Ornithichian dinosaurs of Thailand: systematics, evolution and palaeobiogeography

Sita Manitkoon

A Thesis Submitted in Partial Fulfillment of Requirements for
degree of Doctor of Philosophy in Palaeontology (International Program)
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ABSTRACT

Southeast Asian ornithischian dinosaurs have been discovered in Thailand, Laos, and Malaysia. These bird-hipped herbivores remain relatively lacking by comparison with saurischian dinosaurs.

The oldest fossil evidence is from the Late Jurassic, represented by stegosaurs and basal neornithischians from Thailand. Recently, an exceptional articulated skeleton belonging to a basal neornithischian was found in the lower Phu Kradung Formation of Phu Noi locality, Kalasin Province of Thailand. It shows a combination of both primitive and derived characters, which resemble those Jurassic small-bodied ornithischians from China. The result of the phylogenetic analysis shows that this dinosaur is a new taxon and is positioned among the most basal neornithischians. The preliminary study on the bone histology of Phu Noi neornithischians based on five femora elements suggests an ontogenetic stage was found mainly in the subadult. Annuli/LAGs (Lines of Arrested Growth) were used to assume past behavior or environment, which from the bone samples are found very few. Therefore, it is assumed that this may be caused by low food demand, no migration, and precocial behavior.

There seems to be a lack of ornithischians during the pre-Barremian. They reappeared in the Early Cretaceous (Aptian-Albian), presenting highly abundant advanced iguanodontians and basal ceratopsians, which is indicative of the herbivorous shift from sauropod-dominated to ornithischian-dominated ecosystems. During this time, iguanodontians and psittacosaurids also found in the Grès supérieurs Formation of Laos and Xinlong Formation of southern China show many similarities to the Khok Kruat fauna of Thailand and are considered equivalent in age. One of the important Khok Kruat localities is the Khok Pha Suam in Ubon Ratchathani Province of Thailand. The locality has been known as “the last home of Thai dinosaurs”. Here, the postcranial element of the styracosternan iguanodontian dinosaurs from the Khok Pha Suam locality was described including an overview of vertebrate assemblages from the Khok Kruat Formation. Not only represented one of the most diverse vertebrate assemblages in the Khok Kruat Formation but also underlines the palaeontological value, which is an essential feature of the Pha Chan-Sam Phan Bok Geopark.

This study illustrates the diversity of ornithischians assemblages in this region and provides their palaeobiogeographical implications.

Keyword : Basal Neonithischia, Bone histology, Ontogeny, Southeast Asia, Iguanodontia

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Chapter 1

Introduction

1.1 Rational of the research

Dinosaur fossils from Southeast Asia have been reported in Thailand (Buffetaut et al., 1997), Laos (Allain et al., 2012), Myanmar (Xing et al., 2016), and Malaysia (Sone et al., 2015). In terms of generic-level diversity and numerical abundance are dominated by saurischians (sauropods and theropods), whereas ornithischians have a lesser amount of fossil remains. The valid ornithischian taxa comprises 4 species of iguanodontians, (Buffetaut & Suteethorn, 2011; Hoffet, 1944; Shibata et al., 2011; 2015) and a ceratopsian (Buffetaut & Suteethorn, 1992). So far, ornithischian remains were found in the Khok Kruat Formation of Thailand and the Grès supérieurs Formation of Laos (Early Cretaceous, Aptian-Albian). Some of them have been reported in the Late Jurassic Phu Kradung Formation: an unnamed stegosaurid (Buffetaut et al., 2001), and a small neornithischian (Buffetaut et al., 2003; Buffetaut & Suteethorn, 2007). In 2012, a well-preserved articulated skeleton of a small neornithischian was discovered from the Phu Kradung Formation in the Phu Noi locality, Kalasin Province. It is one of the best dinosaur specimens ever found in Thailand. Although the material is lost its skull, this specimen shows distinct characteristics suggesting that it possibly belongs to the basalmost neornithischian in Southeast Asia. This research aims to study ornithischians in Thailand. To describe new materials, as well as to better understand the evolution, systematics, and palaeobiology of these herbivorous dinosaurs during the Jurassic-Cretaceous period and their palaeobiogeography in Southeast Asia.

1.2 Objectives

1.2.1 To study the evolution and palaeobiogeography of ornithischian dinosaurs in Southeast Asia and South China

1.2.2 To describe the taxonomy and phylogeny of small basal ornithischian dinosaur from Thailand

1.2.3 To study the ontogeny of ornithischian dinosaur from the Phu Kradung Formation

1.3 Scope of the research

The scope of this work is to describe the morphology of ornithischian dinosaurs, focusing on the small primitive ornithischian from the Phu Kradung Formation, which is a group that has not been intensively studied in terms of taxonomy and phylogeny, including ontogenetic histology. In addition, the diversity of ornithischian assemblages in Southeast Asia and discussion on their palaeobiogeographical implications was illustrated. This study was conducted in institutes of Thailand, including the Palaeontological Research and Education Centre, Mahasarakham University; Sirindhorn Museum; Northeastern Research Institute of Petrified Wood & Mineral Resources (In Honor of His Majesty the King), Nakhon Ratchasima Rajabhat University; Wittaya Nimngam Museum; and collections of other countries.

1.4 Significance of the research

The main expected result is to create the systematics and the life reconstruction of the basal neornithischian dinosaurs from the late Jurassic Phu Kradung Formation of Thailand, including a study on their bone histology. To go along with an understanding of the evolution, and palaeobiogeography of ornithischian dinosaurs in Southeast Asia.

1.5 Institutional abbreviations

PRC: Palaeontological Research and Education Centre, Mahasarakham University, Maha Sarakham Province, Thailand.

SM: Sirindhorn Museum, Kalasin Province, Thailand.

NRRU: Northeastern Research Institute of Petrified Wood & Mineral Resources (In Honor of His Majesty the King) Nakhon Ratchasima Rajabhat University, Nakhon Ratchasima Province, Thailand.

WNM: Wittaya Nimngam Museum, Surin Province, Thailand

FPDM: Fukui Prefectural Dinosaur Museum, Katsuyama, Japan

UM: University of Malaya, Wilayah Persekutuan Kuala Lumpur, Malaysia

IVPP: Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Science, Beijing, China

Chapter 2

An overview of Asian ornithischian dinosaurs

2.1 Introduction

Ornithischia or ‘bird-hipped" is an extinct clade of mainly herbivorous dinosaurs characterized by a pelvic structure superficially like that of birds. The two most distinct characters are an opisthopubic and predentary structure (Seeley, 1888). Some studies placed ornithischians and theropods together in the clade Ornithoscelida (Baron et al., 2017a).

The basalmost ornithischian remains controversial (Baron & 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 (Baron et al., 2017b; Baron & Barrett, 2017; Butler et al., 2008). However, some palaeontologists considered they were primitive dinosauriforms (Madzia et al., 2021; Müller et al., 2018). Other primitive true ornithischians also discovered from the Early Jurassic in southern Gondwana e.g. *Eocursor parvus* (potentially as Sinemurian) in South Africa (Butler et al., 2007), *Heterodontosaurus tucki* (potentially as Sinemurian) in South Africa (Sereno, 2012), *Lesothosaurus diagnosticus* (=*Stormbergia dangershoeki*) in Lesotho and South Africa (Baron et al., 2017b), and *Laquintasaura venezuelae* (Hettangian) in Venezuela (Barrett et al., 2014). Early ornithischians were small size and fast runner bipedal animals (Colbert, 1981). After that, ornithischians evolved to become very diverse in the Jurassic and one of the most successful groups of herbivores in the Cretaceous.

Phylogenetic analysis of ornithischians was carried out by many authors for long time since 1980s. In 2021, Madzia and team published the phylogenetic nomenclature and an overview of ornithischian relationships. They intended to make the standard under the *International Code of Phylogenetic Nomenclature* (*ICPN*, or *PhyloCode*) (Fig. 1).

In this chapter, Ornithischian dinosaurs found in Asia have reviewed, which are represent the diversity and phylogenetic nomenclature of them.

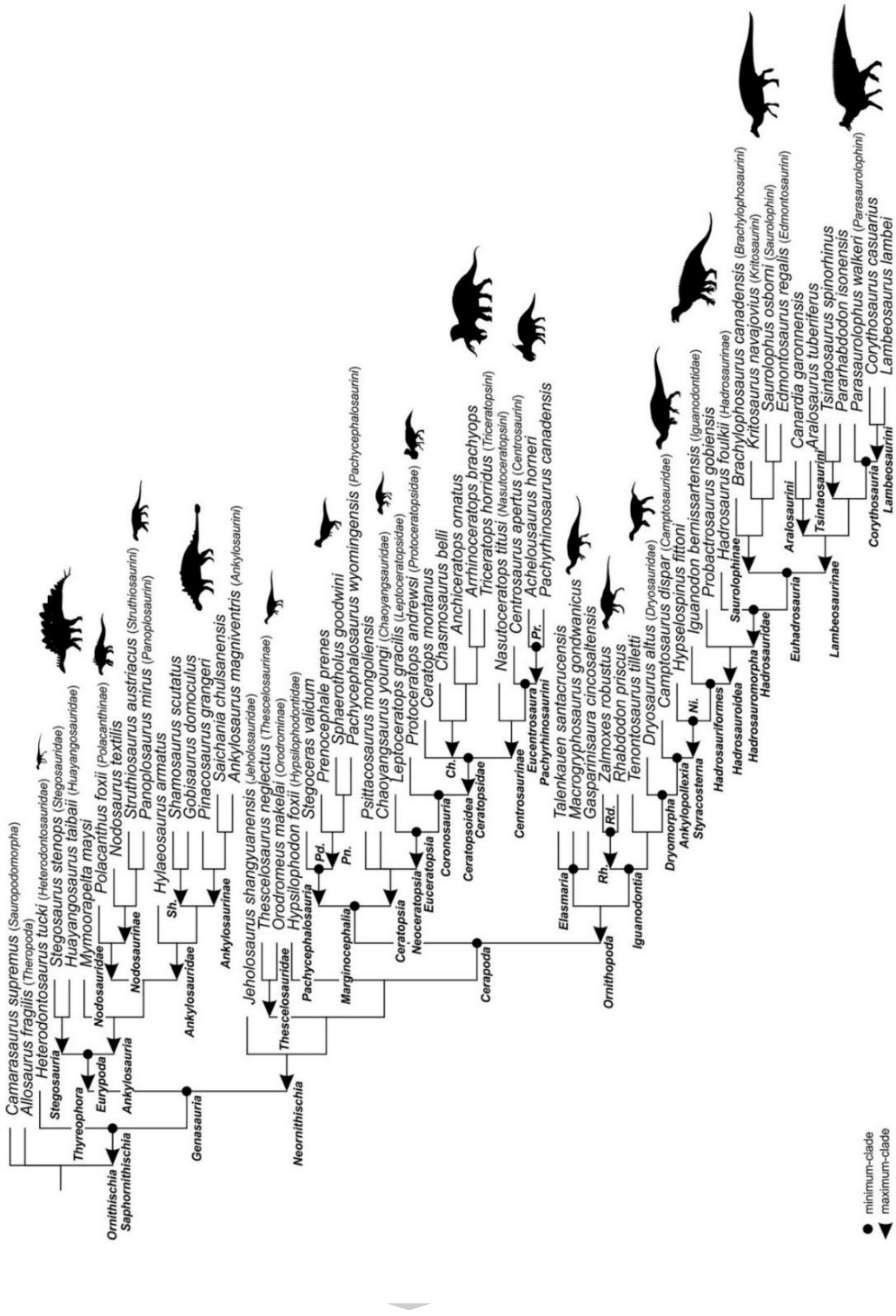

Figure 1 Specifier-based phylogeny of Ornithischia by Madzia et al., 2021. Abbreviations: Ch.–Chasmosaurinae; Ni.–Neoiguanodontia; Pd.–Pachycephalosauridae; Pn.–Pachycephalosaurinae; Pr.–Pachyrostra; Rh.–Rhabdodontomorpha; Rd.–Rhabdodontidae; and Sh.–Shamosaurinae

2.2 Classification of Asian ornithischian dinosaurs

Dinosauria Owen, 1842
Ornithischia Seeley, 1888

Heterodontosauridae Kuhn, 1966

Definition: The clade containing *Heterodontosaurus tucki* Crompton & Charig, 1962 but not *Iguanodon bernissartensis* Boulenger in Beneden, 1881, *Pachycephalosaurus wyomingensis* (Gilmore, 1931), *Stegosaurus stenops* Marsh, 1887, and *Triceratops horridus* Marsh, 1889 (Madzia et al., 2021).

Comment: They were small bipedal with characteristic teeth, including enlarged canine-like tusks and cheek teeth adapted for chewing. Their diet was herbivorous or possibly omnivorous. Their phylogenetic position is uncertain, but they are most commonly found to be primitive, outside genasaurian (Butler et al., 2008; Madzia et al., 2021; Sereno, 2012). Most heterodontosaurids were restricted to the Early Jurassic of South Africa, except *Fruitadens* from the Late Jurassic of the US, and *Echinodon* from the Earliest Cretaceous of England. Only one taxon found in Asia.

Tianyulong confuciusi Zheng et al., 2009

Age and occurrence: Late Jurassic Tiaojishan Formation (?Bathonian-Oxfordian) of Western Liaoning Province, China

Comment: The holotype (STMN 26-3) consists of an incomplete skeleton preserving a partial skull with mandible, partial postcranial elements, as well as remains of filamentous integumentary structures (Sereno, 2012; Zheng et al., 2009). The hollow rigid filaments are parallel to each other and are singular with no evidence of branching, making them more like the structures found on *Psittacosaurus*.

Genasauria Sereno, 1986

Definition: *Ankylosaurus magniventris* Brown 1908, *Stegosaurus stenops* Marsh, 1877, *Parasaurolophus walker* Parks, 1922, *Triceratops horridus* Marsh, 1889, *Pachycephalosaurus wyomingensis* (Gilmore, 1931), their most recent common ancestor and all descendants (Butler et al., 2008).

Comment: A clade comprising Thyreophora and Neornithischia (Madzia et al., 2021).

Thyreophora Nopcsa 1915

Definition: The clade containing *Ankylosaurus magniventris* Brown, 1908 and *Stegosaurus stenops* Marsh, 1887 but not *Iguanodon bernissartensis* Boulenger in Beneden, 1881 and *Triceratops horridus* Marsh, 1889 (Madzia et al., 2021).

Comment: "Armored dinosaurs" member comprises basal members from the Early Jurassic e.g. *Scutellosaurus lawleri* (from USA), *Emausaurus ernsti* (from Germany), *Scelidosaurus harrisonii* (from British Isles), and more derived members in the clade Eurypoda (Ankylosauria and Stegosauria) (Madzia et al., 2021). Some dubious Chinese taxa are still problematic, such as *Tatisaurus oehleri* (Norman, Butler & Maidment, 2007) and *Bienosaurus lufengensis* (Raven et al., 2019).

Tatisaurus oehleri Simmons, 1965

(=*Scelidosaurus oehleri* Lucas, 1996, =?*Bienosaurus lufengensis* Dong, 2001)

Age and occurrence: Early Jurassic Lower Lufeng Formation (Sinemurian) of Yunnan Province, China.

Comment: The holotype (FMNH CUP 2088) consists of a partial left mandible with teeth. It is a dubious basal thyreophoran, and is one of the oldest known members of the group (Norman et al., 2007). Another basal thyreophoran taxon, *Bienosaurus lufengensis*, has been described from the same formation in 2001. The holotype (IVPP V15311), was discovered since 1938, consists of a partial right lower jaw with teeth and several cranial fragments. Later study concluded that *B. lufengensis* was a *nomen dubium*, possibly identical to *Tatisaurus* (Raven et al., 2019).

Yuxisaurus kopchicki Yao et al., 2022

Age and occurrence: Early Jurassic Fengjiahe Formation (?late Sinemurian–Toarcian) of Yunnan Province, China.

Comment: The holotype **(**CVEB 21,701) including skull, axial, limb, and armor elements. Phylogenetic analysis recovers it as either the sister taxon of *Emausaurus* or of the clade *Scelidosaurus*+Eurypoda. (Yao et al., 2022a).

Eurypoda Sereno, 1986

Definition: The clade containing *Ankylosaurus magniventris* Brown, 1908 and *Stegosaurus stenops* Marsh, 1887.(Madzia et al., 2021).

Comment: Eurypoda comprises members of the clades Ankylosauria and Stegosauria.

Stegosauria Marsh, 1877

Definition: The clade containing *Stegosaurus stenops* Marsh, 1887 but not *Ankylosaurus magniventris* Brown, 1908 (Madzia et al., 2021).

Comment: Stegosaurian have been found predominantly in the Northern Hemisphere from the Jurassic to early Cretaceous rocks, in what is now North America, Europe, Africa, and Asia. Some dubious Chinese taxa are still problematic and considered as *nomina dubia*, such as *Chialingosaurus kuani* from China and *Monkonosaurus lawulacus* from Tibet (Maidment & Wei, 2006). Other ambiguous remains also found in Kyrgyzstan, Thailand and Siberia of Russia (Averianov et al., 2009; Averianov et al., 2007; Buffetaut et al., 2001; Skutschas et al., 2021).

Bashanosaurus primitivus Hui et al., 2022

Age and occurrence: Middle Jurassic Lower Shaximiao Formation (Bajocian) of Chongqing Province, China.

Comment: The holotype (CLGPR V00006-1) consists of limb bones, back and tail vertebrae, plates and a spike. It represents the earliest record of stegosaurs in Asia and one of the earliest records in the world. Phylogenetic analysis shows that it is the earliest-diverging stegosaur (Hui et al., 2022).

Chialingosaurus kuani Young, 1959

Age and occurrence: Late Jurassic Upper Shaximiao Formation (Oxfordian-Kimmeridgian) of Sichuan Province, China.

Comment: The holotype (IVPP 2300) consists of six vertebrae, two coracoids, left femur, two humeri, right radius and three dermal spines. The second specimen was later discovered to the same individual as the type specimen, including a fragmentary skull, vertebrae, limbs, and dermal plates (Dong et al., 1983; Jinling et al., 2008). It was considered as a *nomen dubium* (Maidment et al., 2008).

Monkonosaurus lawulacus Zhao, 1986

Age and occurrence: Late Jurassic/Early Cretaceous Loe-ein Formation of eastern Tibet (or the Early Cretaceous Lura Formation of China).

Comment: The holotype (IVPP unnumbered) consists of two partial vertebrae, three dermal plates and a complete ilio-sacral block. It was considered as a *nomen dubium* (Maidment et al., 2008).

Gigantspinosaurus sichuanensis Ouyang, 1922

Age and occurrence: Late Jurassic Upper Shaximiao Formation (Oxfordian) of Sichuan Province, China.

Comment: It is distinct by greatly enlarged shoulder spines. The first specimen (holotype: ZDM 0019) from Zigong consists of a partial skeleton and an impression of the skin. In 2005, the second specimen (ZDM 0156) was repored at Chenjia near Fuquan. It was an intermediate basal member, sharing basal traits with Huayangosauridae as well as somewhat more advanced traits with other Stegosauridae (Hao et al., 2018).

Huayangosauridae Dong, Tang & Zhou, 1982

Definition: The clade containing *Huayangosaurus taibaii* Dong, Tang & Zhou, 1982 but not *Stegosaurus stenops* Marsh, 1887 (Madzia et al., 2021).

Comment: There are only two taxa in this clade, they were found in the Middle Jurassic Fomation of China (Madzia et al., 2021).

Huayangosaurus taibaii Dong, Tang & Zhou, 1982

Age and occurrence: Middle Jurassic Lower Shaximiao Formation (Bathonian-Callovian) of Sichuan Province, China.

Comment: One of the smallest known stegosaurians, it had several types of osteoderms. The holotype (IVPP V6728) consists of a relatively complete skull, and a partial skeleton. Referred specimen (ZDM T7001) includes a skull and more complete skeleton (Dong et al., 1983; Jinling et al., 2008).

Chungkingosaurus jiangbeiensis Dong et al., 1983

Age and occurrence: Late Jurassic Upper Shaximiao Formation of Sichuan Province, China.

Comment: The holotype (CV 206) was apparently an adult, judging by the ossification of the sacrum, consists of anterior portion of skull, dorsal vertebrae, a pelvis with sacrum, caudal vertebrae, the lower end of a humerus, femora, a tibia, and dermal plates. It is one of the smallest stegosaurs (about 4 meters in length) (Dong et al., 1983; Jinling et al., 2008). Phylogenetic analysis by Hui et al. (2022) shows that it is the earliest-diverging stegosaur, along with *Bashanosaurus*,

Stegosauridae Marsh, 1880

Definition: The clade containing *Stegosaurus stenops* Marsh, 1887 but not *Huayangosaurus taibaii* Dong, Tang & Zhou, 1982 (Madzia et al., 2021).

Comment: Stegosauridae comprises taxa from North America, Europe, Africa, and Asia.

Jiangjunosaurus junggarensis Jia et al., 2007

Age and occurrence: Late Jurassic Shishugou Formation (Oxfordian) of Xinjiang, China.

Comment: The holotype (IVPP V 14724) includes the partial skull, complete mandible, articulated 11 cervical vertebrae with 2 plated, ribs, a scapula, a coracoid. It represents a subadult individual (Chengkai et al., 2007).

Tuojiangosaurus multispinus Dong et al., 1977

Age and occurrence: Late Jurassic Upper Shaximiao Formation of Sichuan Province, China.

Comment: The holotype (CV 209) consists of a nearly complete skeleton, which is the most complete stegosaurian skeleton found in Asia. The paratype (CV 210) includes a fragmentary skull, vertebrae, scapula, and a dermal plate. The plates at neck and front trunk were pear-shaped; and became triangular at the rear back (Dong et al., 1983; Jinling et al., 2008).

Wuerhosaurus homheni Dong, 1973

Age and occurrence: Early Cretaceous Lianmuqin Formation (?Valanginian) of Xinjiang, western China

Comment: *W. homheni* (IVPP V 4006) was described from a nearly complete pelvis and sacrum, caudal vertebrae, dorsal vertebrae, a scapulocoracoid, humerus, phalanx, and dermal plates which are rounder or flatter than other stegosaurids (Dong et al., 1983; Jinling et al., 2008; Maidment & Wei, 2006). A smaller specimen (IVPP V6877) which is from a similar age and has a similar anatomy from the Ejinhoro Formation in Inner Mongolia was described in 1993, it was named as the second species "*W. ordosensis*". However, the latter species was considered as a *nomen dubium* because lacking unique character combinations, and the holotype and referred material is missing from the collection (Maidment et al., 2008).

Mongolostegus exspectabilis Tumanovaa and Alifanova, 2018

Age and occurrence: Early Cretaceous Dzunbain Formation (Aptian-Albian) of Mongolia.

Comment: The holotype (PIN, no. 3779-15:) was described as the dubius taxon "*Wuerhosaurus mongoliensis*". It belongs to the latest Stegosauridae known so far (Tumanova & Alifanov, 2018).

Ankylosauria Osborn, 1923

Definition: The clade containing *Ankylosaurus magniventris* Brown, 1908 but not *Stegosaurus stenops* Marsh, 1887 (Madzia et al., 2021).

Comment: Ankylosauria has appeared in the Middle Jurassic until the end of the Cretaceous. Most members are in clade Euankylosauria (Ankylosauridae + Nodosauridae), known from the Northern Hemisphere. A few less known basal members in the clade Parankylosauria are from the Cretaceous of Antarctica, Australia, and South America (Soto-acuña et al., 2021). Some dubious species has no diagnostic features, and thus is a *nomen dubium* (e.g., *Crichtonsaurus bohlini*; Dong, 2002 *Zhejiangosaurus lishuiensis* Lü et al., 2007)

Crichtonsaurus bohlini Dong, 2002

Age and occurrence: Early Cretaceous Sunjiawan Formation (Cenomanian-Turonian) of Liaoning Province, China

Comment: The holotype (IVPP V12745) consists of a left lower jaw with teeth and referred materials from postcranial element (IVPP V12746 and LPM 101) such as vertebrae. scapula, coracoid, humerus, pes, cervical halfring and osteoderms (Dong, 2002). However, a lack of overlapping material between those specimens were pointed out, *C. bohlini* was concluded as a *nomen dubium* (Arbour & Currie, 2016).

Heishansaurus pachycephalus Bohlin, 1953

Age and occurrence: Late Cretaceous Minhe Formation (Campanian or Maastrichtian) of Gansu Province, northwestern China

Comment: It was known from fragmentary skull, vertebrae, and osteoderms (no specimen number given). So far, only casts (AMNH 2062) of some material available. It was mistaking as a member of the pachycephalosaurs. Arbour and Currie (2015) suggested that it is an ankylosaur rather than a pachycephalosaur by the caudal vertebrae characters and considered it as *nomen dubium*.

Tianchiasaurus nedegoapeferima Dong, 1993

Age and occurrence: Middle-Late Jurassic Toutunhe Formation (Bathonian–Oxfordian) of China.

Comment: One of the earliest members of Ankylosauria. The type specimen was informally referred to as "*Jurassosaurus*" after the movie Jurassic Park, and the species epithet is formed from the surnames of the movie's main actors (Dong, 1993).

?*Sinankylosaurus zhuchengensis* Wang et al., 2020

Age and occurrence: Late Cretaceous Xingezhuang Formation of Shandong Province, China.

Comment: It is known from the holotype (ZJZ-183) based on an incomplete right ilium (Wang et al., 2020). However, it has no ankylosaur diagnostic features and was considered as an invalid taxon, even not an ankylosaur. (Zheng et al., 2021).

Ankylosauridae Brown, 1908

Definition: The clade containing *Ankylosaurus magniventris* Brown, 1908 but not *Nodosaurus textilis* Marsh, 1889 (Madzia et al., 2021).

Comment: Ankylosauridae comprises of the clades Shamosaurinae and Ankylosaurinae, and other members more closely related to them from North America (e.g., *Aletopelta coombsi*), ?Europe (*Hylaeosaurus armatus*) and Asia (Madzia et al., 2021).

Bissektipelta archibaldi Parish & Barrett, 2004

Age and occurrence: Late Cretaceous Bissekty Formation (Turonian-Coniacian) of Uzbekistan.

Comment: The holotype (ZIN PH 1/6,) consists of braincase with a partial skull roof, isolated teeth and osteoderms. It was named as the second species of the dubius ankylosaur "*Amtosaurus*" from the Upper Cretaceous Bayan Shireh Formation (Cenomanian - Santonian) of Mongolia (Alexander O. Averianov, 2002; Parish & Barrett, 2004).

Liaoningosaurus paradoxus Xu et al., 2001

Age and occurrence: Early Cretaceous Yixian Formation (Aptian) of Liaoning Province, China.

Comment: Fish remain was preserved in gut contents suggested that *Liaoningosaurus* may have eaten fish. Moreover, some features of its skeleton showing aquatic adaptions. The holotype (IVPP V12560) is an articulated skeleton of juvenile. It was initially placed into Nodosauridae (Xing Xu et al., 2001), and was being classified as basal ankylosauridae later (Arbour & Currie, 2016).

Chuanqilong chaoyangensis Han et al., 2014

Age and occurrence: Late Cretaceous Jiufotang Formation (Aptian) of Liaoning Province, China.

Comment: The holotype (CJPM V001) is a nearly complete skeleton missing only the distal portion of the caudal series. It is the sister taxon of *Liaoningosaurus* near the base of the Ankylosauridae (Han et al., 2014). However, some palaeontologists suggested that it could be the older ontogeny stage of the smaller ankylosaur *Liaoningosaurus* (Xiaobo & Reisz, 2019).

Maleevus disparoserratus Tumanova, 1987

Age and occurrence: Late Cretaceous Bayan Shireh Formation (Cenomanian-Santonian), Mongolia

Comment: The holotype (PIN 554/1) consists of two fragments of the left and right maxillae. It cannot be considered diagnostic features from other ankylosaurids, and must therefore be considered a *nomen dubium* (Arbour & Currie, 2016).

Ankylosaurinae Nopcsa, 1918

Definition: The clade containing *Ankylosaurus magniventris* Brown, 1908 but not *Shamosaurus scutatus* Tumanova, 1983 (Madzia et al., 2021).

Comment: Ankylosaurinae comprises members of the clade Ankylosaurini and other members more closely related to them from Asia (Madzia et al., 2021). Some dubious taxa are still problematic e.g., *Dyoplosaurus giganteus* Maleev, 1956.

Crichtonpelta benxiensis (=*Crichtonsaurus benxiensis*) Lü et al., 2007

Age and occurrence: Late Cretaceous Sunjiawan Formation (Cenomanian) of Liaoning Province, China.

Comment: The ankylosaurids *Crichtonsaurus bohlini* (Dong, 2002) and *Crichtonsaurus benxiensis* (Junchang et al., 2007) were named from the same formation. In 2014, Arbour considered *C. bohlini* lacks diagnostic characters and should be a *nomen dubium*. However, the skull holotype (BXGMV0012) of *C. benxiensis* can be differentiated from other ankylosaurs. It was proposed a new combination *Crichtonpelta benxiensis* to receive the diagnostic material of "*C.*" *benxiensis* (Arbour & Currie, 2016).

Jinyunpelta sinensis Zheng et al., 2018

Age and occurrence: Early to Late Cretaceous Liangtoutang Formation (Albian-Cenomanian) of Zhejiang, China.

Comment: The holotype (ZMNH M8960) consists of a complete skull, and partial skeleton. The paratype (ZMNH M8963) was found nearby, including the left lower leg and a complete tail club. It would be the oldest and basalmost ankylosaurid that possess a tail club (Zheng et al., 2018).

Minotaurasaurus ramachandrani Miles & Miles, 2009

Age and occurrence: Late Cretaceous Djadokhta Formation (Campanian), Mongolia.

Comment: The holotype (INBR21004) consists of a skull with complete lower jaws and predentary. The paratype (MAE 98 179) consisting of a skull, axis, and first cervical half-ring. It was suggested that probably a junior synonym of *Tarchia* (Arbour et al., 2014). However, it was redescribed and concluded that a valid taxon (Penkalski & Tumanova, 2017).

Pinacosaurus grangeri Gilmore, 1933 (Type species)
(=*Pinacosaurus ninghsiensis* Young, 1935; =*Syrmosaurus viminocaudus* Maleev, 1952; =*Syrmosaurus viminicaudus* Maleev, 1954)
Pinacosaurus mephistocephalus Godefroit et al., 1999

Age and occurrence: Late Cretaceous Djadokhta Formation (Campanian) of Mongolia and Late Cretaceous Bayan Mandahu Formation (Campanian) of Inner Mongolia, China.

Comment: *Pinacosaurus* is well-known with numerous specimens having been discovered. The two valid taxa can be distinguished from each other. *P. grangeri* (the holotype no. AMNH 6523 found in the Djadokhta Formation) differs from *P. mephistocephalus* (the holotype no. IMM 96BM3/1 found in the Bayan Mandahu) in having short squamosal horns that do not extend far past posterior margin of skull; width across squamosal horns is not greater than width across supraorbitals; and has lacrimal incisure (Arbour & Currie, 2016). The postcranial remains referred to *Pinacosaurus* sp. also found in Wangshi Group of Shandong Province, China (Eric Buffetaut, 1995).

Tsagantegia longicranialis Tumanova, 1993

Age and occurrence: Late Cretaceous Bayan Shireh Formation (Cenomanian - Santonian), Mongolia.

Comment: The holotype specimen (MPC 700/17) is a complete skull that is unique amongst ankylosaurids by having flat cranial caputegulae that are predominantly rhomboidal and trapezoidal (Arbour & Currie, 2016).

Mongolian ankylosaurid indet. Park et al., 2021

Age and occurrence: Late Cretaceous Barun Goyot Formation (middle-upper Campanian), Mongolia.

Comment: The holotype (MPC-D 100/1359) preserved in a resting posture, consists of a nearly complete postcranial skeleton that lacks the tail but includes dorsal vertebrae, ribs, pectoral girdles, forelimbs, pelvic girdles, hindlimbs, and osteoderms. It shows that Asian ankylosaurids evolved rigid bodies with a decreased number of pedal phalanges (Park et al., 2021).

Shanxia tianzhenensis Barrett et al., 1998

Age and occurrence: Late Cretaceous Huiquanpu Formation (Cenomanian-Campanian) of Shanxi Province, China

Comment: The holotype (IVPP V11276) consists of the fragmentary skull, axis, cervicals, dorsals, caudals, humerus, femora, and osteoderm (Barrett et al., 1998). Arbour & Currie (2015) suggested *Shanxia* and *Tianzhenosaurus* to be junior synonyms of *Saichania* because there are no unique characteristics that distinguish between them. If correct, this would make an occurrence of *Saichania* in China.

Tianzhenosaurus youngi Pang & Cheng, 1998

Age and occurrence: Late Cretaceous Huiquanpu Formation (Cenomanian-Campanian) of Shanxi Province, China.

Comment: The holotype (HBV-10001) consists of a partial skull. Two paratype specimens were referred (HBV-10002: an incomplete mandible; HBV-10003: cervical vertebrae, dorsal vertebrae, caudal vertebrae, a sacral, ilia, pectoral girdles, pelvic girdles, fore and hind limbs with fore and hind feet, tail club and osteoderms). Based on skull characters, it was considered as a junior synonym of *Tianzhenosaurus* and *Saichania* (Arbour et al., 2014; Sullivan, 1999).

Saichania chulsanensis Maryańska, 1977

Age and occurrence: Late Cretaceous Barun Goyot Formation (Campanian-Maastrichtian), Mongolia.

Comment: The holotype (MPC 100/151) consists of complete skull, cervical vertebrae, dorsal vertebrae, ribs, sternum, scapulocoracoids, humerus, ulna, radius, manus, osteoderms including cervical half rings (Maryańska, 1977). It shared the habitat with *Tarchia* and *Zaraapelta*. The skull ornamentation would then have served recognition between taxa, there is no evidence for sexual dimorphism (Arbour et al., 2014).

Tarchia kielanae Maryanska, 1977 (Type species)

Age and occurrence: Late Cretaceous Barun Goyot Formation (Campanian - Maastrichtian) of Ömnögovi Province, Mongolia.

Comment: The holotype of type species *T. kielanae* (ZPal MgD-I/111) consists of a skull and rear elements.

Tarchia teresae Penkalski & Tumanova, 2016 (Type species)
Tarchia tumanovae Park et al., 2021

Age and occurrence: Late Cretaceous Nemegt Formation (Maastrichtian), Mongolia.

Comment: The other species of *Tarchia*: *T. teresae* (holotype specimens: PIN 3142/250) and *T. tumanovae* (holotype specimens: MPC-D 100/1353) were found in same formation. They coexisted with other megaherbivores, such as hadrosaurids and sauropods. Both species had a shovel-shaped beak, which is a morphological character of selective feeders. The dietary shifts of Mongolian ankylosaurs in Cenomanian to Maastrichtian stages probably relate to habitat change (Park, Lee, Kobayashi, et al., 2021).

Zaraapelta nomadis Arbour et al., 2014

Age and occurrence: Late Cretaceous Barun Goyot Formation (Campanian - Maastrichtian), Mongolia.

Comment: The holotype (MPC D-100/1388) consists of a partial skull missing the rostrum. It is different from other ankylosaurs by having unique smooth-textured keel offset from the rest of the squamosal horn (Arbour et al., 2014).

Ankylosaurini Arbour & Currie, 2016

Definition: The clade containing *Ankylosaurus magniventris* Brown, 1908 but not *Pinacosaurus grangeri* Gilmore, 1933 and *Saichania chulsanensis* Maryańska, 1977 (Madzia et al., 2021).

Comment: Ankylosaurini comprises North American members (e.g., *Akainacephalus johnsoni*, *Ankylosaurus magniventris*, *Anodontosaurus lambei*, *Dyoplosaurus acutosquameus*, *Euoplocephalus tutus*, *Nodocephalosaurus kirtlandensis*, *Scolosaurus cutleri*, *Ziapelta sanjuanensis*, *Zuul crurivastator*), and only one Asian taxon (Madzia et al., 2021).

Talarurus plicatospineus Maleev, 1952

Age and occurrence: Late Cretaceous Bayan Shireh Formation (Cenomanian-Santonian) of Mongolia.

Comment: The holotype specimen (PIN 557) consists of partial skull and postcranial skeleton. It is a close relative with *Nodocephalosaurus* from North America, represented by similar facial osteoderms (Arbour & Currie, 2016). Additional skulls have been recovered in 2007. Evidence seems to indicate that it had a grazer feeding-method by having a broad and rectangular snout, useful for low vegetation, whereas *Tsagantegia*, another ankylosaurid from the same formation, filled the niche of a browser herbivore by having more elongated and shovel-shaped beak, useful for high vegetation (Park et al., 2020).

Shamoaurinae Tumanova, 1983

Definition: The clade containing *Gobisaurus domoculus* Vickaryous et al., 2001 and *Shamosaurus scutatus* Tumanova, 1983 but not *Ankylosaurus magniventris* Brown, 1908 (Madzia et al., 2021).

Comment: Shamosaurinae comprises a few members from Asia (Madzia et al., 2021).

Shamosaurus scutatus Tumanova, 1983

Age and occurrence: Early Cretaceous Dzunbain Formation Formation (Aptian - Albian) of Dornogovi Province, Mongolia.

Comment: The holotype (PIN 3779/2) insists of skull and partial postcranial skeleton; the skull and two cervical half rings. The referred specimens including portion of skull (PIN 3779/1), and fragmentary mandible (PIN 3101). It has a rather flat skull and sharp upper beak obliquely appending to the front (Arbour & Currie, 2016).

Gobisaurus domoculus Vickaryous et al., 2001

Age and occurrence: Late Cretaceous Ulansuhai Formation (possibly Turonian) of Inner Mongolia, China.

Comment: The holotype (IVPP V12563) consists of a skull and the yet undescribed postcranial elements (Vickaryous et al., 2001). It shares many cranial similarities with *Shamosaurus*, e.g., triangular skulls with small squamosal horns and supraorbitals that are less prominent than in other ankylosaurids, and both possess a distinct longitudinal groove on the dorsal surface of the premaxillary beak (Arbour & Currie, 2016).

Zhongyuansaurus luoyangensis Xu et al., 2007

Age and occurrence: Early Cretaceous Haoling Formation (Aptian-Albian) of the Henan Province, China.

Comment: The holotype (HGM 41HIII-0002) consists of a nearly complete skull, a cervical neural spine, dorsal vertebrae, caudal vertebrae, posterior caudal centra, ribs, a humerus, both ischia, a pubis, and osteoderms (Li et al., 2007). It was considered that it was a probable junior synonym of *Gobisaurus* (Arbour & Currie, 2016).

Nodosauridae Marsh, 1890

Definition: The containing *Nodosaurus textilis* Marsh, 1889 but not *Ankylosaurus magniventris* Brown, 1908 (Madzia et al., 2021).

Comment: Nodosauridae comprises members of the clades Nodosaurinae, Polacanthinae, and other members more closely related to them from North America (e.g., *Gastonia burgei* and *Gargoyleosaurus parkpinorum*), Asia, and probably Europe (e.g., *Acanthopholis horrida* and *Sarcolestes leedsi*) (Madzia et al., 2021).

Dongyangopelta yangyanensis Chen et al., 2013

Age and occurrence: Early to Late Cretaceous Chaochuan Formation (Albian-Cenomanian) of Zhejiang Province, China.

Comment: The holotype (DYM F0136) includes dorsosacral vertebrae, sacral vertebrae, dorsal ribs, partial ilium, right femur, pedal phalanges, osteoderms and ossified tendons (Chen et al., 2013). It is one of only a few ankylosaur species from Asia known to have possessed a pelvic shield of fused osteoderms (Arbour & Currie, 2016).

Sauroplites scutiger Bohlin, 1953

Age and occurrence: Early Cretaceous (Barremian-Aptian) near Tebch of Inner Mongolia, China

Comment: The hototype were not given a specimen number. Only casts in the American Museum of Natural History (AMNH 2074) of some of the materials are available. Although extremely fragmentary and poorly preserved, the pelvic shield character of this taxon can be differentiated from other ankylosaurs (Arbour & Currie, 2016).

Hokkaido nodosaurid indet. Hayakawa et al., 2005

Age and occurrence: Late Cretaceous Hikagenosawa Formation (?late Cenomanian) of Hokkaido Prefecture, Japan

Comment: The specimen (MCM A522) consists of the left rear half of the skull, along with various cheek teeth in the orbit and adductor fossa, and the atlas articulated with the occipital condyle. It was collected since 1995 and was donated to Mikasa City Museum (Hawakaya et al., 2005).

Nodosaurinae Abel, 1919

Definition: The clade containing *Nodosaurus textilis* Marsh, 1889, but not *Hylaeosaurus armatus* Mantell, 1833, *Mymoorapelta maysi* Kirkland & Carpenter, 1994, and *Polacanthus foxii* Owen in Anonymous, 1865 (Madzia et al., 2021).

Comment: Nodosaurinae comprises members of the clades Panoplosaurini (from the Cretaceous of North America e.g., *Animantarx ramaljonesi*, ‘*Denversaurus*’ *schlessmani*, *Edmontonia longiceps*, and *Panoplosaurus mirus*), Struthiosaurini (from the Cretaceous of Europe and North America e.g., *Europelta carbonensis*, *Hungarosaurus tormai*, *Pawpawsaurus campbelli*, and *Struthiosaurus* spp.), and other members more closely related to them from North America (e.g., *Acantholipan gonzalezi*, *Borealopelta markmitchelli*, *Nodosaurus textilis*, *Sauropelta edwardsi*) (Madzia et al., 2021).

Polacanthinae Lapparent & Lavocat, 1955

Definition: The clade within Ankylosauridae or Nodosauridae containing *Polacanthus foxii* Owen in Anonymous, 1865 but not *Ankylosaurus magniventris* Brown, 1908 and *Nodosaurus textilis* Marsh, 1889 (Madzia et al., 2021).

Comment: Polacanthinae living from the Late Jurassic through Early Cretaceous of Europe (e.g., *Polacanthus foxii*) and potentially North America and Asia

Taohelong jinchengensis Yang et al., 2013

Age and occurrence: Early Cretaceous Hekou Group (Barremian) of Gansu Province, China

Comment: The holotype (GSDM 00021) including caudal vertebra, ilium, and osteoderms. The outer rim of the ilium is like a mirrored "S" in dorsal view. It was the first polacanthine to be described from Asia, and was placed to be the sister taxon to *Polacanthus foxii* from Europe (Yang et al., 2013).

Neornithischia Cooper, 1985

Definition: All genasaurians more closely related to *Parasaurolophus walkeri* than to *Ankylosaurus magniventris* or *Stegosaurus stenops* (Butler et al., 2008). Member of neornithischians including Ornithopoda, Marginocephalia (ornithopods + marginocephalians = Cerapoda), Jeholosauridae, Thescelosauridae, and a variety of basal forms (comprises *Agilisaurus louderbacki*, *Hexinlusaurus multidens*, *Hypsilophodon foxii*, *Kulindadromeus zabaikalicus*, *Leaellynasaura amicagraphica*, *Lesothosaurus diagnosticus*, *Othnielosaurus consors* (= *Nanosaurus agilis*), *Yandusaurus hongheensis*) (Madzia et al., 2021).

Comment: A variety of ornithischian basal forms that traditionally referred to as hypsilophodontids (Barrett et al., 2005; Butler et al., 2008; Sereno, 1999). The problematic classification among basal neornithischians is still unclear (Boyd, 2015; N. Li et al., 2019; Madzia et al., 2019).

Sanxiasaurus modaoxiensis Li et al., 2019

Age and occurrence: Middle Jurassic Xintiangou Formation of Chongqing Municipality, China

Comment: The holotype is a partial postcranial skeleton consisting of 2 cervical vertebrae, 11 dorsal vertebrae, 4 sacral vertebrae, 18 caudal vertebrae, both humeri, radii and ulnas, partial right ilium, partial right ischium, both femora and tibiae, left fibula, 3 metatarsi and 4 phalanges. It was more derived than *Lesothosaurus* and less derived than *Hexinlusaurus*. (Li et al., 2019).

Agilisaurus louderbacki Peng, 1992

Age and occurrence: Middle Jurassic Lower Shaximiao Formation (?Bathonian-Callovian) of Sichuan Province, China.

Comment: The complete skeleton, which is only a few parts of its left forelimb and hindlimb are missing. It was originally referred to the Fabrosaurid, and to be one of the most basal neornithischian in the recent studies (Barrett et al., 2005; Peng, 1992).

Hexinlusaurus multidens Barrett et al., 2005 after He & Cai, 1983

Age and occurrence: Middle Jurassic Lower Shaximiao Formation (?Bathonian-Callovian) of Sichuan Province, China.

Comment: *H. multidens* was originally referred to the second species of *Yandusaurus* and *Agilisaurus* (He & Cai, 1984; Peng, 1992). After study of the morphology and taxonomy by Barrett, Butler & Knoll (2005), led them to erect a new taxon. It is slightly more derived than *A.louderbacki* (Barrett et al., 2005; D. B. Norman et al., 2004). The holotype is a nearly complete, articulated skull and postcranial skeleton. Paratype is partial skull and postcranial skeleton.

Xiaosaurus dashanpensis Dong & Tang, 1983

Age and occurrence: Middle Jurassic Lower Shaximiao Formation (?Bathonian-Callovian) of Sichuan Province, China.

Comment: The holotype of *X. dashanpensis* is too fragmentary consists of a jaw fragment, 2 cervical vertebrae, 4 caudal vertebrae, a humerus, a partial left femur and a complete right hindlimb (Z. Dong & Tang, 1983). It has sometimes been considered a *nomen dubium*, but some paleontologists concluded it to be valid by possessed a mediolaterally straight humerus, which is a single unique derived trait (autapomorphy) (Barrett et al., 2005).

Yandusaurus hongheensis He, 1979

Age and occurrence: Middle Jurassic Upper Shaximiao Formation (?Bathonian-Callovian) of Hongheba, Zigong in Sichuan Province, China.

Comment: *Y. hongheensis* known from the basis of a fragmentary skull and partial postcranial remains (Barrett et al., 2005; He, 1979). The phylogenetic analysis recovered it in a position in Basal neornithischia (Butler et al., 2008). It is noted that bigger size than other basal neornithischian from the Lower Shaximioa Formation (*Agilisaurus, Hexinlusaurus* and *Xiaoaurus*) (Li et al., 2011)

Kulindadromeus zabaikalicus Godefroit et al., 2014

Age and occurrence: Middle Jurassic Ukureyskaya Formation (Bathonian) of Siberia, Russia

Comment: It possess feather-like integument (protofeathers). The two genera latter published *Kulindapteryx ukureica* and *Daurosaurus olovus* (Alifanov & Saveliev, 2014) were considered as synonym with *K. zabaikalicus* (Pascal Godefroit et al., 2014).

Gongbusaurus shiyi Dong, Zhou & Zhang, 1983

Age and occurrence: Late Jurassic Upper Xiaximiao Formation of Sichuan, China

Comment: A dubious ornithischian which was originally assigned to the Fabrosauridae from the isolated premaxillary tooth and cheek teeth (Dong et al., 1983; Jinling et al., 2008).

"Gongbusaurus" (=*Eugongbusaurus*) *wucaiwanensis* Dong, 1989

Age and occurrence: Late Jurassic Shishugou Formation of Wucaiwan, Xinjiang, China

Comment: The holotype includes a partial lower jaw, caudal vertebrae, and a partial forelimb, and paratype consisting of sacral vertebrae, caudal vertebrae, and hind limbs. Some paleontologists have suggested replacement name, "*Eugongbusaurus*" (Dong, 1989; Jinling et al., 2008).

Phu Noi neornithischian This study

Age and occurrence: Late Jurassic Phu Kradung Formation of Kalasin Province, Thailand

Comment: description in Chapter 3 and 4.

Silusaurus zhangqiani Dong, 1997

Age and occurrence: Early Cretaceous (Aptian-Albian) Xinminbao Group of Gansu, China

Comment: The holotype includes a premaxillary tooth and maxillary tooth. It was originally to hypsilophodontid taxon (Jinling et al., 2008).

Jeholosauridae Han et al., 2012

Definition: The clade outside Hypsilophodontidae or Thescelosauridae containing *Jeholosaurus shangyuanensis* Xu, Wang & You, 2000 but not *Hypsilophodon foxii* Huxley, 1869, *Iguanodon bernissartensis* Boulenger in Beneden, 1881, *Pachycephalosaurus wyomingensis* (Gilmore, 1931), *Thescelosaurus neglectus* Gilmore, 1913, and *Triceratops horridus* Marsh, 1889 (Madzia et al., 2021).

Comment: Jeholosauridae comprises *Jeholosaurus shangyuanensis* and *Yueosaurus tiantaiensis* (Madzia et al., 2021). It is apparently endemic group of Cretaceous East Asia.

Jeholosaurus shangyuanensis Xu et al., 2000

Age and occurrence: Early Cretaceous Yixian Formation (Aptian) of Liaoning Province, China

Comment: A small bipeds known from two juvenile specimens, the holotype (IV PP V 12529) is a nearly complete skull and partial postcranial (Xu et al., 2000).

Yueosaurus tiantaiensis Zheng et al., 2012

Age and occurrence: Early to Late Cretaceous Liangtoutang Formation (Albian-Cenomanian) of Zhejiang Provincce, China.

Comment: The holotype (ZMNH M8620) consists of an articulated, partial but well-preserved postcranial skeleton (Zheng et al., 2012).

Thescelosauridae Sternberg, 1937

Definition: The clade containing *Thescelosaurus neglectus* Gilmore, 1913 but not *Iguanodon bernissartensis* Boulenger in Beneden, 1881, provided that it does not include *Hypsilophodon foxii* Huxley, 1869 (Madzia et al., 2021).

Comment: Thescelosauridae comprises members of the clades Thescelosaurinae and Orodrominae (Madzia et al., 2021). The clade Parksosauridae Buchholz, 2002 has been considered as synonym with Thescelosauridae (Madzia et al., 2021).

Orodrominae Brown et al., 2013

Definition: The clade within Thescelosauridae containing *Orodromeus makelai* Horner & Weishampel, 1988 but not *Hypsilophodon foxii* Huxley, 1869 and *Thescelosaurus neglectus* Gilmore, 1913 (Madzia et al., 2021).

Comment: Three taxa known from Asia and a few members known from North America (e.g. *Orodromeus*, *Oryctodromeus*, and *Zephyrosaurus*) (Madzia et al., 2021).

Changchunsaurus parvus Zan et al., 2005

Age and occurrence: Early Cretaceous Quantou Formation (Aptian) of Jilin Province, China

Comment: The holotype (JLUM L0403-j–Zn2) is a skeleton and skull, with a premaxilla and partial lower jaw. It shows a combination of features between basal ornithischians (e.g., five teeth in each premaxilla, short toothless portion of upper beak, and a small gap between beak teeth and cheek teeth) and more derived ornithopods (reduction in size or loss of some skull fenestrae or holes) (Butler et al., 2011; Zan et al., 2005).

Haya griva Makovicky et al., 2011

Age and occurrence: Late Cretaceous Javkhlant Formation (Santonian-Campanian) of Mongolia

Comment: The holotype (IGM 100/2017) consists of a complete skull with some postcranial elements. Other several well-preserved specimens also found including a large mass of gastroliths, representing the second occurrence next to *Gasparinisaura* (Makovicky et al., 2011).

Koreanosaurus boseongensis Huh et al., 2011

Age and occurrence: Late Cretacous Seonso Conglomerate (?Santonian-Campanian) of Boseong, South Korea

Comment: The holotype (KDRC-BB2) is a partial skeleton without skull. According to the morphological, phylogenetic, and taphonomic data, it was possibly a burrowing dinosaur, like *Oryctodromeus* from USA (Huh et al., 2011).

Cerapoda Sereno,1986

Definition: The clade containing *Iguanodon bernissartensis* Boulenger in Beneden, 1881, *Pachycephalosaurus wyomingensis* (Gilmore, 1931), and *Triceratops horridus* Marsh,

1889 (Butler, Upchurch & Norman, 2008).

Comment: Cerapoda comprises members of the clades Ornithopoda and Marginocephalia (Madzia et al., 2021).

Ornithopoda Marsh 1881

Definition: The clade containing *Iguanodon bernissartensis* Boulenger in Beneden, 1881 but not *Pachycephalosaurus wyomingensis* (Gilmore, 1931) and *Triceratops horridus* Marsh, 1889 (Madzia et al., 2021).

Comment: Member in this clade is uncertain. Madzia et al. (2021) difined as Ornithopoda comprised *Burianosaurus augustai*, *Gideonmantellia amosanjuanae*, and members of the clades Elasmaria (known from Cretaceous rocks in South America, Antarctica, and Australia) and Iguanodontia. Some analysis defined *Hypsilophodon foxii*, and members of the clades Jeholosauridae and Thescelosauridae within ornithopods (Baron et al., 2017b; Dieudonné et al., 2020; Dieudonné et al., 2016).

Iguanodontia Baur, 1891

Definition: The clade containing *Dryosaurus altus* (Marsh, 1878), *Iguanodon bernissartensis* Boulenger in Beneden, 1881, *Rhabdodon priscus* Matheron, 1869, and *Tenontosaurus tilletti* Ostrom, 1970, but not include *Hypsilophodon foxii* Huxley, 1869 (Madzia et al., 2021).

Comment: Iguanodontia comprises members of the clade Rhabdodontomorpha (from Europe and Gondwana), *Tenontosaurus* spp. (from North Ameica), and Dryomorpha (Madzia et al., 2021).

Dryomorpha Sereno, 1986

Definition: The clade containing *Dryosaurus altus* (Marsh, 1878) and *Iguanodon bernissartensis* Boulenger in Beneden, 1881 (Madzia et al., 2021).

Comment: Dryomorpha comprises members of the clades Dryosauridae (primitive iguanodonts. from Middle Jurassic to Early Cretaceous of Africa, Europe, and North America) and Ankylopollexia (Madzia et al., 2021).

Ankylopollexia Sereno, 1986

Definition: The clade containing *Camptosaurus dispar* (Marsh, 1879) and *Iguanodon bernissartensis* Boulenger in Beneden, 1881. (Madzia et al., 2021).

Comment: Ankylopollexia comprises Camptosauridae and members of the clade Styracosterna. (Madzia et al., 2021). Clade was named from the cone-shaped thumb that characterizes Iguanodon-grade ornithopods.

Styracosterna Sereno, 1986

Definition: The clade containing *Iguanodon bernissartensis* Boulenger in Beneden, 1881 but not *Camptosaurus dispar* (Marsh, 1879) (Madzia et al., 2021).

Comment: Styracosterna comprises uncertain and/or basal taxa (such as *Hippodraco scutodens*, *Iguanacolossus fortis*), and members of the clade Hadrosauriformes (Madzia et al., 2021).

Bayannurosaurus perfectus Xu et al, 2018

Age and occurrence: Early Cretaceous Bayingebi (Bayin-Gobi) Formation (Early Aptian) of Mongolia.

Comment: The holotype (IMMNH PV00001) is a nearly complete, semi-articulated skeleton, including the entire caudal series. It is a non-hadrosauriform ankylopollexian that is more derived than *Hypselospinus*, yet less derived than *Ouranosaurus* and just outside of the Hadrosauriformes (Xu et al., 2018).

Fukuisaurus tetoriensis Kobayashi & Azuma, 2003

Age and occurrence: Early Cretaceous Kitadani Formation (Barremian) of Fukui Prefecture, Japan.

Comment: The holotype (FPDM-V-40-1, FPDM-V-40-2) is a right maxilla and a right jugal. Further of a skull element and a right sternal plate had been referred. It was described as more derived than *Iguanodon* and *Ouranosaurus*, but less derived than *Altirhinus*. (Kobayashi & Azuma, 2003). However, later cladistic analyses showed *F. tetoriensis* in many positions of the styracostern such as a basal member of Hadrosauroidea (Ramírez-Velasco et al., 2012), or a non-hadrosauroid styracostern (Bertozzo et al., 2017; Madzia et al., 2021).

Koshisaurus katsuyama Shibata and Azuma, 2015

Age and occurrence: Early Cretaceous Kitadani Formation (Barremian) of Fukui Prefecture, Japan.

Comment: The holotype (FPDM-V9079) consists of maxillary, vertebral, pubic and femur. A phylogenetic analysis by the authors indicates that it is a basal member of Hadrosauroidea and is more derived than the contemporaneous *Fukuisaurus*. (Shibata & Azuma, 2015). However, later phylogenetic analysis presented its position in Styracosterna more basal than *Iguanodon bernisartensis* (Tsogtbaatar et al., 2019).

Lanzhousaurus magnidens You, Ji & Li, 2005

Age and occurrence: Early Cretaceous Hekou Group (Barremian) of Gansu Province, China.

Comment: The holotype (GSLTZP 1-1) consists of partial skeleton of a single individual including mandible, isolated maxillary teeth, isolated right dentary teeth and complete a series of fourteen vertebrae, sternal plates, ribs, and pubes. It is a large non-hadrosauriform iguanodontian has the largest known herbivorous dinosaur teeth. Unlike its hadrosauriform relatives possessing tooth batteries of many small teeth, *L. magnidens* utilized a small number (14) of very large teeth (~10 cm long) to create a large, continuous surface for mastication (Suarez et al., 2017; You et al., 2005).

Napaisaurus guangxiensis Ji & Zhang, 2022

Age and occurrence: Early Cretaceous Xinlong Formation (?Aptian-Albian) of Guangxi Zhuang Autonomous Region, China.

Comment: The holotype (FS-20-007 to 008) is a right ischium and right ilium. It is the first named basal iguanodontian taxon from southern China, and also provides more crucial evidence for understanding the relationships of the Early Cretaceous dinosaur faunas between the Napai Basin and Thailand in Southeast Asia (Ji & Zhang, 2022).

Neoiguanodontia Norman, 2014

Definition: The clade containing *Hypselospinus fittoni* (Lydekker, 1889), *Iguanodon bernissartensis* Boulenger in Beneden, 1881, and *Parasaurolophus walkeri* Parks, 1922 (Madzia et al., 2021).

Comment: Neoiguanodontia comprises *Hypselospinus fittoni* (from UK) and members of the clade Hadrosauriformes (Madzia et al., 2021).

Hadrosauriformes Sereno, 1997

Definition: The clade containing *Hadrosaurus foulkii* Leidy, 1858 and *Iguanodon bernissartensis Boulenger* in Beneden, 1881 (Madzia et al., 2021).

Comment: Hadrosauriformes comprises members of the clades Hadrosauroidea, Iguanodontidae (=Iguanodontoidea; such as *Iguanodon* spp. From Europe) and other member more closely related to them (Madzia et al., 2021).

Hadrosauroidea von Huene, 1952

Definition: The clade containing *Hadrosaurus foulkii* Leidy, 1858 but not *Iguanodon bernissartensis* Boulenger in Beneden, 1881 (Madzia et al., 2021).

Comment: Hadrosauroidea comprises the clade Hadrosauromorpha and other member more closely related to them (Madzia et al., 2021).

Altirhinus kurzanovi Norman, 1998

Age and occurrence: Early Cretaceous Khuren Dukh Formation (Barremian-Albian) of Dornogovi Province, Mongolia.

Comment: In 1952, its remains were originally referred to as the species *Iguanodon orientalis*. The holotype (PIN 3386/8) is a skull, a distinctive tall arch on top of its snout similar structure seen in *Muttaburrasaurus* from Australia, including some postcranial material (Norman, 1998).

Batyrosaurus rozhdestvenskyi Godefroit et al., 2012

Age and occurrence: Late Cretaceous Bostobe Formation (Santonian-Campanian) of central Kazakhstan.

Comment: The holotype (AEHM 4/1) consists of a partial skeleton, including a partial skull. The authors considered *B. rozhdestvenskyi* possibly the same taxon as the dubius *Arstanosaurus akkurganensis*a Shilin & Suslov, 1982 , known from the left maxilla (holotype: AAIZ 1/1) and the lower end of a left femur (AAIZ 1/2), as both were found from the same formation (Pascal Godefroit et al., 2012).

Bolong yixianensis Wu, Godefroit & Hu, 2010

Age and occurrence: Early Cretaceous Yixian Formation (earliest Aptian) of Liaoning Province, China

Comment: The holotype (YHZ-001) consists of a skull with lower jaws. The second specimen (ZMNH-M8812) was later described consists of an almost complete skeleton of a young individual. It differs from *Jinzhousaurus*, which is previously found in the same formation by at least 14 cranial and dental characters (Wu et al., 2010).

Choyrodon barsboldi Gates et al., 2018

Age and occurrence: Early Cretaceous Khuren Dukh Formation (Barremian-Albian) of Dornogovi Province, Mongolia.

Comment: The holotype (MPC-D 100/801) is a partial disarticulated skull, metacarpals, and cervical ribs of a subadult animal. Differences in morphology and results of the phylogenetic analyses support that *C. barsboldi* distinct from *Altirhinus kurzanovi*, which is found in the same formation, but is a sister taxon with the North American species *Eolambia caroljonesa* (Gates et al., 2018).

Equijubus normani You et al., 2003

Age and occurrence: Early Cretaceous Xinminbao Group (Aptian) of Gansu Province, China

Comment: The holotype (IVPP V12534) consists of a complete skull with articulated lower jaws and associated incomplete postcrania. This study also suggests that the hadrosauroids had most likely originated in Asia in the Early Cretaceous before this clade diversified and spread to other Laurasian continents during the Late Cretaceous (You et al., 2003).

Gongpoquansaurus mazongshanensis Lü, 1997
(=*Probactrosaurus mazongshanensis* Lü, 1997)

Age and occurrence: Early Cretaceous Zhonggou Formation (Albian) of Gansu Province, China

Comment: The holotype (IVPP V. 11333) is a caudal part of an incomplete skull. It was first described as the third species of *Probactrosaurus mazongshanensis* (Lü, 1997). In 2014, the species was redescribed, and the describers erected *Gongpoquansaurus* (You et al., 2014). It is less derived than the type species *P. gobiensis*.

Jinzhousaurus yangi Wang & Xu, 2001

Age and occurrence: Early Cretaceous Yixian Formation (Aptian) Liaoning Province, China

Comment: The holotype (IVPP V12691) consists of a nearly complete skeleton, compressed on a slab. It represents the first reported large-sized dinosaur from Jehol fauna in western Liaoning, (Wang & Xu, 2001).

"*Mandschurosaurus*" *laosensis* Hoffet, 1944

Age and occurrence: Early Cretaceous Grès supérieurs Formation (Aptian-Albian) of Muong Phalane, Laos

Comment: Three iguanodontians have been placed within the hadrosaurid genus *Mandschurosaurus* (type species *M. amurensis* is from China). Hoffet (1944) described *M. laosensis* from three distal ends of femora, an ilium, and a scapula, he also referred some cervical and caudal vertebrae as this taxon (Buffetaut, 1991). It was considered as *nomen dubium* (Buffetaut & Suteethorn, 2011; Horner et al., 2004).

Nanningosaurus dashiensis Mo et al., 2007

Age and occurrence: Late Cretaceous Nalong Basin of Guangxi Zhuang Autonomous Region, China.

Comment: The holotype (NHMG8142) is an incomplete skeleton including skull. The paratype (NHJM8143) is a right maxilla. This animal was claimed first hadrosaurid named from southern China (Jinyou et al., 2007). However, many latter phylogenic analyses suggested that it is on the position of the hadrosauroid (Kobayashi et al., 2021; Xing et al., 2014).

Penelopognathus weishampeli Godefroit, Li, and Shang, 2005

Age and occurrence: Early Cretaceous Bayin-Gobi Formation (Albian) of Inner Mongolia, China

Comment: The holotype (IMM 2002-BYGB-1) is a right dentary, which is resemble those taxa from Lower Cretaceous of Gobi area: *Altirhinus kurzanovi* and *Probactrosaurus gobiensis* (Pascal Godefroit et al., 2005).

Probactrosaurus gobiensis Rozhdestvensky, 1966
(=*Probactrosaurus alshanicus* Rozhdestvensky, 1966)

Age and occurrence: Early Cretaceous Dashuigou Formation (Barremian-Albian) of Inner Mongolia, China

Comment: The holotype (PIN 2232/1) is a partial skull, and the referred material (PIN 2232/10) is partial skeleton. Unfortunately, the specimen referred to the second species, *P. alashanicus* which was based on fragmentary material, had been lost after being dispatched from Moscow to Beijing. The latter species was concluded as synonym of *P. gobiensis* (Norman, 2002; Rozhdestvenskiy, 1967).

Ratchasimasaurus suranareae Shibata et al., 2011

Age and occurrence: Early Cretaceous Khok Kruat Formation (Aptian) of Nakhon Ratchasima Province, Thailand

Comment: The holotype (NRRU-A2064) is an elongated and flat left dentary, the length is six times longer than the height (Shibata et al., 2011).

Siamodon nimngami Buffetaut and Suteethorn, 2011

Age and occurrence: Early Cretaceous Khok Kruat Formation (Aptian) of Nakhon Ratchasima Province, Thailand

Comment: The holotype (PRC-4) is a well-preserved left maxilla and the referred materials, an isolated maxillary tooth (PRC-5) and a braincase (PRC-6) (Buffetaut & Suteethorn, 2011).

Sirindhorna khoratensis Shibata et al., 2015

Age and occurrence: Early Cretaceous Khok Kruat Formation (Aptian) of Nakhon Ratchasima Province, Thailand

Comment: The holotype (NRRU3001-166) is an articulated braincase including referred skull element. Phylogenetic analysis revealed *S. khoratensis* as among the most basal hadrosauroids. It is the best-preserved iguanodontian in Southeast Asia so far (Shibata et al., 2015).

Xuwulong yueluni You, Li & Liu, 2011

Age and occurrence: Early Cretaceous Xinminpu Group (Aptian-Albian) of Gansu Province, China

Comment: The holotype (GSGM F00001) is an articulated specimen including a complete cranium, almost complete axial skeleton, and complete left pelvic girdle (You et al., 2011).

Zuoyunlong huangi Wang et al., 2017

Age and occurrence: Late Cretaceous Zhumapu Formation (Cenomanian) of Shanxi Province, China

Comment: The holotype (SXMG V 00 004) consists of two bones from the right-hand half of the pelvis, a partial right ilium, and the lower end of the shaft of the right ischium. It is one of the oldest known hadrosauroid also date from the Cenomanian (Wang et al., 2017).

Hadrosauromorpha Norman, 2014

Definition: The clade containing *Hadrosaurus foulkii* Leidy, 1858 but not *Probactrosaurus gobiensis* Rozhdestvensky, 1966 (Madzia et al., 2021).

Comment: Hadrosauromorpha comprises the clade Hadrosauridae and other member more closely related to them (Madzia et al., 2021).

Bactrosaurus johnsoni Gilmore, 1933

(="*Bakesaurus*" Zhou, 2005; =*Cionodon kysylkumensis* Riabinin, 1931)

Age and occurrence: Late Cretaceous Iren Dabasu Formation (Cenomanian) of Inner Mongolia, China.

Comment: The holotype specimens (AMNH 6553), was composed of partial skeletons more than one individual, consists of dentary, maxillary and other skull parts; dorsal, sacral, and caudal vertebrae, most of which were found in series; left scapula, left sternal, both pubes, both ischia, left femur, fibula and complete left hind foot and part of right (Gilmore, 1933).

Datonglong tianzhenensis Xu et al., 2016

Age and occurrence: Late Cretaceous Huiquanpu Formation (Cenomanian-Campanian) of Shanxi Province, China.

Comment: The holotype (SXMG V 00005) consists of complete right dentary with some preserved teeth (Xu et al., 2016).

Gilmoreosaurus mongoliensis Gilmore, 1933
(=*Mandschurosaurus mongoliensis* Gilmore, 1933)

Age and occurrence: Late Cretaceous Iren Dabasu Formation (Cenomanian) of Inner Mongolia, China.

Comment: In 1933, Charles W. Gilmore published two iguanodontian taxa from the Iren Dabasu of Inner Mongolia. One was the genus *Bactrosaurus*. The second (the holotype: AMNH 6551) was named as a new species of *Mandschurosaurus*, *M. mongoliensis* (Gilmore, 1933). After that, Michael K. Brett-Surman considered the later taxon as a distinct genus. He erected the genus *Gilmoreosaurus* in 1979, honoring Gilmore. It is known from not less than four adult animals (Brett-Surman, 1979).

Gobihadros mongoliensis Tsogtbaatar et al., 2019

Age and occurrence: Late Cretaceous Bayan Shireh Formation (Cenomanian-Santonian) of Mongolia.

Comment: The holotype (MPC-D100/746) consists of a nearly complete articulated skeleton with a partly disintegrated skull. Numerous specimens have been referred especially the specimen MPC-D100/763, a complete articulated skull, with a hand. The specimens have partly been found in other sites in the Bayan Shireh Formation. It is the most completely known non-hadrosaurid hadrosauroid from Asia (Tsogtbaatar et al., 2019).

Jintasaurus meniscus You & Li, 2009

Age and occurrence: Early Cretaceous Yujingzi Basin (?Albian) of Gansu Province, China.

Comment: The holotype (FRDC: GJ 06-2-52) includes an articulated posterior portion of the skull roof and an almost complete braincase (You & Li, 2009).

Levnesovia Transoxiana Sues and Averianov, 2009

Age and occurrence: Late Cretaceous Bissekty Formation (Middle-Late Turonian) of Uzbekistan

Comment: The holotype (USNM 538191) consists of postorbital region of skull roof with nearly complete braincase (Sues & Averianov, 2009a).

Nanyangosaurus zhugeii Xu et al., 2000

Age and occurrence: Late Cretaceous Xiaguan Formation (Turonian-Campanian) of Henan Province, China

Comment: The authors considered *N. zhugeii* is an Albian iguanodontian, but the type of horizon is now believed to be Turonian-Campanian in age based on plant and invertebrate fossils (Wang et al., 2013). The holotype (IVPP V 11821) consists of a partial skeleton lacking the skull. It is more derived than *Probactrosaurus* but lies outside hadrosaurids (Xu et al., 2000).

Plesiohadros djadokhtaensis Tsogtbaatar et al., 2014

Age and occurrence: Late Cretaceous Alagteeg Formation (split out from the overlying Djadochta Formation) (Campanian) of Mongolia.

Comment: The holotype (MPC-D100/751) is a partial skeleton, lower jaw, cervical vertebra, hyoid, metatarsals, and phalanges. It is a derived hadrosauroid proximate to Hadrosauridae. The complete replacement of non-hadrosaurid hadrosauoids with true hadrosaurids in the Maastrichtian of Mongolia represents the complex pattern of faunal interchange between Asia and North America in the latest Cretaceous (Tsogtbaatar et al., 2014).

Tanius sinensis Wiman, 1929 (Type species)

Age and occurrence: Late Cretaceous Jiangjunding Formation of the Wangshi Group (?Campanian), China.

Comment: The holotype (PMU R.240) of type species *T. sinensis* consists of the back of the skull, which was collected in 1923 (below the Jingangkou Formation, where *Tsintaosaurus spinorhins* were found). It was referred to basal hadrosauroid. The second species "*T.*" *chingkankouensis* Young, 1958 erected based on a few postcranial bones collected in the same area with *Tsintaosaurus* at Jingangkou, Laiyang. However, Zhang et al (2017) suggested that the sacrum and ilium of "*T.*" *chingkankouensis* shows typical hadrosaurid features should not be referred to genus *Tanius*. The third species "*T.*" *laiyangensis* Zhen, 1976 was inferred to be a member of the clade Kritosaurini , the first record from Asia (Zhang et al., 2019).

Shuangmiaosaurus gilmorei You et al., 2003

Age and occurrence: Late Cretaceous Sunjiawan Formation (Early Cenomanian) of Liaoning Province, China

Comment: The holotype (LPM 0165) consists of a partial left upper jaw and lower jaw, including the maxilla, part of the praemaxilla, elements of the lacrimal and the dentary (You et al., 2003).

Yunganglong datongensis Wang et al., 2013

Age and occurrence: Late Cretaceous lower Zhumapu Formation (Cenomanian) of Shanxi Province, China

Comment: The holotype (SXMG V 00001) consists of the skull material, and an associated but disarticulated partial postcranium came from a single individual. It helps to elucidate the origin and evolution of Hadrosauridae (Wang et al., 2013).

Zhanghenglong yangchengensis Xing et al., 2014

Age and occurrence: Late Cretaceous Majiacun Formation (Middle Santonian) of Henan Province, China

Comment: The holotype (XMDFEC V0013) consists of a partial skull and lower jaw. The paratype (XMDFEC V0014) is a partial skeleton lacking the skull, including five back vertebrae, ribs, a shoulder blade and the right ulna. It displays a unique combination of plesiomorphic and derived features of hadrosauroids, and is clearly morphologically transitional between basal hadrosauroids and hadrosaurids. (Xing et al., 2014).

Hadrosauridae Cope, 1869

Definition: The clade containing *Hadrosaurus foulkii* Leidy, 1858, *Lambeosaurus lambei* Parks, 1923, and *Saurolophus osborni* Brown, 1912 (Madzia et al., 2021).

Comment: Hadrosauridae, the so-called duck-billed dinosaurs, comprises the clade Euhadrosauria and other member more closely related to them (e.g. *Hadrosaurus foulkii* and *Eotrachodon orientalis* from North America) (Madzia et al., 2021). The phylogenetic position of some dubious taxa is still unclear.

Mandschurosaurus amurensis Riabinin, 1930 (Type species)

Age and occurrence: Late Cretaceous Yuliangze Formation (Maastrichtian) of Heilongjiang Province, China.

Comment: It was the first dinosaur genus named from China. The holotype (IVP AS coll.) collected from the banks of the Amur River, China in 1914. It was initially referred to the genus "*Trachodon*" *amurense* Riabinin, 1925, but was later reassigned to a new genus by Riabinin (1930). *M. amurensis* is a large hadrosaurid based on a poorly preserved and incomplete skeleton, and often considered as a *nomen dubium* (Horner et al., 2004).

Microhadrosaurus nanshiungensis Dong, 1979

Age and occurrence: Late Cretaceous Yuanpu Formation (=Nanxiong Formation: Campanian/Maastrichtian) of Guangdong Province, China.

Comment: The holotype (IVPP V4732) is a partial dentary with tooth battery from a juvenile individual. It was considered as a *nomen dubium* (Horner et al., 2004).

Yamatosaurus izanagii Kobayashi et al. 2021

Age and occurrence: Late Cretaceous Kita-Ama Formation (Maastrichtian) of Awaji Island, Japan.

Comment: The holotype (MNHAH D1-033516) consists of a right dentary, a right surangular, twelve isolated dentary teeth, four cervical vertebrae, a distal caudal vertebra, three cervical ribs, and a coracoid. It is a basal hadrosaurid, more derived than *Hadrosaurus* but less than Saurolophinae+Lambeosaurinae. The biogeographic analyses show that basal hadrosaurids were widely distributed in Asia and Appalachia, that the clade of Saurolophinae and Lambeosaurinae originated in Asia, and that eastern Asia may have served as a refugium of relict hadrosauroid taxa such as *Plesiohadros djadokhtaensis, Tanius sinensis*, and *Yamatosaurus izanagii* during the Late Cretaceous (Kobayashi et al., 2021).

Euhadrosauria Weishampel, Norman & Grigorescu, 1993

Definition: The clade containing *Lambeosaurus lambei* Parks, 1923 and *Saurolophus osborni* Brown, 1912, provided that it does not include *Hadrosaurus foulkii* Leidy, 1858 (Madzia et al., 2021).

Comment: Euhadrosauria comprises members of the clades Saurolophinae and Lambeosaurinae (Madzia et al., 2021).

Saurolophinae Brown, 1914 (=**Hadrosaurinae** Lambe, 1918)

Definition: The clade containing *Saurolophus osborni* Brown, 1912 but not *Lambeosaurus lambei* Parks, 1923, provided that it does not include *Hadrosaurus foulkii* Leidy, 1858. (Madzia et al., 2021).

Comment: Saurolophinae comprises members of the clades Brachylophosaurini (from North America e.g. *Brachylophosaurus* and *Maiasaura*), Edmontosaurini, Kritosaurini (from North America e.g. *Gryposaurus* and *Kritosaurus*), and Saurolophini (Madzia et al., 2021).

Barsboldia sicinskii Maryańska & Osmólska, 1981

Age and occurrence: Late Cretaceous Nemegt Formation (Maastrichtian), Mongolia.

Comment: With only one partial skeleton known, it was described as a lambeosaurine and has been considered dubious (Norman & Sues, 2000). A newer study suggests that it is actually a valid saurolophine (Prieto-Márquez, 2011).

Brachylophosaurini Gates et al., 2011

Definition: The clade containing *Brachylophosaurus canadensis* Sternberg, 1953 but not *Edmontosaurus regalis* Lambe, 1917, *Hadrosaurus foulkii* Leidy, 1858, *Kritosaurus navajovius* Brown, 1910, and *Saurolophus osborni* Brown, 1912. (Madzia et al., 2021).

Comment: The largest ornithischian is in this clade, Edmontosaurini comprises *Edmontosaurus* spp. From North America and other members from Asia (Madzia et al., 2021) and potentially Asia (Xing et al., 2012).

Wulagasaurus dongi Godefroit et al., 2008

Age and occurrence: Late Cretaceous Yuliangze Formation (Maastrichtian) of Heilongjiang Province, China.

Comment: It is known from a right dentary (holotype: GMH W184) and additional remains including braincases, jugal, maxillae, scapulae, sternals, humeri, and ischium. It was analyzed as the most basal saurolophine (Pascal Godefroit et al., 2008). However, Xing and his team re-evaluated and re-described of both original and recent specimens of *W. dongi*, they concluded that it shared many morphological similarities with *Brachylophosaurus* and *Maiasaura*, suggesting that the only member in clade Brachylophosaurini outside North America (Xing et al., 2012).

Edmontosaurini Glut, 1997

Definition: The clade containing *Edmontosaurus regalis* Lambe, 1917 but not *Brachylophosaurus canadensis* Sternberg, 1953, *Hadrosaurus foulkii* Leidy, 1858, *Kritosaurus navajovius* Brown, 1910, and *Saurolophus osborni* Brown, 1912 (Madzia et al., 2021).

Comment: Most of members are discovered from North America (Madzia et al., 2021).

Kamuysaurus japonicus Kobayashi et al., 2019

Age and occurrence: Late Cretaceous Hakobuchi Formation (Yezo Group) (Early Maastrichtian) of Hokkaido Prefecture, Japan

Comment: The holotype (HMG-1219) consists of a nearly complete skeleton with skull of an adult individual. It is, one of the most complete dinosaur skeletons found in Japan. It has been found in a marine layer, which was likely washed into the sea as a carcass (Kobayashi et al., 2019).

Kerberosaurus manakini Bolotsky & Godefroit, 2004

Age and occurrence: Late Cretaceous Udurchukan Formation (Maastrichtian) of Blagoveschensk, Russia.

Comment: The holotype (AENM 1/319) is a cranial material. This study provides additional support for land links and faunal interchange between eastern Asia and North America at the end of the Cretaceous. Several independent hadrosaurid lineages migrated from western North America to eastern Asia, probably by late Campanian to early Maastrichtian time. At the end of the Maastrichtian, completely different dinosaur faunas developed in both regions, indicating geographical or palaeoecological barrier (Bolotsky & Godefroit, 2004).

?*Kundurosaurus nagornyi* Godefroit et al., 2012

Age and occurrence: Late Cretaceous Udurchukan Formation (Maastrichtian) of Kundur, Russia.

Comment: The holotype (AENM 2/921) is a disarticulated skull. The referred specimens may belong to other individuals including skull and postcranial element, which were found at the same level as the holotype. However, some researcher considered *K. nagornyi* to be a junior synonym of *Kerberosaurus manakini* on the basis of their co-occurrence within the same formation and presence of morphological characters (Xing et al., 2014).

Laiyangosaurus youngi Zhang et al., 2017

Age and occurrence: Late Cretaceous Jingangkou Formation of Wangshi Group (?Campanian), China.

Comment: The holotype (IVPP V 23401) consists of a large left maxilla, a right squamosal, and a left dentary. It shows typical saurolophine morphologies that can be distinguished from the equivalent bones of the other two Laiyang hadrosauroids, the non-hadrosaurid hadrosauroid *Tanius* and the Lambeosaurine *Tsintaosaurus* (Zhang et al., 2017).

Shantungosaurus giganteus Hu, 1973
(=*Zhuchengosaurus maximus* Zhao et al., 2007;
=*Huaxiaosaurus aigahtens* Zhao et al., 2011)

Age and occurrence: Late Cretaceous Xingezhuang Formation (?Campanian-Maastrichtian stages) of Shandong Province, China.

Comment: *S. giganteus*, the largest ornithischian taxon in the world, is the single hadrosaurid from the Zhucheng area that is considered valid. *Zhuchengosaurus* and *Huaxiaosaurus*, both of which are known from the same region, have been interpreted by phylogenetic analyses as junior synonyms of *S. giganteus*. All unequivocal morphological discrepancies among these three taxa could be caused from ontogenetic and polymorphic variation including specimen distortion (Xing et al., 2014).

Saurolophini Glut, 1997

Definition: The clade containing *Saurolophus osborni* Brown, 1912 but not *Brachylophosaurus canadensis* Sternberg, 1953, *Edmontosaurus regalis* Lambe, 1917, *Hadrosaurus foulkii* Leidy, 1858, and *Kritosaurus navajovius* Brown, 1910 (Madzia et al., 2021).

Comment: Saurolophini comprises *Augustynolophus morrisi*, *Prosaurolophus maximus*, and *Saurolophus* spp. (Madzia et al., 2021).

Saurolophus angustirostris Rozhdestvensky, 1952

Age and occurrence: Late Cretaceous Nemegt Formation (Maastrichtian), Mongolia.

Comment: The type species *Saurolophus osborni* Brown, 1912 was found from the Horseshoe Canyon Formation of western Canada. The second species, *S. angustirostris*, known by numerous specimens from Mongolia. The latter species was larger than American species and was one of the largest herbivores of the Nemegt Formation (Bell, 2011).

Lambeosaurinae Parks, 1923

Definition: The clade containing *Lambeosaurus lambei* Parks, 1923 but not *Hadrosaurus foulkii* Leidy, 1858 and *Saurolophus osborni* Brown, 1912 (Madzia et al., 2021).

Comment: Lambeosaurinae comprises members of the clades Corythosauria, Tsintaosaurini, and other member more closely related to them (Madzia et al., 2021). Some dubious taxa are still problematic.

Aralosaurus tuberiferus Rozhdestvensky, 1968

Age and occurrence: Late Cretaceous Bostobe Formation (Upper Santonian-Lower Campanian) of central Kazakhstan.

Comment: The holotype (Paleontological Institute No. 2229/1) is an incomplete skull (Rozhdestvenskiy, 1968). At the time, its skull was reconstituted resemblance with the skull of *Gryposaurus*, the Saurolophinae from North American, with the presence of an arch snouted. The re-examination of its skull revealed that *A. tuberiferus* had a hollow bony structure located far in front of the orbits. It has been identified as the most basal Lambeosaurinae, which is the group that originated from Asia and then migrated to North America before or at the beginning of the late Campanian (Godefroit et al., 2004).

Jaxartosaurus aralensis Riabinin, 1937

Age and occurrence: Late Cretaceous Dabrazhin Formation (Santonian) of southern Kazakhstan.

Comment: A medium-sized hadrosaur known from the lectotype (The Museum of the Central Science and Research Institute for Geological Exploration (Leningrad), No. 1/5009): incomplete skull. The skull is wide and low with a helmet-like crest in which the frontals and prefrontals do not participate (Rozhdestvenskiy, 1968). The second species from Xinjiang of China, *J. fuyunensis*, was described by Wu (1984) for a dentary, but is dubious (Horner et al., 2004).

Kazaklambia convincens Bell & Brink, 2013
(=*Corythosaurus convincens* Rozhdestvensky, 1968;
=*Procheneosaurus convincens* Rozhdestvensky, 1968)

Age and occurrence: Late Cretaceous Dabrazhin Formation (Santonian) of southeatern Kazakhstan

Comment: The holotype (PIN 2230/1) consists of a virtually complete skull and skeleton of an immature individual lacking most of the preorbital region of the skull, distal parts of the forelimbs, distal left hindlimb, and distal caudal vertebrae. It is in a basal position of Lambeosaurinae, which was seen as proving an Asian origin of the clade (Bell & Brink, 2013).

Nipponosaurus sachalinensis Nagao, 1936

Age and occurrence: Late Cretaceous Yezo Group (?Late Santonian or Early Campanian) of Sakhalin Island, Russia.

Comment: The holotype (Regist. No. 6590) known from a single juvenile specimen, it was the first dinosaur named based on a discovery on Japanese territory at the time of naming. A cladistic analysis in 2017 found its position outside of the clade Parasaurolophini and Lambeosaurini (Takasaki et al., 2017).

Corythosauria Madzia et al., 2021

Definition: The new clade by Madzia et al. (2021) containing *Corythosaurus casuarius* Brown, 1914, *Lambeosaurus lambei* Parks, 1923, and *Parasaurolophus walkeri* Parks, 1922.

Comment: Corythosauria comprises members of the clades Lambeosaurini and Parasaurolophini (Madzia et al., 2021).

Parasaurolophini Glut, 1997

Definition: The clade containing *Parasaurolophus walkeri* Parks, 1922 but not *Aralosaurus tuberiferus* Rozhdestvensky, 1968, *Lambeosaurus lambei* Parks, 1923 and *Tsintaosaurus spinorhinus* Young, 1958.(Madzia et al., 2021).

Comment: Parasaurolophini comprises members from North America (e.g. *Parasaurolophus* spp. and *Tlatolophus galorum*) and *Charonosaurus jiayinensis* from Asia (Madzia et al., 2021; Ramírez Velasco et al., 2021).

Charonosaurus jiayinensis Godefroit, Zan & Jin, 2000

Age and occurrence: Late Cretaceous Yuliangze Formation (Maastrichtian) of Heilongjiang Province, northeastern China.

Comment: The holotype (CUST J-V1251-57) is a partial skull, resembles that of *Parasaurolophus*. It is one of the largest hadrosaurs currently known from Asia, and is only one parasaurolophine outside North America (Pascal Godefroit et al., 2000).

Lambeosaurini Sullivan et al., 2011

Definition: The clade containing *Lambeosaurus lambei* Parks, 1923 but not *Aralosaurus tuberiferus* Rozhdestvensky, 1968, *Parasaurolophus walkeri* Parks, 1922, and *Tsintaosaurus spinorhinus* Young, 1958 (Madzia et al., 2021). Lambeosaurini is synonym of the discouraged clade Corythosaurini Glut, 1997 (Madzia et al., 2021).

Comment: Lambeosaurine (or hollow-crested duckbill) comprises member from Asia, Europe (*Arenysaurus ardevoli* and *Blasisaurus canudoi*), North America (*Corythosaurus* spp., *Hypacrosaurus* spp., *Lambeosaurus* spp., *Magnapaulia laticaudus*, and *Velafrons coahuilensis*) (Madzia et al., 2021).

Amurosaurus riabinini Bolotsky & Kurzanov, 1991

Age and occurrence: Late Cretaceous Udurchukan Formation (Maastrichtian) of Blagoveschensk, Russia.

Comment: The holotype (AEHM 1/12) consists of left side of a maxilla and dentary from the same individual. Other skeleton material was described more recently, making it the most abundant on the Russian territory (Godefroit, Bolotsky, et al., 2004).

Olorotitan arharensis Godefroit et al., 2003

Age and occurrence: Late Cretaceous Udurchukan Formation (Maastrichtian) of Kundur, Russia.

Comment: It is based on the holotype (AEHM 2/845), an articulated, but incomplete adult skeleton including the skull and most of the postcranium. The high diversity and mosaic distribution of hadrosaurids in the Amur−Heilongjiang region are the result of a complex palaeogeographical history and imply that many independent hadrosaurid lineages dispersed readily between western America and eastern Asia at the Maastrichtian stage (Pascal Godefroit et al., 2003).

Sahaliyania elunchunorum Godefroit et al., 2008

Age and occurrence: Late Cretaceous Yuliangze Formation (Maastrichtian) of Heilongjiang Province, China.

Comment: The holotype (GMH W453) consists of a partial skull (Pascal Godefroit et al., 2008), which was discovered in a bonebed alongside rarer remains of Wulagasaurus. Its phylogenetic analysis performed as a sister taxon with *A. riabinini* (Xing et al., 2014).

Tsintaosaurini Prieto-Márquez et al., 2013

Definition: The clade containing *Pararhabdodon isonensis* Casanovas-Cladellas, Santafé-Llopis & Isidro-Llorens, 1993 and *Tsintaosaurus spinorhinus* Young, 1958 but not *Aralosaurus tuberiferus* Rozhdestvensky, 1968, *Lambeosaurus lambei* Parks, 1923 and *Parasaurolophus walkeri Parks, 1922* (Madzia et al., 2021).

Comment: Tsintaosaurini comprises *Pararhabdodon isonensis* from Spain and *Tsintaosaurus spinorhinus* (Madzia et al., 2021).

Tsintaosaurus spinorhinus Young, 1958

Age and occurrence: Late Cretaceous Jingangkou Formation of Wangshi Group (?Campanian), China.

Comment: The holotype (IVPP AS V725) consists of a partial skeleton with skull. It was originally reconstructed with a unicorn-like horn on its skull, but was concluded from the paratype specimen that it just the rear part of a larger hollow tubular crest that started from the tip of the snout (Prieto-Márquez & Wagner, 2013).

Marginocephalia Sereno 1986

Definition: The clade containing *Ceratops montanus* Marsh, 1888, *Pachycephalosaurus wyomingensis* (Gilmore, 1931), and *Triceratops horridus* Marsh, 1889 (Madzia et al., 2021).

Comment: Marginocephalia comprises members of the clades Ceratopsia and Pachycephalosauria (Madzia et al., 2021).

Ceratopsia Marsh, 1890

Definition: The clade containing *Ceratops montanus* Marsh, 1888 and *Triceratops horridus* Marsh, 1889 but not *Pachycephalosaurus wyomingensis* (Gilmore, 1931) (Madzia et al., 2021).

Comment: Ceratopsia comprises *Psittacosaurus* spp., and members of the clades Chaoyangsauridae and Neoceratopsia (Madzia et al., 2021). The problematic classification of some basal taxon is still unclear.

Albalophosaurus yamaguchiorum Ohashi & Barrett, 2009

Age and occurrence: Early Cretaceous Kuwajima Formation (?Valanginian—Hauterivian) of Ishikawa Prefecture, Japan.

Comment: The holotype (SBEI 176) consists of an incomplete cranial bone (Ohashi & Barrett, 2009). The first description pointed it was as a basal cerapodan, and then was resolved within basal ceratopsias (Han et al., 2012).

Micropachycephalosaurus hongtuyanensis Dong, 1978

Age and occurrence: Late Cretaceous Wangshi Formation (Campanian) of Shandong Province, China.

Comment: The holotype (IVPP V 5542) consists of partial skull and skeleton, which was originally described as a pachycephalosaurians. After hat, it was recovered as a basal ceratopsian (Butler et al., 2008, 2011).

Psittacosaurus mongoliensis Osborn, 1923 (Type species)

Age and occurrence: Early Cretaceous Formation (Albian – Aptian) of Mongolia.

Comment: *Psittacosaurus* was a basal ceratopsian from the Early Cretaceous Formations (Late Barremian–Aptian) in the family Psittacosauridae by Osborn in 1923, which is not been formally defined yet (Madzia et al., 2021; Osborn, 1923). It was in an early branch of the ceratopsian phylogeny and was probably not directly ancestral to any other ceratopsians. All species of *Psittacosaurus* had four manus digits and lost antorbital fenestra, whereas other ceratopsians retained antorbital fenestra same as most other archosaurs and possess the fifth digits. It is the highest number of valid species named than any non-avian dinosaur genus. Although possibly as many as 19 species have been referred to this genus, about 9-12 are currently considered valid (Napoli et al., 2019) from across China, Mongolia, Siberia, and possibly Thailand and Laos.

- *P. sinensis* Young, 1958
- *P. meileyingensis* Sereno et al., 1988
- *P. xinjiangensis* Sereno & Zhao, 1988
- *P. sattayaraki* Buffetaut & Suteethorn, 1992
- *P. neimongoliensis* Russell & Zhao, 1996
- *P. ordosensis?* Russell & Zhao, 1996
- *P. mazongshanensis?* Xu, 1997
- *P. sibiricus* Leshchinskiy et al., 2000
- *P. lujiatunensis* Zhou et al., 2006 (=*P. major* Sereno et al., 2007; = *P. houi* (=*Hongchanosaurus houi*) You et al., 2003)
- *P. gobiensis* Sereno, Zhao and Lin, 2010
- *P. amitabha* Napoli et al., 2019

Chaoyangsauridae Zhao, Cheng & Xu, 1999

Definition: The clade containing *Chaoyangsaurus youngi* Zhao, Cheng & Xu, 1999 but not *Psittacosaurus mongoliensis* Osborn, 1923 and *Triceratops horridus* Marsh, 1889 (Madzia et al., 2021).

Comment: Chaoyangsauridae comprises 4 members from China (Madzia et al., 2021).

Chaoyangsaurus youngi Zhao, Cheng, & Xu, 1999

Age and occurrence: Late Jurassic Tuchengzi Formation (late Tithonian) of Liaoning Province, China

Comment: The holotype (IGCAGS V371) consists of the lower part and braincase of the skull, the lower jaws, seven neck vertebrae, the right scapula and the right humerus (Zhao et al., 1999).

Hualianceratops wucaiwanensis Han et al., 2015

Age and occurrence: Late Jurassic Shishugou Formation (Oxfordian) of Xinjiang, China

Comment: The holotype (IVPP V18641) including an incomplete skull, lower jaws, sacral vertebrae, the right lower hindlimb, a nearly complete left pes (Han et al., 2015).

Xuanhuaceratops niei Zhao et al., 2006

Age and occurrence: Late Jurassic Houcheng Formation (Tithonian) of Hebei Province, China

Comment: The holotype (IVPP 12722) was probably a fully grown individual, it consists of an incomplete skull and partial skeleton (Zhoa et al., 2006).

Yinlong downsi Xu et al., 2006

Age and occurrence: Late Jurassic Shishugou Formation (Oxfordian) of Xinjiang Province, China

Comment: It is the earliest known ceratopsian. The holotype (IVPP VI4530) is a nearly complete skeleton including with gastroliths preserved in the abdominal cavity (Xu et al., 2006).

Neoceratopsia Sereno, 1986

Definition: The clade containing *Triceratops horridus* Marsh, 1889 but not *Chaoyangsaurus youngi* Zhao, Cheng & Xu, 1999 and *Psittacosaurus mongoliensis* Osborn, 1923 (Madzia et al., 2021).

Comment: Neoceratopsia comprises members of the clade Euceratopsia, and other members more closely related to them from North America (e.g. *Aquilops americanus*), Europe (e.g., *Ajkaceratops kozmai* and *Stenopelix valdensis*), and Asia (Madzia et al., 2021; Osi et al., 2010; Tanoue & Okazaki, 2014).

Archaeoceratops oshimai Dong & Azuma, 1997 (Type species)

Archaeoceratops yuijingziensis You et al., 2010

Age and occurrence: Early Cretaceous Xinminbao Group (=Xinminpu Group) (Aptian) Gansu Province, north central China.

Comment: The holotype of *A. oshimai* (IVPP V 11114) consists of a nearly complete skull, caudal vertebrae, pelvis, and most of a hind foot. The paratype (IVPP V 11115) a somewhat smaller than the holotype, consists of caudal series, a partial hind limb, and a completely preserved foot (You & Dodson, 2003). The second species *A. yujingziensis* was found 100 km southeast from the type species locality (You et al., 2010).

Asiaceratops salsopaludalis Nesov et al., 1989

Age and occurrence: Late Cretaceous Khodzhakul Formation (Early Cenomanian) of Uzbekistan

Comment: The type species, *A. salsopaludalis,* consists of the limited material: teeth, cranial fragments, phalanx. It has often been considered a *nomen dubium* (You & Dodson, 2004). Some cladistic analyses indicated it is a basal position in the Leptoceratopsidae (Ryan et al., 2012).

Auroraceratops rugosus You et al., 2005

Age and occurrence: Early Cretaceous Xinminpu Group (Aptian) of Gansu Province, China

Comment: The type specimen (IG-2004-VD-001) consists of a nearly complete subadult skull. It is the second basal neoceratopsian to be found in the Mazong Shan area, after *Archaeoceratops* (You et al., 2005).

Beg tse Yu et al., 2020

Age and occurrence: Early-Late Cretaceous Ulaanoosh Formation (Albian-Cenomanian) of Ömnögovi Province, Mongolia

Comment: It is the most basal neoceratopsian currently known and shows transitional features between basal ceratopsians and other neoceratopsians. The holotype (IGM 100/3652) is a partial skeleton including an articulated partial skull and fragmentary postcranial elements (Yu et al., 2020).

Graciliceratops mongoliensis Sereno, 2000

Age and occurrence: Late Cretaceous Bayan Shireh Formation (Cenomanian-Santonian) of Mongolia.

Comment: In 1975, the specimen (ZPAL MgD-I/156) was referred to the genus *Microceratops* Bohlin 1953 (=*Microceratus*, which was renamed by Mateus in 2008). However, *Microceratus* was considered a *nomen dubium* by Sereno, he noted that this genus lacked any diagnostic features. The specimen ZPAL MgD-I/156, consists of a very fragmented skull and skeleton, was redescribed by him, creating a new dinosaur: *Graciliceratops mongoliensis* (Sereno, 2000).

Helioceratops brachygnathus Jin et al., 2009

Age and occurrence: Early-Late Cretaceous Quantou Formation (Albian-Cenomanian) of Jilin Province, China

Comment: The holotype (JLUM L0204-Y-3) is a right dentary, the paratype (JLUM L0204-Y-4) is a left maxilla, which were discovered at a close distance from each other (Jin et al., 2009).

Koreaceratops hwaseongensis Lee et al., 2011

Age and occurrence: Early Cretaceous Sihwa Formation (Albian) of South Korea.

Comment: The holotype (KIGAM VP 200801) is a nearly complete tail with tall neural spines; both ischia; partial distal hind limbs; and feet (Lee et al., 2011). The bone histology suggests that it was about eight years old when it died (Baag & Lee, 2022).

Kulceratops kulensis Nesov, 1995

Age and occurrence: Early Cretaceous Khodzhakul Formation (Albian) of Uzbekistan

Comment: The holotype (CCMGE No. 495/12457) consists of a left maxilla. Due to the poorness of the remains, it is considered a *nomen dubium* (You & Dodson, 2004).

Liaoceratops yanzigouensis Xu, 2002

Age and occurrence: Early Cretaceous Yixian Formation (Barremian) of Liaoning Province, China

Comment: The holotype (IVPP V12738) consists of an almost complete skull. It possess jugal horns and a small skull frill, which are distinct features help understand the early evolution of horned dinosaurs and confirm that Asia is the origin of ceratopsians (X. Xing et al., 2002).

Mosaiceratops azumai Zheng, Jin & Xu, 2015

Age and occurrence: Late Cretaceous Xiaguan Formation (lower-middle Turonian—middle Campanian) of Henan Province, China

Comment: The holotype (ZMNH M8856) consists of an incomplete and disarticulated skeleton with skull, several features in the premaxilla and nasal bones are shared with *Psittacosaurus*. This study supports the hypothesis that *Psittacosaurus* is a relatively derived clade, rather than the most basal group of the Ceratopsia (Zheng et al., 2015).

Yamaceratops dorngobiensis Makovicky & Norell, 2006

Age and occurrence: Late Cretaceous Javkhlant Formation (Santonian-Campanian) of Mongolia

Comment: The holotype (IGM 100/1315) consists of a partial skull (Makovicky & Norell, 2006). In 2020, an articulated skeleton (MPC-D 100/553) juvenile specimen was reported. This taxon represents one of the basalmost neoceratopsians with a broad, thin frill and hyper-elongated middle caudal neural spines while still being bipedal (Son et al., 2022).

Euceratopsia Madzia et al., 2021

Definition: The clade containing *Leptoceratops gracilis* Brown, 1914b, *Protoceratops andrewsi* Granger & Gregory, 1923, and *Triceratops horridus* Marsh, 1889 (Madzia et al., 2021).

Comment: Euceratopsia comprises members of the clades Leptoceratopsidae and Coronosauria (Madzia et al., 2021).

Leptoceratopsidae Nopcsa, 1923

Definition: The clade containing *Leptoceratops gracilis* Brown, 1914b but not *Protoceratops andrewsi* Granger & Gregory, 1923 and *Triceratops horridus* Marsh, 1889 (Madzia et al., 2021).

Comment: Leptoceratopsidae comprises members from North America (e.g., *Cerasinops hodgskissi*, *Ferrisaurus sustutensis*, *Gryphoceratops morrisoni*, *Leptoceratops gracilis*, *Montanoceratops cerorhynchus*, *Prenoceratops pieganensis*, *Unescoceratops koppelhusae*) and Asia (Madzia et al., 2021).

?Bainoceratops efremovi Tereschenko & Alifanov, 2003

Age and occurrence: Late Cretaceous Djadokhta Formation (Campanian), Mongolia.

Comment: It is known from a vertebral series (PIN, no. 614-33) which is distinguished from the common of Djadokhta deposits *Protoceratops andrewsi*. It shows close relationships to Leptoceratopsids such as *Udanoceratops tschizhovi* and *Leptoceratops gracilis* (Tereschenko & Alifanov, 2003).

Ischioceratops zhuchengensis He et al., 2015

Age and occurrence: Late Cretaceous Wangshi Group (Coniacian-Campanian) of Shandong Province, China.

Comment: The holotype (ZCDM V0016) is partially articulated postcranial element: the entire sacrum, ossified tendons, the pelvis, the anteriormost fifteen caudal vertebrae, and the right femur, tibia and fibula. It is recovered as a derived leptoceratopsid, and as the sister taxon to *Montanoceratops* from North America (He et al., 2015).

Udanoceratops tschizhovi Kurzanov, 1992

Age and occurrence: Late Cretaceous Djadokhta Formation (Campanian), Mongolia.

Comment: The holotype (PIN 3907/11) comprising a well-preserved skull with a short frill and no horns, and some vertebrae. It is the largest leptoceratopsid known so far (You & Dodson, 2004).

Zhuchengceratops inexpectus Xu et al., 2010

Age and occurrence: Late Cretaceous Xingezhuang Formation (?Campanian-Maastrichtian stages) of Shandong Province, China.

Comment: The holotype (ZCDM V0015) is a partial, articulated skeleton including skull with mandibles, anterior 14 presacral vertebrae and associated ribs, and some additional fragments (Xu et al., 2010).

Coronosauria Sereno, 1986

Definition: The clade containing *Protoceratops andrewsi* Granger & Gregory, 1923 and *Triceratops horridus* Marsh, 1889 (Madzia et al., 2021).

Comment: Coronosauria comprises members of the clades Protoceratopsidae and Ceratopsoidea (Madzia et al., 2021).

Protoceratopsidae Granger and Gregory,1923

Definition: The clade containing *Protoceratops andrewsi* Granger & Gregory, 1923 but not *Ceratops montanus* Marsh, 1888, *Leptoceratops gracilis* Brown, 1914b, and *Triceratops horridus* Marsh, 1889 (Madzia et al., 2021).

Comment: All members of Protoceratopsidae were found in Asia (Madzia et al., 2021).

Bagaceratops rozhdestvenskyi

Age and occurrence: Late Cretaceous Barun Goyot Formation (Campanian - Maastrichtian), Mongolia.

Comment: The holotype (ZPAL MgD-I/126), a medium-sized skull, was described in 1975. So far, the growth stages of this animal are relatively well understood known from many individuals. Four neoceratopsians were considered as synonyms with *B. rozhdestvenskyi* including *Gobiceratops minutus* Alifanov, 2008; *Lamaceratops tereschenkoi* Alifanov, 2003; *Magnirostris dodsoni* You & Dong, 2003; and *Platyceratops tatarinovi* Alifanov, 2003 (Czepiński, 2020).

Breviceratops kozlowskii Kurzanov, 1990

Age and occurrence: Late Cretaceous Barun Goyot Formation (Campanian-Maastrichtian), Mongolia.

Comment: The holotype (ZPAL MgD-I/117) was found in the Khulsan locality, which consists of a partial postcranial skeleton with skull belonging to juvenile stage. Other specimens were referred from the Hermiin Tsav and Khulsan localities (Kurzanov, 1990).

Protoceratops andrewsi Granger and Gregory, 1923 (Type species)

Protoceratops hellenikorhinus Lambert et al., 2001

Age and occurrence: Late Cretaceous Djadokhta Formation (Campanian) of Mongolia, and Bayan Mandahu Formation of Inner Mongolia, China

Comment: The type species, *P. andrewsi*, was described in 1923. In 2001, *P. hellenikorhinus*, was named as a second valid species from the Bayan Mandahu Formation (same age with Djadokhta Formation) in Inner Mongolia, China and. The latter species was notably larger, had a slightly different frill, and had more robust jugal horns (Lambert et al., 2001).

Ceratopsoidea Hay, 1902

Definition: The clade containing *Ceratops montanus* Marsh, 1888 and *Triceratops horridus* Marsh, 1889 but not *Protoceratops andrewsi* Granger & Gregory, 1923 (Madzia et al., 2021).

Comment: Ceratopsoidea comprises *Turanoceratops tardabilis* from Uzbekistan, *Zuniceratops christopheri* from New Mexico, and members of the clade Ceratopsidae (Madzia et al., 2021).

Turanoceratops tardabilis Nesov et al., 1989

Age and occurrence: Late Cretaceous Bissekty Formation (Turonian), Uzbekistan.

Comment: It has a pair of postorbital horns like those seen in the Ceratopsidae, which is representing transitional between earlier ceratopsians and advanced ceratopsids (Sues & Averianov, 2009b).

Ceratopsidae Marsh, 1888

Definition: The clade containing *Centrosaurus apertus* Lambe, 1905, *Ceratops montanus* Marsh, 1888, *Chasmosaurus belli* (Lambe, 1902), and *Triceratops horridus* Marsh, 1889 (Madzia et al., 2021).

Comment: Ceratopsidae comprises members of the clades Centrosaurinae and Chasmosaurinae and other members more closely related to them. All of them found in the Late Cretaceous rocks from North America except *Sinoceratops* from China. A possible ceratopsid tooth has been reported from the Imuta Formation (Campanian-Maastrichtian) of Kyushu, Japan (Manabe et al., 2016).

Sinoceratops zhuchengensis Xu et al., 2010

Age and occurrence: Late Cretaceous Xingezhuang Formation (?Campanian-Maastrichtian stages) of Shandong Province, China.

Comment: It is the first ceratopsid dinosaur discovered in out of North America, and is one of the largest known Centrosaurines (Xing Xu, Wang, Zhao, & Li, 2010).

Pachycephalosauria Maryańska & Osmólska, 1974

Definition: The clade containing *Pachycephalosaurus wyomingensis* (Gilmore, 1931) but not *Ceratops montanus* Marsh, 1888 and *Triceratops horridus* Marsh, 1889 (Madzia et al., 2021).

Comment: Pachycephalosauria lived during the Late Cretaceous, it comprises *Wannanosaurus yanshiensis* and members of the clade Pachycephalosauridae (Madzia et al., 2021). *Ferganocephale adenticulatum* (Averianov et al., 2005) from the Middle Jurassic Balabansai Svita of Kyrgyzstan is considered as dubious taxon (Sullivan, 2006).

Wannanosaurus yansiensis Hou, 1977

Age and occurrence: Late Cretaceous Xiaoyan Formation (Campanian) of Anhui Province, China.

Comment: The holotype (Field No. 70101.2; IVPP V4447) consists of right posterior skull cap, left jugal, left mandible with teeth, left humerus, femora, right tibia, a portion of ilium, and a cervical vertebra. It has been considered primitive member by having a flat skull roof with large openings (Butler & Zhao, 2009; Hou, 1977).

Pachycephalosauridae Sternberg, 1945

Definition: The clade containing *Pachycephalosaurus wyomingensis* (Gilmore, 1931) and *Stegoceras validum* Lambe, 1902, provided that it does not include *Heterodontosaurus tucki* Crompton & Charig, 1962 (Madzia et al., 2021).

Comment: Pachycephalosauridae comprises members of the clade Pachycephalosaurinae, and other members more closely related to them from North America e.g. *Colepiocephale lambei*, *Hanssuesia sternbergi*, *Stegoceras* spp. (Madzia et al., 2021).

Pachycephalosaurinae Sereno, 1997

Definition: The clade containing *Pachycephalosaurus wyomingensis* (Gilmore, 1931) but not *Stegoceras validum* Lambe, 1902 (Madzia et al., 2021).

Comment: Pachycephalosaurinae comprises members of the clade Pachycephalosaurini (from North America e.g., *Alaskacephale gongloffi*, *Dracorex hogwartsia*, *Pachycephalosaurus wyomingensis*, and *Stygimoloch spinifer*), and other members more closely related to them from North America (e.g., *Acrotholus audeti*, *Foraminacephale brevis*, and *Sphaerotholus* spp.) and Asia (Madzia et al., 2021).

Amtocephale gobiensis Watabe, Tsogtbaatar & Sullivan, 2011

Age and occurrence: Late Cretaceous Bayan Shireh Formation (Turonian-Santonian) of Mongolia.

Comment: The holotype (MPC-D 100/1203) is a nearly complete frontoparietal dome of a subadult individual. It may be the oldest known pachycephalosaurid as it comes from rocks that are no younger than late Santonian (Watabe et al., 2011).

Goyocephale lattimorei Perle et al., 1982

Age and occurrence: Late Cretaceous Djadokhta Formation (Campanian), Mongolia.

Comment: The primitive pachycephalosaurine known from the holotype (GI SPS 100/1501) including an flat skull, part of the forelimb and hindlimb, some of the pelvic girdle, and some vertebrae. (Perle et al., 1982).

Homalocephale calathocercos Maryanska & Osmolska, 1974

Age and occurrence: Late Cretaceous Nemegt Formation (Maastrichtian), Mongolia.

Comment: The holotype (MPC-D 100/1201) consists of an incomplete skull and postcranial material. Unlike the rounded and sloping dome head *Prenocephale,* it has flattened head which is a possible adult growth stage also potentially seen in genus *Pachycephalosaurus* from North America (John R. Horner & Goodwin, 2009; Maryanska et al., 1974). Longrich et al. (2010) suggested that *Homalocephale* is the juvenile or sub-adult stage of *Prenocephale* from the same locality.

Prenocephale prenes Maryńska & Osmólska, 1974

Age and occurrence: Late Cretaceous Nemegt Formation (Maastrichtian), Mongolia.

Comment: The holotype (Z. Pal. No. MgD-I /I04) including perfectly preserved skull without mandibles, and some fragmentary postcranial elements (Maryanska et al., 1974). In 2018, the juvenile specimens of *Prenocephale* were reported and provided new ontogenetic data that reinforces the taxonomic distinction between it and *Homalocephale* (Evans et al., 2018).

Sinocephale bexelli Bohlin, 1953

Age and occurrence: Late Cretaceous Ulansuhai Formation. (?Turonian) of Inner Mongolia, China.

Comment: It was originally misunderstood as a species of the theropod genus *Troodon*, and later transferred to the genus *Stegoceras*. The original holotype was lost, with modern research conducted using rediscovered plaster cast of holotype parietal (PMU 23186) (Evans et al., 2021).

Tylocephale gilmorei Maryańska & Osmólska, 1974

Age and occurrence: Late Cretaceous Barun Goyot Formation (Campanian - Maastrichtian), Mongolia.

Comment: The holotype (Z. Pal. MgD-I/105) is poorly preserved skull probably being a subadult. The doming is not pronounced and appears to be transitional between the flat-headed (*Homalocephale*) and more fullydomed (*Prenocephale*) forms (Sullivan, 2006).

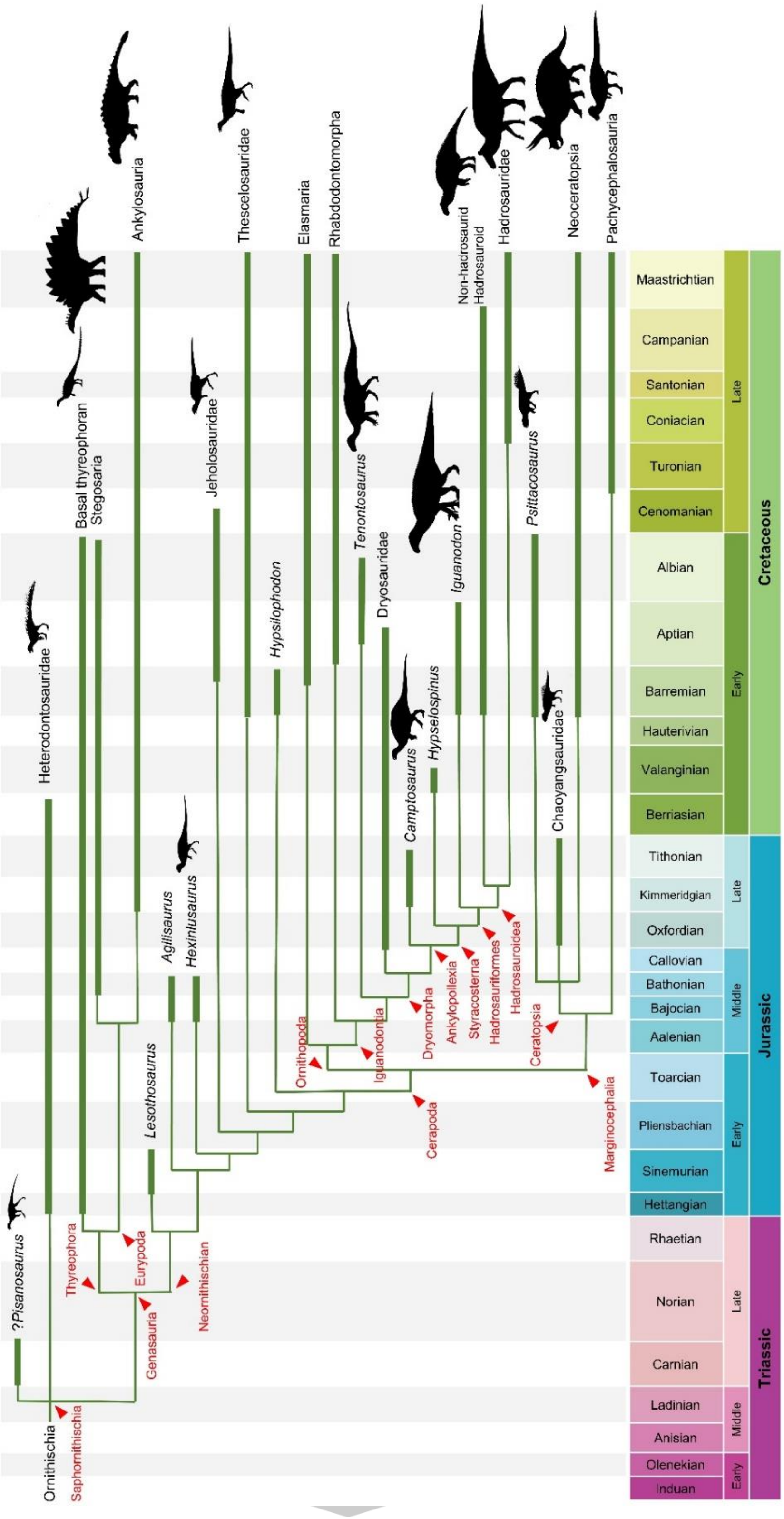

Figure 2 Phylogenetic and temporal relationships among ornithischian dinosaurs (Modified from Baron et al. 2017; Godefroit et al., 2014; Madzia et al., 2018; Madzia et al., 2021; Riguetti et al., 2022; Soto-acuña et al., 2021).

Table 1 Ornithischian dinosaurs in Asia

Period	Epoch	Clade	Country
Cretaceous	Late (Cenomanian-Maastrichtian)	Ankylosauridae	China, Mongolia, Uzbekistan
		Nodosauridae	Japan
		Thescelosauridae	Mongolia, South Korea
		Non-hadrosaurid Iguanodontia	China, Kazakhstan, Mongolia, ?Oman, Uzbekistan
		Hadrosauridae	China, Japan, Kazakhstan, Mongolia, Russia
		Basal Neoceratopsia	China, Mongolia, Uzbekistan
		Leptoceratopsidae	China, Mongolia
		Protoceratopsidae	China, Mongolia
		Ceratopsoidea	China, ?Japan, Uzbekistan
		Pachycephalosauria	China, Mongolia
	Early (Berriasian-Albian)	Stegosauridae	China, Mongolia, ?Russia
		Ankylosauria indet.	China, ?Malaysia
		Ankylosauridae	China, Mongolia
		Nodosauridae	China, ?Japan
		Basal Neornithischia	China
		Jeholosauridae	China
		Thescelosauridae	China
		Non-hadrosaurid Iguanodontia	China, Japan, Laos, ?Malaysia, Mongolia, Thailand
		Basal Marginocephalia	China, Japan
		Psittacosaurus	China, ?Laos, Mongolia, Russia, Thailand
		Basal Neoceratopsia	China, Japan, Mongolia, South Korea, ?Uzbekistan
Jurassic	Late (Oxfordian-Tithonian)	Huayangosauridae	China
		Stegosauridae	China, Thailand
		?Ankylosauria indet.	China
		Basal Neornithischia	China, Thailand
		Chaoyangsauridae	China
	Middle (Aalenian-Callovian)	Heterodontosauridae	China
		Stegosauria indet.	China, Kyrgyzstan, Russia
		Huayangosauridae	China
		?Ankylosauria indet.	China
		Basal Neornithischia	China, Russia
	Early (Hettangian-Toarcian)	Basal Thyreophora	China

2.3 Discussion

China and Mongolia represent the richest assemblage at the generic level of ornithischian dinosaurs in Asia (Table 1). So far, Asian ornithischians have been found from five epochs as follows:

1) The Early Jurassic

A few basal thyreophorans were reports in Yunnan Province of China. During this epoch, the basal thyreophorans also discovered from Africa (e.g. *Laquintasaura*), Europe (e.g. *Scelidosaurus* and *Emausaurus*), and North America (e.g. *Scutellosaurus*).

2) The Middle Jurassic

At least six basal neornithischians were reported from China and Russia, they were the only members of this clade that were discovered during this epoch around the world. One heterodontosaurid, one ankylosaurian (its rock formation is between Middle-Late Jurassic), and at least two stegosaurian taxa appeared in China. Interestingly, filamentous integumentary structures were found only from Asian ornithischians so far (*Tianyulong* and *Kulindadromeus* and appeared again in *Psittacosaurus* in the Early Cretaceous*)*. It is evidence for protofeathers being basal to ornithischians, rather than just to theropods, as previously suspected (Godefroit et al., 2014).

3) The Late Jurassic

Asian ornithischians were still dominated by stegosaurs same as in Africa, Europe, and US. Some basal neornithischians reported from China and Thailand. Even no evidence of iguanodontian ornithopods in Asia so far, but there were the earliest known marginocephalians, Chaoyangsauridae, in China. The presence of Jurassic ceratopsians only in Asia indicates an Asian origin for the group.

4) The Early Cretaceous

The number of stegosaurids had decreased, two taxa from China and Mongolia, and were eventually lost. In contrast to the apparent increased of ankylosaurians in China, Japan, and Mongolia. Two jeholosaurids, apparently endemic group of East Asia, and one thescelosaurid from China. Ornithopods was getting much bigger. and became greatly dominant herbivores in the ecosystem. Several non-hadrosaurid iguanodontians have been reported from China, Japan, Mongolia, Thailand, Laos, and possibly Malaysia. Several species of *Psittacosarus* and basal neoceratopsians found in China, Japan, Mongolia, Russia, South Korea, Thailand, Laos, and possibly Uzbekistan.

5) The Late Cretaceous

The Beringian land bridge between present-day Siberia and Alaska, which opened during the Aptian-Albian, served route for terrestrial vertebrates to migrate 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 ankylosaurid, hadrosaurid, neoceratopsian, pachycephalosaurian, tyrannosaurid, and troodontid) supposedly originated in Asia (Bell, 2011). Asian ornithischian dinosaurs much diverged in the Late Cretaceous. Non-hadrosaurid hadrosauroids were replaced with hadrosaurids, the medium to large-sized duck-billed dinosaurs. Hadrosaurids became the most dominant, and roamed China, Japan, Kazakhstan, Mongolia, and Russia. Two thescelosaurids from Mongolia and South Korea. Several pachycephalosaurians, exclusively lived in Laurasia, were found in China and Mongolia. Several ankylosaurians reported from China, Japan, Mongolia, and Uzbekistan. Several neoceratopsians (e.g., leptoceratopsids and protoceratopsids) were reported from China, Mongolia, and Uzbekistan, but there is only one taxon of ceratopsids from China contrary to the prevalent in North America.

Chapter 3

Ornithischian dinosaurs in Southeast Asia: a review with palaeobiogeographic implications

Some part of this chapter was presented in Manitkoon, S., and Deesri, U. 2019. Evolutionary Stages of Ornithischian Dinosaurs in the Khorat Group of Thailand. The 1st Asian Palaeontological Congress. Beijing, China. It was published in Manitkoon, S., Deesri, U., Warapeang, P., Nonsrirach, T., and Chanthasit, P. (2022). Ornithischian dinosaurs in Southeast Asia: a review with palaeobiogeographic implications. Fossil Record, (in progress)

3.1 Introduction

Southeast Asia consists of a mosaic of microcontinents. In the late Palaeozoic and Mesozoic, the northern margin of eastern Gondwana, which, after drifting northward, collided with each other and with South China (Metcalfe, 1998). Numerous of vertebrate fossils have been discovered from the Khorat Plateau of northeastern Thailand, as well as southern Laos, from the non-marine Mesozoic formations of the Indochina block (Buffetaut, 1991; Buffetaut & Suteethorn, 1998). Whereas, the record of non-marine Mesozoic vertebrates from other SE Asian terranes is much less well known (Buffetaut et al., 2005). Southeast Asian dinosaur fossils have been discovered from Thailand, Laos, Myanmar, Malaysia, and Cambodia (Allain et al., 1999; Buffetaut et al., 1995; Buffetaut et al., 2003; Buffetaut et al., 2021; Sone et al., 2015; Xing et al., 2016). They are dominated by sauropods and theropods by amount of bones and diversity level, 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 ornithischian in Southeast Asia have been reported limited in the Late Jurassic and the late Early Cretaceous (Aptian-Albian) formations (Table 2).

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

Most of ornithischians in Southeast Asia known from the Khorat Group of Thailand. After the first discovered of a dinosaur bone in 1976 from Khon Kaen Province, northeastern Thailand, the collaboration of a Thai-French team began excavation in 1981, and more dinosaur remains were found (Grote et al., 2009). Ornithischian bones were presented 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 together with basal neornithischians were excavated (Buffetaut et al., 2001; Buffetaut et al., 2014; Manitkoon et al., 2019). Contrary with the late Early Cretaceous Khok Kruat Foramation (Aptian-Albian), highly abundant neornithischian dinosaurs comprises 3 taxa of iguanodontians *Siamodon nimngami* (Buffetaut & Suteethorn, 2011), *Ratchasimasaurus suranareae* (Shibata et al., 2011), and *Sirindhorna khoratensis* (Shibata et al., 2015), plus one taxon of basal ceratopsian *Psittacosaurus sattayaraki* (Buffetaut & Suteethorn, 1992). The Khok Kruat Formation of Thailand is considered the lateral equivalent to the Grès Supérieurs Formation of southern Laos.

The fauna assemblage from the Xinlong Formation of southern China shows many similarities to the Khorat Group of Thailand. It seems to be especially close to the Khok Kruat Formation, as shown by hybodont sharks, turtles and dinosaurs, and was proposed as Aptian in age (Cuny et al., 2017; Mo et al., 2016). Ornithischians have been found including iguanodontian (*Napaisaurus guangxiensis* (Ji & Zhang, 2022)) and a possibly basal ceratopsian (Mo et al., 2016).

In Peninsular Malaysia, the Jurassic-Cretaceous rocks are mostly of continental deposits, but the record of dinosaurs remains rather scanty (Rahman, 2019). The first discovery was led by the University of Malaya's paleontological 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 fish assemblage has strong affinities with Early Cretaceous Sao Khua Formation of Thailand (Teng et al., 2019). Another report was carried out by the Mineral and Geoscience Department Malaysia and the Malaysian Geological Heritage Group in the interior district of Terengganu in 2014, the teeth of iguanodontians has been referred (Akhir et al., 2015).

The principal purpose of this study is to illustrate the diversity of ornithischian assemblages in Southeast Asia and Southern China (Fig. 3), focusing on Thailand where most of them have been reported, and discuss their evolution and paleobiogeography.

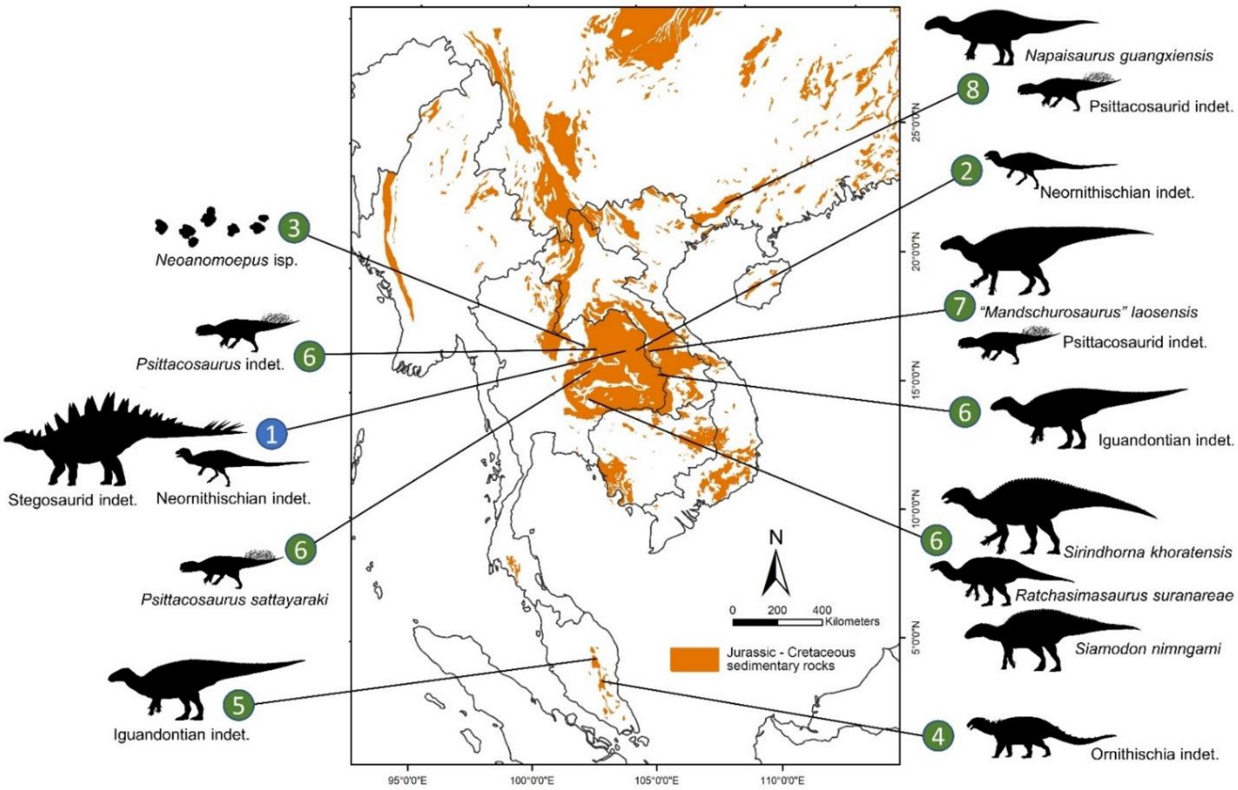

Figure 3 Southeast Asia map showing the distribution of Jurassic–Cretaceous nonmarine sediments in Southeast Asia (map is modified from Lee et al., 2014; Thanh & Khuc, 2006; Uchida et al., 2017; Yan et al., 2019)

.

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

Table 2 Ornithischian taxa in Southeast Asia plus southern China

Formation	**Age**	**Taxa**	**Country**	**References**
Xinlong	late Early Cretaceous (Aptian)	*Napaisaurus guangxiensis* Iguanodontian indet. ?Psittacosaurid	China	Ji & Zhang, 2022 Mo et al., 2016 Mo et al., 2015, Cuny et al., 2017
Grès Supérieurs	late Early Cretaceous (Aptian-Albian)	"*Mandschurosaurus*" *laosensis* Iguanodontian indet. ?Psittacosaurid	Laos	Hoffet, 1944 Hoffet, 1944, Buffetaut, 1991 Allain et al., 1999
Khok Kruat	late Early Cretaceous (Aptian-Albian)	*Siamodon nimngami* *Ratchasimasaurus suranareae* *Sirindhorna khoratensis* Iguanodontian indet. *Psittacosaurus sattayaraki* *Psittacosaurus* sp.	Thailand	Buffetaut & Suteethorn, 2011 Shibata et al., 2011 Shibata et al., 2015 Manitkoon et al., 2022 Buffetaut & Suteethorn, 1992 Buffetaut et al., 2007
Gagau Group	?Early Cretaceous	Iguanodontian indet.	Malaysia	Akhir et al., 2015
?Tembeling Group	Early Cretaceous (?late Valanginian -early Hauterivian))	Ornithischian indet.,	Malaysia	Sone et al., 2015
Phra Wihan	?Beriasian-Valanginian	*Neoanomoepus* isp. (footprint)	Thailand	Lockley et al., 2009
Upper Phu Kradung	Early Cretaceous (?Beriasian)	Basal neornithischian indet.	Thailand	Buffetaut et al., 2001, Buffetaut et al., 2014
Lower Phu Kradung	Late Jurassic	Stegosaurid indet., Basal neornithischian new taxon	Thailand	Buffetaut et al., 2001, Chapter 4

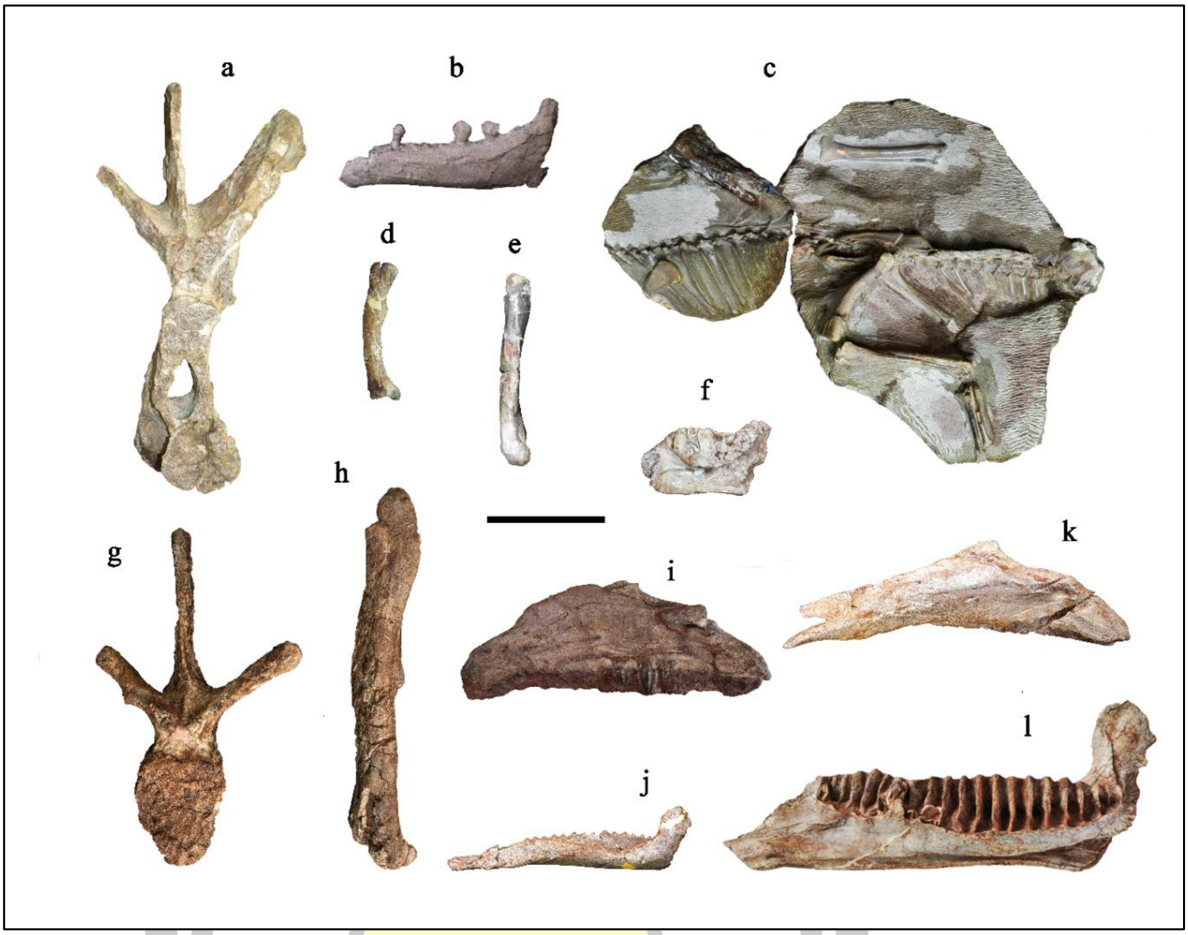

Figure 4 Exceptional specimen of ornithischian dinosaurs from Thailand.

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* left maxilla (k; NRRU-A2048), *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; a, c-e, and g-l scale bar equals 10 cm; b and f scale bar equals 5 cm.

3.2 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 separated by Nan-Uttaradit suture (Racey et al., 1996). The Mesozoic Khorat Group is a Thai stratigraphic group of non-marine rocks from Late Jurassic to Early Cretaceous in northeastern Thailand consists of 5 formations: Phu Kradung, Phra Wihan, Sao Khua, Phu Phan, and Khok Kruat (Racey, 2009). Three of the formations (Phu Kradung, Sao Khua, and Khok Kruat) have yielded rich vertebrate remains including selachians, actinopterygians, sarcopterygians, amphibians, turtles, crocodyliformes, pterosaurs, non-avian dinosaurs, and birds (Buffetaut et al., 2003b; Buffetaut et al., 2005; Buffetaut and Suteethorn, 1998; Buffetaut et al., 2006).

3.2.1 Phu Kradung Formation

The formation is considered as forming the base the Khorat Group which outcrops mostly on the Khorat Plateau in Northeastern, Thailand (Racey, 2009). The age of the Phu Kradung Formation is still uncertain, with contradictory signals coming from vertebrate palaeontology and palynology, it is conventionally considered as Late Jurassic or Early Cretaceous in age (Racey et al., 1996). The presence of *Dicheiropollis etruscus* in the Phu Kradung Formation seem to confirm an Early Cretaceous age, although some of the lower part of the Phu Kradung Formation could still be Late Jurassic (?Tithonian) (Racey & 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 assemblage similar to those found in the Middle-Late Jurassic of China (Buffetaut et al., 2003; Chanthasit et al., 2019; Cuny et al., 2014).

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. 5).

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

Previous study: It is the first scientifically evidence of thyreophoran dinosaur in Southeast Asia. The typical specimen is identified as belonging to the family Stegosauridae, which is more advanced than the primitive taxa such as huayangosaurid *Huayangosaurus* from the Middle Jurassic of China (Buffetaut et al., 2001). SM2011-1-001 has a much higher neural arch and more upright transverse processes, indicates that it should be referred to the Stegosauridae (Buffetaut et al., 2001).

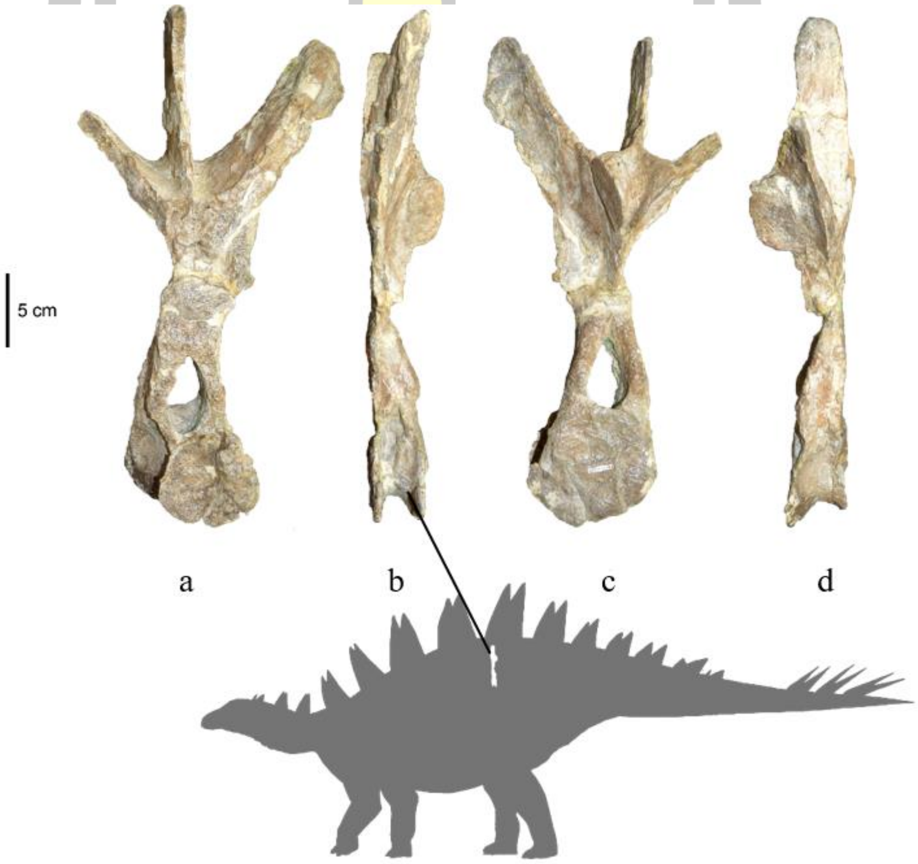

Figure 5 A posterior dorsal vertebra of a stegosaurid (SM2011-1-001) in anterior (a), left lateral (b) posterior (c), and (d) right lateral views.

Basal neornithischian indet. (so-called the ‘Phu Noi neornithischian’) (Buffetaut et al., 2014; Manitkoon et al., 2019)

Material: PRC 149 (Fig. 4b; 6a-b) (renumbered from PN 13-09 in Buffetaut et al., 2014), a lower jaw; PRC 150, an articulated postcranial skeleton (Fig. 4c) (Manitkoon et al., 2019).

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 fan-shaped teeth with a strongly ridged crown and asymmetry enamel distribution suggested 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 preacetabular process of the ilium is narrow, long with a perfectly rounded termination, and slightly ventrally curved. The postacetabular 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: The systematics of basal neornithischians is still problematic (Barrett et al., 2005; Butler et al., 2008). Many taxa, were once considered as early member of ornithopods, have been changed into the basal neornitischians (Madzia et al., 2019, 2021). With similarity to those Chinese taxa, suggesting that the PRC 149 to the basal position of neornithischian outside clade Ornithopoda and might belong to same animal as PRC 150 in older stage. Numerous specimens of limb bones with various sizes of basal neornithischians were also found from the Phu Noi site, indicates that these dinosaurs were abundant and common in this area, it is the oldest neornithischian known so far from southeast Asia. Even postcranial characters of PRC 150 show resemblance to *Agilisaurus louderbacki* and *Hexinlusaurus multidens* from the lower Shaximiao Formation, the dentary teeth of PRC 149 and other isolated teeth from Phu Noi are different by having asymmetrically distributed enamel on the teeth. *Agilisaurus louderbacki* and *Hexinlusaurus multidens* exhibit symmetrically distributed enamel (Barrett et al., 2005; Peng, 1992), but teeth from Phu Noi possesses the advance condition of asymmetrically distributed enamel same as

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; Carpenter & Galton, 2018; Galton, 2009). Preliminary comparisons seem to indicate that it is new taxa (Buffetaut et al., 2014; Manitkoon et al., 2019), these will be done in our next study.

Basal neornithischian indet. (so-called the 'Khok Sanam neornithischian')

Material: WNM-Ks-001 (Fig. 6c-e), an isolated tooth.

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

Comments: It is possibly closely related with the Phu Noi neornithischians. A dentary tooth shows the fan-shaped crown, and looks like characters as the posterior teeth present in the dentary teeth of PRC 149 (Buffetaut et al., 2014) and *Nanosaurus agilis* (Carpenter & Galton, 2018). Even the enamelled surface is a bit thin, a well-developed ornamentation of ridges is still noticeable on the lingual side, the enamel is asymmetrically distributed. The margin of the laterally compressed crowns bears distinct denticles. The labial side of the tooth bear no enamel and show wear facets. The ornamented lingual side do 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 is preserved and curved to the labial side.

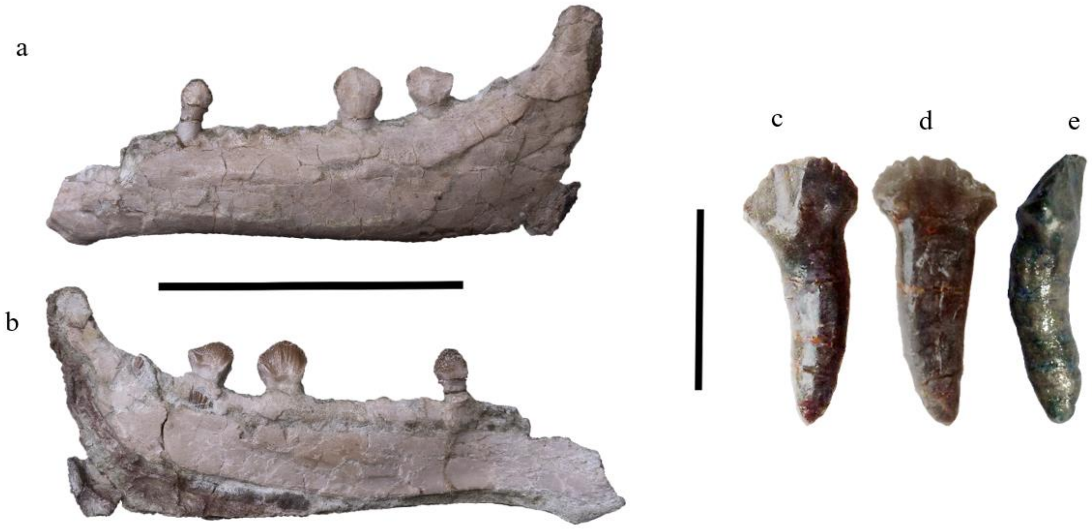

Figure 6 Basal neornithischian specimens from the lower Phu Kradung Formation. (left) Left dentary (PRC 149) from Phu Noi locality, in lateral (a) and medial (b) views; (right) isolated tooth (WNM-Ks-001) from Khok Sanam locality, in lingual (c), labial (d) and mesial/distal (e) views. a-b scale bar equals 5 cm; c-e scale bar equals 1 cm.

Basal neornithischian indet. (so-called the 'Dan Luang neornithischian')

Material: SM2016-1-081 (Fig. 7), a left femur (Buffetaut et al., 2003; 2014; 2006).

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

Previous study: The first specimen that belong to basal neornithischian in Thailand. it was excavated in 1996 but has not been described yet (Buffetaut et al., 2001, 2003; Buffetaut et al., 2002, 2006; Buffetaut & Suteethorn, 1998a). Buffetaut and Suteethorn roughly considered that it is similar to *Yandusaurus* (=*Hexinlusaurus multidens*) from China (Buffetaut & Suteethorn, 1998a).

Description: The left femur is robust and almost complete except distal end is eroded. It is 12.08 cm in length, and has a transverse midshaft diameter 1.57 mm. The shaft of the femur is bowed in lateral view resembles that of *Hexinlusaurus multidens* (He & Cai, 1984b), *Agilisaurus louderbacki* (Peng, 1992), *Hypsilophodon foxii* (Galton, 2009) and the Phu Noi neornithischian (Manitkoon et al., 2019). The end of the femoral head is unpreserved. The anterior end of the greater trochanter is slightly convex, while 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 portion of fourth trochanter is lost, but likely to form a pendant shaped that located on the medial margin of the proximal half of the femur as the same position with PRC 150 as well as other basal neornithischians. An oval shallow occurs between the base of the fourth trochanter and the femoral shaft for muscle insertion. The distal portion of the femoral shaft shows mediolaterally expanding towards the distal condyles although it was damaged, posteriorly the distal condyles are separated by a caudal intercondylar groove.

Comments: Dan Luang locality has yielded mamenchisaurid teeth (Suteethorn et al., 2013), possibly mamenchisaurid rib, theropod teeth, crocodyliforms osteoderms, and large teeth resembling pholidosaurid *Chalawan thailandicus* (Buffetaut & Ingavat, 1980; Martin et al., 2014), shell fragments of basal trionychoid turtle *Basilochelys macrobios* (Tong et al., 2009), petrified wood, and amber. Fossil assemblage indicates early Cretaceous in age, which is supposed to be the upper part of the Phu Kradung Formation based on the appearance of large pholidosaurid and large trionychoid turtle. Contrary to semi-aquatic fauna from the Lower Phu Kradung locality such as Phu Noi, which is outstanding by the small xinjiangchelyid turtles *Phunoichelys thirakhupti* and *Kalasinemys prasarttongosothi* (Tong et al., 2015; Tong et al., 2019), and teleosaurid *Indosinosuchus potamosiamensis* (Martin et al., 2019). SM2016-1-081 is possibly in the basal position of neornithischian same as the older Phu Noi taxon, but more specimen is needed to increase our understanding of basal neornithischians from the Upper Phu Kradung Formation.

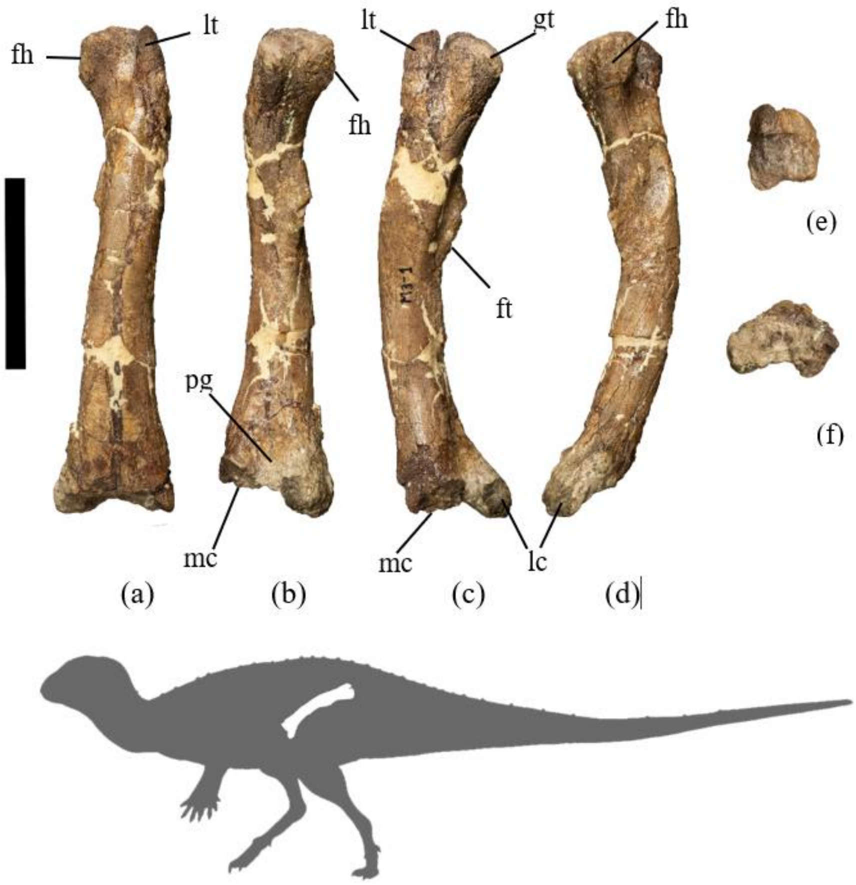

Figure 7 Left femur of the 'Dan Luang neornithischian' (SM2016-1-081) in anterior (a), posterior (b), lateral (c) medial (d) proximal (e) and distal (f) views.

Abbreviation: 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.

3.2.2 Phra Wihan Formation

The Phra Wihan Formation underlies the Sao Khua Formation and is underlain by the Phu Kradung Formation. Dating as Lower Cretaceous (Berriasian to Early Barremian) age from a rich palynological assemblage (Racey, 2009; Racey & Goodall, 2009). Lithology and stratigraphy indicate a depositonal environment of braided streams and occasional meandering rivers in humid climate (Racey, 2009). The Formation has not yielded skeletal material, but the biodiversity of dinosaurs can be approached by the study of the footprints. The site 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 & Suteethorn, 1993), the palaeoenvironment is estimated brackish water region or fluvial shallow (Kozu, 2017). At least one trackway was made by a small-sized theropod. Others have belonged to small quadrupedal ornithischian, which is 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). It is classified as an ichnogenus *Neoanomoepus* isp. (Fig. 8) on the basis of type material from Canada, suggests that these hitherto unknown earliest Cretaceous ichnofaunas may represent a radiation of small basal ornithopods (Kozu, 2017; Le Loeuff et al., 2002; Lockley et al., 2009).

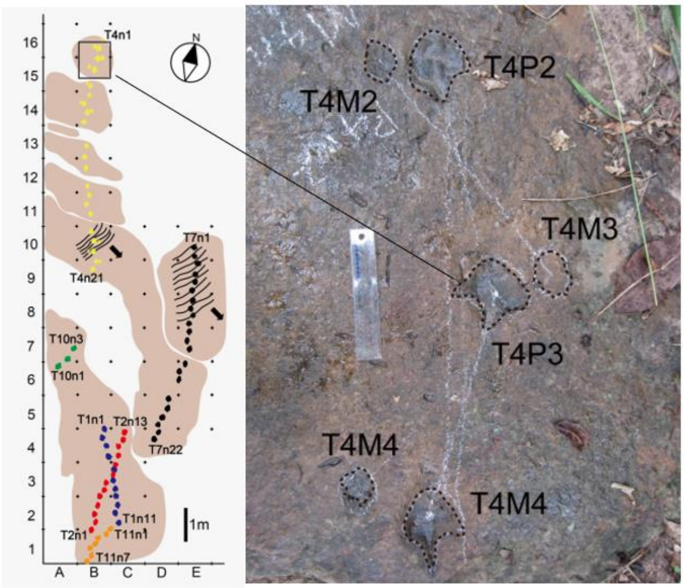

Figure 8 (left) Meshmap of the outcrop at the site Hin Lat Pa Chad. Arrows indicate paleocurrent directions estimated by ripple-marks the trackway. (right) trackway of *Neoanomoepus* isp. (Kozu, 2017)

3.2.3 Khok Kruat Formation

The formation comprises with reddish-brown, reddish purple sandstone, siltstone and mudstone, with some conglomerate beds (Department of Mineral Resources, 2014). The Khok Kruat Formation is conformably overlying the Phu Phan Formation, it widely spread in the outer parts of the Phu Phan Range. The Khok Kruat Formation of Thailand is equivalent to upper part of the Grès Supérieurs Formation of southern Laos (Weishampel et al., 2004), they are considered as Aptian-Albian in age on the basis of their vertebrate fauna and palynology (Buffetaut et al., 2005a, 2009; Cappetta et al., 1990; Racey & Goodall, 2009). On the contrary with other formation in Khorat Group, ornithischian dinosaur remains are fairly abundant at various localities in northeastern of Thailand.

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

Ratchasimasaurus suranareae Shibata et al., 2011

Material: holotype NRRU-A2064, a left dentary (Fig. 4j).

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

Previous study: *R. suranareae* is member of hadrosauroids (Madzia et al., 2020; Shibata et al., 2015), 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, the ratio of length (from the rostral to the caudal margin)/height (at the middle of the dentary) is 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, it is relatively small when compared to other skull material of iguanodontians in Thailand. The result from CT scan cannot conclude that it is an immature or mature individual (Shibata et al., 2011). Comparison with a nearly complete right dentary of *Sirindhorna khoratensis* (NRRU3001-167) from the nearby area, it is about 38 cm in length with 20 alveoli (Shibata et al., 2015). In iguanodontians, the tooth number increases during growth and single teeth are also becoming relatively wider such as *Dysalotosaurus lettowvorbecki* and *Zalmoxes robustus,* there is a slight ontogenetic increase of dentary tooth positions from 10 to 13 and 8 to 10 respectively (Hübner & Rauhut, 2010; Weishampel et al., 2003). In hadrosauroids, many ontogenetic changes in region of the skull and mandible, the dentary experienced an elongation of the mandibular ramus during growth (Bell, 2011; Campione & Evans, 2011; Prieto-Marquez & 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 and Suteethorn, 2011

Material: holotype PRC-4 (Fig. 4i), a left maxilla 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 & Suteethorn, 2011).

Previous study: *S. nimngami* showing a combination features of iguanodontian following: maxilla shaped like an isosceles triangle, with the dorsal process located at about mid-length of the bone; 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 & Suteethorn, 2011). There may have been as many as 25 tooth positions in the maxilla (Buffetaut & Suteethorn, 2011). It differs from hadrosaurids in the area for the jugal, with 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 & Suteethorn, 2011). *S. nimngami* and *R. suranareae* was mentioned as member 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-KS-001 (Fig. 5.4D), an isolated dentary tooth from the same locality is therefore 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 midline makes the crown asymmetric. The secondary ridge is positioned mesial to and is less prominent. As opposed to *S. khoratensis* dentary teeth that the crowns appear to be apicobasal erect. *S. nimngami* dentary tooth appear to be curved apicobasal. Shibata and his team noted that no other accessory ridges on the crown of *S. khoratensis* (Shibata et al., 2015), 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 considered *S. nimngami* as *nomen dubium* taxon based on its material does not show any autapomorphy characters, and possibly referable to other taxa from the same area (Norman, 2014). However, Shibata and his team showed the possibility of the existence of three iguanodontians in the Khok Kruat Formation (Shibata et al., 2015). 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 to be different animals, while comparisons to *R. suranareae* are not feasible as long as the overlapping material have not been discovered.

Shibata and his team (2015) were latter insisted the type locality of *S. nimngami* by Buffetaut and Suteethorn (2011) as Ban Nong Rangka, located in the adjacent subdistrict of Ban Saphan Hin locality but the same age. Here, I would like to confirm the information by asking from, the holotype collector, Mr.Witaya Nimngam that the site locality of *S. nimngami* is at Ban Saphan Hin. Far from the point where *S. khoratensis* is found and definitely not from Ban Nong Rangka (Fig. 9).

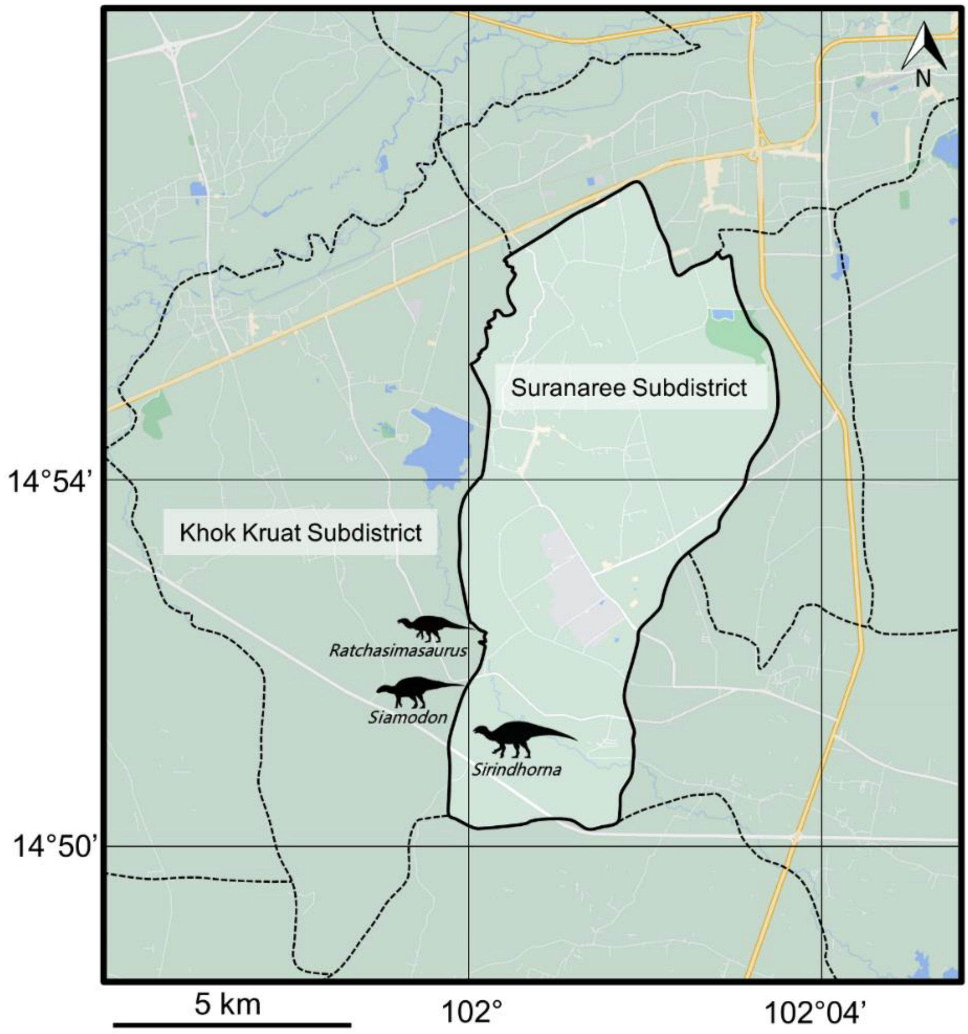

Figure 9 Locality map of *Siamodon*, *Ratchasimasuarus* and *Sirindhorna.*

Sirindhorna khoratensis Shibata et al., 2015

Material: holotype NRRU3001-166, an articulated braincase including referred skull element following: 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), a right maxilla (NRRU-A2047) (Fig. 4k), 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. 4l), 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 where the *S. nimngami* was found), Khok Kruat Subdistrict, Nakhon Ratchasima Province; Late Early Cretaceous Khok Kruat Formation (Aptian)

Previous study: It is known from several duplications of braincases and dentaries that indicate an inclusion of at least four individuals. The holotype material, a braincase, shows an autapomorphy: sagittal crest extending along entire dorsal surface of the parietal and reaching the frontoparietal suture (Shibata et al., 2015). Referred material display unique combination of characters such as antorbital fossa of the maxilla not visible, slightly rostrally deepening dentary ramus, and dentary teeth with primary and secondary ridges but no accessory ridges (Shibata et al., 2015). It was analyzed in the basal position of non-hadrosaurid hadrosauroids (Shibata et al., 2015). However, later analysis recovered it near the base of Hadrosauromorpha, more advance than *R. suranareae* (Madzia et al. 2020). *S. khoratensis* maxilla (NRRU-A2048) has low-angled triangular shaped and the caudally positioned lacrimal process, 24 alveoli are rostrocaudally arranged and slightly curved caudolaterally. It is distinctive to the isosceles triangular shaped with the dorsally process positioned at the middle of the maxilla of *S. nimngami* (Shibata et al., 2015). *R. suranareae* has a low and elongate dentary ramus and the robust coronoid process different from a robust and straight dentary ramus with the subvertical coronoid process of *S. khoratensis* (Shibata et al., 2015).

Comment: It is claimed as the best-preserved iguanodontian ornithopod in Southeast Asia (Shibata et al., 2015). Not only published cranial material, Ban Saphan Hin locality also yielded the postcranial skeleton that assumed to belong to *S. khoratensis* because discovered five braincase show no features to imply the differences taxa (Shibata et al., 2018). The result of CT-scanning revealed brain morphology of *S. khoratensis*, it has general endocast features resemble those of non-hadrosaurid hadrosauroids (Shibata et al., 2018).

Iguanodontian indet. (so-called the ‘Khok Pha Suam iguanodontian’)

Material: Isolated teeth and postcranial material including cervical vertebra (PRC 155); dorsal vertebra (SM2021-1-113); 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); right femur (SM2021-1-118); tibia (SM2021-1-119); fibula (PRC 158); and phalanx (SM2021-1-120) (see all figures in chapter 6).

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 in Khok Pha Suam, but too fragmentary (Manitkoon et al., 2022). Some isolated postcranial bones belonging to iguanodontians were discovered, including vertebrae and limb bones from different individuals based on varies greatly size of the left and right femur (Manitkoon et al., 2022; Samathi & Suteethorn, 2022). Samathi and Suteethorn assumed most of the Khok Pha Suam iguanodontian material to be a single taxon, they analyzed its phylogenetic position as a non-hadrosauriform styracosternan (Samathi & Suteethorn, 2022).

Comment: The teeth of Thai iguanodontians show the robust primary ridge displaced distally relative to the crown apicobasal axis is a derived feature of iguanodontians among ornithopods (Norman, 2004, 2014). They also possess the mammillate shape of the 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. nimngami* (Fig. 10C-D), *S. khoratensis* (Fig. 10A-B), and Khok Pha Suam taxon (Fig. 10E-F), 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). They have the different characteristics of maxillary teeth, briefly as follows: *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 & Suteethorn, 2011); *S. khoratensis*: lanceolate-shaped crown, primary ridge separates the labial surface unevenly, distal portion of the labial surface bears weak subsidiary ridges and slightly broader than the mesial portion (Shibata et al., 2015); 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 of the accessory ridges on the crowns of maxillary teeth, and the shifting of the primary ridge on the maxillary tooth crown to the midline (You et al., 2003).

The dentary teeth of Thai forms, including *S. khoratensis* (Fig. 10G-H), *S. nimngami* (Fig. 10I-J), and Khok Pha Suam taxon (Fig. 10K-L) (not preserved in *R. suranareae*) possess prominent primary ridge. The crowns allowed the teeth to interlock, resulting in the more elaborate structure of the dental battery. The different characteristics briefly as follow: *S. khoratensis*: wide with leaf-shaped crown, the secondary ridge is positioned mesial to and is less prominent than the primary ridge, no other accessory ridge (Shibata et al., 2015); *S. nimngami*: leaf-shaped crown, the secondary ridge is positioned mesial to and is less prominent than the primary ridge, at least one faint accessory ridge on the mesial side, crown appear to be curved apicobasal; 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 on the mesial and the distal portion. The dentary tooth of *S. nimngami* and Khok Pha Suam iguanodontian show accessory ridges, which is absence in *S. khoratensis*. This character appeared in basal hadrosauroids (Prieto-Márquez et al., 2016). In this respect, *S. khoratensis* is probably more advance than *S. nimngami* and 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 will provide geographic distribution about 400 km to the far east (Fig. 3). However, Khok Pha Suam locality is closer to Savannakhet of than Nakhon Ratchasima. The comparison between them had to be very careful, and overlapping elements are required. It would be incredible if Khok Pha Suam iguanodont is a new taxon, this means that there is a diversity of species up to five to six in the region. and is necessary to compare the postcranial material between Khok Pha Suam taxa and *S. khoratensis*.

The high diversity of iguanodontians is found simultaneously in Southeast Asia. A careful consideration is needed, and more materials are awaited. As the case of *Edmontosaurus*, the duck-billed edmontosaurine was widely distribution in the Late Cretaceous (Campanian-Maastrichtian) ranging from Colorado to Alaska of North America, two species are validated in the only single genus, and show the result of ontogenetic change (Campione & Evans, 2011; Takasaki et al., 2020).

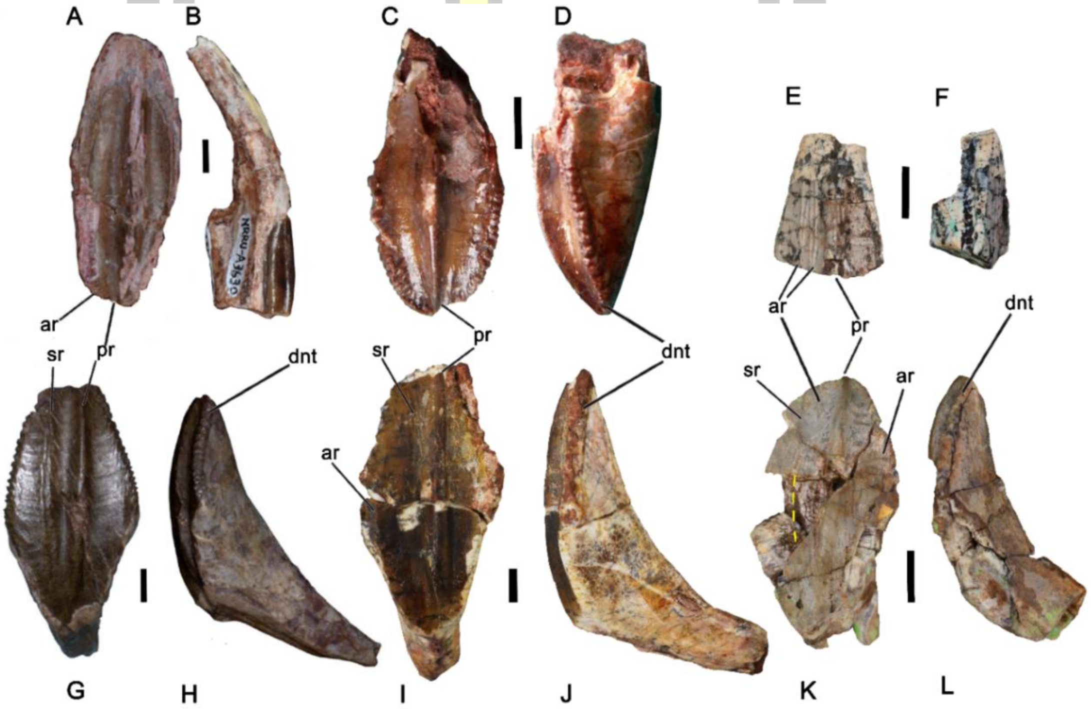

Figure 10 Isolated Thai iguanodontian teeth.

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

Psittacosaurus sattayaraki Buffetaut and Suteethorn, 1992

Material: holotype SM2016-1-163 (renumbered from TF 2449a by Buffetaut & Suteethorn, 1992) right dentary (Fig. 4f), SM2016-1-164 (renumbered from TF 2449b by Buffetaut & Suteethorn, 1992) maxilla fragment

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

Previous study: Apart from those ornithopods that mentioned above, another one 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), it is the southernmost known occurrences of this genus (Buffetaut & Suteethorn, 1992). However, an incomplete material makes the existence of the taxa remains questionable (Sereno, 2000; You & Dodson, 2004). Buffetaut and Suteethorn attributed the validity to *P. sattayaraki*, which is supported by typical tooth and dentary morphology such as clearly show a bulbous primary ridge typical for *Psittacosaurs*, a symmetrical crown and lack of a basal cingulid (Buffetaut et al., 2007). The taxon was 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 the material of *Psittacosaurus* seems to be scarce in Southeast Asia. In Thailand, only fragmentary materials were discovered from Chaiyaphum and Khon Kaen Provinces, but not found in any other Khok Kruat localities (Manitkoon et al., 2022).

***Psittacosaurus* indet.** Buffetaut et al., 2007

Material: SM2016-1-080 (Fig. 4e), a right femur; unnumbered material including isolated tooth, a dentary fragment, a dorsal vertebra, and a fragmentary sacrum.

Locality and age: only SM2016-1-080 was collect from 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 district, Khon

Kaen Province; all specimens belong to Late Early Cretaceous Khok Kruat Formation (Aptian-Albian)

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

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

3.3 Laos

3.3.1 Grès Supérieurs Formation (=Khok Kruat Formation)

All the dinosaur-bearing beds in Savannakhet basin belong to the top of the Grès Supérieurs Formation (Cavin et al., 2018; Racey, 2009). 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., 2018). The Grès Supérieurs Formation is considered the lateral equivalent to the Khok Kruat Formation of neighbouring Thailand. Both are considered as Aptian-Albian in age based on their vertebrate assemblages, bivalves, and palynomorphs (Allain et al., 2012; Buffetaut et al., 2005; Cappetta et al., 1990; Racey, 2009). Not only skeletal materials, Laos also yielded possibly 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 (Fig. 11).

Locality and age: Muong Phalane, Savannakhet Province of Laos; The Grès Supérieurs Formation (≈ the Khok Kruat Formation), Aptian–Albian

Previous study: *Mandschurosaurus* was the first dinosaur taxon 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 reassigned in 1930 to a new genus *Mandschurosaurus amurensis* (Godefroit et al., 2011). *M. amurensis* is a large hadrosaurid (duck-billed dinosaurs) based on a poorly preserved and incomplete skeleton, and often considered as a *nomen dubium* (Horner et al., 2004). Over the years, Josué-Heilmann Hoffet, a French geologist, discovered the first dinosaur fossils from Southeast Asia (Brett-Surman et al., 2012). He described those ornithopod material as "*Mandschurosaurus*" *laosensis* (Hoffet, 1944), and was considered as Late Cretaceous (Senonian) in age (Buffetaut, 1991). However, some palaeontologists considered "*M.*" *laosensis* a *nomen dubium* (Buffetaut, 1991; Horner et al., 2004). "*M*". *laosensis* potential being a non-hadrosaurid iguanodontian such as *Siamodon*, *Ratchasimasaurus*, and *Sirindhorna* from the same age of Thailand. Hoffet also considered the another ilium which is more robust than "*Mandschurosaurus*" *laosensis*, indicating the presence of a second type taxon (Allain et al., 1999; Buffetaut, 1991).

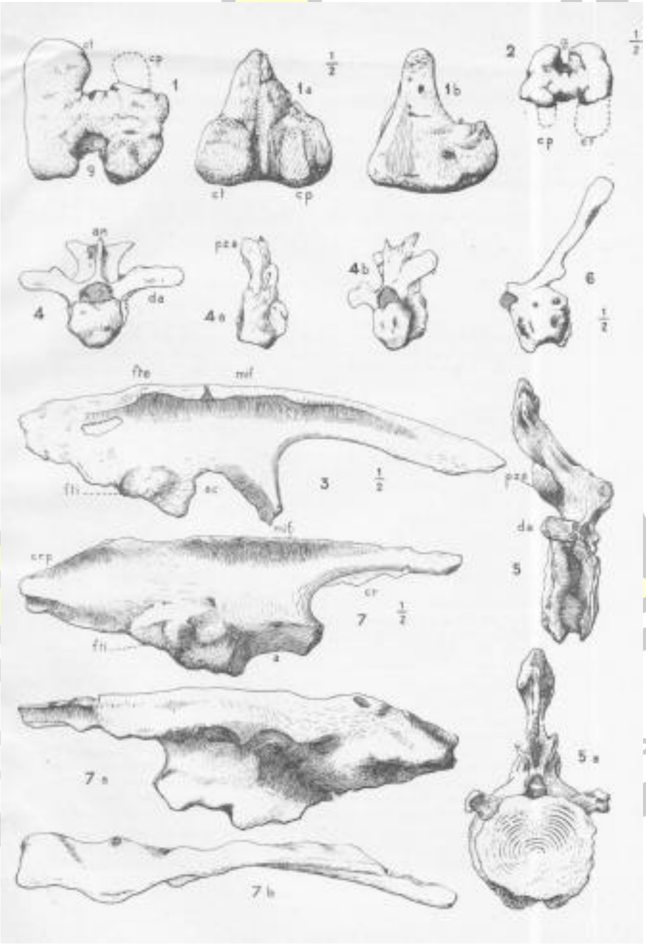

Figure 11 (1-6) Sketch of *M. laosensis* specimens, (7) ilium of an iguanodontian possibly second type taxon (Hoffet, 1944).

Iguanodontian indet.

Material: unnumbered specimen consists of series of dorsal vertebrae, rib, pubis, and ischium (Fig. 12).

Locality and age: Ban Lamthouay, Tang Vay District, Savannakhet Province; The Grès Supérieurs Formation (≈ the Khok Kruat Formation), Aptian–Albian

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

Psittacosaurid indet. (so-called the 'Savannakhet psittacosaurid')

Material: unnumbered specimen of left mandible (Fig. 12).

Locality and age: Ban Lamthouay, Tang Vay District, Savannakhet Province; The Grès Supérieurs Formation (≈ the Khok Kruat Formation), Aptian–Albian

Comments: The unpublished specimen of psittacosaurid indet. was reported, and the cast of this specimen displayed in the Dinosaur Museum of Savannakhet (Allain et al., 1999; Buffetaut et al., 2007; Cavin et al., 2018). Detailed comparison with *Psittacosaurus sattayaraki* of Thailand is needed after a full description of this material.

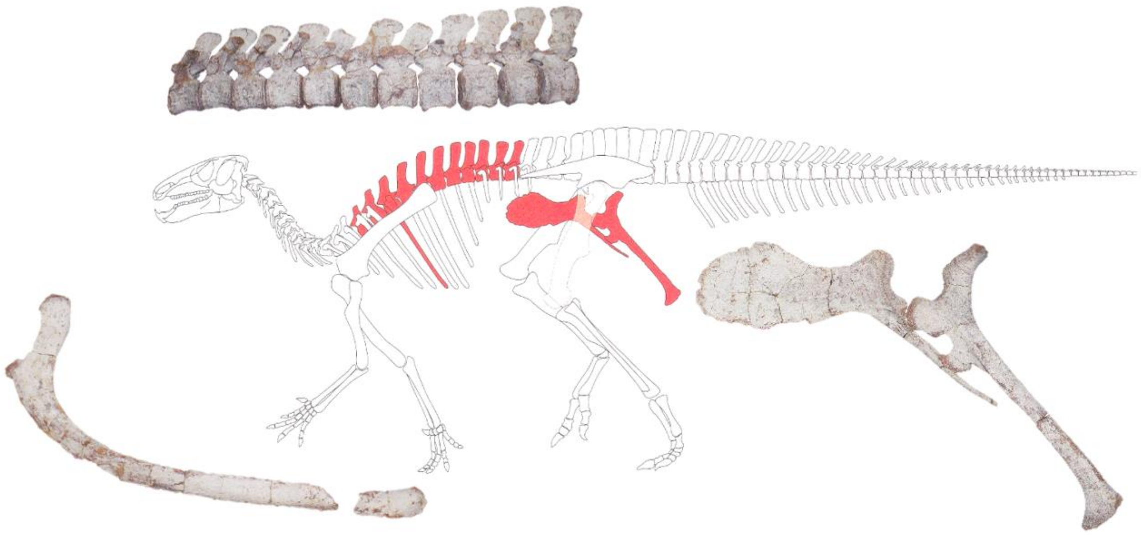

Figure 12 Material of iguanodontian indet. from Laos (modified from FPDM, 2015). Not to scale.

Figure 13 Mandible of psittacosaurid indet. from Laos (modified from FPDM, 2015)

3.4 Malaysia

3.4.1 The Tembeling Group

The non-marine fossil-bearing unit was informally referred to as ‘the Pahang vertebrate bed’ located in the interior of Pahang State, the site has been kept confidential. Hybodont sharks and ray-finned fish fishes were reported from this assemblage, which has strong affinities with faunas 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 equal to the Sao Khua Formation of Thailand in age based on faunal composition and biostratigraphic correlation (Teng et al., 2019).

So far, ornithischian from the Tembling Group has not been scientific published yet, but was released some details in the Malaysian medias (University of Malaya, 2014). This study is unable to provide further details current

Ankylosaurian indet. Sone et al., 2022

Material: UM10580 an isolated tooth.

Locality and age: Taman Negara region of Pahang State, Western Malaysia; The Tembeling Group (≅ the Sao Khua Formation), ? late Valanginian - early Hauterivian

Previous study: The tooth is about 13 mm long and 10.5 mm wide in preserved dimension (University of Malaya, 2014). The crown of the tooth is relatively small, the ornamented faces do not show a prominent median ridge. A strong cingulum round the base of the crown.

Comments: Initially, it is classified as ankylosaurian tooth (Sone et al., 2022), suggesting the first discovery of the clade in Asia.

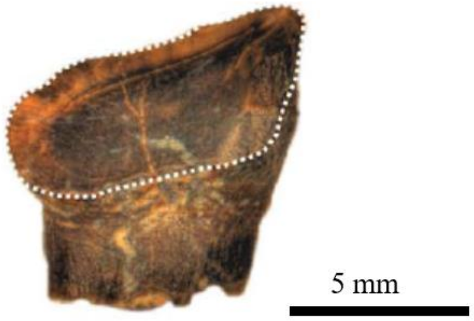

Figure 14 the isolated nodosaurid tooth from North America (Mallon & Anderson, 2014).

3.4.2 The Gagau Group

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

Iguanodontian indet.

Material: The unnumbered isolated tooth (Fig.15).

Locality and age: Hulu Terengganu at northeastern part of Mount Gagau Area; The Gagau Group, ?late Early Cretaceous

Description: The crown of the tooth is leaf-shaped, which bear a prominent median primary ridge and weak subsidiary ridges. It shows a well-developed ornamentation on the enamelled surface. The margins of the crown bear distinct denticles.

Comments: The features indicate that it was the tooth of iguanodontian dinosaur, which restricted found from Aptian-Albian stages of Thailand and Laos. We suppose that this fossil bed is possibly late Early Cretaceous in age.

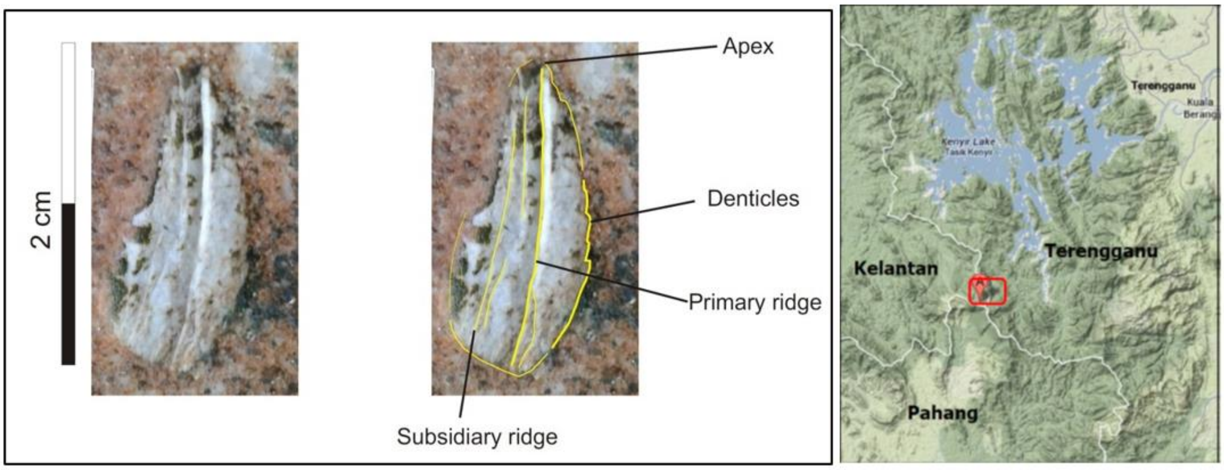

Figure 15 (Left) The tooth of iguanodontian indet. from Mount Gagau Area, and (Right) the site locality at the Gagau Mountain Terengganu-Kelantan-Pahang border (Rahman, 2017).

3.5 Southern China

3.5.1 Xinlong Formation

The material of ornithischains was report from the Napai Basin in the south-western part of 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 Southeast Asia (Mo et al., 2016). The four species of hybodonts from the assemblage (*Acrorhizodus khoratensis*, "*Hybodus*" *aequitridentatus*, *Thaiodus ruchae* and *Khoratodus foreyi*) are indeed endemic to Southeast Asia and South China, and are restricted to the Aptian-Albian interval (Cuny, 2012; Cuny et al., 2017). The vertebrate fossil supports the Xinlong Formation is coeval with the Khok Kruat Formation of Thailand and the 'Grès supérieurs' Formation of Laos, in age (Mo et al., 2016).

***Napaisaurus guangxiensis* Ji & Zhang, 2022**

Material: The holotype, FS-20-007 to 008, a right ischium and right ilium (Fig. 16).

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

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

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

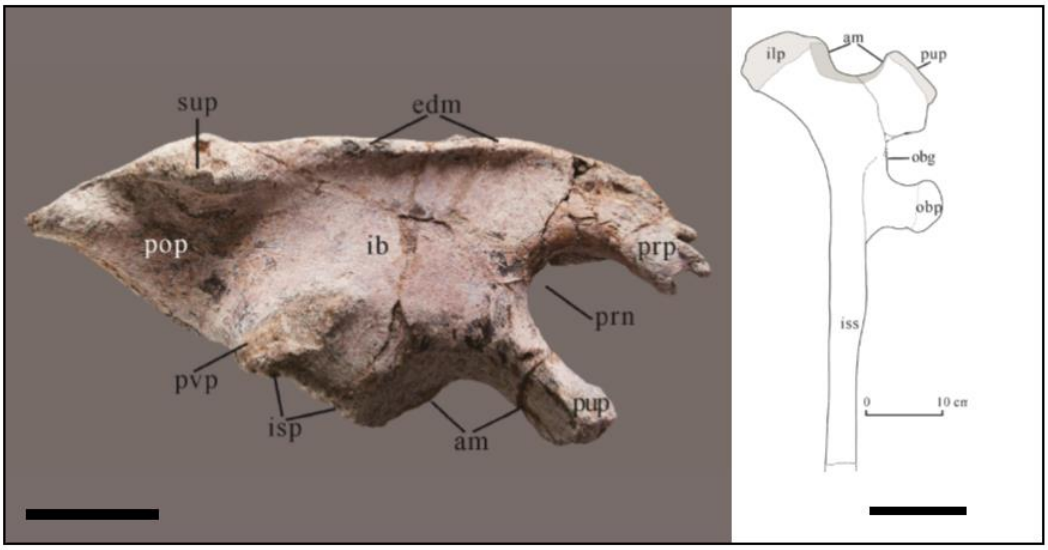

Figure 16 (Left) Right ilium (FS-20-008) and (Right) right ischium (FS-20-007) of *N. guangxiensis* in lateral view; Scale bars:10 cm (Ji & Zhang, 2022).

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 (Fig. 17).

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

Previous study: The not well-preserved vertebrae, limb bones, and teeth cannot be identified taxa more precisely. However, some lower tooth showing bears a strong median primary ridge and at least one subsidiary ridge suggesting a relatively advanced iguanodontian (Mo et al., 2016).

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

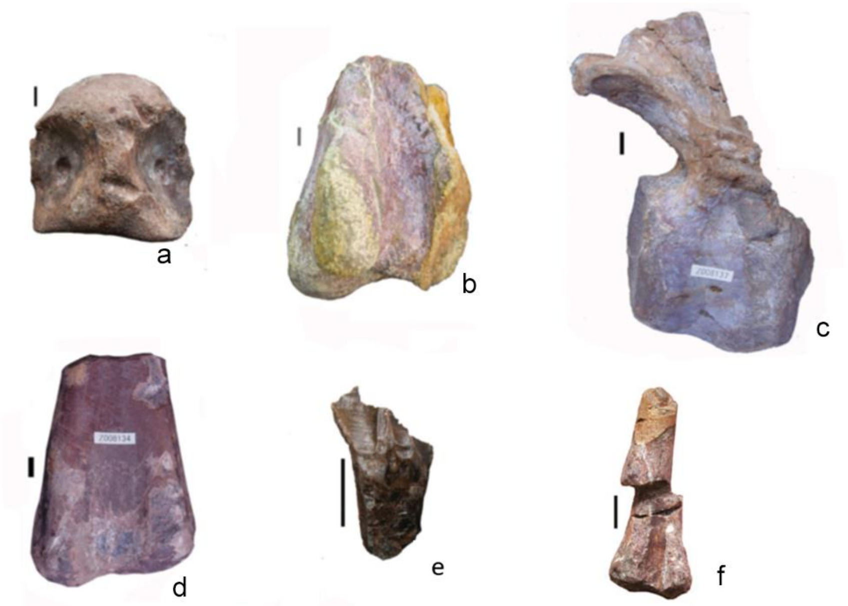

Figure 17 Iguanodontian material from the Xinlong Formation of the Napai Basin: (a) cervical vertebra, ventral view; (b) distal end of left femur, posterior view; (c) dorsal vertebra, right lateral view; (d) distal end of left humerus, anterior view; and (e) tooth. (f) Distal end of ?psittacosaurid right femur in posterior view; Scale bars: 10 mm (Mo et al., 2016).

?Psittacosaurid indet. Mo et al., 2016

Material: unnumbered specimens including distal end of right femur (Fig. 17f).

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

Previous study: Mo and his team (2016) reported an incomplete femur, which is resembled to psittacosaurid. Although the condition of the specimen is poor preserved, but this group has widely distributed in the Early Cretaceous of China, Mongolia, Siberia, Thailand, and Laos. It is possible that this basal ceratopsian could be found in the Xinlong Formation (Buffetaut & Suteethorn, 1992; Buffetaut et al., 2007; Mo et al., 2016).

3.6 Discussion

3.6.1 Evolution of Southeast Asian ornithischians.

The origin of ornithischian remains controversial (Baron & 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 (Baron et al., 2017b; Baron & Barrett, 2017; Butler et al., 2008). However, some palaeontologists considered they were primitive dinosauriforms (Madzia et al., 2021; Müller et al., 2018). Other primitive true ornithischians also discovered from the Early Jurassic in southern Gondwana e.g. *Eocursor parvus* (potentially as Sinemurian) in South Africa (Butler et al., 2007), *Heterodontosaurus tucki* (potentially as Sinemurian) in South Africa (Sereno, 2012), *Lesothosaurus diagnosticusand* (=*Stormbergia dangershoeki*) in Lesotho and South Africa (Baron et al., 2017b), and *Laquintasaura venezuelae* (Hettangian) in Venezuela (Barrett et al., 2014). After that, ornithischians evolved to become very diverse in the Jurassic and one of the most successful groups of herbivores in the Cretaceous.

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

1) The Early Jurassic

A few basal thyreopharans were reports in Yunnan Province of China (Norman et al., 2007; Yao et al., 2022b). During this epoch, the basal thyreophorans also discovered from Africa, Europe and North America (Barrett et al., 2014). However, evidence of their existence is yet to be seen in Southeast Asia. Even the Late Triassic-Early Jurassic Nam Phong Formation has been found in northeastern Thailand, but 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 Mesozoic red bed of northern of Thailand, sauropod indet. from Chiang Muan district, Phayao Province has been found and was dating as post-Toarcian age, possibly boundary between early and middle Jurassic (Chanthasit et al., 2018). However, ornithischian material is yet to be discovered.

2) The 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 of ornithischians were found only from Asian taxa so far (*Tianyulong* and *Kulindadromeus* and appeared again in *Psittacosaurus* in the Early Cretaceous). It is 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) The Late Jurassic

Asian ornithischians were dominated by stegosaurs same as in Africa, Europe, and US. Some basal neornithischians reported from US, China and Thailand. At this time, basal iguanodontians (such as *Dryosaurus*, *Dysalotosaurus* and *Camptosaurus*) evolved in North America, Africa, and Europe but there is even no evidence in Asia (Norman, 2004; Xu et al., 2018). However, there were the earliest known marginocephalians, Chaoyangsauridae, in China. The presence of Jurassic ceratopsians restricted in Asia indicates an Asian origin for the group (Zhao et al., 1999). In Thailand, the lower part of Phu Kradung Formation yields stegosaurids and basal neornithischians similar to those found in China. While the upper part, which is likely considered as basal Cretaceous in age (Tong et al., 2015; Tong et al., 2019), still have the appearance of basal neornithischians and other groups of dinosaurs (such as metricanthosaurids and mamenchisaurids) similar to those found from the lower Phu Kradung Formation.

4) The Early Cretaceous

The number of stegosaurids had decreased and were eventually lost (Tumanova & Alifanov, 2018). In contrast to the apparent increased of ankylosaurians. Jeholosaurids, apparently endemic group of East Asia (Xu et al., 2000). During the late Early Cretaceous, iguanodontians evolution shifted, they were getting much bigger and became greatly 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 *Psittacosarus* and basal neoceratopsians found in China, Japan, Mongolia, Russia, South Korea, Thailand, Laos, and possibly Uzbekistan (Averianov et al., 2006; You & Dodson, 2004).

5) The Late Cretaceous

The Beringian land bridge between present-day Siberia and Alaska, which opened during the Aptian-Albian, served route for terrestrial vertebrates to migrate 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 ankylosaurid, hadrosaurid, neoceratopsian, pachycephalosaurian, tyrannosaurid, and troodontid) supposedly originated in Asia (Bell, 2011). Asian Ornithischian dinosaurs much diverged in the Late Cretaceous. Non-hadrosaurid hadrosauroids were replaced with hadrosaurids, the medium to large-sized duck-billed dinosaurs (Kobayashi et al., 2021; Tsogtbaatar et al., 2019). Hadrosaurids became the most dominant, and roamed China, Japan, Kazakhstan, Mongolia, and Russia. Two thescelosaurids from Mongolia and South Korea. Several pachycephalosaurians, exclusively lived in Laurasia, were found in China and Mongolia (Sullivan, 2006). Several ankylosaurians reported from China, Japan, Mongolia, and Uzbekistan (Park et al., 2021). Several neoceratopsians (e.g. leptoceratopsids and protoceratopsids) were reported from China, Mongolia, and Uzbekistan, but there is only one taxa of ceratopsids from China contrary to the prevalent in North America (Xu et al., 2010). However, even the diversity of ornithischian dinosaurs during this epoch was highest, but no deposits of any dinosaur bones have been reported in Southeast Asia.

3.6.2 Paleobiogeographic implications

Southeast Asia consists of a mosaic of microcontinents. In the late Palaeozoic and Mesozoic, the northern margin of eastern Gondwana, which, after drifting northward, collided with each other and with South China (Metcalfe, 1998). Most of dinosaur fossils in northeastern Thailand, Laos, and Cambodia have been found from Indochina Terrane.

Stage 1 Late Jurassic to Early Cretaceous (Fig. 18a)

The oldest record of ornithischian dinosaurs in southeast Asia so far is from the Phu Kradung Formation of northeastern 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 Phu Noi locality and the nearby Khok Sanam locality, which is considered as the lowermost part of Phu Kradung Formation (Buffetaut et al., 2001; Chanthasit et al., 2019; Cuny et al., 2014; Manitkoon & Deesri, 2019). Racey & Goodall (2009) supposed that the lower Phu Kradung Formation could be Late Jurassic (?Tithonian) in age, as well as supporting 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 southern peninsular belongs to the Sibumasu Terrane (Buffetaut et al., 2005; Cuny et al., 2014) such as hybodont sharks (Cuny et al., 2014), Brachyopoidea 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., 2005; Suteethorn et al., 2013) indicates a faraway distant distribution. While the upper part of Phu Kradung Formation is Early Cretaceous in age based on the presence of the pollen, *Dicheiropollis etruscus* (Racey & Goodall, 2009), and a turnover of hybodont shark, turtle and crocodylomorph faunas (Cuny et al., 2014; Martin et al., 2019; Tong et al., 2009, 2019).

The microremains of hybodont *Acrodus kalasinensis*, *Jaiodontus* sp. and similar to denticles from the Khlong Min Formation are found in the lower Phu Kradung localites (Cuny et al., 2014). The genus *Acrodus* known from Triassic and Jurassic deposits (Rees & Underwood, 2006), and *Jaiodontus* restricted in the Oxfordian of China (Klug et al., 2010). In addition, the absence of the common in the Early Cretaceous assemblage *Heteroptychodus*, but known from upper levels of the

Phu Kradung Formation such as the Ban Kham Phok locality of Mukdahan Province, supports the age difference between lower and upper 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 abundant from the Late Jurassic of China as following: 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, whereas records of this group in Early Cretaceous deposits are scarce in mainland Asia (Tong et al., 2015; Tong et al., 2019). The turtle faunas from the lower Phu Kradung are distinct from other assemblages placed in the upper part, which include abundant remains of more advanced turtles, the trionychoid such as *Basilochelys macrobios* (Tong et al., 2015; Tong et al., 2009; Tong et al., 2019).

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

The saurischian dinosaur faunas from both the lower and the upper Phu Kradung Formation are mamenchisaurids and metriacanthosaurids, which are well-known Chinese groups from the Middle-Late Jurassic/Early Cretaceous Formations in the Sichuan-Yunnan-Northern Junggar Basin. Mamenchisaurids (such as *Mamenchisaurus* and *Omeisaurus*) are eusauropods, and also present in the Chuanjie Formation, Shishugou Formation, Lower and Upper Shaximiao Formations, Suining Formation, and Penglaizhen Formation (Buffetaut et al., 2006; Ren et al., 2021; Wang et al., 2019; Xing et al., 2015). Metriacanthosaurids (=sinraptorids) from Phu Noi show similar characteristics to *Sinraptor dongi* from Upper Jurassic Shishugou Formation of the Junggar Basin in northwestern 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 was once thought to be endemic group of eastern Asia. However, the report of isolated fossils from Itat Formation from 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* the closely relate of *Sinraptor* has been found in upper Oxford Clay of England.

A single bone of stegosaur from the Lower Phu Kradung Formation cannot provide the definitive proof, except itself is more advance than the Middle Jurassic *Huayangosaurus* and likely to be closer to those from Late Jurassic taxa such as *Tuojiangosaurus* (Buffetaut et al., 2001). Basal neornithischians from Phu Noi showing combined characters resemble to those taxa from the Lower and Upper Shaximiao Formation of China and Late Jurassic Morrison Formation of US (Barrett et al., 2005; Carpenter & Galton, 2018; Manitkoon et al., 2019).

As mentioned above, the dinosaur faunas including metriacanthosaurids and mamenchisaurids, and basal neornithischians have been found in both lower and upper part of the Phu Kradung Formation indicated that, despite the change in other groups of vertebrate faunas, dinosaurs remained the same group and had long stratigraphic range. Another noteworthy point is the Phu Kradung Formation, and the Klong Min Formation shows a remarkable biodiversity and reveals a close relationship with Chinese Jurassic vertebrate assemblages suggests that group of vertebrate faunas are more widespread than previously thought. Accordingly, these continental terranes had been in contact with mainland Asia before Jurassic time.

Stage 2 Early Cretaceous (?Berriasian to pre-Barremian) (Fig. 18b)

The trackway of a small quadrupedal ornithopod is found in the Phra Wihan Formation of Thailand. This formation was dating as Lower Cretaceous (Berriasian-Early Barremian) age from a rich palynological assemblage (Racey, 2009; Racey & Goodall, 2009). However, a subsequent study suggested that the dates for the underlies Sao Khua Formation had been altered by geologic processes (Tucker et al., 2022), and there dating the sedimentation of the upper part of the Sao Khua

Formation to no earlier than early Hauterivian, which means that 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 from 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 faunas including turtles and theropod dinosaurs are considered to be a Barremian assemblage (Samathi et al., 2019b; Tong et al., 2019), and following a more refined regional biostratigraphic correlation of the freshwater bivalves *Pseudohyria* (*Matsumotoina*) *matsumotoi* suggest a Late Barremian in age (Tumpeesuwan et al., 2010). Lastly, the geochronological data based on radiometric dating of detrital zircons indicating a tightly restricted late Valanginian-early Hauterivian age (133.6-132.1 Ma) for the Sao Khua Formation establishes that the dinosaur fauna is ~5-9 million years older than currently known (Tucker et al., 2022).

The Sao Khua Formation is dominated by sauropods (somphospondylian titanosauriformes, another type titanosauriformes and diplodocoids) and theropods (spinosaurids, megaraptorans and coelurosaurs) at the generic diversity level and overall abundance (Buffetaut et al., 2002; Buffetaut & Suteethorn, 1998a; Samathi et al., 2019). Among the thousands of saurischian bones have been collected from northeastern Thailand, no evidence of ornithischians has yet been found in this formation (Buffetaut et al., 2015). The seeming unusual absence of ornithischian dinosaurs in the Sao Khua Formation is most consistent with the ecological composition of Valanginian/Hauterivian aged assemblages from Gondwanan mainland for example the “wood beds” of the upper Kirkwood Formation of South Africa and the Bajada Colorado Formation of South America, which are dominant of various sized theropods and multiple cohabiting species of sauropods (Tucker et al., 2022). This is contrast to those pre-Barremian dinosaur assemblages of Laurasian landmasses from Europe and North America, which is a diverse ornithischian record including ankylosaurians and iguanodontians shared habitats with other sauropod and theropod dinosaurs (Kirkland et al., 2016; Norman, 2010; Tucker et al., 2022). Comparison with the contemporaneous formations in Asia, ornithischian remains still somewhat poorly constrained (Tucker et al., 2022). Material of stegosaurian indet. is reported from the Mengyin Formation (Berriasian-Valanginian), Shandong Province of China (Tucker et al., 2022). A stegosaurine *Wuerhosaurus homheni* and probably basal ceratopsians have been reported from the Lianmuqin Formation (?Valanginian) of Tugulu Group, Xinjiang Region of China (Maidment et al., 2008; Sereno & Shichin, 1988).

Although during late Valanginian-early Hauterivian seems to be a crucial period of 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 show 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 in southeasth Asia during this time.

The early Cretaceous Phu Phan Formation is unconformably underlying 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 an exception of a large sauropod limb bone is found in a cliff face at Phu Kum Kao locality, Kalasin Province (Buffetaut et al., 2003; Buffetaut et al., 2002). No evidence of ornithischians has hitherto been reported.

Stage 3 Middle Cretaceous (Aptian to Albian) (Fig. 18c)

In contrast with the Sao Khua Formation, the younger Khok Kruat Formation contains abundant neornithischian dinosaurs remains including iguanodontians and basal ceratopsian, fewer theropods (spinosaurids and carcharodontosaurians) and titanosauriformes sauropods have been found (Buffetaut et al., 2005; Chokchaloemwong 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 palaeobiogeographic supporting by vertebrate fossil (Cuny et al., 2017; Mo et al., 2016), and have yield five iguanodontian taxa, and at least one taxon of

Psittacosaurus (Buffetaut & Suteethorn, 1992; Buffetaut & Suteethorn, 2011; Ji & Zhang, 2022; Shibata et al., 2015). This stage represents the highest diversity of ornithischians, and also refine the temporal shift from sauropod-dominated to iguanodontian-dominated ecosystems during the Cretaceous in southeast Asia. Both iguanodontians and ceratopsian possibly spread in this region during the Aptian. A hypothesis attributes Cerapoda (ornithopods+ceratopsians) dentition are suited for efficiently grinding the vegetation as a reason for them successful competition than other herbivorous in the latter Cretaceous time (Strickson et al., 2016).

Basal iguanodontians are originated 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 elongate archipelago around the Jurassic-Cretaceous boundary (Fig. 18a), probably associated with the coeval global marine regression (Xu et al., 2018). Asian basal ankylopollexians were diversified during the Early Cretaceous such as *Fukuisaurus* and *Koshisaurus* (Barremian) from Japan (Shibata & Azuma, 2015), *Lanzhousaurus* (Barremian) from China (You et al., 2005), and *Bayannurosaurus* (early Aptian) of Inner Mongolia, China (Xu et al., 2018). Later, the non-hadrosaurid hadrosauroids are mainly discovered from middle Cretaceous (Aptian-Albian). For instance, *Altirhinus* and *Choyrodon* from Mongolia (Gates et al., 2018; Norman, 1998); *Equijubus*, *Gongpoquansaurus*, *Jintasaurus*, and *Xuwulong* from Gansu Province of China (You et al., 2003, 2014; You & Li, 2009); *Probactrosaurus* and *Penelopognathus* from Inner Mongolia, China (Godefroit et al., 2005; Rozhdestvenskiy, 1967); *Ratchasimasaurus*, *Sirindhorna*, and possibly *Siamodon* from Thailand (Shibata et al., 2015).

The earliest known ceratopsians (or even marginocephalian dinosaurs) is a family Chaoyangsauridae (such as *Chaoyangosaurus* and *Yinlong*), during the Late Jurassic of China (You & 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 possibly 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* often found in lacustrine deposits (Averianov et al., 2006; Buffetaut et al., 2007), which is greatly different 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 uncovered in Thailand and Laos (Manitkoon et al., 2022).

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

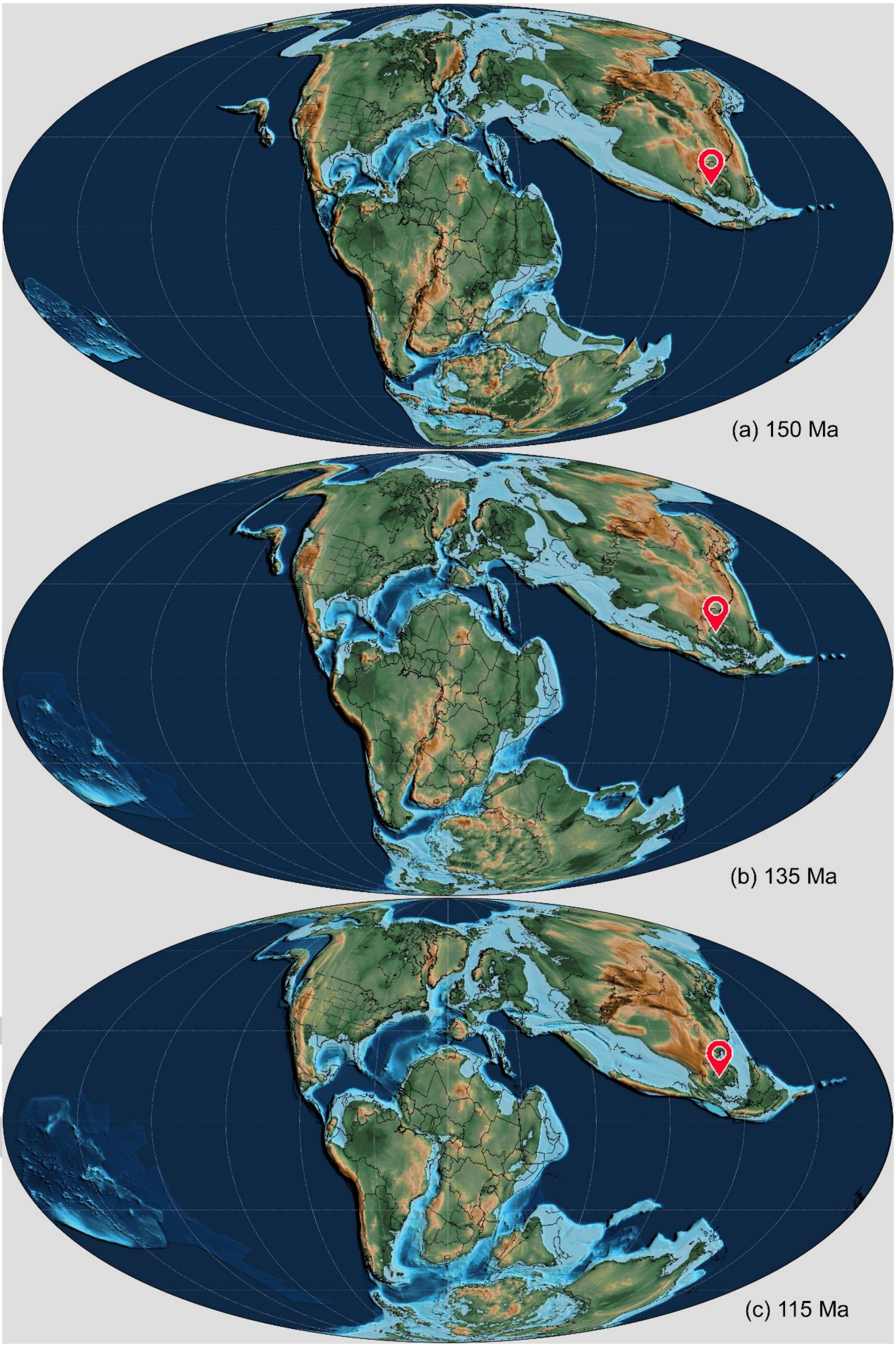

Figure 18 Paleogeographic maps showing the location of Thailand (red pins) in each stages (modified from Scotese, 2021).

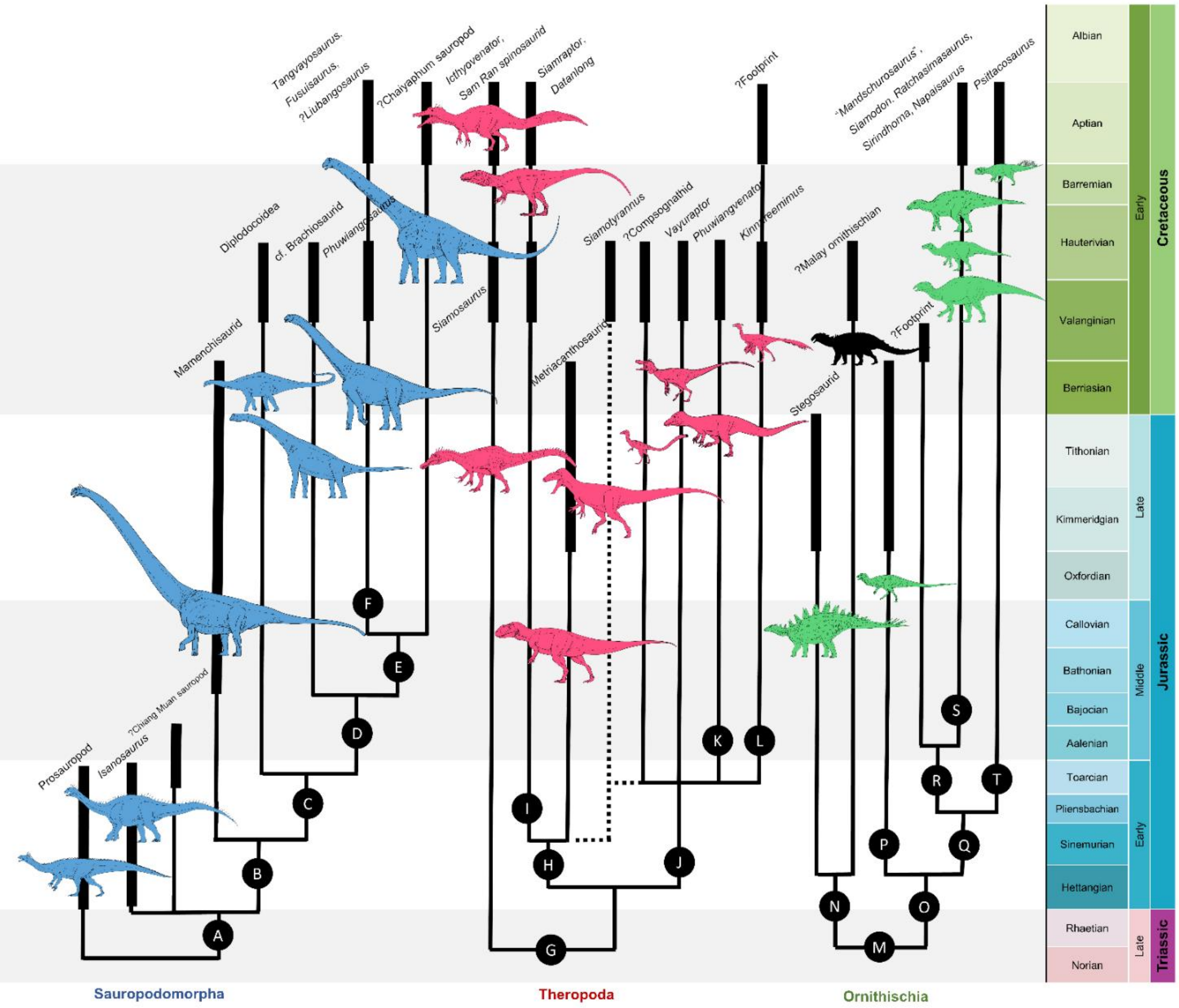

Figure 19 Phylogenetic relationships of non-avian dinosaurs in southeast Asia and southern China.

Abbreviation: 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 (Chanthasit et al., 2018; Cuny et al., 2014; Laojumpon et al., 2017; Mo et al., 2016; Samathi et al., 2019; Teng et al., 2019).

3.7 Conclusion

So far, most of the southeast Asian ornithischian fossils have been found in the Khorat Group of northeastern Thailand. At least six taxa have been reported and date from the Late Jurassic to the late Early Cretaceous. The oldest is known from the Jurassic Phu Kradung Formation represented by stegosaurids and basal neornithischians. The ornithischian footprints from the Phra Wihan Formation shows the evidence of ornithischians before pre-Barremian. There appears to be an absence of ornithischian dinosaurs during the Sao Khua Formation. Until the Early Cretaceous Khok Kruat Formation (Aptian-Albian) presents high abundant advanced iguanodontians plus basal ceratopsians, which is refine the herbivorous shift from sauropod-dominated to ornithischian-dominated ecosystems. The iguanodontians and psittacosaurids also found in the Grès supérieurs Formation of Laos and Xinlong Formation of southern China show many similarities to the Khok Kruat fauna of Thailand and are considered equivalent in age. The scarce dinosaur specimens from Malaysia are also an age ambiguity. However, the ornithischian tooth from the Tembeling Group represents the existence of ornithischians that were missing from the equivalent time in the Sao Khua Formation of Thailand. This study illustrated the diversity of ornithischian assemblages in Southeast Asia, providing an updated review and a discussion about their paleobiogeographic implications.

Chapter 4

A new basal neornithischian dinosaur from the Late Jurassic Phu Kradung Formation of Thailand

Some part of this chapter was presented in Manitkoon, S., Sueethorn, S., Deesri, U., and Suteethorn, V. 2019. An Articulated Skeleton of the Neornithischian Dinosaur from the Late Jurassic–Early Cretaceous, Phu Kradung Formation of Thailand. The 4th International Symposium on Asian Dinosaur in Mongolia 2019. Ulaanbaatar, Mongolia.

4.1 Introduction

Neornithischia is a clade of herbivourous dinosaurs including; ornithopods, marginocephalians and a variety of small bodied bipedal basal forms that historically referred to as hypsilophodonts (Barrett et al., 2005; Butler et al., 2008; Sereno, 1999). The problematic classification among basal neornithischians is still unclear (Table 3) (Boyd, 2015; Li et al., 2019; Madzia et al., 2019). In Asia, *Sanxiasaurus modaoxiensis* is the earliest neornithischian from the Middle Jurassic Xintiangou Formation of China (N. Li et al., 2019). Other taxa have been described from the Middle Jurassic of Sichuan, China: *Agilisaurus louderbacki*, *Hexinlusaurus multidens*, and *Xiaosaurus dashanpensis* from the lower Shaximiao Formation, and *Yandusaurus hongheensis* from the upper Shaximiao Formation (Barrett et al., 2005; Dong & Tang, 1983; He & Cai, 1984b; Li et al., 2011; Peng, 1992). Including a primitive feather-like *Kulindadromeus zabaikalicus* from Siberia (Godefroit et al., 2014).

In Southeast Asia, the more advanced neornithischians have been described, including iguanodontian ornithopods and basal ceratopsians: *Mandschurosaurus laosensis* from the Grès Supérieurs Formation of Laos (Hoffet, 1944), *Siamodon ninngami* (Buffetaut & Suteethorn, 2011), *Ratchasimasaurus suranareae* (Shibata et al., 2011), *Sirindhorna khoratensis* and *Psittacosaurus sattayaraki* (Buffetaut & Suteethorn, 1992) from the Khok Kruat Formation of Thailand, all of these cerapodan neornithischians (ornithopods and marginocephalians) have been discovered from the Early Cretaceous (Aptian-Albian). Nevertheless, no valid taxon had been described yet from older formation. A few elements of basal neornithischians were reported from the Late Jurassic Phu Kradung Formation of Thailand including a left femur from the Dan Luang locality, Mukdahan Province (Buffetaut et al., 2003; Buffetaut & Suteethorn, 2007), a lower jaw with the distinct characters of fan-shaped teeth and asymmetrically distributed enamel on the lingual surface from the Phu Noi locality, Kalasin Province (Buffetaut et al., 2014).

In 2012, a team by the Palaeontological Research and Education Centre, Mahasarakham University excavated remains in the solid rock from the Phu Noi locality in the Late Jurassic Phu Kradung Formation. After lab preparation revealed a well-preserved articulated skeleton of a new basal neornithischian dinosaur, which is the earliest neornithischian taxon in Southeast Asia. Discovery of this dinosaur providing biodiversity, biogeography, and early evolutionary information on the neornithischians during the Jurassic-Cretaceous period.

4.2 Institutional abbreviations

PRC: Palaeontological Research and Education Centre, Mahasakakham University, Thailand
SM: Sirindhorn Museum, Kalasin Province, Thailand

4.3 Geological setting

The Phu Kradung Formation is considered as forming the base of the Mesozoic Khorat Group and is distributed on the Khorat Plateau in northeastern Thailand. The sedimentological aspects and vertebrate fossils indicate that it was deposited by meandering rivers, with a high-energy regime along the palaeochannels, followed by deposition in a floodplain and lacustrine environment. (Department of Mineral Resources, 2014; Meesook, 2000).

The specimens was excavated from the Phu Noi locality (Fig. 20) belongs to the lower part of the Phu Kradung Formation, which could be the Upper Jurassic in age (Cuny et al., 2014; Martin et al., 2019). Stratigraphically, characterized by brownish-purple and greenish-grey sandy siltstone which sedimentary deposited in a natural levee with low energy, the elevation of the bone bed is about 243-258 meters (Boonchai et al., 2019; Ditbanjong & Chanthasit, 2019).

Phu Noi locality is located at Ban Din Chi, Kham Muang District, Kalasin Province, Thailand. It is one of the richest Southeast Asian non-marine vertebrate bones where PRC and Sirindhorn Museum has worked more than ten years. Several new taxa was named including freshwater shark; *Acrodus kalasinensis* (Cuny et al., 2014), ginglymodian fish; *Isanichthys lertboosi* (Deesri et al., 2014), lungfish; *Ferganoceratodus annekempae* (Cavin et al., 2020), xinjiangchelyid turtles; *Phunoichelys thirakupti* and *Kalasinemys prasarttongosothi* (Tong et al., 2015; Tong et al., 2019), and teleosaurid crocodylomorph; *Indosinosuchus potamosiamensis* and *Indosinosuchus kalasinensis* (Martin et al., 2019; Wilberg, et al., 2019). This site has also produced the Brachiopidae temnospondyls (Nonsrirach et al., 2021), rhamphorhynchid pterosaurs and numerous dinosaur elements; mamenchisaurid sauropods, metriacanthosaurid (=sinraptorid) theropods and small basal neornithischians (Buffetaut et al., 2014; Buffetaut et al., 2015; Chanthasit et al. , 2015; Nonsrirach et al., 2021; Unwin et al., 2018) that are currently under study. The Phu Noi site is close to the Late Jurassic Phu Kradung Formation outcrop of Ban Khok Sanam village (about 3 km away from Phu Noi) that found a dorsal vertebra of stegosaurid (Buffetaut et al., 2001). The group of vertebrate fauna resembles those Middle Jurassic from China.

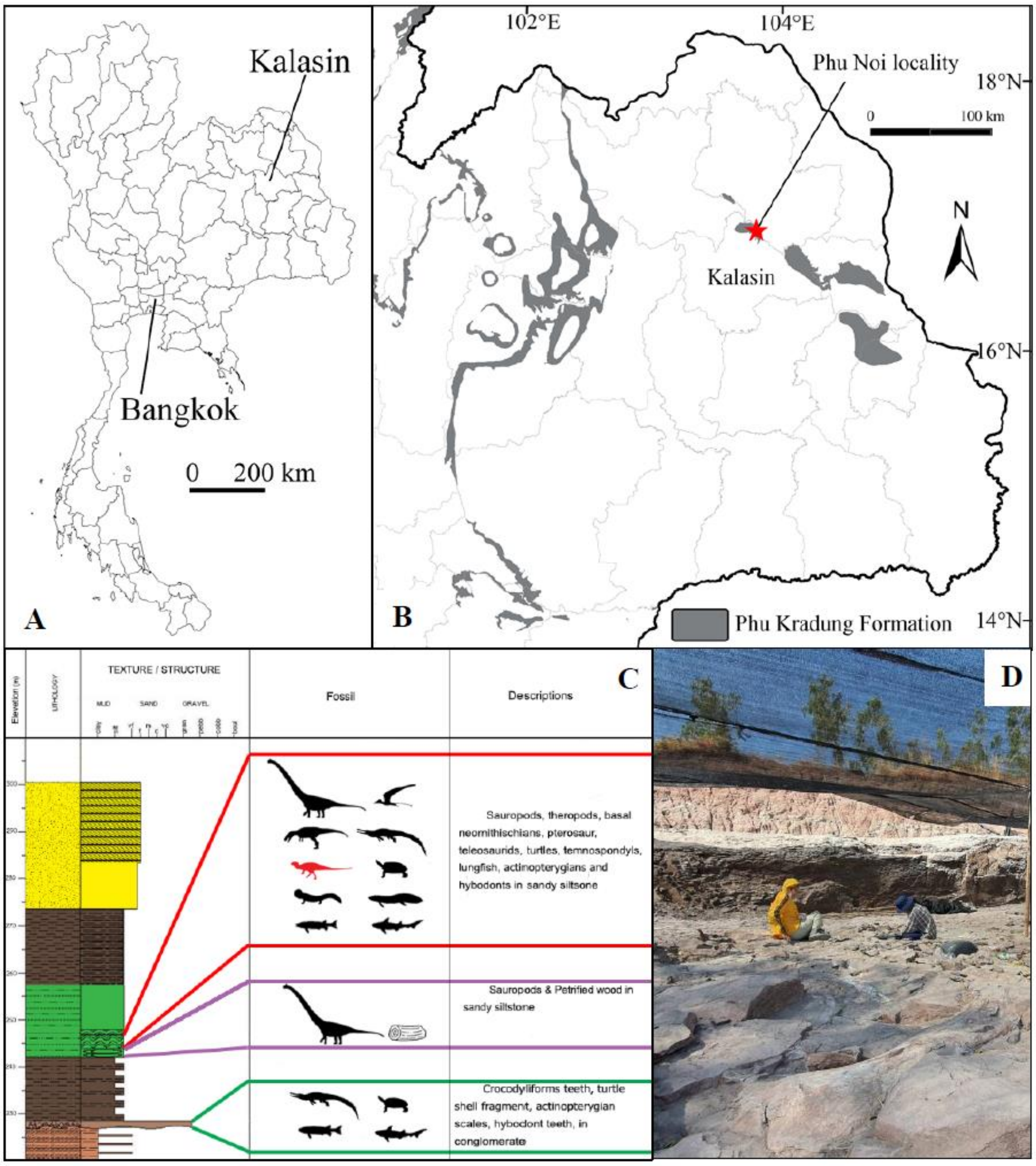

Figure 20 Locality map and stratigraphy of Phu Noi neornithischia new taxon. A, map of Thailand, showing the location of Bangkok and Kalasin Province; B, map of Khorat Plateau, showing the distribution of the Lower Phu Kradung formation and the location of Phu Noi locality (a red star); C, stratigraphic column of Phu Noi (applied from Boonchai et al., 2019), D, a photograph of the excavation site.

4.4 Materials and methods

The fossil preparation was done by removal of the fossiliferous bones from the hard rock matrix. I used a pneumatic pen and fixed it by cyanoacrylate glue. The holotype specimen spent time more than 2 year for preparation. Measurements of the bones were taken with a digital caliper.

The holotype of Phu Noi neornithischia new taxon (PRC 150) is known from the more than 60% completed skeleton from the material comprising postcranial element including a well-preserved articulated series of vertebrae, the entire pelvic girdle, the left and right femurs, tibias and fibulas, ossified tendons, the left scapula and manus, the left tarsals, metatarsals, and an ungual. (Fig 21). It was collected from the Phu Noi locality in Kham Muang District, Kalasin Province. The specimen is now housed in PRC collection. Additional materials of the basal neornithischians from Phu Noi locality are collected in Palaeontological Research and Education centre, Mahasarakham University and Sirindhorn Museum.

4.5 Results

4.5.1 Systematic paleontology

Dinosauria Owen, 1842
Onithischia Seeley, 1888
Neornithischia Cooper, 1985
Phu Noi neornithischia new taxon

Holotype. PRC 150; A well preserved articulated series of vertebrae (from probably 6th cervical to 10th caudal vertebrae), the entire pelvic girdle, the left and right femurs, tibiae and fibulae, a few ossified tendons, an incomplete tooth, the left scapula and manus, the left tarsals, metatarsals and an ungual.

Referred material. PRC 149 (renumbered from PN 13-09 in Buffetaut et al. 2014), a lower jaw (Fig. 6); SM2021-1-132, a left pes with tibia (Fig. 31). All from the type locality.

Type locality and horizon. Phu Noi locality (a small hill as the Thai name indicates), Ban Din Chi Sub-district, Kham Muang District, Kalasin Province, Thailand; Upper Jurassic Phu Kradung Formation, Khorat Group.

Diagnosis. The holotype can be referred as a basal neornithischian and distinguished by an autapomorphy: ossified tendons which are a defining character for ornithischian restricted to the dorsal and sacral regions. Phu Noi neornithischian new taxon shows combination of both primitive and derived characters resembles those small-bodied ornithischian: the axial skeleton is composed of 15 dorsal and 5 sacrals; Brevis shelf of the ilium is visible in lateral view along entire length; a distinct supraacetabular flange on the pubic peduncle of the ilium; prepubis tip extends beyond distal end of preacetabular process of ilium; manus digit formula is 2-3-4-3-1. Mc III and Mc IV are longest, digits nearly equal in length.

Table 3 Occurrence of basal neornithischians in the Middle Jurassic – Early Cretaceous

Taxa	**Age**	**Formation**	**Occurrence**	**Reference**
Sanxiasaurus modaoxiensis	Aalenian-Toarcian	Xintiangou	China (Chongqing)	Li et al., 2019
Agilisaurus louderbacki	?Bajocian	Lower Shaximiao	China (Sichuan)	Peng, 1999
Hexinlusaurus multidens	?Bajocian	Lower Shaximiao	China (Sichuan)	He & Cai, 1983
Xiaosaurus dashanpensis	?Bajocian	Lower Shaximiao	China (Sichuan)	Dong & Tang, 1983
Kulindadromeus zabaikalicus	Bathonian	Ukureyskaya	Russia (Cherynyshevsky)	Godefroit et al., 2014
Yandusaurus hongheensis	?Oxfordian	Upper Shaximiao	China (Sichuan)	He, 1979
Phu Noi neornithischia new taxon	**?**	**Phu Kradung**	**Thailand (Kalasin)**	**This study**
Nanosaurus agilis	Kimmeridgian-Tithonian	Morrison	USA (Colorado, Wyoming)	Marsh, 1877
Hypsilophodon foxii	Berriasian-Barremian	Wessex	England (Isle of Wight)	Huxley, 1869; Galton, 1974
Leaellynasaura micagraphica	Albian	Eumeralla	Australia (Victoria)	Rich & Rich, 1989

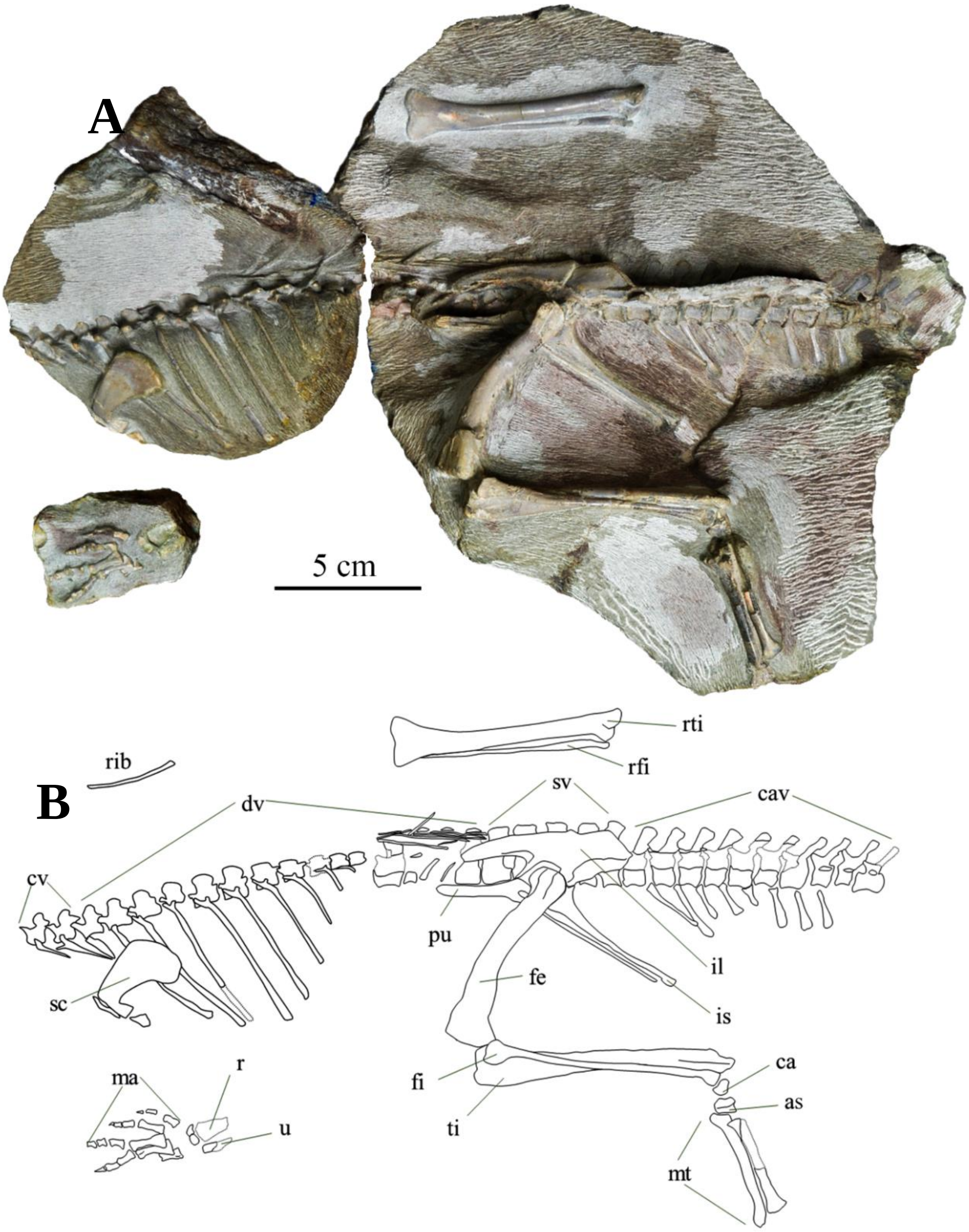

Figure 21 The holotype of Phu Noi neornithischia new taxon (PRC 150) in left lateral view. Photograph (A), and drawing (B).

Abbreviations: as, astragalus; ca, calcaneum; cav, caudal vertebrae; cv, cervical vertebrae; dv, dorsal vertebra; fe, femur; fi, fibula; il, ilium; is, ischium; ma, manus; mt, metatarsal; pu, pubis; r, radius; rfi, right fibula; rti, right tibia; sc, scapula; sv, sacral vertebra; as, astragalusrsal; ti, tibia; u, ulna.

Figure 22 The holotype of Phu Noi neornithischia new taxon in right lateral view.

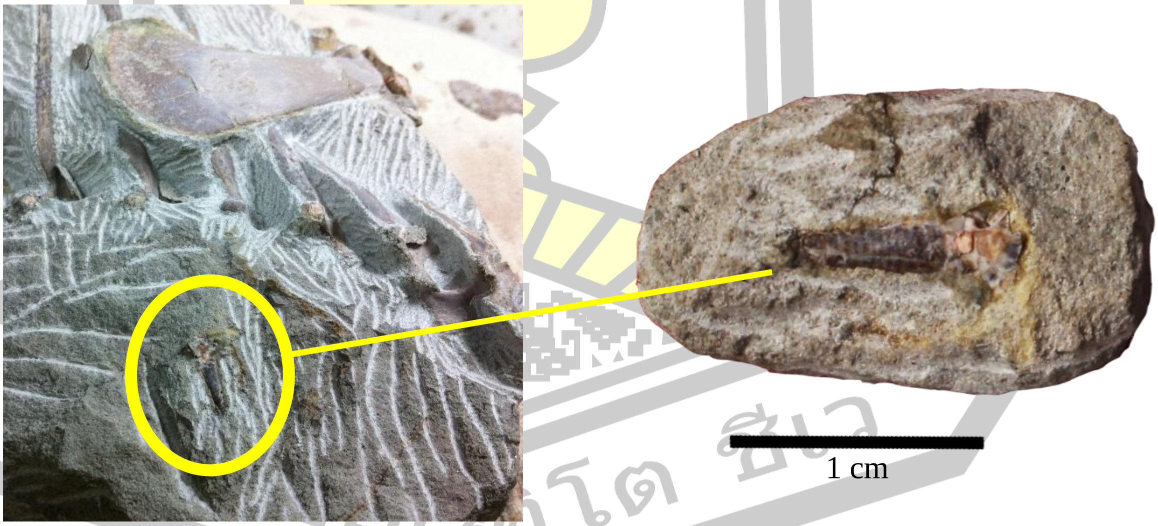

Figure 23 Isolated tooth of the holotype of Phu Noi neornithischia new taxon.

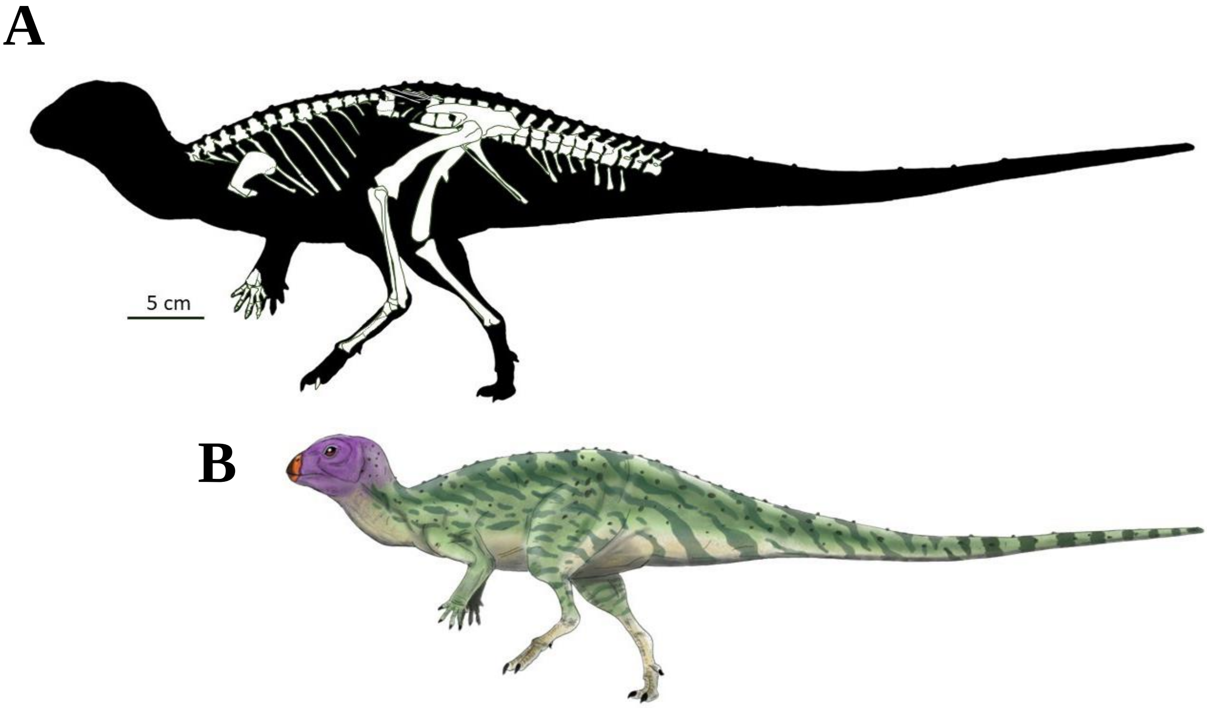

Figure 24 Reconstruction of Phu Noi neornithischia new taxon (PRC 150) in left lateral view. A composite skeletal of holotype individual (A), and life restoration (B). Drawing by Sita Manitkoon.

4.5.2 Description

Tooth

Only a single isolated tooth is preserved with the holotype specimen (Fig. 23). The crown is broken but still shows the fan-shaped. The cylindrical root has been preserved and curves to the labial side.

Cervical vertebrae

The last two posterior end of the cervical vertebrae are visible articulated in lateral view, being still largely buried in matrix (Fig. 21). Phu Noi neornithischian new taxon possibly has nine cervical vertebrae same as in the Jurassic basal neornithischians *Agilisaurus* and *Hexinlusaurus* (Table 4), if so, the preserved vertebrae are cv8 and cv9. The neural spines are small triangular shape. The shape of the centrum can't see clearly, cv3-9 are opisthocoelus (centrum is convex and the posterior is concave) in *Agilisaurus and Hypsilophodon* (Hulke, 1882; Peng, 1992), and are amphiplatyan in *Hexinlusaurus* (He & Cai, 1984b). The dorsal spine is small and triangular. Postzygopophyses are short and slightly higher than prezygopophyses. The diapophysis is approximately 90˚ from horizontal. The ribs are gradually broadened proximally. The position of the diapophyses seems higher up the neural arch.

Dorsal vertebrae

All 15 articulated dorsal vertebrae are preserved on the holotype (Fig. 21), and the left lateral side preserves all the ribs. The shape of the centra seems rectangular in dc12-dv15 in the right lateral view, same as *Agilisaurus*, *Hexinlusaurus* and *Yandusaurus* (He & Cai, 1984a; Peng, 1992). Dv11 has posterior articular end plane of centra slightly convex, and dv12 has anterior end somewhat concave. Diapophyses are horizontally extended, and slightly inclined dorsally. Anterior dorsal ribs are relatively long with relatively large curvature, while the posterior ribs gradually shorten and straighten. The neural spines of dv2-dv15 are a thin rectangular plate, except dv1 is triangular similar to neural spines of cervical vertebrae. A distinct suture line delineates the neural arch from the centrum of dv12-dv15, indicates that this animal is a juvenile stage (Fig. 4.8).

Sacral vertebrae

There are five sacral vertebrae present. Distinct suture lines separate the neural arch from the centrum of sv1-2 (Fig. 25). Most of the sacral vertebrae being still buried in matrix. The neural spines are rectangular plates and seems relatively low.

Figure 25 The pin is sticked in point of a suture line between the neural arch and the centrum of dv15 of Phu Noi neornithischia new taxon.

Caudal vertebrae

The holotype preserves 10 articulated anterior caudal vertebrae (Fig. 26). The shape of the centra is unclear, but possibly is amphicoelus same as in *Agilisaurus* (Peng, 1992). The size of the posterior centra seems to be gradually getting smaller. The neural spine is narrow, long, and posteriorly inclined. Neural spines gradually lower anterior to posterior, with a gradual decrease in angle to the centrum as in *Agilisaurus and Hexinlusaurus* (He & Cai, 1984a; Peng, 1992). The diapophyses of anterior caudals are long but gradually shorten. The diapophyses are horizontally extended with shaped like a long thin plate. Haemal arches 1-8 have been preserved in position, and there is some slight damage to the distal end of arches 5, 6, and 8. Ha1-2 possesses the longest haemal arch with a laterally flattened and slightly posteriorly curved shaft. Posteriorly the arches (ha6-8) gradually decrease in size, the shafts become straight, and the distal ends become flattened and thinned.

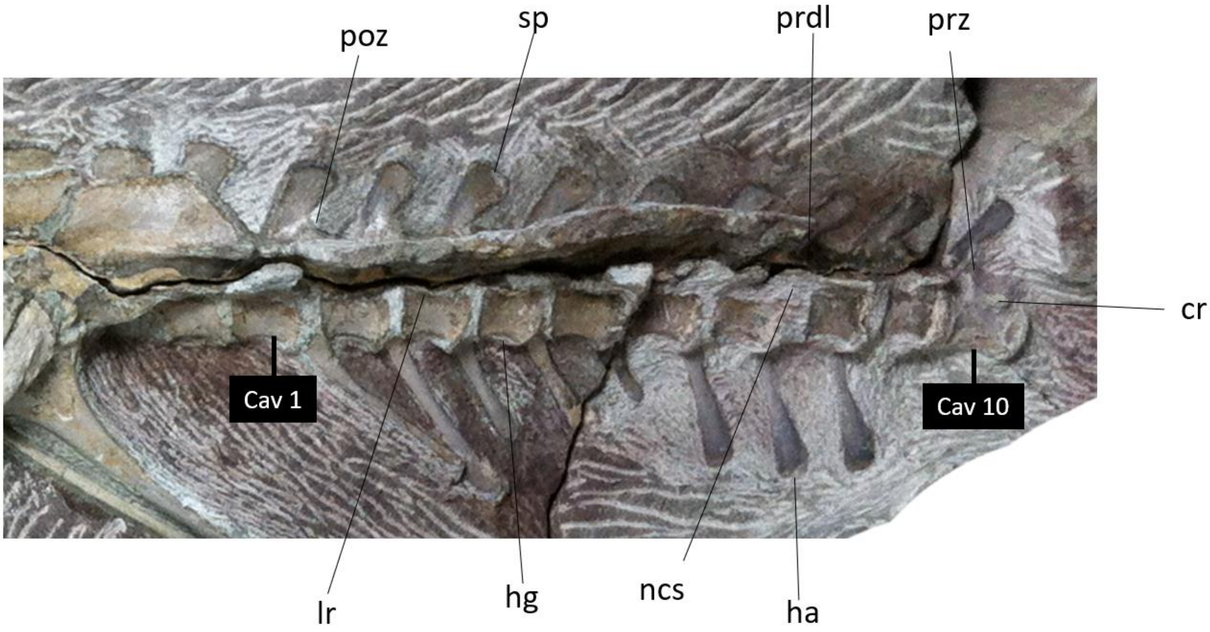

Figure 26 Anterior to middle caudal vertebrae of Phu Noi neornithischia new taxon.

Abbreviations: Cav, caudal vertebra and position; cr, caudal rib (transverse processes or pleurapophyses); ha, haemal arch/process; hg, haemal groove; lr, lateral ridge; ncs, neurocentral suture; pcdl, posterior centrodiapophyseal lamina; poz, postzygapophysis; prdl, prezygodiapophyseal lamina; prz, prezygapophysis; sp, spinal process.

Ossified tendons

The ossified tendons confirm that the specimen belongs to an ornithischian. This is the first report of the ossified tendons in Southeast Asian dinosaurs. Ossified tendons run longitudinally along the lateral surfaces of the neural spines of the dorsal vertebrae (They are clearly visible from the dv7) and terminate at the first sacral vertebra (Figs. 25,27). They are long, slender, and round in cross section, and appear to be parallel with each other. This type of ossified tendon is similar to that in the basal neornithischians *Agilisaurus louderbacki*, *Jeholosaurus shangyuanensis*, *Haya griva*, some basal ceratopsians such as *Ischioceratops zhuchengensis* (Han et al., 2012; He et al., 2015; Makovicky et al., 2011; Peng, 1992).

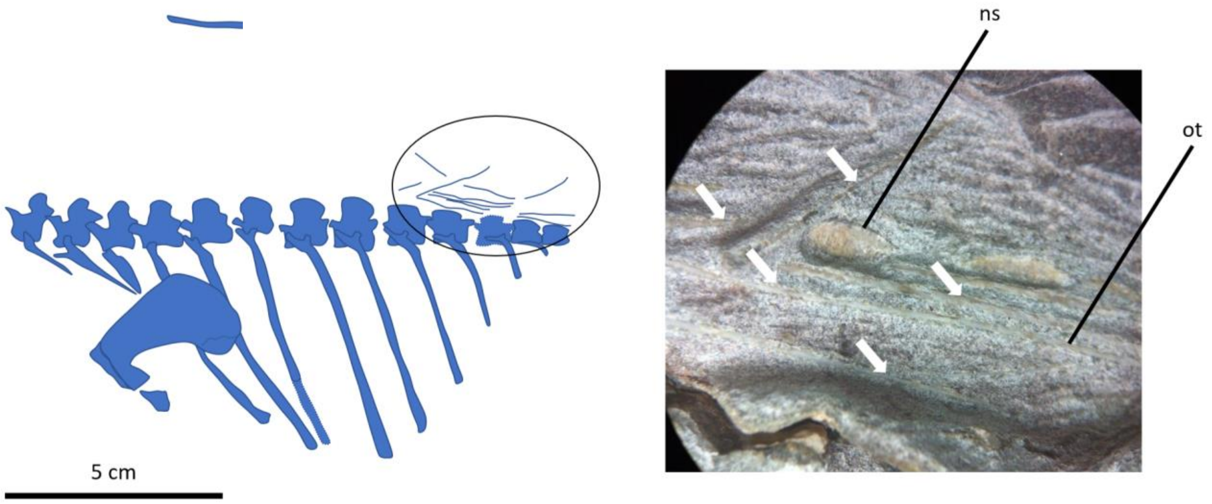

Figure 27 Articulated dorsal vertebrae held by ossified tendons.

Abbreviations: ns, neural spine; ot, ossified tendons.

Table 4 Vertebrae count of some ornithischian dinosaurs

Taxa	**Cervical**	**Dorsal**	**Sacral**	**Caudal**	**Reference**
Heterodontosaurus tucki	9	12	6	34-37	(Galton, 2014)
Lesothosaurus diagnosticus	9	15	5	35-50	(Baron et al., 2017b)
Agilisaurus louderbacki	9	15	5	44	(Peng, 1992)
Hexinlusaurus multidens	9	15	5	14+	(He & Cai, 1984a)
Phu Noi neornithischia new taxon	**?**	**15**	**5**	**?**	**This study**
Nanosaurus agilis	9	15	6	?	(Galton & Jensen, 1973)
Hypsilophodon foxii	9	15-16	5-6	45-50	(Galton, 1974)
Orodromeus makelia	9	15	6	30+	(Scheetz, 1999)
Convolosaurus marri	9	15	6	43	(Andrzejewski et al., 2019)

Appendicular skeleton

Pectoral girdle and anterior limb

Only the left scapula and left manus are preserved in the holotype of Phu Noi neornithischia new taxon

Scapula

The scapula blade is rather broad and short with a relatively straight anterior margin and slightly anteriorly curved posterior margin similar to *Hexinlusaurus* (He & Cai, 1984a). The distal end is relatively thin and distinctly expanded, attached the dorsal ribs of dv1-3 (Fig. 21). Near the ventral end is a ventral protuberance of the scapula. There is some damage to the scapula neck and coracoid facet.

Manus

The right forelimb is completely lost, but the left manus is articulated preserved with relatively complete digits and carpals (Fig. 27). The trace of the distal end of radius and the damaged ulna were still visible in the holotype specimen. the radiale articulates proximally with the medial margin of the radius, close to the metacarpal I. The intermedium articulates with radiale, and the medial margin of the distal radius. The carpus is less known in basal neornithischian (Norman et al., 2004). *Hexinlusaurus multidens* is formed an ulnare, intermedium, and radiale (He & Cai, 1984a). *Hypsilophodon foxii* bears only of the ulnare, intermedium, and one distal carpal (Galton, 1971). There is an ulnare, intermedium, and a single distal carpal in *Orodromeus makelai* (Scheetz, 1999). Finally, Phu Noi neornithischian new taxon is preserved only a radiale and intermedium.

The digit formula is 2-3-4-3-1 (Table 5). Mc III and Mc IV are longest, nearly equal in length, and have greatly expanded proximal ends and constricted shafts. This is different from other basal neornithischians such as *Hexinlusaurus multidens* and *Hypsilophodon foxii*, which are Mc II and Mc III are longest (Galton, 1971; He & Cai, 1984a), and it's probably the diagnosis character of this dinosaur. Mc I and Mc II are thin and flat. Mc V is the shortest metacarpal, there is no any phalanges after this bone similar to *Hypsilophodon foxii* (Galton, 1971). Ungual phalanges of digits I, II, and IV are clawed, but damaged in digit III.

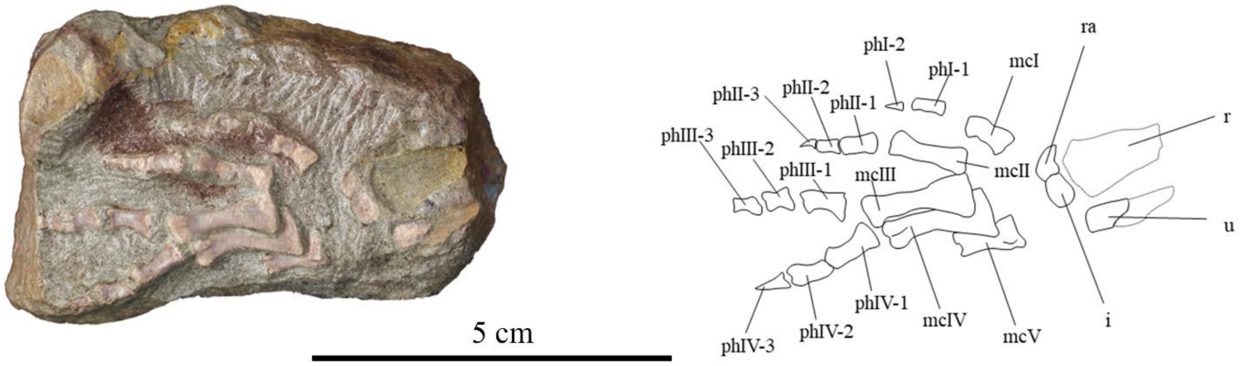

Figure 28 Posterior view of the left manus of Phu Noi neornithischia new taxon.

Abbreviations: i, intermedium; mc, metacarpal; ph, phalange; I-V, digits I-V; R, radius; ra, radiale; U, ulna.

Table 5 Manus and Pes formula of ornithischian dinosaurs

Taxa	**Family/clade**	**Age**	**Manus**	**Pes**	**Source**
Heterodontosaurus tucki	Heterodontosauridae	Early Jurassic,	2-3-4-3-2	2-3-4-5-0	(Norman et al., 2004)
Xiaosaurus dashanpensis	Basal neornithischia	Middle Jurassic	-	2?-3-4-5-0	(Dong & Tang, 1983)
Agilisaurus louderbacki	Basal neornithischia	Middle Jurassic,	-	2-3-4-5-0	(Peng, 1992)
Hexinlusaurus multidens	Basal neornithischia	Middle Jurassic	2-3-4-2?-2	2-3-4-5-0	(He & Cai, 1984b)
Phu Noi neornithischia new taxon	Basal neornithischia	**Late Jurassic**	**2-3-4-3-1**	**2-3-4-5-0**	**This study**
Hypsilophodon foxii	Basal neornithischia	Early Cretaceous,	2-3-4-3?-1?	2-3-4-5-0	(Galton, 1971)
Orodromeus makelai	Parksosauridae	Late Cretaceous	?-3-4-3-?	2-3-4-5-0	(Norman et al., 2004).
Dryosaurus altus	Iguanodontia	Late Jurassic,	2-3-4-3-2	0-3-4-5-0	(Norman et al., 2004)
Tenontosaurus tilletti	Iguanodontia	Early Cretaceous,	2-3-3-2-1	2-3-4-5-0	(Dodson 1980; Forster 1990a)
Camptosaurus dispar	Iguanodontia	Late Jurassic	2-3-3-2-1	2-3-4-5-0	(Gilmore 1909; Erickson 1988
Iguanodon bemissartensis	Iguanodontidae	Early Cretaceous,	2-3-3-2-4	0-3-4-5-0	(Norman 1980)
Edmontosaurus regalis	Hadrosauridae	Late Cretaceous,	0-3-3-3-3	0-3-4-5-0	(Norman et al., 2004).

Table 6 Pectoral, pelvic girdles, and limb bones measurements of Phu Noi neornithischia new taxon.

Element	**Measurement (mm)**	
Scapula (L)	Length	48.12
	Proximal width	18.0
	Distal width	25.70
	Smallest diameter of shaft	10.44
Ilium (L)	Length	70.37
	Height	14.66
	Length of anterior lobe	?
	Breadth of acetabulum	7.26
Pubis (L)	Length	103.04
	Length of preprocess	?
	Length of postprocess	?
Ischium (L)	Length	65.38
	Proximal width	16.41
	Distal width	4.11
	Smallest breadth shaft	3.27
Femur (L)	Length	82.08
	Proximal width	14.07
	Distal width	19.69
	Smallest shaft diameter	9.78
Tibia (L)	Length	100.82
	Proximal width	15.86
	Distal width	?
	Smallest shaft diameter	9.29
Fibula (L)	Length	95.41
	Proximal width	9.64
	Distal width	7.38
	Smallest shaft diameter	3.74

Pelvic girdle and posterior limb

The relatively well preserved left pelvic girdle and left hind limb are present in situ on the holotype of Phu Noi neornithischia new taxon. The isolated right femur, tibia with fibula is fall-off apart. The most right lateral side of the pelvic girdle is laterally compressed.

Ilium

The left ilium is well preserved (Figs. 21, 25), and the outline is similar to *Agilisaurus*, *Hexinlusaurus* and some basal neornithischians (Fig. 28). The iliac blade is thinly plate and slightly concave laterally. The preacetabular process of the ilium is narrow, long with a perfectly rounded termination, and slightly ventrally curved. The postacetabular process is short and high. There is a distinct suture between preacetabular process and post acetabular process, above the ischial peduncle. The acetabulum is semicircle shaped. The dorsolateral side of the acetabulum is distinctly thickened to compose a round and smooth supraacetabular flange/crest same as in *Agilisaurus*, *Sanxiasaurus*, and *Jeholosaurus* (Han et al., 2012; Li et al., 2019; Peng, 1992). This supra-acetabular flange was subsequently lost in neornithischians more derived than *Agilisaurus* as an improvement of their bipedal stance (Dieudonné et al., 2020). The brevis shelf of the ilium is directed ventromedially along its entire length and is clearly visible in lateral view, as in *Agilisaurus*, *Sanxiasaurus*, *Lesothosaurus*, and basal thyreophoran such as *Scelidosaurus* (Barrett et al., 2005; Li et al., 2019; Peng, 1992). The ischial peduncle of the ilium projects ventrally.

Pubis

The left pubis is thin and long with a sharply pointed anterior end. The prepubic blade is rod-like shape, elongated into distinct anterior process and extends beyond distal end of preacetabular process of ilium as in *Hexinlusaurus* and other neornithischians, but contrary with *Agilisaurus* (He & Cai, 1984a, Peng, 1992). The pubis rotated posteroventrally to lie alongside the ischium. The body of pubis makes substantial contribution to the margin of the acetabulum. The obturator foramen is obscured in lateral view. The posterior process is particularly elongated and terminates nearly at the same point as the ischium. The shaft is rotated at its midpoint, and the distal end is thin as in *Hexinlusaurus* (He & Cai, 1984a).

Ishium

The ischium is long, and flat with a broad proximal end for articulation with the pubis (Fig. 21). The ischial shaft is relatively straight and twisted mediolaterally as in most basal neornithischians such as *Lesothosaurus*, *Sanxiasaurus*, *Agilisaurus*, *Hexinlusaurus*, *Nanosaurus*, and *Kulindadromeus* (Baron et al., 2017; Carpenter & Galton, 2018; Godefroit et al., 2014; He & Cai, 1984a; Li et al., 2019; Peng, 1992). There is tap-shaped obturator process located much proximally. The ischial shaft gradual broadens and becomes broadest at the distal end. There is no groove on the dorsal margin as in some basal ornithischians such as *Eocursor*, *Lesothosaurus*, and *Agilisaurus* (Baron et al., 2017b; Barrett et al., 2005; Butler, 2010; Peng, 1992).

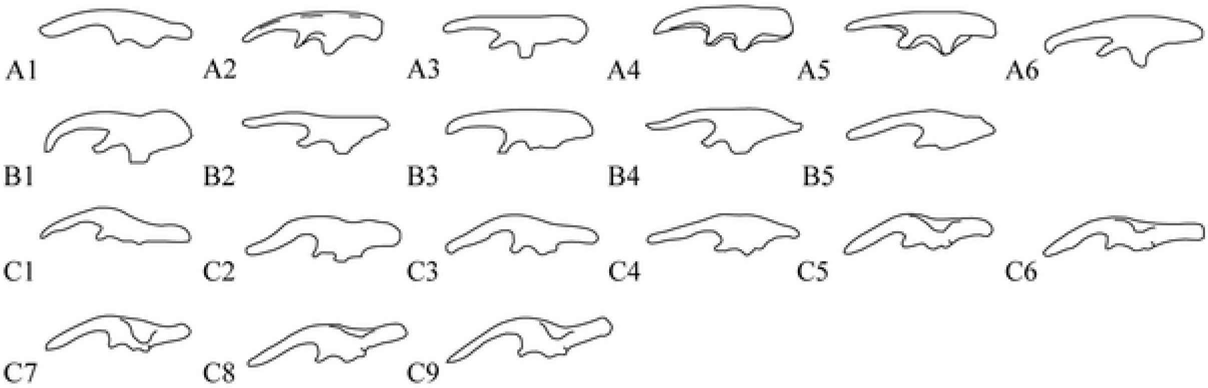

Figure 29 Ornithischian left ilia in lateral view. (He et al., 2015). All figures are just outlines, similar but not identical to the original image. All figures are for illustrative purposes only. Outlines are not to scale.

A1, *Heterodontosaurus tucki;* A2, *Othnielia agilis;* A3, *Hypsilophidon foxii*, A4; *Hexinlusaurus multidens*; A5 *Agilisaurus louderbacki*; A6, *Jeholosaurus shangyuanensis*;

B1, *Tenontosaurus tilleti;* B2, *Dryosaurus;* B3, *Camptosaurus dispar;* B4, *Iguanodon atherfieldensis*; B5, *Ouranosaurus nigeriensis*;

C1, *Gryposaurus incurvimanus*; C2, *Parasaurolophus cyrtocristatus*; C3, *Corythosaurus casuarius*; C4, *Gilmoreosaurus mongoliensis*; C5, *Brachylophosaurus canadensis*; C6, *Edmontosaurus regalis*; C7, *Saurolophus osborni*; C8, *Maiasaura peeblesorum*; C9, *Kritosaurus navajovius*.

Femur

The left and right femur are preserved (Figs. 21-22). They are robust and almost complete. The shaft of the femur is bowed in lateral view resembles that of *Hexinlusaurus multidens* (He & Cai, 1984b), *Agilisaurus louderbacki* (Peng, 1992) *Hypsilophodon foxii* (Galton, 2009) (Fig. 29) and the Dan Luang neornithischian (see chapter 3). The right femur possess a well-developed femoral head (caput femoris) which perpendicular to the shaft as in most basal neornithischians (Makovicky et al., 2011). The anterior end of the greater trochanter is slightly convex, while 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 portion of fourth trochanter is form a pendant shaped that lies posteromedially one-third the distance proximal end of the femur. Early ornithischian dinosaurs are uniquely characterized by a fourth trochanter with a prominent pendant process (Persons & Currie, 2020). An oval foramen occurs at medial surface laterally base of the fourth trochanter and the femoral shaft for muscle insertion. The distal portion of the femoral shaft shows mediolaterally expanding towards the distal condyles, posteriorly the distal condyles are separated by a caudal intercondylar groove, *M. caudofemoralis* longus (Andrzejewski et al., 2019; Butler, 2010), as in other basal neornithischian such as *Sanxiasaurus*, *Agilisaurus*, *Hexinlusaurus* (He & Cai, 1984a; Li et al., 2019; Peng, 1992).

Tibia

Both left and right tibiae are preserved together with fibulae (Fig. 21), they are longer than the femora as in other basal neornithischians, indicated fast-running adaptation (Galton, 1971). The left tibia rests in lateral view while the right tibia shows in posterior view.

The tibia shaft is robust, long, straight, and twisted along its long axis. Its proximal end is strongly inflated into a triangular surface and shows a division into three distinct processes: cnemial crest, fibular condyle and medial condyle. The well-developed cnemial crest projects forward and curves laterally to form a fossa for accommodating the head of the fibula. The distal end is a distinctly transversely broadened triangle with a concave anterior surface, convex posterior surface, and a swollen ridge at its midpoint as in *Agilisaurus* (Peng, 1992). The proximal tibia also contributes to the platform for the lateral femoral condyle and contributes to the base of the cnemial crest. The medial malleolus extends farther distally for accommodation the distal end of the fibula on its anterior surface.

Fibula

The fibula is straight, long, and gracile. It is enlarged to form a head for fitting to the fibular fossa of the proximal tibia. The distal end is transversely flattened to accommodate with the lateral tibia and the calcaneum.

Pes

The left astragalus and calcaneum comprise the only preserved tarsal elements. Generally, the astragalus bone is located directly below the tibia and medial to the calcaneum, and frequently fused together. In the holotype specimen of Phu Noi neornithischia new taxon, the astragalus is bigger, but it is fall-off apart below the calcaneum (Fig. 21). From a possibly anterodorsal view, the astragalus is smooth, slightly concave in the middle of the plate, and quite inclined on the side to be attached to the calcaneum. The calcaneum posits in the lateral view. It is represented as a small nubbin of bone that articulates proximally with the fibula and tibia. The astragalus and calcaneum are formed as upper series between the metatarsals below and the tibia and fibula above. In *Hexinlusaurus*, there are the lower series of small bones under astragalus and calcaneum called distal tarsus (including tarsi 1 and 2) (X. He & Cai, 1984a). However, there is no evidence of the distal tarsus in Phu Noi neornithischia new taxon.

The possibly left metatarsal III and IV are present (Fig. 21), but the proximal half of metatarsal IV is almost lost. They are long, slender and straight in lateral view as in *Agilisaurus*, *Hexinlusaurs*, and *Sanxiasaurus* (X. He & Cai, 1984a; N. Li et al., 2019; Peng, 1992),but different from that of *Lesothosaurus* and *Eocursor* which curved laterally distally (Baron et al., 2017b; Butler, 2010). The metatarsals seem an ovoid cross-section at the mid-shaft. The phalangeal formula is usually 2-3-4-5-0 in other neronithischians such as *Agilisaurus*, *Hexinlusaurus*, *Xiaosaurus*, *Hypsilophodon*, *Orodromeus* (Dong & Tang, 1983; Galton, 1971; He & Cai, 1984; Norman et al., 2004; Peng, 1992) (Table 5). The proximal and distal ends are expanded anteroposteriorly. Distally, metatarsal III possess facet for accommodation the medial surface of metatarsal IV.

Although the pedal phalanges are missing, a single isolated ungual is preserved at the right lateral side of the specimen, above the right ilium (Fig. 22). It is tapering, narrow pointed, claw-like in lateral view, and dorsoventrally flattened.

Referred material.

Material: PRC 149 (renumbered from PN 13-09 in Buffetaut et al. 2014), a lower jaw (Fig. 6A-B).

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

Comment: see in chapter 3.

Material: SM2021-1-132, a left pes with tibia, astragalus, and calcaneum (Fig. 30)

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

Comment:

This left tibia is approximately 2.3 times longer than the tibia of the holotype specimen. Metatarsal V is absent. The left pes preserves the complete phalangeal formula is 2-3-4-5-0 as in other neronithischians such as *Agilisaurus*, *Hexinlusaurus*, *Xiaosaurus*, *Hypsilophodon*, *Orodromeus* (Dong & Tang, 1983; Galton, 1971; He & Cai, 1984; Norman et al., 2004; Peng, 1992) (Table 5). Mt III is the longest, and Mt I is the shortest. The phalanges are long and slender. The claws are sharp and triangular, but not very recurved.

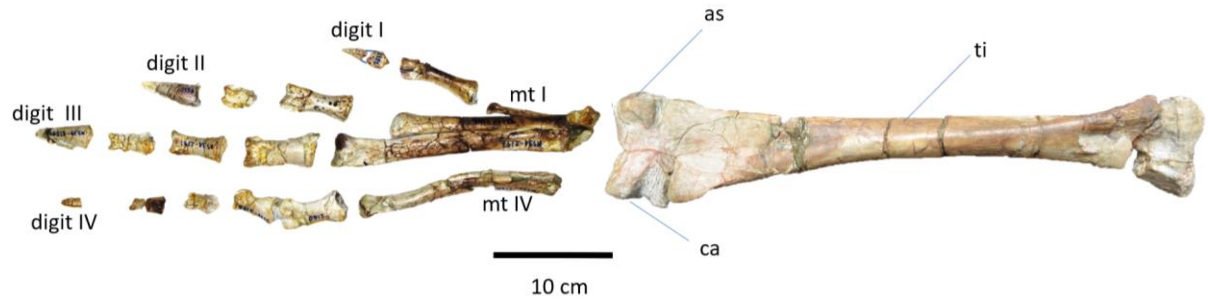

Figure 30 SM2021-1-132, a left pes with tibia in dorsal view.

Abbreviations: as, astragalus; ca, calcaneum; mt, metatarsal; pph, pedal phalanx; ti, tibia.

Table 7 Dental count and enamel distribution on tooth crowns of some ornithischians.

Taxa	**Premaxilla**	**Maxilla**	**Enamel distribution**	**Mandible**	**Enamel distribution**
Pisanosaurus mertii	?	11+ (17-18?)	symmetry	15	symmetry
Heterodontosaurus tucki	3	12	asymmetry	?	asymmetry
Echinodon becklessii	3	~11	symmetry	10	symmetry
Tatisaurus oehleri	?	?	symmetry	18	symmetry
Lesothosaurus diagnosticus	6	~14	symmetry	~14	symmetry
Agilisaurus louderbacki	5	14	symmetry	20	symmetry
Hexinlusaurus multidens	?	18	symmetry	20	symmetry
Xiaosaurus dashanpensis	?	?	symmetry	?	?
Yandusaurus hongheensis	?	15	asymmetry	?	?
Phu Noi neornithischia new taxon.	**?**	**?**	**?**	**?**	**asymmetry**
Nanosaurus agilis	?	?	asymmetry	13	asymmetry
Kulindadromeus zabaikalicus	?	?	?	?	asymmetry
Leaellynasaura amicagraphica	?	?	asymmetry	?	?
Hypsilophodon foxii	5	10-11	asymmetry	13-14	asymmetry
Convolosaurus marri	4	8-10	asymmetry	11	asymmetry
Dysalotosaurus lettowvorbecki	0	13	asymmetry	11-12	asymmetry

4.5.3 Phylogenetic Analysis

The systematics of basal neornithischians is still problematic (Barrett et al., 2005; Butler et al., 2008). A variety of basal forms that traditionally referred to as hypsilophodontids (Barrett et al., 2005; Butler et al., 2008; Sereno, 1999). Many taxa, were once considered as early member of ornithopods, have been changed into the basal neornitischians (Madzia et al., 2019, 2021).

In order to assess the phylogenetic position of Phu Noi neornithischia taxon, a cladistic analysis was performed. The data matrix was based on that of Baron et al. (2017) modified from Butler and Sullivan (2009) (Appendix 1), which consists of 55 tata and 227 characters. Six unstable ‘wild card’ taxa including *Yandusaurus*, *Anabisetia*, *Echinodon*, *Yueosaurus*, *Koreanosaurus*, and *Laquintasaura* were excluded from the final data set creating a matrix of 49 taxa. *Euparkeria capensis* was included in the analysis as the outgroup. The data matrix was compiled in Mesquite v3.02. In our analysis, character of the holotype specimen (PRC 150) was added. The limit of the maxtree was set up at 30,000. A new technology search in TNT using sectorial search, ratchet, tree drift, and tree fuse options with default parameters and 100 random addition sequences. Our phylogenetic analysis generated 75 most parsimonious trees (MPTs) of 565 steps (consistency index (CI)=0.446; retention index (RI)=0.696).

This analysis confirmed that Phu Noi neornithischian new taxon was a basal neoceratopsian close to *Agilisaurus* and *Hexinlusaurus* from China.

Characteristic coding of Phu Noi neornithischia new taxon based on the matrix published by Baron et al., (2017).

```
?????  ?????  ?????  ?????  ?????  ?????  ?????  ?????  ?????  ?????
?????  ?????  ?????  ?????  ?????  ?????  ?????  ?????  ?????  ?????
?????  ?????  ?????  ?????  ?????  ?????  ???0?  012??  00?00  10??0
10???  ?0000  00001  00000  0?010  00100  0001?  110?0  01111  10120
20000  11110  ????0  10000  0??00  01
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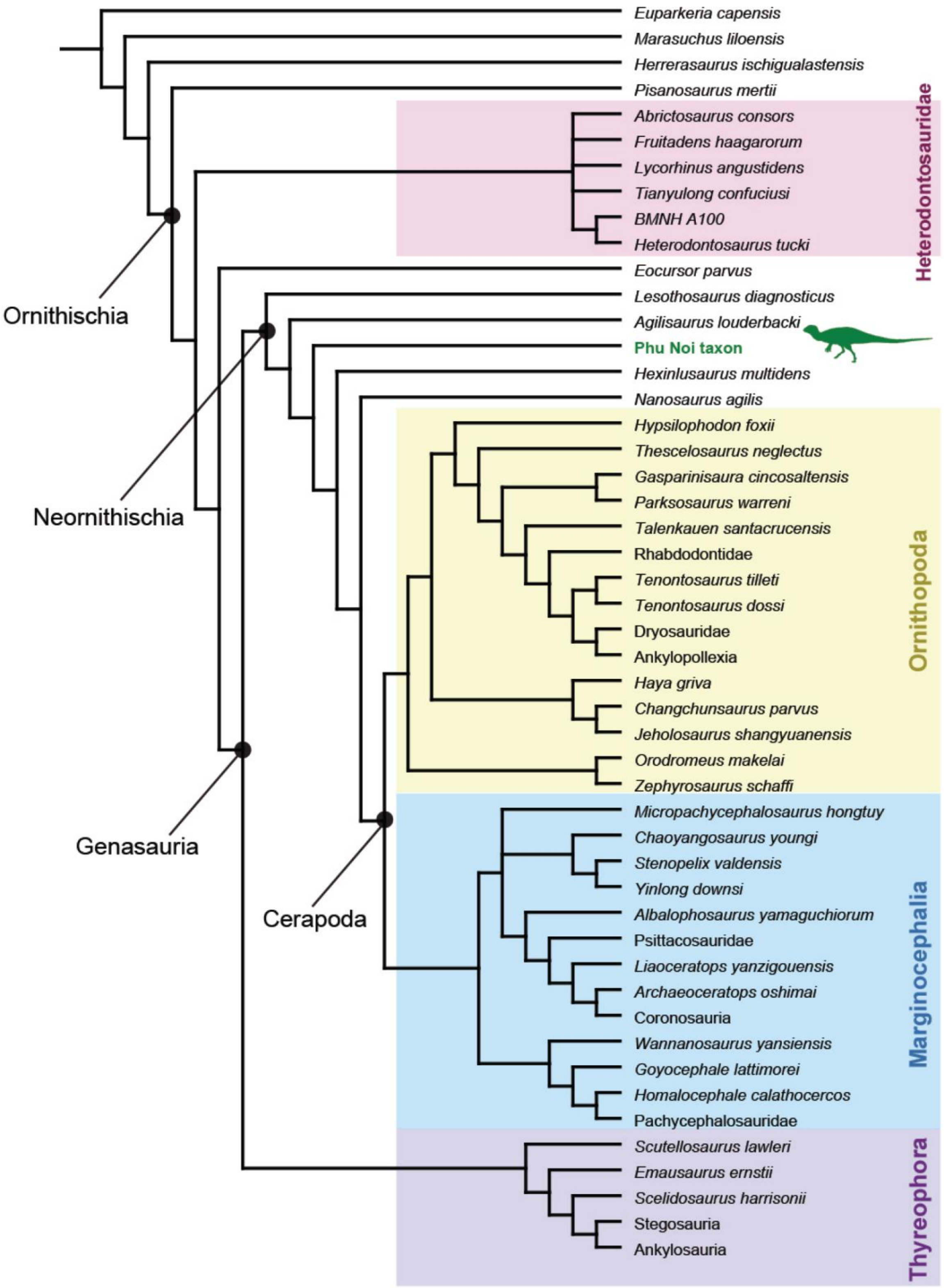

Figure 31 50% majority rule tree showing the phylogenetic relationships of Phu Noi neornithischia new taxon. Numbers on nodes indicate the percentage of trees that recovered that node.

4.6 Comparison and discussion

The strict consensus tree recovers Phu Noi taxon as among the most basal neornithischians (Fig. 31). The manus is unique and presumably autapomorphic, with Mc III and Mc IV are longest, nearly equal in length. This is different from other basal neornithischians such as *Hexinlusaurus multidens* and *Hypsilophodon foxii*, which are Mc II and Mc III are longest (Galton, 1971; He & Cai, 1984a).

Phu Noi neornithischian new taxon. shows combination of both primitive and derived characters of small basal neornithischians. The dorsolateral side of the acetabulum is distinctly thickened to compose a round and smooth supraacetabular flange same as in *Agilisaurus*, *Sanxiasaurus*, and *Jeholosaurus* (Han et al., 2012; Li et al., 2019; Peng, 1992). This supraacetabular flange was subsequently lost in neornithischians more derived than *Agilisaurus* (Dieudonné et al., 2020). The brevis shelf of the ilium is directed ventromedially along its entire length and is clearly visible in lateral view, as in *Agilisaurus, Sanxiasaurus, Lesothosaurus* (Barrett et al., 2005; Li et al., 2019; Peng, 1992). The prepubic blade is elongated into distinct anterior process and extends beyond distal end of preacetabular process of ilium as in *Hexinlusaurus* and other neornithischians, but contrary with *Agilisaurus* (He & Cai, 1984a, Peng, 1992). Phu Noi neornithischian new taxon has 15 dorsal and 5 sacrals as in other basal neornithischians (Table 4). The digit formula is 2-3-4-3-1 same as *Hypsilophodon* (Galton, 1971). The portion of fourth trochanter is form a pendant shaped, which is a unique character among the basal neornithischians (Persons & Currie, 2020).

Numerous specimens of limb bones from various sizes of basal neornithischians were also found at the Phu Noi site, indicating that these dinosaurs were abundant in this area. I infer that many isolated bones of basal neornithischians from this site are the same animal, but of different ages (see chapter 5). The referred materials provide further information of this taxon, including PRC 149, a lower jaw; SM2021-1-132, a left pes with tibia, astragalus, and calcaneum. The dentary teeth of PRC 149 and other isolated teeth from Phu Noi are different in having asymmetrically distributed enamel on the teeth (Table 7). *Agilisaurus louderbacki* and *Hexinlusaurus multidens* exhibit symmetrically distributed enamel (Barrett et al., 2005; Peng, 1992), but teeth from Phu Noi possess the advance condition of asymmetrically distributed enamel 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; Carpenter & Galton, 2018; Galton, 2009). The ornamented lingual side do not show a prominent median ridge contrasting with the European Early Cretaceous *Hypsilophodon foxii* (Galton, 2009) and other derived neornithischians. The pes phalangeal formula of Phu Noi neornithischia new taxon is 2-3-4-5-0 as in other neronithischians such as *Agilisaurus*, *Hexinlusaurus*, *Xiaosaurus*, *Hypsilophodon*, *Orodromeus* (Dong & Tang, 1983; Galton, 1971; He & Cai, 1984; Norman et al., 2004; Peng, 1992).

The femur length of the holotype is 8.2 cm (Table 6). The body length of this dinosaur estimated to be about 0.6 m. comparison with *Agilisaurus* (Peng, 1992). However, distinct suture lines appear on the vertebrae, indicates that it is a juvenile stage. I assume that an adult stage can be up to 2 meters long, compared to the longest femur found (about 26.6 cm. in length).

Phu Noi neornithischia new taxon shows the oldest record of ornithischian dinosaurs in southeast Asia so far. They lived together with mamenchisaurid sauropods, metricanthosaurid theropods, and possibly stegosaurids from the lower part of the Late Jurassic Phu Kradung Formation. (Buffetaut et al. 2001, Chanthasit et al. 2019, Cuny et al. 2014, Manitkoon and Deesri 2019). Racey and Goodall (2009) supposed that the lower Phu Kradung Formation could be Late Jurassic in age, which was also supported by the evidence from vertebrate remains (Buffetaut et al. 2001, Buffetaut et al. 2006).

4.7 Conclusion

The Phu Noi locality contains a wealth of specimens providing an exceptional articulated skeleton, represents one of the best-preserved dinosaurs ever found from Southeast Asia. The specimens reveal a new species of basal neornithischian with a unique set of both basal and derived characters. The unique aspect of the Phu Noi neornithischian new taxon is the manus, Mc III and Mc IV are longest different from other basal neorithischians. Phu Noi neornithischian new taxon is the earliest record of neornithischian in Southeast Asia. The finding adds diversity and helps elucidate the evolution of basal neornithischian dinosaurs in this region. Many of the remaining bones are still in the process of fossil preparation, including part of the skull. These examples may provide a better understanding of biology and more information of this dinosaur in the future.

Chapter 5

Preliminary study on the bone histology of basal neornithischian from the Phu Noi locality, Phu Kradung Formation of Thailand

Some part of this chapter was presented in Manitkoon, S., Deesri, U., Chanthasit, P., and Wannachan, A., 2022. Preliminary study on the bone histology of basal neornithischian dinosaur from the Late Jurassic Phu Kradung Formation of Thailand. The 6th International Palaeontological Congress in Khon Kaen, Thailand 2022.

Figure 32 Mounted skeleton of *Dysalotosaurus* in Museum für Naturkunde, Berlin (Source: https://prometheus.med.utah.edu/~bwjones/2012/07/museum-fur-naturkunde-berlin/)

5.1 Introduction

Histologic studies have been utilized by the palaeontologist to understand the life history of those extinct animals. With the combination of data from the tissue structure with morphological, taphonomical, and statistical data (Reizner, 2010), it is possible to get a much better established and higher significant view of the life history and sometimes even the social structure and behavior of extinct species (Hübner, 2012).

All terms and study on bone histology in this study are following the study of Hübner (2012), who studied on the bone histology of a small ornithopod *Dysalotosaurus lettowvorbecki*. It is known from thousands of bones and several ontogenetic stages and was found in a single locality within the Tendaguru Formation of southeastern Tanzania, possibly representing a single herd. *Dysalotosaurus* provides a case study for examining variation in bone microstructure and life history and helps to unravel the growth pattern of small ornithischian dinosaurs (Hübner, 2012).

Palaeontologists usually estimate the age of extinct tetrapods by observing the growth cycle (Chinsamy-Turan, 2005; Erickson, 2005; Varricchio, 1993). The degree of vascularization, the orientation of vascular canals, and the degree of organization of the collagenous matrix are direct reflections of the local bone growth rate. When growth slows down and/or stops completely, which typically occurs annually, it is marked by a line of arrested growth (LAGs) or other types of growth marks. The schematized structures may not all necessarily be found together within a single section (Bailleul et al., 2019).

However, an accurate count of the number of annuli/LAGs is often interrupted by the ontogenetic expansion of the marrow cavity and/or secondary remodeling (Hübner, 2012). This problem was often solved by the examination of an ontogenetic series or by the back-calculation of the lost/obscured number of annuli/LAGs (Erickson, 2000; Horner et al., 2000; Horner & Padian, 2004; Hübner, 2012; Klein & Sander, 2007). There is also a high variability in the number of annuli/LAGs between different individuals within a single population, between different skeletal elements of one individual, and sometimes even in the cross-section of a single bone (John R. Horner et al., 2000; Klein & Sander, 2007; Ricqlès de, 1983). The method used to estimate the relative age of extinct animals is ‘Amprino’s Rule’ (Klein & Sander, 2007), which can help to estimate the growth rate of an extinct species, but, as for skeletochronology, the results are strongly dependent on body size, ontogenetic stage, and skeletal element and should always be considered in comparison with other individuals, populations, and species (Hübner, 2012).

Among dinosaur groups, ornithopods are one of the best-studied concerning bone histology, because several species are known from many individuals of different growth stages (Chinsamy, 1995; John R. Horner et al., 2000; Hübner, 2012; Vanderven et al., 2014). It has even proved possible to reconstruct the breeding strategy and life history of some taxa. The growth pattern of large ornithopods is quite well known, whereas the bone histology of many small ornithopods and basal neornithischians still has problematic for their growth patterns (Chinsamy-Turan, 2005; Chinsamy, 1995; Chinsamy et al., 1998; John R. Horner et al., 2009). In particular, the scarcity of annuli/LAGs, the usual tool for age estimations, has considerably complicated the reconstruction of their life history. The discovery that annuli/LAGs are present in *Dysalotosaurus* and *Dryosaurus* helped interpretations of their growth patterns (John R. Horner et al., 2009; Hübner, 2012). However, the inconsistent development of annuli/ LAGs made it necessary to examine another type of growth cycle for the reconstruction of the life history of *Dysalotosaurus* (Hübner, 2012). Due to the scarcity of annuli/LAGs, the reconstruction of the life history of *Dysalotosaurus* was carried out using regularly developed and alternating slow and fast-growing zones.

Hübner (2012) indicated the ontogenetic stages in femora of *Dysalotosaurus* as 5 stages.

Stage 1 or Embryonic/Perinatal Stage. This stage, already described in some other ornithopods, is not represented in the sampled femora of *Dysalotosaurus*, and the overall size of other known specimens indicates that none of the preserved femora would fit into this stage.

Stage 2 or Early Juvenile Stage. The marrow cavity is very large compared to the bone wall thickness. The internal anterior wedge, if present, consists of compacted coarse cancellous bone (CCCB) that is not yet compacted. The posterolateral corner and the respective Plug are weakly pronounced. The periosteal compact bone tissue has a high number of longitudinal vascular canals. The primary osteons are often isolated from each other by thick bands of well-organized and relatively uniformly birefringent woven-fibered matrix (knitted texture). Particularly in the internal part anteriorly, only simple vascular canals are present. There is at most one slow-growing zone developed at the external edge of the cortex.

Stage 3 or Late Juvenile Stage. The external circumferential profile is more pronounced, and the Posterolateral Plug is well visible. The drift of the marrow cavity from approximately anterior to posterior is in progress, which is indicated by the well-compacted CCCB of a larger anterior wedge as well as a deeper incision into the posterior bone wall. The primary osteons are more numerous and there is a decrease in the proportion of knitted texture. There are the first occurrences of isolated secondary osteons. Growth cycles are well distinguishable and reach two to three in number.

Stage 4 or Sexually Immature Stage. The development of the external cross-sectional profile as well as of distinct areas (e.g. the Posterolateral Plug) is now complete. The anterior wedge of the CCCB is more pronounced, although this also depends on the relative position of the cross section within the shaft. The marrow cavity is deeply incised into the posterior wall. The density of well-developed primary osteons is very high in the thick and fast-growing parts of the sections. Secondary osteons are more abundant and can also occur in the Posterolateral Plug and the anterior corner. The number of growth cycles is three to five.

Stage 5 or Sexually Mature Stage. The units of the cross-sectional bone wall are strongly diversified. The anteroposterior migration of the marrow cavity interrupts up to four growth cycles posteriorly. Secondary osteons are numerous forming clusters anteriorly and posterolaterally at different distances from the external surface. The number of growth cycles reaches up to nine and the transition from well-distinguishable fast and slow-growing zones internally to the diffuse and more uniform wide zone externally is visible in five of the largest cross sections.

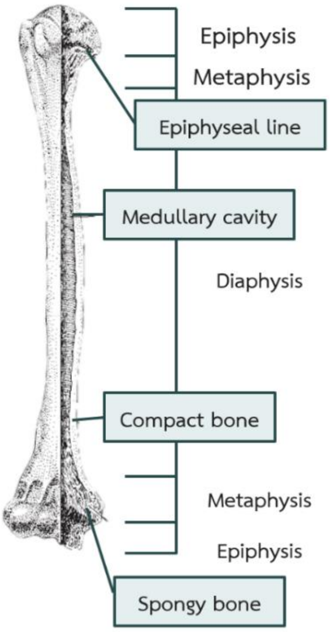

Figure 33 Composition of long bone (modified from Kardong, 1997)

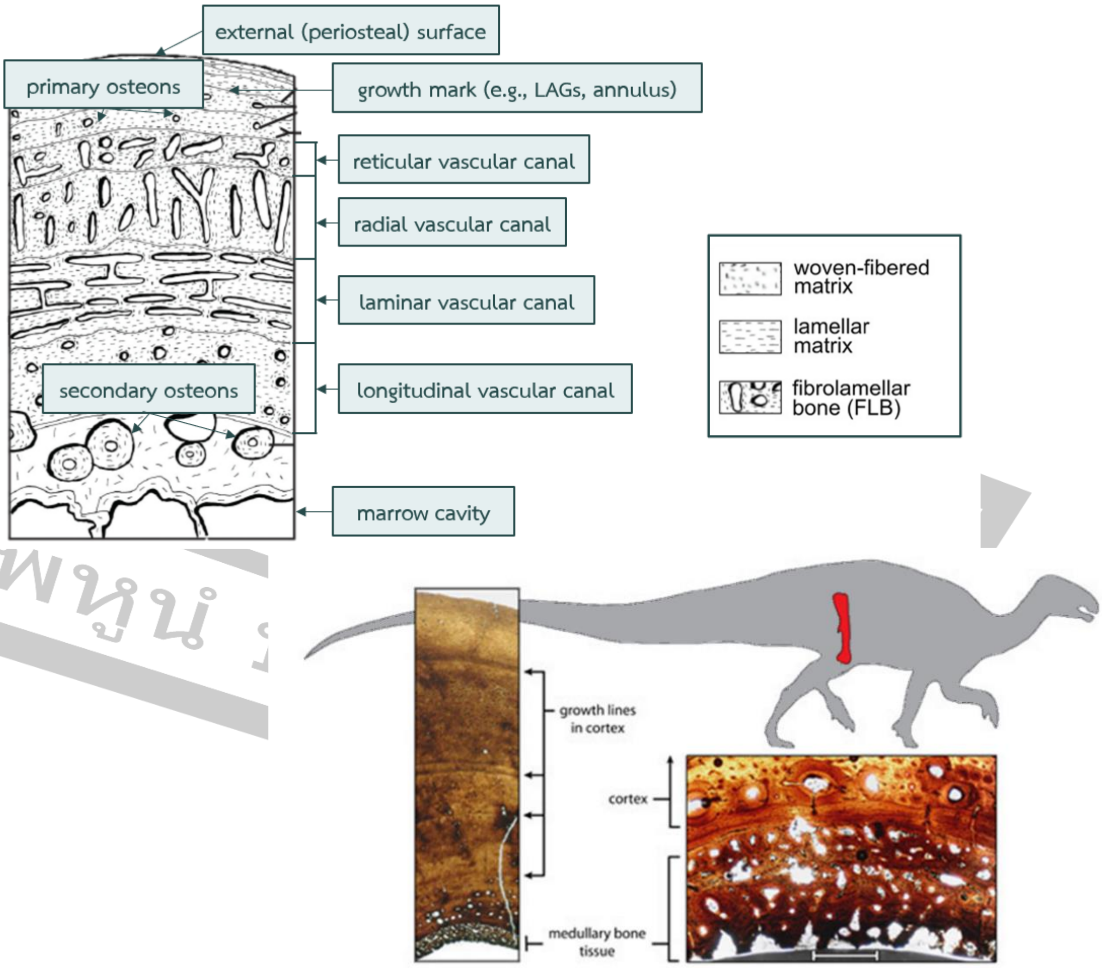

Figure 34 (above) Schematic representation of the cortex of a long bone seen in cross-section (modified from Huttenlocker, Woodward & Hall, 2013). (below) Bone histology of femur of ornithopod dinosaur (modified from Sarah Werning/UC Berkeley & Andrew Lee/Ohio University, fossil courtesy of the Oklahoma Museum of Natural History)

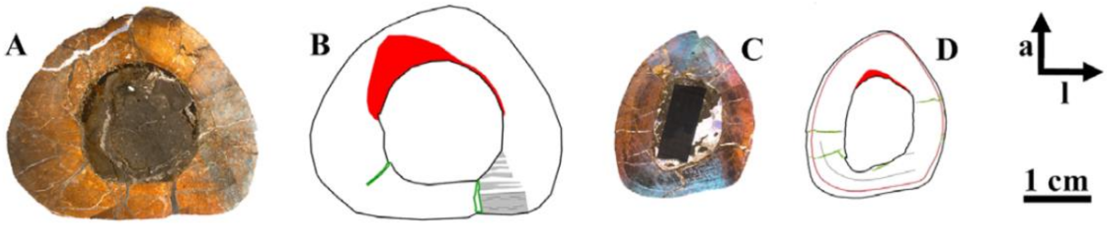

Figure 35 Representative cross sections and corresponding sketches of *Dysalotosaurus* femora.

A–B: Large femur GPIT/RE/ 3588, cut distally to the base of the fourth trochanter; C–D: Medium sized femur GPIT/RE/3587, cut close to the base of the fourth trochanter; All sections are oriented and scaled consistently. Internal red area represents CCCB or an endosteal layer (B, D). Lines in green mark cross sectional damage. Growth cycles are shaded (B) or lined (D) in gray, annuli/LAGs are lined in red (Modified from Hübner, 2012).

5.2 Material and methods

The materials used for thin sectioning, were housed in the Palaeontological Research and Education, Mahasarakham University. Five femora were chosen for this study, including PN14-300, PN14 -271, PN15-11, PN14-320, and PN-unnumbered (Figs. 36A-E). The sections are standardized to a single interval along the bone shaft and not to a single level (Fig. 36F). Distinct processes or expansions helped to verify the relative position of the section. Proximal femora possessed the fourth trochanter and distal femora a strong proximodistal, laterally expanding shelf (Hübner, 2012). All femoral sections were made either at the base of the fourth trochanter or approximately at the proximal end of the lateral shelf, except for the PN-unknow that only preserved the distal end.

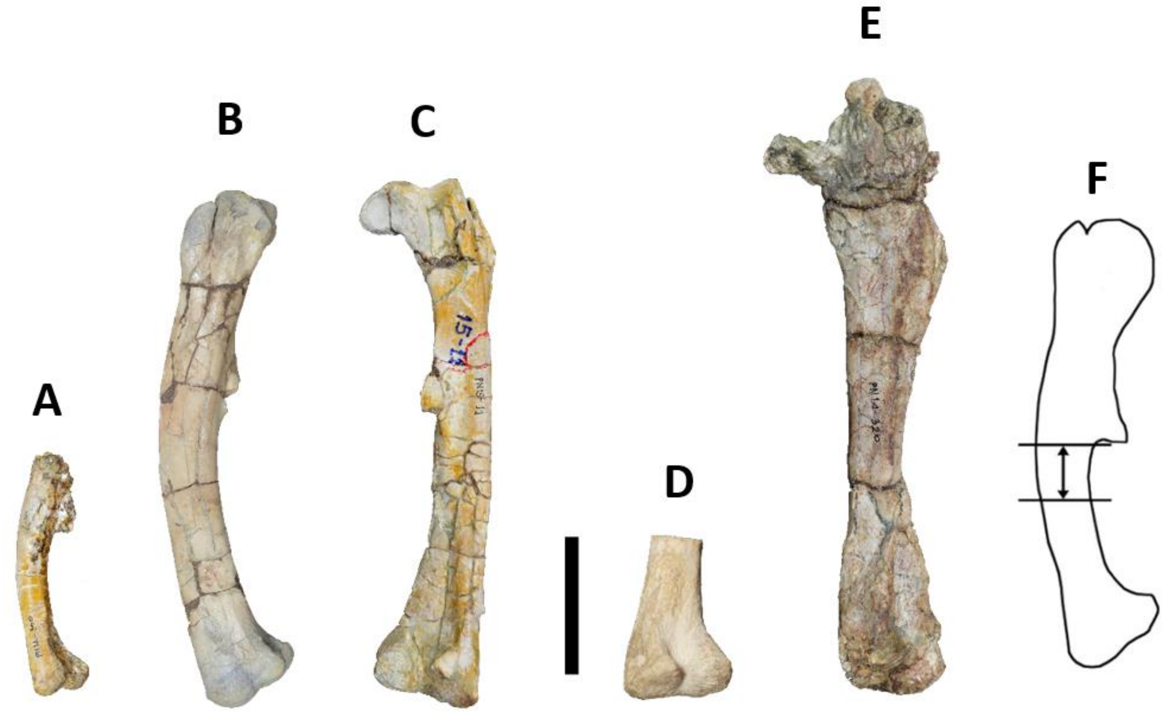

Figure 36 Femora elements of Phu Noi neornithischians for this study.

A: left femur PN14-300 in lateral view; B: left femur PN14-271 in lateral view; C: right femur PN15-11 in posterior view; D: left femur PN-unnumbered in posterior view; E: right femur PN14-320 in posterior view; F: interval cutting level in the femur (lateral view) modified from Hübner (2012). (Scale bar A-E = 5cm).

Figure 37 Method of thin section.

1: specimens for thin section, 2: Crosscutting the specimen with the stone cutting machine (Hillquist), 3: Flatten the surface of the specimen with silicon-carbide powder (SiC), 4-5: Mount the specimen to the slide with thermoplastic, 6-7: Grinding the specimen slide until thin enough for microscopy. Mounting and labeling the stub, 8: Microscopy of thin section (Nikon eclipse E200).

5.3 Results

5.3.1 PN14-300

The thin section of the left femur PN14-300 (Fig 36A) shows a distinctive feature with the marrow cavity which is large relative to the bone wall (Fig. 38A). Fibrolamellar bone tissue, which is a disorganized arrangement or arrangement of collagen fibers, and another type of tissue, compacted coarse cancellous bone (CCCB), usually lies close to the marrow cavities.

On examination under a microscope, most of the vascular canals are found to resemble fossa, or cavities called vascular canals, which vary in size and distribution. Most types of vascular canals are longitudinal vascular canals, including primary osteons that are grouped together in a knitted pattern (Fig. 38B-D). In general, the secondary osteons are rarely found in of the femora (Hübner, 2012), which does not contain in the PN14-300 sample.

In the inner cortex of the posteromedial section, a thin layer of parallel fibered bone is found attached to the marrow cavities. The incompletely developed CCCB. Thus, CCCB is not yet compacted in this example (Fig. 38C).

The zonation pattern is not found the annuli/LAGs in this specimen. There are two growth cycles, which consist of fast-growing zones show a darker band appearance, and the slow-growing zones show a lighter color characteristic (Fig. 38B). The growth cycle is clearly demonstrated in the posterolateral section

The histology study of the PN14-300 revealed a large size of the bone marrow cavity with the isolated primary osteons. The CCCB is not tightly compressed. Only two growth cycles were found. By comparison with *Dysalotosaurus* by Hübner 's study, this led to the conclusion that the PN14-300 belonging to the early juvenile stage.

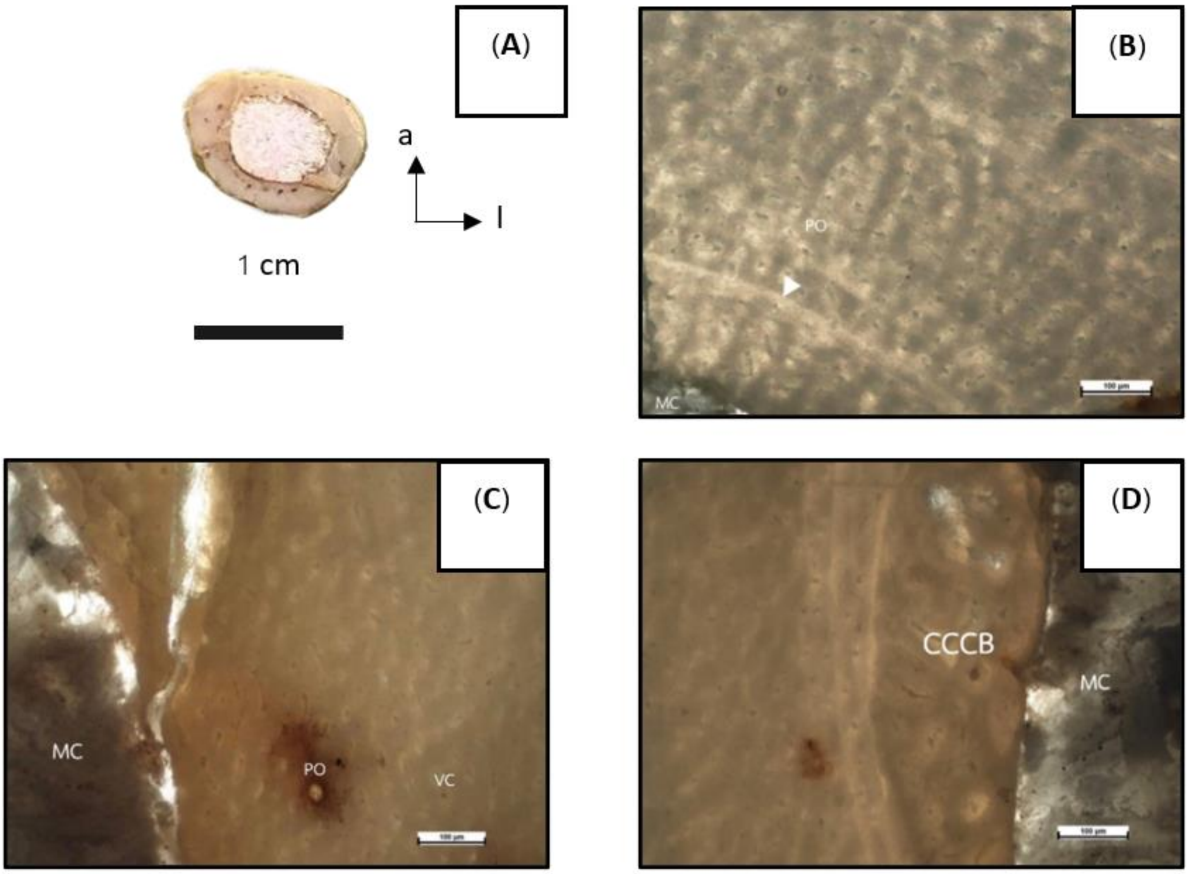

Figure 38 PN14-300

(A) An overview of the oriented cross section (a = anterior, l = lateral), under normal light. (B,C,D) Vascular organization in cross sections under normal light. (B) Part of the posterolateral section with organized primary osteons and vascular canals, white triangle indicates the outer edge of a growth cycle. (C) Part of posteromedial section close to the marrow cavities showing many simple vascular canals. (D) Part of the wedge of CCCB that are developing next to the bone marrow cavity; Abbreviations: vascular canals–VC, primary osteons-PO, compacted coarse cancellous bone-CCCB, marrow cavity-MC.

5.3.2 PN14-271

PN14-271 is the left femur (Fig. 36B). Most of the tissue in this specimen is the fibrolamellar bone tissue, which is the arrangement of collagen fibers, including a woven fiber matrix and primary osteons. The other tissue found is CCCB-wedge, which originates from the endosteal tissue, is usually located near the marrow cavities.

On examination under a microscope, most of the vascular canals are found resemble fossa or cavities, which vary in size and distribution. Most types of vascular canals are longitudinal vascular canals.

Moreover, the developing primary osteons are found near the vascular canals (Fig. 39B). The secondary osteons are generally rare in the femoral region. In the part of anterolateral section of PN14-271, a newly developed of secondary osteons exhibits a circular overlapping lamella and the haversian canals in the middle (Fig. 39C).

Parallel fibered bone is found in the inner cortex of the anterolateral section, it is a collagen fiber wrapped around the bone and wide arranged parallel to each other attached to the marrow cavities. Another type of tissue is CCCB, a type of tissue formed by filling the gaps in the coarse cancellous bone or spongy bone, where the endosteal is accumulation (Fig. 39D).

Only 2 annuli/LAGs found in the zonation pattern (Fig. 39 C). The growth cycle is clearly seen in the lateral section, there are 4 growth cycles (Fig. 5.8 B). The fast-growing zone shows a darker color, and the slow-growing zone shows a lighter shade (Fig. 39B). By comparison with *Dysalotosaurus* by Hübner 's study, this led to the conclusion that the PN14-271 belonging to the sexuality immature stage.

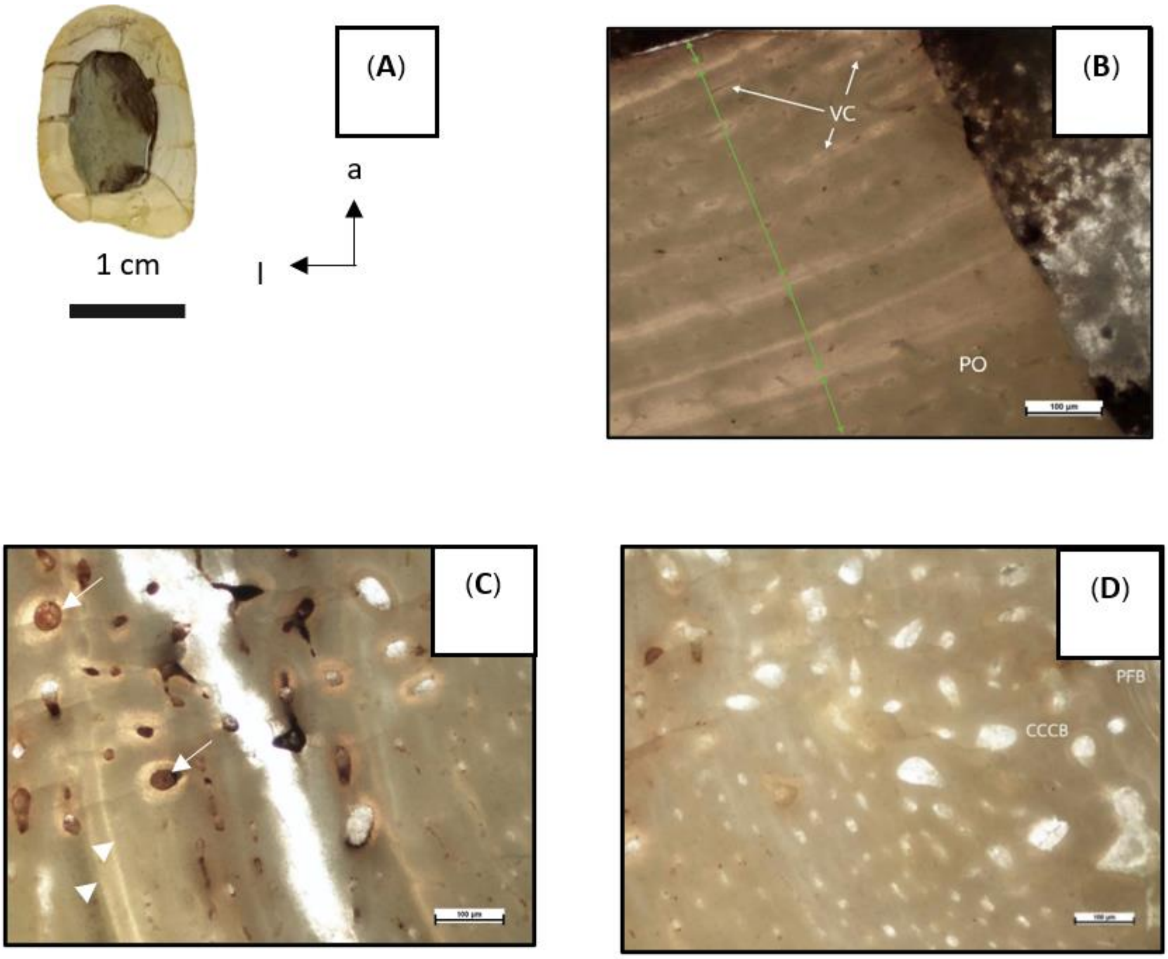

Figure 39 PN14-271

(A) An overview of the oriented cross section (a = anterior, l = lateral), under normal light. (B,C,D) Vascular organization in cross sections under normal light. (B) Part of the lateral section with developing vascular canals, green arrow indicates growing zone. (C) Part of anterolateral section, arrow showing the secondary osteons, white triangle showing annuli/LAGs. (D) parallel-fibered tissue attached to the top right marrow cavity and the developing CCCB.; Abbreviations: vascular canals–VC, primary osteons-PO, parallel fibered bone–PFB, compacted coarse cancellous bone-CCCB

5.3.3 PN15-11

PN15-11 is the right femur (Fig. 36C). Most of the tissue in this specimen is the fibrolamellar bone tissue, which has a disorganized arrangement of collagen fibers, including a vascular canals and primary osteons. The other tissue found is CCCB-wedge, which originates from the endosteal tissue, is usually located near the marrow cavities.

On examination under a microscope, most of the vascular canals are found resemble fossa or cavities, which vary in size and distribution. Most types of vascular canals are longitudinal vascular canals. The developing primary osteons are found near the vascular canals (Fig. 40B). The developed secondary osteons are found in the part of anterolateral section (Fig. 40C).

Usually, the annuli/LAGs are rarely found in the femur. Only 2 annuli/LAGs found in the zonation pattern (Fig. 40D). There are 4 growth cycles show in the posterolateral section (Fig. 40D). The fast-growing zone shows a darker color, and the slow-growing zone shows a lighter shade.

The histology of the PN15-11 revealed that the CCCB characteristics became more visible, and the compression began. Developed primary bone cells are highly distributed, predominantly in the outer cortex, with the longitudinal vascular canals visible in the peripheral area. Secondary osteons appear in the part anterior section, clearly showing the features of the internal components. By comparison with *Dysalotosaurus* by Hübner 's study (2012), this led to the conclusion that the PN15-11 belonging to the sexuality immature stage.

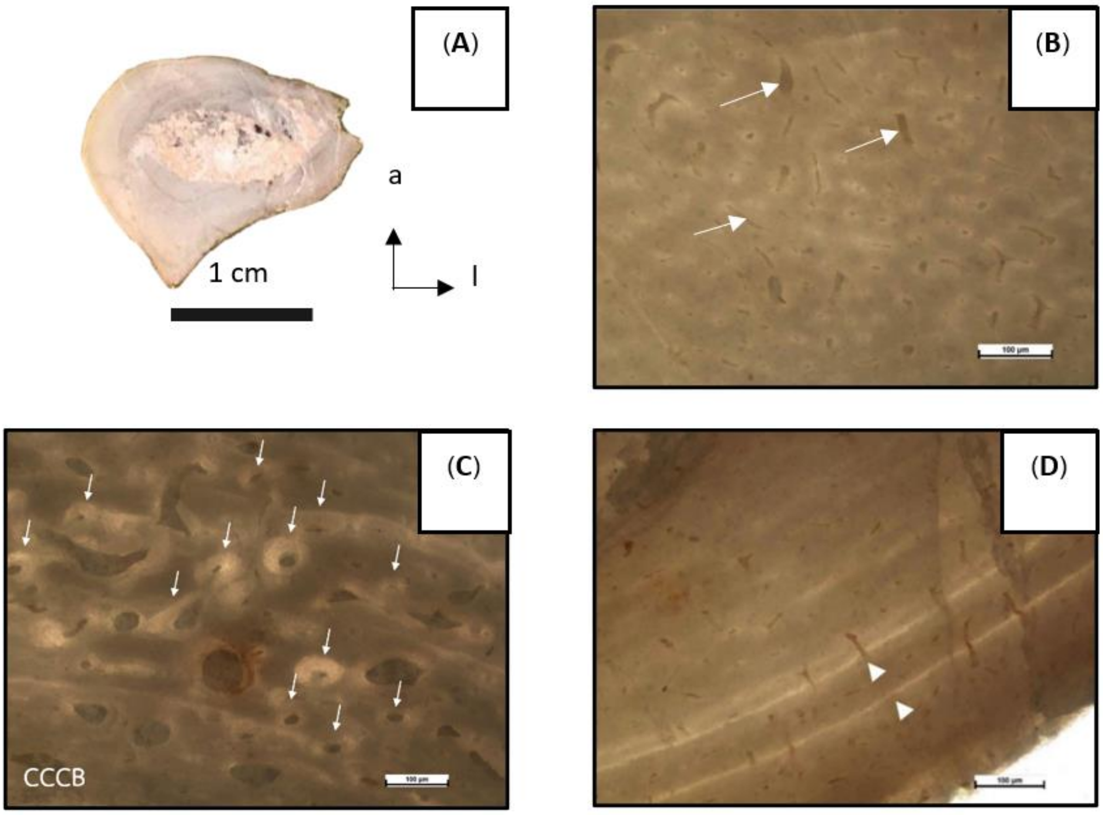

Figure 40 PN15-11

(A) An overview of the oriented cross section (a = anterior, l = lateral), under normal light. (B,C,D) Vascular organization in cross sections under normal light. (B) Part of anterolateral section with developing of the primary osteons, arrows showing the vascular canals. (C) Part of anterior section, arrows showing the secondary osteons. (D) Part of posterior section with growth cycle, white triangle showing annuli/LAGs.; Abbreviations: compacted coarse cancellous bone-CCCB

5.3.4 PN-unnumbered

PN-unnumbered is the left femur (Fig. 36D), the part used for this study is the distal metaphysis, the junction between the diaphysis, the shaft of the femur, and the epiphysis, the distal part of the femur (Figure 33). It shows the two types of bones including compact and spongy bone. The compact bone is a type of bone tissue that is dense and arranged as the surface of the bone. While, the spongy bone/cancellous bone, is a type of bone tissue that is less dense and rigid. but has a greater surface area than a compact bone.

The bone tissue found in the compact bone is the fibrolamellar bone tissue in outer cortex of the anterior section, consists of the s distributed secondary osteons (Fig. 41B). In the inner cortex found another type of tissue, CCCB, which is tight compression characteristics that can be seen very clearly (Fig. 41C).

In the spongy bone, parallel fibered bone tissue is found along the circumference. The secondary osteons are found in the surrounding area. Under a microscope, ruptures of the bone marrow cavity caused by process of bone remodeling are called resorption cavities (Hübner, 2012), and marrow spaces are also found (Fig. 41D).

As for the growth level of PN-unnumbered, the results were inconclusive. Because the specimen is the distal part of the diaphysis, which is a spongy area, no clusters of primary osteons, vascular canals, and especially the growth cycle. Based on the presence of secondary osteons and compression of the CCCB, it may be assumed that this specimen belongs to a sexually immature stage to sexually mature stage by comparison with Hübner’s study (2012).

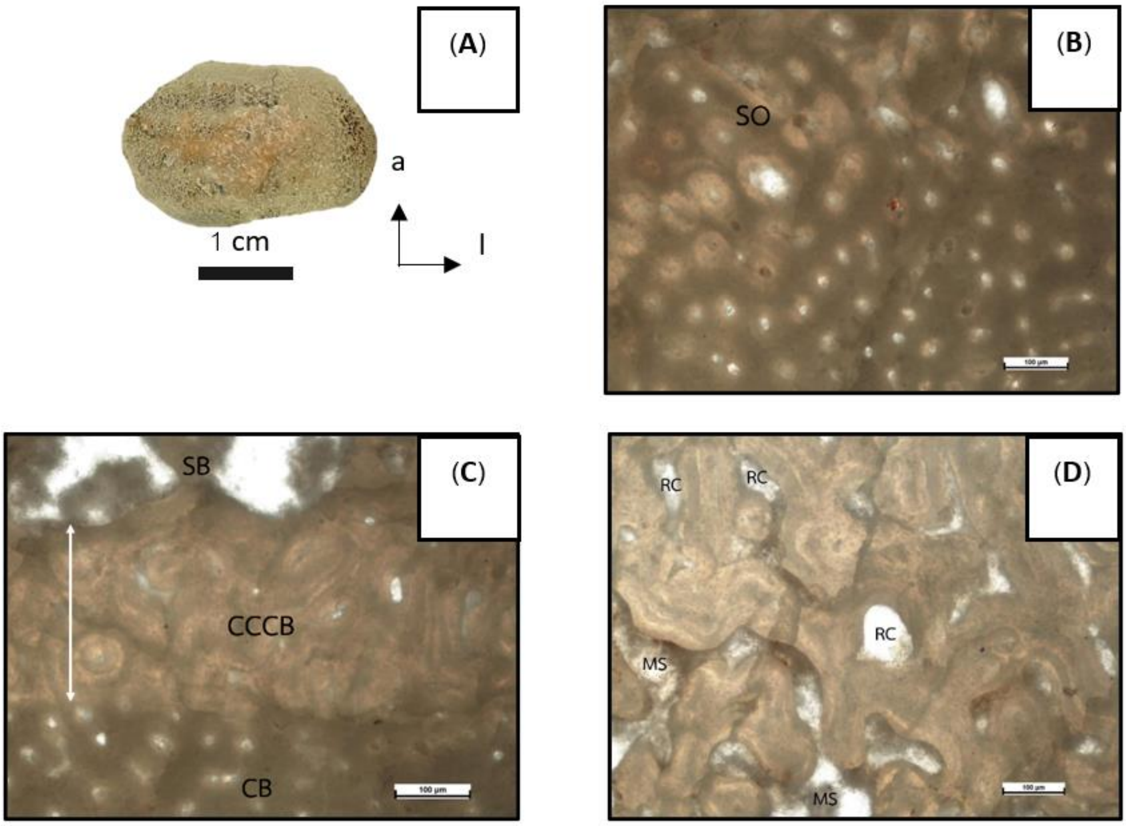

Figure 41 PN-unnumbered

(A) An overview of the oriented cross section (a = anterior, l = lateral), under normal light. (B-D) Vascular organization in cross sections under normal light. (B) Part of anterior section showing the secondary osteons in the outer cortex. (C) Part of anterolateral section showing CCCB between the compact and spongy bones. (D) Part of anterolateral section showing spongy bone; Abbreviations: secondary osteons-SO, compacted coarse cancellous bone-CCCB, compact bone-CB, spongy bone-SB, resorption cavities-RC, marrow space-MS

5.3.5 PN14-320

PN14-320 is the right femur (Fig. 36E). Most of the tissue in this specimen is the fibrolamellar bone tissue, which has a disorganized arrangement of collagen fibers, including a vascular canals and primary osteons. The other tissue found is CCCB-wedge, which originates from the endosteal tissue, is usually located near the marrow cavities.

On examination under a microscope, most of the vascular canals are found resemble fossa or cavities, which vary in size and distribution. Most types of vascular canals are longitudinal vascular canals. The developing primary osteons are found near the vascular canals (Fig. 42B). The developed secondary osteons are rarely found in the part of posterolateral section, a newly developed of secondary osteons exhibits a circular overlapping lamella and the haversian canals in the middle (Fig. 42C). Parallel fibered bone is found in the inner cortex of the posterolateral section, it is a collagen fiber wrapped around the bone and wide arranged parallel to each other attached to the marrow cavities. Another type of tissue is CCCB (Fig. 42C).

Only 1 annuli/LAGs found in the zonation pattern (Fig. 42D). There are 7 growth cycles show in the lateral section (Fig. 42D). The fast-growing zone shows a darker color, and the slow-growing zone shows a lighter shade.

The outermost cortex of the PN14-320 shows a layered tissue, closely spaced of the annuli/LAGs called the External Fundamental System (EFS). This tissue indicates that this femur reached its developed to the maximum peak and is in the reproductive stage (Fig. 42D).

The histology of the PN14-320 revealed that the CCCB characteristics are clearly visible. Developed primary bone cells are highly distributed, predominantly in the outer cortex, with the visible longitudinal vascular canals in the lateral section. By comparison with *Dysalotosaurus* by Hübner 's study (2012), this led to the conclusion that the PN1 4-320 belonging to the sexuality mature stage because the discovery of EFS, which is a symbol of the development of maturity. Relative to the size of the bone that is the largest compared to the other femur.

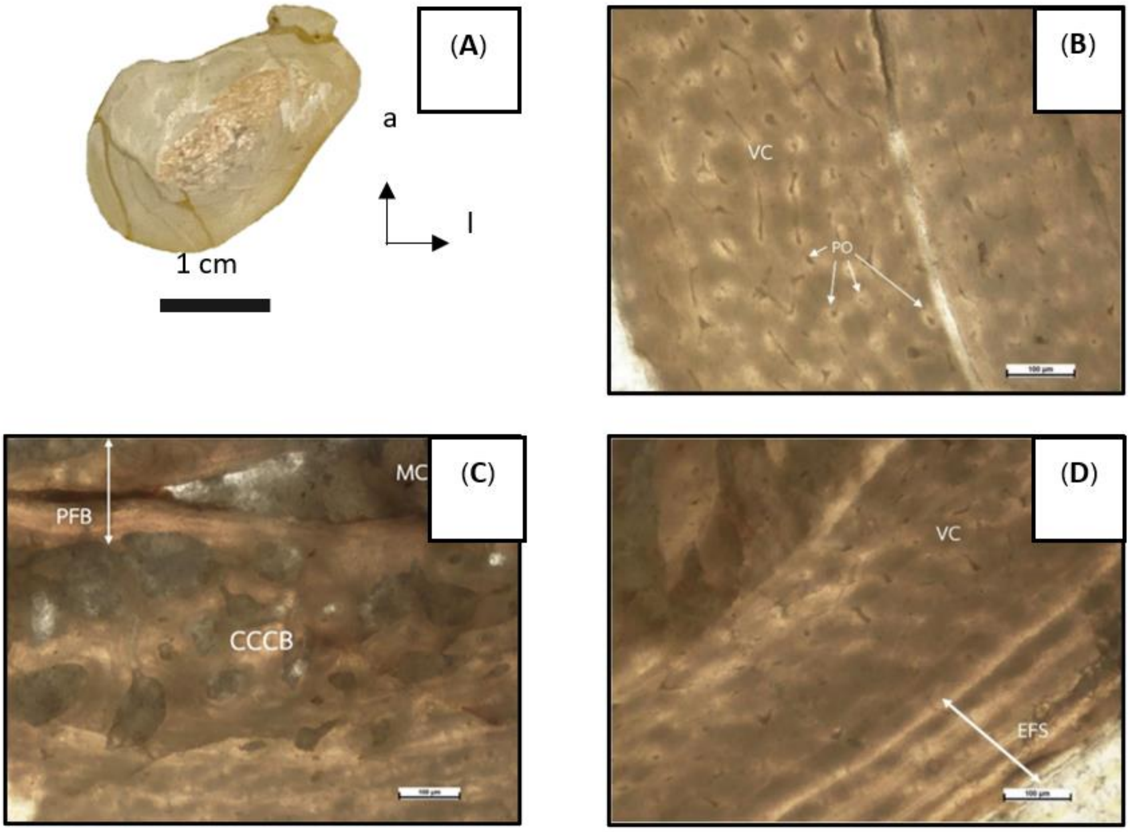

Figure 42 PN14-320

(A) An overview of the oriented cross section (a = anterior, l = lateral), under normal light. (B-D) Vascular organization in cross sections under normal light. (B) Part of the posterior section showing the many isolated primary osteons and vascular canals being developed. (C) CCCB is fully compressed, and a layer of parallel fibered bone tissue attached to the bone marrow cavity. (D) Part of lateral section showing EFS; Abbreviations: vascular canals–VC, primary osteons-PO, compacted coarse cancellous bone-CCCB, marrow cavities-MC, parallel fibered bone–PFB, External Fundamental System-EFS.

5.4 Discussion and conclusion

The study on bone histology of basal neornithischian dinosaur from Phu Noi locality, Late Jurassic Phu Kradung Formation of Thailand provides data of the ontogenetic stage of this dinosaur group, following the study of *Dysalotosaurus* by Hübner (2012). In the five femur materials, most were found to be in the subadult stage. Most of the internal tissues in the bone were characterized by the completely development of primary osteons. The developing vascular canals are found from primary osteons. The secondary osteons are formed from the process of bone remodeling when the body of the animal undergoes changes or maturation. Compacted coarse cancellous bone, or CCCB are found, most have not yet begun to compress. The External Fundamental System (EFS) is not found at the outermost cortex in many specimens, indicates that they belong to sub-adult stage (Table 8).

Phu Noi taxon exhibits a growth pattern same as *Dysalotosaurus* and other small ornithischians, where annuli/LAGs as representatives of a zonal bone tissue are rather scarce, completely absent, or are replaced by less obvious growth cycles (Hübner, 2012). On the other hand, large ornithopods, other ornithischians show a relative consistent growth pattern with annuli/LAGs representing the usual kind of growth cycles (Fondevilla et al., 2018; Hübner, 2012; Vanderven et al., 2014). Small ornithischians had probably less seasonal environmental stress than large ornithopods and different growth patterns had existed in large and small taxa, respectively (Hübner, 2012).

The appearance of annuli/LAGs can also be generated as data to study past behavior or palaeoenvironment (Bailleul et al., 2019; Hübner, 2012). I hypothesized that this might be caused by

1) Food demand

Normally, small ornithischians were predominantly selective low-browsers (Norman et al., 2004). The size of Phu Noi taxon is quite small (approximated the length of an adult, about 2 meters), they need less food than other large-bodied herbivorous such as stegosaur and mamenchisaurid in the same area (Buffetaut et al., 2001; Chanthasit et al., 2015).

2) Migration

Phu Noi taxon is possibly no need to migrate or relocate. Migration can occur due to inappropriate environmental conditions. The evidence of eroded calcrete found in Phu Noi locality, indicates a semi-humid to arid environment (Boonchai et al., 2019). This environment may have driven the temporary migration of animals to find new food sources. This herbivorous dinosaur has a good adaptation to the environment. Therefore, there is no interruption of growth.

Some smaller ornithischians were able to withstand harsh environmental conditions through adaptation. For example, *Oryctodromeus* has adapted to stressful environments by digging hole to escape the cold weather (Varricchio et al., 2007). The larger ornithischian dinosaurs, for example, *Edmontosaurus* from North America migrated from Alaska to Canada during the winter to finding the new food sources with a warmer climate (Bell & Snively, 2008).

3) Breeding strategy

There are two types of parenting behavior in dinosaurs (John R. Horner, 1992). The precocial behavior: parents only take care for their children during the egg and incubation period. This causes the baby to develop slow growth during juvenile and begin to develop rapidly after juvenile. The altricial behavior: will raise their children since they are in the egg, provide food, protect from predators until they reach full maturity. This causes the youth to grow rapidly until reaching full maturity, it begins to develop and decrease.

Hübner (2012) has created a graph simulating the growth of *Dysalotosaurus* compare with *Tenontosaurus* (which is larger ornithopod). *Tenontosaurus* shows higher initial and juvenile growth rates and reached their asymptotic growth plateau relatively earlier than *Dysalotosaurus* (Fig. 43). The growth pattern of *Tenontosaurus* is similar to the large hadrosaurids *Maiasaura* and *Hypacrosaurus*, so that altricial behavior can be assumed as well. Thus, altricial behavior was probably one of the key strategies within ornithopod dinosaurs to become large in a short time and the resulting growth pattern (higher juvenile growth rates, early sexual and somatic maturity compared to small ornithischians, consistent development of annuli/LAGs) reflects this seasonally much more stressful strategy (Hübner, 2012).

The Phu Noi taxon is probably precocial as hatchlings same as *Dysalotosaurus* and other small ornithischians (Hübner, 2012).

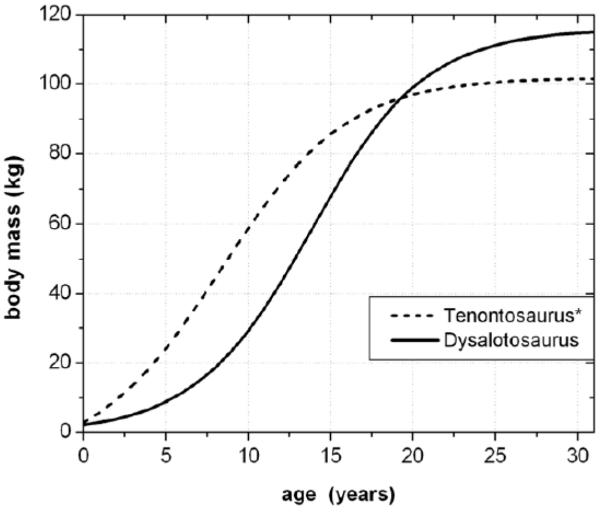

Figure 43 Comparison of growth curves of *Tenontosaurus tilletti* and *Dysalotosaurus lettowvorbecki*. *Note that the maximum body mass of *Tenontosaurus* is app. ten times higher than in *Dysalotosaurus*. Thus, for a better comparison, the body mass values of *Tenontosaurus* were divided by 10 and then used for the growth curve calculation (Hübner, 2012).

In conclusion, the study on bone histology of the basal neornithischian from Phu Noi indicates that most of material in this study were in the sub-adult stage. Same as other small ornithischians often lack regularly developed annuli/LAGs due to lower food demands, no need for migration, and precocial behavior. This is just a preliminary study. The study of the leftover femora that are kept at the Sirindhorn Museum, including other long bones will allow us to understand the behavior and growth of this dinosaur more in the future.

Table 8 Ontogeny stages of Phu Noi neornithischian compare with *Dysalotosaurus*

Ontogenetic stage of *Dysalotosaurus* (Hubner, 2012)	Phu Noi taxon	Specimen number	Stage
Stage 1 Embryonic/Perinatal			Sub-adult
Stage 2 Early juvenile	/	PN14-300	
Stage 3 Late juvenile			
Stage 4 Sexually immature	/	PN14-271 PN15-11 PN-unnumbered	
Stage 5 Sexually mature	/	PN14-320	Adult

Table 9 Basic dataset of all cross sections of femora

Labels	**Ant-Post Ø**	**Med-Lat Ø**	**Ant-Post Cavity**	**Med-Lat Cavity**	**Number growth cycles**	**Number annuli/LAGs**	**Ontogenetic stage**
PN14-300	11.20	9.10	6.80	5.90	2	-	Early juvenile
PN14-271	11.20	20.80	8.90	13.10	4	2	Sexuality immature
PN15-11	14.40	18.20	6.80	12.80	4	2	Sexuality immature
PN-unknow	17.80	25.80	11.80	13.20	-	-	Sexuality immature - Sexuality mature
PN14-320	15.20	21.00	8.90	13.70	7	-	Sexuality mature

Explanation of heading-abbreviations: Ant-post Ø – Diameter of cross section in anteroposterior direction; Med-lat Ø – Diameter of cross section in mediolateral direction; Ant-post cavity – Diameter of marrow cavity in anteroposterior direction; Med-lat cavity – Diameter of marrow cavity in mediolateral direction (All data in mm).

Chapter 6

Material of the Khok Pha Suam iguanodontian dinosaurs: An overview of vertebrate diversity from the Early Cretaceous Khok Kruat Formation (Aptian-Albian) of Thailand

Some part of this chapter was published as Manitkoon, S., Deesri, U., Lauprasert, K., Warapeang, P., Nonsrirach, T., Nilpanapan, A., Wongko, K., and Chanthasit, P. (2022). Fossil assemblage from the Khok Pha Suam locality of northeastern, Thailand: an overview of vertebrate diversity from the Early Cretaceous Khok Kruat Formation (Aptian-Albian). Fossil Record, 25 (1), 83–98. (Appendix 2)

6.1 Introduction

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

(Jin-Geng and Meesook, 2013). The Khok Kruat Formation is considered the lateral equivalent to the Grès Supérieurs Formation of southern Laos. Both are considered as Aptian-Albian in age based on their vertebrate assemblages, bivalves, and palynomorphs (Allain et al., 2012; Buffetaut et al., 2005, 2009; Cappetta et al., 1990; Racey and Goodall, 2009). In contrast to the Sao Khua Formation, which contains no evidence of ornithischians, three taxa of non-hadrosaurid iguanodontians and a basal ceratopsian have been described from the Khok Kruat Formation (Buffetaut et al., 2005; Shibata et al., 2015). Khok Pha Suam is part of the Pha Chan-Sam Phan Bok Geopark. It is the third national geopark that has been created after the Satun Global Geopark (Satun Province) and the Khorat Geopark (Nakhon Ratchasima Province). This geopark has many outstanding geological sites and contains three main spots: 'land of the last Thai dinosaurs' in the Khok Pha Suam locality; unique natural places such as Pha Chan (high cliffs above the Mekong River), the Sam Pan Bok (known as the 'Grand Canyon of Thailand', which consists of extensive bedrock with many potholes outcropping in the Mekong River), Pha Taem (ancient cliff paintings in the Pha Taem National Park); and the two-color river viewpoint where the blue water of the Mun River mixes with the brown water of the Mekong River (Department of Mineral Resources, 2021; Singtuen & Won-in, 2019). The creation of a geopark will help to promote trade investment and tourism, improve the quality of its inhabitants, strengthen the communities, and contribute substantially to both geoconservation and geotourism by promoting a new type of tourism in Thailand (Singtuen & Won-in, 2019). This study summarises the palaeontological data that illustrates to the general public what Khok Pha Suam looked like a hundred million years ago and will also improve the academic interest in the geopark.

6.2 Geological settings and palaeoenvironment

Khok Pha Suam is located in the Na Kham Subdistrict, Si Muang Mai District, Ubon Ratchathani Province. The outcrop was discovered in 1993 by villagers near the forested area maintained by the Na Kham Subdistrict Administrative Organization. The site has been extensively eroded by water into a badlands-type landscape (Figure 6.1d) (Cappetta et al., 2006).

The thickness of the lithostratigraphic section is about 4 meters (Fig. 44c). The exposed deposits are composed of siltstone and very fine sandstone with some carbonate caliche pebble conglomerates. The fining-upward sequence is pale red to grayish-red and reddish brown. The dip of the strata is 10/135 to the south-east. The lower part is 1 meter thick and consists of reddish brown very thin to thin bedded claystone grading up to thin bedded siltstone interbedded with fine-grained sandstone. The fragile vertebrate remains are found on the eroded surface of this layer which can be collected directly. The upper part is 3 meters thick and consists of reddish-brown, thin-to medium bedded, medium-grained sandstones interbedded siltstones, claystones. A calcrete horizon (palaeosol) has been found at the top of the succession (Wongko, 2018; Wongko et al., 2019).

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

6.3 Material

The specimens were collected from Khok Pha Suam locality, Na Kham Subdistrict, Si Muang Mai District, Ubon Ratchathani Province (Fig. 4a-b) and are now housed in the collections of the Palaeontological Research and Education Centre, Mahasarakham University and Sirindhorn Museum. This work includes a review of published specimens and new records from recent discoveries.

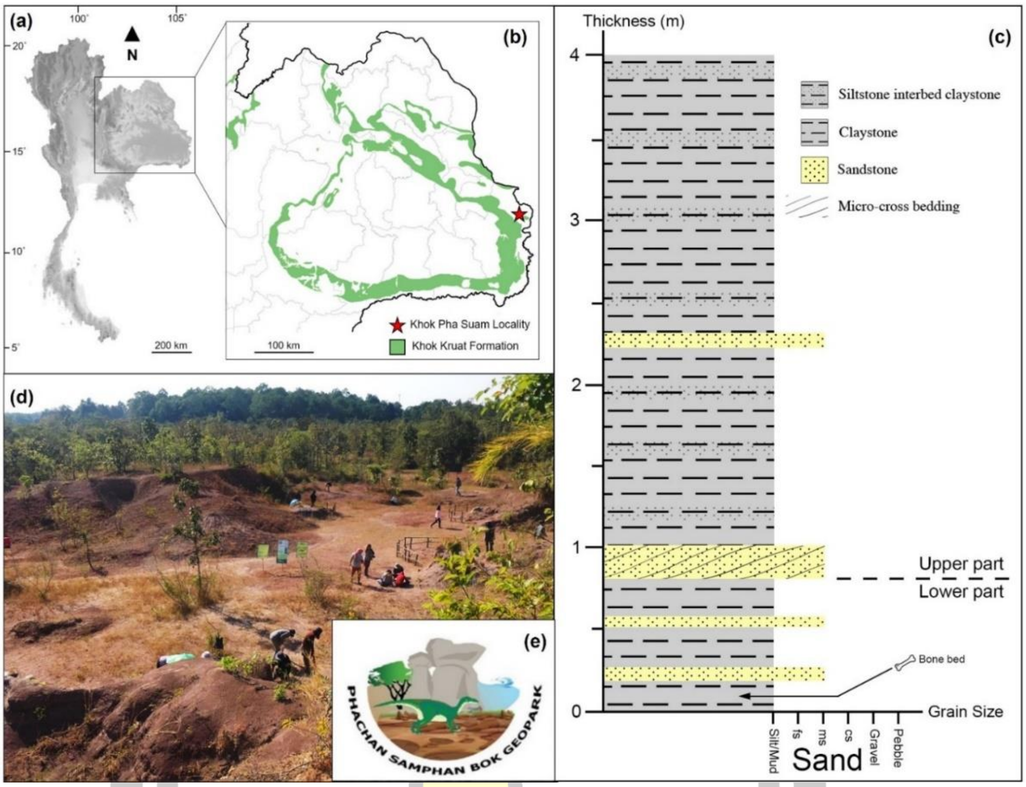

Figure 44 Locality map and lithostratigraphic section of Khok Pha Suam locality (Manitkoon et al., 2022).

a, map of Thailand, showing the location of the Khorat Plateau; b, distribution of the Khok Kruat Formation in northeastern Thailand (green color; modified from DMR, 2004), location of Khok Pha Suam locality (red star); c, stratigraphic column of Khok Pha Suam, d, a photograph of the excavation site; e, logo of The Pha Chan-Sam Phan Bok Geopark.

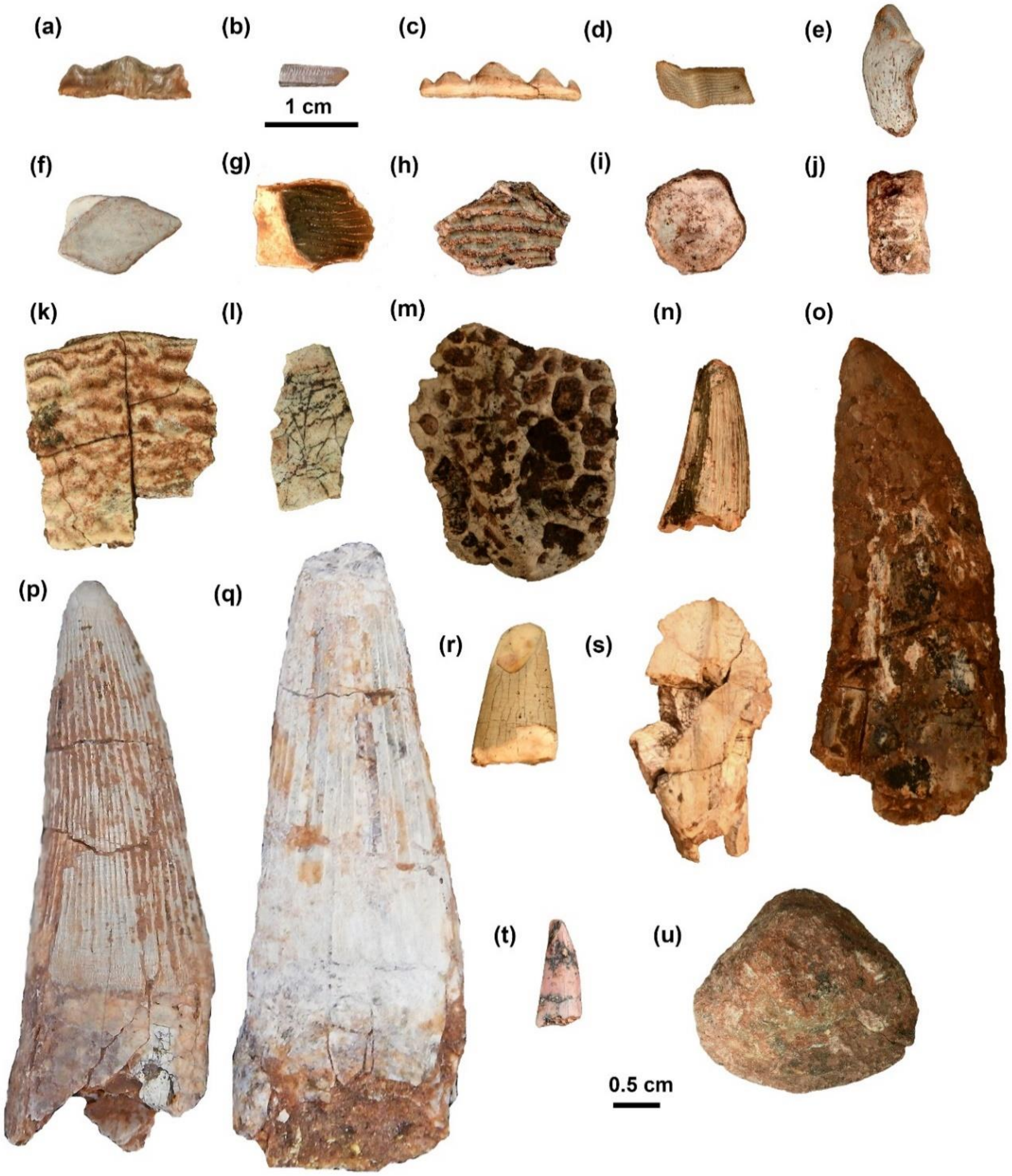

Figure 45 Isolated microremains from Khok Pha Suam locality (Manitkoon et al., 2022).

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

6.4 Khok Pha Suam iguanodontians

The vertebrates found at the Khok Pha Suam locality comprise five taxa of hybodont sharks, at least two taxa of ginglymodians, a sinamiid fish, carettochelyid and adocid turtles, neosuchian crocodyliforms, pterosaurs, dinosaurs (iguanodontians, sauropods, and at least two taxa of theropods). The faunal diversity described in this article together with additional data from other localities allows us to propose a preliminary reconstruction of the Early Cretaceous Khok Kruat Formation ecosystem (Fig. 52).

Although Khok Pha Suam vertebrates are mostly known from microremains and fragmentary larger remains, some isolated postcranial bones belonging to iguanodontians were discovered (Figs 46-51), including vertebrae and limb bones from different individuals. For this reason, these herbivores are outstanding from all the other tetrapods of the Khok Pha Suam locality, becoming therefore an iconic symbol of Pha Chan-Sam Phan Bok Geopark (Figure 44).

Postcranial material of iguanodontians from Khok Pha Suam including cervical vertebra (PRC 155); dorsal vertebra (SM2021-1-113); 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); right femur (SM2021-1-118); tibia (SM2021-1-119); fibula (PRC 158); and phalanx

(SM2021-1-120). Because the size of the left and right femur varies greatly. Therefore, it can indicate the inclusion of at least 2 individuals. The bigger individual is possibly adult stage, based on the fusion of the neurocentral suture of the vertebrae.

Teeth

See in chapter 3.4.3 Iguanodontian indet. (so-called the 'Khok Pha Suam iguanodontian') (Fig. 10)**Cervical vertebra**

The caudal vertebra (PRC 155, Fig. 46a-f) is in fixed by plaster, the posterior part is concave of the centrum while the anterior part is unpreserved. The heart-shaped centrum which is tends to be opisthocoelous like cervical vertebrae of the other basal hadrosauroids and hadrosaurids. The parapophysis is broken, but the contact forming is observable in the lateral view. The forked shape postzygapophysis arches over the intervertebral joint to contact the adjacent prezygapophysis which is missing. The neural spine is slightly low, the tip is disappeared. The diapophysis is approximately 45˚ from horizontal. Although the exact position of PRC 155 is unclear, it is definitely a distal cervical vertebra based on comparisons with *Gobihadros mongoliensis* (MPC-D 100/746) (Tsogtbaatar et al., 2019), *Ouranosaurus nigerensis* (MSNVE 3714) (Bertozzo et al., 2017), and *Kamuysaurus japonicus* (HMG-1219) (Kobayashi et al., 2019).

Dorsal vertebra

The dorsal vertebra (SM2021-1-113; Fig. 46g-j) is anterolateral compressed. An outline of the centrum is heart-shaped in posterior view similar to middle dorsal vertebrae of *Kamuysaurus japonicus* (Kobayashi et al., 2019) and spool-shaped in ventral view. The parapophysis is absent. The diapophyses project dorsolaterally and slightly rostrally at an angle of about 45˚ from the horizontal. The neural spine is platelike and thin transversely, it is rectangular shape in cross-section.

Caudal vertebra and chevron

The caudal vertebra (SM2021-1-114, Fig. 47a-f) is in a rather bad condition and fixed by plaster. However, it represents the character of the proximal caudal vertebra. The shape of the centrum is nearly circular, the central surface is biconcave (slightly amphicoelous). The facet at the caudoventral margin of the centrum for accommodating the haemal arch (chevron) is unpreserved. The pre-and postzygapophyses are prominent pedestals from the base of the neural spine. The neural spine is slightly tall, but about half of its height was missing. The cross-section of the neural spine is rectangular. The caudal ribs angling approximately 45˚ to the horizontal.

Two distal caudal vertebrae (PRC 156, Fig. 47i) are nearly complete, the posterior tendency of the neural spine becomes larger posteriorly, but a distal portion of the neural spine is missing. The lateral surfaces of the centrum are rather broken, the central surface is amphicoelous. SM2021-1-115 (Fig. 47j) is poorly preserved, half of the left side was destroyed.

A proximal chevron (PRC 157, Fig. 47g-h) consisting of a slender distal blade which is the tip is unpreserved. One side of the atop process which will form the haemal canal is missing.

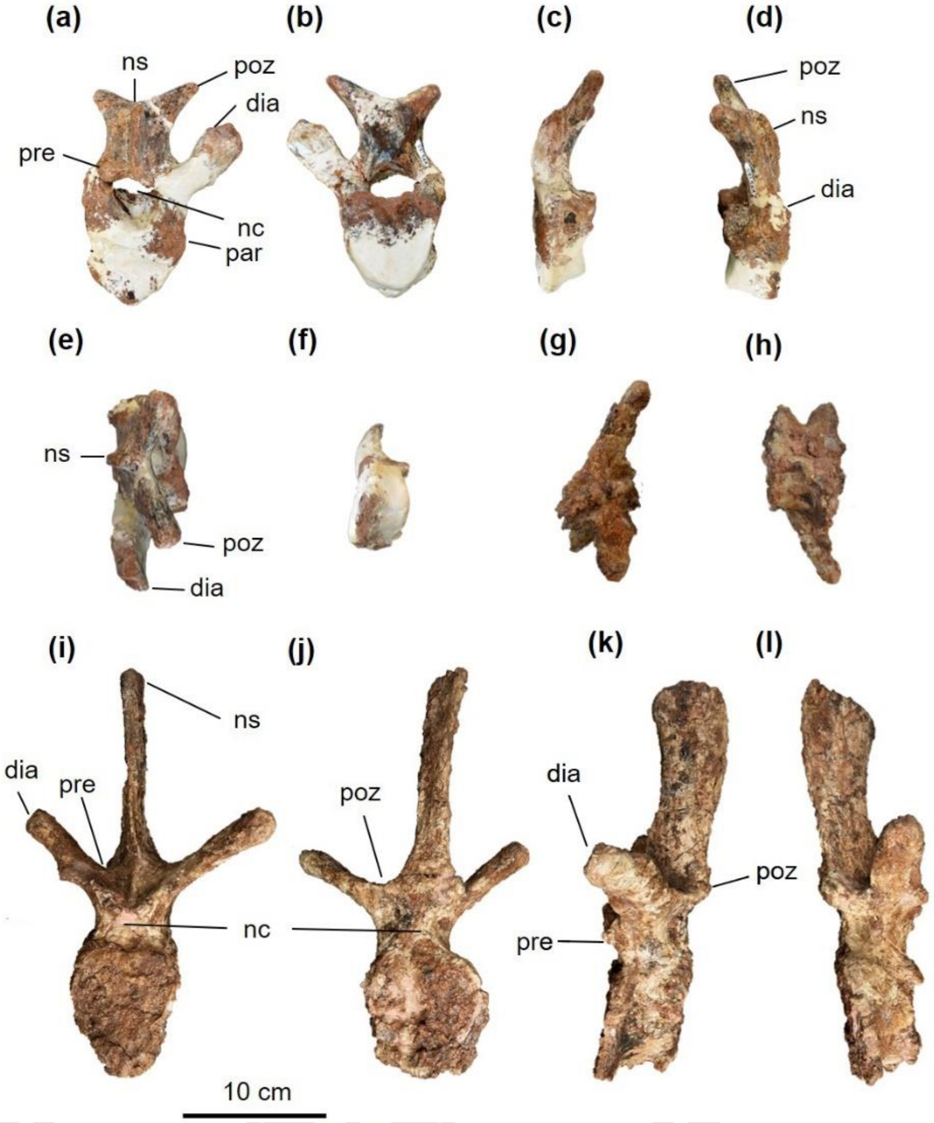

Figure 46 Cervical vertebra (a-h: PRC 155) and dorsal vertebra (i-l: SM2021-1-113) of the Khok Pha Suam iguanodontian

In anterior (a), posterior (b), left lateral, (c) right lateral (d), dorsal (e), ventral (f), dorsal (g), ventral (h), anterior (i), posterior (j), left lateral (k), and right lateral (l) views. Abbreviation: dia; diapophysis, nc; neural canal, ns; neural spine, par; parapophysis, poz; postzygapophysis, prz; prezygapophysis.

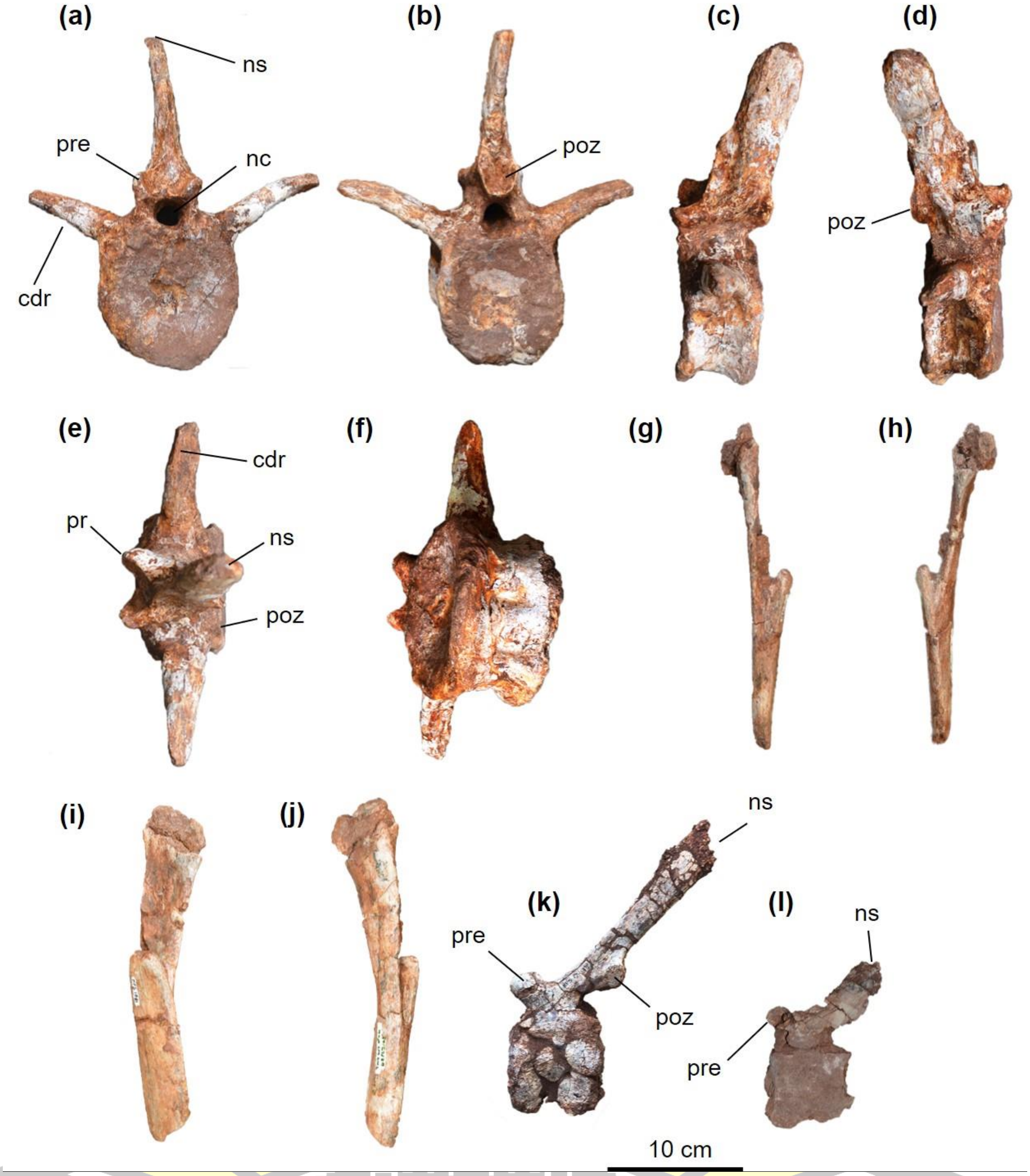

Figure 47 Proximal caudal vertebra (a-f: SM2021-1-114), distal caudal vertebra (i, PRC 156; j, SM2021-1-115), and chevron (i-j: PRC 157) of the Khok Pha Suam iguanodontian

In anterior (a), posterior (b), left lateral (c), right lateral (d), dorsal (e), ventral (f), anterior (g), posterior (h), left lateral (i), right lateral (j), (k-l) left lateral view. Abbreviation: cdr; caudal rib, nc; neural canal, ns; neural spine, poz; postzygapophysis, prz; prezygapophysis.

Manus

The metacarpal (SM2021-1-116; Fig. 48a-f) is possibly the right metacarpal IV, it is robust and slightly S-curved in dorsal views. The proximal and distal ends are expanded craniocaudally in lateral and medial views. There is the lateral ridge in lateral view, the craniomedial surface of the proximal end possesses a medial concavity which would contact the craniolateral surface of the proximal end of metacarpal III.

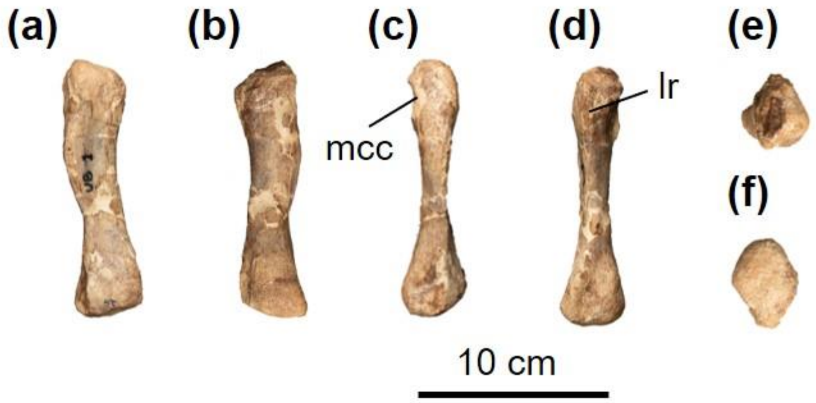

Figure 48 Metacarpal (SM2021-1-119) of the Khok Pha Suam iguanodontian

In dorsal (a) ventral (b) medial (c), lateral (d), proximal (e) and distal (f) views. Abbreviation: lr, lateral ridge; mcc, medial concavity.

Femur

The right femur (SM2021-1-117; Fig. 49a-f) is robust and almost complete. It is 52 cm in length and possess a transverse midshaft diameter of 7.51 cm. The shaft of the femur is slightly straight in lateral view. The lower end of the femur is mediolaterally compressed and twisted about one-third distally. The femoral head (caput femoris) is not well preserved. The greater trochanter lies upon the same plane as the femoral. The flattened and rather blade-like lesser trochanter (cranial or anterior trochanter) is distinguished from the greater trochanter by a narrow cleft, it is beyond the anterolateral corner of the greater trochanter. The tip of the fourth trochanter is lost but shows the triangular shaped crest located on the medial margin of the proximal half of the femur similar with *Iguanodon bernissartensis* (IRSNB. 1534)

(Norman, 1980), *Mantellisaurus atherfielden* (BMNHR5764) (Norman, 1986), *Probactrosaurus gobiensis* (PIN 2232/18-9) (Norman, 2002), *Jinzhousaurus yangi* (IVPP V12691) (Wang et al., 2010; Wang and Xu, 2001), *Ouranosaurus nigerensis* (MSNVE 3714) (Bertozzo et al., 2017), and *Gobihadros mongoliensis* (MPC-D 100/746) (Tsogtbaatar et al., 2019). At the distal portion of the femur, the medial and lateral condyles are prominent and expanded. The medial condyle of the femur is larger than lateral condyle. The anterior and posterior intercondylar grooves (intercondylar extensor and intercondylar flexor grooves) are well-developed and clearly visible.

The left femur (SM2021-1-118; Fig. 49g-l) is smaller than SM2021-1-117, indicated that possibly belong to juvenile stage. It is 30 cm in length and has a transverse midshaft diameter of 3.75 cm which indicates that belongs to another individual, and possibly juvenile. The femoral shaft is slightly straight, the femoral head is not well preserved as in SM2021-1-117, but more retains its original shape. The lesser trochanter is more anteriorly flattened than SM2021-1-117. The tip of the fourth trochanter is unpreserved. The medial and lateral condyles are distinct but less curved than SM2021-1-117, the lateral condyle is considerably bigger than the medial condyle. The anterior intercondylar groove almost invisible whereas the posterior intercondylar groove is appeared but not deep as much as in SM2021-1-117.

Tibia and fibula

The right tibia (SM2021-1-119; Fig. 50a-b) is twisted along its long axis. The proximal portion is mediolaterally compressed, the cnemial crest is well-developed and protrudes forward. The lateral condyle and the medial condyle posit on the caudal half of the proximal end. The midshaft is oval in cross-section. The distal end which is contact surface for fibular and calcaneum is not well-preserved.

The proximal portion of the left fibula (PRC 158; Fig. 50c-d) is unpreserved. The distal part is long and narrow, enlarges for articulation of distal end of the tibia.

Pes

The phalanx (SM2021-1-120; Fig. 50g-j) is possibly the phalanx III-1 because of approximately symmetrical however the tip on one side of the proximal portion was missing. It is robust and slightly longer than wide, the proximal and distal articular surfaces are elliptical.

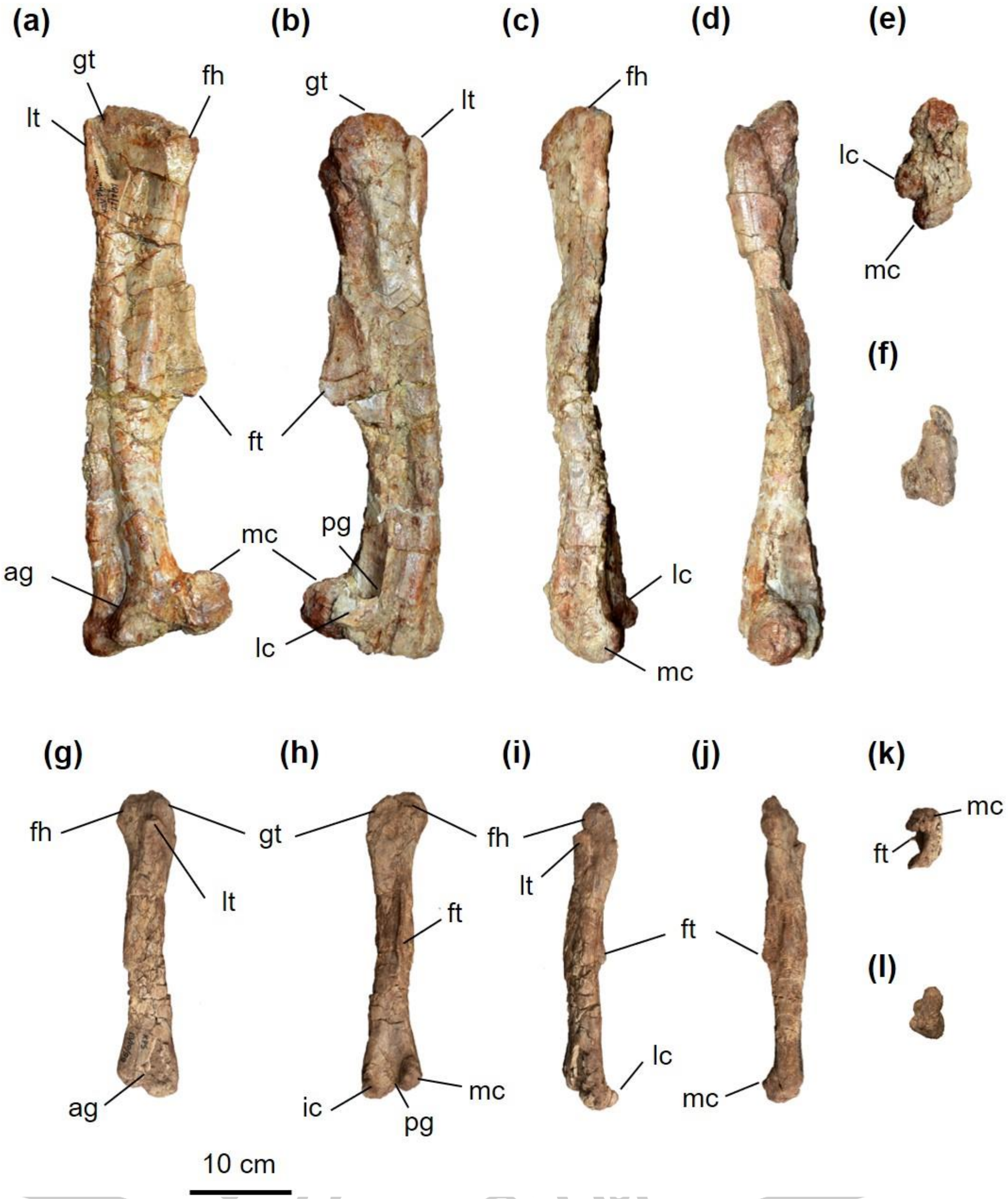

Figure 49 Right femur (a-f: SM2021-1-117), left femur (g-l: SM2021-1-118) of the Khok Pha Suam iguanodontian

In anterior (a), posterior (b), lateral (c), medial (d), distal (e), proximal (f), anterior (g), posterior (h), lateral (i), medial (j), distal (k), and proximal (l) views.

Abbreviation: ag, anterior intercondyle groove; fh, femoral head; ft, fourth trochanter; gt, greater trochanter; mc, medial condyle; lc, lateral condyle; lt, lesser trochanter; pg, posterior intercondyle groove.

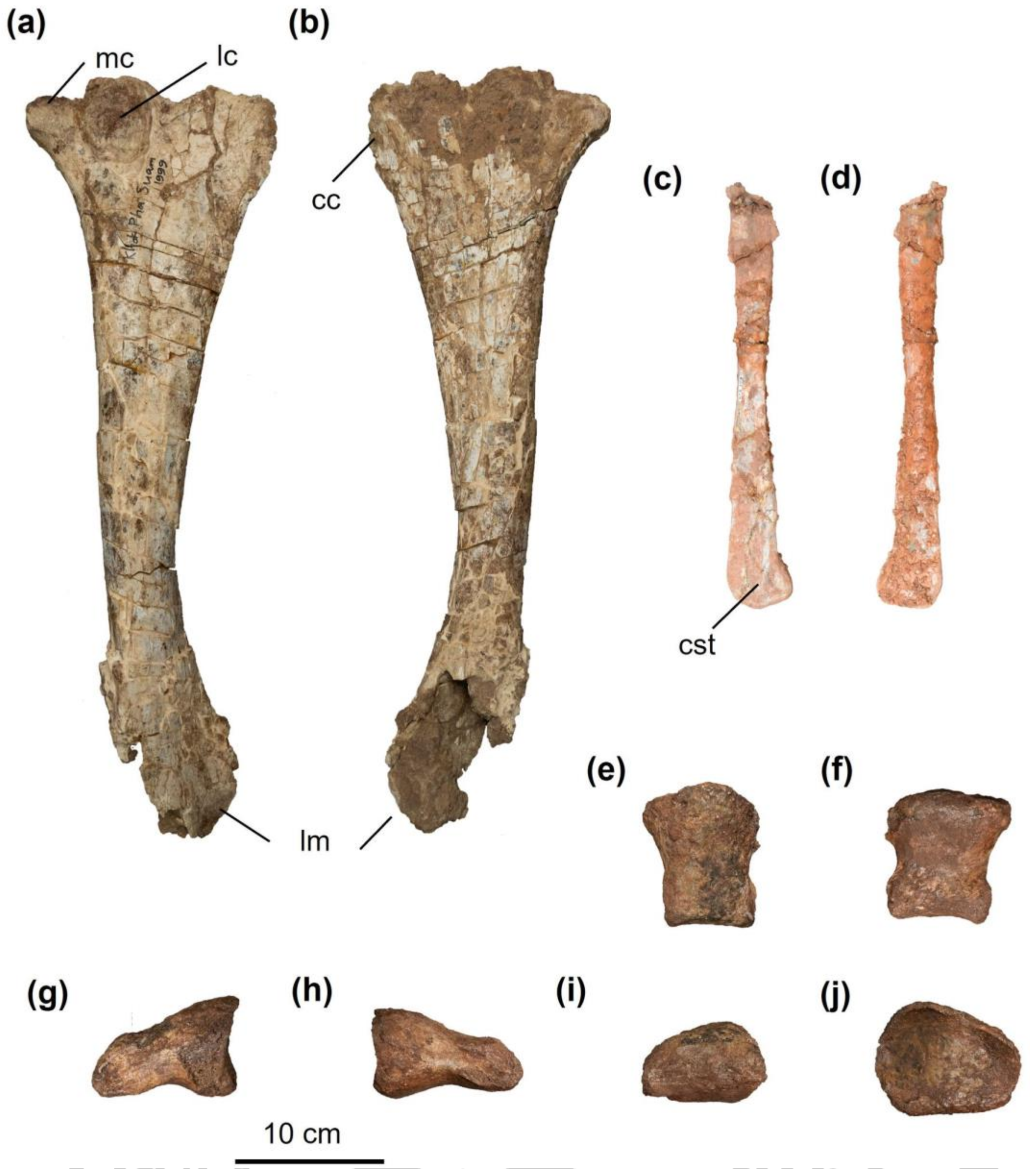

Figure 50 Right tibia (a-b: SM2021-1-119), left fibula (c-d: PRC 158), and phalanx (e-j: SM2021-1-120) of the Khok Pha Suam iguanodontian

In lateral (a), medial (b), anterior (c), posterior (d), dorsal (e), ventral (f), lateral (g), medial (h), anterior (i) and posterior (j) views. Abbreviation: cc, cnemial crest; cst, contact surface for tibia; lc, lateral condyle; lm, lateral malleolus; mc, medial concavity.

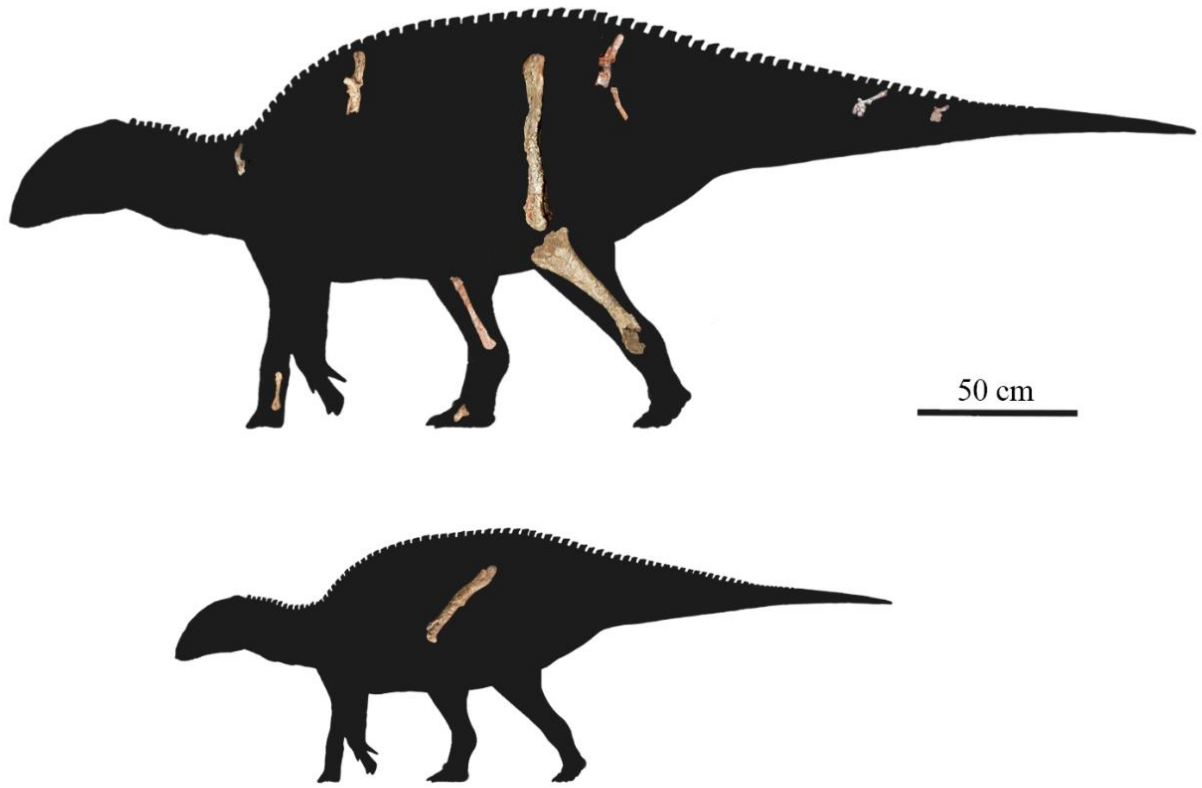

Figure 51 Tentative reconstruction of Khok Pha Suam iguanodontian indet. showing recovered bones in left lateral view

6.5 Overview of other Khok Kruat localities.

The sedimentology of Khok Kruat localities shows that the vertebrate fossils were deposited in a fluvial system including flood plains and channels of meandering rivers. At Ban Saphan Hin, Nakhon Ratchasima Province, various vertebrate remains were found scattered and fragmentary in a medium to thick-bedded reddish-brown conglomerate. The conglomerates are locally cross-bedded. These elements indicate that the fossils were transported with medium to high energy and deposited in the channel. Carbonate clasts are commonly found and well cemented by calcite. These shreds of evidence suggest a semi-arid environment. This locality has yielded *Thaiodus ruchae*, *Heteroptychodus steinmanni*, *Lanxangichthys* sp. *Shachemys* sp., *Kizylkumemys khoratensis*, *Khoratosuchus jintasakuli*, Eusuchian indet., *Sirindhorna khoratensis*, *Siamraptor suwati* (Cuny et al., 2008; Cavin et al., 2018;

Chokchaloemwong et al., 2019; Kubo et al., 2018; Lauprasert et al., 2009; Shibata et al., 2015; Tong et al., 2005, Tong et al., 2009).

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

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

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

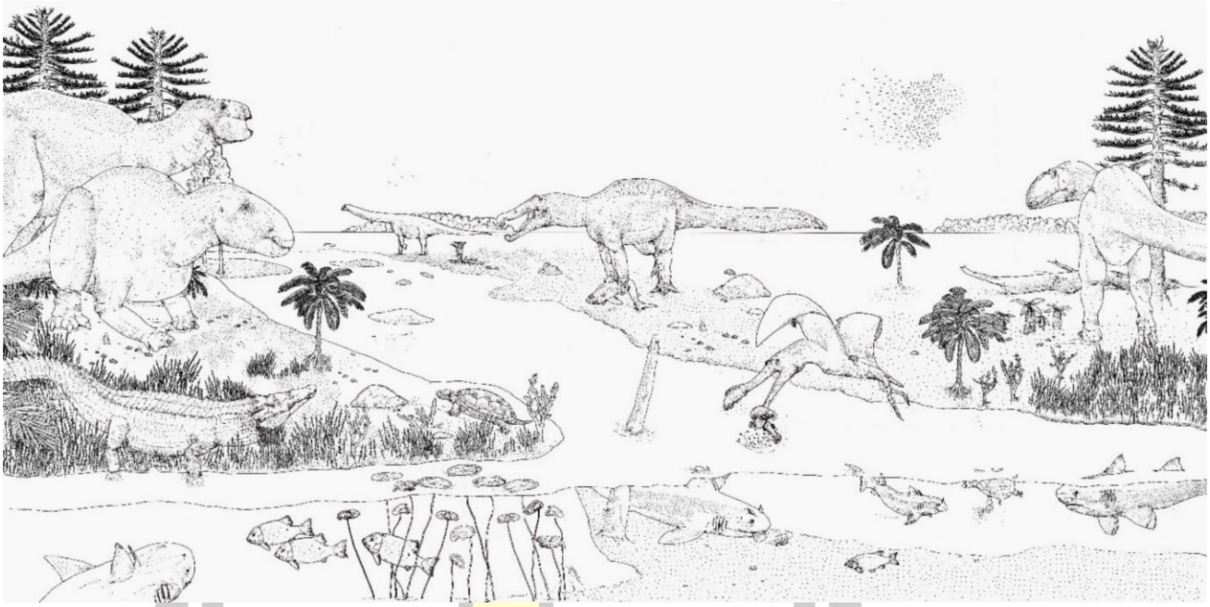

Figure 52 Palaeoenvironmental interpretation of the Early Cretaceous (Aptian-Albian) Khok Pha Suam Locality. Drawing by Sakka Weerataweemat.

6.6 Discussion

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

Hundreds of isolated teeth and many dorsal fin spine fragments of hybodonts representing up to five different genera have been recovered so far. Pattern and form variation of these shark teeth show adaptations towards various diets: cutting (*Thaiodus*), crushing (*Khoratodus*, "*Hybodus*" and *Acrorhizodus*), and grinding (*Heteroptychodus*) (Cuny et al., 2017). Bivalve internal molds (Figure 5u) which have been found in Khok Pha Suam resemble *Trigonioides trigonus* (Hoffet, 1937) from the Grès Supérieurs Formation of southern Laos and *Pseudohyria (Matsumotoina) somanai* (Tumpeesuwan et al., 2010) from the older Sao Khua Formation based only on comparison with external shell morphology. Additional comparisons of hinge teeth characters are needed to establish more taxonomic precision. These bivalves could potentially have been food for *H. steinmanni*. The five species of hybodonts from the same assemblage have also been found in the Xinlong Formation in southern China

(Cuny et al., 2017). They are indeed endemic to Southeast Asia and South China, four of them (*Acrorhizodus*, “*H.*” *aequitridentatus*, *Thaiodus* and *Khoratodus*) are restricted to the Aptian-Albian interval (Cuny, 2012). The fifth genus, *Heteroptychodus* is currently restricted to Thailand, Japan, Kyrgyzstan, South China and Mongolia, and is the most common hybodont species found in the Khorat Group (Cuny et al., 2008; Cuny et al.,2014), exhibiting a large stratigraphic distribution, from the Upper Phu Kradung Formation to the Khok Kruat Formation (Cuny et al., 2014). Three species are currently recognized including *H. steinmanni*, *H. kokutensis*, and *H. chuvalovi* (Cuny et al., 2008). One thing important to notice is that Khok Pha Suam has yielded a few large teeth compared to the number of small ones, contrary to Ban Saphan Hin, where only large teeth are recovered. If the large teeth are considered as belonging to adult specimens, small ones to juveniles, then Khok Pha Suam may appear as a potential nursery for these sharks.

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

The teeth of Khok Kruat spinosaurids can be categorized into two morphotypes (Wongko et al., 2019) and indicate that two distinct spinosaurid taxa potentially occur in the Albian-Aptian of Thailand. If these morphotypes are not related to differences between taxa, they are due to a dimorphism within a single species. However, there are evidence of several spinosaurid taxa in the same area from many formations such as *Spinosaurus aegyptiacus* and *Sigilmassasaurus brevicollis* from the Cenomanian Kem Kem beds of Morocco and *Ceratosuchops inferodios* and *Riparovenator milnerae* from the Barremian Wessex Formation of UK (Barker et al., 2021; Hendrickx et al., 2016; Richter et al., 2013). This suggests the possibility of a co-occurrence of two distinct spinosaurid taxa in the Khok Kruat Formation.

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

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

From the available materials currently, the Khok Pha Suam iguanodont represents characters of styracosternan iguanodontian such as triangular-shaped crest of the femur, the medial and lateral condyles are prominent and expanded at the distal end of femur. Three taxa of styracosternan iguanodontians, including *Siamodon ninngami*, *Ratchasimasaurus suranareae*, and *Sirindhorna khoratensis*, have been described from the Khok Kruat Formation in Nakhon Ratchasima Province plus one Laotian taxon *Mandschurosaurus laosensis* from the Grès Supérieurs Formation of Laos. If Khok Pha Suam iguanodontian is one of the previously named taxa from Nakhon Ratchasima, this will provide geographic distribution about 400 km to the far east. However, Khok Pha Suam locality is closer to Savannakhet of laos than Nakhon Ratchasima. The comparison between them had to be very careful, and overlapping elements are required. It would be incredible if Khok Pha Suam iguanodont is a new taxon, this means that there is a diversity of species up to five in the region. However, *S. khoratensis* is the best-preserved iguanodontian ornithopod in Southeast Asia, described from a composite individual including skull and mandible, as well as postcranial elements (Shibata et al., 2018). Therefore, it is necessary to compare the postcranial material between Khok Pha Suam taxa and *S. khoratensis* in our further study.

6.7 Conclusions

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

Chapter 7

Summary

The study of this thesis can be concluded as follows:

7.1 Evolutionary stages of ornithischian dinosaurs in Southeast Asia

Southeast Asian ornithischian fossils have been found in Thailand, Laos, Malaysia plus southern China. Their appearance can be divided into three stages. The oldest is known from the late Jurassic Phu Kradung Formation of Thailand represented by stegosaurids and basal neornithischians. There seems to be a lack of ornithischians during the pre-Barremian. However, the ankylosaurian tooth from the Tembeling Group represents the existence of ornithischians that were missing from the equivalent time in the Sao Khua Formation of Thailand. The last stage is the Early Cretaceous Khok Kruat Formation (Aptian-Albian) presents highly abundant advanced iguanodontians plus basal ceratopsians, which is refine the herbivorous shift from sauropod-dominated to ornithischian-dominated ecosystems. The iguanodontians and psittacosaurids also found in the Grès supérieurs Formation of Laos and Xinlong Formation of southern China show many similarities to the Khok Kruat fauna of Thailand and are considered equivalent in age.

7.2 Basal neornithischian new taxon from Phu Noi locality

The study of undescribed specimen PRC150, which is one of the best-preserved dinosaurs ever found from Southeast Asia, reveals a new species of basal neornithischian. The unique aspect of the Phu Noi neornithischian new taxon is the manus, Mc III and Mc IV are longest different from other basal neorithischians. It is the earliest record of neornithischian in Southeast Asia. Phylogenetic analysis confirmed that Phu Noi neornithischian new taxon was a basal neoceratopsian close to *Agilisaurus* and *Hexinlusaurus* from China. The finding adds diversity and helps elucidate the evolution of basal neornithischian dinosaurs in this region.

7.3 Preliminary study on the bone histology of Phu Noi neornithischians

Many isolated bones of basal neornithischians have been found in the Phu Noi locality. They are possibly the same animal, but of different ages based on different sizes. This study was conducted on five femora elements. According to differentiation and organizational patterns of the tissues within the bone suggest an ontogenetic stage in 5 femora was found mainly in the subadult based on the study of Hübner (2012), who studied the bone histology of a small ornithopod *Dysalotosaurus lettowvorbecki*. Annuli/LAGs were used to study past behavior or environment, which from the bone samples are found very few. Therefore, it is assumed that this may be caused by low food demand, no need for migration or relocation, and precocial behavior. This is the first study on bone histology and ontogeny of basal ornithischians in Thailand.

7.4 Khok Pha Suam iguanodontians

From the available materials currently, the Khok Pha Suam iguanodont represents characters of styracosternan iguanodontian such as the triangular-shaped crest of the femur, the medial and lateral condyles are prominent and expanded at the distal end of the femur. If Khok Pha Suam iguanodontian is one of the previously named taxa from Nakhon Ratchasima, this will provide geographic distribution about 400 km to the far east. However, Khok Pha Suam locality is closer to Savannakhet of laos than Nakhon Ratchasima. The comparison between them had to be very careful, and overlapping elements are required. It is necessary to compare the postcranial material with other taxa in our further study.

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APPENDIX 1

The ornithischian phylogenetic data matrix

The phylogenetic analysis in this study was based on that of Baron et al. (2017) modified from Butler and Sullivan 2009), which consists of 55 tata and 227 characters.

1. Skull proportions: 0. Preorbital skull length more than 45 per cent of basal skull length; Preorbital length less than 40 per cent of basal skull length.
2. Skull length (rostral–quadrate): 0. 10 per cent or less of body length; 1. 13 per cent or more of body length (modified following Xu *et al*. 2006).
3. Neomorphic rostral bone, anterior to premaxilla: 0. Absent; 1. Present.
4. Rostral bone, anteriorly keeled and ventrally pointed: 0. Absent; 1. Present.
5. Rostral bone, ventrolateral processes: 0. Rudimentary; 1. Well-developed.
6. Premaxilla, edentulous anterior region: 0. Absent, first premaxillary tooth is positioned adjacent to the symphysis; 1. Present, first premaxillary tooth is inset the width of one or more crowns.
7. Premaxilla, posterolateral process, length: 0. Does not contact lacrimal; 1. Contacts the lacrimal, excludes maxilla–nasal contact.
8. Oral margin of the premaxilla: 0. Narial portion of the body of the premaxilla slopes steeply from the external naris to the oral margin; 1. Ventral premaxilla flares laterally to form a partial floor of the narial fossa.
9. Position of the ventral (oral) margin of the premaxilla: 0. Level with the maxillary tooth row; 1. Deflected ventral to maxillary tooth row.
10. Premaxillary foramen: 0. Absent; 1. Present.
11. Premaxillary palate: 0. Strongly arched, forming a deep, concave palate; 1. Horizontal or only gently arched.
12. Overlap of the dorsal process of the premaxilla onto the nasal: 0. Present; 1. Absent.
13. Fossa-like depression positioned on the premaxilla–maxilla boundary: 0. Absent; 1. Present.
14. Premaxilla–maxilla diastema: 0. Absent, maxillary teeth continue to anterior end of maxilla; 1. Present, substantial diastema of at least one crowns length between maxillary and premaxillary teeth.

15. Form of diastema; 0. Flat; 1. Arched ‘subnarial gap’ between the premaxilla and maxilla.
16. Narial fossa surrounding external nares on lateral surface of premaxilla, position of ventral margin of fossa relative to the ventral margin of the premaxilla: 0. Closely approaches the ventral margin of the premaxilla; 1. Separated by a broad flat margin from the ventral margin of the premaxilla
17. External nares, position of the ventral margin: 0. Below the ventral margin of the orbits; 1. Above the ventral margin of the orbits.
18. External naris size: 0. Small, entirely overlies the premaxilla; 1. Enlarged, extends posteriorly to overlie the maxilla.
19. Deep elliptic fossa present along sutural line of the nasals: 0. Absent; 1. Present.
20. Internal antorbital fenestra size: 0. Large, generally at least 15 per cent of the skull length; 1. Very much reduced, less than 10 per cent of skull length, or absent.
21. External antorbital fenestra: 0. Present; 1. Absent.
22. External antorbital fenestra, shape: 0. Triangular; 1. Oval or circular.
23. Additional opening(s) anteriorly within the antorbital fossa: 0. Absent; 1. Present.
24. Maxilla, prominent anterolateral boss articulates with the medial premaxilla: 0. Absent; 1. Present.
25. Maxilla, accessory anterior process: 0. Absent; 1. Present.
26. Maxilla, buccal emargination: 0. Absent; 1. Present.
27. Eminence on the rim of the buccal emargination of the maxilla near the junction with the jugal: 0. Absent; 1. Present.
28. Slot in maxilla for lacrimal: 0. Absent; 1. Present.
29. Accessory ossification(s) in the orbit (palpebral/supraorbital): 0. Absent; 1. Present.
30. Palpebral/supraorbital: 0. Free, projects into orbit from contact with lacrimal/prefrontal; 1. Incorporated into orbital margin.
31. Palpebral, shape in dorsal view: 0. Rod-shaped; 1. Plate-like with wide base.
32. Palpebral/supraorbital, number: 0. One; 1. Two; 2. Three.
33. Free palpebral, length, relative to anteroposterior width of orbit: 0. Does not traverse entire width of orbit; 1. Traverses entire width of orbit.

34. Exclusion of the jugal from the posteroventral margin of the external antorbital fenestra by lacrimal–maxilla contact: 0. Absent; 1. Present.

35. Anterior ramus of jugal, proportions: 0. Deeper than wide, but not as deep as the posterior ramus of the jugal; 1. Wider than deep; 2. Deeper than the posterior ramus of the jugal.

36. Widening of the skull across the jugals, chord from frontal orbital margin to extremity of jugal is more than minimum interorbital width: 0. Absent; 1. Present, skull has a triangular shape in dorsal view.

37. Position of maximum widening of the skull: 0. Beneath the jugal–postorbital bar; 1. Posteriorly, beneath the infratemporal fenestra.

38. Jugal (or jugal–epijugal) ridge dividing the lateral surface of the jugal into two planes: 0. Absent; 1. Present.

39. Epijugal: 0. Absent; 1. Present.

40. Jugal boss: 0. Absent; 1. Present.

41. Node-like ornamentation on jugal, mostly on, or ventral to, the jugal–postorbital bar: 0. Absent; 1. Present.

42. Jugal–postorbital bar, width broader than infratemporal fenestra: 0. Absent; 1. Present.

43. Jugal–postorbital joint: 0. Elongate scarf joint; 1. Short butt joint.

44. Jugal, form of postorbital process: 0. Not expanded dorsally; 1. Dorsal portion of postorbital process is expanded posteriorly.

45. Jugal–squamosal contact above infratemporal fenestra: 0. Absent; 1. Present.

46. Jugal posterior ramus, forked: 0. Absent; 1. Present.

47. Jugal, posterior ramus: 0. Forms anterior and ventral margin of infratemporal fenestra; 1. Forms part of posterior margin, expands towards squamosal.

48. Jugal–quadratojugal contact: 0. Overlapping; 1. Tongue-and-groove.

49. Postorbital, orbital margin: 0. Relatively smooth curve; 1. Prominent and distinct projection into orbit.

50. Postorbital: 0. T-shaped; 1. Triangular and plate-like.

51. Postorbital–parietal contact: 0. Absent, or very narrow; 1. Broad.

52. Contact between dorsal process of quadratojugal and descending process of the squamosal: 0. Present; 1. Absent.

53. Quadratojugal, shape: 0. L-shaped, with elongate anterior process; 1. Subrectangular with long axis vertical, short, deep anterior process.

54. Quadratojugal, ventral margin: 0. Approaches the mandibular condyle of the quadrate; 1. Well-removed from the mandibular condyle of the quadrate.

55. Quadratojugal, orientation: 0. Faces laterally; 1. Faces posterolaterally.

56. Quadratojugal, transverse width: 0. Mediolaterally flattened; 1. Transversely expanded and triangular in coronal section.

57. Prominent oval fossa on pterygoid ramus of quadrate: 0. Absent; 1. Present.

58. Quadrate lateral ramus: 0. Present; 1. Absent.

59. Quadrate shaft: 0. Anteriorly convex in lateral view; 1. Reduced in anteroposterior width and straight in lateral view.

60. Paraquadratic foramen or notch, size: 0. Absent or small, opens between quadratojugal and quadrate; 1. Large.

61. Paraquadratic foramen, orientation: 0. Posterolateral aspect of quadrate shaft; 1. Lateral aspect of quadrate or quadratojugal.

62. Paraquadratic foramen, position: 0. On quadrate-quadratojugal boundary; 1. Located within quadratojugal.

63. Quadrate mandibular articulation: 0. Quadrate condyles subequal in size; 1. Medial condyle is larger than lateral condyle; 2. Lateral condyle is larger than medial.

64. Paired frontals: 0. Short and broad; 1. Narrow and elongate (more than twice as long as wide).

65. Supratemporal fenestrae: 0. Open; 1. Closed.

66. Supratemporal fenestrae, anteroposteriorly elongated: 0. Absent, fenestrae are subcircular to oval in shape 1. Present.

67. Parietal septum, form: 0. Narrow and smooth; 1. Broad and rugose.

68. Parietosquamosal shelf: 0. Absent; 1. Present.

69. Parietosquamosal shelf, extended posteriorly as distinct frill: 0. Absent; 1. Present.

70. Composition of the posterior margin of the parietosquamosal shelf: 0. Parietal contributes only a small portion to the posterior margin;1. Parietal makes up at least 50 per cent of the posterior margin.

71. Postorbital–squamosal bar: 0. Bar-shaped; 1. Broad, flattened.

72. Postorbital–squamosal tubercle row: 0. Absent; 1. Present.

73. Enlarged tubercle row on the posterior squamosal: 0. Absent; 1. Present.

74. Frontal and parietal dorsoventral thickness: 0. Thin; 1. Thick.

75. Paroccipital processes: 0. Extend laterally and are slightly expanded distally; 1. Distal end pendent and ventrally extending.

76. Paroccipital processes, proportions: 0. Short and deep (height ≥ 1/2 length); 1. Elongate and narrow.

77. Posttemporal foramen/fossa, position: 0. Totally enclosed with the paroccipital process; 1. Forms a notch in the dorsal margin of the paroccipital process, enclosed dorsally by the squamosal.

78. Supraoccipital, contribution to dorsal margin of foramen magnum: 0. Forms entire dorsal margin of foramen magnum; 1. Exoccipital with medial process that restricts the contribution of the supraoccipital.

79. Basioccipital, contribution to the border of the foramen magnum: 0. Present; 1. Absent, excluded by exoccipitals.

80. Basisphenoid: 0. Longer than, or subequal in length to, basioccipital; 1. Shorter than basioccipital.

81. Prootic–basisphenoid plate: 0. Absent; 1. Present.

82. Basal tubera, shape: 0. Knob-shaped; 1. Plate-shaped.

83. Basipterygoid processes, orientation: 0. Anteroventral; 1. Ventral; 2. Posteroventral.

84. Premaxilla–vomeral contact: 0. Present; 1. Absent, excluded by midline contact between maxillae.

85. Dorsoventrally deep (deeper than 50% of snout depth) median palatal keel formed of the vomers, pterygoids and palatines: 0. Absent; 1. Present.

86. Pterygovomerine keel, length: 0. Less than 50% of palate length; 1. More than 50% of palate length.

87. Pterygoid–maxilla contact at posterior end of tooth row: 0. Absent; 1. Present.

88. Pterygoquadrate rami, posterior projection of ventral margin: 0. Weak; 1. Pronounced.

89. Cortical remodeling of surface of skull dermal bone: 0. Absent; 1. Present.

90. Predentary: 0. Absent; 1. Present.

91. Predentary size: 0. Short, posterior premaxillary teeth oppose anterior dentary teeth; 1. Roughly equal in length to the premaxilla, premaxillary teeth only oppose predentary.
92. Predentary, rostral end in dorsal view: 0. Rounded; 1. Pointed.
93. Predentary, oral margin: 0. Relatively smooth; 1. Denticulate.
94. Tip of predentary in lateral view: 0. Does not project above the main body of predentary; 1. Strongly upturned relative to main body of predentary.
95. Predentary, ventral process: 0. Single; 1. Bilobate.
96. Predentary, ventral process: 0. Present, well-developed; 1. Very reduced or absent.
97. Dentary symphysis: 0. V-shaped; 1. Spout shaped.
98. Dentary tooth row (and edentulous anterior portion) in lateral view: 0. Straight; 1. Anterior end downturned.
99. Dorsal and ventral margins of the dentary: 0. Converge anteriorly; 1. Subparallel.
100. Ventral flange on dentary: 0. Absent; 1. Present.
101. Coronoid process: 0. Absent or weak, posterodorsally oblique, depth of mandible at coronoid is less than 140% depth of mandible beneath tooth row; 1. Well-developed, distinctly elevated, depth of mandible at coronoid is more than 180% depth of mandible beneath tooth row.
102. Anterodorsal margin of coronoid process formed by posterodorsal process of dentary: 0. Absent; 1. Present.
103. Coronoid process, position: 0. Posterior to dentition; 1. Lateral to dentition.
104. External mandibular fenestra, situated on dentary-surangular-angular boundary: 0. Present; 1. Absent.
105. Small fenestra positioned dorsally on the surangular-dentary joint: 0. Absent; 1. Present.
106. Ridge or process on lateral surface of surangular, anterior to jaw suture: 0. Absent; 1. Present, anteroposteriorly extended ridge; 2. Present, dorsally directed finger-like process.
107. Retroarticular process: 0. Elongate; 1. Rudimentary or absent.
108. Node-like ornamentation of the dentary and angular: 0. Absent; 1. Present.

109. Level of jaw joint: 0. Level with tooth row, or weakly depressed ventrally; 1. Strongly depressed ventrally, more than 40% of the height of the quadrate is below the level of the maxilla.

110. Mandibular osteoderm: 0. Absent; 1. Present.

111. Premaxillary teeth: 0. Present; 1. Absent, premaxilla edentulous.

112. Premaxillary teeth, number: 0. Six; 1. Five; 2. Four; 3. Three; 4. Two; 5. One.

113. Premaxillary teeth, crown expanded above root: 0. Crown is unexpanded mesiodistally above root, no distinction between root and crown is observable; 1. Crown is at least moderately expanded above root.

114. Premaxillary teeth increase in size posteriorly: 0. Absent, all premaxillary teeth subequal in size; 1. Present, posterior premaxillary teeth are significantly larger in size than anterior teeth.

115. Maxillary and dentary crowns, shape: 0. Apicobasally tall and blade-like; 1. Apicobasally short and sub-triangular; 2. Diamond-shaped.

116. Maxillary/dentary teeth, marginal ornamentations: 0. Fine serrations set at right angles to the margin of the tooth; 1. Coarse serrations (denticles) angle upwards at 45 degrees from the margin of the tooth.

117. Enamel on maxillary/dentary teeth: 0. Symmetrical; 1. Asymmetrical.

118. Apicobasally extending ridges on maxillary/dentary teeth: 0. Absent; 1. Present.

119. Apicobasally extending ridges on lingual/labial surfaces of maxillary/dentary crowns confluent with marginal denticles: 0. Absent; 1. Present.

120. Prominent primary ridge on labial side of maxillary teeth: 0. Absent; 1. Present.

121. Prominent primary ridge on lingual side of dentary teeth: 0. Absent; 1. Present.

122. Position of maxillary/dentary primary ridge: 0. Centre of the crown surface, giving the crown a relatively symmetrical shape in lingual/labial view; 1. Offset, giving crown asymmetrical appearance.

123. At least moderately developed labiolingual expansion of crown (‘cingulum’) on maxillary/dentary teeth: 0. Present; 1. Absent.

124. Heterodont dentary dentition: 0. No substantial heterodonty is present in dentary dentition; 1. Single, enlarged, caniform anterior dentary tooth, crown is not mesiodistally expanded above root; 2. Anterior dentary teeth are strongly

recurved and caniform, but have crowns expanded mesiodistally above their roots and are not enlarged relative to other dentary teeth.

125. Peg-like tooth located anteriorly within dentary, lacks denticles, strongly reduced in size: 0. Absent; 1. Present.

126. Alveolar foramina (‘special foramina’) medial to maxillary/dentary tooth rows: 0. Present; 1. Absent.

127. Recurvature in maxillary and dentary teeth: 0. Present; 1. Absent.

128. Overlap of adjacent crowns in maxillary and dentary teeth: 0. Absent; 1. Present.

129. Crown is mesiodistally expanded above root in cheek teeth: 0. Absent; 1. Present.

130. Position of maximum apicobasal crown height in dentary/maxillary tooth rows: 0. Anterior portion of tooth row; 1. Central portion of tooth rows; 2. Caudal portion of tooth rows.

131. Close-packing and quicker replacement eliminates spaces between alveolar border and crowns of adjacent functional teeth: 0. Absent; 1. Present.

132. Fusion between the intercentum of the atlas and the neural arches: 0. Absent; 1. Present.

133. Epipophyses on anterior (postaxial) cervicals: 0. Present; 1. Absent.

134. Cervicals 4-9, form of central surfaces: 0. Amphicoelous; 1. At least slightly opisthocoelous.

135. Cervical number: 0. Seven/eight; 1. Nine; 2. Ten or more.

136. Articulation between the zygapophyses of dorsal vertebrae: 0. Flat; 1. Tongue-and-groove.

137. Dorsals, number: 0. 12–13; 1. 15; 2. 16 or more.

138. Sacrals, number: 0. Two; 1. Three; 2. Four/five; 3. Six or more.

139. Sacrum, accessory articulation with pubis: 0. Absent; 1. Present.

140. Posterior sacral ribs are considerably longer than anterior sacral ribs: 0. Absent; 1. Present.

141. Anterior caudal vertebrae, length of transverse processes relative to neural spine height: 0. Subequal; 1. Longer than neural spine.

142. Proximal caudal neural spines: 0. Height the same or up to 50 per cent taller than the centrum; 1. More than 50 per cent taller than the centrum.

143. Elongate tail (59 or more caudals): 0. Absent; 1. Present.
144. Chevron shape: 0. Rod-shaped, often with slight distal expansion; 1. Strongly asymmetrically expanded distally, width greater than length in mid caudals.
145. Sternal segments of the anterior dorsal ribs: 0. Unossified; 1. Ossified.
146. Gastralia: 0. Present; 1. Absent.
147. Ossified clavicles: 0. Absent; 1. Present.
148. Sternal plates, shape: 0. Absent; 1. Kidney-shaped; 2. Shafted or hatchet-shaped (rod-like posterolateral process, expanded anterior end).
149. Proportions of humerus and scapula: 0. Scapula longer or subequal to the humerus; 1. Humerus substantially longer than the scapula.
150. Scapula blade, length relative to minimum width: 0. Relatively short and broad, length is 5-8 times minimum width; 1. Elongate and strap-like, length is at least 9 times the minimum width.
151. Scapula acromion shape: 0. Weakly developed or absent; 1. Well-developed spine-like.
152. Scapula, blade-shape: 0. Strongly expanded distally; 1. Weakly expanded, near parallel-sided.
153. Humeral length: 0. More than 60% of femoral length; 1. Less than 60% of femoral length.
154. Deltopectoral crest development: 0. Well-developed, projects anteriorly as a distinct flange; 1. Rudimentary, is at most a thickening on the anterolateral margin of the humerus.
155. Humeral shaft form, in anterior or posterior view: 0. Relatively straight; 1. Strongly bowed laterally along length.
156. Longest manual phalanx as percentage of length of humerus: 0. Less than 10% ; 1. More than 15%.
157. Metacarpals with block-like proximal ends: 0. Absent; 1. Present.
158. Metacarpals 1 and 5: 0. Substantially shorter in length than metacarpal 3; 1. Subequal in length to metacarpal 3.
159. Penultimate phalanx of the second and third fingers: 0. Shorter than first phalanx; 1. Longer than the first phalanx.
160. Manual digit 3, number of phalanges: 0. Four; 1. Three or fewer.

161. Manual digits 2–4: 0. First phalanx relatively short compared to second phalanx; 1. First phalanx more than twice the length of the second phalanx.

162. Extensor pits on the dorsal surface of the distal end of metacarpals and manual phalanges: 0. Absent or poorly developed; 1. Deep, well-developed.

163. Manual unguals strongly recurved with prominent flexor tubercle: 0. Absent; 1. Present.

164. Acetabulum: 0. At least a small perforation; 1. Completely closed.

165. Preacetabular process, shape / length: 0. Short, tab-shaped, distal end is posterior to pubic peduncle; 1. Elongate, strap-shaped, distal end is anterior to pubic peduncle.

166. Preacetabular process, length: 0. Less than 50% of the length of the ilium; 1. More than 50% of the length of the ilium.

167. Preacetabular process, lateral deflection: 0. 10–20 degrees from midline; 1. More than 30 degrees.

168. Dorsal margin of preacetabular process and dorsal margin of ilium above acetabulum: 0. Narrow, not transversely expanded; 1. Dorsal margin is transversely expanded to form a narrow shelf.

169. In dorsal view preacetabular process of the ilium expands mediolaterally towards its distal end: 0. Absent; 1. Present.

170. Dorsal margin of the ilium in lateral view: 0. Relatively straight or slightly convex; 1. Sinuous, postacetabular process is strongly upturned.

171. Subtriangular process extending medially from the dorsal margin of the iliac blade: 0. Absent; 1. Present.

172. Subtriangular process, form and position: 0. Short and tab-like, above acetabulum; 1. Elongate and flange-like, on postacetabular process.

173. Brevis shelf & fossa: 0. Fossa faces ventrolaterally and shelf is near vertical and visible in lateral view along entire length, creating a deep postacetabular portion; 1. Fossa faces ventrally and posterior of shelf portion cannot be seen in lateral view.

174. Length of the postacetabular process as a percentage of the total length of the ilium: 0. 20% or less; 1. 25-35%; 2. More than 35%.

175. Medioventral acetabular flange of ilium, partially closes the acetabulum: 0. Present; 1. Absent.

176. Supra-acetabular ‘crest’ or ‘flange’: 0. Present; 1. Absent.

177. Ischial peduncle of the ilium: 0. Projects ventrally; 1. Broadly swollen, projects ventrolaterally.

178. Pubic peduncle of ilium: 0. Large, elongate, robust; 1. Reduced in size, shorter in length than ischial peduncle.

179. Pubic peduncle of ischium, shape: 0. Transversely compressed; 1. Dorsoventrally compressed.

180. Ischium, shape of shaft: 0. Relatively straight; 1. Gently curved along length; 2. Distinct bend at midlength.

181. Ischial shaft, cross-section: 0. Compressed mediolaterally; 1. Subcircular and bar-like.

182. Ischial shaft: 0. Expands weakly, or is parallel-sided, distally; 1. Distally expanded into a distinct ‘foot’; 2. Tapers distally.

183. Groove on the dorsal margin of the ischium: 0. Absent; 1. Present.

184. Tab-shaped obturator process on ischium: 0. Absent; 1. Present.

185. Ischial symphysis, length: 0. Ischium forms a median symphysis with the opposing blade along at least 50% of its length; 1. Ischial symphysis present distally only.

186. Pubis, orientation: 0. Anteroventral; 1. Rotated posteroventrally to lie alongside the ischium (opisthopubic).

187. Shaft of pubis (postpubis), shape in cross-section: 0. Blade-shaped; 1. Rod-shaped.

188. Shaft of pubis (postpubis), length: 0. Approximately equal in length to the ischium; 1. Reduced, extends for half or less the length of the ischium.

189. Reduction of postpubic shaft: 0. Postpubic shaft extends for around half the length of ischium; 1. Postpubic shaft is very short or absent.

190. Body of pubis, size: 0. Relatively large, makes substantial contribution to the margin of the acetabulum; 1. Reduced in size, rudimentary, nearly excluded from the acetabulum.

191. Body of the pubis, massive and dorsolaterally rotated so that obturator foramen is obscured in lateral view: 0. Absent; 1. Present.

192. Prepubic process: 0. Absent; 1. Present.

193. Prepubic process: 0. Compressed mediolaterally, dorsoventral height exceeds mediolateral width; 1. Rod-like, mediolateral width exceeds dorsoventral height; 2. Dorsoventrally compressed; 3. Twisted along length – dorsoventrally compressed at its base and transversely compressed distally.

194. Prepubic process, length: 0. Stub-like and poorly developed, extends only a short distance anterior to the pubic peduncle of the ilium; 1. Elongated into distinct anterior process.

195. Prepubic process, extends beyond distal end of preacetabular process of ilium: 0. Absent; 1. Present.

196. Extent of pubic symphysis: 0. Elongate; 1. Restricted to distal end of pubic blade, or absent.

197. Femoral shape in medial/lateral view: 0. Bowed anteriorly along length; 1. Straight.

198. Femoral head: 0. Confluent with greater trochanter, fossa trochanteris is groove-like; 1. Fossa trochanteris is modified into distinct constriction separating head and greater trochanter.

199. ‘Anterior’ or ‘lesser’ trochanter, morphology: 0. Absent; 1. Trochanteric shelf ending in a small, pointed, spike; 2. Broadened, prominent, ‘wing’ or ‘blade’ shaped, sub-equal in anteroposterior width to greater trochanter; 3. Reduced anteroposterior width, closely appressed to the expanded greater trochanter.

200. Level of most proximal point of anterior trochanter relative to level of proximal femoral head: 0. Anterior trochanter is positioned distally on the shaft, and separated from ‘dorsolateral’ trochanter/greater trochanter by deep notch visible in medial view; 1. Anterior trochanter positioned proximally, approaches level of proximal surface of femoral head, closely appressed to ‘dorsolateral’/greater trochanter (no notch visible in medial view).

201. Fourth trochanter of femur, shape: 0. Low eminence, or absent; 1. Prominent ridge; 2. Pendent.

202. Fourth trochanter, position: 0. Located entirely on proximal half of femur; 1. Positioned at midlength, or distal to midlength.

203. Anterior (extensor) intercondylar groove on distal end of femur: 0. Absent; 1. Present.

204. Posterior (flexor) intercondylar groove of the femur: 0. Fully open; 1. Medial condyle inflated laterally, partially covers opening of flexor groove.

205. Lateral condyle of distal femur, position and size in ventral view: 0. Positioned relatively laterally, and slightly narrower in width than the medial condyle; 1. Strongly inset medially, reduced in width relative to medial condyle.

206. Distal tibia: 0. Subquadrate, posterolateral process is not substantially developed; 1. Elongate posterolateral processs, backs fibula.

207. Fibular facet on the lateral margin of the proximal surface of the astragalus: 0. Large; 1. Reduced to small articulation.

208. Calcaneum, proximal surface: 0. Facet for tibia absent; 1. Well-developed facet for tibia present.

209. Medial distal tarsal: 0. Articulates distally with metatarsal 3 only; 1. Articulates distally with metatarsals 2 and 3.

210. Metatarsal arrangement: 0. Compact, closely appressed to one another along 50-70% of their length, spread distally; 1. Contact each other only at proximal ends, spread strongly outwards distally.

211. Digit 1: 0. Metatarsal 1 robust and well-developed, distal end of phalanx 1-1 projects beyond the distal end of metatarsal 2; 1. Metatarsal 1 reduced & proximally splint like, end of phalanx 1-1 does not extend beyond the end of metatarsal 2; 2. Metatarsal 1 reduced to a vestigal splint or absent, does not bear digits.

212. Pedal digit 4 phalangeal number: 0. Five; 1. Four or fewer.

213. Metatarsal 5, length: 0. More than 50 per cent of metatarsal 3; 1. Less than 25 per cent of metatarsal 3.

214. Metatarsal 5: 0. Bears digits; 1. Lacks digits.

215. Pedal unguals, shape: 0. Tapering, narrow pointed, claw-like; 1. Wide, blunt, hoof-like.

216. Epaxial ossified tendons present along vertebral column: 0. Absent; 1. Present.

217. Ossified hypaxial tendons, present on caudal vertebrae: 0. Absent; 1. Present.

218. Ossified tendons, arrangement: 0. Longitudinally arranged; 1. Basket-like arrangement of fusiform tendons in caudal region; 2. Double-layered lattice.

219. Parasagittal row of dermal osteoderms on the dorsum of the body: 0. Absent; 1. Present.

220. Lateral row of keeled dermal osteoderms on the dorsum of the body: 0. Absent; 1. Present.

221. U-shaped cervical / pectoral collars composed of contiguous keeled osteoderms: 0. Absent; 1. Present.

222. Wear facets on teeth: 0. Absent or sporadically developed; 1. Systematic development of wear facets along the entire tooth row.

223. Head of humerus is separated from prominent medial tubercle on proximal surface by a groove: 0. Absent; 1. Present.

224. Pendent fourth trochanter, rod-like with subparallel anterior and posterior surfaces: 0. Absent; 1. Present.

225. Fibula, distal end is strongly reduced and splint-like: 0. Absent; 1. Present.

226. Astragalus and calcaneum are indistinguishably fused to one another: 0. Absent; 1. Present.

227. Maximum expansion of distal tibia relative to proximal: 0. Distal tibia is considerably less expanded than proximal; 1. Maximum expansion of distal tibia is subequal to that of proximal tibia.

APPENDIX 2

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

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

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Abstract

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

Key Words

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

1. Introduction

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

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

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

2. Institutional abbreviations

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

3. Geological settings and palaeoenvironment

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

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

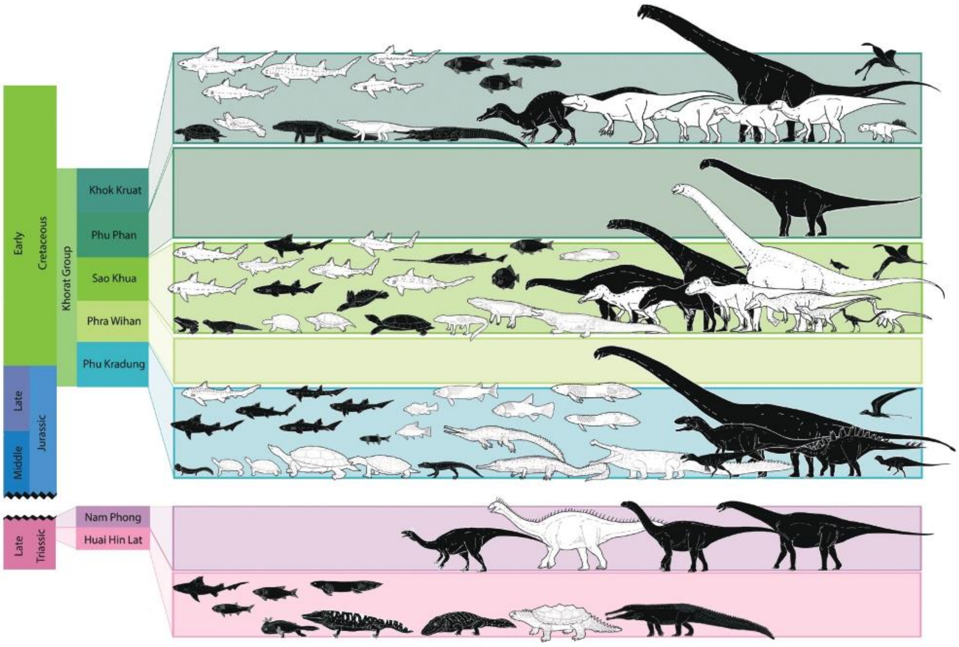

Figure 1. Mesozoic vertebrate fauna from the Indochina Terrane of NE Thailand, species-level identified taxa shown in white silhouettes, tentatively identified taxa in black silhouettes, further details in Suppl. material 1 (Modified from Lionel Cavin: All not to scale).

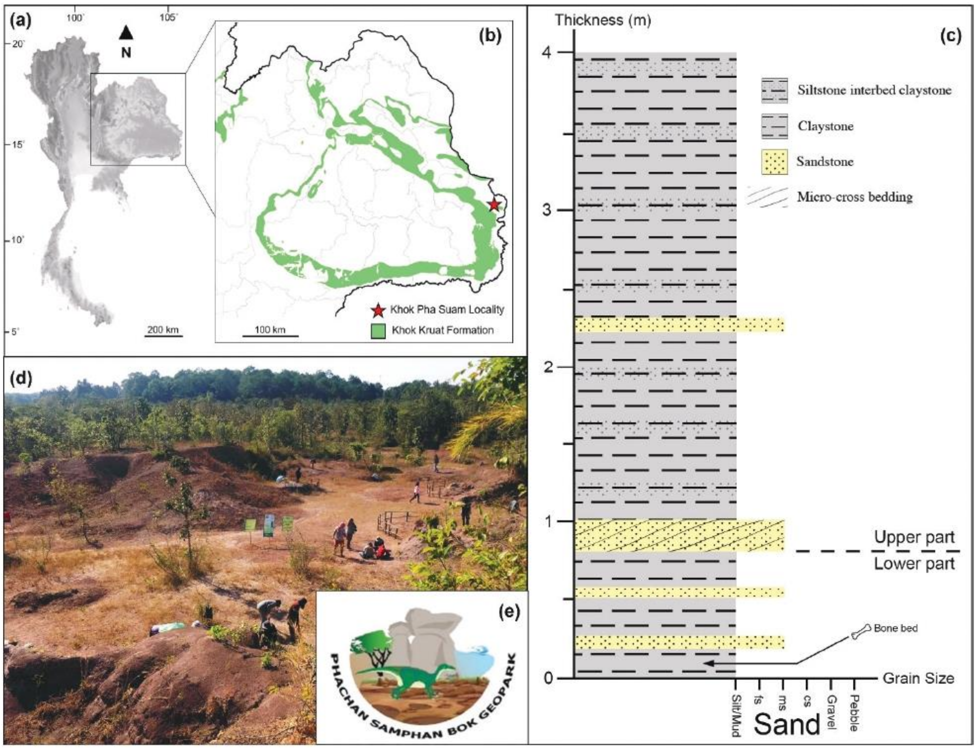

Figure 2. Locality map and Lithostratigraphic section of Khok Pha Suam locality. **a.** Map of Thailand, showing the location of the Khorat Plateau; **b.** Distribution of the Khok Kruat Formation in northeastern Thailand (green color; modified from DMR, 2004), location of Khok Pha Suam locality (red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

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

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

4. Material

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

5. Vertebrate palaeontology

The vertebrates found at the Khok Pha Suam locality comprise five taxa of hybodont sharks, at least two taxa of ginglymodians, a sinamiid fish, carettochelyid and adocid turtles, neosuchian crocodyliforms, pterosaurs, dinosaurs (iguanodontians, sauropods, and at least two taxa of theropods). The faunal diversity described in this article together with additional data from other localities allows us to propose a preliminary reconstruction of the Early Cretaceous Khok Kruat Formation ecosystem (Fig. 6).

5.1 Selachians

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

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

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

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

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

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

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

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

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

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

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

5.2. Actinopterygians

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

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

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

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

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

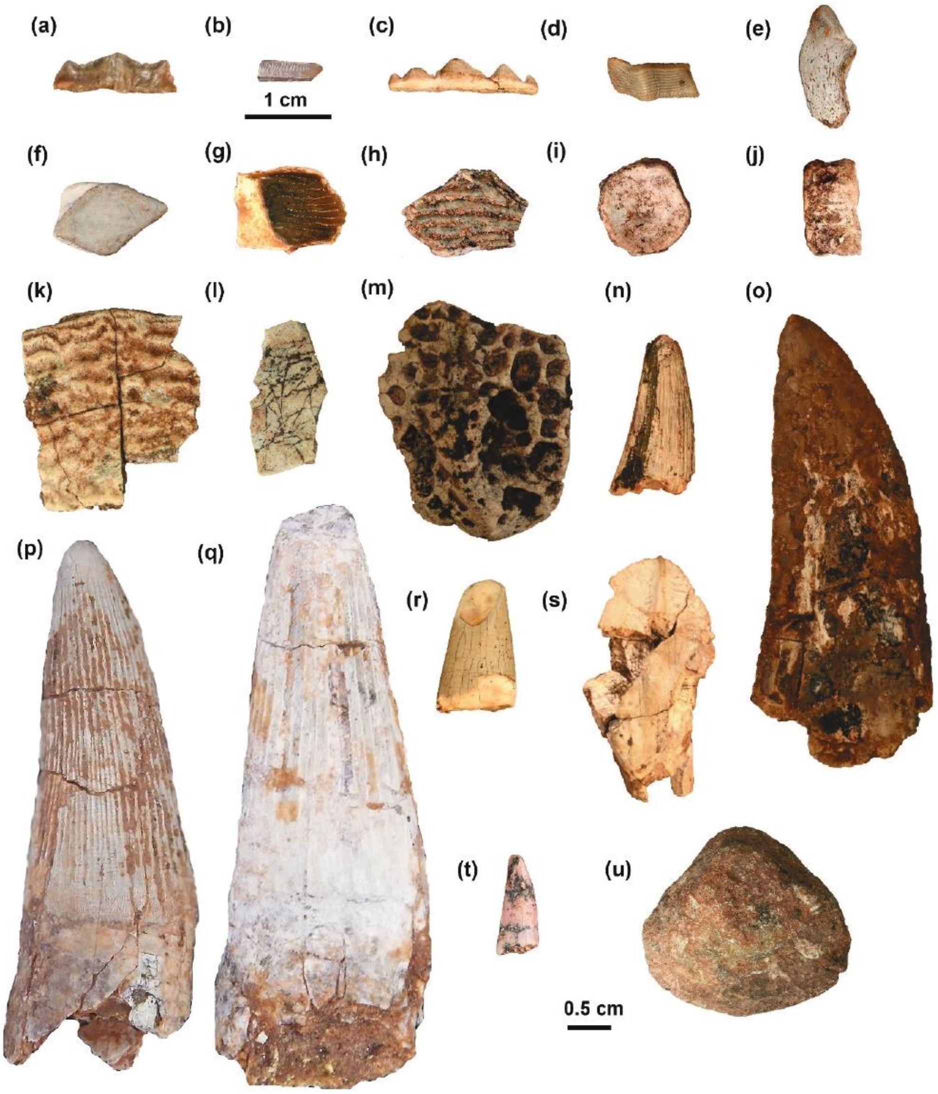

Figure 3. Isolated microremains from Khok Pha Suam locality. *Thaiodus ruchae* tooth (**a.** PRCMR301) in labial view, *Khoratodus foreyi* tooth (**b.** PRCMR302) in lingual view, "*Hybodus*" *aequitridentatus* tooth (**c.** PRCMR303) in labial view, *Heteroptychodus steinmanni* tooth (**d.** PRCMR304)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

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

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

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

5.3. Turtles

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

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

5.4. Crocodyliforms

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

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

Family Goniopholididae Cope, 1875 (Fig. 4)

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

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

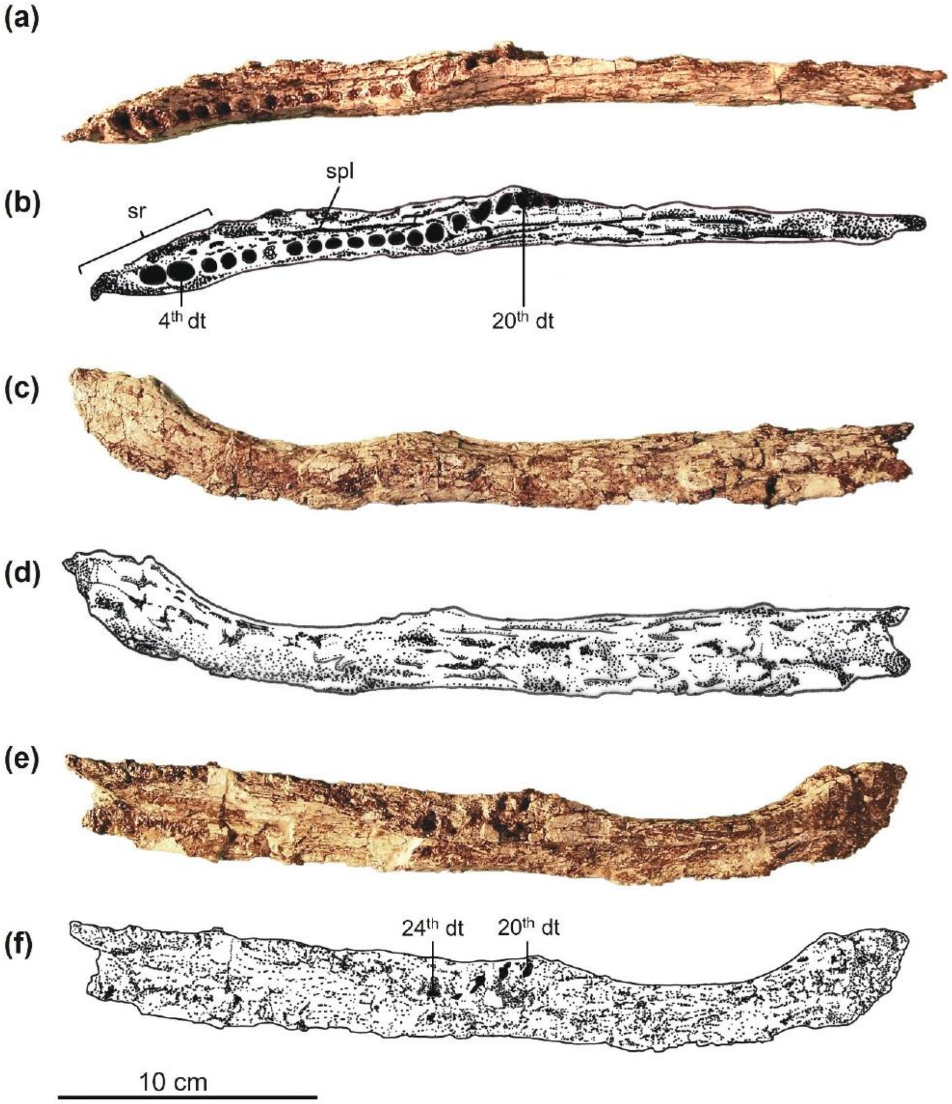

Figure 4. Photos and drawing of a nearly complete left mandible of Goniopholididae indet. from Khok Pha Suam (SM2021-1-112) in dorsal (**a, b**), lateral (**c, d**) and lingual (**e, f**) views. Abbreviation: dt, dentary tooth; spl, splenial; sr, symphyseal region.

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

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

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

5.5. Sauropods

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

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

5.6. Theropods

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

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

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

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

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

5.7. Iguanodontians

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

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

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

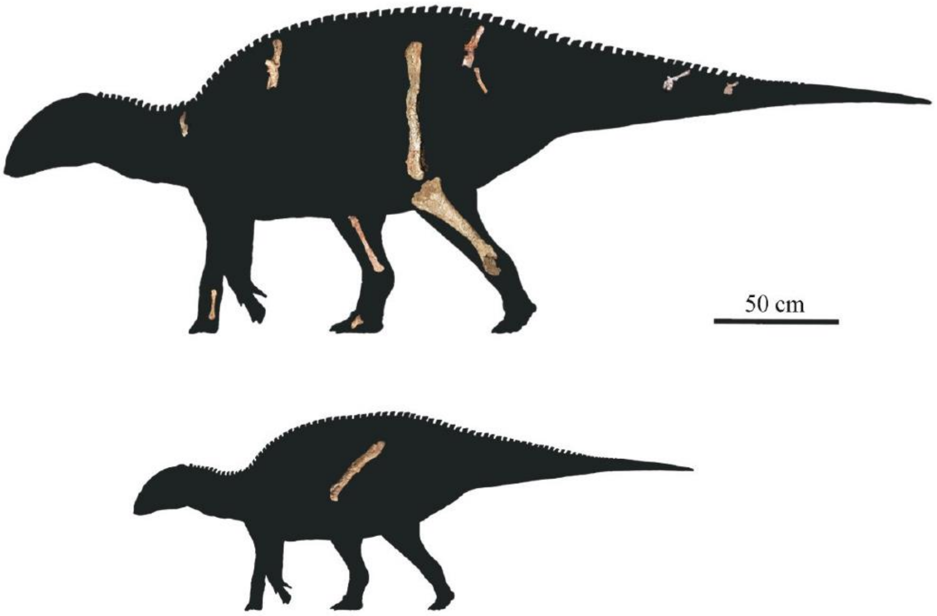

Figure 5. Tentative reconstruction of Khok Pha Suam iguanodontian indet. showing recovered bones in left lateral view

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

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

5.8. Pterosaurs

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

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

6. Overview of other Khok Kruat localities

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

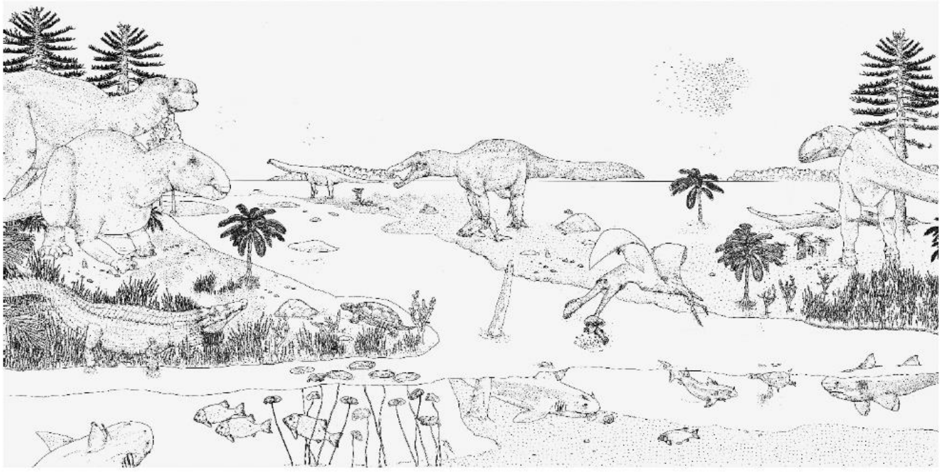

Figure 6. Palaeoenvironmental interpretation of the Early Cretaceous (Aptian-Albian) Khok Pha Suam Locality. Drawing by Sakka Weerataweemat.

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

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

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

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

7. Discussion

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

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

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

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

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

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

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

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

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

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

8. Conclusions

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

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Supplementary material 1

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

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Data type: Images

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

Link: https://doi.org/10.3897/fr.25.83081.suppl1

Supplementary

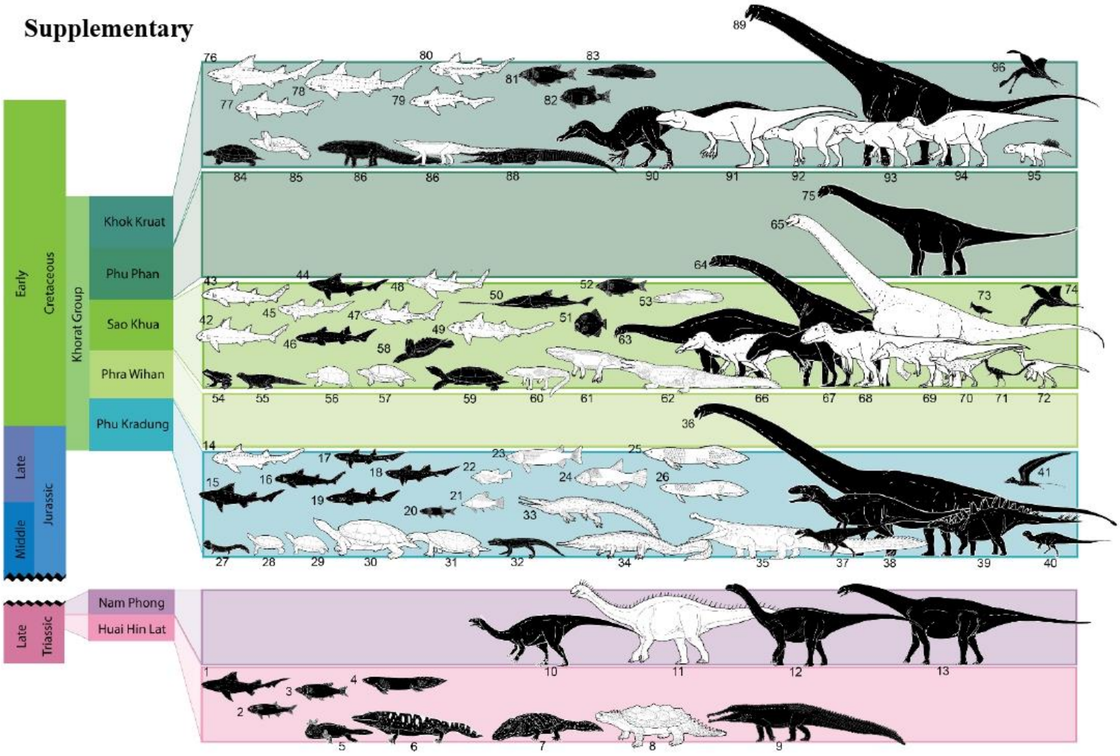

Figure 1. Mesozoic vertebrate fauna from the Indochina Terrane of Thailand, species-level identified taxa shown in white silhouettes, tentatively identified taxa in black silhouettes (Modified from Lionel Cavin: All not to scale).

Huai Hin Lat Formation
1. *Hybodus* sp.
2. Palaeonisciformes indet.
3. Semionotiformes indet.
4. Ceratodontoidei indet.
5. Plagiosauridae indet.
6. Stereospondyli indet.
7. *Cyclotosaurus* cf. *posthumus*
8. *Proganochelys ruchae*
9. Phytosauria indet.

Footprints (archosauria indet.)

Nam Phong Formation
10. Basal sauropodomorpha indet.
11. *Isanosaurus attavipachi*
12. Sauropoda cf. Vulcanodontidae
13. Sauropoda cf. *Tazoudasaurus*

Footprints (tetrapod indet., sauropoda and theropoda)

Phu Kradung Formation
14. *Acrodus kalasinensis*
15. *Hybodus* sp.
16. *Heteroptychodus* sp.
17. *Lonchidion* sp.
18. *Lissodus* sp.
19. *Jiaodontus* sp.
20. Ptycholepidae indet.
21. *Thaiichthys buddhabutrensis*
22. *Khoratichthys gibbus*
23. *Isanichthys palustris*
24. *Isanichthys lertboosi*
25. *Ferganoceratodus martini*
26. *Ferganoceratodus annekempae*

27. Brachyopidae indet.
28. *Phunoichelys thirakhupti*
29. *Kalasinemys prasarttongosothi*
30. *Basilochelys macrobios*
31. *Yakemys multiporcata*
32. *Atoposauridae indet.*
33. *Indosinosuchus potamosiamensis*
34. *Indosinosuchus kalasinensis*
35. *Chalawan thailandicus*
36. Mamenchisauridae indet.
37. Theropoda indet.
38. Metriacanthosauridae indet.
39. Stegosauridae indet.
40. Basal neornithischia indet.
41. Rhamphorhynchoidea indet

Phra Wihan Formation

Footprints (crocodyliformes, sauropoda, theropoda and ornithopoda)

Sao Khua Formation

42. *Heteroptychodus steinmanni*
43. *Heteroptychodus kokutensis*
44. *Hybodus* sp.
45. *Lonchidion khoratensis*
46. *Parvodus* sp.
47. *Isanodus paladeji*
48. *Isanodus nongbualamphuensis*
49. *Mukdahanodus trisivakulii*
50. Sclerorhynchoid indet.
51. Pycnodontiformes indet.
52. Ginglymodi indet.
53. *Siamamia naga*
54. Anura indet.
55. Anguimorpha indet. (egg fossil)
56. *Isanemys srisuki*
57. *Protoshachemys rubra*
58. *Kizylkumemys* sp.
59. Trionychoidea indet.
60. *Theriosuchus grandinaris*
61. "*Goniopholis*" *phuwiangensis*
62. *Siamosuchus phuphokensis*
63. Sauropoda cf. Diplodocoidea
64. Sauropoda cf. Brachiosauridae
65. *Phuwiangosaurus sirindhornae*
66. *Siamosaurus suteethorni*
67. Carcharodontosauria indet.
68. *Siamotyrannus isanensis*
69. *Phuwiangvenator yaemniyomi*
70. *Vayuraptor nongbualamphuensis*
71. Compsognathidae indet.
72. *Kinnareemimus khonkaenensis*
73. Aves indet.
74. Ornithocheridae indet.

Footprints (theropoda)

Phu Phan Formation

75. Sauropod indet.

Footprints (theropoda)

Khok Kruat Formation

76. "*Hybodus*" *aequitridentatus*
77. *Heteroptychodus steinmanni*
78. *Thaiodus ruchae*
79. *Khoratodus foreyi*
80. *Acrorhizodus khoratensis*
81. *Lanxangichthys* sp.
82. Ginglymodi indet.
83. *Siamamia* sp.
84. *Kizylkumemys khoratensis*
85. *Shachemys* sp.
86. Goniopholididae indet.
87. Eusuchia indet.
88. *Khoratosuchus jintasakuli*
89. Titanosauriformes indet.
90. Spinosauridae indet.
91. *Siamraptor suwati*
92. *Siamodon nimngami*
93. *Ratchasimasaurus suranareae*
94. *Sirindhorna khoratensis*
95. *Psittacosaurus sattayaraki*
96. Pterosauria indet.

Footprints (crocodyliformes, theropoda and ornithopoda)

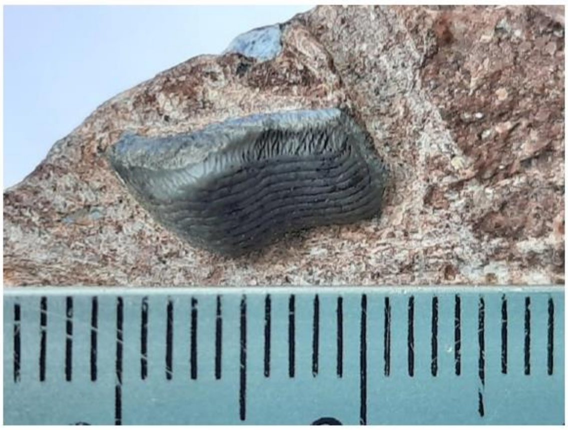

Figure 2. Tooth of *Heteroptychodus steinmanni* from Ban Saphan Hin (housed in private colletion), Nakhon Ratchasima Province in apical view: Photo courtesy of Witaya Nimngami

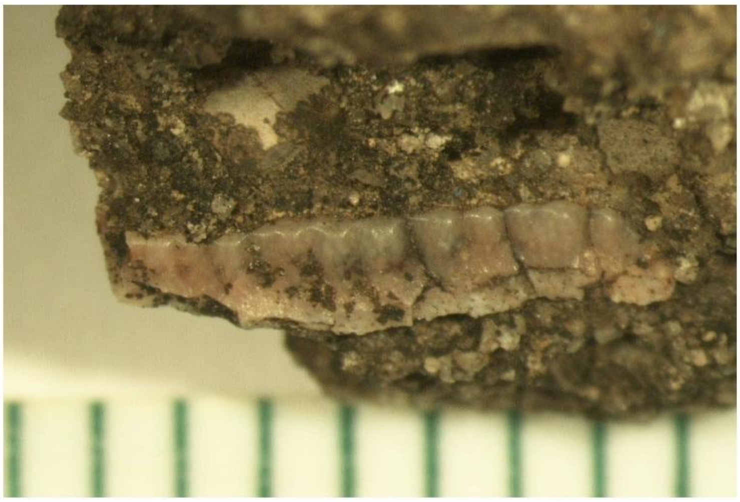

Figure 3. Tooth of *Thaiodus ruchaea* from Lam Pao Dam, Kalasin Province in lingual view: Photo courtesy of Gilles Cuny.

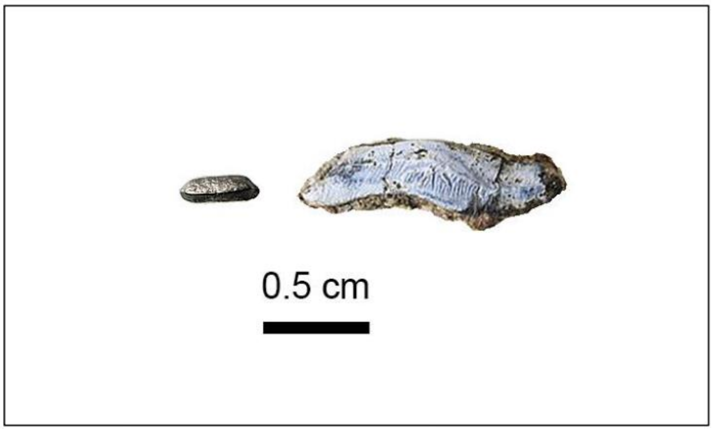

Figure 4. Teeth of Hybodonts indet. from Lam Pao Dam (housed in Sirindhorn Museum colletion), Kalasin Province in apical view: Photo courtesy of Wansiri Boonla.

Figure 5. A left femur approximately 40 cm in length of a probable juvenile sauropod from Khok Pha Suam in posterior view. It is on an exhibit at the local museum under the supervision of Na Kham Subdistrict Administrative Organization.

APPENDIX 3

Manuscript
“Ornithischian dinosaurs in Southeast Asia: a review with palaeobiogeographic implications)”

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Ornithischian dinosaurs in Southeast Asia: a review with palaeobiogeographic implications

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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).

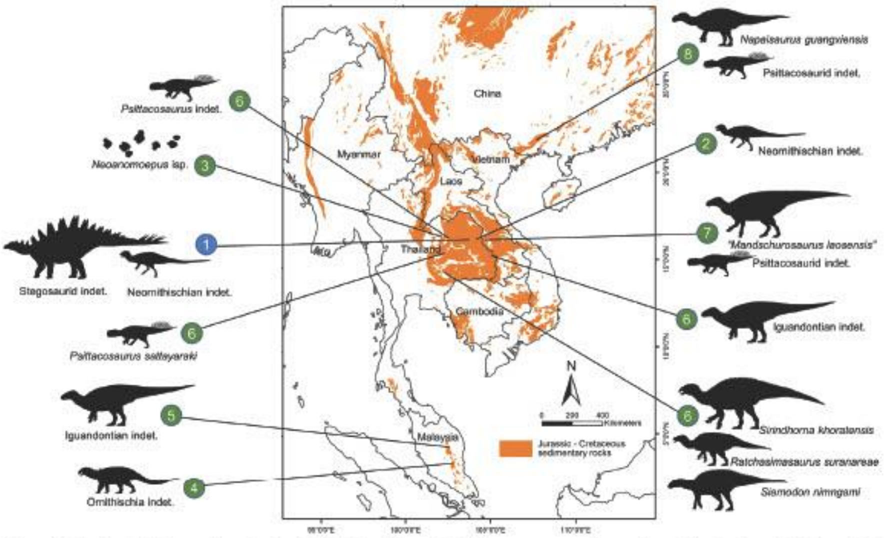


Figure 1. Southeast Asia map showing the distribution of Jurassic–Cretaceous non-marine sediments in Southeast Asia (modified from CCOP's 1:2 million Geologic map of East and Southeast Asia), Number in circles = rock formations: 1, Lower Phu Kradung; 2, Upper Phu Kradung; 3, Phra Wihan; 4, ?Tembling 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 sattayaraki* (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).

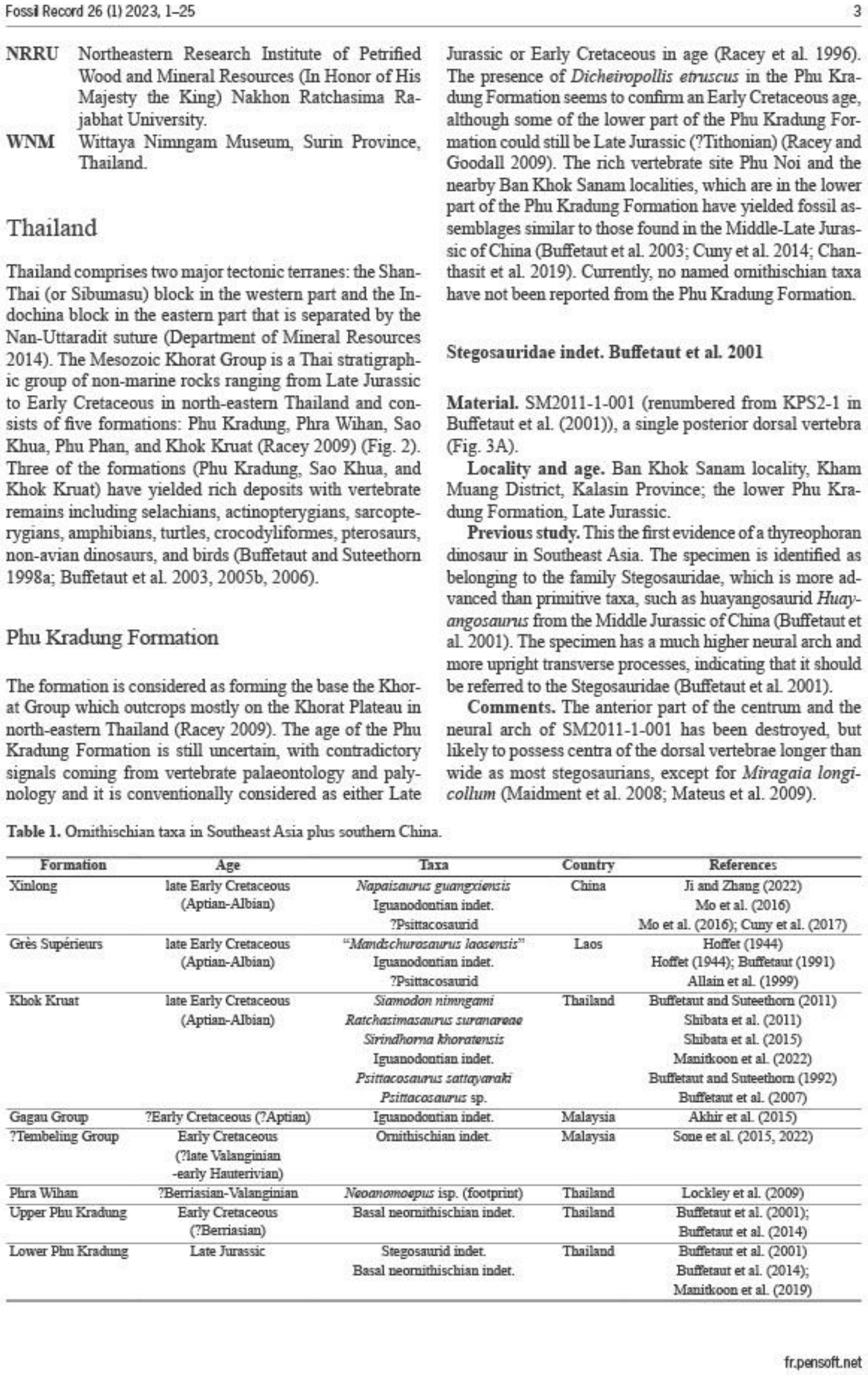
The faunal assemblage from the Aptian Xinlong Formation of southern China shows many similarities to the Khok Kruat Formation of the Khorat Group of Thailand, especially the presence of the four endemic genera of hybodont sharks restricted to Southeast Asia and South China (Cuny 2012; Cuny et al. 2017). 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 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).

Table 1. Ornithischian taxa in Southeast Asia plus southern China.

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

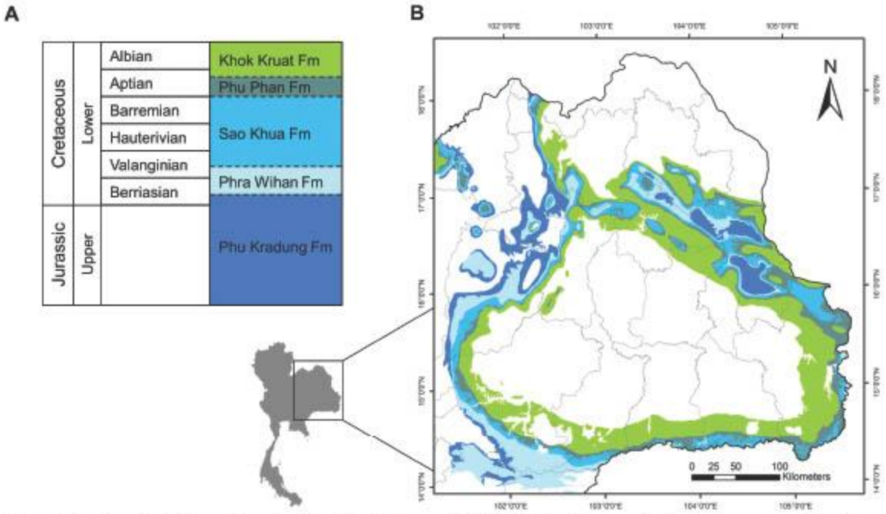


Figure 2. Stratigraphy of Khorat Group (modified from Tucker et al. (2022)) **A.** Location map showing the formations of the Khorat Group on the Khorat Plateau of north-eastern Thailand (**B**).

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 fan-shaped 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

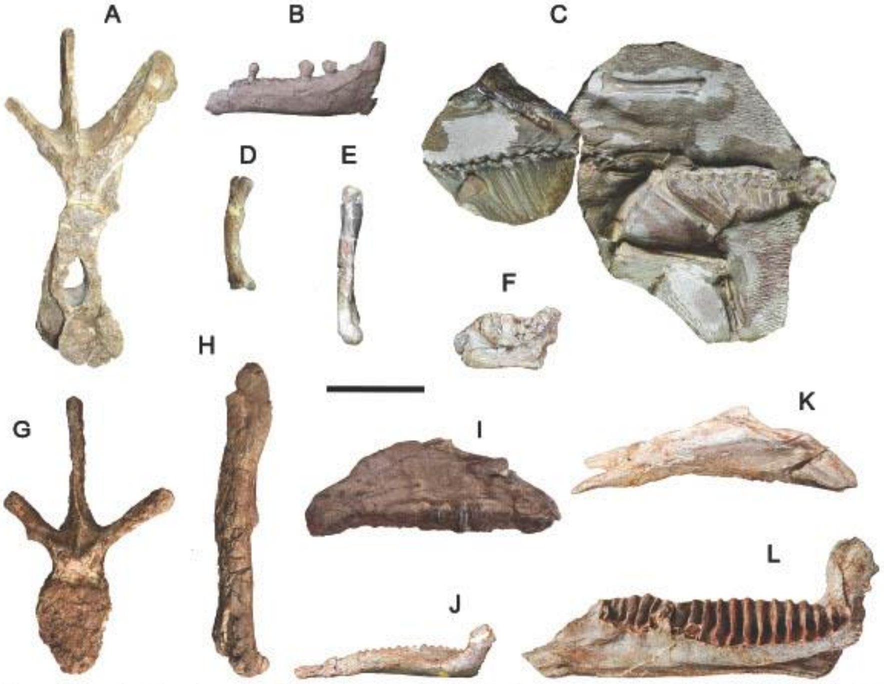


Figure 3. Exceptional specimen of ornithischian dinosaurs from Thailand. Stegosaurid vertebra (**A.** SM2011-1-001), Phu Noi neornithischian left dentary (**B.** PRC149), Phu Noi neornithischian articulated skeleton (**C.** PRC150), Dan Luang neornithischian left femur (**D.** SM2016-1-081), *Psitacosaurus* 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* left maxilla (**K.** NRRU-A2048), *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 multidens*) 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

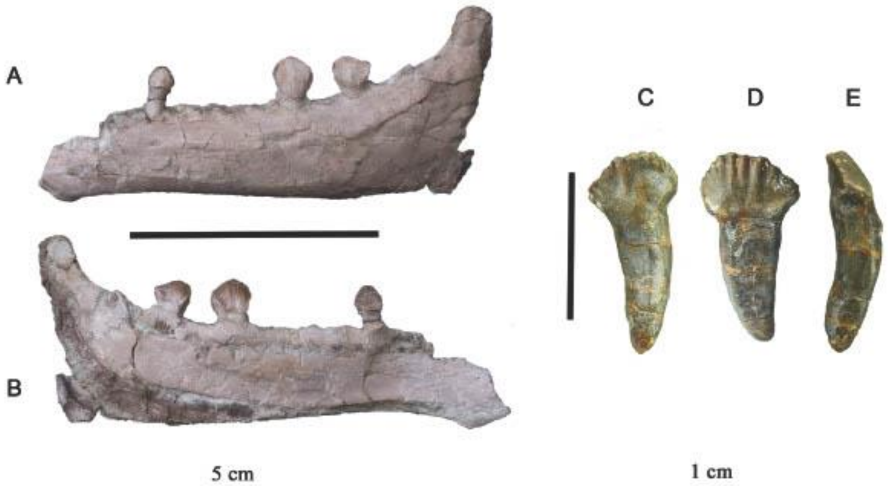


Figure 4. Basal neornithischian specimens from the lower Phu Kradung Formation. (left) Left dentary (PRC 149) from Phu Noi locality, in lateral (**A**) and medial (**B**) views; (right) isolated tooth (WNM-Ks-001) from Khok Sanam locality, in labial (if dentary) (**C**), lingual (**D**) and mesial/distal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

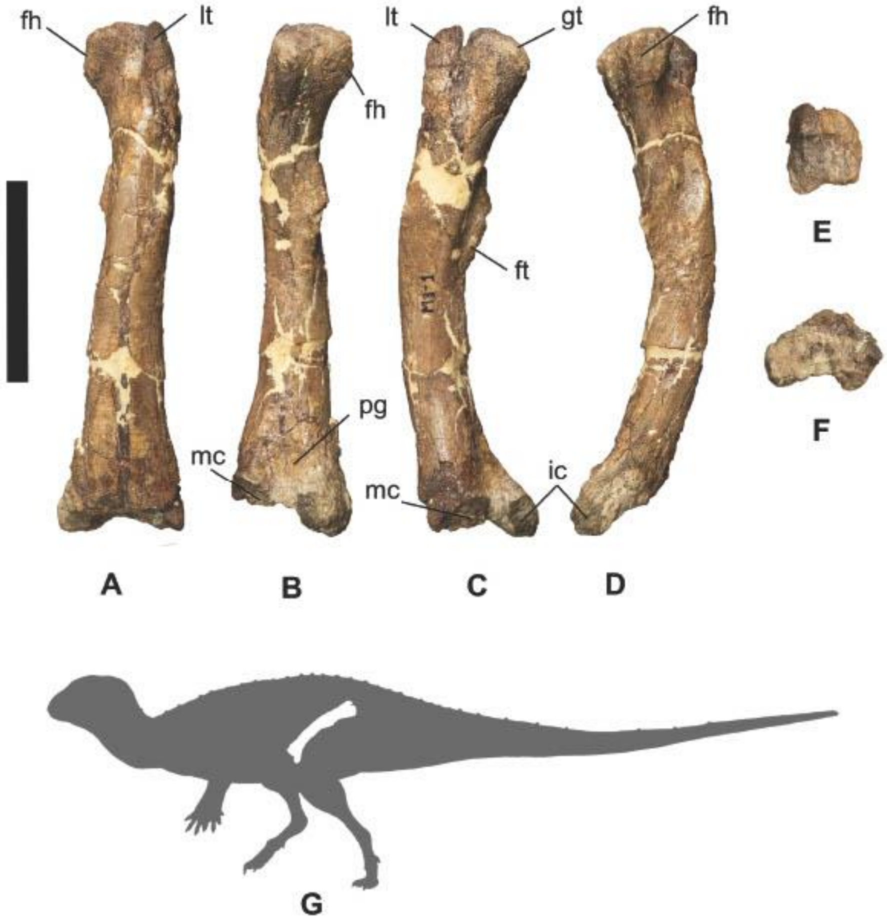


Figure 5. Left femur of the 'Dan Luang neornithischian' (SM2016-1-081) in anterior (**A**), posterior (**B**), lateral (**C**) medial (**D**) proximal (**E**) and distal (**F**) views; Reconstruction showing the bone in left lateral view (**G**); Abbreviations: fh, femoral head; ft, fourth trochanter; 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. nimngami* 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).

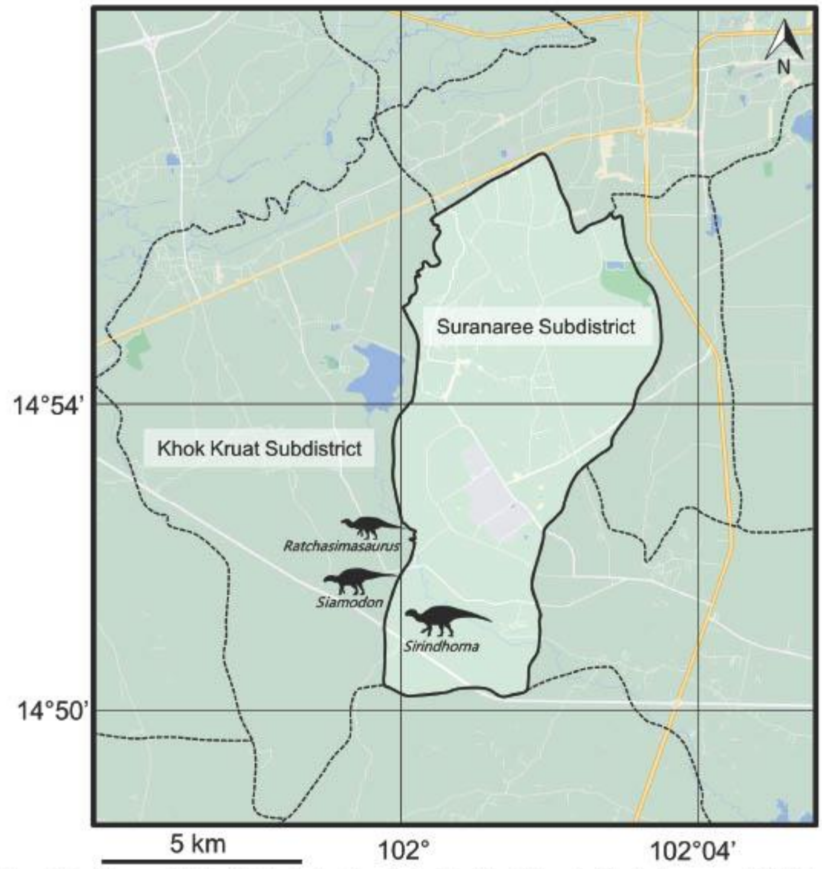


Figure 7. Locality map of Nakhon Ratchasima Province, showing localities of *Siamodon*, *Ratchasimasaurus* and *Sirindhorna*.

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

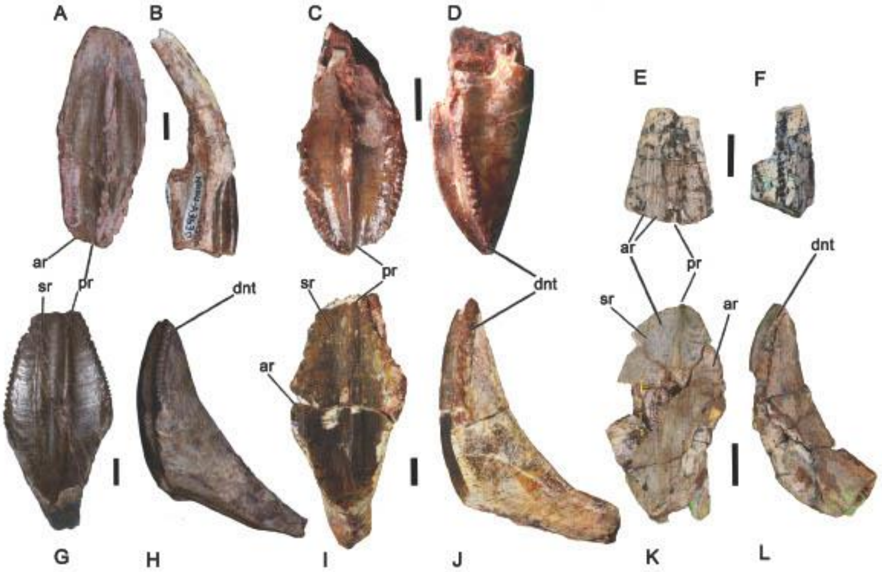


Figure 8. Isolated Thai iguanodontian teeth; *Sirindhorna khoratensis* maxillary tooth (**A, B.** NRRU-A1959) and dentary tooth (**G, H.** NRRU3001-28); *Siamodon nomngami* maxillary tooth (**C, D.** PRC-5) and dentary tooth (**I, J.** WNM-Sp-001); Khok Pha Suam iguanodontian maxillary tooth (**E, F.** 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*: leaf-shaped 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 (≈ 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 (≈ 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 (≈ 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*.

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 ~ 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; Chokchaloemwong 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

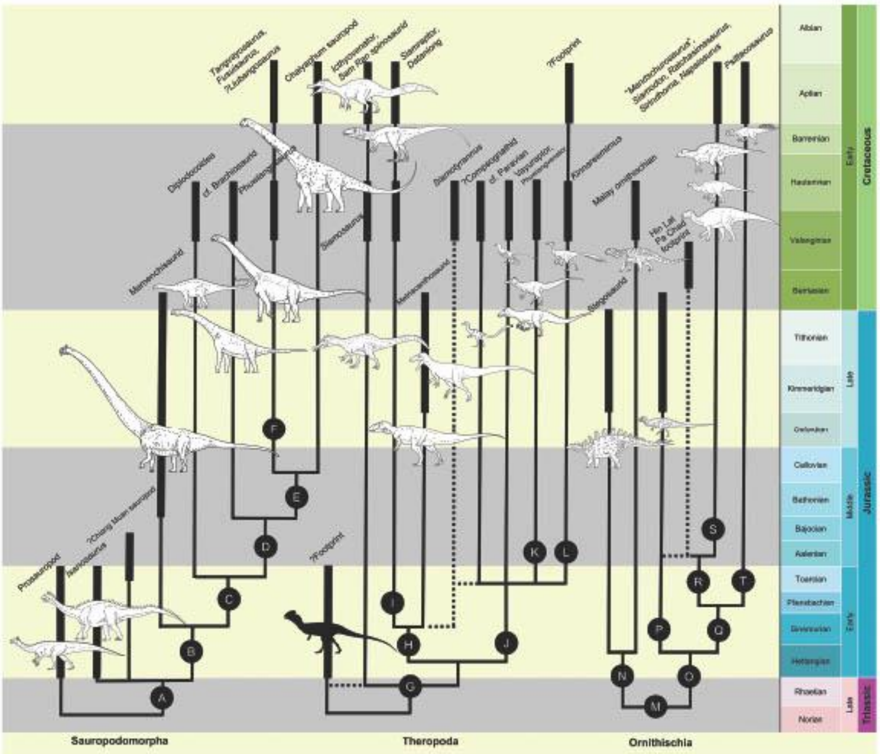


Figure 9. Phylogenetic relationships of non-avian dinosaurs in southeast Asia and southern China. Abbreviations: A, Sauropoda; B, Eusauropoda; C, Neosauropoda; D, Macronaria; E, Titanosauriformes; F, Somphospondyli; G, Tetanurae; H, Allosauroidea; I, Carcharodontosauria; J, Coelurosauria; K, Megaraptora; 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.

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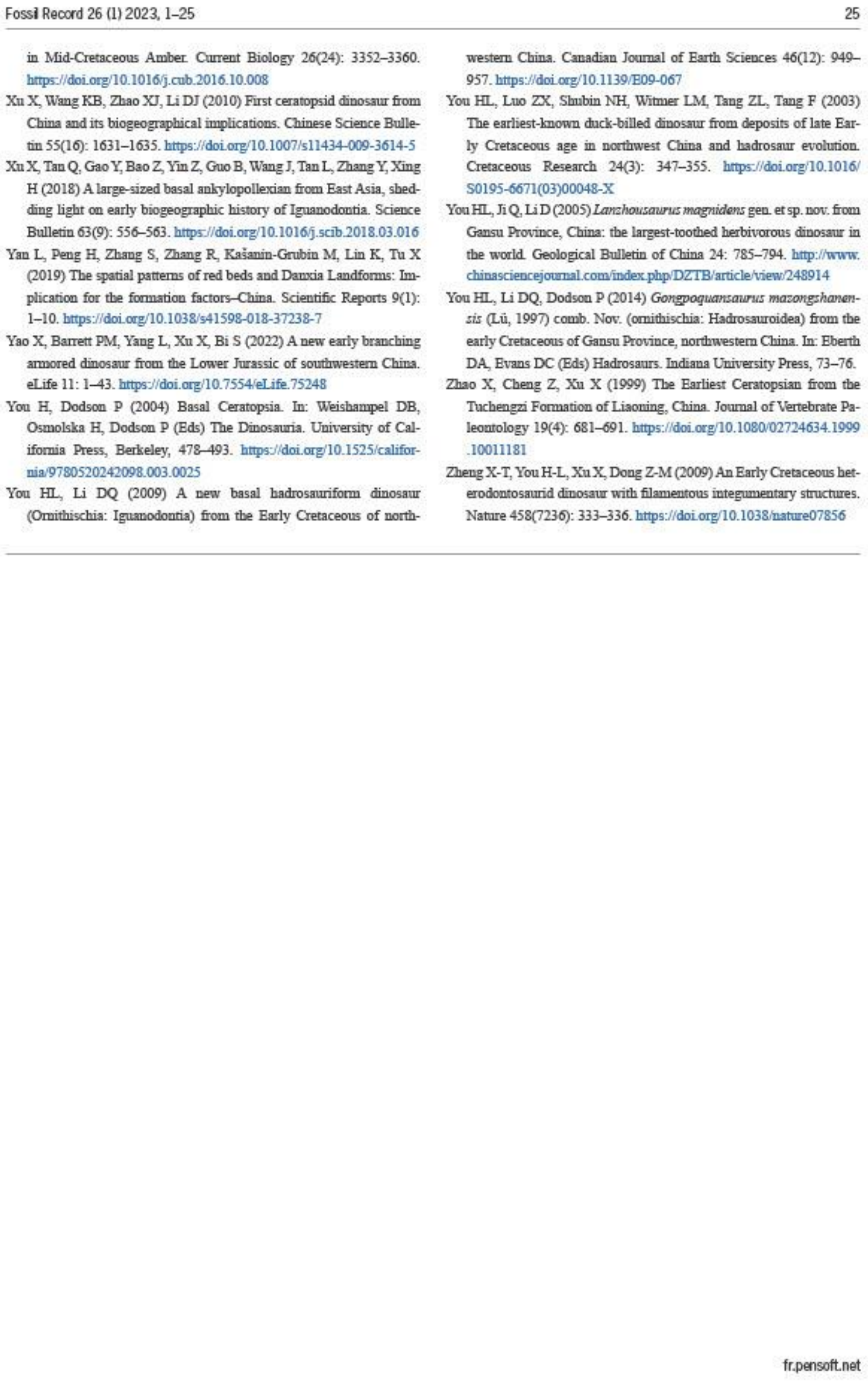

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