi and Suteethorn 2022). Samathi and Suteethorn assumed that most of the Khok Pha Suam iguanodontian material belonged to a single taxon, and found its phylogenetic position to be a non-hadrosauriform styracosternan (Samathi and Suteethorn 2022).

Comment. The teeth of Thai iguanodontians exhibit a robust primary ridge displaced distally relative to the crown apicobasal axis, which is a derived feature of iguanodontians amongst ornithopods (Norman 2004, 2014). They also possess mammillate marginal denticles, which is a synapomorphy of taxa closer to hadrosaurids than basal ankylopollexians, such as *Camptosaurus* (Fanti et al. 2016).

The maxillary teeth of Thai forms, including S. khoratensis (Fig. 8A), S. nimngami (Fig. 8C), and the Khok Pha Suam taxon (Fig. 8E), are diagnostic of the level of ankylopollexian iguanodontian by displaying the prominent primary ridge, accessory ridges, and the vertical channels marking the positions occupied by successional tooth crowns (Norman 2014). The different maxillary teeth characteristics are as follows: S. khoratensis: lanceolate-shaped crown, primary ridge separates the labial surface unevenly, distal portion of the labial surface bears weak subsidiary ridges and is slightly broader than the mesial portion (Shibata et al. 2015); S. nimngami: diamond-shaped crown, primary ridge in a median position, no/one short weak accessory ridge is present in what is presumably the mesial half of the crown, in the apical part. (Buffetaut and Suteethorn 2011); Khok Pha Suam iguanodontian: possibly diamond-shaped crown, primary ridge divides the crown into two asymmetrical halves, at least four weak accessory ridges in what is presumably the mesial portion along the apicobasal axis. The more derived hadrosauroids usually lose the accessory ridges on the crowns of maxillary teeth, and show a shifting of the primary ridge on the maxillary tooth crown to the mid-line (You et al. 2003).

The dentary teeth of the Thai forms, including S. khoratensis (Fig. 8B), S. nimngami (Fig. 8D), and Khok Pha Suam taxon (Fig. 8F) (not preserved in R. suranareae) possess a prominent primary ridge. The crowns allowed the teeth to interlock, resulting in the more elaborate structure of the dental battery. The different characteristics are as follow: S. khoratensis: wide with leaf-shaped crown, the secondary ridge is positioned mesial to and is less prominent than the primary ridge, with no other accessory ridges (Shibata et al. 2015); S. nimngami: leafshaped crown, the secondary ridge is positioned mesial to and is less prominent than the primary ridge, at least one faint accessory ridge is present on the mesial side, crown appears to be curved apicobasally; Khok Pha Suam iguanodontian: leaf-shaped crown, the less prominent secondary ridge is positioned mesial to and is less prominent than the primary ridge and at least two weak accessory ridges are present on the mesial and the distal portion. The dentary teeth of S. nimngami and the Khok Pha Suam iguanodontian show accessory ridges, which are absent in S. khoratensis. This character appeared in basal hadrosauroids (Prieto-Márquez et al. 2016). In this respect, S. khoratensis is probably more advanced than S. nimngami and the Khok Pha Suam iguanodontian.

So far, three taxa of styracosternan iguanodontians, including *S. ninngami*, *R. suranareae*, and *S. khoratensis*, have been described from the Khok Kruat Formation in Nakhon Ratchasima Province plus one Laotian taxon "*M. laosensis*" from the Grès Supérieurs Formation of Laos. If Khok Pha Suam iguanodontian is one of the previously-named taxa from Nakhon Ratchasima, this would provide a geographic distribution of about 400 km to the far east (Fig. 1). However, the Khok Pha Suam locality is closer to Savannakhet than Nakhon Ratchasima. The

comparison between them has to be very careful, and overlapping elements are required. It would be significant if the Khok Pha Suam iguanodont is a new taxon, as it would mean that there was a diversity of up to five to six species in the region. It is necessary to compare the postcranial material between the Khok Pha Suam taxon and *S. khoratensis*.

If a high diversity in iguanodontians is present in Southeast Asia, then careful consideration and more materials will be required. This may be similar to the case of *Edmontosaurus*, the duck-billed edmontosaurine that was widely distributed in the Late Cretaceous (Campanian-Maastrichtian) ranging from Colorado to Alaska of North America, where several genera were consolidated into two species under a single genus, based on ontogenetic variation, morphometrics and several other factors (Campione and Evans 2011; Takasaki et al. 2020).

Psittacosaurus sattayaraki Buffetaut & Suteethorn, 1992

Material. holotype SM2016-1-163 (renumbered from TF 2449a by Buffetaut and Suteethorn (1992)), right dentary (Fig. 3F); SM2016-1-164 (renumbered from TF 2449b by Buffetaut and Suteethorn (1992)) maxilla fragment.

Locality and age. Ban Dong Bang Noi, Lat Yai Subdistrict, Mueang District, Chaiyaphum Province; late Early Cretaceous Khok Kruat Formation (Aptian).

Previous study. Apart from the ornithopods mentioned above, another valid taxon from the Khok Kruat Formation is a small basal ceratopsian. P. sattayaraki was described from a well-preserved dentary (SM2016-1-163) and a maxilla fragment (SM2016-1-164), and it is the southernmost known occurrence of this genus (Buffetaut and Suteethorn 1992). However, the incompleteness of the material makes the validity of the taxa questionable (Sereno 2000; You and Dodson 2004). Buffetaut, Suteethorn, and Khansubha (2007) defended P. satayaraki as a species of *Psittacosaurus*, based on the tooth and dentary morphology clearly exhibiting fan-shaped tooth crowns bearing bulbous primary ridge, and a markedly convex alveolar border in lateral or medial view and an incipient ventral flange of the dentary. The taxon has been accepted as a valid species of Psittacosaurus in other reviews (Averianov et al. 2006; Lucas 2006).

Comment. Although *Psittacosaurus* was abundant in the Early Cretaceous of Eastern Asia (especially China, Mongolia, and Siberia), it is worth noting that material of *Psittacosaurus* seems to be scarce in Southeast Asia. In Thailand, only fragmentary materials were discovered in Chaiyaphum and Khon Kaen Provinces, and have not been found in other Khok Kruat localities (Manitkoon et al. 2022).

Psittacosaurus sp. Buffetaut et al., 2007

Material. SM2016-1-080, a right femur (Fig. 3E); unnumbered material including isolated tooth, a dentary fragment, a dorsal vertebra, and a fragmentary sacrum.

Locality and age. SM2016-1-080 was collected from the banks of the Nam Phong River, Ban Bueng Klang Village, Nam Phong District, Khon Kaen Province; other materials were collected from Phu Hin Rong, Mancha Khiri District, Khon Kaen Province; all specimens belong to late Early Cretaceous Khok Kruat Formation (Aptian-Albian).

Previous study. Additional postcranial specimens referred to as *Psittacosaurus* have been found in Khon Kaen Province (Buffetaut et al. 2007). The alveolar margin of the dentary fragment is markedly convex resembling the holotype of *P. sattayaraki*, but it is a larger individual (Buffetaut et al. 2007).

Comment. Only the femur is still kept in the Sirindhorn Museum.

Laos

Grès Supérieurs Formation (= Khok Kruat Formation)

All of the dinosaur-bearing beds in the Savannakhet Basin belong to the top of the Grès Supérieurs Formation (Racey 2009; Cavin et al. 2019). The age of dinosaurs in Savannakhet Province is Aptian–Albian, constrained by the non-marine Cretaceous bivalve *Trigonioides kobayashi-Plicatounio Suzuki* (Allain et al. 1999; Cavin et al. 2019). The Grès Supérieurs Formation is considered the lateral equivalent of the Khok Kruat Formation in neighbouring Thailand. Both are considered as Aptian-Albian in age, based on their vertebrate assemblages, bivalves, and palynomorphs (Cappetta et al. 1990; Buffetaut et al. 2005b; Racey 2009; Allain et al. 2012) . Laos has yielded not only skeletal materials, but possibly an ornithopod trackway from Muong Phalane (Allain et al. 1997; Le Loeuff et al. 2009).

"Mandschurosaurus laosensis" Hoffet, 1944

Material. unnumbered specimen consists of vertebrae, ilium, and femora.

Locality and age. Muong Phalane, Savannakhet Province of Laos; Grès Supérieurs Formation (\approx the Khok Kruat Formation), Aptian–Albian.

Previous study. *Mandschurosaurus* was the first dinosaur named from China, its material collected from the Late Cretaceous Yuliangze Formation (Maastrichtian) in Heilongjiang (Amur) River area between China and Russia (Godefroit et al. 2011). It was initially referred to the genus "*Trachodon*" *amurense* (Riabinin 1925), but was later re-assigned in 1930 to a new genus as *Mandschurosaurus amurensis* (Godefroit et al. 2011). *M. amurensis* is a large hadrosaurid (duck-billed dinosaurs), based on a poorly preserved and incomplete skeleton, and is often considered as a *nomen dubium* (Horner et al. 2004). Hoffet described the Laotian ornithopod material as "Mandschurosaurus laosensis" (Hoffet 1944), which was considered Late Cretaceous (Senonian) in age (Buffetaut 1991). However, some palaeontologists consider "M. laosensis" a nomen dubium (Buffetaut 1991; Horner et al. 2004). "M. laosensis" is potentially a non-hadrosaurid iguanodontian, such as Siamodon, Ratchasimasaurus, and Sirindhorna from rocks of the same age in Thailand. Hoffet also suggested that another ilium which is more robust than "M. laosensis", indicated the presence of a second taxon (Buffetaut 1991; Allain et al. 1999).

Iguanodontian indet. ('Savannakhet iguanodontian B')

Material. unnumbered specimen consists of series of dorsal vertebrae, rib, pubis, and ischium.

Locality and age. Ban Lamthouay, Tang Vay District, Savannakhet Province; The Grès Supérieurs Formation (\approx the Khok Kruat Formation), Aptian-Albian.

Comments. These unpublished materials are kept in the Dinosaur Museum of Savannakhet. It is necessary to compare these with the unpublished postcranial material of *S. khoratensis*.

Psittacosaurid indet. ('Savannakhet psittacosaurid')

Material. unnumbered specimen of left mandible.

Locality and age. Ban Lamthouay, Tang Vay District, Savannakhet Province; Grès Supérieurs Formation (\approx the Khok Kruat Formation), Aptian–Albian.

Comments. The unpublished specimen of psittacosaurid indet. was reported and the cast of this specimen is displayed in the Dinosaur Museum of Savannakhet (Allain et al. 1999; Buffetaut et al. 2007; Cavin et al. 2019). Detailed comparison with *Psittacosaurus sattayaraki* of Thailand is needed after a full description of this material has been completed.

Malaysia

The Tembeling Group

This non-marine fossil-bearing unit was informally referred to as 'the Pahang vertebrate bed' and is located in the interior of Pahang State, but the exact location of the site has been kept confidential. Hybodont sharks and ray-finned fish fishes were reported from this assemblage, which have strong affinities with fauna in the Early Cretaceous of Thailand (Teng et al. 2019). The four hybodont taxa, including *Heteroptychodus kokutensis, Isanodus paladeji, Lonchidion* aff. *khoratensis*, and *Mukdahanodus* aff. *trisivakulii*, were previously known only from the Sao Khua Formation (Khorat Group) and equivalent strata of Ko Kut (Kut Island) (Teng et al. 2019). Plants, bivalves, turtles and dinosaurs (teeth of a spinosaurid and an ornithischian) also reported from the same bonebed (Sone et al. 2015; Teng et al. 2019). They considered this site is correlated to the Early Cretaceous part (Temus Shale) of the Tembeling Group, and is equal to the Sao Khua Formation of Thailand in age based on faunal composition and biostratigraphic correlation (Teng et al. 2019).

So far, the ornithischians from the Tembling Group have not been published, but some information was released in the Malaysian media (University of Malaya 2014). We are unable to provide further details currently.

The Gagau Group

Far northeast from the Pahang vertebrate bed, another dinosaur site was found in the Chichir River of Hulu Terengganu in the north-eastern part of the Mount Gagau Area (Rahman 2019). The fossil area is underlain by the Jurassic-Cretaceous Gagau Group, comprising footprints and teeth within the Lotong Sandstone (Akhir et al. 2015). The teeth were found in ex-situ conglomerate boulders, and identified as belonging to iguanodontian dinosaurs.

Southern China

Xinlong Formation

Material of ornithischians was reported from the Napai Basin in south-western Guangxi Zhuang Autonomous Region (Dong 1979). The assemblage belongs to the Early Cretaceous (Aptian) Xinlong Formation (sometimes called the Napai Formation), and shows resemblance to the Khok Kruat Formation Southeast Asia (Mo et al. 2016). The four species of hybodonts from the assemblage (*Acrorhizodus khoratensis*, "*Hybodus*" *aequitridentatus*, *Thaiodus ruchae* and *Khoratodus foreyi*) are endemic to Southeast Asia and South China, and restricted to the Aptian-Albian interval (Cuny 2012; Cuny et al. 2017). These vertebrate fossils support the Xinlong Formation as coeval with the Khok Kruat Formation of Thailand and the 'Grès Supérieurs' Formation of Laos (Mo et al. 2016).

Napaisaurus guangxiensis Ji & Zhang, 2022

Material. The holotype, FS-20-007 to 008, a right ischium and ilium.

Locality and age. Napai Basin, Fusui County; Xinlong Formation, Early Cretaceous (Aptian).

Previous study. This is the first named basal iguanodontian taxon from southern China, based on characteristics of the ilium and ischium which differ from other known iguanodontian taxa (Ji and Zhang 2022).

Comments. The authors did not perform a phylogenetic analysis of the taxon. It is necessary to compare with the unpublished ischium and ilium of *S. khoratensis*.

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Iguanodontian indet. Mo et al., 2016

Material. Unnumbered specimens including cervical vertebra, dorsal vertebra, distal end of left humerus, distal end of left femur, and isolated teeth.

Locality and age. Napai Basin, Guangxi Zhuang Autonomous Region; Xinlong Formation, Early Cretaceous (Aptian).

Previous study. These poorly preserved specimens cannot be identified more precisely. However, some lower teeth bear a strong median primary ridge and at least one subsidiary ridge suggesting a relatively advanced iguanodontian (Mo et al. 2016).

Comments. There are many taxa of iguanodontians in Thailand and Laos, but it cannot be concluded whether these materials belong to *Napaisaurus guangxiensis* or not.

?Psittacosaurid indet. Mo et al., 2016

Material. Unnumbered specimens including distal end of a right femur.

Locality and age. Napai Basin, Guangxi Zhuang Autonomous Region; Xinlong Formation, Early Cretaceous (Aptian).

Previous study. Mo et al. (2016) reported an incomplete femur, which resembles a psittacosaurid. Although the condition of the specimen is poor, this group is widely distributed in the early Cretaceous of China, Mongolia, Siberia, Thailand, and Laos. It is possible that this basal ceratopsian could be present in the Xinlong Formation (Buffetaut and Suteethorn 1992; Buffetaut et al. 2007; Mo et al. 2016).

Discussion

Evolution of Southeast Asian ornithischians

The origin of ornithischians remains controversial (Baron and Barrett 2018). Chilesaurus diegosuarezi from the Late Jurassic (Tithonian) of Chile and Pisanosaurus mertii from the Early Late Triassic (Carnian) of Argentina, were considered to be the most basal ornithischians (Butler et al. 2008; Baron and Barrett 2017; Baron et al. 2017). However, some palaeontologists consider them as primitive dinosauriforms (Müller et al. 2018; Madzia et al. 2021). Other primitive true ornithischians were also discovered from the Early Jurassic in southern Gondwana, for example, Eocursor parvus (potentially Sinemurian) in South Africa (Butler et al. 2007), Heterodontosaurus tucki (potentially Sinemurian) in South Africa (Sereno 2012), Lesothosaurus diagnosticus (= Stormbergia dangershoeki) in Lesotho and South Africa (Baron et al. 2017), and Laquintasaura venezuelae (Hettangian) in Venezuela (Barrett et al. 2014). Ornithischians evolved later to become remarkably diverse in the Jurassic and one of the most successful groups of Cretaceous herbivores.

So far, Asian ornithischians have been found from five epochs as follows:

1) Early Jurassic

A few basal thyreophorans have been reported from Yunnan Province, China (Norman et al. 2007; Yao et al. 2022). During this epoch, basal thyreophorans are known from Africa, Europe and North America (Barrett et al. 2014). However, evidence of their existence is yet to be found in Southeast Asia. Although dinosaur remains have come from the Late Triassic-Early Jurassic Nam Phong Formation of north-eastern Thailand, the fossils discovered include only postcranial material of sauropodomorphs (Buffetaut et al. 2000; Laojumpon et al. 2017) and large theropod footprints (Liard et al. 2015). In the Mesozoic red beds of northern Thailand, an indeterminate sauropod from the Chiang Muan District, Phayao Province was found and dated as post-Toarcian in age, possibly at the boundary between the Early and Middle Jurassic (Chanthasit et al. 2018). However, ornithischian material has yet to be discovered.

2) Middle Jurassic

A few basal neornithischians (such as *Agilisaurus* and *Kulindadromeus*) were reported from China and Russia (Barrett et al. 2005; Godefroit et al. 2014). Heterodontosaurids, possibly ankylosaurians and stegosaurians appeared in China (Dong et al. 1983; Dong 1993; Zheng et al. 2009). Interestingly, filamentous integumentary structures in ornithischians have only been from Asian taxa so far (*Tianyulong* and *Kulindadromeus* and appeared again in *Psittacosaurus* in the Early Cretaceous). These provide evidence for protofeathers being basal to ornithischians, rather than just to theropods, as previously suspected (Godefroit et al. 2014). The Middle Jurassic dinosaurs in Southeast Asia are still obscure.

3) Late Jurassic

As in Africa, Europe, and the USA, Asian ornithischian faunas were dominated by stegosaurs during this time. Some basal neornithischians are reported from the USA, China, and Thailand. Basal iguanodontians (such as Dryosaurus, Dysalotosaurus and Camptosaurus) evolved in North America, Africa, and Europe, but there is no evidence for these taxa in Asia (Norman 2004; Xu et al. 2018). However, there were the earliest known marginocephalians, the Chaoyangsauridae, in China. The presence of Jurassic ceratopsians restricted to Asia indicates an Asian origin for the group (Zhao et al. 1999). In Thailand, the lower part of the Phu Kradung Formation yields stegosaurians and basal neornithischians. While the upper part, which is likely considered as Lower Cretaceous in age (Tong et al. 2015, 2019b), still includes basal neornithischians and other groups of dinosaurs (such as metricanthosaurids and mamenchisaurids) similar to those from the lower Phu Kradung Formation.

4) Early Cretaceous

By this time, the number of stegosaurids decreased and these were eventually lost (Tumanova and Alifanov 2018). In contrast, we observe an apparent increase of ankylosaurians and the appearance of jeholosaurids, considered to have been an endemic group in East Asia (Han et al. 2012). During the late Early Cretaceous, iguanodontians evolved larger body sizes and became the dominant herbivores in the ecosystem. Several non-hadrosaurid iguanodontians have been reported from China, Japan, Mongolia, Thailand, Laos, and possibly Malaysia (Norman 2004). Several species of *Psittacosaurus* and basal neoceratopsians have been found in China, Japan, Mongolia, Russia, South Korea, Thailand, Laos, and possibly Uzbekistan (You and Dodson 2004; Averianov et al. 2006).

5) Late Cretaceous

The Beringian land bridge between present-day Siberia and Alaska, which opened during the Aptian-Albian, served as a migration route for terrestrial vertebrates between Asia and North America during the Late Cretaceous (Russell 1993). Hence, we can see the similarities between the dinosaur fauna from these two continents. Many dinosaur groups (including ankylosaurids, hadrosaurids, neoceratopsians, pachycephalosaurians, tyrannosaurids and troodontids) supposedly originated in Asia (Bell 2011). Asian ornithischian dinosaurs diverged considerably in the Late Cretaceous. Non-hadrosaurid hadrosauroids were replaced with hadrosaurids, the medium to large-sized duck-billed dinosaurs (Tsogtbaatar et al. 2019; Kobayashi et al. 2021). Hadrosaurids became dominant, and extended across China, Japan, Kazakhstan, Mongolia, and Russia. There are two thescelosaurids known from Mongolia and South Korea (Huh et al. 2011; Makovicky et al. 2011). Several pachycephalosaurians, exclusively known from Laurasia, were found in China and Mongolia (Sullivan 2006). Several ankylosaurians are reported from China, Japan, Mongolia, and Uzbekistan (Park et al. 2021). Several neoceratopsians (such as leptoceratopsids and protoceratopsids) were reported from China, Mongolia, and Uzbekistan, but there is only one taxon of ceratopsid from China, contrary to their prevalence in North America (Xu et al. 2010). However, although the diversity of ornithischian dinosaurs during this epoch was highest, no dinosaur bones of this age have been reported in Southeast Asia.

Palaeobiogeographic implications

Southeast Asia consists of a mosaic of microcontinents. In the late Palaeozoic and Mesozoic, the northern margin of eastern Gondwana, after drifting northwards, collided with South China and other microcontinents (Metcalfe 1998). These terranes were united by the Late Triassic. Most of the dinosaur fossils in north-eastern Thailand, Laos, and Cambodia have been found on the Indochina Terrane.

Stage 1: Late Jurassic to Early Cretaceous

The oldest record of ornithischian dinosaurs in southeast Asia so far is from the Phu Kradung Formation of north-eastern Thailand, which is the basal unit of the Khorat Group (Racey et al. 1996; Racey 2009). Stegosaurids and small-bodied basal neornithischians have been unearthed, together with mamenchisaurid sauropods, and metricanthosaurid theropods, from the rich vertebrate assemblages of the Phu Noi locality and the nearby Khok Sanam locality, which is considered as the lowermost part of Phu Kradung Formation (Buffetaut et al. 2001; Cuny et al. 2014; Chanthasit et al. 2019; Manitkoon and Deesri 2019). Racey and Goodall (2009) supposed that the lower Phu Kradung Formation could be Late Jurassic (?Tithonian) in age, which was also supported by the evidence from vertebrate remains (Buffetaut et al. 2001; Buffetaut et al. 2006).

Interestingly, the vertebrate faunas from the lower Phu Kradung Formation share similarities with the those from the Middle-Late Jurassic (Bathonian-Callovian) Khlong Min Formation of the Thai southern peninsula from the Sibumasu Terrane (Buffetaut et al. 2005a; Cuny et al. 2014). Hybodont sharks (Cuny et al. 2014), brachyopoid temnospondyls (Buffetaut et al. 1994; Nonsrirach et al. 2021), teleosaurid crocodylomorphs (Buffetaut et al. 1994; Cuny et al. 2009; Martin et al. 2019), and mamenchisaurid sauropods (Buffetaut et al. 2005a; Suteethorn et al. 2013) from both the lower Phu Kradung and Khlong Min Formations indicate a wide distribution.

The upper part of Phu Kradung Formation is Early Cretaceous in age, based on the presence of Dicheiropollis etruscus (Racey and Goodall 2009) and a turnover of hybodont shark, turtle and crocodylomorph faunas (Tong et al. 2009, 2019b; Cuny et al. 2014; Martin et al. 2019). Microremains of the hybodont Acrodus kalasinensis, Jaiodontus sp. and related denticles from the Khlong Min Formation are found in the lower Phu Kradung (Cuny et al. 2014). The genus Acrodus is known from the Triassic and Jurassic (Rees and Underwood 2006), and Jaiodontus is restricted to the Oxfordian of China (Klug et al. 2010). In addition, the absence of the more common Heteroptychodus from the Early Cretaceous assemblages and its presence in the upper Phu Kradung Formation supports the age difference between the upper and lower parts of the Phu Kradung Formation (Cuny et al. 2014).

The xinjiangchelyid turtles (such as *Phunoichelys kalasinensis* and *Kalasinemys prasarttongosothi*) from Phu Noi can be correlated with those from the Late Jurassic of China as follows: the Late Jurassic Shangshaximiao (= upper Shaximiao) Formation of Sichuan Basin, the Middle-Late Jurassic Shishugou, Toutunhe and Qigu formations of the Junggar and Turpan Basins, and the Middle Jurassic Chuanjie Formation in Yunnan Basin. In contrast, records of this group in Early Cretaceous deposits are scarce in Asia (Tong et al. 2015, 2019b). The turtle fauna from the lower Phu Kradung are distinct from assemblages in the upper part, which include abundant remains of more advanced turtles, such as the trionychoid *Basilochelys macrobios* (Tong et al. 2009, 2015, 2019b).

The presence of teleosaurid crocodylomorphs (such as *Indosinosuchus potamsiamensis*) from Phu Noi suggest a Middle-Late Jurassic age contrary to crocodylomorphs from the upper part, which are characterised by pholidosaurids (such as *Chalawan thailandicus*) and atoposaurids (Lauprasert et al. 2011; Martin et al. 2014), indicating a faunal turnover in Southeast Asia through the Jurassic-Cretaceous (Martin et al. 2019).

The saurischian dinosaur faunas from both the lower and the upper Phu Kradung Formation consist of mamenchisaurids and metriacanthosaurids, which are well-known from the Middle-Late Jurassic/Early Cretaceous Formations in the Sichuan-Yunnan-Northern Junggar Basin of China. Mamenchisaurids (such as Mamenchisaurus and Omeisaurus) are eusauropods, and are also present in the Chuanjie Formation, Shishugou Formation, lower and upper Shaximiao Formation, Suining Formation, and Penglaizhen Formation (Buffetaut et al. 2006; Xing et al. 2015; Wang et al. 2019; Ren et al. 2021). Metriacanthosaurids (= sinraptorids) from Phu Noi show similar characteristics to Sinraptor dongi from the Upper Jurassic Shishugou Formation of the Junggar Basin in north-western China, and Yangchuanosaurus from the Middle-Late Jurassic Shaximiao Formation and possibly Late Jurassic-Early Cretaceous Suining Formation (Chanthasit et al. 2019). Both mamenchisaurids and metrianthosaurids were once thought to be endemic to east Asia. However, the report of isolated fossils from the Itat Formation of Russia and the taxon Wamweracaudia from Tendaguru extends the geographic distribution of mamenchisaurids into Siberia and Africa (Averianov et al. 2019; Mannion et al. 2019). Furthermore, Metriacanthosaurus, a close relative of Sinraptor, has been found in the upper Oxford Clay Formation of England.

The single stegosaur bone from the lower Phu Kradung Formation cannot provide definitive proof, except that it is more advanced than the Middle Jurassic *Huayangosaurus* and likely to be closer to those from the Late Jurassic taxa, such as *Tuojiangosaurus* (Buffetaut et al. 2001). Basal neornithischians from Phu Noi show characters that resemble taxa from the lower and upper Shaximiao Formation of China and the Late Jurassic Morrison Formation of US (Barrett et al. 2005; Carpenter and Galton 2018; Manitkoon et al. 2019).

As mentioned above, the dinosaur faunas including metriacanthosaurids and mamenchisaurids, and basal neornithischians have been found in both the lower and upper parts of the Phu Kradung Formation indicating that, despite the change in other groups of vertebrate faunas, dinosaurs remained the same and had long stratigraphic ranges. Another noteworthy point is the Phu Kradung Formation, and the Klong Min Formation show a remarkable biodiversity and reveal a close relationship with Chinese Jurassic vertebrate assemblages suggesting that the vertebrate faunas are more widespread than previously thought. This is probably not surprising as the vertebrate-bearing terranes of Southeast Asia and China were fused by the Late Triassic and Mesozoic terrestrial sandstones are widespread from China south to Malaysia (Sone and Metcalfe 2008; Cai and Zhang 2009; Choong et al. 2022).

Stage 2: Early Cretaceous (?Berriasian to pre-Barremian)

The trackway of a small quadrupedal ornithopod is found in the Phra Wihan Formation of Thailand. This Formation was dated as Lower Cretaceous (Berriasian-Early Barremian) from a rich palynological assemblage (Racey 2009; Racey and Goodall 2009). However, a subsequent study using radiometric dating on detrital zircon grains suggested that the dates for the underlying Sao Khua Formation are much older than previously suspected (Tucker et al. 2022). The study restricted the upper part of the Sao Khua Formation to no earlier than early Hauterivian, which means that the Phra Wihan Formation is likely not younger than Valanginian in age (Tucker et al. 2022).

The Sao Khua Formation of Thailand was assigned to the Early Cretaceous on palynological evidence (Racey et al. 1996), and probably Valanginian-Barremian on the basis of dinosaurs and bivalves (Meesook 2000). In the most recent publications, Sao Khua vertebrate fauna, including turtles and theropod dinosaurs, are considered to be Barremian (Samathi et al. 2019b; Tong et al. 2019a), and following a more refined regional biostratigraphic correlation of the freshwater bivalves Pseudohyria (Matsumotoina) matsumotoi suggesting a late Barremian age (Tumpeesuwan et al. 2010). Lastly, the radiometric data on detrital zircon grains indicated a tightly restricted late Valanginian-early Hauterivian age (133.6–132.1 Ma) for the Sao Khua Formation, and establishes that the dinosaur fauna is $\sim 5-9$ million years older than currently known (Tucker et al. 2022).

The Sao Khua Formation is dominated by sauropods (somphospondylian titanosauriforms, other titanosauriforms and diplodocoids) and theropods (spinosaurids, megaraptorans and coelurosaurs) in terms of species-richness and overall abundance (Buffetaut and Suteethorn 1998a; Buffetaut et al. 2002; Samathi et al. 2019a) (Fig. 9). Amongst the thousands of saurischian bones that have been collected from north-eastern Thailand, no evidence of ornithischians has yet been found in this formation (Buffetaut et al. 2015). The lack of ornithischians in the Sao Khua Formation is possibly consistent with the ecological composition of Valanginian/Hauterivian aged assemblages from Gondwana, for example, the "wood beds" of the upper Kirkwood Formation of South Africa and the Bajada Colorado Formation of South America, which are dominated by various-sized theropods and multiple cohabiting species of sauropods (Tucker et al. 2022). This is in contrast to those pre-Barremian dinosaur assemblages of Laurasian landmasses from Europe and North America, which have a diverse ornithischian record including ankylosaurians and iguanodontians and which shared habitats with other sauropod and theropod dinosaurs (Norman 2010; Kirkland et al. 2016; Tucker et al. 2022). By comparison with contemporaneous formations in Asia, ornithischian remains are still somewhat limited (Tucker et al. 2022). Material of an indeterminate stegosaurian has been reported from the Mengyin Formation (Berriasian-Valanginian), Shandong Province of China (Tucker et al. 2022). A stegosaurine *Wuerhosaurus homheni* and probable basal ceratopsians have been reported from the Lianmuqin Formation (?Valanginian) of Tugulu Group, Xinjiang Region of China (Sereno and Shichin 1988; Maidment et al. 2008).

Although the late Valanginian-early Hauterivian seems to be a crucial period for the ornithischian dinosaurs in southeast Asia, it does not mean that they were completely absent, but possibly reflected niche overlap, competition between herbivores considerably, and/or different timing of biogeographic dispersal. However, the vertebrate assemblage from 'the Pahang vertebrate bed' of Malaysia shows strong affinities with faunas in the Sao Khua of Thailand (Teng et al. 2019). An ornithischian tooth from this site may help fill the gap in the disappearance of ornithischian dinosaurs from Southeast Asia during this time.

The Early Cretaceous Phu Phan Formation is unconformably underlain by the red siltstones of the Sao Khua Formation, whereas the contact with the overlying Khok Kruat Formation is conformable suggesting that the Phu Phan Formation must fall within the interval early Hauterivian to Aptian, based on the ages of the over- and underlying formations (Racey 2009; Tucker et al. 2022). Theropod tracks have been reported, while vertebrate bones are extremely rare. Only a large sauropod limb bone has been found in a cliff face at Phu Kum Kao locality, Kalasin Province (Buffetaut et al. 2002; Buffetaut et al. 2003). No evidence of ornithischians has hitherto been reported.

Stage 3: Middle Cretaceous (Aptian to Albian)

In contrast with the Sao Khua Formation, the younger Khok Kruat Formation contains abundant neornithischian dinosaurs remains including iguanodontians and basal ceratopsians, fewer theropods (spinosaurids and carcharodontosaurians) and titanosauriforms sauropods have been found (Buffetaut et al. 2005b; Chokchaloem-wong et al. 2019; Manitkoon et al. 2022).

The Khok Kruat Formation of Thailand, together with the Grès Supérieurs Formation of Laos and the Xinlong Formation of southern China share the same palaeobiogeography, supported by vertebrate fossils (Buffetaut and Suteethorn 1998b; Mo et al. 2016; Cuny et al. 2017), and have yielded five iguanodontian taxa, and at least one taxon of *Psittacosaurus* (Buffetaut and Suteethorn 1992; Buffetaut and Suteethorn 2011; Shibata et al. 2015; Ji and Zhang 2022). This stage represents the highest diversity of ornithischians, and also refines the temporal shift from sauropod-dominated to iguanodontian-dominated ecosystems during the Cretaceous in southeast Asia. Both iguanodontians and ceratopsians possibly spread in this region during the Aptian. One hypothesis suggests Cerapoda (ornithopods+ceratopsians) dentitions are suited



Figure 9. Phylogenetic relationships of non-avian dinosaurs in southeast Asia and southern China. Abbreviations: A, Sauropoda; B, Eusauropoda; C, Neosauropoda; D, Macronaria; E, Titanosauriformes; F, Somphospondyli; G, Tetanurae; H, Allosauroidea; I, Carcharodontosauria; J, Coelurosauria; K, Megaraptora; L, Ornithomimosauria; M, Genasauria; N, Thyreophora; O, Neornithischia; P, Basal neornithischian; Q, Cerapoda; R, Ornithopoda; S, Iguanodontia; T, Ceratopsia (Cuny et al. 2014; Mo et al. 2016; Laojumpon et al. 2017; Chanthasit et al. 2018; Samathi et al. 2019a; Rolando et al. 2022; Sone et al. 2022; Sriwisan et al. 2022).

for efficiently grinding vegetation as a reason for their successful competition with other herbivores in later Cretaceous time (Strickson et al. 2016).

Basal iguanodontians first appeared in North America, Africa, and Europe during the late Jurassic (possibly Kimmeridgian) (Norman 2004). Ankylopollexia, a derived clade of iguanodontian, is inferred to have immigrated to West Europe from North America prior to the Valanginian, and dispersed into East Asia from West Europe via the elongated archipelago around the Jurassic-Cretaceous boundary, probably associated with the coeval global marine regression (Xu et al. 2018). Asian basal ankylopollexians were diverse during the Early Cretaceous including taxa like *Fukuisaurus* and *Koshisaurus* (Barremian) from Japan (Shibata and Azuma 2015), *Lanzhousaurus* (Barremian) from China (You et al. 2005), and *Bayannurosaurus* (early Aptian) from Inner Mongolia, China (Xu et al. 2018). Later, the non-hadrosaurid hadrosauroids are mainly known from the middle Cretaceous (Aptian-Albian). For instance, *Altirhinus* and *Choyrodon* from Mongolia (Norman 1998; Gates et al. 2018); *Equijubus*, *Gongpoquansaurus, Jintasaurus*, and *Xuwulong* from Gansu Province, China (You et al. 2003, 2014; You and Li 2009); *Probactrosaurus* and *Penelopognathus* from Inner Mongolia, China (Rozhdestvenskiy 1967; Godefroit et al. 2005); *Ratchasimasaurus, Sirindhorna*, and possibly *Siamodon* from Thailand (Shibata et al. 2015).

The earliest known ceratopsians (or even marginocephalian dinosaurs) are in the family Chaoyangsauridae (*Chaoyangosaurus* and *Yinlong*), from the Late Jurassic of China (You and Dodson 2004). Until the Early Cretaceous (late Barremian-Aptian), the genus *Psittacosaurus* roamed across China, Mongolia, Russia, Thailand and possibly Laos (Buffetaut et al. 2007). Although as many as 19 species have been referred to this genus, about 9–12 are currently considered valid (Napoli et al. 2019). Although psittacosaurids were abundant in the Early Cretaceous of Eastern Asia, they appear to be scarce in Southeast Asia (Buffetaut and Suteethorn 1992; Buffetaut et al. 2007). Specimens of *Psittacosaurus* are often found in lacustrine deposits (Averianov et al. 2006; Buffetaut et al. 2007), which differs from the fluvial deposits with an arid or semi-arid subtropical climate of the Khok Kruat Formation and the Grès Supérieurs Formation (Racey et al. 1996; Wongko 2018). Both factors, depositional environment and palaeoclimate, may provide an explanation for the scarcity of psittacosaurid materials in Thailand and Laos (Manitkoon et al. 2022).

After the Aptian-Albian stages, no further Mesozoic vertebrate fossils have been reported from Southeast Asia. The Khok Kruat Formation is unconformably overlain by the Maha Sarakham Formation (Albian-Cenomanian), which was deposited in a hypersaline, land-locked salt lake within an arid, continental desert, coinciding with worldwide high sea level in the Late Cretaceous and the flooding of marine-sourced water over what is now the Khorat Plateau (Racey et al. 1996).

Conclusions

So far, most southeast Asian ornithischian dinosaur fossils have been found in the Khorat Group of north-eastern Thailand. At least six taxa have been reported and dated from the Late Jurassic to the late Early Cretaceous. The oldest are known from the Late Jurassic Phu Kradung Formation represented by stegosaurids and basal neornithischians. There appears to be an absence of ornithischian dinosaurs during the pre-Barremian of the Sao Khua Formation. The Early Cretaceous Khok Kruat Formation (Aptian-Albian) contains abundant advanced iguanodontians plus basal ceratopsians, which reflects the shift from sauropod-dominated to ornithischian-dominated ecosystems. Iguanodontians and psittacosaurids are also found in the Grès Supérieurs Formation of Laos and the Xinlong Formation of southern China with many similarities to the Khok Kruat fauna of Thailand and these formations are considered equivalent in age. The rare dinosaur specimens from Malaysia are also an age anomaly. However, we propose that the ornithischian tooth from the Tembeling Group represents the existence of ornithischians that are missing from the time-equivalent Sao Khua Formation of Thailand. This study illustrates the diversity of ornithischian assemblages in Southeast Asia, providing an updated review and a discussion about their palaeobiogeographic implications.

Acknowledgements

We would like to thank many colleagues for useful suggestions and comments; Clive Burrett and Thitiwoot Sethapanichsakul for their help with the English language. Kamonlak Wongko, Sasa-On Khansubha, Wilailuck Naksri, and Kantanat Trakunweerayut for providing data on ornithischian specimen and map preparation. Witaya Nimgnam for material from Ban Khok Sanam and Ban Saphan Hin localities. We are grateful to the staff of the Palaeontological Research and Education Centre of Mahasarakham University, Sirindhorn Museum, and Northeastern Research Institute of Petrified Wood and Mineral Resources (In Honor of His Majesty the King) Nakhon Ratchasima Rajabhat University, who took part in our fieldwork and helped during visits to the collection. This research project was financially supported by Mahasarakham University.

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