THEROPOD DINOSAURS FROM THAILAND AND SOUTHEAST ASIA
PHYLOGENY, EVOLUTION, AND PALEOBIOGEOGRAPHY

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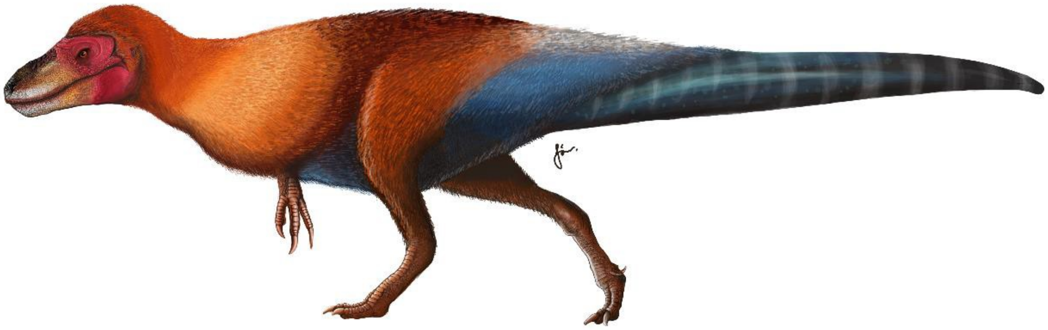

ACKNOWLEDGMENTS

This is a long journey since I was a bachelor student at Mahidol University (Bangkok, Thailand), and first had an opportunity to study paleontology, specifically,Thai dinosaurs. The first paleontological research that I did was a bachelor project studying dorsal vertebrae of the theropod *Siamotyrannus*. Since then, I knew what I wanted to be and what I wanted to do in the rest of my life. After finished bachelor study, I got a scholarship to study abroad. I decided to come to Germany to study theropod paleontology. Struggling with German language courses in Göttingen for over a year, I finally got a place in Munich doing a master program in evolution and systematics, and finally, in Bonn for PhD study. I continued to study Thai theropods, from those dorsal vertebrae of *Siamotyrannus* as a bachelor project, to study the anatomy of *Siamotyrannus* as a master project, and finally, I had an opportunity to study theropods in Thailand and Southeast Asia as my PhD topic (as you are reading it now), which is a dream come true in my life for about 10 years.

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My deepest thank goes to my family, my parents Wichien and Aree Samathi, who don't know much about paleontology or biology but always understand and support me since I was young, whatever I wanted to do or to be, either art or science. Thanks to my grandmom, my sisters (and brothers in law), and my nieces and nephews (my sisters' daughters and sons), who always wait to see me once a year, as well as my girlfriend, Wijanee Sendang, who always support and understand me. Thank all of you for being patient with me and loving me.

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Finally, I would like to deeply thank my PhD supervisor, Prof. Martin Sander, who gave me the opportunity to study theropod dinosaurs under his supervision, who inspires me a lot in the field of paleontology and biology, and for working patiently with me. Without him, his encouragement, his understanding, his supervision, and his support, it would be hard for me to finish this long- term project that I wanted to do since I was a bachelor student in Thailand.

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SUMMARY

Southeast Asia played an important role in dinosaur study during the Late Jurassic to mid-Cretaceous. Thailand is roughly in the third place in dinosaur discovery in Asia, after China and Mongolia. Nevertheless, there are few palaeontologists. Focussing on theropod dinosaurs in Southeast Asia, they mainly consist of non-maniraptoran tetanurans. They show similarity to Chinese plus Japanese theropods during the Early Cretaceous in broad systematic terms. During this time, some theropods such as spinosaurids and carcharodontosaurs were almost cosmopolitant. Whereas some theropods such as metriacanthosaurids were endemic to Europe and Asia including China and Thailand during the Middle to Late Jurassic.

In this thesis, my team and I added knowledge and updated information on theropod diversity and taxonomy in Southeast Asia. The diversity of non-avian theropods from the Khorat Plateau in northeastern Thailand is high compared with previous works.

In the Sao Khua Formation, which shows the highest theropod diversity, two new theropod taxa have been described and named. These include the basal coelurosaur *Vayuraptor nongbualamphuensis* gen. et sp. nov. and the basal megaraptoran *Phuwiangvenator yaemniyomi* gen. et sp. nov. This find suggests that the Megaraptora might originate in Southeast Asia. The problematic avetheropod *Siamotyrannus* has been revised and found here to be a basal coelurosaur, not an allosauroid as previous studies. This tells us that the basal coelurosaurs were probably evolved into large bodied at early stages. New phylogenetic analyses found *Kinnareemimus* is a basal ornithomimosaur, more basal than previously thought. Postcranial materials of a spinosaurid from the Phu Wiang Mountain, Khon Kaen Province, which might belong to *Siamosaurus*, have been described. A juvenile theropod from the Phu Wiang Mountain has been reported and described for the first time. Several theropod fragmentary materials from Thailand have been re-studied and discussed.

In the Phu Kradung Formation, a new metriacanthosaurid (sinraptorid), which is being described by Chanthasit and team, was briefly mentioned here.

In the Khok Kruat Formation, a yet unnamed and undescribed spinosaurid from Thailand has been preliminary studied here. We found that it differs from the spinosaurid from Laos, suggested that it could be a new taxon. A new carcharodontosaur, which is being described by Chokchaloemwong and team, was briefly mentioned here.

Furthermore, theropod materials in Southeast Asia including Myanmar, Laos, and Malaysia, as well as southern China, have been here discussed. The supposed to be a ceratosaur *Camarillasaurus* from the Early Cretaceous of Spain was found here to be a spinosaurid, not a ceratosaur as in the original study, adding number of spinosaurid taxa into the Iberian Peninsula. Finally, a tibial fragment of a spinosaurid has been identified and studied. It was concluded to belong to the subclade Spinosaurinae and shows some level of aquatic adaptation.

INTRODUCTION

Theropod dinosaurs form a morphologically and taxonomically diverse clade of bipedal tetrapods which include extant birds. They appeared in the Late Triassic until recent. They are generally classified within the Saurischia, together with the sauropodomophs. While some studies placed theropods in the clade Ornithoscelida and are the closest relatives of the Ornithischia (Baron 2017; Baron & Barrett 2017; Baron et al. 2017; Parry et al 2017; Langer et al. 2017).

The most abundant and diverse theropod fossils found in Southeast Asia are from Thailand. Most of them are from the Sao Khua Formation, but also can be found in the Khok Kruat and Phu Kradung formations. Some of these finds were studied almost twenty years ago, whereas others have been discovered recently and need careful study. In this thesis, theropod dinosaurs found in Thailand have been studied, with a specific emphasis on new specimens and new information on theropods. The discovery of theropod dinosaurs from Thailand started in the late 1980s. Until now, eleven non-avian theropods and a Mesozoic bird have been reported. They pertain to various groups and date from the Late Jurassic to the Early Cretaceous (Samathi et al., 2019b).

Aim of this research is to study theropods in Thailand. To describe new taxa, as well as re- analyze and revise the old materials that have been found and studied almost 30 years ago.

This thesis consists of 8 chapters.

Chapter 1 is an overview of non-maniraptoran theropods in Asia. It was presented in the GeoBonn 2018 meeting as a poster.

Chapter 2 is a review of theropods in Southeast Asia including southern China and was published in Annales de Paléontologie (Samathi et al., 2019b).

Chapter 3 is the descriptions of two new theropods from Thailand. It was published in Acta Paleontologica Polonica (Samathi et al., 2019a).

Chapter 4 is the phylogenetic analysis of the ornithomimosaur *Kinnareemimus* from Thailand. It was presented as a poster at the 15th EAVP (European Association of Vertebrate Palaeontologists) 2017 in Munich, Germany, and the 5th IPC (International Palaeontological Congress) 2018 in Paris, France.

Chapter 5 is a study of the osteology and phylogeny of *Siamotyrannus* from Thailand. It started as my MSc thesis with updated information. I added, modified, and improved the description and discussion, and did more thorough comparison after I examined several theropod specimens first hand in various museums. I also analysed the phylogenies with new and updated data matrices.

Chapter 6 is a description and phylogeny of new material of a spinosaurid from the Early Cretaceous of Thailand and a reassessment of *Camarillasaurus*, a probable spinosaurid from the Early Cretaceous of Spain.

Chapter 7 is a description of a juvenile theropod from Thailand, possibly a spinosaurid. This is the first report of juvenile theropod from Thailand.

Finally, **Chapter 8** is on a spinosaurine from Brazil corroborating semi-aquatic adaptation in the Spinosaurinae. It was published in Cretaceous Research in 2018 (Aureliano et al.,2018).

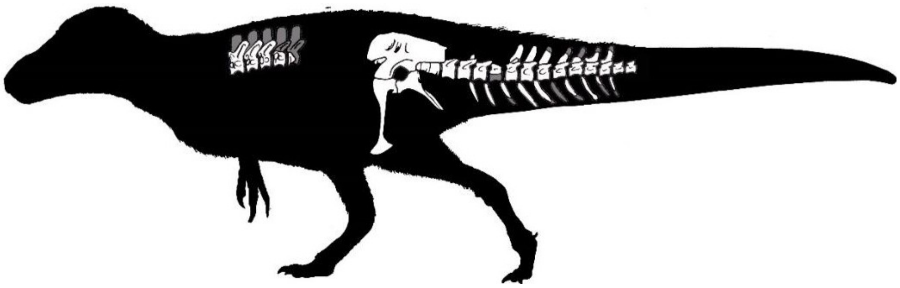
Author contribution:

All the chapters, except the chapter 8, were mainly performed by me. I did the research as a main investigator. I acquired and analyzed the data, wrote the manuscripts, prepared the figures, and corrected and approved the manuscripts with help from my co-authors and supervisor. They provided me materials, co-investigated, participated in data acquisition, and read and approved the final version of the manuscripts.

For the chapter 8, I took a major part in the anatomical and taxonomical analyses. I wrote the part on the morphology, taxonomy and comparison, and corrected other parts. I contributed to the final version of the manuscript, read it, and approved it. Other parts were done by Aureliano and others.

CHAPTER I

Asian Non-Maniraptoran Neotheropoda: An Overview



CHAPTER 1

ASIAN NON-MANIRAPTORAN NEOTHEROPODA: AN OVERVIEW

Published as **Samathi, A.** 2018. Biodiversity of non-maniraptoran theropod dinosaurs during the Mesozoic in Asia. Abstract volumn *GeoBonn 2018 Bonn*.

Abstract:

In this review, non-maniraptoran theropod dinosaurs found in Asia including India are summarized starting with the basal neotheropods to non-maniraptoran coelurosaurs. They are the main groups of theropods that have been found, or possibly found, in Thailand and Southeast Asia so far. The purpose of this work is to collect and summarize the theropod groups in Asia for best understand their evolution, diversification, and paleobiogeography.

Theropods in Asia first appeared in the Early Jurassic, they consist of coelophysoids and basal tetanurans. During the Middle Jurassic, Asia was roamed by large-bodied metriacanthosaurids and basal tetanurans, a contrast to Europe and North America which dominated by megalosaurids and allosaurids. In the Late Jurassic, Asia was still dominated by metriacanthosaurids with one possible megalosaurid, whereas in Europe, the megalosaurids and metriacanthosaurids were present together. This suggests that the mega-carnivore faunal exchange occurred between Asia and Europe during the Late Jurassic. This assumption, however, depends on the position of the Chinese Middle Jurassic *Monolophosaurus* which some studies found it to be a basal tetanuran or to nest within Megalosauroidea, or Allosauroidea and the Chinese Middle Jurassic *Xuanhanosaurus* which some studies found it to belong to Metriacanthosauridae or Megalosauroidea. The metriacanthosaurids also migrated to Southeast Asia during the Late Jurassic. In the Early Cretaceous, theropod faunas in Asia were much diverged than other time. In the Late Cretaceous, Asia was the place of tyrannosaurids and ornithomimids, with a small number of non-tyrannosaurid tyrannosauroids and one report of carcharodontosaurid, whereas the India subcontinent was roamed by the abelisaurid ceratosaurs.

INTRODUCTION

Theropoda is a clade of carnivorous dinosaurs originated possibly in the Late Triassic of Gondwana, this depends on the position of *Eoraptor* and herrerasaurids (see Martinez et al, 2011; Sereno et al, 2013; Baron et al 2017). One of the most basal theropods is *Eodromaeus murphi* (Martinez et al, 2011), *Tawa hallae* (Nesbitt et al, 2009), and *Daemonosaurus chauliodus* (Sues et al, 2011).

In this brief review, I will focus on non-maniraptoran theropod dinosaurs found in Asia including India, since they are the main groups of theropods that have been found in Thailand and Southeast Asia so far. I will start with the basal neotheropods to non-maniraptoran coelurosaurians. I do not cover all Asian theropods, only the groups that found or possibly found in Thailand and Southeast Asia.

Non-maniraptoran Theropoda in Asia

Dinosauria Owen, 1842

Theropoda Marsh, 1881

Coelophysoidea (Nopcsa, 1928) Holtz, 1994

Definition: A stem-based taxon defined by the most inclusive clade containing *Coelophysis bauri* but not *Carnotaurus sastrei*, *Ceratosaurus nasicornis*, and *Passer domesticus* (Sereno 2005).
Comment: There are two reports of coelophysoids from Asia. Both are from the Lower Jurassic Lufeng Formation, Yunnan Province, China. One is limb fragments of cf. *Megapnosaurus* sp. (Irmis, 2004) and other is the well-preserved skeleton of *Panguraptor lufengensis* (You et al., 2014).

cf. *Megapnosaurus* sp. Irmis, 2004

Age: The Lower Jurassic Lufeng Formation.
Occurrence: Yunnan Province, China.
Comment: It consists of limb fragments. It was assigned to Ceratosauria by the fusion of distal tarsals and metatarsals, excluded from Tetanurae because of its metatarsal III is not hourglass shaped, and was referred to cf. *Megapnosaurus* based on the fusion of metatarsal II and III (Irmis, 2004).

Panguraptor lufengensis You et al., 2014

Age: The Lower Jurassic Lufeng Formation.
Occurrence: Yunnan Province, China.
Comment: A well-preserved skeleton of a coelophysid theropod diagnosed by a unique combination of characters including an anterodorsal-posteroventral ridge on lateral surface of the maxilla, within antorbital fossa; elliptical, laterally facing fenestra posterodorsal to the anterodorsal-posteroventral ridge of maxilla; and distal tarsal IV with a hooked anteromedial corner (You et al., 2014).

Ceratosauria Marsh, 1884b

Definition: A stem-based taxon defined as the most inclusive clade containing *Ceratosaurus nasicornis* but not *Passer domesticus* (Sereno, 2005 *sensu* Holtz and Padian, 1995).
Comment: Ceratosaurs in Asia were found mainly from India with some reports from China. The only one named and valid ceratosaur from China is *Limusaurus inextricabilis* (Xu et al., 2009). The three valid abelisauroid ceratosaurs from India that included in the study of Carrano and Sampson (2008) consist of *Indosaurus matleyi* (Huene and Matley,1933), *Rajasaurus narmadensis* (Wilson et al., 2003), and *Laevisuchus indicus* (Huene and Matley, 1933). And one

abelisaurid ceratosaur from India, *Rahiolisaurus*, was reported later by Novas et al. in 2010.

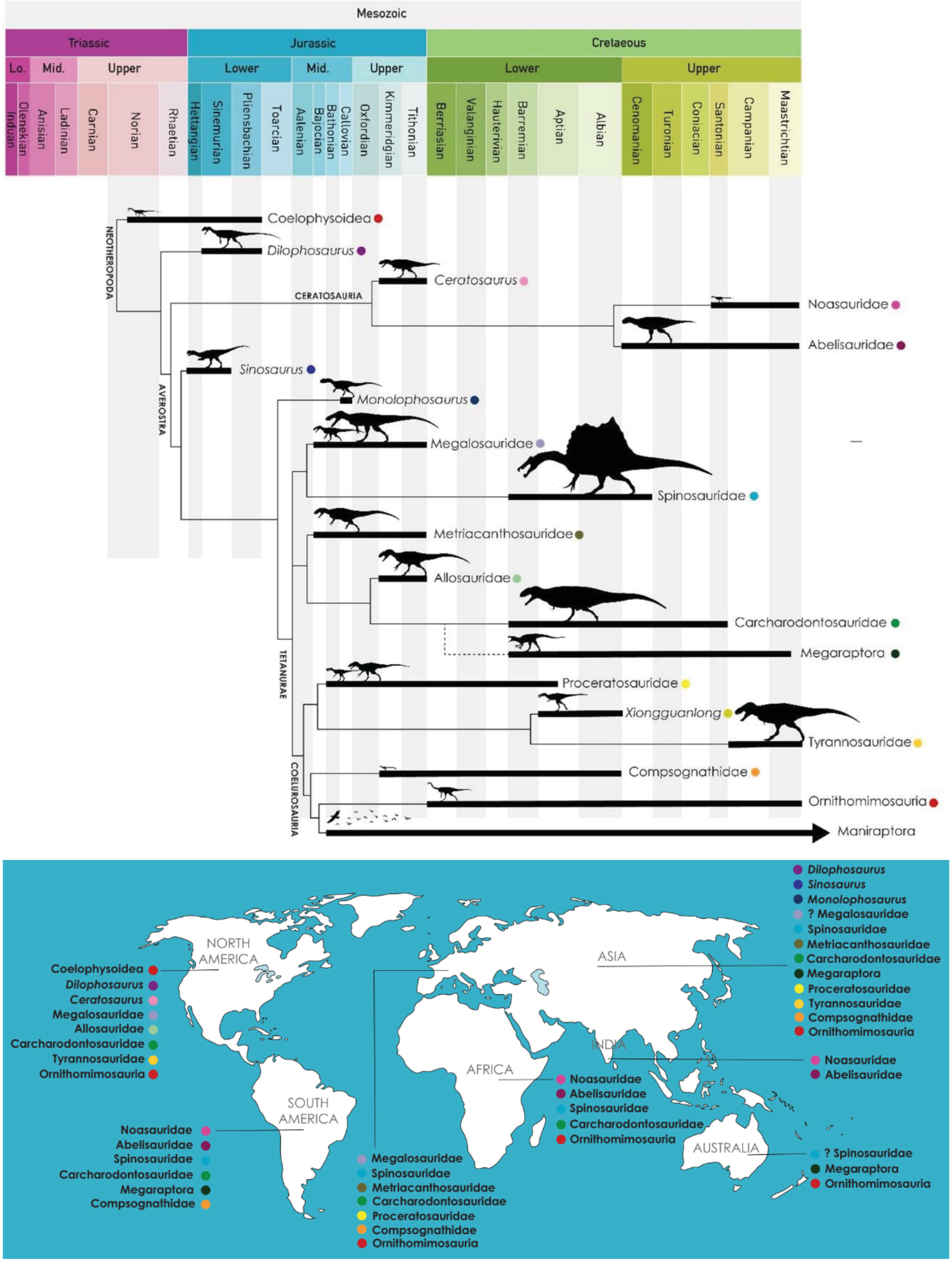


Fig. 1. Phylogeny and stratigraphic distribution of theropod clades. Modified from Carrano et al 2012; Ezcurra & Novas 2016; Brusatte et al 2016.

Limusaurus inextricabilis Xu et al., 2009

Age: Oxfordian, the upper part of the Shishugou Formation.
Occurrence: Wucaiwan, Junggar Basin, Xinjiang, China.
Comment: A small ceratosaur diagnosed by the autapomorphies on its skull and appendicular elements, for example, short skull; toothless; nasal with a lateral shelf; premaxilla with a convex buccal edge; large external mandibular fenestra; flange on anterior margin of scapular blade; metacarpal II much more robust than other metacarpals; phalanx II-1 with distinct lateral process proximodorsally; pubis with laterally ridged, prominent posterior boot; metatarsus forming a strong transverse arch (see Xu et al., 2009).

Abelisauroidea (Bonaparte and Novas, 1985) Bonaparte, 1991

Definition: The most inclusive clade containing *Carnotaurus sastrei* and *Noasaurus leali* (Sereno 2005).
Comment: Abelisauroidea comprises Abelisauridae and Noasauridae are found in India subcontinent.

Abelisauridae Bonaparte and Novas, 1985

Definition: The most inclusive clade containing *Carnotaurus sastrei* but not *Noasaurus leali* (Sereno 2005).
Comment: at least three valid taxa of abelisaurids presented in India subcontinent.

Indosaurus matleyi Huene and Matley, 1933

Age: Lameta Formation, Maastrichtian, Late Cretaceous.
Occurrence: Bara Simla Hill, Jabalpur, Madhya Pradesh, India.
Comment: It was considered to be problematic by Carrano & Sampson (2008).

Rahiolisaurus Novas et al. 2010

Age: Lameta Formation, Maastrichtian, Late Cretaceous.
Occurrence: Near Rahioli village, Kheda District, Gujarat, western India.
Comment: An abelisaurid theropod diagnosed by premaxillary interdental plates fused and lacking vertical ridges; dental foramina absent; premaxillary teeth with teardrop-shaped cross- section; a faint mesial keel but a rounded distal edge; iliac blade with a deep caudal notch on the postacetabular process; metatarsal I rod-like; metatarsal II strongly narrow proximally (Novas et al. 2010).

Rajasaurus narmadensis Wilson et al., 2003

Age: Lameta Formation, Maastrichtian, Late Cretaceous.
Occurrence: Temple Hill, near Rahioli village, Kheda District, Gujarat, western India.

Comment: Abelisaurid theropod diagnosed by median nasal–frontal prominence with frontal forming the posterior rim; anteroposteriorly elongate upper temporal fenestrae; a robust ilium with a transverse ridge separating the brevis fossa from the acetabulum (Wilson et al., 2003).

Noasauridae Bonaparte & Powell 1980

Laevisuchus indicus Huene and Matley, 1933

Age: Lameta Formation, Maastrichtian, Late Cretaceous.
Occurrence: Bara Simla Hill, Jabalpur, Madhya Pradesh, India.
Comment: The validity of this theropod was accepted but it cannot be diagnosed due to the incompleteness of the materials (Carrano & Sampson 2008).

Other fragmentary taxa consist of *Coeluroides*, *Dryptosauroides*, *Indosuchus*, *Lametasaurus*, *Ornithomimoides mobilis*, and *Majungasaurus crenatismus*, they were regarded as abelisaurid indet. (Carrano and Sampson, 2008). *Compsosuchus*, *Jubbulpuria*, and *Ornithomimoides*? were suggested to belong to Abelisauroidea possibly Noasauridae (Carrano and Sampson, 2008). There are several abelisaurids indet., noasaurid indet., abelisauroids indet., and one ceratosaur indet. from China (Carrano and Sampson, 2008).

Tetanurae Gauthier, 1986

Definition: The most inclusive clade containing *Passer domesticus* but not *Ceratosaurus nasicornis* (Allain et al, 2012).

'Basal' Tetanurae

Chuandongocoelurus He 1984

Age: Xiashaximiao Formation, Middle Jurassic.
Occurrence: Chuandong, Sichuan, China.
Comment: It shows tetanuran and non-tetanuran features (Benson, 2010; Benson et al., 2010; Carrano et al., 2012).

Gasosaurus constructus Dong & Tang, 1985

Age: Bathonian-Callovian Middle Jurassic, Lower Shaximiao.
Occurrence: Dashanpu, Sichuan, China.
Comment: Understudy by D. Hone (Carrano et al., 2012).

Monolophosaurus jiangi Zhao & Currie 1993

Age: Middle Bathonian-late Callvonian, Middle Jurassic Shishugou Formation (Brusatte et al 2010).
Occurrence: Junggar Basin, Xinjiang, China.

Comment: large-bodied tetanuran diagnosed by nasal process of premaxilla bifurcated posteriorly; lateral surface of premaxilla with deep groove between subnarial foramen and foramen on base of nasal process; large midline crest formed by nasals with straight dorsal margin nearly parallel to maxillary alveolar margin; two enlarged, subequal pneumatic fenestrae in posterodorsal part of narial fossa; lacrimal with discrete, tab-like process projecting dorsally above preorbital bar; rectangular frontals, much wider than long (Zhao et al., 2010; Brusatte et al., 2010). *Monolophosaurus* was originally classified as a *'megalosaur-grade'* theropod closely related to *Allosaurus* by Zhao and Currie (1993).

Monolophosaurus and *Chuandongocoelurus* formed an endemic theropod clade limited to the Middle Jurassic of Asia (Zhao et al., 2010). *Monolophosaurus* was found to belong to basal Tetanurae by Brusatte et al. (2010) based on skull anatomy, which is a contrast to most analyses which place *Monolophosaurus* within the more derived Allosauroidea (Brusatte et al., 2010). It was also found to be basal Tetanurae by Carrano et al (2012). But it was recovered to nest within Megalosauroidea by Rauhut et al (2016).

Sinosaurus triasicus Young 1948
(=*'Dilophosaurus' sinensis* Hu 1993)

Age: Lower Lufeng Formation Early Jurassic (Hettangian-Sinemurian) age (Xing et al 2013).
Occurrence: Yunnan Province, China.
Comment: A theropod diagnosed by vertical groove on lateral premaxilla adjacent to contact with maxilla. *Sinosaurus triasicus* formerly known as *'Dilophosaurus' sinensis* (Hu 1993; Smith 2007; Xing, 2012; Xing et al., 2013) was placed in *'stem Tetanurae'* by Carrano et al. (2012) and places outside Tetanurae by Xing (2012). It was concluded to belong to '*Dilophosaurus* clade' by Langer et al. (2014).

Shuangbaisaurus anlongbaoensis Wang et al., 2017

Age: Fengjiahe Formation, Lower Jurassic.
Occurrence: Liuna Village, Anlongbao Town, Shuangbai County, Chuxiong Yi Autonomous Prefecture, Yunnan Province, China.
Comment: Large-bodied theropod diagnosed by parasagittal crests at least along orbital dorsal rims; elevated ventral edge of the premaxilla; the premaxillary body is higher than long; and small upper temporal fenestra (Wang et al., 2017).

Megalosauroidea (Fitzinger, 1843) Walker, 1964
(=**Spinosauroidea** Stromer, 1915)

Definition: The most inclusive clade containing *Megalosaurus bucklandi* but not *Passer domesticus* (Benson 2010; Holtz et al., 2004).

Spinosauridae Stromer, 1915
(=**Baryonychidae** Charig and Milner, 1986)

Definition: The most inclusive clade containing *Spinosaurus aegyptiacus* but not *Torvosaurus tanneri*, *Allosaurus fragilis*, and *Passer domesticus* (Sereno 2005).

Comment: Traditionally the spinosauridae can be divided into two groups (e.g. Sereno et al., 1998; Hone & Holtz 2017; Candeiro et al., 2017) but was found later that the subclade Baryonychinae might be a paraphyletic group (Sales & Schultz 2017).

Ichthyovenator laosensis Allain et al., 2012

Age: Early Cretaceous Grés Superior Formation.

Occurrence: Ban Kalum, Tang Vay Area, Savannakhet Province, Lao PDR.

Comment: A spinosaurid diagnosed by unique characters including a dorsosacral sinusoidal sail; penultimate dorsal neural spine is 410 % of centrum length with anterodistal finger-like process; fan-shaped sacral neural spines 3 and 4; transverse processes of first caudal vertebra with sigmoid profile in dorsal view; deep prezygapophyseal centrodiapophyseal fossae in the first caudal vertebra; long iliac blade (all from Allain et al., 2012). *Ichthyovenator* was first placed in Baryonychinae by Allain *et al.* (2012) but was later suggested to be closely related to Spinosaurinae than Baryonychinae by Allain 2014 based on new material discovered from the type locality (Allain et al., 2012; Allain, 2014).

Siamosaurus suteethorni Buffetaut and Ingawat, 1986

Age: Sao Khua Formation, Early Cretaceous.

Occurrence: Khonkaen province, northeastern Thailand.

Comment: Its teeth show fluted enamel display on both the labial and lingual faces with approximately 15 flutes per side (Bertin, 2007), and show less recurved profile and relatively rounded cross section (Carrano et al., 2012). The carinae lack serrations, a characteristic associated with teeth of Spinosaurinae (Bertin, 2007). Theropod affinities of *Siamosaurus* have been questioned by Sues et al (2002). It was concluded by some workers as Spinosauridae indet. (e.g. Bertin 2010; Carrano et al 2012), Theropoda indet. by Holtz et al 2004, and considered to be *nomen dubum* by Sales and Schultz (2017).

As-yet-undescribed spinosaurid from Thailand (Milner et al., 2007)

Age: Khok Kruat Formation, Early Cretaceous.

Occurrence: Khon Kaen province.

Comment: The vertebrae resemble *Baryonyx* and *Spinosaurus* (Milner et al., 2007) "with baryonychine characters" (Bertin, 2010).

Sinopliosaurus fusuiensis Hou, Yeh, & Zhao 1975

Age: The Early Cretaceous Napai Formation.
Occurrence: Fusui County, Guangxi Zhuang Autonomous Region, Southern China.
Comment: It was originally assigned to the sauropterygian by Hou et al (1975) and was found later to belong to the Spinosauridae by Buffetaut et al (2008).

Some fragmentary materials reported in Asia including possible spinosaurid teeth from Japan (Hasegawa et al., 2003; Katsuhiro et al 2017); a probable baryonychine tooth from China (Hone et al., 2010); a possible spinosaurine tooth from China (Lü et al., 2009); and spinosaurid teeth from Malaysia (Sone et al 2015).

Megalosauridae (Fitzinger, 1843) Bonaparte, 1850

Definition: The most inclusive clade containing *Megalosaurus bucklandii* but not *Allosaurus fragilis*, *Spinosaurus aegyptiacus*, and *Passer domesticus* (Holtz et al, 2004).
Comment: There is only one possible megalosaurid recovered in Asia.

Leshansaurus qianweiensis Li et al., 2009

Age: Shangshaximaio Formation, Late Jurassic.
Occurrence: Sichuan, China.
Comment: A medium to large-bodied theropod diagnosed by a distinct ventral ridge on all sacral vertebral centra. It was originally placed within Metriacanthosauridae by Li et al (2009) but later found to may be an Asian megalosaurid by Carrano et al. (2012) based on similarities of the braincase to those of *Piveteausaurus* and *Dubreuillosaurus*, and its maxilla resembles those of *Afrovenator* and *Duriavenator* (Li et al 2009; Carrano et al 2012).

Avetheropoda Paul, 1988a
(=**Neotetanurae** Sereno et al., 1994)

Definition: The least inclusive clade containing *Allosaurus fragilis* and *Passer domesticus* (Holtz et al 2004).

Allosauroidea (Marsh 1878) Currie and Zhao, 1994

Definition: The most inclusive clade containing *Allosaurus fragilis* but not *Passer domesticus* (Sereno, 2005) or defined by a stem-based taxon that encompasses all dinosaurs closer to *Allosaurus* than to birds (Brusatte and Sereno, 2008).

Metriacanthosauridae (Paul, 1988a) Carrano, Benson, and Samson, 2012
(=**Sinraptoridae** Currie and Zhao, 1994)

Definition: The most inclusive clade containing *Metriacanthosaurus parkeri* but not *Allosaurus fragilis*, *Carcharodontosaurus saharicus*, or *Passer domesticus* (Sereno, 2005).

Comment: Metriacanthosauridae formerly known as Sinraptoridae is a clade of large-bodied theropods previously thought to be endemic to the Middle to Late Jurassic of central Asia. Some studies later found *Metriacanthosaurus* from England belong to this clade (Benson 2010; Carrano et al 2012). *Poekilopleuron* from France, *Lourinhanosaurus* from Portugal, and *Siamotyrannus* from Thailand might belong to this group (Benson 2010; Carrano et al 2012). Metriacanthosaurids probably originated in China before the Middle Jurassic and later spread to Europe and Southeast Asia. Depending on the affinities of *Siamotyrannus*, they might have survived into the Early Cretaceous (Samathi 2016).

Metriacanthosaurinae Paul, 1988a

Definition: The most inclusive clade containing *Metriacanthosaurus parkeri* but not *Yangchuanosaurus shangyouensis* (Carrano et al, 2012).

Shidaisaurus jinae Wu et al., 2009

Age: Upper Lufeng Formation, early Middle Jurassic.

Occurrence: A'na, Laochangjing village, Chuanjie township, Lufeng County, Yunnan, China.

Comment: A medium to large-bodied theropod diagnosed by the combination of characters including supraoccipital excluded from foramen magnum by exoccipitals; paroccipital process down turned slightly; axis with a large, sharply pointed epipophysis and a thin lamina between the epipophysis and neural spinethat is broader than in other theropods; anteroventral to dorsoposterior pubic length is almost the same as the height of the iliac blade; lacks a ventral notch distal to the obturator process on the ischium; ischium is relatively long almost the same length as the pubis (Wu et al, 2009).

Siamotyrannus isanensis Buffetaut et al 1996

Age: Sao Khua Formation, Early Cretaceous.

Occurrence: Phuwiang District, Khonkaen Province.

Comment: *Siamotyrannus* was concluded to be a basal tyrannosaurid by Buffetaut et al (1996) and Holtz (2001). It was found to be a basal allosauroid by some workers (e.g. Holtz 2004, Rauhut 2003; 2009), a sinraptorid by Carrano et al. (2012), and found to be a basal coelurosaur by Samathi (2013) and Samathi et al. (2015; 2017).

Sinraptor dongi, Currie and Zhao, 1993

Age: Shishugou Formation, ?Bathonian Oxfordian.
Occurrence: Xinjiang China.
Comment: A large-bodied allosauroid with enlarged lateral temporal fenestra with relatively straight postorbital-squamosal bar; very short squamosal ramus of postorbital; and palatine very deeply pneumatic between internal naris and postpalatine fenestra (all from Currie and Zhao,1993).

Sinraptor hepingensis (Gao, 1998).
(=*Yangchuanosaurus hepingensis* Gao, 1992)

Age: Upper Shangshaximiao, Late Jurassic, Oxfordian-early Kimmeridgian.
Occurrence: Zigong, Sichuan, China.
Comment: Some workers referred it to the genus *Yangchuanosaurus* (Gao 1992; 1999) and *Sinraptor* (Currie & Zhao 1994; Rauhut 2003; Holtz et al 2004). It was found to nest within the subclade Metriacanthosaurinae by Carrano et al (2012).

The *'Yangchuanosaurus'* group

Szechuanosaurus campi Young, 1942

Age: Shangshaximiao Formation, Oxfordian–early Kimmeridgian, Late Jurassic.
Occurrence: Zigong, Sichuan, China.

Comment: The holotype of *Szechuanosaurus campi* (IVPP V.235, V.236, V.238, V.239) consists of undiagnostic teeth and is considered as *nomen dubium* by some authors (Chure 2000; Carrano et al 2012). The referred specimen (CV 00214) consists of the incomplete skeleton but no tooth preserved (Dong 1983; Chure 2000; Carrano et al 2012), thus cannot be referred to *Szechuanosaurus campi*. The CV 00214 was found to represent a new taxon (Chure 2000; Carrano et al 2012).

Yangchuanosaurus shangyouensis Dong, Chang, Li & Zhao, 1978

Age: Upper Shangshaximiao, Late Jurassic, Oxfordian-early Kimmeridgian.
Occurrence: Yongchuan County, Sichuan, China.
Comment: The holotype CV 00215 is a complete skull and skeleton. It was referred to 'Sinraptoridae' by some authors (i.e. Currie and Zhao 1994; Sereno et al 1994; 1996) but distinct from *Sinraptor dongi* (Currie and Zhao 1994; Carrano et al 2012).

Yangchuanosaurus magnus Dong, Zhou & Zhang, 1983

Age: Upper Shaximiao, Late Jurassic.

Occurrence: Sichuan, China.
Comment: The holotype CV 00216 is a complete skull and skeleton. Carrano et al (2012) considered *Y. magnus* and *Y. shangyuensis* as a single species and suggested the differences are due to intraspecific variation, possibly ontogeny (Carrano et al 2012).

Yangchuanosaurus zigongensis (Gao, 1993).
(=*'Szechuanosaurus' zigongensis* Gao, 1993)

Age: Lower Xiashaximiao Formation, Bathonian-Callovian.
Occurrence: Zigong, Sichuan, China.
Comment: The holotypic materials consist of ZDM 9011, 9012, 9013, 9014. The type species of the genus is considered to be *nomen dubium* by some authors (see Chure 2000; Holtz 2004; Carrano et al 2012). *'S'. zigongensis* was referred to *Yangchuanosaurus* by Carrano et al (2012) based on the broad phylogenetic analysis of basal theropods.

Metriacanthosauridae *incertae sedis*

Xuanhanosaurus qilixiaensis Dong, 1984

Age: Lower Shaximiao Formation, Bathonian-Callovian, the Middle Jurassic.
Occurrence: Xuanhan, Sichuan, China.
Comment: A tetanuran diagnosed by a pronounced posterior ridge on an articular facet of humeral head that overhangs shaft (Rauhut 2003); and dorsal neural spines transversely thick with gently concave lateral surfaces (Carrano et al 2012). *Xuanhanosaurus* was found to be a basal tetanuran by Holtz et al (2004), a megalosauroid by Benson (2010), Benson et al (2010), and Rauhut et al (2016), and a metriacanthosaurid *incertae sedis* by Carrano et al. (2012).

There are at least two materials of metriacanthosaurids found in Thailand including a left tibia (Buffetaut and Suteethorn, 2007), and skull and postcranial skeleton (Chantasit and Suteethorn, 2013; Chantasit et al 2015; Samathi et al 2016).

Carcharodontosauria Benson, Carrano, and Brusatte, 2009

Definition: the most inclusive clade comprising *Carcharodontosaurus saharicus* and *Neovenator salerii* but not *Allosaurus fragilis* or *Sinraptor dongi* (Benson et al., 2009).
Comment: There are four named Asian carcharodontosaurians found mainly from China and two reported materials from Thailand.

Chilantaisaurus tashuikouensis Hu, 1964

Age: The Early Cretaceous, Ulansuhai Formation.
Occurrence: Nei Mongol, Alanshan, China.
Comment: A large-bodied theropod diagnosed by autapomorphies of the humerus

including subrectangular, anteromedially curving deltopectoral crest that protrudes almost as far anteriorly as it is long proximodistally and bears a pitted scar on its anterior surface; an obliquely oriented ulnar condyle (Benson and Xu, 2008). *Chilantaisaurus* was found to be a neovenatorid carcharodontosaurian by Carrano et al (2012). It was found to be possible a basal coelurosaur by Benson and Xu (2008) and Porfiri et al (2014).

Datanglong guangxiensis Mo et al., 2014

Age: The Early Cretaceous Xinlong Formation.
Occurrence: Guangxi, China.
Comment: A large-bodied, basal carcharodontosaurian diagnosed by long parapophysis on the last dorsal vertebra, brevis fossa with short, ridge-like medial blade, and pubic peduncle of the ilium with posteroventrally expanded margin (Mo et al, 2014). It was found to possibly be a basal member of Megaraptora by Samathi and Chanthasit (2017) based on the pneumaticity on the ilium.

Kelmayisaurus petrolicus Dong, 1973

Age: The Early Cretaceous, Tugulu Group.
Occurrence: Xinjiang, China.
Comment: A basal carcharodontosaurid diagnosed by a concave groove positioned anteriorly on the lateral surface of the dentary and a unique combination of some characters on the maxilla and on the dentary (Brusatte et al., 2012). *Kelmayisaurus* was named by Dong (1973) and was considered invalid by Rauhut and Xu (2005). It was later redescribed and found to be a valid taxon within Carcharodontosauridae by Brusatte et al (2012).

Shaochilong maortuensis (Hu, 1964)
(=*Chilantaisaurus maortuensis* Hu, 1964)

Age: The Early to Late Cretaceous, Albian; Dashuigou Formation.
Occurrence: Maortu, Inner Mongol, China.
Comment: A carcharodontosaurid with maxillary antorbital fossa reduce and nearly absent; paradental groove of maxilla absent; deep, vertical grooves located dorsally on maxillary interdental plates; frontal sagittal crest; and some pneumatic on nasal and prootic (Brusatte et al., 2009; 2010). *Shaochilong* was first referred to be a new species of *Chilantaisaurus tashuikouensis* by Hu (1964) but with the absence of the overlapping material with *Chilantaisaurus*, it was re- described and re-diagnosed by Brussatte et al (2009) and was found to be a member of carcharodontosaurid, and they named it *Shaochilong* (Brussatte et al, 2009).

There are two reported materials of carcharodontosaurians from the Early Cretaceous of Thailand (Azuma et al., 2011; Buffetaut and Suteethorn, 2012).

Coelurosauria Huene, 1914a

Definition: The most inclusive clade containing *Passer domesticus* but not *Allosaurus fragilis*, *Sinraptor dongi* and *Carcharodontosaurus saharicus* (Sereno 2005).
Comment: There are three 'basal' coelurosaurs from Asia.

'Basal' Coelurosauria

Fukuivenator paradoxus Azuma et al, 2016

Age: The Early Cretaceous Kitadani Formation (Barremian to Aptian).
Occurrence: Kitadani Dinosaur Quarry, Katsuyama City, Fukui, Japan.
Comment: A small-bodied theropod diagnosed by unique features on its skull, teeth, and postcranial skeleton.

Xinjiangovenator parvus Rauhut and Xu, 2005

Age: The Early Cretaceous.
Occurrence: Xinjiang, China.
Comment: A small-bodied theropod diagnosed by fibular condyle of tibia extending farther posteriorly than the lateral side of the proximal end of this bone; fibula with a longitudinal groove on the anterior side of the proximal end (Rauhut and Xu, 2005). *Xinjiangovenator* is another basal coelurosaur from the Early Cretaceous of Xinjiang, China (Rauhut and Xu, 2005; Choiniere et al., 2010). It was concluded to be a maniraptoran by Rauhut and Xu (2005) but later found to be a basal coelurosaur by Choiniere et al. (2010).

Zuolong salleei Choiniere et al., 2010

Age: The Late Jurassic Shishugou Formation.
Occurrence: Wucaiwan, Xinjiang, China.
Comment: A basal coelurosaur which is differ from all other theropods in possessing a large, slit- like quadrate foramen inclined medially at approximately 45^0 with associated deep fossa on the quadrate; sacral centrum 5 with an obliquely oriented posterior articular surface that is angled anterodorsally; fovea capitis very large, occupying almost the entire posterodorsal surface of the femoral head; distal condyle of metatarsal III large relative to that of other metatarsals and bearing an anteromedially projecting flange on its anteromedial margin (all from Choiniere et al., 2010).

Non-avialan coelurosaur from Myanmar (DIP-V-15103) Xing *et al.*, 2016b

Age: Early Cenomanian (98.8 ± 0.6 Ma), mid-Cretaceous based on U-Pb dating of zircons or Albian – Cenomanian (105 – 95 Ma), mid-Cretaceous based on ammonite biostratigraphy and palynology.
Occurrence: Hukawng Valley, Angbamo site, Tanai Township, Myitkyina District, Kachin Province of Myanmar.
Comment: A feathered, mid to distal tail of a non-avialan coelurosaurian theropod, possibly juvenile preserved in amber with plumage and soft tissues.

Tyrannosauroidea (Osborn, 1906) Walker, 1964

Definition: The most inclusive clade containing *Tyrannosaurus rex* but not *Ornithomimus edmontonicus*, *Troodon formosus*, or *Velociraptor mongoliensis* (Sereno 2005).

Proceratosauridae Rauhut, Milner, and Moore-Fay, 2010

Definition: All theropods that are more closely related to *Proceratosaurus* than to *Tyrannosaurus*, *Allosaurus*, *Compsognathus*, *Coelurus*, *Ornithomimus*, or *Deinonychus* (Rauhut et al, 2010).

Guanlong wucaii Xu et al., 2006

Age: The Late Jurassic Oxfordian, Shishugou Formation.
Occurrence: Wucaiwan, Xinjiang, China.
Comment: A medium-sized tyrannosauroid with a complex and highly pneumatic crest on the skull together with other unique characters on the skull, axial skeleton, and limbs (Xu et al., 2006).

Kileskus aristotocus Averianov et al., 2010

Age: The Middle Jurassic Bathonian, Itat Formation.
Occurrence: Sharypovo District, Krasnoyarsk Territory, West Siberia, Russia.
Comment: A proceratosaurid tyrannosauroid diagnosed by the unique combination of characters which includes the sagittal crest on the cranial; elongated external naris; premaxilla with short ventral margin; and the ratio of the depth of the antorbital fossa ventral to antorbital fenestra relative to the maxilla ventral to the antorbital fossa which the former is much higher than the latter (all from Averianov et al., 2010).

Sinotyrannus kazuoensis Ji et al., 2009

Age: The Early Cretaceous Jiufotang Formation.
Occurrence: Kazuo County, Western Liaoning, China.
Comment: A large-bodied tyrannosauroid diagnosed by combined characters including large external naris; a concave anterior portion of the dorsal margin of maxilla; maxillary fenestra connected to the anterior margin of the antorbital fossa but separated from the ventral margin of the antorbital fossa; short preacetabular blade of the ilium and lacking an anterior hook (Ji et al., 2009).

Yutyrannus huali Xu et al, 2012

Age: Lower Cretaceous Yixian Formation.
Occurrence: Batuyingzi, Beipiao, Liaoning Province, China.
Comment: A large-bodied tyrannosauroid diagnosed by unique characters such as

rugose, highly fenestrated cranial crest formed by premaxillae and nasals together with other unique characters on the skull and ilium elements (Xu et al, 2012).

Non-tyrannosaurid tyrannosauroids

Dilong paradoxus Xu et al., 2004

Age: The Early Cretaceous Yixian Formation.
Occurrence: Lujiatun, Beipiao, Western Liaoning, China.
Comment: A small-bodied tyrannosauroid diagnosed by the presence of two pneumatic recesses dorsal to the antorbital fossa on the maxilla; Y-shaped cranial crest formed by the nasals and lacrimals; extremely long descending process of the squamosal; lateral projection of the basisphenoid; cervical vertebrae with very deep, subcircular interspinous ligamentous fossae; robust scapula; hypertrophied coracoid (Xu et al., 2004).

Raptorex kriegsteini Sereno et al., 2009

Age: The Early Cretaceous (Sereno et al 2009) or the Late Cretaceous (Newbrey et al 2013; see Fowler et al 2009).
Occurrence: China (Sereno et al 2009) or possible Mongolia (Fowler et al 2009).
Comment: A small-bodied tyrannosauroid diagnosed by a narrow accessory pneumatic fossa within the antorbital fossa dorsal to the maxillary fenestra; jugal suborbital ramus of particularly narrow depth; and absence of a vertical, medial crest on the iliac blade (Sereno et al., 2009). Some considered it as a juvenile *Tarbosaurus* or other large-bodied Tyrannosaurid (Fowler et al 2010).

Timurlengia euotica Brusatte et al., 2016

Age: Bissekty Formation, Upper Cretaceous, Middle-Upper Turonian.
Occurrence: Dzharakuduk, central Kyzylkum Desert, Navoi Viloyat, Uzbekistan.
Comment: *Timurlengia* was diagnosed mainly based on the holotypic braincase. It is an intermediate-grade tyrannosauroid phylogenetically proximal to *Xiongguanlong* (Brusatte et al.,2016).

Xiongguanlong baimoensis Li et al., 2009

Age: The Early Cretaceous, possibly Aptian-Albian age.
Occurrence: Yujingzi Basin, Gansu, China.
Comment: A medium-sized tyrannosauroid diagnosed by a uniquely elongate preorbital region reaching over two-thirds of skull length. It can be distinguished from other tyrannosauroids by the characters on the skull elements, premaxillary teeth, and cervical vertebrae (Li et al., 2009).

Tyrannosauridae Osborn, 1905

Definition: The least inclusive clade containing *Tyrannosaurus rex*, *Gorgosaurus libratus* and *Albertosaurus sarcophagus* (Sereno 2005).

Alioramus alti Brusatte et al., 2009

Age: The Late Cretaceous Maastrichtian Nemegt Formation.
Occurrence: Tsagaan Khushuu, Mongolia.
Comment: A tyrannosaurine diagnosed by the features on the skull such as pneumaticity on the skull elements, cervical vertebrae, and dorsal ribs, as well as the anterodorsally inclined of the medial ridge on the ilium (Brusatte et al 2009).

Alioramus remotus Kurzanov, 1976b

Age: The Late Cretaceous, Beds of Nogon-Tsav, ?Maastrichtian.
Occurrence: Mongolia.
Comment: A long-snouted and gracile predator with an extreme degree of cranial ornamentation (Brusatte et al 2009).

Alectrosaurus olseni Gilmore 1933

Age: The Late Cretaceous, Cenomanian-?Campanian, Iren Dabasu Formation, Bayanshiree Svita.
Occurrence: Inner Mongolia, China; Mongolia.
Comment: A mid-sized tyrannosauroid which might closely relate to *Xiongguanlong* and lie outside Tyrannosauridae (Loewen et al 2013).

Qianzhousaurus sinensis Lü et al., 2014

Age: Nanxiong Formation, Upper Cretaceous, Maastrichtian.
Occurrence: Longling Town, Nankang, Ganzhou City, Jiangxi Province, China.
Comment: A mid to large-sized tyrannosaurid diagnosed by possessing an extremely long and low skull, its snout is two thirds or more of skull length; elongate maxillary fenestra; pronounced rugosities on the nasals; and on the number of dentary teeth (Lü et al., 2014).

Tarbosaurus bataar Maleev 1955

Age: The Late Cretaceous, Nemegt Formation, Subashi Formation, Yuanpu Formation, Wangshi Group, Quiba Formation, unnamed Formation.
Occurrence: Mongolia, Xinjiang, Guandong, Shandong, Henan, China.

Comment: *Tarbosaurus* was found to differ from *Tyrannosaurus* by Hurum & Sabath (2003) and closer to *Zhuchengtyrannus* than to *Tyrannosaurus* by Loewen et al (2013). It was found to be closer to *Tyrannosaurus* than to *Zhuchengtyrannus* by Brusatte & Carr (2016) and Carr et al (2017) and considered to be sister taxon to *Tyrannosaurus* and named *'Tyrannosaurus' bataar* by Carr et al (2017).

Zhuchengtyrannus magnus Hone et al., 2011

Age: The Late Cretaceous Wangshi Group.
Occurrence: Zangjiazhuang, Zhucheng City, Shandong Province, China.
Comment: A large-bodied tyrannosaurid diagnosed by a unique combination of characters including the ventral margin of the antorbital fenestra lies well above that of the ventral rim of the antorbital fossa, and the anteroposterior length of the maxillary fenestra is more than half the distance between the anterior margins of the antorbital fossa and fenestra (Hone et al., 2011). It was distinguished by other tyrannosaurines by a horizontal shelf on the lateral surface of the base of the ascending process, and a rounded notch in the anterior margin of the maxillary fenestra (Hone et al., 2011).

Megaraptora Benson, Carrano, and Brusatte 2010

Definition: The most inclusive clade comprising *Megaraptor namunhuaiquii* but not *Chilantaisaurus tashuikouensis*, *Neovenator salerii*, *Carcharodontosaurus saharicus* or *Allosaurus fragilis* (Benson *et al.,* 2010).
Comment: Megaraptora is a clade of theropods with large-clawed, highly pneumatized, and long and gracile metatarsals (Coria & Currie 2016; Benson et al 2010). The basal member was recovered from the Barremian of Japan (Azuma & Currie 2000; Benson et al 2010; Porfiri et al 2014), whereas the more derived clade, the Megaraptoridae, are known from the Cenomanian to Santonian rocks of Gondwana (Porfiri et al 2014; Novas et al 2016). Until now, there are two newly reported megaraptoran specimens from Thailand which looks similar to *Fukuiraptor* and *Australovenator* (Samathi & Chanthasit 2015; 2017).

Fukuiraptor kitadaniensis Azuma and Currie, 2000

Age: The Early Cretaceous Kitadani Formation, Barremian.
Occurrence: Kitadani locality, Katsuyama city, Fukui Prefecture, Japan.
Comment: A mid-sized avetheropod diagnosed by the proportionally long arm; pubic peduncle of the ilium is approximately as broad anteroposteriorly as mediolaterally (Azuma and Currie, 2000); Currie and Azuma, 2006). It was concluded to be a neovenatorid carcharodontosaurian by Carrano et al. (2012) but later found to be a megaraptoran tyrannosauroid by Porfiri et al. (2014).

Compsognathidae Cope, 1871

Definition: The most inclusive clade containing *Compsognathus longipes* but not *Passer domesticus* (Holtz et al, 2004).
Comment: Three compsognathids were reported from China, there are also some fragments reported from Thailand.

Huaxiagnathus orientalis Hwang et al., 2004

Age: The Early Cretaceous Yixian Formation.
Occurrence: Dabangou village, Sihetun Area, Liaoning, China.
Comment: A large-bodied compsognathid differs from other compsognathids in having a very long posterior process of the premaxilla that overlaps the antorbital fossa, a manus as long as the lengths of the humerus plus radius, large manual unguals I and II that are subequal in length and much larger than the manual ungual III, a first metacarpal that has a smaller proximal transverse width than the second metacarpal, and a reduced olecranon process on the ulna (all from Hwang et al., 2004).

Sinocalliopteryx gigas Ji et al., 2007

Age: The Early Cretaceous Yixian Formation.
Occurrence: Western Liaoning, China.
Comment: A large-bodied compsognathid differing from other compsognathids in having a manus as long as the humerus plus radius, very large and subequally long manual unguals I and II, the smaller proximal transverse width of the first metacarpal, and reduced olecranon process on the ulna (all from Ji et al, 2007). *Sinocalliopteryx* differs from *Huaxiagnathus* in having the much larger size, and in some characters on the premaxilla, ulna, ilium, and ischium (Ji et al, 2007).

Sinosauropteryx prima Ji & Ji, 1996

Age: The Jurassic-Cretaceous Yixian Formation.
Occurrence: Liaoning, China.
Comment: A small-bodied coelurosaur with short, stout forelimbs, the first digit is longer than the humerus and the radius, powerful proximomedial flange on the first metacarpal. *Sinosauropteryx* differs from *Compsognathus* in that the forelimb is relatively smaller in comparison with the hindlimbs (Currie and Chen, 2001).

Ornithomimosauria (Marsh 1890) Barsbold, 1976a
(=**Arctometatarsalia** Senter, 2007)

Definition: The most inclusive clade containing *Ornithomimus velox* but not *Allosaurus fragilis*, *Tyrannosaurus rex*, *Compsognathus longipes*, *Alvarezsaurus calvoi*, *Therizinosaurus cheloniformis*, *Deinonychus antirrhopus*, *Troodon formosus*, and *Passer domesticus* (Lee et al, 2014).
Comment: Eight ornithomimosaurs were reported from China, Mongolia, and Thailand.

Aepyornithomimus tugrikinensis Tsogtbaatar et al 2017

Age: Djadokhta Formation, Campanian.
Occurrence: Tögrögiin Shiree locality, Mongolia.
Comment: An ornithomimid diagnosed by an unevenly developed pair of concavities of the third distal tarsal; curved contacts between the proximal ends of second and fourth metatarsals; the elongate fourth digit; and a laterally inclined medial condyle on phalanx IV-1 (Tsogtbaatar et al 2017).

Anserimimus planinychus Barsbold, 1988b

Age: Nemegt Stiva, Early Maastrichtian.
Occurrence: Bayankhongor, Mongolia.
Comment: An ornithomimosaur diagnosed by its expanded deltopectoral crest and large epicondyles of the humerus, as well as its manual unguals, which are straight, mediolaterally expanded, and flat ventrally (all from Makovicky et al 2004).

Archaeornithomimus asiaticus (Gilmore, 1933)

Age: ?Campanian.
Occurrence: Iren Dabasu, Inner Mongolia, China.
Comment: It differs from other ornithomimids in the subequal lengths of metacarpals I and III, which are shorter than metacarpal II, and the stouter proportions of the metatarsus (Russell1972), it is distinguished from all other ornithomimosaurs by the expansion of the ischial boot (Smith and Galton 1990), and it has not enough character information to diagnose with apomorphies (Makovicky et al 2004).

Beishanlong grandis Makovicky et al., 2010

Age: Aptian-Albian, Early Cretaceous.
Occurrence: White Ghost Castle field area, Yujingzi Basin, Gansu, China.
Comment: Large ornithomimosaur with notched anterior caudal neural spine; keeled midcaudal centra with divided neural spines and prominent ridges connecting pre- and postzygapophyses; scapula with pronounced fossa at rostral end of supraglenoid

buttress; shallow coracoid with prominent lateral ridge emanating from coracoid tuber and deep notch between glenoid and postglenoid process; curved pollex ungual, but straighter unguals on digits II and III; curved ischial shaft; third metatarsal proximally pinched but visible along extensor surface of foot; curved pedal unguals (all from Makovicky et al. 2010).

Deinocheirus mirificus Osmólska & Roniewicz, 1970

Age: Nemegt Formation (Upper Campanian or Lower Maastrichtian).
Occurrence: Altan Uul III, Altan Uul IV, and Bugiin Tsav, Mongolia (Lee et al., 2014).
Comment: It was originally diagnosed by the long and large forelimbs (Osmólska & Roniewicz, 1970) and found later within the Ornithomimosauria (Kobayashi and Basbold, 2006) and subclade Deinocheiridae (Lee et al., 2014).

Gallimimus bullatus Osmólska, Roniewicz, & Barsbold, 1972

Age: Nemegt Formation, Early Maastrichtian.
Occurrence: Ömnögov', Mongolia.
Comment: An ornithomimid diagnosed by the very long snout, broad and flattened dorsoventrally at the tip and by the characters on its skull, lower jaw, vertebrae, and fore and hind limbs (Osmólska et al, 1972). The external mandibular fenestra may be more reduced in *G. bullatus* than in other ornithomimosaurs (Makovicky et al 2004).

Garudimimus brevipes Barsbold, 1981

Age: Bayanshiree Svita, Cenomanian-Santonian.
Occurrence: Ömnögov', Mongolia.
Comment: An ornithomimosaur diagnosed by jaw articulation positioned more posterior than the postorbital bar; fossae at the base of dorsal process of supraoccipital; paired depressions on the lateral surface of neural spines at base of the proximal caudal vertebra; and deep groove at the proximal end of the lateral surface of pedal phalanges III-1 and III-2 (Barsbold, 1981) with subarctometatarsalian metatarsals (e.g. Makovicky et al 2004; Buffetaut et al., 2009).

Harpymimus okladnikovi Barsbold & Perle, 1984

Age: Shinekhudag Svita, Late Albian.
Occurrence: Dundgov', Mongolia.
Comment: An ornithomimosaur diagnosed by eleven dentary teeth that are anterior in position; transition between anterior and posterior caudal vertebrae at eighteenth caudal, triangular-shaped depression on dorsal surface of supraglenoid buttress of scapula; low ridge dorsal to depression along posterior edge of scapular blade; small but deep

collateral ligament fossa on lateral condyle of metacarpal III (Barsbold & Perle, 1984). It differs from other ornithomimosaurs by robust humerus and by not have arctometatarsalian metatarsals (Makovicky et al., 2004).

Hexing qingyi Jin et al., 2012

Age: Yixian Formation, Lower Valanginian – Lower Barremian.
Occurrence: Xiaobeigou locality, Lujiatun, Shangyuan, Beipiao City, western Liaoning, China.
Comment: It was diagnosed by the rostral portion of the premaxilla deflected ventrally in front of the lower jaw; a deep antorbital fossa that invades the whole lateral surface of the maxilla; a sagittal crest on the parietal; pendant paroccipital processes that extend ventrally below the level of the foramen magnum; a dentary fenestra; a phalangeal formula for manus of 0-(1 or 2)-3-3-0, and elongated proximal phalanges of digits III and IV (Jin et al, 2012).

Kinnareemimus khonkaenensis Buffetaut et al., 2009

Age: The Early Cretaceous Sao Khua Formation.
Occurrence: Khonkaen Province, north-eastern of Thailand.
Comment: An ornithomimosaurid with metatarsal III is visible in cranial view between the proximal ends of metatarsal II and IV, but become rod-like distally and expands again, with a triangular cross-section, closer to the distal end (Buffetaut et al., 2009). *Kinnareemimus* was found to be possibly more primitive than previous though but that might due to the incompleteness or immature of the materials (Samathi 2017).

Shenzhousaurus orientalis Ji, Norell, Makovicky, Gao, Ji, & Yuan, 2003

Age: Yixian Formation, Barremian.
Occurrence: Liaoning, China.
Comment: An ornithomimosaur distinguished from all others except *Harpymimus* in having teeth restricted to the anterior dentary. It shows primitive characters not found in advanced ornithomimosaurs including a straight ischium and a postacetabular process that is gently curved rather than truncated. It is distinguished from *Pelecanimimus* by the tooth distribution pattern and the primitive configuration of the hand in which the digit I is shorter than digits II and III (all from Ji et al, 2013).

Sinornithomimus dongi Kobayashi and Lü, 2003

Age: The Late Cretaceous, Ulansuhai Formation, Aptian-?Albian.
Occurrence: Inner Mongolia, China.
Comment: An ornithomimid diagnosed by depression on the dorsolateral surface of the

posterior process of parietal; fenestra within quadratic fossa divided into two by vertical lamina; low ridge on the ventral surface of parasphenoid bulla; and loss of posterolateral extension of the proatlas (Kobayashi and Lü, 2003).

Qiupalong henanensis Xu et al., 2011

Age: The Late Cretaceous.
Occurrence: Henan, China.
Comment: An ornithomimid diagnosed by unique features including a notch on the lateral surface of the medial posterior process of the proximal end of the tibia; a small pit at the contact between astragalus and calcaneum. It's also diagnosed by a combination of a primitive feature including short anterior extension of the pubic boot; and derived features including arctometatarsal condition, straight pubic shaft, and the wide angle between pubic shaft and boot (Xu et al., 2011).

Bissekty ornithomimid Sues & Averianov 2016

Age: Bissekty Formation, middle-upper Turonian, Upper Cretaceous.
Occurrence: Dzharakuduk II, central Kyzylkum Desert, Uzbekistan.
Comment: It consists of more than 800 isolated bones. It shows three unambiguous synapomorphies of Ornithomimidae including the length of anterior cervical centra three to five times greater than the transverse width; low and rounded fibular crest of the tibia; metatarsal III pinched between metatarsals II and IV; the proximal end of metatarsal III not visible in the anterior view (Sues & Averianov 2016). Phylogenetic analysis found it at the base of Ornithomimidae (Sues & Averianov 2016; McFeeter 2017).

There was currently a new unnamed ornithomimid from the lower Upper Cretaceous Bayanshiree Formation of south eastern Mongolia briefly reported by Kobayashi et al. in 2014.

Problematic ornithomimosaur
Lepidocheirosaurus Alifanov and Saveliev, 2015

Age: The Late Jurassic (?Tithonian).
Occurrence: Transbaikal Siberia.
Comment: It is extremely fragmentary and consists of left manus and a few caudal vertebrae. It was suggested to be problematic by Sereno (2017) because its identification as an ornithomimosaur is not based on synapomorphies and the diagnosis of the species is not based on autapomorphies (Sereno 2017).

DISCUSSION

Asian theropod diversity and paleobiogeography

A general overview of theropod dinosaurs in Asia during the Mesozoic

1) *The Early Jurassic*
Two coelophysoids and two basal tetanurans were reports from China.
2) *The Middle Jurassic*
One ceratosaurian, three basal tetanurans, at least three metriacanthosaurids from China and one non-tyrannosaurid tyrannosauroid reported from Siberia, Russia.
3) *The Late Jurassic*
There were one megalosaurid, at least three metriacanthosaurids, one basal coelurosaur, and one non-tyrannosaurid tyrannosauroid reported from China and Thailand.
4) *The Early Cretaceous*
Several spinosaurids, carcharodontosaurids, several (five) non-ornithomimid ornithomimosaurs, several non-tyrannosaurid tyrannosauroids, megaraptorans, and basal coelurosaurs (including compsognathids) have been reported from China, Mongolia, Thailand, Japan, and Lao PDR.

Table 1. Mesozoic non-maniraptoran theropod faunas in Asia at the family/superfamily level.

Periods	Epochs	Theropod families/superfamilies	Localities
Jurassic	Early Jurassic	Coelophysoids	China
		basal tetanurans	China
	Middle Jurassic	basal tetanurans	China
		ceratosaurian	China
		metriacanthosaurids	China
		non-tyrannosaurid tyrannosauroid	Russia (Siberia)
	Late Jurassic	Megalosaurid	China
		metriacanthosaurids	China, Thailand
		non-tyrannosaurid tyrannosauroids	China
		basal coelurosaur	China
Cretaceous	Early Cretaceous	metriacanthosaurid?	Thailand?
		non-tyrannosaurid tyrannosauroids	China
		basal coelurosaurs (incl. compsog.)	China, Thailand
		spinosaurids	China, Thailand, Lao PDR, Japan, Malaysia
		carcharodontosaurids	China, Thailand
		non-ornithomimid ornithomimosaurs	China, Thailand, Mongolia
		megaraptorans	Thailand, Japan
	Late Cretaceous	non-tyrannosaurid tyrannosauroids	Uzbekistan, Mongolia?
		tyrannosaurids	China, Mongolia
		carcharodontosaurid	China
		ornithomimids	China, Mongolia, Uzbekistan, Tajikistan, Kazakhstan, Japan
		abelisaurids	India

5) *The Late Cretaceous*

Several abelisaurids from India, one carcharodontosaurid, several ornithomimids, several tyrannosaurids and non-tyrannosaurid tyrannosauroids have been reported from China, Mongolia, Japan, and central Asia. They are mostly medium to large-sized theropods except for some coelurosaurians such as compsognathids, some basal ornithomimosaurs, and some non- tyrannosaurid tyrannosauroids.

Table 2. Mesozoic non-maniraptoran theropod faunas in each continent at the family/superfamily level.

Epochs	Asia+India	Europe	North America	S. America +Africa	Australia +Antarctica
Early Jurassic	Coelophysoids; basal tetanurans		*Coelophysis*; *Dilophosaurus*		*Cryolophosaurus*
Middle Jurassic	basal tetanurans; ceratosaurian; megalosaurid; metriacanthosaurids; non-tyrannosaurid tyrannosauroid	megalosaurids; non-tyrannosaurid tyrannosauroid		Piatnitzkysaurids	
Late Jurassic	Megalosaurid; Metriacanthosaurids; non-tyrannosaurid tyrannosauroids; basal coelurosaur	compsognathids; basal coelurosaur; megalosaurid; ceratosaurian	allosaurids; megalosaurid	Ceratosaurians	
Early Cretaceous	metriacanthosaurid?; non-tyrannosaurid tyrannosauroids; basal coelurosaurs (incl. compsog.); spinosaurids; carcharodontosaurids; non-ornithomimid ornithomimosaurs; megaraptorans	Spinosaurid; Carcharodontosaurids	Carcharodontosaurids	Spinosaurids; Carcharodontosaurids	megaraptoran
Late Cretaceous	non-tyrannosaurid tyrannosauroids; tyrannosaurids; carcharodontosaurid; ornithomimids; abelisaurids		Tyrannosaurids; Ornithomimids	Spinosaurids; Carcharodontosaurids; Megaraptorans; Abelisaurids	megaraptorans

Comparison to Europe and North America

Theropods in Asia first appeared in the Early Jurassic, they consist of coelophysoids and basal tetanurans. During the Middle Jurassic, Asia was roamed by large-bodied Metriacanthosaurids and basal tetanurans, a contrast to Europe and North America which dominated by megalosaurids and allosaurids. In the Late Jurassic, Asia was still dominated by metriacanthosaurids with one possible megalosaurid, whereas in Europe, the megalosaurids and metriacanthosaurids were present together. This suggests that the mega-carnivore faunal exchange occurred between Asia and Europe during the Late Jurassic. This assumption, however, depends on the position of the Chinese Middle Jurassic *Monolophosaurus* which some studies found it to be a basal tetanuran or to nest within Megalosauroidea, or

Allosauroidea and the Chinese Middle Jurassic *Xuanhanosaurus* which some studies found it to belong to Metriacanthosauridae or Megalosauroidea. The metriacanthosaurids also migrated to Southeast Asia during the Late Jurassic. In the Early Cretaceous, theropod faunas in Asia much diverged than other time. In the Late Cretaceous, Asia was the place of tyrannosaurids and ornithomimids, with a small number of non-tyrannosaurid tyrannosauroids and one report of carcharodontosaurid, whereas the India subcontinent was roamed by the abelisaurids.

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CHAPTER 2

A Review of Theropod Dinosaurs from Southeast Asia

CHAPTER 2

A REVIEW OF THEROPOD DINOSAURS FROM THE LATE JURASSIC TO MID-CRETACEOUS OF SOUTHEAST ASIA

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Abstract:

Several non-avian theropod dinosaurs, as well as some Mesozoic birds, have been reported from Southeast Asia. The fossils are dominantly found in northeastern Thailand, however, one bizarre theropod has been described from Laos, one theropod has been reported from Malaysia, and some avian and non-avian theropods have been recently reported from Myanmar. The temporal distribution of Southeast Asian theropods ranges from the Late Jurassic to the mid-Cretaceous. All non-avian theropod faunas from Southeast Asia consist of non-maniraptoran tetanurans. They show similarity to Chinese plus Japanese theropods during the Early Cretaceous in broad systematic terms. During this time, megaraptorans can be found only in Japan, Australia, Brazil, and possibly Thailand, whereas tyrannosauroids can be found in China, Europe, possibly Brazil and Australia. Spinosaurids, carcharodontosaurians, and some coelurosaurs such as ornithomimosaurs were almost cosmopolitan. Metriacanthosaurids, on the other hand, were endemic to Europe and Asia including China and Thailand during the Middle to Late Jurassic.

1. Introduction

The most abundant and diverse non-avian theropod fossils found in Southeast Asia are from Thailand. Most of them are from the Sao Khua Formation, but also can be found in the Khok Kruat and Phu Kradung formations. Some of these finds were studied almost twenty years ago, whereas others have been discovered recently and need careful study. In this paper, an overview of theropod dinosaurs during the Mesozoic in Southeast Asia is provided, with a specific emphasis on new specimens and information on theropods found in Thailand.

The discovery of non-avian theropod dinosaurs from Thailand started in the late 1980s. Until now, eleven non-avian theropods and a Mesozoic bird have been reported. The theropods pertain to various groups and date from the Late Jurassic to the Early Cretaceous of northeastern Thailand (ca. 160–113 million years ago). There are two metriacanthosaurids (= sinraptorids) from the Phu Kradung Formation, which may be Late Jurassic or Early Cretaceous in age (prior to 125 million years ago). The finds consist of a lower leg (left tibi) of a metriacanthosaurid and cranial elements of another metriacanthosaurid (Buffetaut and Suteethorn, 2007; Chanthasit and Suteethorn, 2013). Seven theropods plus a bird from the Early Cretaceous Sao Khua Formation (ca. 130–125 million years ago) include a compsognathid (Buffetaut and Ingavat, 1984); several teeth of a spinosaurid (*Siamosaurus suteethorni*, Buffetaut and Ingavat, 1986); the postcranial skeleton of an ostrich-mimic dinosaur (*Kinnareemimus khonkaenensis,* Buffetaut et al., 2009); a maxilla of a carcharodontosaurid (Buffetaut and Suteethorn, 2012); the putative basal tyrannosauroid *Siamotyrannus isanensis* (Buffetaut et al., 1996), for which new studies suggest that it may not be a tyrannosauroid but an allosauroid (e.g. Rauhut, 2003a; Carrano et al., 2012) or that it could be a basal coelurosaur (Samathi, 2013; Samathi and Chanthasit, 2017); a Mesozoic bird (Buffetaut et al., 2005a); and two newly reported mid-sized, probable megaraptoran coelurosaurs, which look similar to *Fukuiraptor* from Japan (Samathi et al., 2019). Two theropods from the Early Cretaceous Khok Kruat Formation (ca. 125–113 million years ago) include an undescribed partial postcranial skeleton of a spinosaurid (Buffetaut et al., 2005b; Milner et al., 2007) and an undescribed partial skull and postcranial skeleton of a carcharodontosaurian (Azuma et al., 2011).

Other theropods from Southeast Asia have been recovered from Laos, Malaysia, and Myanmar. These include one spinosaurid from Laos named *Ichthyovenator laosensis* from the "Grès supérieurs" Formation reported in 2012 (Allain et al., 2012; Allain, 2014) and two spinosaurid teeth from the late Early Cretaceous of the Malay Peninsula (Sone et al., 2015). One coelurosaur and several enantiornithine birds preserved in amber were also recently reported from the mid-Cretaceous of Myanmar (Xing et al., 2016a, 2016b, 2017, 2018, 2019). Theropods from the Xinlong Formation of southern China, which belongs to the same paleobiogeographic province as Southeast Asia, includes the carcharodontosaur *Datanglong guangxiensis* (Mo et al., 2014b) and several teeth of carcharodontosaurids and spinosaurids (Buffetaut et al., 2008; Mo et al., 2014a, 2016).

Here, we review theropod dinosaurs found on the Southeast Asian mainland, as well as southern China, focusing mainly on Thailand from where most of the theropod faunas have been reported. We discuss their affinities based on recent information and recent finds, as well as comment on their evolution and paleobiogeography. Our review also focuses on the geologic age of, in particular, the finds from northeastern Thailand (Khorat Plateau). There, a circa 3–4km thick sequence of continental redbeds (Morley et al., 2011), the Khorat Group, that has been divided into several formations, yields the dinosaur fossils, including those of theropods. However, as in other parts of the world, the continental redbed sequences of the Khorat Plateau have been notoriously difficult to date, leading to sometimes strongly differing age assignments of the fossils in the older and more recent literature.

2. Institutional abbreviations

DIP: Dexu Institute of Palaeontology, Chaozhou, China; GMG: GeologicalMuseumof Guangxi Zhuang AutonomousRegion, southern China; HPG: Hupoge Amber Museum, Tengchong City Amber Association, China; IVPP: Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; MDS: Dinosaur Museum, Savannakhet, Lao PDR; PRC: Paleontological Research and Education Center, Mahasarakham University, Maha Sarakham, Thailand; SM: Sirindhorn Museum, Department of Mineral Resources, Kalasin, Thailand; UM: University of Malaya, Kuala Lumpur, Malaysia.

3. Theropod dinosaurs in Thailand

The first dinosaur bone from Thailand was found in 1976 by a geologist from the Department of Mineral Resources, Bangkok, in the course of a uranium survey at Phu Wiang District, Khon Kaen Province.The discovery consisted of a fragment of a sauropod femur from the Sao Khua Formation (Buffetaut, 1982). Since then, a collaboration led by the Department of Mineral Resources, Thailand, and the Centre National de la Recherche Scientifique, France, has led to the discovery of many dinosaur remains including ornithischians, sauropods, and theropods (Buffetaut and Suteethorn, 1992; Martin et al., 1994; Suteethorn et al., 2009).

3.1. The Phu Kradung Formation (Late Jurassic–Early Cretaceous)

The Phu Kradung Formation was originally considered to be Late Triassic to Early Jurassic in age by Ward and Bunnag (1964). Later, it was suggested that it could not be older than Jurassic by Buffetaut and Suteethorn (2007) based on the presence of the advanced mesosuchian crocodilian *Chalawan thailandicus* (Buffetaut and Ingavat, 1980; Martin et al., 2014). A Late Jurassic or probably Early Cretaceous age was proposed by Racey et al. (1996), and an Early Cretaceous age was suggested by palynological studies (Buffetaut and Suteethorn, 2007).

The Phu Noi Locality, where many non-marine vertebrate specimens have been found, is in the lower part of the Phu Kradung Formation. The age of the locality could be Late Jurassic based on the similarity to dinosaur faunas from the Late Jurassic of China (Buffetaut et al., 2014; Deesri et al., 2014; Chanthasit et al., 2015).

The dinosaurs reported from the Phu Kradung Formation include euhelopodid sauropods (Buffetaut et al., 2002; Buffetaut and Suteethorn, 2004), later found to be mamenchisaurids by Suteethorn et al. (2012), a stegosaur (Buffetaut et al., 2001), small ornithopods (Buffetaut and Suteethorn, 2007; Buffetaut et al., 2014), two large-bodied theropods (see below), and small theropods (Chanthasit, 2011; Chanthasit et al., 2015). Other vertebrate remains include hybodont sharks (Cuny et al., 2003), actinopterygians and dipnoans (Cavin et al., 2004), temnospondyl amphibians (Buffetaut et al., 1994), turtles (Tong et al., 2009, 2015, 2019), and crocodilians (Buffetaut and Ingavat, 1980, 1983; Martin et al., 2014, 2015, 2019).

The two notable theropods that have been reported from the Phu Kradung Formation are:

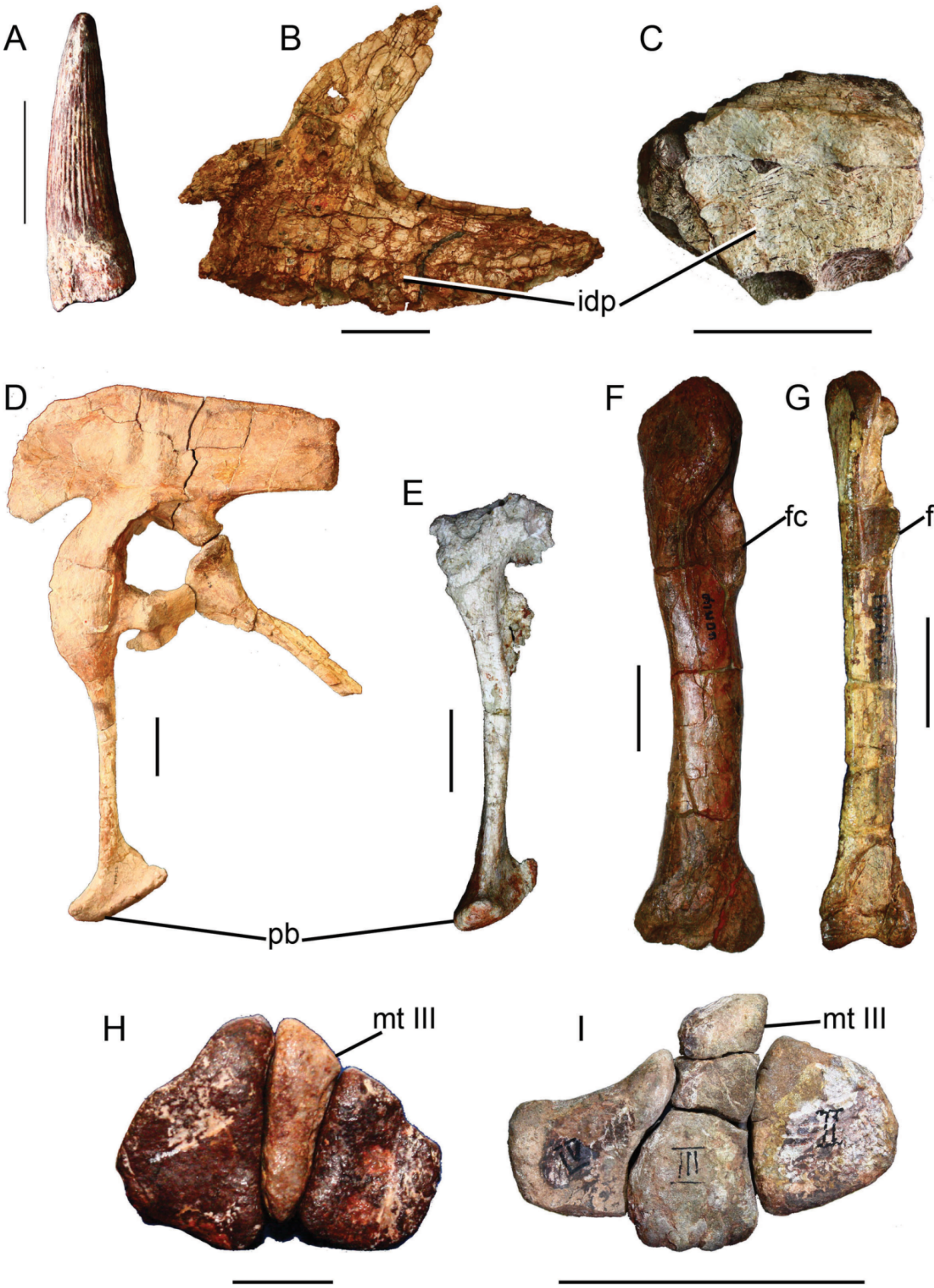


Fig. 1. Selected specimens of theropods from Thailand. Tooth (A) of the spinosaurid *Siamosaurus suteethorni* (SM-TF 2043a). Right maxillae in medial view of (B) Phu Noi metriacanthosaurid (SM-KS34-1498) and (C) Phu Wiang carcharodontosaurid (PRC 61). Pelvis elements in lateral view of (D) *Siamotyrannus isanensis* (SM-PW9-1) and (E) the Khok Kruat spinosaurid (SM-KK14). Left tibiae in anterior view of (F) Kham Phok metriacanthosaurid (SM 10) and (G) *Vayuraptor nongbualamphuensis* (SM-NB A1-2). Metatarsals in proximal view of (H) *Kinnareemimus khonkaenensis* (SM-PW5A) and (I) *Phuwiangvenator yaemniyomi* (SM-PW9B). Abbreviations: idp: interdental plate; fc: fibular crest; mt III: third metatarsal; pb: pubic boot. Scale bars (B–G, I) = 10 cm, (A) = 2.5 cm, (H) = 1 cm.

Metriacanthosauridae indet. (Buffetaut and Suteethorn, 2007; the so-called the 'Kham Phok metriacanthosaurid')

Material: **SM 10**, a nearly complete left tibia (Fig. 1F).

Occurrence: The specimen was found in an outcrop of fluvial grey sandy clays of the Phu Kradung Formation near the village of Kham Phok, Mukdaharn Province. It was lying underneath the shell of a giant turtle (Buffetaut and Suteethorn, 2007). The only damage to the bone consists of some abrasion of the proximal articular head (Buffetaut and Suteethorn, 2007).

Description: The specimen pertains to a medium to large-sized allosauroid theropod. It was excluded from ceratosaurs based on the following characters:

- the cnemial crest is less prominent;
- the fibular crest does not extend to the proximal end;
- the distal articular surface is triangular instead of quadrangular.

It differs from coelurosaurs in having an oblique ridge on the distal tibia instead of being anteriorly flat as in coelurosaurs, and in spinosaurids, which have a nearly vertical ridge on the tibia anteriorly (Buffetaut and Suteethorn, 2007). It was assigned to Allosauroidea based on similarity to this group by Buffetaut and Suteethorn (2007). Within this group, it shows greater similarity to *Sinraptor dongi* than to *Allosaurus fragilis* in that:

- the proximal articular surface of SM 10 is broader and more rounded in the caudal region than in *Allosaurus*;

- the fibular condyle is less sharply defined;

- the cnemial crest is less prominent cranially than in *Allosaurus*;

- the height of the ascending process of the astragalus is closer to *Sinraptor* and much lower than in *Allosaurus* (the ascending process height relative to tibial length is 13% in SM 10, 12% in *Sinraptor*, and 20% in *Allosaurus*);

- the ridge for the astragalar facet is more convex and much lower than in *Allosaurus*;

- the deep medial pit on the distal articular surface is open medially (all information from Buffetaut and Suteethorn, 2007).

Comments: We suggest that the tibia SM 10 belongs to the subclade Metriacanthosaurinae *sensu* Paul 1988a (see Carrano et al., 2012) based on the bulbous fibular crest of the tibia, which is a synapomorphy of this subclade (Carrano et al., 2012).

Unnamed metriacanthosaurid (Chanthasit and Suteethorn, 2013; Chanthasit et al., 2015; the so-called the 'Phu Noi metriacanthosaurid'; Fig. 1B)

Material: Skull elements such as teeth, premaxillae, and maxillae as well as appendicular materials of more than one individual.

Occurrence: Phu Noi Locality, Kham Muang District, Kalasin Province.

Description: A large metriacanthosaurid allosauroid with complex accessory openings on the maxilla (Chanthasit and Suteethorn, 2013).

Comments: The material represents more than one individual based on the recovered bones, which include at least three premaxillae, four maxillae, and two right metatarsals III. Possibly two morphs are present, robust and gracile, which could be due to different sexes or ontogeny. The Phu Noi metriacanthosaurid was suggested to be closer to *Sinraptor* than to *Yangchuanosaurus zigongensis* by Chanthasit et al. (2015) based on the pneumatic openings in antorbital fossa of the maxilla, which are more dominant in Phu Noi metriacanthosaurid and *Sinraptor* than in *Yangchuanosaurus*. Moreover, according to the proportion of the skull with larger and rounder antorbital fenestra and longer jugal suture of the maxilla, the skulls of Phu Noi material and *Sinraptor* are deeper and longer than *Yangchunosaurus* (Chanthasit et al., 2015; pers. obs.). The cranial material is currently under study.

3.2. The Sao Khua Formation (Late Barremian)

The Sao Khua Formation is one of the most fossil-rich formations of the Khorat Group of northeastern Thailand. The formation was originally considered to be Jurassic in age, but it was later shown to be Early Cretaceous based on palynology (Buffetaut et al., 2009). Before the palynological dating, a pre-Aptian age (prior to 125 million years ago) had been proposed (Buffetaut and Suteethorn, 1999) based on vertebrate faunas. A Barremian–Aptian age has also been proposed for this formation by Racey and Goodall (2009) based on palynology, and a late Barremian age (ca. 130–125 million years ago) has been proposed based on non-marine bivalves by Tumpeesawan et al. (2010) (see Buffetaut and Suteethorn, 1999, 2012).

Eight distinct theropods have been reported from the Sao Khua Formation:

Tetanurae indet. (Buffetaut and Ingavat, 1984).

Material: **SM-TF 1739-1**, the proximal part of a left tibia; **SM-TF 1739-2**, the proximal part of a right humerus.

Occurrence: Phu Wiang 1 Locality, also known as 'Phu Pratu Teema' locality, Phu Wiang District, Khon Kaen Province.

Comments: The material represents a small-sized tetanuran based on the following synapomorphy: the fibular crest of the tibia does not extend to the proximal end (Rauhut, 2003a). It was assigned to Compsognathidae by Buffetaut and Ingavat (1984) based primarily on size, shape, and similarity with the European *Compsognathus*. However, the specimen shows plesiomorphic characters including the lack of a deep cleft between the fibular condyle and the medial condyle and the lack of an offset between the cnemial crest and fibular condyle of the tibia. We refer this specimen to Tetanurae indet. and suggest that the precise affinities of this specimen need further careful study.

Spinosaurid *Siamosaurus suteethorni* (Buffetaut and Ingavat, 1986).

Holotype: **SM-TF 2043a**, isolated tooth (Fig. 1A).

Hypodigm: Holotype and referred materials (**SM-TF 2043b-i**), isolated teeth.

Occurrence: PhuWiang1 Locality 'Phu Pratu Teema',PhuWiang District, Khon Kaen Province.

Description: Spinosaurid theropod which teeth showing fluted enamel on both the labial and lingual faces, with approximately 15 flutes per side (Bertin, 2010). The teeth also show a weakly recurved profile and relatively rounded cross-section (Carrano et al., 2012). The carinae lack serrations, a characteristic associated with Spinosaurinae teeth (Sereno et al., 1998; Benson, 2010; Bertin, 2010; Hone and Holtz, 2017). But, in fact, there are very small serrations on unworn teeth (E. Buffetaut pers. comm.; A.S. pers. obs.).

Comments: Because of the lack of tooth-bearing cranial material, the affinities of the teeth among the Spinosauridae are currently uncertain (e.g., Sues et al., 2002). The teeth were assigned by some authors to Spinosauridae indet. (Bertin, 2010), considered to be a nomen dubium by Sales and Schultz (2017), Theropoda indet. by Holtz et al. (2004), ?Spinosauridae indet. by Carrano et al. (2012), and a valid taxon within the subclade Spinosaurinae, closer to *Spinosaurus* than to *Suchomimus*, by Arden et al. (2019). We note that Arden et al. (2019) included geographic and stratigraphic data into their analysis because the spinosaurid taxa are either highly fragmentary or with non-overlapping materials. According to Bertin (2010), a redescription dealing with the generic validity of *Siamosaurus* is currently being prepared by E. Buffetaut, therefore, no further discussion is attempted here.

Two tooth morphotypes of spinosaurids have been recently reported (Suteethorn et al., 2018) from the Pra Prong locality, Sa Kaeo Province. The geological age of the Pra Prong site is still unclear, but it shows similarity with the Sao Khua Formation (Suteethorn et al., 2018).

Avetheropod *Siamotyrannus isanensis* (Buffetaut et al., 1996).

Holotype: **SM-PW9-1**, left half of the pelvis, the sacrum, five isolated dorsal vertebrae, 13 articulated anterior caudal vertebrae with chevrons (Buffetaut et al., 1996) (Fig. 1D).

Referred material: A tibia and a partial sacrum (Buffetaut and Suteethorn, 1999).

Occurrence: Phu Wiang 9 Locality, Phu Wiang District, Khon Kaen Province.

Diagnosis: An avetheropod with a double vertical ridge on the central part of the lateral surface of the iliac blade (Rauhut, 2003a; Carrano et al., 2012).

Comments: *Siamotyrannus* initially was described as a primitive tyrannosaurid (Buffetaut et al., 1996; Holtz, 2001) but later interpreted as an allosauroid (Rauhut, 2003a), a metriacanthosaurid allosauroid (Carrano et al., 2012), and possibly a basal coelurosaur (e.g. Samathi, 2013; Samathi and Chanthasit, 2017).

Siamotyrannus is clearly not tyrannosauroid since it lacks tyrannosauroid synapomorphies (Rauhut, 2003b; Carrano et al., 2012; Brusatte and Benson, 2013; Samathi, 2013). These include a strongly developed and well-defined vertical ridge above acetabulum on the lateral surface of the ilium (Rauhut, 2003b). In tyrannosauroids, the vertical ridge is narrow, sharply defined, rounded, and extends over almost the complete height of the ilium (Brusatte and Benson, 2013). In basal, non-tyrannosaurid tyrannosauroids, the ridges are posterodorsally inclined (Brusatte and Benson, 2013; Brusatte and Carr, 2016). In *Siamotyrannus*, two parallel, vertical ridges are present instead of one ridge. These ridges are wide and do not extend to the dorsal margin of the iliac blade. The second lacking synapomorphy is that the dorsal part of the anterior margin of the preacetabular blade is concave or bilobate shape in tyrannosauroids (Rauhut, 2003b), which is not present in *Siamotyrannus* (characters from Samathi, 2013).

The tibia with partial sacrum provisionally assigned to *Siamotyrannus* by Buffetaut and Suteethorn (1999) more probably belongs to another taxon of theropod found in the Phu Wiang Locality (see below). A revision and phylogenetic analysis of *Siamotyrannus* is currently in progress by Samathi et al.

Mesozoic bird/Neornithes indet. (Buffetaut et al., 2005a).

Material: **SM-K3-1**, the distal part of a left humerus.

Occurrence: Khok Kong Locality, Kalasin Province.

Comments: The humerus represents a medium-sized avian. It was surface-collected in 1992. The specimen is not an enantiornithine but may be an early ornithurine based on two characters, including:

- transversely orientated dorsal condyle (orientated at almost 90 degrees relative to the axis of the bone);

- the humeral brachial fossa developed as a flat scar (characters from Buffetaut et al., 2005a).

Ornithomimosaur *Kinnareemimus khonkaenensis* (Buffetaut et al., 2009) (Fig. 1H).

Holotype: **SM-PW5A-100**, an incomplete left third metatarsal with the distal end and part of the shaft.

Hypodigm: Holotype and referred materials (**SM-PW5A-101** to **131**).

Occurrence: Phu Wiang 5 Locality, Phu Wiang District, Khon Kaen Province.

Diagnosis: An ornithomimosaur with metatarsal III visible in cranial view between the proximal ends of metatarsal II and IV, but becoming rod-like distally and expanding again, with a triangular cross-section, closer to the distal end (all from Buffetaut et al., 2009).

Comments: *Kinnareemimus* is possibly more primitive than previously thought (e.g. nesting outside the Ornithomimidae) based on recent phylogenetic analyses (Samathi, 2017). This conclusion, however, might be due to the incompleteness or immaturity of the material. However, we note that Brusatte et al. (2014) did not find any tree topology in which *Kinnareemimus* was located within the Ornithomimosauria in their phylogenetic analysis and suggested that it is some kind of basal coelurosaur.

Carcharodontosaurid (Buffetaut and Suteethorn, 2012; the socalled the 'Phu Wiang carcharodontosaurid')

Material: **PRC 61**, part of a right maxilla with un-erupted tooth (Fig. 1C).

Occurrence: Surface-collected. Phu Wiang 1A Locality. Phu Wiang District, Khon Kaen Province

Description: A large-bodied carcharodontosaurid with completely fused interdental plates resembling *Carcharodontosaurus*, *Mapusaurus*, and *Shaochilong*. It differs from *Sinraptor* and *Tyrannosaurus* in which the interdental plates are separated and differs from *Allosaurus* where the individual plates can be distinguished although there is some level of fusion (all information from Buffetaut and Suteethorn, 2012).

Comments: Large theropods with fused interdental plates with different levels of fusion can be found among abelisaurids, carcharodontosaurs, *Allosaurus*, and *Torvosaurus* (Sampson and Witmer, 2007; Brusatte et al., 2012; Araújo et al., 2013; Hendrickx and Mateus, 2014). There is some variation in interdental plate wall morphology, such as a smooth or ridged surface, and in the lateral texture of the surface of the maxilla body, such as a rugose or smooth surface texture (Sereno et al., 1996; Brusatte and Sereno, 2007; Sampson and Witmer, 2007; Sereno and Brusatte, 2008). The height-width proportion of interdental plates (Brusatte et al., 2012) should be considered as well. Thus, it is important to compare PRC 61 with other abelisaurids and carcharodontosaurids and also *Torvosaurus* since they are almost cosmopolitan theropods (except the abelisaurids and *Torvosaurus*) and are usually found together, possibly living in the same environment (e.g. Brusatte and Sereno, 2007; Candeiro et al., 2018; Hassler et al., 2018). The comparison will be done in a future study.

Based on size and occurrence, the Phu Wiang carcharodontosaurid might represent the same animal as *Siamotyrannus*. However, more discoveries and further study are needed to test this hypothesis.

Basal coelurosaur *Vayuraptor nongbualamphuensis* (Samathi et al, 2019).

Material: **SM-NB A1-2**, a left tibia with associated astragalocalcaneum, a coracoid, and incomplete referred materials (Fig. 1G).

Occurrence: Phu Wat A1 Locality, Nong Sang, Nong Bua Lamphu Province.

Diagnosis: a basal coelurosaur with (1) the astragalus has two horizontal grooves, two fossae at the base of the ascending process, (2) the ascending process being straight laterally and straight and parallel medially with the medial rim sloping to the tip laterally, (3) a vertical ridge starting from the tip and disappearing just above the middle of the ascending process, and (4) a long and slender astragalar ascending process (all information from Samathi et al., 2019).

Comments: *Vayuraptor* was recently reported and named by Samathi et al., 2019. In addition to *Australovenator* from the Late Cretaceous of Australia, *Vayuraptor* looks similar to the megaraptoran *Fukuiraptor* from the Early Cretaceous of Japan (Samathi et al., 2019; Azuma and Currie, 2000; Hocknull et al., 2009; White et al., 2013). However, with few materials, the phylogenetic position of *Vayuraptor* must await further discovery of additional materials.

Megaraptoran *Phuwiangvenator yaemniyomi* (Samathi et al, 2019).

Material: **SM-PW9B**, dorsal and sacral vertebrae, forelimb and hindlimb elements (Fig. 1I).

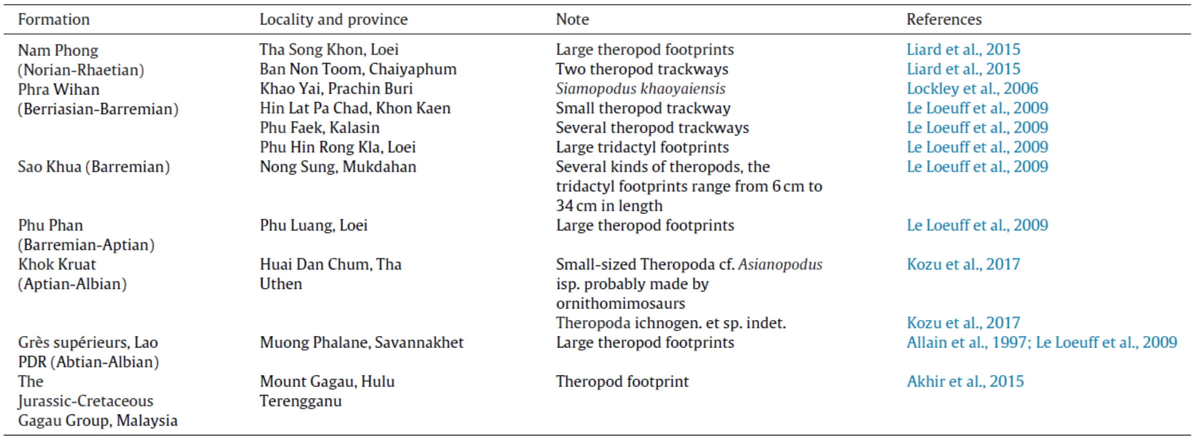
Occurrence: Phu Wiang 9B Locality, Phu Wiang District, Khon Kaen Province.

Diagnosis: a megaraptoran coelurosaur with (1) ventrally flat sacral vertebrae with sulci in the anterior and posterior region of the centra and (2) the anterior rim of metatarsal IV slopes from proximolaterally to distomedially. This way, the distomedial corner of the proximal articular surface of metatarsal IV in anterior view is much lower than the articular surface of metatarsal III. In addition, the distomedial corner is lower than in any other known theropod (all information from Samathi et al., 2019).

Comments: *Phuwiangvenator* was recently reported and named by Samathi et al. in 2019, who found it belongs to the Megaraptora and possibly the most basal member of this group. This finding suggests that Megaraptora might originate in Southeast Asia and had a high diversity and wide distribution during the Early Cretaceous, which became more provincial in the Late Cretaceous (Samathi et al., 2019).

Furthermore, some teeth of theropods from Nakhon Ratchasima Province, northeastern Thailand, were briefly reported by Chokchaloemwong et al. (2015) who suggested them to be close to *Fukuiraptor*.

Table 1. List of theropod footprints known from Southeast Asia. All formations are from Thailand unless indicated otherwise.



Formation	Locality and province	Note	References
Nam Phong (Norian-Rhaetian)	Tha Song Khon, Loei	Large theropod footprints	Liard et al., 2015
	Ban Non Toom, Chaiyaphum	Two theropod trackways	Liard et al., 2015
Phra Wihan (Berriasian-Barremian)	Khao Yai, Prachin Buri	*Siamopodus khaoyaiensis*	Lockley et al., 2006
	Hin Lat Pa Chad, Khon Kaen	Small theropod trackway	Le Loeuff et al., 2009
	Phu Faek, Kalasin	Several theropod trackways	Le Loeuff et al., 2009
	Phu Hin Rong Kla, Loei	Large tridactyl footprints	Le Loeuff et al., 2009
Sao Khua (Barremian)	Nong Sung, Mukdahan	Several kinds of theropods, the tridactyl footprints range from 6 cm to 34 cm in length	Le Loeuff et al., 2009
Phu Phan (Barremian-Aptian)	Phu Luang, Loei	Large theropod footprints	Le Loeuff et al., 2009
Khok Kruat (Aptian-Albian)	Huai Dan Chum, Tha Uthen	Small-sized Theropoda cf. *Asianopodus* isp. probably made by ornithomimosaurs	Kozu et al., 2017
		Theropoda ichnogen. et sp. indet.	Kozu et al., 2017
Grès supérieurs, Lao PDR (Abtian-Albian)	Muong Phalane, Savannakhet	Large theropod footprints	Allain et al., 1997; Le Loeuff et al., 2009
The Jurassic-Cretaceous Gagau Group, Malaysia	Mount Gagau, Hulu Terengganu	Theropod footprint	Akhir et al., 2015

3.3. The Khok Kruat Formation (Aptian)

The Khok Kruat Formation was suggested by Buffetaut et al. (2005a, b) to be Aptian-Albian in age based on the freshwater hybodont shark *Thaiodus ruchae*. The palynological evidence also indicates an Aptian age for the upper part of the formation (Buffetaut et al., 2005a, b; Sattayarak et al., 1991; Racey et al., 1996).

The Khok Kruat Formation has yielded dinosaur remains including the theropods reviewed below, sauropods, the ceratopsian *Psittacosaurus sattayaraki* (Buffetaut et al., 1989; Buffetaut and Suteethorn, 1992; Buffetaut et al., 2007), and three iguanodontian ornithopods. These are *Ratchasimasaurus suranarii* (Shibata and Jintasakul, 2008; Shibata et al., 2011), *Siamodon nimngami* (Buffetaut et al., 2005b; Buffetaut and Suteethorn, 2011), and *Sirindhorna khoratensis* (Shibata et al., 2015). Dinosaur footprints also have been reported from the formation (Buffetaut et al., 2005b). Other fossil remains are hybodont sharks, semionotiform fishes, turtles (Tong et al., 2005), and crocodilians (Lauprasert, 2006). Two theropods have been reported from the Khok Kruat Formation (Buffetaut et al., 2005b; Milner et al., 2007; Azuma et al.,2011).

Undescribed spinosaurid (Buffetaut et al., 2004, 2005b; Milner et al., 2007; the so-called the 'Khok Kruat spinosaurid')

Material: **SM-KK 14**, a partial skeleton including cervical and dorsal vertebrae, pelvic elements, an isolated, elongate neural spine, chevron, and possible metacarpal (Buffetaut et al., 2004, 2005b; pers. obs. Fig. 1E).

Occurrence: Ban Pia Fan, Samran Subdistrict, Muang District, Khon Kaen Province.

Description: The anterior cervical vertebrae are longer than the posterior ones. On the dorsal vertebrae, the infraprezygapophyseal fossae are expanded in size. The chevron lacks an anterior process. This process is also absent in other spinosaurids. The pubis is slightly concave anteriorly in lateral view. The distal end of the pubic boot has an L-shape and closely resembles those of *Ichthyovenator* (Allain et al., 2012) and *Suchomimus* (pers. obs.).

Comments: The vertebrae of SM-KK 14 resemble *Baryonyx* and *Spinosaurus* (Buffetaut et al., 2005b; Milner et al., 2007). We suggest that the cervical vertebrae of SM-KK 14 could be C4, C6, C7, and C10 in comparison with *Baryonyx* (Evers et al., 2015). SM-KK 14 resembles *Ichthyovenator* but differs in some details, for example, SM-KK 14 and *Ichthyovenator* show a posteroventrally open obturator notch of the pubis and relatively tall dorsal neural spines. However, SM-KK 14 has an anteriorly concave pubis and a posteriorly curved chevron, whereas *Ichthyovenator* has a straight pubis and chevrons (Allain et al., 2012; pers. obs.).

Unnamed and undescribed carcharodontosaurian (Azuma et al., 2011; the so-called the 'Khorat carcharodontosaurian')

Material: A premaxilla, maxillae, isolated teeth, cervicals, a dorsal, a caudal, manual ungual, and a metatarsal.

Occurrence: The Dinosaur Quarry, Suranari, Nakhon Ratchasima Province.

Description: A large-bodied allosauroid theropod with arcuate enamel wrinkles on isolated teeth; the ratio of the labial-lingual base width to the fore-aft base length is similar to that of carcharodontosaurids. There is a large and rectangular-shaped premaxilla with four teeth, none of which show a D-shape in cross-section. There are four interdental plates (information from Azuma et al., 2011).

Comments: The description of this theropod is currently being prepared by Chokchaloemwong and team (D. Chokchaloemwong, pers. comm.).

4. Theropod dinosaur in Laos

The spinosaurid from Laos, *Ichthyovenator laosensis* Allain, Xaisanavong, Richir, and Khentavong, 2012, is from the "Grès supérieurs" Formation. This formation might be the same age as the Khok Kruat (Buffetaut, 1991) and Phu Pan Formations and is probably late Barremian to early Cenomanian in age (Allain et al., 2012; Allain, 2014). A non-marine bivalve assemblage recovered in the Tang Vay area suggests *Ichthyovenator* is Aptian in age (Allain et al., 2012).

Material: Holotype: partially articulated skeleton (**MDS BK10- 01** to **15**) including dorsal vertebra, the neural spine of the last dorsal vertebra, caudal vertebrae, sacral vertebrae, ilia, the right pubis, ischia, and a dorsal rib (Allain et al., 2012). Additional materials: a complete series of cervical vertebrae, the first dorsal vertebra, the left pubis, caudal vertebrae, and teeth of the same individual (Allain, 2014).

Occurrence: Ban Kalum, Tang Vay area, Savannakhet Province, Laos.

Description: A spinosaurid diagnosed by unique characters including a dorsosacral sinusoidal sail; penultimate dorsal neural spine is 410% of centrum length with anterodistal finger-like process; fan-shaped sacral neural spines 3 and 4; transverse processes of first caudal vertebra with sigmoid profile in dorsal view; deep prezygapophyseal centrodiapophyseal fossae in the first caudal vertebra; and long iliac blade (all characters from Allain et al., 2012).

Comments: The taxon was originally interpreted as a member of the Spinosauridae subclade Baryonychinae by Allain et al. (2012) but was later found to be more closely related to Spinosaurinae than to Baryonychinae based on additional specimens (Allain, 2014). Within Spinosaurinae, it was found to be closer to *Spinosaurus* than to *Siamosaurus* by Arden et al. (2019).

5. Theropod dinosaur in Malaysia

Spinosaurid teeth from the Malay Peninsula (Sone et al., 2015).

Material: Teeth **UM10575** and **UM10576** (Sone et al., 2015).

Occurrence: The Tembeling Group, which correlates to the Khorat Group. The exact locality is kept secret for protection and conservation (Sone et al., 2015).

Comments: The teeth show sharp vertical ridges and serrated carinae with minute denticles and display a veined microornament over the surface (information from Sone et al., 2015). The teeth show spinosaurid characters including subcircular tooth crowns in cross-section (Benson, 2010) and the presence of striations on tooth crowns (Evers et al., 2015).

Table 2. List of theropod (including the Mesozoic bird) specimens known from SE Asia and S China.

Specimen	Description	Locality	Identification	References
Phu Kradung Fm.				
SM 10	Left tibia	Mukdaharn	Metriacanthosauridae (= Sinraptoridae) indet.	Buffetaut and Suteethorn, 2007
SM-KS 34-1133, etc.	Skull and postcranial elements	Kalasin	As-yet-unnamed Metriacanthosauridae	Chanthasit and Suteethorn, 2013
Sao Khua Fm.				
SM-TF 1739-1, SM-TF 1739-2	Left tibia, right humerus	Khon Kaen	Tetanurae indet.	Buffetaut and Ingavat, 1984
SM-TF 2043a-i	Teeth	Khon Kaen	*Siamosaurus suteethorni*	Buffetaut and Ingavat, 1986
SM-PW5A-100 and referred materials	Postcranial skeleton	Khon Kaen	*Kinnareemimus khonkhaenensis*	Buffetaut et al., 2009
PRC 61	Partial skull	Khon Kaen	Carcharodontosauridae indet.	Buffetaut and Suteethorn, 2012
SM-PW9-1	Postcranial skeleton	Khon Kaen	*Siamotyrannus isanensis*	Buffetaut et al., 2009
SM-K3-1	Humerus	Kalasin	Possible early ornithurine	Buffetaut et al., 2005a
SM-NB A1-2	Tibia with associated astragalocalcaneum	Nong Bua Lam Phu	*Vayuraptor nongbualamphuensis*	Samathi et al. 2019
SM-PW9B	Postcranial skeleton	Khon Kaen	*Phuwiangvenator yaemniyomi*	Samathi et al. 2019
Khok Kruat Fm.				
SM-KK14	Cervicals	Khon Kaen	As-yet-undescribed Spinosauridae	Buffetaut et al., 2004, 2005a, b; Milner et al., 2007
In the collection of Nakhon Ratchasima Rajabhat University	Premaxilla	Nakhon Ratchasima	As-yet-undescribed Carcharodontosauria	Azuma et al., 2011
Grès supérieurs Fm.				
MDS BK10-01 to 15	Vertebrae, pelvis element, chevrons	Savannakhet, Lao PDR	*Ichthyovenator laosensis*	Allain et al., 2012
The Tembeling Gr.				
UM10575, UM10576	Teeth	Malaysia	Spinosauridae indet.	Sone et al., 2015
Mid-Cretaceous				
DIP-V-15100, DIP-V-15101, DIP-V-15102, DIP-V-15105, HPG-15-1	Partial skeleton	Myanmar	Enantiornithine birds	Xing et al., 2016a, 2017, 2018, 2019
DIP-V-15103	Tail		Non-avialan coelurosaur	Xing et al., 2016b
Xinlong Fm.				
GMG 00001	Partial skeleton	Datang Town, Guangxi, China	*Datanglong guangxiensis*	Mo et al., 2014b
IVPP V 4793	Teeth	Fusui County, Guangxi, China	Spinosauridae indet. *“Sinopliosaurus fusuiensis”*	Hou et al., 1975; Buffetaut et al., 2008; Mo et al., 2016

Table 3. Comparison of non-avian theropod faunas from Southeast Asia, China + Japan, and Europe.

	SE Asia	China + Japan	Europe
Late Jurassic	Metriacanthosaurids	Metriacanthosaurids; megalosaurid; basal coelurosaurs; tyrannosauroids; ceratosaur	Metriacanthosaurid; basal allosauroids; megalosaurid; basal coelurosaurs (incl. compsognathids); tyrannosauroids
Early Cretaceous	?metriacanthosaurid; basal coelurosaurs (incl. ?compsognathid); spinosaurids; carcharodontosaurians; ornithomimosaur; ?megaraptoran	Tyrannosauroids; basal coelurosaurs (incl. compsognathids); spinosaurids; carcharodontosaurians; ornithomimosaurs; megaraptoran	Tyrannosauroids; ceratosaurs; spinosaurids; carcharodontosaurians; ornithomimosaur

6. Theropod dinosaurs in Myanmar

Enantiornithine birds (Xing et al., 2016a, 2017, 2018, 2019).

Material: **DIP-V-15100**, **DIP-V-15101**, **DIP-V-15102**, **DIP-V-15105**, and **HPG-15-1**.

Occurrence: All material comes from the mid-Cretaceous Angbamo site, Hukawng Valley, Tanai Township, Myitkyina District, Kachin Province of Myanmar, which might be in the early Cenomanian (98.8±0.6 Ma) or Albian–Cenomanian (105–95 Ma, based on ammonite biostratigraphy and palynology) (Shi et al., 2012; Xing et al., 2016a).

Comments: The specimens DIP-V-15100 and DIP-V-15101 are partial wings of precocial hatchling birds preserved in amber with plumage and integument. The two specimens might belong to the same species (Xing et al., 2016a). HPG-15-1 is nearly half of a hatchling bird individual with soft tissue (Xing et al., 2017). DIP-V-15102 is an articulated skeleton with integumentary structures missing the rostral and middle portions of the skull and most of its right wing and leg. However, this specimen is the most complete individual discovered so far in Burmese amber (Xing et al., 2018). Recently, Xing et al. (2019) reported a partial bird in Burmese amber (DIP-V-15105). It consists of a partial foot (a distal right tarsometatarsus and nearly complete pedal digits) and wing fragments (information from Xing et al., 2019).

Fig. 2. Map of Southeast Asia and southern China showing the localities that have yielded the currently known theropod dinosaurs. 1 = Kachin; 2 = Guangxi; 3 = Khon Kaen; 4 = Kalasin; 5 = Nakhon Ratchasima; 6 = Sa Kaeo; 7 = Savannakhet; 8 = unrevealed locality. The two new theropod taxa described by Samathi et al. (2019) were not incorporated into this figure to avoid delays in publication.

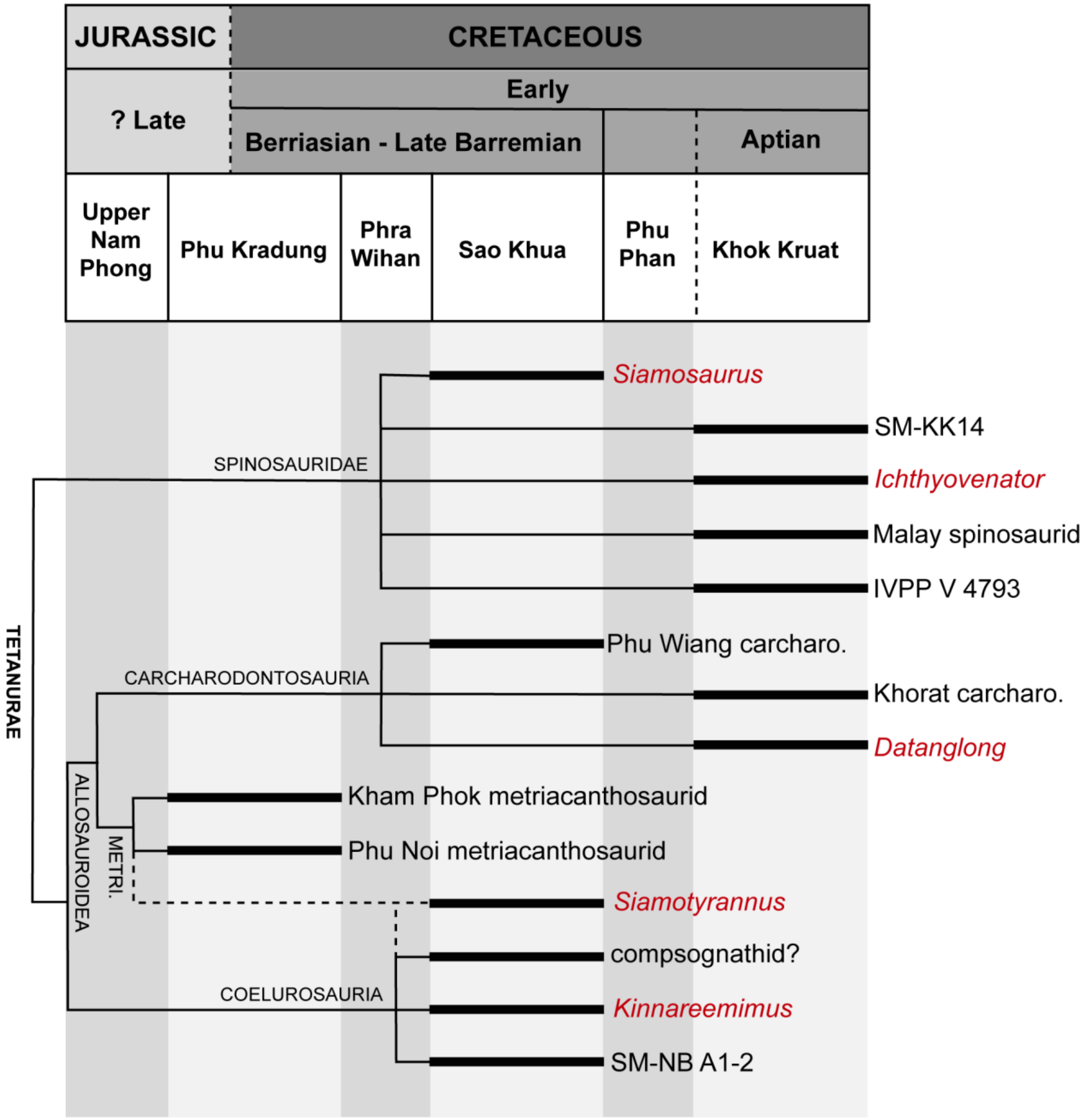


Fig. 3. Theropod dinosaurs and their phylogenetic relationships found in the Late Jurassic–Early Cretaceous of Southeast Asia and southern China. METRI. = Metriacanthosauridae.

Non-avialan coelurosaur (Xing et al., 2016b).

Material: **DIP-V-15103**.

Occurrence: Mid-Cretaceous Angbamo site, Hukawng Valley, Tanai Township, Myitkyina District, Kachin Province of Myanmar which might be in the early Cenomanian (98.8±0.6 Ma) or Albian–Cenomanian (105–95 Ma, based on ammonite biostratigraphy and palynology).

Comments: DIP-V-15103 is a feathered, mid to distal tail of a non-avian coelurosaurian theropod, possibly juvenile, preserved in amber with plumage and soft tissues. DIP-V-15103 was assigned to non-avian Coelurosauria based on:

- there are more than 25 caudal vertebrae (estimated);
- a distinct ventral groove on the caudal centra is present;
- the preserved tail feathers lack closed vanes (the closed vane is a Pennaraptora character).

The presence of open vanes also suggests that DIP-V-15103 is more crownward than compsognathids and tyrannosauroids (see Xing et al., 2016b supplementary information).

7. Theropod dinosaurs in southern China

7.1. The Xinlong Formation

The Early Cretaceous Xinlong Formation of the Napai Basin and Datang Basin, Guangxi, southern China belongs to the same paleobiogeographic province as Southeast Asia. Therefore, adding theropod records from this formation to the present work can help to understand the diversity and paleobiogeography of this region. The Xinlong Formation was found to be equivalent to the Khok Kruat Formation in Thailand and the 'Grès supérieurs' Formation in Laos which are Aptian in age (Mo et al., 2016). From this formation, one carcharodontosaur has been named, as well as several teeth, which have been assigned to the Carcharodontosauridae and Spinosauridae (Mo et al., 2014a, 2014b, 2016).

The carcharodontosaur *Datanglong guangxiensis* (Mo et al., 2014b).

Holotype: **GMG 00001**, partial articulated postcranial skeleton including posteriormost dorsal vertebra, five sacral vertebrae, the first two caudal vertebrae, the first chevron, left and right ilia, and a partial pubis and ischium.

Occurrence: Datang Basin, Datang Town, Nanning City, Guangxi Zhuang Autonomous Region, southern China.

Description: A large-bodied, basal carcharodontosaurian diagnosed by long parapophyses on the last dorsal vertebra, brevis fossa with short, ridge-like medial blade, and pubic peduncle of the ilium with posteroventrally expanded margin (information from Mo et al., 2014b).

Comments: *Datanglong* shares some characters with derived carcharodontosaurids and megaraptorans [e.g., it has a pneumatic dorsal vertebra and ilium, but it shows non-pneumatic sacral vertebrae which are present in megaraptorans (Aranciaga Rolando et al., 2018)], therefore careful analysis is needed before its phylogenetic position can be assessed.

Furthermore, other isolated carcharodontosaurid teeth from the Napai Basin, Xinlong Formation, have been reported, and they are relatively common (Mo et al., 2014a, 2016).

Spinosaurid teeth IVPP V 4793 "*Sinopliosaurus fusuiensis*" (Hou et al., 1975).

Material: **IVPP V 4793**, an almost complete tooth and four fragmentary teeth.

Occurrence: Napai Basin, Fusui County, Guangxi Zhuang Autonomous Region, southern China.

Description: Recurved, laterally compressed teeth with well developed longitudinal ridges on both faces (approximately twelve on each face) of the crown and a finely wrinkled enamel (Buffetaut et al., 2008; Mo et al., 2016).

Comments: IVPP V 4793 shows spinosaurid affinities as mentioned above (see Buffetaut et al., 2008). It was first assigned to Plesiosauria and named "*Sinopliosaurus fusuiensis*" by Hou et al. (1975) and was later found to be a spinosaurid closely similar to *Siamosaurus* by Buffetaut et al. (2008). It was considered as *nomen dubium* by Sales and Schultz (2017), who stated that naming theropod species based on isolated teeth has been problematic. The IVPP V 4793 is considered here as Spinosauridae indet. Awaiting further discovery, no study beyond this is attempted here. In addition, isolated spinosaurid teeth have been reported as relatively common in the Xinlong Formation (Mo et al., 2016).

8. Theropod footprints

Theropod footprints in Southeast Asia are mainly from Thailand with one report from Laos and one recent report from Malaysia (Buffetaut et al., 1985; Liard et al., 2015; Le Loeuff et al., 2009; Kozu et al., 2017; Allain et al., 1997; Akhir et al., 2015), see Table 1.

8.1. Thailand

8.1.1. Nam Phong Formation (Norian-Rhaetian)

Tha Song Khon, Loei Province

Large theropod footprints (Liard et al., 2015).

Ban Non Toom, Chaiyaphum Province

Two theropod trackways (Liard et al., 2015).

8.1.2. Phra Wihan Formation (Berriasian-Barremian)

Khao Yai, Prachin Buri Province

Siamopodus khaoyaiensis (Lockley et al., 2006).

Hin Lat Pa Chad, Khon Kaen Province

Small theropod trackway (Le Loeuff et al., 2009).

Phu Faek, Kalasin Province

Several theropod trackways (Le Loeuff et al., 2009).

Phu Hin Rong Kla, Loei Province

Large tridactyl footprints (Le Loeuff et al., 2009).

8.1.3. Sao Khua Formation (Barremian)

Nong Sung, Mukdahan Province

Several kinds of theropods, the tridactyl footprints range from 6cm to 34cm in length (Le Loeuff et al., 2009).

8.1.4. Phu Phan Formation (Barremian-Aptian)

Phu Luang Wildlife Sanctuary, Loei Province

Large theropod footprints (Le Loeuff et al., 2009).

8.1.5. Khok Kruat Formation (Aptian-Albian)

Huai Dam Chum, Tha Uthen

Small-sized Theropoda, cf. Asianopodus isp., probably made by ornithomimosaurian (Kozu et al., 2017).

Theropoda ichnogen. et sp. indet. (Kozu et al., 2017).

8.2. Laos

8.2.1. Grès supérieurs Formation (≈Khok Kruat Formation Aptian-Albian)

Muong Phalane, Savannakhet Province

Large theropod footprints (Allain et al., 1997; Le Loeuff et al., 2009).

8.3. Malaysia

8.3.1. Jurassic-Cretaceous Gagau Group

Mount Gagau, Hulu Terengganu

Single theropod footprint (Akhir et al., 2015).

9. Discussion

9.1. Theropod Diversity (Table 2)

Theropod faunas from the Late Jurassic to the Early Cretaceous of Southeast Asia include several clades, among them Metriacanthosauridae, Spinosauridae, Carcharodontosauria, Ornithomimosauria, as well as basal Coelurosauria and birds.

In Thailand, The Phu Kradung Formation yields two metriacanthosaurids. However, the Kham Phok and Phu Noi metriacanthosaurids might belong to the same taxon. The reported metriacanthosaurids, together with the mamenchisaurids found at the Phu Noi Locality, comprise essentially the same endemic East Asian fauna previously known from the Middle and Late Jurassic of China (Buffetaut and Suteethorn, 2007; Suteethorn et al., 2012; Chanthasit et al., 2015), suggesting that the Phu Kradung Formation, or at least its lower part, is no younger than Late Jurassic in age (Martin et al., 2015). However, the finding that Metriacanthosaurus from the Late Jurassic of England belongs to the Metriacanthosauridae (formerly Sinraptoridae) suggests that this clade is more widespread than previously thought (Benson and Barrett, 2009; Carrano et al., 2012). This supports the hypothesis that many dinosaur groups with a global distribution in the Late Jurassic and/or Cretaceous probably originated before the separation of Laurasia and Gondwana, as suggested by various authors (e.g., Brusatte and Sereno, 2008; Brusatte et al., 2009; Barrett et al., 2011; Xu et al., 2018).

The Sao Khua Formation of Thailand yields one carcharodontosaurian, one or two spinosaurids, one ornithomimosaur, and probable basal coelurosaurs. Based on size and occurrence, the Phu Wiang carcharodontosaurid might belong to the same taxon asSiamotyrannus. However, more findings and study are needed to test this hypothesis. At the very least, two large-bodied theropods, mid-sized basal coelurosaurs, and small-bodied coelurosaurs, including ornithomimosaurs, were present. This shows a high diversity of theropods from this formation.

The Khok Kruat Formation of Thailand (also the “Grès supérieurs” Formation of Laos and the Xinlong Formation of southern China) yields two carcharodontosaurians and at least two spinosaurids. In Myanmar, the mid-Cretaceous yields non-avian coelurosaur and enantiornithine birds.

There are, until now, no records of abelisauroids in Southeast Asia, which corroborates what is currently known about the distribution of this clade, as abelisauroids have been found only in South America, Africa, Europe, India, and Madagascar (Carrano and Sampson, 2008), underscoring the isolation of eastern Asia during the Cretaceous.

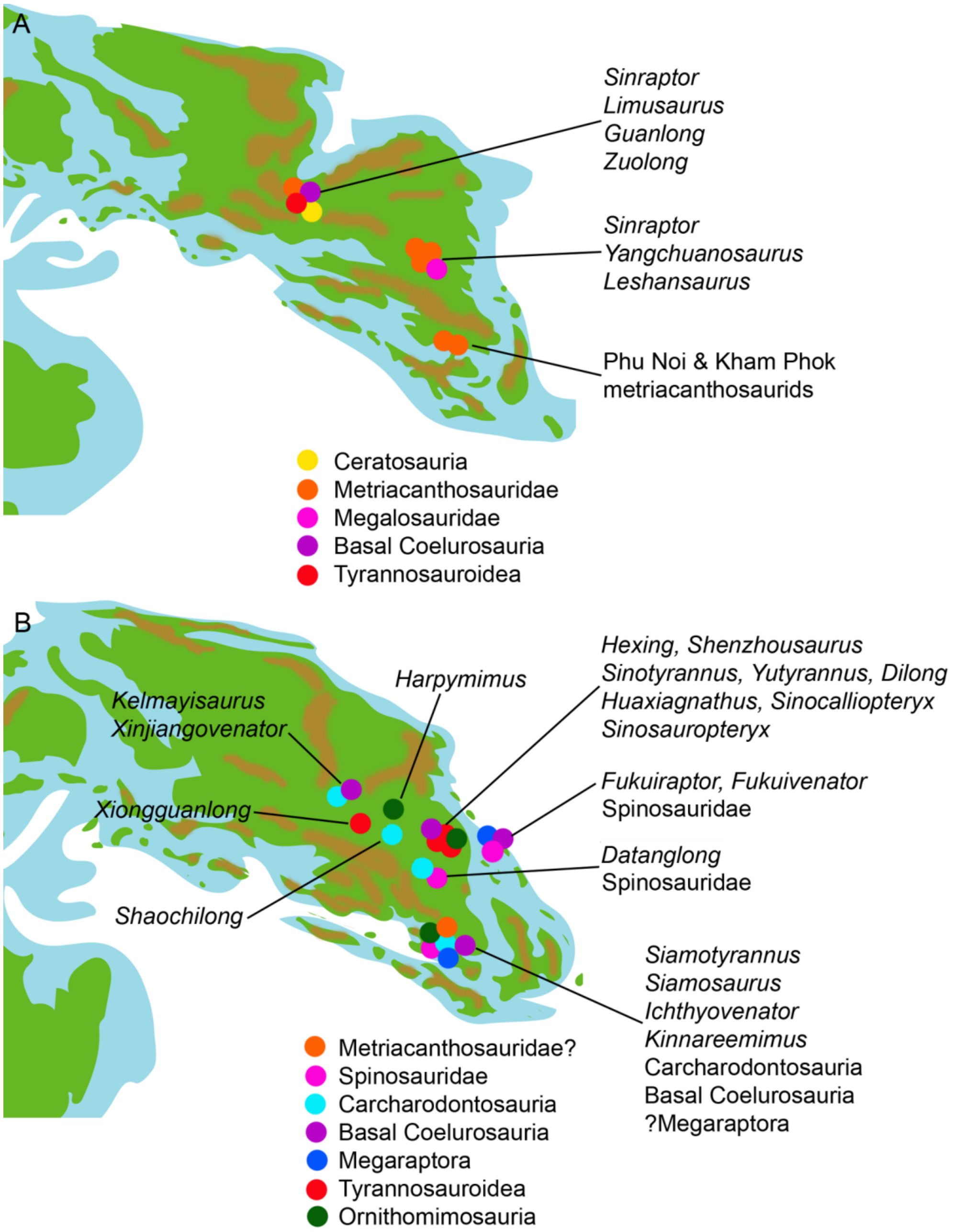


Fig. 4. Paleobiogeography of non-maniraptoran theropod dinosaurs in Asia. (A) Late Jurassic (~150 Ma) and (B) Early Cretaceous (~120 Ma). Paleogeographic maps based on cpgeosystems.com.

9.2. Paleobiogeographic Implications

The dinosaur faunas from the Phu Kradung Formation show similarity with the faunas from the Late Jurassic Upper Shaximiao Formation of Sichuan and the Shishugou Formation of Xinjiang (Buffetaut et al., 2006). The Khok Kruat Formation dinosaur assemblage is similar to those from the Xinminbao Group of Gansu, the Dashuigou Formation of Inner Mongolia (Buffetaut et al., 2006), and the Xinlong Formation of southern China (Mo et al., 2016).

Focusing mainly on the non-maniraptoran theropods, we found that during the Late Jurassic, Southeast Asia was roamed by Metriacanthosauridae, whereas East Asia (China + Japan) was home to Metriacanthosauridae, Megalosauridae, basal Coelurosauria, Tyrannosauroidea, and basal Ceratosauria (e.g., Carrano et al., 2012). In Europe, Metriacanthosauridae, basal Allosauroidea, Megalosauridae, basal Coelurosauria (including Compsognathidae), and Tyrannosauroidea were present (e.g., Carrano et al., 2012; Rauhut et al., 2016), see Table 3. Thus, especially considering the much scantier Southeast Asian theropod record compared to East Asia, Southeast Asia was evidently part of the same faunal province as East Asia (China + Japan). However, the lower diversity in Southeast Asia during this time might be due to sampling biases such as anthropogenic and geologic biases, which have more effects on a global scale than previously thought (Alroy, 2010; Benson and Butler, 2011; Butler et al., 2012; Tennant et al., 2018; Xu et al., 2018).

During the Early Cretaceous, theropod faunas in Southeast Asia consist of ?Metriacanthosauridae, basal Coelurosauria, Spinosauridae, Carcharodontosauria, Ornithomimosauria, and possible Megaraptora, whereas East Asia was home to basal Coelurosauria (including Compsognathidae), Tyrannosauroidea, Spinosauridae, Carcharodontosauria, Ornithomimosauria, and Megaraptora. In Europe, Spinosauridae, Carcharodontosauria, Tyrannosauroidea, Ornithomimosauria, and Ceratosauria were present (e.g., Carrano et al., 2012; Rauhut et al., 2016; Hone and Holtz, 2017). Thus, once again, we can draw the same conclusion as above. The lower number of finds in Southeast Asia seems to suggest a lower diversity of theropods compared to the Chinese and Japanese record, but this may be simply due to sampling biases.

All theropod faunas from Southeast Asia found so far belong to non-maniraptoran tetanurans with the exception of the avian theropods found in Thailand and Myanmar. These show greater similarity to East Asian (China + Japan) theropods during the Early Cretaceous, in broad systematic terms, than to Europe. During this time, megaraptorans can be found in Japan, Brazil, and Australia only (Benson et al., 2010; Aranciaga Rolando et al., 2018). The new report from Thailand, which potentially belongs to this clade, is important since it could answer the question of the origin of Megaraptora and also the position of Megaraptora within theropods. Tyrannosauroids can be found in China, Europe, and possibly Brazil and Australia (Brusatte and Carr, 2016; Delcourt and Grillo, 2018). Spinosaurids, carcharodontosaurians, and some coelurosaurs such as ornithomimosaurs were almost cosmopolitan (e.g., Brusatte et al., 2009; Hone and Holtz, 2017; Samathi, 2017; Candeiro et al., 2018; Hunt and Quinn, 2018). Spinosaurids can be found in Europe, Africa, Asia, South America, possibly Australia, but not North America. In Southeast Asia, two informative spinosaurids have been discovered, from Lao PDR and Thailand. These consist of a postcranial skeleton including vertebrae and pelvic elements. Furthermore, fragmentary materials, especially teeth, have been found throughout northeastern Thailand and, in one instance, from the Malay Peninsula. This suggests a high abundance of these theropods and their paleoenvironments, which were predominantly non-marine, fluvial depositional environments (Buffetaut and Suteethorn, 1999; Buffetaut et al., 2005b). Metriacanthosaurids, on the other hand, were endemic to China and Europe during the Middle to Late Jurassic but can be found in the Late Jurassic of Thailand.

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CHAPTER 3

Two New Basal Coelurosaurs from the Early Cretaceous of Thailand

CHAPTER 3

TWO NEW BASAL COELUROSAURIAN THEROPOD DINOSAURS FROM THE LOWER CRETACEOUS SAO KHUA FORMATION OF THAILAND

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Editors' choice

Two new basal coelurosaurian theropod dinosaurs from the Lower Cretaceous Sao Khua Formation of Thailand

ADUN SAMATHI, PHORNPHEN CHANTHASIT, and P. MARTIN SANDER

Samathi, A., Chanthasit, P., and Sander, P.M. 2019. Two new basal coelurosaurian theropod dinosaurs from the Lower Cretaceous Sao Khua Formation of Thailand. *Acta Palaeontologica Polonica* 64 (2): 239–260.

Megaraptora is a clade of mid to large-sized theropods that are long-snouted, large-clawed, highly pneumatized, and have long and gracile metatarsals. The basal member was reported from the Barremian of Japan. A more derived clade, the Megaraptoridae, is known from the Cenomanian to Santonian of Gondwana. Here two new basal coelurosaurs from the Lower Cretaceous Sao Khua Formation of Thailand are described and named as *Phuwiangvenator yaemniyomi* gen. et sp. nov. and *Vayuraptor nongbualamphuensis* gen. et sp. nov. *Phuwiangvenator* is a megaraptoran coelurosaur and diagnosed by the ventrally flat sacral vertebrae with sulci in the anterior and posterior region of the centra and the anterior rim of metatarsal IV sloping proximolaterally to distomedially and being much lower than that of metatarsal III anteriorly. *Vayuraptor* is a basal coelurosaur and diagnosed by its astragalus which has two horizontal grooves, two fossae at the base of the ascending process, the ascending process being straight laterally and straight and parallel medially with the medial rim sloping to the tip laterally, and a long and slender astragalar ascending process. Although the position of the basal coelurosaur *Vayuraptor* remains unclear and must await further discovery, megaraptoran affinities are likely. The Early Cretaceous megaraptoran fossil record has been recovered from the Barremian to Aptian of Asia. All Asian megaraptorans might be a monophyletic clade or a paraphyletic series relative to the Megaraptoridae. Several specimens have been reported from the Aptian to mid-Cretaceous of Australia, and one report from the Albian of South America. These fossils show a high diversity of the Early Cretaceous megaraptorans and a wide distribution during that time. The clade then became more provincial in the Late Cretaceous.

Key words: Dinosauria, Theropoda, Coelurosauria, Megaraptora, *Phuwiangvenator*, *Vayuraptor*, Cretaceous, Thailand.

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Introduction

Megaraptora (sensu Benson et al. 2010) is a clade of medium to large-sized highly pneumatized theropods with a long-snout, large-manual claws, and long and gracile metatarsals (Benson et al. 2010; Coria and Currie 2016). A basal member was reported from the Barremian of Japan, *Fukuiraptor* (Azuma and Currie 2000; Benson et al. 2010; Porfiri et al. 2014). A more derived clade, the Megaraptoridae (sensu Novas et al. 2013), is known from the Cenomanian to Santonian rocks of Gondwana (Porfiri et al. 2014; Novas et al. 2016). The clade consists of the South American taxa *Megaraptor* (Novas 1998), *Aerosteon* (Sereno et al. 2008), *Murusraptor* (Coria and Currie 2016), *Orkoraptor* (Novas et al. 2008), and *Tratayenia* (Porfiri et al. 2018) as well as *Australovenator* from Australia (Hocknull et al. 2009).

Several fragmentary specimens have been reported and referred to the Megaraptora including an astragalus (NMV P150070) from the Aptian of Australia (Agnolin et al. 2010; Benson et al. 2012b); the Lightning Ridge megaraptorid (LRF 100-106) from the Albian of Australia (Bell et al. 2015); an ulna (NMV P186076) from the Aptian–Albian of Victoria, Australia (Smith et al. 2008), and *Rapator* from Australia (Agnolin et al. 2010; White et al. 2013b). Some specimens have been reported from South America including caudal vertebrae from Brazil (CPPLIP 1324, Martinelli et al. 2013; and MPMA 08-003-94, Mendez et al. 2012), which were suggested to be sacral vertebrae by Motta et al. (2016) (see Sales et al. 2017); another caudal vertebra (UFRGS-PV-032-K, Sales et al. 2017); and sacral vertebrae from Brazil (SMNS 58023; Aranciaga Rolando et al. 2018). Furthermore, a left tibia with associated astragalocalcaneum (SM-NB A1-2) and postcranial material (SM-PW9B) have been recently reported from the Early Cretaceous of Thailand (Samathi and Chanthasit 2015, 2017) and are described here in detail.

Problematic taxa possibly belonging to Megaraptora are *Siats* from North America (Zanno and Makovicky 2013; see Novas et al. 2013 for an alternative interpretation), *Aoniraptor* from South America (Motta et al. 2016), and *Eotyrannus* from Europe (Hutt et al. 2001). This taxon was found to be a megaraptorid nested within Tyrannosauroidea by Porfiri et al. (2014). Other taxa interpreted as related with Megaraptora are *Gualicho* from South America (Apesteguía et al. 2016), *Chilantaisaurus* from China (Hu 1964; Benson and Xu 2008; see Delcourt and Grillo 2018), and *Neovenator* from England (Brusatte et al. 2008). *Chilantaisaurus* and *Siats* were recovered as megaraptorans more derived than *Fukuiraptor* by Bell et al. (2015), however, these two taxa do not exhibit megaraptoran features (Novas et al. 2013). *Siats* may fall among uncertain tetanurans. These results are contradictory due to the fragmentary nature of these theropods or different interpretation (see Porfiri et al. 2014).

Megaraptora phylogeny.—The phylogenetic status of Megaraptora is still debated and deserves further testing. Currently, there are three hypotheses of the phylogenetic position of Megaraptora: (i) deeply nested within Allosauroidea (Benson et al. 2010; Carrano et al. 2012); (ii) nested within Tyrannosauroidea (Novas et al. 2012a; 2013; Porfiri et al. 2014; Cau 2018); and (iii) Megaraptora are the most basal Coelurosauria (Novas et al. 2015; Apesteguía et al. 2016; Ezcurra and Novas 2016; Delcourt and Grillo 2018) (Fig. 1). The reason is the fact that they show "intermediate" or "mixed" characters in their anatomy which could be interpreted as "derived" characters for allosauroids or "basal" characters in Coelurosauria (Benson et al. 2010; Novas et al. 2013; Porfiri et al. 2014). This includes the "primitive" characters, e.g., short and broad scapula, distal tibia with vertical medial ridge, as well as the "derived" characters, e.g., elongate hindlimb, the tall ascending process of the astragalus, and pectoral and pelvic pneumaticity (Benson et al. 2010; Novas et al. 2013). The spinosaurids also show some features such as a short and broad scapula, distal tibia with vertical ridge, relatively tall and sheet-like ascending process of the astragalus, and large manual claws which arose convergently among megaraptorans. However, large manual unguals are also present in comsognathids.

New coelurosaurs, probable megaraptorans, from Thailand.—Currently, nine theropods have been reported from the Khorat Group of northeastern Thailand. Until now, five theropods have been found from the Sao Khua Formation (e.g., Buffetaut and Suteethorn 2012; see the geological setting part in this paper). There are at least two new coelurosaurian theropod specimens from the Sao Khua Formation that may belong to the Megaraptora. These are the focus of the current paper. We here describe *Phuwiangvenator yaemniyomi* gen. et sp. nov. based on a partial postcranial skeleton and a second, smaller coelurosaur, *Vayuraptor nongbualamphuensis* gen. et sp. nov., based on hindlimb elements (Samathi and Chanthasit 2017). The new Thai taxa might inform us about the phylogenetic position of Megaraptora among Avetheropoda and the origin and paleobiogeography of Megaraptora which might have originated in Asia or Southeast Asia.

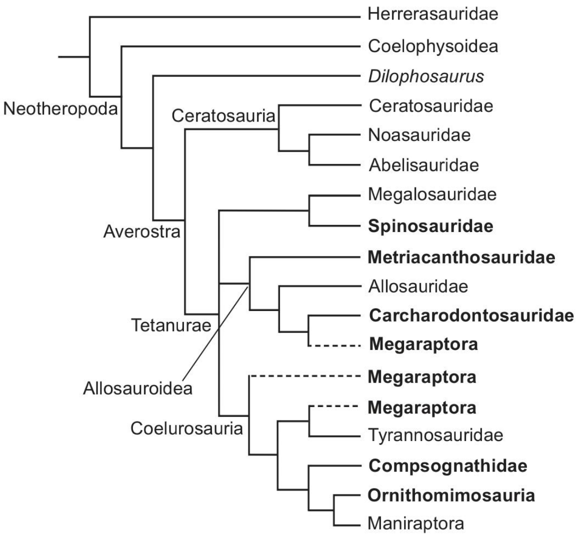

Fig. 1. Three hypotheses of the phylogenetic position of Megaraptora. Megaraptora as derived Carcharodontosauria (Benson et al. 2010; Carrano et al. 2012); basal Coelurosauria (Novas et al. 2015; Apestiguea et al. 2016; Delcourt and Grillo 2018); and basal Tyrannosauroidea (Novas et al. 2012a, 2013; Porfiri et al. 2014; Cau 2018). The tree is modified from Ezcurra and Novas (2016). Bolded are theropods found in Thailand.

Institutional abbreviations.—CPPLIP, Centro de Pesquisas Paleontológicas Llewellyn Ivor Price-Peirópolis, Uberaba County, Minas Gerais, Brazil; FPDM, Fukui Prefectural Dinosaur Museum, Katsuyama, Japan; FSAC, Faculté des Sciences Aïn Chock (University of Casablanca), Casablanca, Morocco; MB, Museum für Naturkunde, Berlin, Germany; MCNA, Museo de Ciencias Naturales y Antropológicas "Cornelio Moyano", Mendoza, Argentina; MNBH, Musée National Boubou Hama, Niamey, Republic of Niger; MPMA, Museu de Paleontologia de Monte Alto, Brazil; MSNM, Museo di Storia Naturale di Milano, Milan, Italy; NMV, Museum Victoria, Melbourne, Australia; PRC, Paleontological Research and Education Center, Maha Sarakham University, Maha Sarakham, Thailand; SM, Sirindhorn Museum, Department of Mineral Resources, Kalasin, Thailand; SMNS, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; UMNH, Natural History Museum of Utah, Salt Lake City, Utah, USA.

Nomenclatural acts.—This published work and the nomenclatural acts it contains, have been registered in ZooBank: urn:lsid:zoobank.org:pub:DE9BDAD4-A657-485F-ADE2-F2DD2CCA1A7B.

Material and methods

The holotype of *Phuwiangvenator yaemniyomi* gen. et sp. nov. described in this paper was discovered by Preecha Sainongkham, a staff member of Phu Wiang Fossil Research Center and Dinosaur Museum in 1993, with some referred material found later. The fossils are housed at the Sirindhorn Museum, Kalasin Province under the Department of Mineral Resources, Thailand. The holotype elements of *Phuwiangvenator yaemniyomi* gen. et sp. nov. seem to represent a single individual, based on size (see SOM: table 1, Supplementary Online Material available at http://app.pan.pl/SOM/app64-Samathi_etal_SOM.pdf), matching articulation, and shared phylogenetic affinity. The referred elements, found about 300 m away from the holotype, seem to belong to the same animal as the holotype, based on the size, matching articulation (e.g., the right astragalocalcaneum fits perfectly to the right tibia) and shared phylogenetic affinity (i.e., the right astragalocalcaneum and the left astragalocalcaneum).

The holotype of *Vayuraptor nongbualamphuensis* gen. et sp. nov. consists of a left tibia with associated astragalocalcaneum with referred material (see description below). They were discovered by Paladej Srisuk (PRC) in 1988. The holotype material is housed at the Sirindhorn Museum, Kalasin Province under the Department of Mineral Resources, Thailand and the referred material is housed at the collection of the PRC, Maha Sarakham University, Maha Sarakham Province, Thailand. All the available elements of *Vayuraptor nongbualamphuensis* gen. et sp. nov. seem to represent a single individual, based on size and shared phylogenetic affinity.

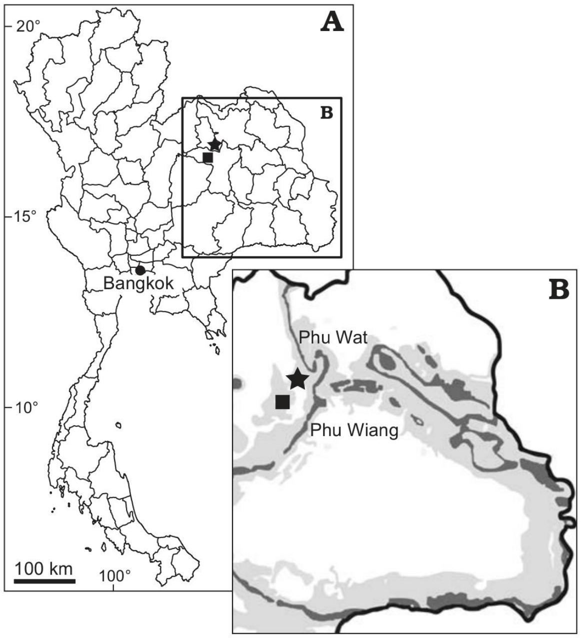

Fig. 2. Map of Thailand (**A**) and close-up of northeastern Thailand (**B**) showing the location of Phu Wiang locality, Khon Kaen Province (square) and Phu Wat locality, Nong Bua Lamphu Province (star). Dark gray, Sao Khua Formation outcrops, light gey, Phu Kradung and Khok Kruat formations.

For phylogenetic analyses, the data matrix was edited in the program Mesquite (Maddison and Maddison 2015), and the program TNT (Goloboff et al. 2008) was used and for finding the shortest tree under the parsimony and optimality criterium. We follow the analytical setting and data matrix of Apesteguía et al. (2016). This is a modified version of the Novas et al. (2013) matrix with additional characters and taxa by Apesteguía et al. (2016) and focused on Allosauroidea and basal Coelurosauria. *Ceratosaurus* serves as the outgroup. The 288 characters used were unordered and equally weighted with 46 theropod taxa in each analysis. We used the "New Technology" search option which included the default settings for sectorial, ratchet, tree drift, and tree fusion. Because the two Thai theropods are fragmentary, we then separated them into two different analyses for better resolution. In the first analysis, we added *Phuwiangvenator* and *Siamotyrannus* into this matrix and excluded *Santanaraptor* for a better resolution since this taxon is fragmentary. In the second analysis, we added *Vayuraptor* and *Siamotyrannus* into the matrix and excluded *Santanaraptor* and *Chilantaisaurus*.

Geological and geographical setting

The first dinosaur bone from Thailand was found in the 1980's at the Phu Wiang Mountain, Khon Kaen Province. It was a fragment of a sauropod femur from the Sao Khua Formation (Buffetaut 1982). Since then, a collaboration led by the Department of Mineral Resources, Thailand and the Centre National de la Recherche Scientifique, France has led to the discovery of many other dinosaur remains including ornithischians, sauropods, and theropods (e.g., Buffetaut and Suteethorn 1992; Martin et al. 1994; Suteethorn et al. 2009).

The Sao Khua Formation, from which the two new basal coelurosaurs from Thailand are described here, is one of the most fossil-rich formations of the Khorat Group of northeastern Thailand (Fig. 2). It consists of red clay, sandstone, and conglomerate, indicating deposition in a floodplain with meandering rivers. The fauna contains freshwater hybodont sharks, actinopterygian fishes, turtles, crocodilians, and dinosaurs (Buffetaut and Suteethorn 1998). The formation was originally considered Jurassic in age, but it was later shown to be in the Early Cretaceous. Buffetaut and Suteethorn (1999) were the first to suggest an Early Cretaceous age based on the vertebrate fossils. Most recently, the age was constrained to the late Barremian based on non-marine bivalves (Tumpeesawan et al. 2010). We follow this age assignment. Until now, five distinct theropods have been reported from the Sao Khua Formation. Theses consists of a possible compsognathid (Buffetaut and Ingavat 1984), teeth of the spinosaurid *Siamosaurus suteethorni* (Buffetaut and Ingavat

1986), the theropod *Siamotyrannus isanensis* (Buffetaut et al. 1996), the ornithomimosaur *Kinnareemimus khonkaenensis* (Buffetaut et al. 2009), and the partial skull of a carcharodontosaurid (Buffetaut and Suteethorn 2012).

Systematic palaeontology

Dinosauria Owen, 1842

Theropoda Marsh, 1881

Tetanurae Gauthier, 1986

Coelurosauria von Huene, 1920

Megaraptora Benson, Carrano, and Brusatte, 2010

Genus *Phuwiangvenator* nov.

Zoobank LCID: urn:lsid:zoobank.org:act:5FF98BC6-5B5E-45AF-8F90-AC12DBDE57E7

Type species: *Phuwiangvenator yaemniyomi* gen. et sp. nov., monotypic, see below.

Etymology: Phu Wiang Mountain, Khon Kaen Province, Thailand, the place where the holotype was found, combined with Latin *venator*, hunter; thus "Hunter of Phu Wiang".

Diagnosis.—Same as for the only known species.

Phuwiangvenator yaemniyomi sp. nov.

Figs. 3–14.

Zoobank LCID: urn:lsid:zoobank.org:act:AA829C5F-84C6-4287-BED7-50DDC551A815

Etymology: In honor of Sudham Yaemniyom, former geologist of the Department of Mineral Resources, Bangkok, who found the first dinosaur bone of Thailand in 1976 at Phu Wiang Mountain.

Holotype: SM-PW9B, a partial skeleton consisting of a dorsal vertebra, three fused sacral vertebrae, right metacarpal II, right manual phalanges and unguals, right and left tibiae, left astragalocalcaneum, left metatarsal I, right metatarsals II–IV, right pedal phalanges and unguals. The bones were found in an area of about 5 square meters.

Type locality: Phu Wiang Site 9B, Phu Wiang Mountain, Khon Kaen Province, Thailand (Fig. 2).

Type horizon: Sao Khua Formation, probably upper Barremian, Lower Cretaceous.

Referred material.—SM-PW9A, an atlantal intercentrum and right astragalocalcaneum which were found together and approximately 300 m away from the holotype (Phu Wiang Site 9A).

Diagnosis.—*Phuwiangvenator* is a megaraptoran diagnosed by the following autapomorphies: (i) short sulci on the sacral vertebrae ventrally along the anterior and posterior part of the centrum; (ii) the anterior rim of metatarsal IV slopes from proximolaterally to distomedially. This way, the distomedial corner of the proximal articular surface of metatarsal IV in anterior view is much lower than the articular surface of metatarsal III. In addition, the distomedial corner is lower than in any other known theropod.

Description.—*General morphology*: *Phuwiangvenator* was a mid to large-sized theropod with an estimated body length of 6 m. The skeletal proportion are shared by other theropods of corresponding sized such as *Australovenator*.

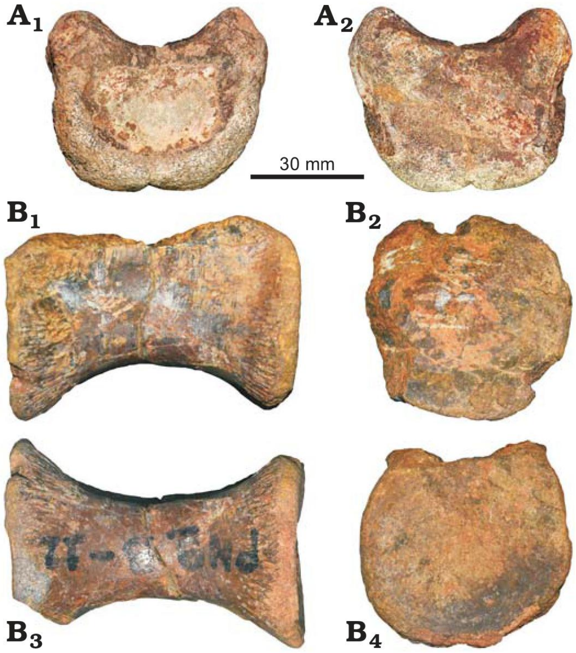

Fig. 3. Coelurosaurian theropod *Phuwiangvenator yaemniyomi* gen. et sp. nov. from the Early Cretaceous Sao Khua Formation of Phu Wiang, Khon Kaen Province, Thailand. **A**. SM-PW9A-1, atlantal intercentrum in anterior (A_1) and posterior (A_2) views. **B**. SM-PW9B-12, dorsal vertebra in left lateral (B_1), anterior (B_2), ventral (B_3), and posterior (B_4) views.

Atlantal intercentrum: The atlantal intercentrum is well preserved, only the posterior portion is slightly eroded. The atlantal intercentrum is concave anteriorly, and high dorsoventrally. The odontoid concavity in the dorsal surface is smooth. The distinct ventrolateral process on the atlantal intercentrum is not present (Fig. 3A).

Dorsal vertebra: The dorsal vertebra (SM-PW9B-12) was recovered (Fig. 3B). The neural arch is missing and possibly was not fused to the centrum. The centrum looks similar to that of *Fukuiraptor* (FPDM-V-8381; AS personal observations) and *Gualicho* (Apesteguía et al. 2016). The centrum has no pleurocoel and no ventral and lateral rugosities in the anterior and posterior end of the centrum, the same as in *Gualicho* (Apesteguía et al. 2016). The centrum is longer than high with a lateral depression on the lateral sides. The anterior face of the centrum is concave, whereas the posterior is flat (platycoelous). The centrum shape is circular anteriorly and posteriorly. The vertebra of *Phuwiangvenator* are highly constricted, hour-glass shaped in ventral view and very concave in the ventral part in lateral view which is same as in dorsal vertebrae of *Fukuiraptor*, *Aerosteon*, *Allosaurus*, *Tyrannosaurus*, *Ornitholestes*, *Coelurus*, and *Zuolong* (Madsen 1976; Brochu 2003; Carpenter et al. 2005b; Choiniere et al. 2010). This differs from caudal vertebrae which normally are less concave in the ventral part in lateral view and less constricted in ventral view compared with dorsal vertebrae. The lack of a parapophysis on the centrum suggest that it belongs to the middle to posterior portion of the dorsal series. The highly constricted posterior dorsal vertebral centrum is present in *Phuwiangvenator* as well as in allosauroids, megaraptorids, and derived tyrannosauroids (Novas et al. 2013). The dorsal vertebra of *Phuwiangvenator* also differs from the sacral vertebrae in the constriction of the centrum in ventral and lateral views. There is no keel or groove on the centrum ventrally. There is no facet for the chevron, so it is clearly not a caudal vertebra. As seen on broken surfaces, the dorsal vertebra appears to have a camellate internal structure.

Sacral vertebrae: Three incomplete fused sacral vertebrae are preserved (SM-PW9B-39). The anterior face of the centrum is flat. The centra are possibly sacral 1, 2, and 3 based on the probable sacral ribs which are situated on the anterodorsal side of the centrum. The neural arches of sacral 1 and 2 are badly preserved and still covered by the matrix. The quality of preservation of the centra is generally good, especially on the right side. The left side is compressed. The centra are flat ventrally, there is no keel and no constriction on the sacrals ventrally. There are small, short sulci on the anterior and posterior part of the sacral 2 and one sulcus on the anterior part of the sacral 3 (the posterior part has no sulci) ventrally (Fig. 4). There are no pleurocoels or any foramina. The centra are longer than high. The sacral rib articulation is located low for sacral 3 anteriorly, at middle for sacral 1, and anteriorly in scaral 2.

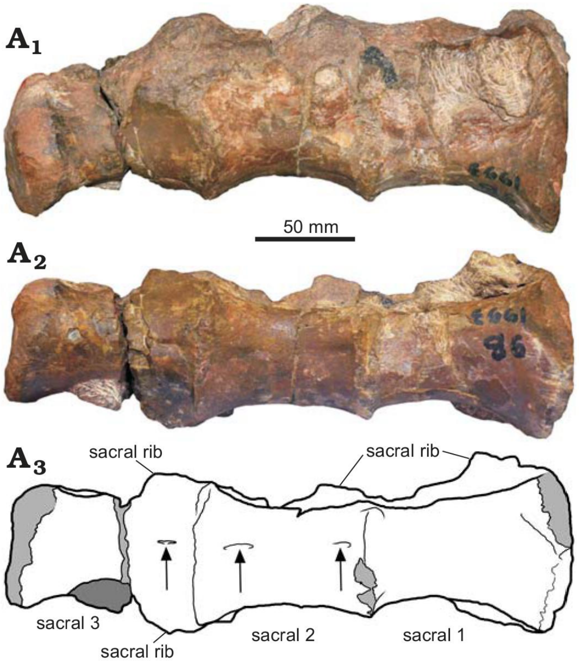

Fig. 4. Coelurosaurian theropod *Phuwiangvenator yaemniyomi* gen. et sp. nov. from the Early Cretaceous Sao Khua Formation of Phu Wiang, Khon Kaen Province, Thailand. SM-PW9B-39, anterior sacral vertebrae in right lateral (A_1) and ventral (A_2) views; line drawing in ventral view (A_3). Arrows indicate ventral sulci, light grey, broken part; dark grey, matrix.

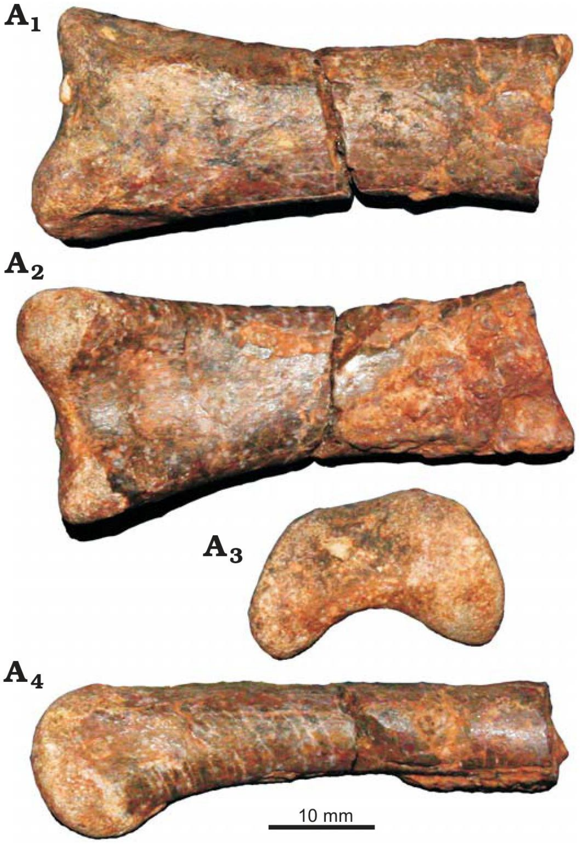

Fig. 5. Coelurosaurian theropod *Phuwiangvenator yaemniyomi* gen. et sp. nov. from the Early Cretaceous Sao Khua Formation of Phu Wiang, Khon Kaen Province, Thailand. SM-PW9B-6, right metacarpal II in dorsal (A_1), ventral (A_2), distal (A_3), and medial (A_4) views.

Manual phalanges and unguals: The manual phalanges and unguals consist of manual phalanx I-1 (SM-PW9B-3); manual ungual I-2 (SM-PW9B-19); metacarpal II (SM-PW9B-6, Fig. 5); manual ungual II-3 (SM-PW9B-23); manual phalanx III-1 (SM-PW9B-4); manual phalanx III-2 (SM-PW9B-7); manual phalanx III-3 (SM-PW9B-5); and manual ungual III-4 (SM-PW9B-21) (Fig. 6, 7).

In general, manual phalanges are referred to the Theropoda based on the presence of deep, well-defined collateral ligament pits and the presence of an extensor fossa on the dorsal surface proximal to the distal articulation (Rauhut 2003).

Only the distal part of the right metacarpal II (SM-PW9B-6) is preserved. It is long and gracile. The metacarpal is dorsoventrally flattened and resembles the metacarpal II of the basal tyrannosauroid *Kileskus* from Siberia (Averianov et al. 2010) and identified here to be a distal part of the right metacarpal II. The distal end of metacarpal II is asymmetrical; it is slightly expanded and divided

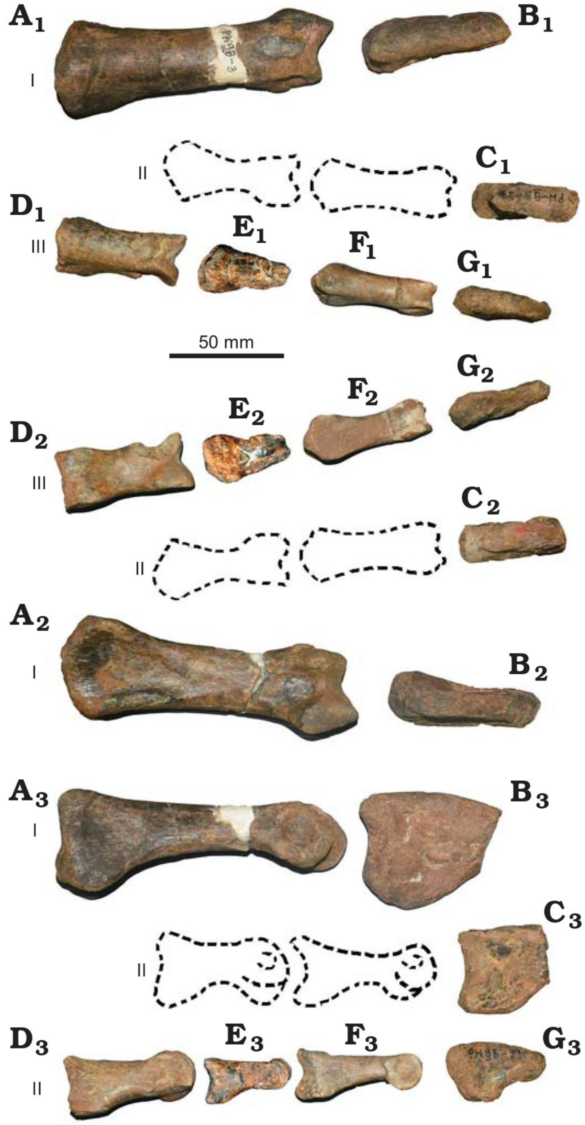

Fig. 6. Coelurosaurian theropod *Phuwiangvenator yaemniyomi* gen. et sp. nov. from the Early Cretaceous Sao Khua Formation of Phu Wiang, Khon Kaen Province, Thailand. SM-PW9B-3 (**A**), SM-PW9B-19 (**B**), SM-PW9B-23 (**C**), SM-PW9B-4 (**D**), SM-PW9B-7 (**E**), SM-PW9B-5 (**F**), SM-PW9B-21 (**G**); manual phalanges I–III (A, D, E, F) and unguals I–III (B, C, G), in dorsal (A_1–G_1), ventral (A_2–G_2), and lateral (A_3–G_3) views. Dashed lines are the reconstruction of manual phalanges II-1 and II-2.

into two distinct condyles. The distal surface of the medial condyle is larger than the lateral condyle, as in *Kileskus* and *Australovenator* (White et al. 2012). The medial condyle protrudes slightly more distally than the lateral condyle. The pits for the collateral ligaments are not well developed on both condyles. There is no distinct extensor pit on the anterior surface of the shaft proximal to the distal condyle, only a small concavity is present.

The manual phalanx I-1 (SM-PW9B-3) has deep, well-defined collateral ligament pits which are larger on the medial side than the lateral one. There is an extensor fossa on the dorsal surface proximal to the distal articulation. The shaft is proximodistally elongate, shows a high ratio of proximodistal length to transverse width and has a ginglymoid articulation which is asymmetrical and elongated mediodistally. The lateral condyle is about the same height dorsoventrally but shorter proximo-distally than the medial condyle, as in *Australovenator*, in which the lateral condyle is also shorter proximo-distally than the medial condyle (White et al. 2012). The lateral condyle is expanded proximally. The proximal end is asymmetrical, with the medial articular surface larger than the lateral surface. The proximal articular surface is transversely wider on its ventral margin than on its dorsal margin. A ridge on the proximal articular surface slopes slightly laterally rather than being in the middle of the articular surface. This feature is also present in *Gualicho* (Apesteguia et al 2016). The manual phalange I-1 of *Phuwiangvenator* has a longitudinal ventral furrow and longitudinal ridges, and it is convex ventrally in proximal view (Fig. 7A).

The manual phalanx III-1 (SM-PW9B-4) has well-defined collateral ligament pits. There is a shallow, poorly defined extensor fossa on the dorsal surface proximal to the distal articulation. There is no shallow furrow on the ventral surface of the phalanx. The shaft is proximodistally short and relatively robust. The ratio of proximodistal length to transverse width is approximately 2.8. The bone also has a ginglymoid articulation and is asymmetrical and elongated mediodistally. Two prominent ligament scars on the ventral surface proximal to the proximal articulation and one facet for articulation on the proximal end are present as in *Allosaurus.*

The manual phalanx III-2 (SM-PW9B-7) is not well preserved especially on the distal articulation. However, this bone shows deep, well-defined collateral ligament pits on the condyles and no extensor fossa on the dorsal surface proximal to the distal articulation. It is relatively shorter than the manual phalanx III-2 of other theropods.

The manual phalanx III-3 (SM-PW9B-5) has deep, well-defined collateral ligament pits on both condyles. There is no extensor fossa on the dorsal surface proximal to the distal articulation. There is no shallow furrow on the ventral surface of the phalanx. The bone is proximodistally elongate and slender, the ratio of proximodistal length to transverse width is 4. The bone has a ginglymoid articulation which is symmetrical. Two ligamental scars on the ventral surface proximal to the proximal articulation are present but not prominent or well defined. The shaft is slender, and its proximal part is extended ventrally. Two facets for articulation on the proximal end are present. Digit III is much more slender compared with *Australovenator* (White et al. 2012) and *Allosaurus* (Madsen 1976). Phalanx III-3 is as long and slender as phalanx III-3 of *Australovenator* (White et al. 2012).

The manual unguals consist of three unguals in this study. The manual ungual I-2 (SM-PW9B-19) is large, missing the distal portion and the surface of the lower half of the

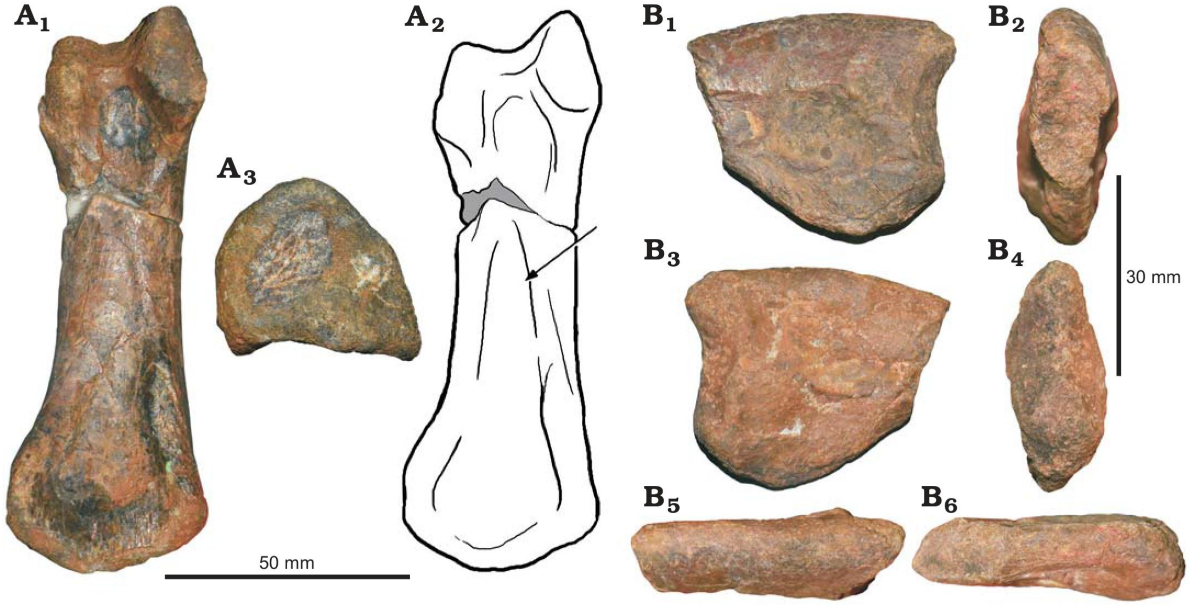

Fig. 7. Coelurosaurian theropod *Phuwiangvenator yaemniyomi* gen. et sp. nov. from the Early Cretaceous Sao Khua Formation of Phu Wiang, Khon Kaen Province, Thailand. **A**. SM-PW9B-3, manual phalanx I-1 in ventral (A_1) and proximal (A_3) views; line drawing in ventral view (A_2). **B**. SM-PW9B-19, manual ungual I-2 in medial (B_1), distal (B_2), lateral (B_3), proximal (B_4), dorsal (B_5), and ventral (B_6) views. Arrow indicates the longitudinal ventral furrow.

left side. There is a small depression on the right side. In proximal view, the articular surface is almost symmetrical. The medial condyle has almost the same height dorsoventrally as the lateral condyle, but it is slightly broader than the lateral condyle. Based on the distal articular surface of phalange I-1, we suggest that this ungual is an ungual I-2 and belongs to the first digit. The proximal end is slightly broader mediolaterally than the distal-most preserved portion. The prominent, sub-oval, mound-like flexor tubercle is present proximally on the ventral surface (Fig. 7). The vascular grooves are present on the lateral and medial surfaces, and are symmetrical. The proximal height/width ratio is 2.4. The manual ungual II-3 (SM-PW9B-23) is medium to large sized and missing the distal portion. The vascular groove is preserved on the medial side. It is symmetrical, the proximal end and the distal-most preserved portion are slightly equal in width mediolaterally. The sub-oval, mound-like flexor tubercle is present proximally on the ventral surface. The proximal height/width ratio is 2.67. The manual ungual III-4 (SM-PW9B-21) is small to medium sized and missing the distal portion. The vascular groove cannot be observed due to the preservation. The articular surface is symmetrical. The proximal end is slightly broader mediolaterally than the distal-most preserved portion. A prominent, sub-oval, mound-like flexor tubercle is present proximally on the ventral surface. The proximal height/width ratio is 2.27.

Tibiae: The right tibia is complete but fractured in the distal portion. The left tibia is not complete, lacking the tibial shaft, only the proximal and distal ends are preserved. The proximal part of the right tibia is better preserved than that of the left one. The tibial shaft is long and almost straight. The cnemial crest is expanded. The anterolateral process of the lateral condyle of *Phuwiangvenator* curves ventrally as a point process as in *Neovenator* (Brusatte et al. 2008), *Australovenator* (Hocknull et al. 2009), *Allosaurus* (UMNH VP 7148, 7922, 7932, 7938, 7939, 7940; AS personal observations), *Lythronax* (UMNH VP 20200; AS personal observations), *Teratophoneus* (UMNH VP 16690; AS personal observations), and *Tyrannosaurus* (Brochu 2003), but not in *Fukuiraptor* and *Vayuraptor*. The presence of this process may be more widespread than previously thought as suggested by Novas et al. (2013). The tibia shows derived states, the elongated and expanded medial malleolus and a distally expanded lateral malleolus (Brusatte and Sereno 2008; Figs. 8, 9).

The morphology of the distal cnemial process of the tibia is rounded. The lateral condyle is small relative to the tibial shaft. It offset from the lateral side of the proximal end of the tibia by a notch (posterior cleft) posteriorly. The fibular crest (the fibular flange) of the tibia is present on the proximal half as a pronounced longitudinal ridge. The fibular crest is clearly offset from the proximal articular facet of the tibia. It does not connect with the proximal end of the tibia (the ridge continuing from the fibular flange to the proximal articular surface of the tibia is absent). The fibular crest morphology is teardrop-shaped in lateral view. The primary nutrient foramen is present and situated posterior to the distal portion of the fibular crest. In the proximal end, the posterior rim of the lateral condyle is short and does not reach the same level as the medial condyle. The lateral malleolus of the distal

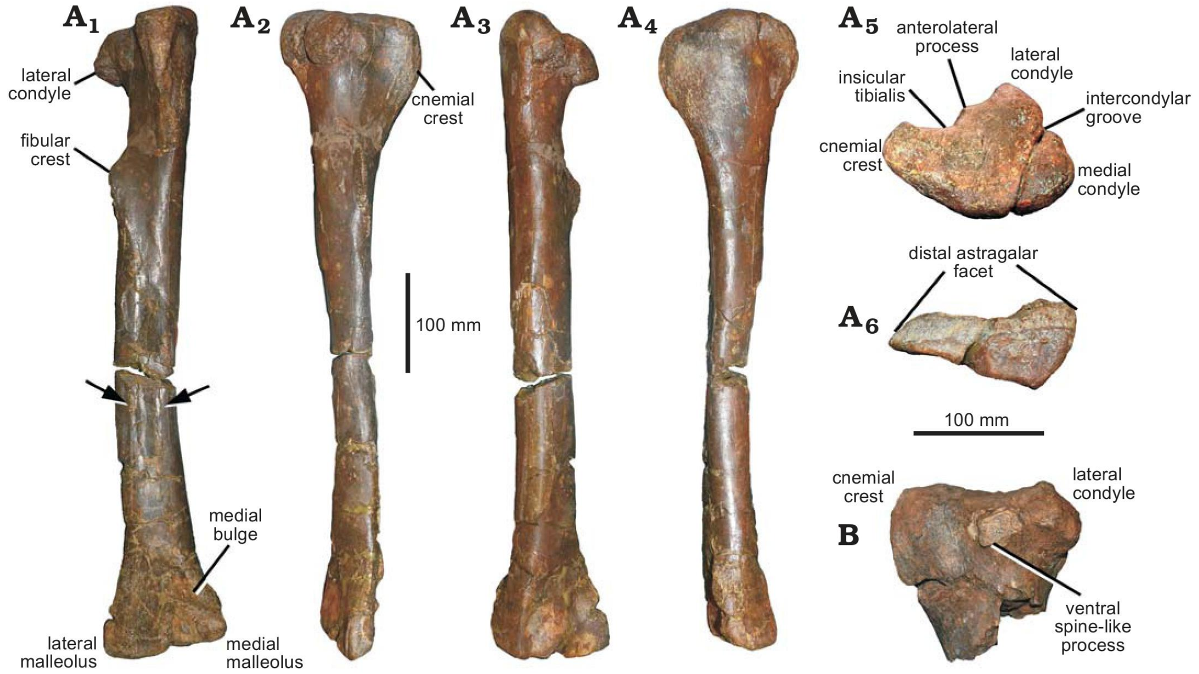

Fig. 8. Coelurosaurian theropod *Phuwiangvenator yaemniyomi* gen. et sp. nov. from the Early Cretaceous Sao Khua Formation of Phu Wiang, Khon Kaen Province, Thailand. **A**. SM-PW9B-41, right tibia in anterior (A_1), lateral (A_2), posterior (A_3), medial (A_4), proximal (A_5), and distal (A_6) views. **B**. SM-PW9B-40, proximal left tibia in lateral view. Arrow indicates vertical ridge on the tibia.

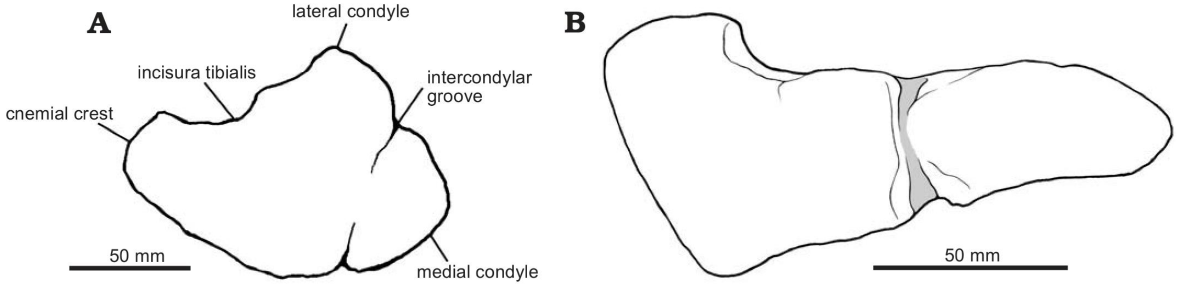

Fig. 9. Coelurosaurian theropod *Phuwiangvenator yaemniyomi* gen. et sp. nov. from the Early Cretaceous Sao Khua Formation of Phu Wiang, Khon Kaen Province, Thailand. **A**. SM-PW9B-41, right tibia in proximal view. **B**. SM-PW9B-40, left tibia in distal view. Light grey indicates broken bone.

tibia is overlapped by the calcaneum. The distal end of the tibia is triangular in outline, flattened anteroposteriorly, and strongly expanded laterally and medially. The lateral malleolus of the distal expansion extends laterally and extends further distally than the medial malleolus. The anteromedial buttress for the astragalus is a bluntly rounded vertical ridge on the medial side. The tibia length of *Phuwiangvenator* is more than 12 times its anteroposterior width at mid-length. This is a synapomorphy of megaraptorans and coelurosaurs (Porfiri et al. 2014) but also present in *Spinosaurus* (AS personal observations; see Discussion; SOM: table 17).

Astragalocalcaneum.—The left astragalocalcaneum (SM-PW9B-18) is nearly complete, lacking only the body of the ascending process of the astragalus (Fig. 10B). The astragalus is 103 mm wide, the calcaneum is 25 mm wide. The astragalar width/calcaneum width ratio is 4.12. The morphology of the ascending process of the astragalus is laminar. It is approximately 90 mm long estimated from the scar for the reception of the ascending process of the astragalus on the distal end of the tibia, approximately 15% of the total length of the tibia. However, this scar does not necessarily correspond to the shape and height of the ascending process of the astragalus (Rauhut and Xu 2005; Rauhut 2012). It is offset from the anterior border of the astragalar body by a shallow groove. The ascending process height relative to the depth of the astragalar body is approximately 1.7 times. The ascending process is slightly transversely narrow compare to more derived coelurosaurs, but it is wider than in *Allosaurus* (UMNH VP 11003; AS personal observations).

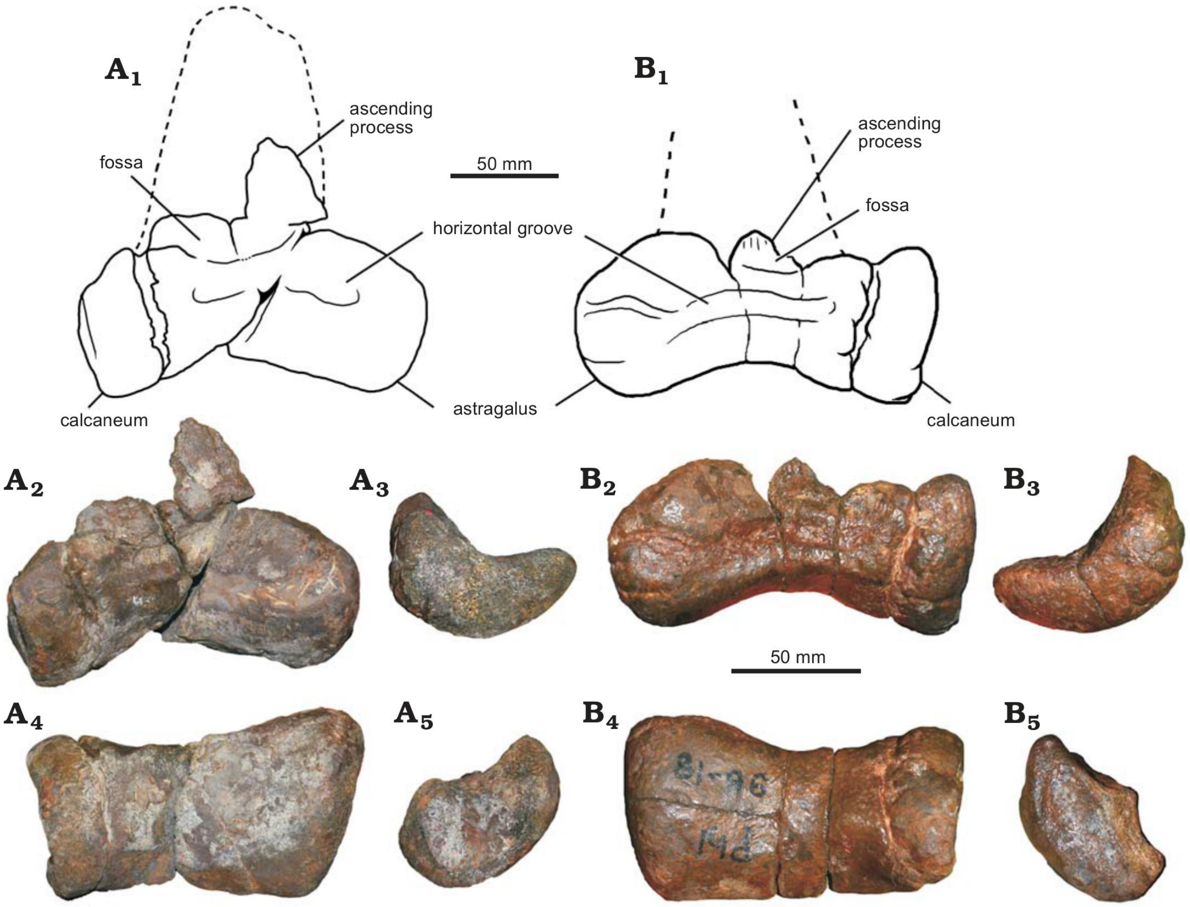

Fig. 10. *Phuwiangvenator yaemniyomi* gen. et sp. nov. from the Early Cretaceous Sao Khua Formation of Phu Wiang, Khon Kaen Province, Thailand. SM-PW9A-B17, right (**A**) and SM-PW9B-18, left (**B**); astragalocalcaneum in anterior (A$_2$, B$_2$), medial (A$_3$, B$_3$), distal (A$_4$, B$_4$), and lateral (A$_5$, B$_5$) views; line drawings in anterior view (A$_1$, B$_1$). Dashed lines are the reconstruction of the ascending processes of the astragali.

The ascending process of the astragalus arises from more than half of the breath of the astragalar body. A round fossa at the base of the ascending process of the astragalus is present.

The cranioproximal process is present, but small compared to other theropods. A distinct anterior development of the lateral condyle (in ventral view) of the astragalar body is present. A proximolateral extension of the astragalus is also present as in *Fukuiraptor* (AS personal observations), but with some damaged on its tips.

The trapezoidal outline of the bone in distal view looks similar to *Australovenator* and the megaraptoran astragalus NMV P150070 (Benson et al. 2012b). In distal view, the astragalar body is concave anteriorly and straight posteriorly. Its surface is flat on the lateral half and convex on the medial half.

The astragalus condyle is significantly expanded proximally on the anterior side of the tibia and faces anterodistally. The orientation of the distal condyles of the astragalus is 30–45° anteriorly. A horizontal groove across the astragalar condyle is present anteriorly. The development of the articular surface for the distal end of the fibula in the astragalus is reduced and situated laterally. A posterolateral crest and a posteromedial crest on the astragalus are not present. The articulation between the ascending process and the fibula is not preserved. Both astragalus and calcaneum are unfused. The calcaneum bears a well-developed facet for the tibia. The calcaneum transverse development is moderate, being approximately 24% (left) and 23% (right) of the width of the astragalus.

The right astragalocalcaneum (SM-PW9A-B17) is referred to the same taxon and the same individual as the holotype of *Phuwiangvenator* since it perfectly matches with the right tibia of the holotype and shows the same size and characters as the left astragalocalcaneum (Fig. 10A; SOM: tables 6–9).

Metatarsals: The metatarsals of *Phuwiangvenator* comprises a left metatarsal I (SM-PW9B-1) and right metatarsals II–IV (SM-PW9B-42, 43, and 44, respectively).

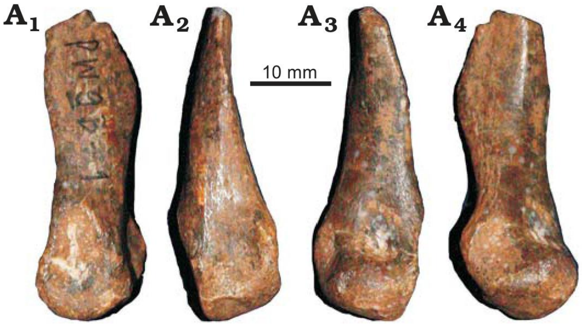

Fig. 11. Coelurosaurian theropod *Phuwiangvenator yaemniyomi* gen. et sp. nov. from the Early Cretaceous Sao Khua Formation of Phu Wiang, Khon Kaen Province, Thailand. SM-PW9B-1, left metatarsal I in lateral (A$_1$), posterior (A$_2$), anterior (A$_3$), and medial (A$_4$) views.

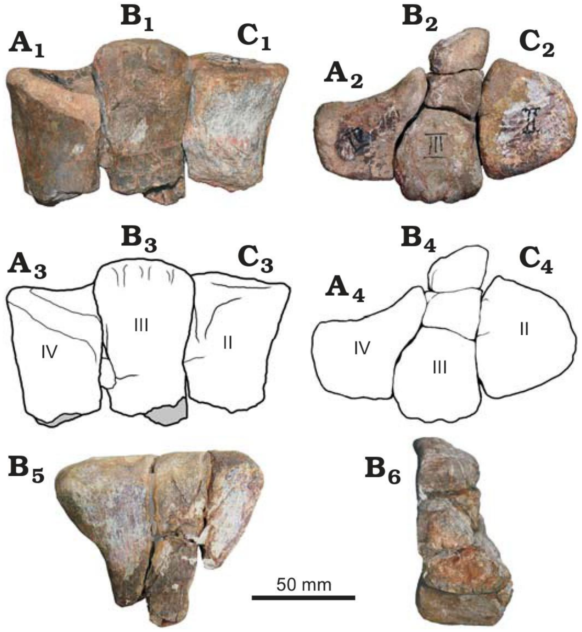

Fig. 12. Coelurosaurian theropod *Phuwiangvenator yaemniyomi* gen. et sp. nov. from the Early Cretaceous Sao Khua Formation of Phu Wiang, Khon Kaen Province, Thailand. SM-PW9B-44 (**A**), SM-PW9B-43 (**B**), SM-PW9B-42 (**C**); metatarsals in anterior (A$_1$–C$_1$) and proximal (A$_2$–C$_2$) views; line drawings in anterior (A$_3$–C$_3$) and proximal (A$_4$–C$_4$) views; metatarsal III in medial (B$_5$) and distal (B$_6$) views.

The left metatarsal I (SM-PW9B-1) has well-defined collateral ligament pits which are deeper on the right side than on the left one. An extensor fossa on the dorsal surface proximal to the distal articulation is present. There is one shallow fossa on the ventral surface proximal to the distal articulation. It is proximodistally elongate. The ratio of proximodistal length to transverse width is approximately 5.2. The bone is asymmetrical and lacks a ginglymoid articulation (Fig. 11).

The metatarsal II is subequal in width to the Mt III and Mt IV proximally (see Rauhut 2003). The shape of the proximal end of the metatarsal III has a deep notch or "hourglass" shaped or "notched" outline which is most pronounced in avetheropods (Carrano et al. 2012). At the broken part, distally below the proximal end, the posterior part of the shaft of the metatarsal III is strongly pinched between the shafts of metatarsals II and IV. In proximal view, metatarsal III is anteroposteriorly oriented, not anterolateral to posteromedial. The anteroposterior orientation of the metatarsal III can be found in *Australovenator*, *Chilantaisaurus*, and *Neovenator*, but not in *Tanycolagreus* and *Ornitholestes*. The anterior rim of metatarsal IV slopes from proximolaterally to distomedially. This way, the distomedial corner of the proximal articular surface of metatarsal IV in anterior view is much lower than the articular surface of metatarsal III (Fig. 12).

Pedal phalanges and unguals: The pedal phalanges consist of phalanges II-1, II-2, III-2, III-3, IV-1, and IV4 (SM-PW9B-5–9 and SM-PW9B-45, respectively; Fig. 13). The pedal phalanges are as in normal theropods in shape.

The pedal unguals in this study consist of unguals I-2, II-3, III-4, and IV-5 (SM-PW9B-11, 22, 19, and 10, respectively). Specimens SM-PW9B-22 and SM-PW9B-19 are medium to large sized and missing the distal portion. They have a rounded cross-section that is symmetrical. SM-PW9B-10 is complete. It has flat ventral surface as in *Australovenator* (Fig. 14). Two vascular grooves are present on both sides. The flexor tubercle is poorly developed. It is higher dorsoventrally than broader mediolaterally and weakly curved. In general, the pedal unguals have the same shape as in other theropods. They do not show extreme dorsoventral flattening in lateral view as in *Spinosaurus* and some ornithomimosaurs.

Stratigraphic and geographic range.—Type locality and horizon only.

Genus *Vayuraptor* nov.

Zoobank LCID: urn:lsid:zoobank.org:act:7CCF3718-D9BE-4FE3-A191-8754C7892CF1

Type species: *Vayuraptor nongbualamphuensis* gen. et sp. nov., monotypic, see below.

Etymology: From Sanskrit *Vayu*, God of Wind and Latin *raptor*, thief; "Raptor of Wind or Wind raptor" in reference to its long and slender tibia, which suggest a fast running animal.

Diagnosis.—Same as for only known species.

Vayuraptor nongbualamphuensis sp. nov.

Figs. 15–17.

Zoobank LCID: urn:lsid:zoobank.org:act:10988651-4C41-4062-A70F-13BC6DE0D722

Etymology: From Nong Bua Lamphu Province where the specimen was recovered.

Holotype: SM-NB A1-2, left tibia with associated astragalocalcaneum (collected in August 1988 by Paladej Srisuk).

Type locality: Phu Wat Site A1 Locality, Nong Sang, Nong Bua Lamphu Province, Thailand, Fig. 2.

Type horizon: Sao Khua Formation, probably upper Barremian?, Lower Cretaceous.

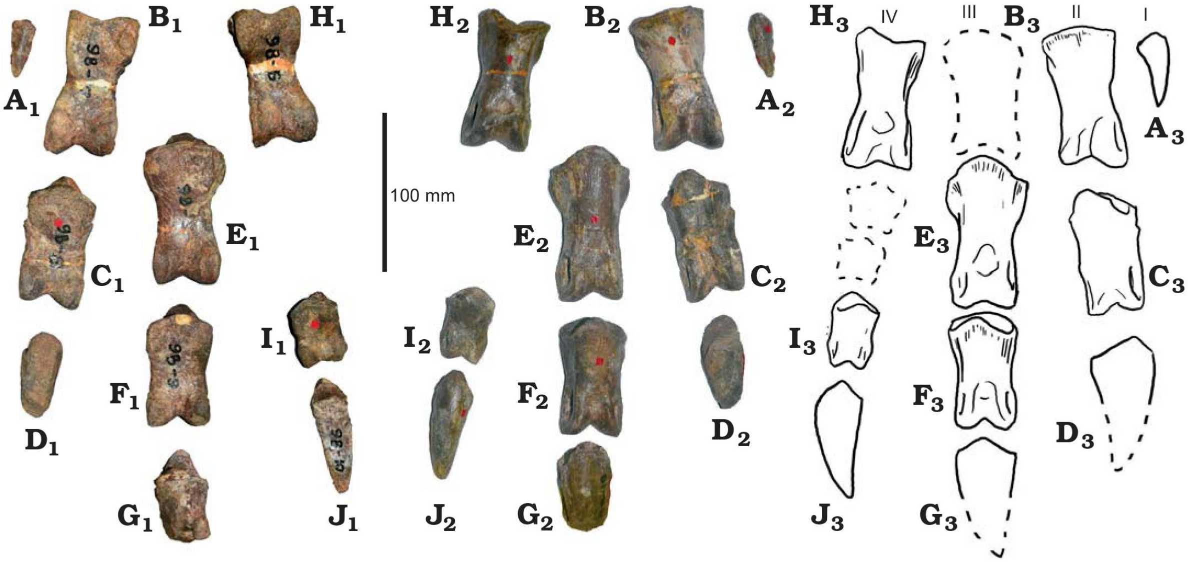

Fig. 13. Coelurosaurian theropod *Phuwiangvenator yaemniyomi* gen. et sp. nov. from the Early Cretaceous Sao Khua Formation of Phu Wiang, Khon Kaen Province, Thailand. SM-PW9B-11 (**A**), SM-PW9B-7 (**B**), SM-PW9B-8 (**C**), SM-PW9B-22 (**D**), SM-PW9B-5 (**E**), SM-PW9B-9 (**F**), SM-PW9B-19 (**G**), SM-PW9B-6 (**H**), SM-PW9B-45 (**I**), SM-PW9B-10 (**J**); right pedal phalanges (B, C, E, F, H, I) and unguals (A, D, G, J), in ventral (A_1–J_1) and dorsal (A_2–J_2) views; line drawings in dorsal view (A_3–J_3). Dashed lines are the reconstruction of pedal phalanges III-1, IV-2, and IV-3 and pedal unguals II-3 and III-4.

Referred material.—PRC-NB A1-11, right coracoids; PRC-NB A1-4, fibula fragment; PRC-NB A1-10 rib; PRC-NB A1-3, probable pubis fragment; PRC-NB A2-20, manual phalanx, and PRC-NB A2-16, probable pedal phalanx; all from the type locality and horizon.

Diagnosis.—*Vayuraptor* is a basal coelurosaur and is diagnosed by the following autapomorphies: (i) astragalus has two short horizontal grooves and two foramina on the astragalar body, and two fossae at the base of the ascending process; (ii) the ascending process of the astragalus is straight laterally and straight and parallel medially at the base. In the middle of the ascending process, the medial rim slopes to the tip laterally; (iii) there is a vertical ridge starting from the tip and disappearing just above the middle of the ascending process; and (iv) extremely high and narrow ascending process of the astragalus, with a ratio of the ascending process height/ascending process width of 1.66.

Fig. 14. Coelurosaurian theropod *Phuwiangvenator yaemniyomi* gen. et sp. nov. from the Early Cretaceous Sao Khua Formation of Phu Wiang, Khon Kaen Province, Thailand. SM-PW9B-10, right pedal ungual IV-5 in lateral (A_1) and ventral (A_2) views.

Description.—*General morphology*: *Vayuraptor* was a mid to large-sized theropod with an estimated body length of 4–4.5 m. The skeletal proportions are shared by other theropods of corresponding sized such as *Fukuiraptor*.

Rib fragment: A rib fragment (PRC-NB A1-10) that is lacking the proximal and distal portion. There is no pneumaticity on the rib fragment.

Coracoid: The posteroventral process of the coracoid (PRC-NB A1-11) is tapering posteroventrally (the posteroventral process is broken). The ventral margin of the coracoid is expanded beyond the rim of the glenoid facet (inferred from the broken part). The coracoid is higher than long and semicircular in shape. The infraglenoid groove is absent (Fig. 15).

Phalanges: Only the distal part of manual phalanx (PRC-NB A2-20) is preserved. It lacks well-defined extensor pits on the dorsal surface proximal to the distal articulation. This was pointed out to be a coelurosaurian character by Rauhut (2003) (see Novas et al. 2016). A probable pedal phalanx (PRC-NB A2-16) is very incomplete so there is not much information to be obtained from this material.

Pubis fragment: A proximal mid-portion of a left pubis

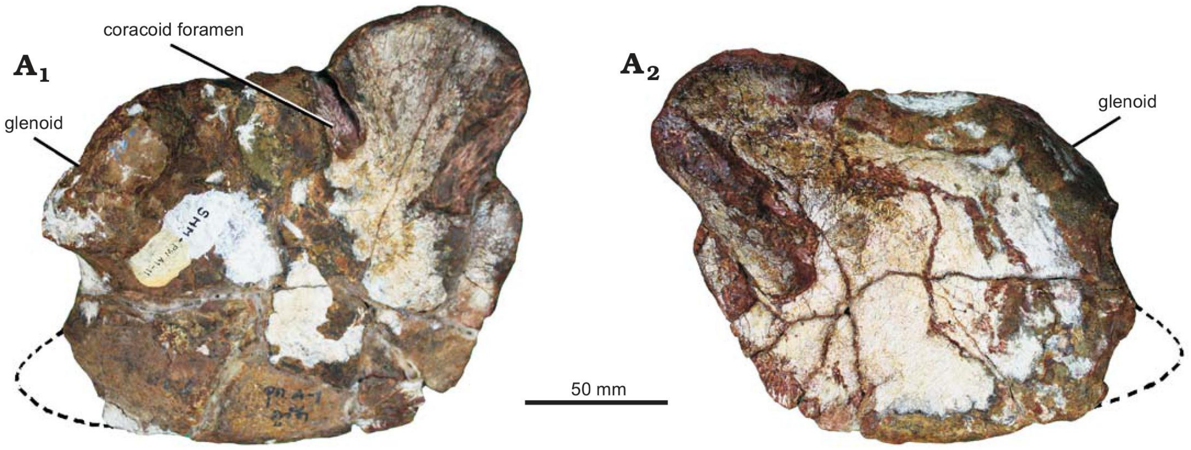

Fig. 15. Coelurosaurian theropod *Vayuraptor nongbualamphuensis* gen. et sp. nov. from the Early Cretaceous Sao Khua Formation of Phu Wat, Nong Bua Lamphu Province, Thailand. PRC-NB A1-11, right coracoid in lateral (A_1) and medial (A_2) views. Dashed lines are the reconstruction of the posteroventral process of the coracoid.

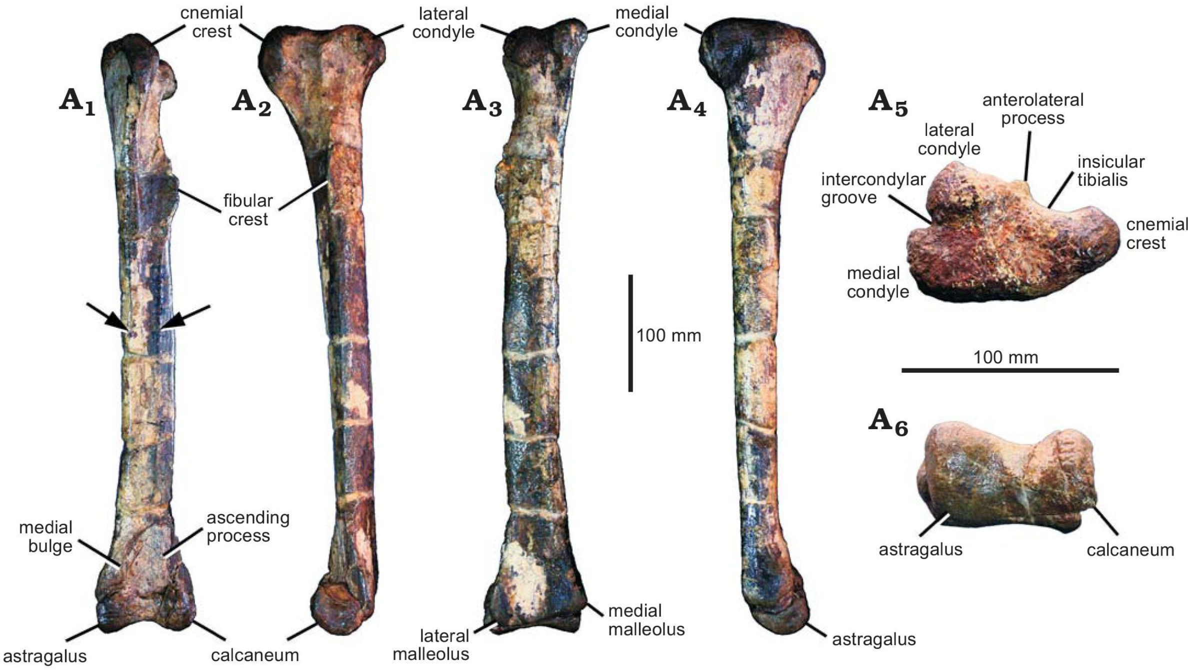

Fig. 16. Coelurosaurian theropod *Vayuraptor nongbualamphuensis* gen. et sp. nov. from the Early Cretaceous Sao Khua Formation of Phu Wat, Nong Bua Lamphu Province, Thailand. SM-NB A1-2, left tibia with associated astragalocalcaneum in anterior (A_1), lateral (A_2), posterior (A_3), medial (A_4), proximal (A_5), and distal (A_6) view. Arrow indicates vertical ridge on the tibia.

(PRC-NB A1-3) preserves a portion of the medial laminar of the pubic shaft. It looks similar to other theropods such as the middle portion of the pubis of *Neovenator* (see Brusatte et al. 2008).

Tibia and fibula: The left tibia (SM-NB A1-2; Fig. 16) is complete. It is long and slender. The cnemial crest is expanded. The morphology of the distal cnemial process is rounded. The anterolateral process of lateral condyle forms a horizontal projection. The tibial shaft is almost straight but the distal portion is slightly curved medially (slightly convex laterally in anterior view). The mid-shaft cross-section is sub-circular with a flattened anterior side (D-shaped cross-section at mid-shaft) as in *Australovenator* (Hocknull et al. 2009) and *Aerosteon* (cast of MCNA-PV-3139; AS personal observations) as well as other coelurosaurs. The cnemial crest is not projected proximally. The lateral condyle

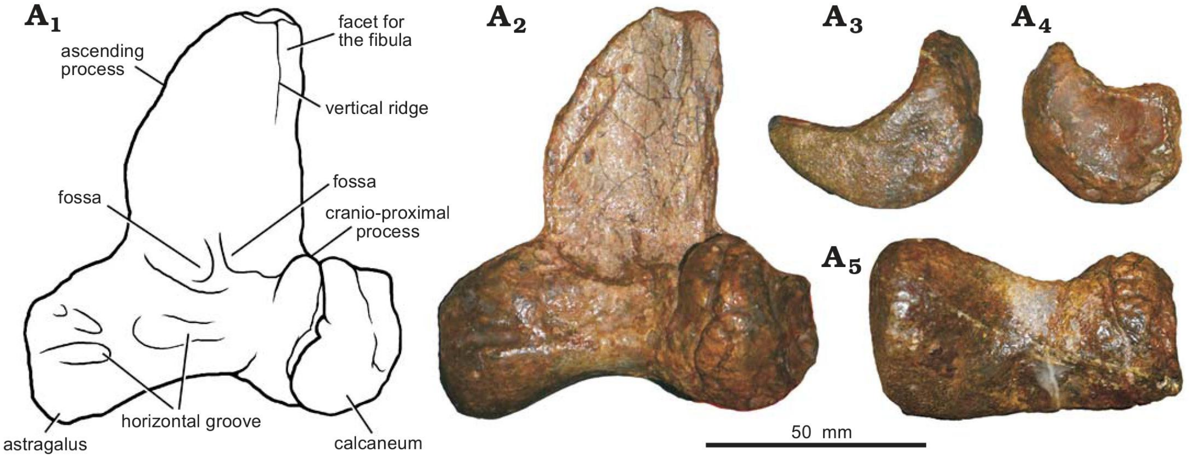

Fig. 17. Coelurosaurian theropod *Vayuraptor nongbualamphuensis* gen. et sp. nov. from the Early Cretaceous Sao Khua Formation of Phu Wat, Nong Bua Lamphu Province, Thailand. SM-NB A1-2, left astragalocalcaneum in anterior (A$_2$), medial (A$_3$), lateral (A$_4$), and distal (A$_5$) views; line drawing in anterior view (A$_1$).

is small relative to the tibial shaft and offset from the lateral side of the proximal end of the tibia by a notch (posterior cleft) posteriorly. It does not reach the same level as the medial side posteriorly. The fibular crest (the fibular flange) of the tibia is present on the proximal half as a pronounced longitudinal ridge. The fibular crest is clearly offset from the proximal lateral surface of the tibia. It does not connect with the proximal end of the tibia (the ridge continuing from the fibular flange to the proximal articular surface of the tibia is absent). The ridge emerges 85 mm from the proximal end of the tibia. The fibular crest is sheet-like. The primary nutrient foramen cannot be observed, due to bad preservation.

The lateral malleolus of the distal expansion extends further distally and laterally than the medial malleolus. The lateral malleolus is overlapped by the calcaneum. The shape of the edge of lateral malleolus is a tabular notch. The distal tibia is most probably flat. The medial vertical ridge or medial bulge of the tibia anteriorly for the ascending process of the astragalus is present. This medial vertical ridge is also present in *Phuwiangvenator, Australovenator*, *Chilantaisaurus*, *Aerosteon* (Benson et al. 2010), and *Juratyrant* (Benson 2008; Rauhut 2012; Brussate and Benson 2013). The distal end of the tibia is triangular in outline, flattened anteroposteriorly, and strongly expanded laterally and medially.

The tibial length of *Vayuraptor* is more than 12 times its anteroposterior width at mid-length. This is a synapomorphy of megaraptorans and coelurosaurs (Benson et al. 2010) or a synapomorphy of Coelurosauria, including Megaraptora (Novas et al. 2013; Porfiri et al. 2014). In *Vayuraptor* this ratio is 13.9. For measurement of the tibiae see SOM: table 17. A fragment of probable fibula (PRC-NB A1-4) is preserved. It is very incomplete and does not offer much information.

Astragalocalcaneum: The left astragalus and calcaneum (SM-NB A1-2) are well preserved, only the tip of the ascending process of the astragalus is missing (Fig. 17). The astragalus is 70 mm wide, the calcaneum is 18 mm wide. The astragalar width/calcaneum width ratio is 3.8. The ascending process of the astragalus is sheet-like, it is 70 mm long, 14% of the total length of the tibia. It is offset from the anterior border of the astragalar body by a shallow groove. Its shape is straight laterally and straight and parallel medially at the base before it slopes to the tip laterally. There is a vertical ridge on the ascending process, from the proximal end to the middle of the process. There are two horizonal grooves and two foramina at the base of the astragalar body. The distal side of the astragalus is strongly concave in anterior view. The trapezoidal outline of the bone in distal view looks similar to that of *Australovenator* and the megaraptoran astragalus NMV P150070 (Benson et al. 2012b). It shows an extremely high and narrow ascending process of the astragalus, with a ratio of the ascending process height/ascending process width of approximately 1.66.

The astragalar body has a concave distal surface. The ascending process of the astragalus of *Fukuiraptor* is 1.7 times the height of its body (Benson et al. 2010) which is the same as in *Vayuraptor* (= 1.7).

The ascending process of the astragalus arises more than half of the breath of the astragalus body, and it is more than twice the height of the astragalus body (7:2.5). The astragalar condyle is significantly expanded proximally on the anterior side of the tibia and faces anterodistally.

The angle of the dorsal margin of the ascending process is almost horizontal. The articulation between the ascending process and the fibula is restricted to the lateral side. The shape of the astragalar ascending process looks similar to that of *Australovenator*, *Fukuiraptor*, *Aerosteon*, *Qianzhousaurus* (Lü et al. 2014), *Raptorex* (Sereno et al. 2009), and *Alioramus* (Brusatte et al. 2012). Two fossae at the base of the ascending process are present. There is an anteroproximal (= proximolateral) expansion of the astragalar lateral condyle, as in

Australovenator and *Fukuiraptor* (Benson et al. 2010). The development of the articular surface for the distal end of the fibula is reduced and situated on the lateral side. The posterolateral crest and posteromedial crest are absent. The calcaneum has a well-developed facet for the tibia. Both the astragalus and calcaneum are unfused. The calcaneum transverse development is moderately wide. The width of the calcaneum is approximately 25.7% of the width of the astragalus.

Remarks.—*Atlantal intercentrum*: The atlantal intercentrum of *Phuwiangvenator* is high in proportion and looks more similar to that of *Allosaurus* (UMNH VP 11289; AS personal obsevations) than to *Sinraptor* (Currie and Zhao 1993), *Aerosteon* (cast of MCNA-PV-3137; AS personal obsevations), and *Orkoraptor* (Novas et al. 2008) in which they are low dorsoventrally.

Dorsal vertebra: In general, the dorsal vertebra of *Phuwiangvenator* looks similar to that of *Fukuiraptor* (AS personal observations). Based on the broken bone surface, the dorsal vertebra apparently has a camellate internal structure. There are no pleurocoels, but a lateral depression and striation on the lateral and ventral side of the centrum are present as in *Fukuiraptor* (AS personal observations).

Sacral vertebrae: The proportion of the sacral centra of *Phuwiangvenator* is longer than high, the same as SMNS 58023, a megaraptoran from the Early Cretaceous of Brazil (Aranciaga Rolando et al. 2018; AS personal observations), *Gualicho* (Apesteguía et al. 2016), MPMA 08-003-94 (Mendez et al. 2012; AS personal observations), CPPLIP 1324 (Martinelli et al. 2013; AS personal observations), *Suchomimus* (MNBH GAD 500 and MNBH GAD70; AS personal observations), and *Spinosaurus* (FSAC-KK 11888; AS personal observations). This proportion is shorter than high in *Aoniraptor* (Motta et al. 2016), *Datanglong* (Mo et al. 2014), and *Megaraptor* (Porfiri et al. 2014; Aranciaga Rolando et al. 2018).

The median transverse constriction is not present in *Phuwiangvenator*, SMNS 58023, and *Suchomimus* (MNBH GAD 500 and MNBH GAD70). The constriction is present in *Datanglong* and *Siamotyrannus*.

Pleurocoels are present in SMNS 58023, *Megaraptor*, and *Aoniraptor*, but absent in *Phuwiangvenator*, *Datanglong*, and *Siamotyrannus*.

The flattened ventral surface of the sacrum is present in *Phuwiangvenator*, *Aoniraptor*, *Falcarius* (Zanno 2010), MPMA 08-003-94, CPPLIP 1324, and some derived coelurosaurs (Rauhut 2003), but convex in the SMNS 58203 (AS personal observations), *Suchomimus* MNBH GAD 500 (AS personal observations), *Datanglong* (Mo et al. 2014), and *Spinosaurus*.

The camellate internal structure is present in SMNS 58023, *Megaraptor*, *Aoniraptor*, and *Phuwiangvenator*. Generally, the vertebral pneumaticity in basal theropods is camerate, where as in ceratosaurs, carcharodontosaurs, and many coelurosaurs, a camellate internal structure is present (Benson et al. 2012a).

The sacral centra are ventrally less concave (in lateral view) in *Phuwiangvenator*, *Megaraptor*, *Aoniraptor*, and *Datanglong*, whereas they are concave in SMNS 58023, *Suchomimus* (MNBH GAD 500 and MNBH GAD70), and *Spinosaurus* (FSAC-KK 11888).

We note that the ventral groove on the sacral centra is present in some theropods such as *Falcarius* (Zanno 2010; AS personal observations), *Neovenator* (Brusatte et al. 2008), and *Condorraptor* (Rauhut 2005), but there is usually one longitudinal groove instead of two sulci which is longer and wider than in *Phuwiangvenator* (see SOM: fig. 1).

Metacarpal: An elongate metacarpal is a coelurosaurian synapomorphy (Novas et al. 2013) which is present in *Phuwiangvenator*. The metacarpal II of *Phuwiangvenator* looks similar to that of *Kileskus* and *Falcarius*, e.g., the shaft is straight, slender, and dorsoventrally flattened. The shaft of metacarpal II is slender in *Phuwiangvenator*, *Megaraptor*, *Australovenator*, *Tanycolagreus*, *Coelurus*, *Gualicho*, *Kileskus*, *Guanlong*, and *Yutyrannus* (Carpenter et al. 2005a, b; Xu et al. 2006, 2012; Averianov et al. 2010; Apesteguía et al. 2016; Novas et al. 2016), however, it differs from that of *Megaraptor* in which it is more slender and straight than in *Megaraptor* (Calvo et al. 2004; Novas et al. 2016). The distal end of metacarpal II is asymmetrical and divided into two condyles in *Phuwiangvenator* as well as in other theropods. The distal surface of the medial condyle is larger than the lateral condyle in *Phuwiangvenator*, *Australovenator*, *Gualicho*, and *Kileskus*. The medial condyle protrudes slightly more distally than the lateral condyle in *Phuwiangvenator*, *Coelurus*, and *Kileskus*. The pits for the collateral ligaments are not well developed on both condyles in *Phuwiangvenator*. There is no distinct extensor pit on the anterior surface of the shaft proximal to the distal condyle, only a small concavity is present in *Phuwiangvenator* and *Kileskus*. The shaft is straight (in dorsal view) in *Phuwiangvenator*, *Australovenator*, *Tanycolagreus*, *Coelurus*, *Gualicho*, *Kileskus*, and *Guanlong*.

Manual phalanges: Manual phalanx I-1 of *Phuwiangvenator* is concave ventrally in proximal view. This character is present in *Australovenator*, *Megaraptor*, NMV P199050 (Benson et al. 2012b), *Suchomimus* (MNBH GAD 500; AS personal observations), *Kileskus* (Averianov et al. 2010), *Falcarius* (Zanno 2006), and *Deinocheirus* (Osmólska and Roniewicz 1970).

A deep and wide furrow along the ventral surface of the manual phalanx I-1 is present in *Megaraptor* and *Australovenator* (Novas et al. 2016). A longitudinal ventral furrow and longitudinal ridges are present in *Phuwiangvenator*. This furrow is also present in *Suchomimus* and *Spinosaurus*, but it is restricted to the proximal part. However, the manual phalanx I-1 of *Phuwiangvenator* exhibits a triangular contour at the proximal end, not a square-shaped contour as present in the megaraptorids *Megaraptor* and *Australovenator* (see Novas et al. 2016).

Manual unguals: The manual ungual I-2 of *Phuwiangvenator* is strongly transversely compressed, being oval with a distinct dorsoventral axis in proximal view (see Novas 1998; Porfiri et al. 2014). This character is also found in

Fukuiraptor, *Megaraptor*, *Australovenator*, and *Chilantaisaurus*. However, the manual ungual I-2 of *Phuwiangvenator*, in relation to its phalanx, is proportionally smaller than in *Megaraptor* and *Australovenator* (Calvo et al. 2004; White et al. 2012; Novas et al. 2016). The manual ungual I-2 of *Phuwiangvenator* has a curved flexor tubercle which is found in *Fukuiraptor* (FPDM-V43-11; AS personal observations) and *Chilantaisaurus* (Benson and Xu 2008), but this character is widely present among Ornithodira. The ratio of the proximal height/width of the manual ungual I-2 of *Phuwiangvenator* is 2.4, compared with 1.95 in *Torvosaurus* (Benson et al. 2010), 1.78 in *Suchomimus* (MNBH GAD 500; AS personal observations), 1.9 in *Baryonyx* (cast of BMNH R9951; AS personal observations), 1.9 in *Allosaurus* (UMNH VP5676; AS personal observations), 2.7 in *Chilantaisaurus* (Benson and Xu 2008), 2.7 in *Fukuiraptor* (FPDM-V43-11; AS personal observations), 2.4 in *Australovenator* (Benson et al. 2010), and 2.75 in *Megaraptor* (Benson et al. 2010). The manual ungual III-4 of *Phuwiangvenator* is small and much smaller than the manual unguals I-2 and II-3 as in other theropods. We note that the character of the manual ungual I-2 with an asymmetrical lateral groove and well-developed ventral ridge of *Megaraptor* and *Australovenator* (White et al. 2012; Novas et al. 2016) is not present in *Phuwiangvenator* and *Fukuiraptor* (FPDM-V43-11; AS personal observations).

Tibia: In proximal view, the lateral condyle of the tibia is level with the posterior margin of the medial condyle. This character is found in *Phuwiangvenator*, *Vayuraptor*, *Australovenator* (White et al. 2013a), *Fukuiraptor* (AS personal observations), *Orkoraptor* (Novas et al. 2008), *Neovenator* (Brusatte et al. 2008), *Tyrannosaurus* (Brochu 2003), *Falcarius* (AS personal observations), *Gualicho* (Apestiguea et al. 2016), and *Murusraptor* (Coria and Currie 2016), but not in *Suchomimus* (MNBH GAD 500, MNBH GAD 98, and MNBH GAD 72). In *Torvosaurus* (Britt 1991), *Piatznitskysaurus*, and *Spinosaurus* this character is independently evolved.

The character: "tibial lateral condyle of proximal end curves ventrally as a pointed process"; this character is present in *Phuwiangvenator*, Megaraptora, some coelurosaurs, and *Neovenator*, but not in *Fukuiraptor* and *Vayuraptor*.

The median prominence in the anterior surface of the distal end of the tibia (tibial vertical medial ridge or medial bulge) is present in *Phuwiangvenator*, *Vayuraptor*, *Australovenator* (White et al. 2013a), *Suchomimus* (MNBH GAD 500; MNBH GAD 97; and MNBH GAD 72; AS personal observations), *Coelurus* (Carpenter et al. 2005b), *Chilantaisaurus* (Benson and Xu 2008), *Falcarius* (Zanno 2010; AS personal observations), *Spinosaurus* (cast of FSAC-KK 11888; AS personal observations), *Chuandongocoelurus* (Rauhut 2012), *Juratyrant* (Benson 2008; Rauhut 2012; Brussate and Benson 2013). *Masiakasaurus* (Carrano et al. 2002), theropod indet. MB.R.2351 (AS personal observations), the abelisauroid MB.R.1750 (AS personal observations), the abelisauroid MB.R.1751 (AS personal observations), *Aniksosaurus* (Martinez and Novas 2006), possibly *Bicentenaria* (Novas et al. 2012b), *Aerosteon*, *Stokesosaurus* (Rauhut 2012), *Ozraptor* (Long and Molnar 1998), *Tanycolagreus* (Carpenter et al. 2005a), *Segnosaurus* (Zanno 2010), *Erliansaurus* (Xu et al. 2002), possibly NMV P150070 (Benson et al. 2012b), and possibly *Fukuiraptor* (AS personal observations). The posteroventral ridge of the tibia is present in *Vayuraptor*, *Australovenator*, and *Tachiraptor* (Langer et al. 2014). The tibia facet for the reception of the ascending process of the astragalus at the distal end which is flat anteriorly is an apomorphy shared by megaraptorans and coelurosaurians (Porfiri et al. 2014).

The character: "tibia anteriorly flat at mid-length with vertical ridges anterolaterally and anteromedially" can be found in *Phuwiangvenator*, *Vayuraptor*, *Neovenator* (Brusatte et al. 2008), *Australovenator* (White et al. 2013a), and *Aerosteron* (cast of MCNA-PV-3139; AS personal observations).

The character: "tibia anteriorly flat or slightly flat but no such vertical ridges" is present in *Spinosaurus* (cast of FSAC-KK 11888; AS personal observations), *Chilantaisaurus* (Benson and Xu 2008), a sinraptorid tibia from Thailand (SM 10; AS personal observations), *Murusraptor* (Coria and Currie 2016), and *Acrocanthosaurus* (Stovall and Langston 1950; see SOM: table 18).

The character: "tibia anteriorly convex or slightly convex but ridge present" can be found in *Allosaurus* (UMNH VP 6402, 7145, 7926, 7936, 7939) and *Fukuiraptor* (FPDM-V43-20).

The tibia is long and slender in the Thai theropods. The length/width ratio is more than 12 in *Phuwiangvenator* (13.82), *Vayuraptor* (13.9), *Australovenator* (12.53), *Fukuiraptor* (approximately 14.3–14.5), *Aerosteon* referred material (14), and *Spinosaurus* neotype (12.09) (Ibrahim et al. 2014) compared with *Murusraptor* (11.9), the *Suchomimus* holotype (MNBH GAD 500, 9.6), *Suchomimus* "subadult" (MNBH GAD97, 10.86), and *Suchomimus* "juvenile" (MNBH GAD72, 11.67) (see SOM: table 17).

Astragalus: The ascending process height of astragalus being more than 0.5 times the width of the astragalar body can be found in *Vayuraptor*, *Fukuiraptor*, *Australovenator*, possibly in *Phuwiangvenator*, and all other coelurosaurs. The transverse width of the ascending process of astragalus occupies the total width of the anterior surface of distal tibia (coelurosaurian character), distinct anterior development of the lateral condyle of the astragalar body and a strong inflection in the anterior margin of the astragalar body in distal view (Novas et al. 2013) (coelurosaurian characters) are present in *Phuwiangvenator*, *Vayuraptor*, *Australovenator*, *Aerosteon*, and other coelurosaurs. The presence of an astragalus with a prominent proximolateral extension is a megaraptoran synapomorphy (Novas et al. 2013). This latter feature is observed in *Vayuraptor* and possibly *Phuwiangvenator* (in the latter it is small and damaged). Transverse development of the calcaneum which is moderately wide (plesiomorphic character) is present in *Phuwiangvenator* and *Vayuraptor*. The shape of the calcaneum in lateral or medial view is strongly asymmetric, with a right angle at the posterior border (Novas et al. 2013) (coelurosaurian character). This character possibly unites the Megaraptora within Coelurosauria.

The character: "ascending process of the astragalus which is offset from distal condyles by a pronounced groove (possible coelurosaurian character)" is present in *Vayuraptor* and *Phuwiangvenator*.

The ratio of the ascending process height/astragalar body height is high in *Vayuraptor* (1.7), *Fukuiraptor* (1.7), *Aerosteron* (1.9), *Alioramus* (2.5), and *Phuwiangvenator* (estimated 1.73). This ratio is lower in NMV P150070 (1.43), *Australovenator* (1.4), *Falcarius* (1.3), *Suchomimus* (MNBH GAD97, 1.3; MNBH GAD98, 1.25), compared with *Allosaurus* (1.14) which has the much lower ratio (see SOM: table 19). This ratio is also low in *Coelurus*, *Bicentenaria*, and *Tugulusaurus*.

The ascending process of astragalus arises from the lateral side of astragalar body (not from its complete width) in *Phuwiangvenator*, *Vayuraptor*, *Australovenator*, *Fukuiraptor*, *Tugurusaurus*, *Bicentenaria*, and *Coelurus*. It arises from the complete width of the astragalar body in *Tanycolagreus* and *Aerosteon*. The ratio of the ascending process width at base/astragalar body width is low and the ascending process is restricted to the lateral side of the astragalar body in basal tetanurans (e.g., Novas et al. 2013) and some basal coelurosaurs. This ratio is 50% in *Allosaurus*, *Bicentenaria* (Novas et al. 2012b), *Tugulusaurus* (Rauhut and Xu 2005), and *Coelurus* (Carpenter et al. 2005b), 55% in NMV P150070, 56% in *Suchomimus* (MNBH GAD97), 63% in *Vayuraptor*, unknown in *Fukuiraptor*, 65% in *Phuwiangvenator*, 66% in *Falcarius*, 70% in *Australovenator*, 78% in *Alioramus*, and 83% in *Aerosteon* (see SOM: table 19).

The ratio of the astragalar ascending process height/ascending process width at base is high in *Vayuraptor* (approximately 1.66), compared with *Alioramus* (1.4), *Phuwiangvenator* (estimated 1.39), NMV P150070 (1.3), *Fukuiraptor* (1.1), *Falcarius* (1.1), *Australovenator* (1), *Aerosteon* (1), *Allosaurus* (UMNH VP11003, 1), and *Suchomimus* (MNBH GAD97, 0.88; MNBH GAD98, 0.8).

An anterior development of the lateral condyle of the astragalus in distal view is present in *Phuwiangvenator*, *Vayuraptor*, *Australovenator*, *Aerosteon*, probable *Fukuiraptor*, NMV P150070, *Appalachiosaurus* (Carr et al. 2005), *Bicentenaria* (Novas et al. 2012b), *Coelurus*, *Tugulusaurus*, and *Alioramus*. The accessory posterolateral ascending process of the astragalus is present in *Fukuiraptor* and NMV P150070 (see Agnolin et al. 2010; see SOM: fig. 2). The prominent proximolateral extension of the astragalus (Benson et al. 2010; Carrano et al. 2012; Porfiri et al. 2014) that projects from the anterior articular facet as a rounded triangular process is present in *Australovenator*, *Aerosteon*, *Fukuiraptor* (small process), *Phuwiangvenator* (small process), and *Vayuraptor*. This process forms the anterior border of the fibular facet of the astragalus and the fibular facet is shallow and bordered posteriorly by the lateral margin of the ascending process (Hocknull et al. 2009). In *Fukuiraptor*, the astragalus has a shallow notch for a process from the calcaneum but it is not well developed (Azuma and Currie 2000; AS personal observations). The astragalar notch for a process from the calcaneum is present in *Aerosteon*, *Phuwiangvenator*, but not *Vayuraptor*. The astragalus has a distinct socket that embraced the mediodistal end of the fibula (Azuma and Corrie 2000; AS personal observations), this present in *Fukuiraptor*, *Phuwiangvenator*, and *Vayuraptor*. The fibular contact extending up the anterolateral margin of the ascending process of the astragalus is present in *Fukuiraptor* (Azuma and Currie 2000; AS personal observations), *Vayuraptor*, and possibly *Phuwiangvenator*.

The long and sheet-liked ascending process of the astragalus with a slope or convex medially and straight laterally can be found in *Vayuraptor*, *Australovenator*, *Fukuiraptor*, *Qianzhousaurus* (Lü et al. 2014), *Raptorex* (Sereno et al. 2009), and *Appalachiosaurus* (Carr et al. 2005). However, the shape of the ascending process of *Vayuraptor* is different from the other theropods mentioned above. The ascending process with vertical ridge proximally which ends in the middle is present in *Vayuraptor* and *Qianzhousaurus* (Lü et al. 2014). Two fossae at the base of the ascending process of the astragalus can be found in *Vayuraptor* and *Appalachiosaurus* (Carr et al. 2005). One fossa is present in *Qianzhousaurus*, *Alioramus*, *Raptorex*, and other tyrannosauroids and ornithomimosaurs (e.g., White et al. 2013a; Lü et al. 2014; Sereno et al. 2009; Brusatte et al. 2012; Choiniere et al. 2012), whereas there is no fossa in *Coelurus*, *Tugurusaurus*, and *Bicentenaria*. There is a cranio-proximal process at the base of the astragalus in *Vayuraptor*, *Australovenator*, *Aerosteon*, and *Coelurus*, small in *Fukuiraptor* and *Phuwiangvenator*.

Calcaneum: In *Phuwiangvenator*, the facet for the fibula of the calcaneum is small and smaller than in the allosauroid *Allosaurus* (UMNH VP 9965). The area for astragalocalcaneum attachment in *Allosaurus* is small and restricted to the anteroventral part, clearly different from *Phuwiangvenator*. The calcaneum of *Phuwiangvenator* is wider anteroposteriorly than high dorsoventrally. This is in contrast to the tyrannosauroid *Appalachiosaurus* (Carr et al. 2005). The facet for the fibula of the calcaneum is larger and not restricted to the dorsal part as in *Appalachiosaurus*. In *Phuwiangvenator* and *Vayuraptor*, the calcaneum is thick and differed from *Falcarius* (UMNH VP 12365), which has a disk-like calcaneum.

The calcaneum of *Phuwiangvenator* looks more similar to that of *Murusraptor* than to *Baryonyx* and *Allosaurus* in the shape and ratio of the fibular facet of the calcaneum. In *Baryonyx* and *Allosaurus*, there are large fibular facets dorsal to the calcaneum, the tibia facets is situated on the medial side. In *Phuwiangvenator* and *Murusraptor*, lateral view, the fibular facet is almost the same size as the tibia facet, and the tibia facet is situated on the mediodorsal side of the calcaneum. In the evolution from basal theropods to moderately derived coelurosaurs, there is a trend of enlargement of the tibial facet of the calcaneum and a concurrent reduction of the fibular facet. As a result, the tibial facet is much larger than the fibular facet in moderately derived coelurosaurs. The calcaneum is relatively wide transversely in *Phuwiangvenator*, *Vayuraptor*, *Murusraptor*, *Aerosteon*, and *Tugulusaurus*. It is strongly compressed in *Tanycolagreus*, *Alioramus*, and derived coelurosaurs. The calcaneum is roughly symmetrical with a wide angle on the posterior border in *Murusraptor* and *Aerosteon*. It is asymmetrical with a right angle on the posterior border in *Phuwiangvenator*, *Vayuraptor*, and *Tanycolagreus* (Novas et al. 2013). The ratio of the width of the calcaneum/the width of the astragalus is 25.7% in *Vayuraptor*, 24% (left) and 23% (right) in *Phuwiangvenator*, and whereas the ratio of the width of the calcaneum/astragalus is less than 20% in coelurosaurs (Rauhut and Pol 2017).

Metatarsals: In proximal view, the lateral margin of metatarsal II is straight in *Australovenator*, *Fukuiraptor* (White et al. 2013a), and *Tanycolagreus* (Carpenter et al. 2005a), but the lateral margin is convex or slightly convex in *Phuwiangvenator*, *Ornitholestes*, and *Allosaurus*.

In proximal view, the metatarsal III is slightly concave medially in *Phuwiangvenator*, *Torvosaurus*, *Ornitholestes*, and possibly *Fukuiraptor*. It is straight in *Australovenator*, *Afrovenator*, possibly *Neovenator*, *Tanycolagreus*, *Mapusaurus*, and almost straight in *Zuolong* and *Allosaurus* (UMNH VP 16038). It is concave in *Chilantaisaurus* and *Sinraptor*.

In the proximal view, the shape of the medial margin of metatarsal IV is sigmoidal in *Phuwiangvenator*, *Mapusaurus*, *Chilantaisaurus*, *Allosaurus*, and *Tanycolagreus*. It is step-like in *Australovenator*, *Megaraptor*, *Ornitholestes*, and *Coelurus*, whereas there is a convex medial margin in *Zuolong*. The shape of the posterolateral margin of metatarsal IV is slightly concave in *Phuwiangvenator*, *Australovenator*, and *Zuolong*, whereas it is almost straight in *Megaraptor*, *Mapusaurus*, *Chilantaisaurus*, and *Ornitholestes*.

In *Phuwiangvenator*, metatarsal III is anteriorposteriorly oriented in proximal view, which is similar to *Australovenator* (White et al. 2013a), *Chilantaisaurus* (Benson and Xu 2008), *Neovenator* (Brusatte et al. 2008), *Falcarius* (Zanno 2010), *Garudimimus* (Kobayashi and Barsbold 2005), and *Acrocanthosaurus* (Stovall and Langston 1950; Currie and Carpenter 2000), but differs from *Suchomimus* (MNBH GAD70; AS personal observations), *Sinraptor* (cast of holotype in FPDM; AS personal observations), *Tanycolagreus* (Carpenter et al. 2005a), *Allosaurus* (UMNH VP 9892, 16038, 9877; AS personal observations), *Majungasaurus* (Carrano 2007), *Afrovenator* (Sereno et al. 1994), and *Dilophosaurus* (Welles 1984) in which the metatarsal III is anterolaterally-posteromedially oriented in proximal view.

In *Phuwiangvenator*, the low anterior rim of the metatarsal IV, which is its autapomorphy, is independently present in *Pandoravenator* (a basal tetanuran from the Late Jurassic of Argentina, Rauhut and Pol 2017), but in *Pandoravenator* the anterior rim of the metatarsal IV, which is much lower than metatarsal III, does not slope proximolaterally to distomedially.

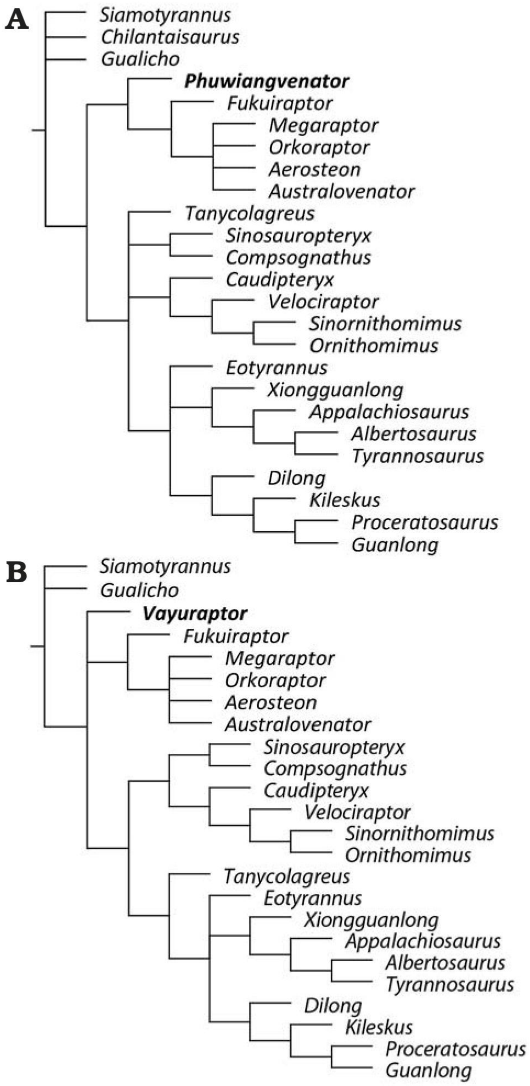

Fig. 18. Strict consensus trees of all the recovered MPTs of the phylogenetic analyses from the present study (modified from Apesteguía et al. 2016). **A**. Data matrix including *Phuwiangvenator yaemniyomi* gen. et sp. nov. **B**. Data matrix including *Vayuraptor nongbualamphuensis* gen. et sp. nov.

Pedal and ungual phalanges: The pedal phalanges of *Phuwiangvenator* are clearly different from *Suchomimus* (MNBH GAD70) and *Spinosaurus* (FSAC-KK 11888) because in spinosaurids, their pedal phalanges are strongly dorsoventrally flattened. Ventrally flattened unguals are present in *Phuwiangvenator*, *Australovenator*, *Spinosaurus*, and ornithomimosaurs. However, the unguals of *Spinosaurus* are extremely dorsoventrally flattened and less curved than in other theropods (FSAC-KK 11888, MSNM V6897; see Maganuco and Dal Sasso 2018).

Phylogenetic analyses

The analytical method and data matrix of Apesteguía et al. (2016) with additional information for the Thai theropods was used (see Material and methods). The phylogenetic analyses were done in the TNT program (Goloboff et al. 2008) with 46 taxa (excluded *Santanaraptor*) and 288 characters. The first analysis recovered five most parsimonious trees (MPTs) of 923 steps with a consistency index (CI) = 0.380 and a retention index (RI) = 0.656. The second analysis with 45 taxa (excluded *Santanaraptor* and *Chilantaisaurus*) and 288 characters recovered seven MPTs of 913 steps with a CI = 0.384 and a RI = 0.662 (Fig. 18).

Synapomorphies recovered in the present analyses include:

Coelurosauria: tibia length is more than 12 times its width (character 186); astragalus ascending process height is more than 0.5 times the width of the astragalar body (character 195); astragalus ascending process occupying total width of anterior surface of distal tibia (character 196); distinct anterior development of the lateral condyle of the astragalar body in distal view is present (character 197); fibular facet of astragalus reduced (character 199); calcaneum strongly asymmetric in lateral or medial view (character 201); distal end of tibia is anteriorly flat (character 208); long and gracile metatarsal III (character 209); ascending process of astragalus is offset from distal condyle by a pronounced groove (character 211); tibia lateral condyle position is shorter than the medial condyle in proximal view (character 221); tibia lateral condyle curves ventrally as pointed process (character 246).

Megaraptora: manual phalanx I-1 with a ventral groove (character 138); strongly transversely compressed manual ungual I-2 (character 141); median prominence in the anterior surface of the tibia distal end (character 188); astragalus with proximolateral extension (character 198); sacrum ventrally flattened (character 214).

Megaraptoridae: manual ungual I lateral groove asymmetrical (character 144); manual ungual I and II with the well-developed ventral ridge (character 145). These two megaraptorid characters are not present in *Phuwiangvenator*.

The analyses recovered *Phuwiangvenator* and *Vayuraptor* within basal Coelurosauria, and as a non-megaraptorid Megaraptora for *Phuwiangvenator*.

Discussion

Systematic and taxonomic analysis.—*Phuwiangvenator yaemniyomi* gen. et sp. nov. and *Vayuraptor nongbualamphuensis* gen. et sp. nov. show the following avetheropod and coelurosaurian characters listed below: (1) the trapezoidal or wedge-shaped, plantar surface pinched of the third metatarsal which is absent in megalosauroids and was suggested to be a possible avetheropod (= neotetanuran) synapomorphy by Benson and Xu (2008) and Holtz et al. (2004) (see Carrano et al. 2012). In fact, this character is present in *Suchomimus* (unknown in *Vayuraptor*; AS personal observations); (2) the tibia length is more than 12 times its anteroposterior width at mid-length. This is a synapomorphy of Coelurosauria, including Megaraptora (Novas et al. 2013; Porfiri et al. 2014), but can also be found in the tibia of the *Spinosaurus* neotype (Ibrahim et al. 2014; AS personal observations).

The following characters that place *Phuwiangvenator* and *Vayuraptor* within Coelurosauria, and *Phuwiangvenator* probably within Megaraptora are based on the present phylogenetic analyses (Fig. 17) and marked by an asterisk.

Phuwiangvenator yaemniyomi is identified as Coelurosauria and non-megaraptorid Megaraptora by the following characters: (1) sacrum ventral surface is flattened/without ventral keel* (Megaraptora synapomorphy) (Rauhut 2003); (2) manual phalanx I-1 is long and slender and has a furrow ventrally* (Megaraptora synapomorphy) (Novas et al. 2016); (3) the ventral margin of the proximal articular surface of the manual phalanx I-1 is concave (Novas et al. 2016); (4) manual ungual I-2 is strongly transversely compressed, being oval with a distinct dorsoventral axis in proximal view* (Megaraptora synapomorphy) (Novas 1998); (5) tibia lateral condyle position in the proximal end at its posterior margin is placed well posteriorly to the level of the posterior edge of the medial condyle* (Novas et al. 2013); (6) tibia lateral condyle of the proximal end curves ventrally as a pointed process* (Benson et al. 2010); (7) tibial median prominence in the anterior surface of the distal end is present* (Novas et al. 2013); (8) tibia length is more than 12 times its anteroposterior width at mid-length* (Coelurosauria synapomorphy) (Novas et al. 2013); (9) tibia flattened anteriorly at mid-length, usually with vertical ridges anterolaterally and anteromedially; (10) tibia facet for the reception of the ascending process of the astragalus at the distal end is more or less flat* (Coelurosauria synapomorphy) (Rauhut 2003; Benson et al. 2010; Novas et al. 2013); (11) the height of the ascending process of the astragalus is more than 0.5 times the width of the astragalar body* (Harris, 1998; Novas et al., 2013); (12) transverse width of ascending process of astragalus is occupying total width of anterior surface of distal tibia* (Rauhut 2003); (13) distinct anterior development of the lateral condyle of the astragalar body is present, strong inflexion of the anterior margin of the astragalar body in distal view* (Coelurosauria synapomorphy) (Novas et al. 2013); (14) astragalus with an anteroproximal extension is present* (Megaraptora synapomorphy) (Benson et al. 2010); (15) atragalus ascending process is offset from distal condyles by a pronounced groove* (Coelurosauria synapomorphy) (Holtz et al. 2004); (16) calcaneum, shape in lateral or medial view is strongly asymmetric, with a right angle at the posterior border* (Coelurosauria synapomorphy) (Novas et al. 2013); and (17) the pedal ungual is flattened ventrally (shared with *Australovenator*).

Vayuraptor nongbualamphuensis is identified as Coelurosauria by the following characters: (1) tibia lateral condyle position in the proximal end at its posterior margin is placed well posteriorly to the level of the posterior edge of the medial condyle* (Novas et al. 2013); (2) tibial median prominence in the anterior surface of the distal end is present* (Novas et al. 2013); (3) tibia length is more than 12 times its anteroposterior width at mid-length* (Novas et al. 2013); (4) tibia is flattened anteriorly at mid-length, usually with vertical ridges anterolaterally and anteromedially; (5) tibia facet for the reception of the ascending process of the astragalus at the distal end is more or less flat* (Rauhut 2003; Benson et al. 2010; Novas et al. 2013); (6) astragalus with a prominent anteroproximal extension is present* (Benson et al. 2010); (7) astragalus distinct anterior development of the lateral condyle of the astragalar body is present and there is a strong inflexion in the anterior margin of the astragalar body in distal view* (Novas et al. 2013); (8) astragalus ascending process is offset from distal condyles by a pronounced groove* (Holtz et al. 2004); (9) transverse width of the ascending process of the astragalus is occupying total width of anterior surface of distal tibia* (Rauhut 2003); (10) the height of the ascending process of the astragalus is more than 0.5 times the width of the astragalar body* (Harris 1998; Novas et al. 2013); (11) fibular facet of the ascending process of the astragalus reduced and laterally oriented (Novas et al. 2013); (12) calcaneum, shape in lateral or medial view is strongly asymmetric, with a right angle on the posterior border* (Novas et al. 2013).

***Phuwiangvenator* vs. *Siamotyrannus*: why are they not the same taxon?**—In *Phuwiangvenator*, the dorsal vertebrae are longer than high, contrary to the dorsal vertebrae of *Siamotyrannus* which higher than long. The sacral vertebrae of *Phuwiangvenator* are also longer than high. Their centra are ventrally flattened and not constricted in ventral view. There is no median transverse constriction on the sacrum, in contrast to *Siamotyrannus*, where the sacral vertebrae are higher than long. The centra of this taxon are ventrally convex and also have a median transverse constriction. The ventral rims of the sacral centra of *Siamotyrannus* are much more convex in lateral view than those of *Phuwiangvenator*. *Phuwiangvenator* also differs from *Siamotyrannus* in being a smaller animal.

***Vayuraptor* vs. *Phuwiangvenator*: why are they not the same taxon?**—These two new theropods belong to the basal Coelurosauria, based on their morphologies as described above. Because the fossils were recovered from the same rock formation within approximately 40 km of each other, careful comparison is needed to determine whether they belong to the same taxon or not. The overlapping materials of these two theropods are the tibia and astragalocalcaneum.

Phuwiangvenator is larger than *Vayuraptor* (tibial length 615 vs. 515 mm, respectively). Although the cranioproximal process of the astragalus is present in *Vayuraptor* and *Phuwiangvenator*, it is more prominent in *Vayuraptor* than in *Phuwiangvenator*. Two short horizontal grooves on the astragalar body are present in *Vayuraptor*, whereas only one horizontal groove is present in *Phuwiangvenator*. There are two fossae at the base of the ascending process of the astragalus in *Vayuraptor* whereas there is only one fossa in *Phuwiangvenator*. The calcaneum of *Vayuraptor* is narrower mediolaterally proximally than that of *Phuwiangvenator* in anterior view. A shallow notch of the astragalus for the calcaneum process is present in *Phuwiangvenator*. This notch is not present in *Vayuraptor*. The character "tibia anterolateral process of the lateral condyle curves as a pointed process" is present in *Phuwiangvenator*, not in *Vayuraptor*. This character has been compared with various ontogenetic stages of *Allosaurus* (UMNH VP 7148, 7922, 7932, 7938, 7939, 7940), and this process was found in all observed specimens (AS personal observations), so we conclude that the differences between *Phuwiangvenator* and *Vayuraptor* are not due to ontogeny. The shape of the fibular crest is different as well (e.g., the fibular crest is expanded proximolaterally in *Phuwiangvenator* vs. being expanded distolaterally in *Vayuraptor*). The shape of the proximal end of the tibia is different, the proximal articular surface of the medial condyle being more convex in *Phuwiangvenator* than *Vayuraptor*.

***Vayuraptor* vs. *Siamotyrannus*: why are they not the same taxon?**—*Vayuraptor* and *Siamotyrannus* are represented by skeletally mature animals based on the fusion of their bones (e.g., astragalocalcaneum in *Vayuraptor*, and pelvis, dorsal and caudal vertebrae in *Siamotyrannus*). There is no overlapping material, so anatomical comparison is impossible. *Vayuraptor* is found here to be a basal coelurosaur. *Siamotyrannus* is an avetheropod, possibly a basal coelurosaur (Samathi 2013; Samathi and Chanthasit 2017; present work) or basal allosauroid (e.g., Rauhut 2003; Carrano et al. 2012). *Vayuraptor* differs from *Siamotyrannus* in being a much smaller animal. *Vayuraptor* is approximately 4–4.5 m in length (similar to *Fukuiraptor*), whereas *Siamotyrannus* is approximately 6.5–7 m in length (Buffetaut et al. 1996). Based on the above information, it is reasonable to conclude that *Vayuraptor* represents a different taxon from *Siamotyrannus*.

Conclusions

The present study describes the anatomy of the two new basal coelurosaurs from Southeast Asia in detail. One of them, *Phuwiangvenator*, is here referred to the Megaraptora. These findings extend the diversity of basal megaraptorans and support the origin of Megaraptora in Asia. The Asian megaraptorans might be a monophyletic clade or a paraphyletic series relative to the Megaraptoridae. Recently, Early Cretaceous fossils of megaraptorans have been recovered from the Barremian to Aptian of Asia. Several materials have been reported from the Aptian to mid-Cretaceous of Australia, whereas there is only one report from the Albian of South America. These show a high diversity and wide distribution during the Early Cretaceous which became more provincial in the Late Cretaceous. However, the phylogenetic position of the basal coelurosaur *Vayuraptor* must await further discovery of additional material and remains open to future analyses.

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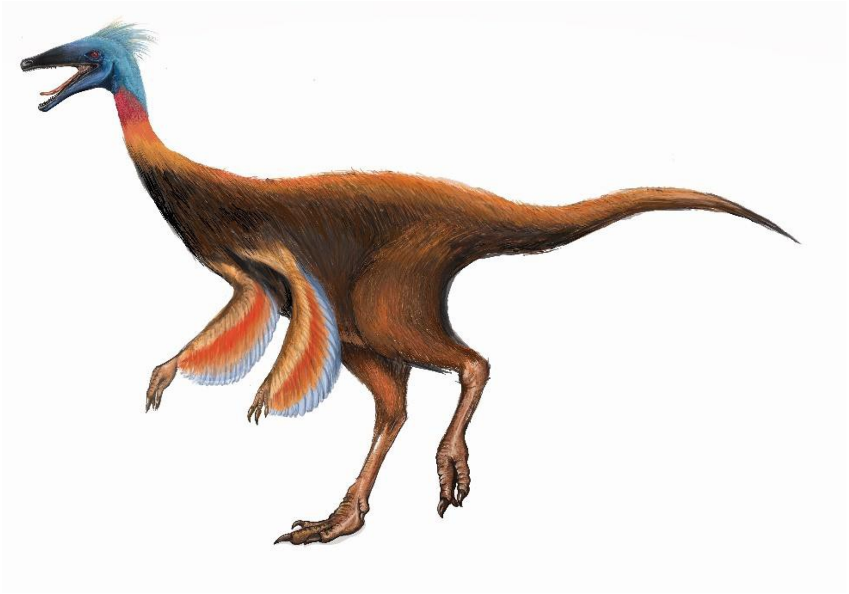
CHAPTER 4

Phylogeny of an Ornithomimosaur *Kinnareemimus khonkaenensis* from the Early Cretaceous of Thailand



CHAPTER 4

PHYLOGENETIC POSITION OF THE ORNITHOMIMOSAUR *KINNAREEMIMUS KHONKAENENSIS* FROM THE EARLY CRETACEOUS OF THAILAND

Abstract published as **Samathi, A.** 2018. Phylogenetic Position of the Ornithomimosaur *Kinnareemimus khonkaenensis* from the Early Cretaceous of Thailand. In: *The Fifth International Palaeontological Congress* 2018 Paris, p. 672 and *15th Annual Meeting of the European Association of Vertebrate Palaeontologists* 2017 Munich, p. 79.

Abstract:

A small-bodied ornithomimosaur *Kinnareemimus khonkaenensis* Buffetaut, Suteethorn, and Tong, 2009 from the Early Cretaceous Sao Khua Formation of northeastern Thailand was first reported in 1999 then named in 2009 by Buffetaut et al. It is the only report of this group in Southeast Asia and was concluded to be a member of Ornithomimosauria more derived than *Harpymimus* and *Garudimimus* but more basal than *Archaeornithomimus*. *Kinnareemimus* has since then never been included in any cladistical analysis. Only one phylogenetic analysis has been done by Brusatte et al. (2014) and they did not find the support of *Kinnareemimus* within the Ornithomimosauria. Here, the phylogenetic analyses for assessing the relationships of *Kinnareemimus* within Ornithomimosauria were performed. The results suggested it might be a basal ornithomimosaur (104 taxa, 568 characters) or belongs to the subclade Deinocheiridae (98 taxa, 568 characters). Generally, the tree topologies agreed with previous studies, i.e. the Ornithomimosauria consists of the subclades Ornithomimidae and Deinocheiridae, and the basal forms. *Kinnareemimus* looks similar to *Garudimimus* in the shape of the fibula in proximal view. Its metatarsal III shows subarctometatarsalian condition which might have evolved independently from other ornithomimids. However, the basal position of *Kinnareemimus* could also be due to the immaturity and the incompleteness nature of this animal.

This study shows that the evolution of the arctometatarsalia condition in ornithomimosaurs was not a simple linear process. Furthermore, it appears that during the Early Cretaceous the basal ornithomimosaurs were more widespread than in the Late Cretaceous when they were restricted to central Asia and North America. *Kinnareemimus* is one of the oldest and more basal ornithomimosaurs. This indicates that Southeast Asia played an important role in the early radiation of the Ornithomimosauria.

Keywords: Ornithomimosauria, Southeast Asia, subarctometatarsalian metatarsus, Early Cretaceous Sao Khua Formation, paleobiogeography

1. INTRODUCTION

Ornithomimosauria, or ostrich dinosaurs, is a clade of coelurosaurian theropods. Within Coelurosauria they were placed within basal-most Maniraptoriformes close to Maniraptora (Makovicky et al 2004). They are characterized by small skull, long neck, long fore and hindlimbs (Makovicky et al 2004; Sues & Averianov 2016). They were known mainly from the Early to Late Cretaceous of Asia and North America with the oldest member from Africa, some reports from Europe, and one report from Southeast Asia (Lee et al 2014; Choiniere et al 2012; Perez-Morelo et al 1994; Buffetaut et al 2009). Ornithomimosauria consists of the clade Ornithomimidae, Deinocheiridae, and basal taxa (Lee et al 2014; Sues & Averianov 2016; McFeeters et al 2016).

In 1995, a Thai – French expedition discovered several individuals of a small theropod from the Early Cretaceous Sao Khua Formation in Khon Kaen Province, North eastern Thailand (Buffetaut & Suteethorn 1999; Buffetaut et al 2009). It was later named *Kinnareemimus khonkaenensis* by Buffetaut et al in 2009 (fig. 1). However, *Kinnareemimus* has never been put in any cladistical analysis before. Only one phylogenetic analysis has been done by Brusatte et al. (2014) and they did not find the support of *Kinnareemimus* within the Ornithomimosauria and suggested it is a kind of basal coelurosaur. We here re-accessed the holotype specimen and thorough re-examined the type material. Data of other ornithomimosaurs were from published literature. We put the character states of *Kinnareemimus* into the data matrices of Choiniere et al 2012 (plus *Deinocheirus*, Lee et al 2016) and McFeeters et al 2016.

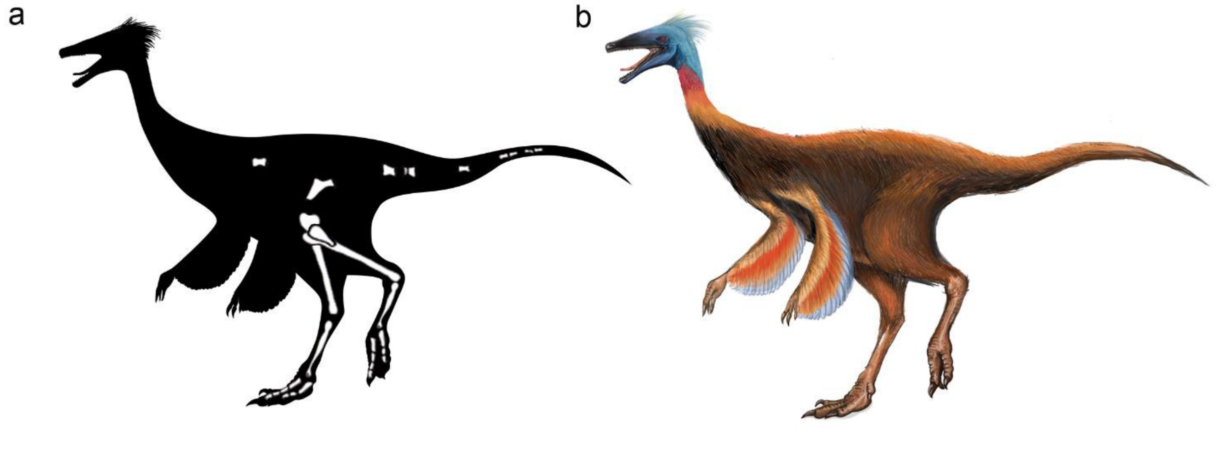


Fig. 1. Skeleton (a) and life (b) reconstruction of *Kinnareemimus khonkaenensis.*

1.1 An overview of the Ornithomimosauria

The Asian ornithomimosaurs: until now, ten ornithomimosaurs were named from China, Mongolia, and Thailand with fragmentary materials from Kazakhstan, Uzbekistan, Tajikistan, and Japan (see Chapter 1 for details). These including: *Anserimimus planinychus* (Barsbold, 1988b) from Nemegt Stiva, early Maastrichtian of Bayankhongor, Mongolia; *Aepyornithomimus* from the Upper Cretaceous Djadokhta Formation, Mongolia (Tsogtbaatar et al. 2017); *Beishanlong* from the Early Cretaceous of China (Makovicky et al. 2010); *Deinocheirus mirificus* (Osmólska & Roniewicz, 1970) from the Late Cretaceous, Nemegt Formation, early Maastrichtian of Ömnögov', Mongolia (Kobayashi and Basbold, 2006; Lee et al., 2014); *Gallimimus bullatus* (Osmólska, Roniewicz, & Barsbold, 1972) Nemegt Formation, early Maastrichtian of Ömnögov', Mongolia; *Garudimimus brevipes* (Barsbold, 1981) from Bayanshiree Svita, Cenomanian-Santonian of Ömnögov', Mongolia; *Harpymimus okladnikovi* (Barsbold & Perle, 1984) from Shinekhudag Svita, late Albian of Dundgov', Mongolia; *Hexing qingyi* (Jin et al., 2012) from the Yixian Formation, lower Valanginian – lower Barremian of Xiaobeigou locality, Lujiatun, Shangyuan, Beipiao City, western Liaoning, P.R. China; *Kinnareemimus khonkaenensis* (Buffetaut et al., 2009) from the Early Cretaceous Sao Khua Formation of Thailand; *Shenzhousaurus orientalis* (Ji, Norell, Makovicky, Gao, Ji, & Yuan, 2003) from the Yixian Formation, Barremian of Liaoning, China; *Sinornithomimus dongi* (Kobayashi and Lü, 2003) from the Late Cretaceous, Ulansuhai Formation, Aptian-?Albian of Inner Mongolia, China; *Qiupalong henanensis* (Xu et al., 2011) from the Late Cretaceous of Henan, China; Bissekty ornithomimid (Sues & Averianov 2016). And a new unnamed ornithomimosaur from the Late Cretaceous of Mongolia (Kobayashi et al., 2014).

The European ornithomimosaurs consist of *Valdoraptor* from the Early Cretaceous Valanginian of West Sussex, England (Allain et al. 2014) and *Pelecanimimus* from the Early Cretaceous of Las Hoyas, Cuenca, Spain (Perez-Moreno et al. 1994).

The African ornithomimosaurs consist of *Nqwebasasaurus* from the Early Cretaceous of Africa (De Klerk et al. 2000) and *Afromimus* from the Early Cretaceous of Niger (Sereno 2017).

The North American ornithomimosaurs consist of *Arkansaurus* from the Early Cretaceous of North America (Hunt and Quinn 2018), *Ornithomimus* (Marsh 1890), *Struthiomimus* (Osborn 1917), *Tototlmimus* (Serrano-Branas et al. 2016), *Qiupalong* sp. (McFeeters et al. 2017), and *Rativates* (McFeeters et al. 2016).

The fragmentary materials have been reported from Kazakhstan (Averianov et al. 2017), Uzbekistan (Sues and Averianov 2016), Tajikistan (Alifanov and Averianov 2006), Japan (Azuma et al. 2013; Naoki 2016), and Australia (Benson et al. 2012).

The problematic taxa including *Nedcolbertia* from North America (Kirkland et al. 1998), *Timimus* from Australia (Vickers-Rich and Rich 1993), *Thecocoelurus* from England (Huene 1923), and *Lepidocheirosaurus* from Russia (Alifanov and Saveliev 2015) remain problematic.

Coelurosaurian Synapomorphies

From Cau (2018), the coelurosaur synapomorphies consist of 1) distinct posteroventral process of lacrimal; 2) distal surface of pubic foot subrectangular; 3) posterior part of pubic foot elongate; 4) distal half of metatarsal IV shaft contacting metatarsal III. The coelurosaurian synapomorphies with the exclusion of *Aorun* (after Cau 2018) including 5) the medially opened maxillary recess; 6) the elongation of the cervical centra beyond the posterior level of the neural arch; 7) fan-shaped dorsal neural spines; 8) the fibular crest not reaching the proximal end of tibia; 9) absence of the anterior distal fossa in the tibia (tibia anteriorly flat); 10) tibial length more than 12 times its anteroposterior width at mid-length (after Porfiri *et al.* 2014).

Ornithomimosaurian Synapomorphies

From Rauhut (2003), the ornithomimosaur synapomorphies consist of 1) maxilla excluded from external nares by broad posterior ascending process of the premaxilla; 2) humerus long, slender and straight; 3) manual unguals only slightly curved or straight, with reduced, distally placed flexor tubercles; 4) obturator process on ischium is small, triangular and placed entirely on the uppermost fifth of the ischial shaft; 5) pedal unguals ventrally flattened, with a semicircular depression instead of a flexor tubercle.

From Holtz et al (2004) five unambiguous synapomorphies of ornithomimosaurs are 1) a pneumatic cultriform rostrum (bulla); 2) an expanded narial process of the premaxilla that separates the nasal and the maxilla caudal to the naris; 3) a subtriangular dentary; 4) a dorsolateral flange on the surangular that forms an expanded articulation with the quadrates; 5) the radius and ulna tightly appressed distally.

Ornithomimidae synapomorphies

From Holtz et al (2004), the ornithomimid synapomorphies are 1) a reduced proximal metatarsal III forming and arctometatarsalian foot; 2) loss of the first pedal digit (see Brownstein 2017; McFeeters et al. 2018).

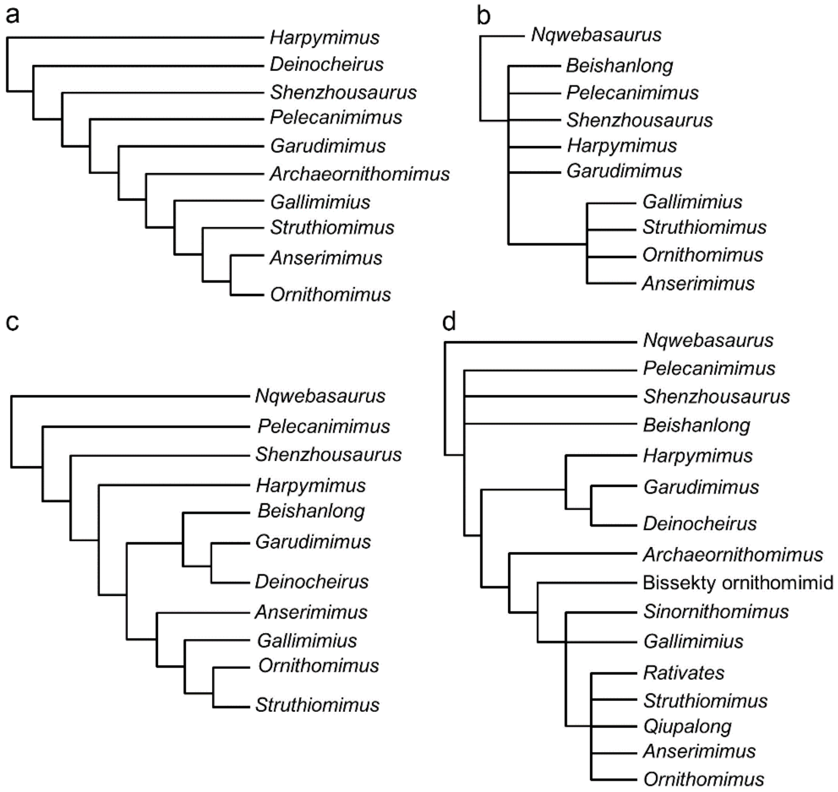


Fig. 2. Previous cladistic analyses from a) Senter, 2007; b) Choiniere *et al.,* 2012; c) Lee *et al.,*2014; d) McFeeters *et al.,* 2017.

1.2 Recent cladistic analyses

Almost all cladistics analyses agreed that the clade Ornithomimosauria consists of *Nqwebasaurus* as the most primitive ornithomimosaur, the clade Ornithomimidae as the most derived ornithomimosaurs, and the intermediate forms (Senter 2007; Xu et al 2011; Choiniere *et al.,* 2012; Lee et al 2014; Sues & Averianov 2016; McFeeters et al 2017; fig. 2).

1.3 Institutional abbreviation

SM: Sirindhorn Museum, Department of Mineral Resources, Kalasin, Thailand. **PW** is for Phu Wiang locality where the specimens were found.

2 MATERIAL AND METHODS

2.1 Data matrix and method followed Choiniere et al 2012 plus *Deinocheirus* (Lee et al. 2014).

2.2 Follow the method and matrix of McFeeters et al. 2016 which was modified from Sues & Averianov 2016 which is the modified version of Choiniere et al. 2012. We used both traditional search and new technology search options in the TNT program (Goloboff et al. 2008) for comparison.

2.3 Drawing/ line drawing, Pictures compare with other ornithomimosaurs, Skeleton reconstruction.

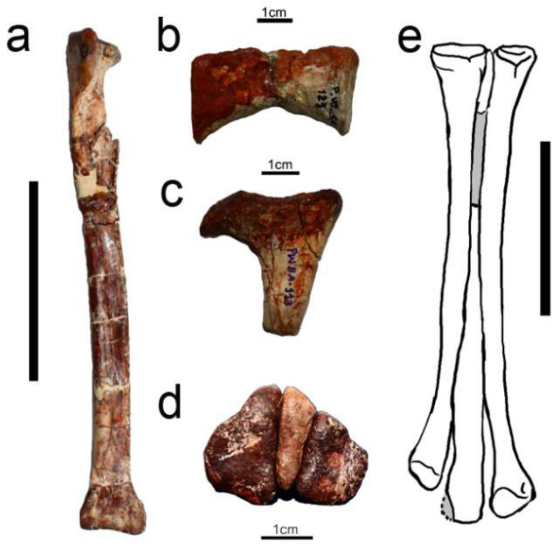


Fig. 3. Selected materials a) left tibia; b) dorsal vertebra; c) pubis; d) metatarals; e) reconstruction of metatarsals. Scale bar a = 10 cm, b – d = 1 cm, e = 5 cm.

3. RESULT

3.1 Systematic paleontology

Dinosauria Owen, 1842 (*sensu* Padian and May, 1993)
Theropoda Marsh, 1881
Coelurosauria von Huene, 1914
Ornithomimosauria Barsbold, 1976 (*sensu* Sereno, 2005b)
Ornithomimoidea Marsh, 1890 (*sensu* Sereno, 2017)
Kinnareemimus khonkaenensis Buffetaut, Suteethorn, and Tong, 2009

Material: The Holotype **SM-PW5A-100** consists of an incomplete left third metatarsal with the distal end and part of the shaft and the referred materials consist of metatarsals, pedal phalanges, pedal ungula phalanx, tibiae, fibular, pubis fragment, dorsal and caudal vertebrae (fig. 3, 4).
Horizon: Sao Khua Formation, Early Cretaceous, ~Late Barremian.
Diagnosis: An ornithomimosaur with combination of following characters: subarctometatarsalian condition of the metatarsals (as in basal ornithomimosaurs) with a triangular cross-section of the mt III closer to the distal end (as in derived ornithomimids) (modified from Buffetaut et al. 2009).

4. PHYLOGENETIC ANALYSIS

4.1 After Choiniere et al., 2012

The data matrix and method followed Choiniere et al. (2012) plus *Deinocheirus*, it consists of 568 characters with 98 taxa. The material of *Kinnareemimus* could be scored for 47 of the 568 characters (8.27%) from the data matrix. The matrix was analyzed heuristically using the software package TNT v. 1.1 (Goloboff et al., 2003), under the parsimony criterion. Most- parsimonious trees were obtained using the following heuristic search parameters: New Tech Search; hold 10,000 trees; 'Driven search' stabilizing consensus twice with a factor of 75 using Sectorial Search, Ratchet, Drift, and Tree Fusing with default settings. The phylogenetic analysis produced 6 MPTs, 568 characters, 98 taxa, 2937 steps, CI = 0.228, RI = 0.594 (fig. 5A).

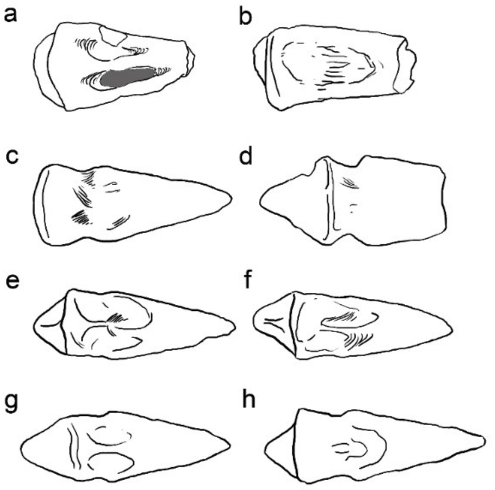


Fig. 4. Pedal unguals of a) *Kinnareemimus*; b) *Nqwebasaurus* Choiniere et al. 2012; c) cf. *Qiupalong* sp. McFeeters et al. 2017; d) *Deinocheirus* Lee et al. 2014; e) and f) Bissekty ornithomimid Sues & Averianov 2016; g) *Garudimimus* Kobayashi and Barsbold 2005; h) Kazak Ornithomimid Averianov et al. 2016. Not to scale.

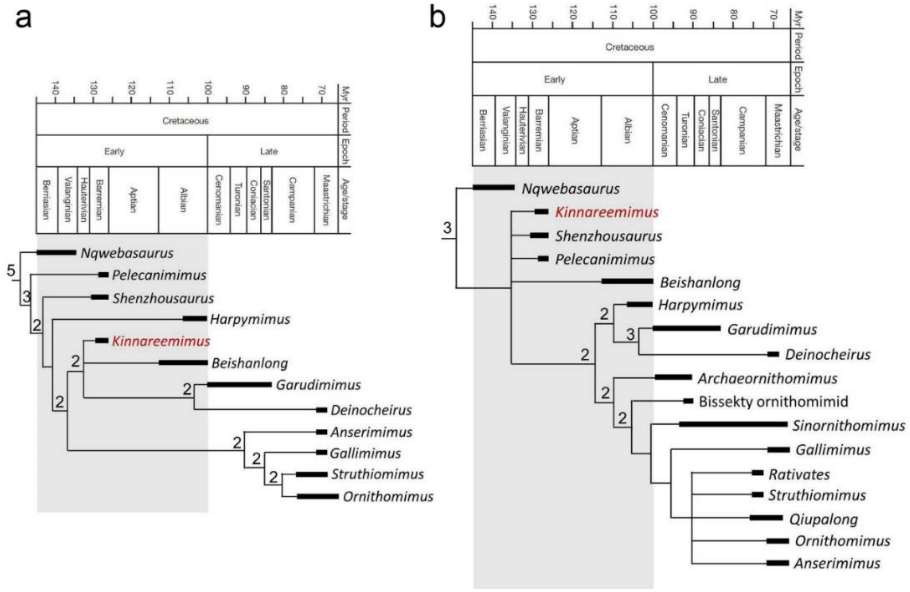


Fig. 5. Phylogenetic analyses a) modified after Choiniere et al. (2012) and found *Kinnareemimus* within the Deinocheiridae, b) modified after McFeeters et al. (2016) and found *Kinnareemimus* as a basal ornithomimosaur. Numbers next to nodes are Bremer support values.

4.1.1 Synapomorphy list

1) *Tawa* + neotheropoda: 256, 392
2) Neotheropoda: 21, 35, 98, 400, 413, 423, 495, 547
3) Averostra: 299, 336, 495, 538, 539
4) Tetanurae: 16, 26, 36, 179, 191, 394, 405, 410, 426, 444, 516, 555
5) Coelurosauria: 27, 32, 76, 278, 316, 457
6) (*Haplocheirus* + Ornithomimosauria) + Maniraptora: 107, 223, 229, 230, 275, 501, 513, 522
7) *Haplocheirus* + Ornithomimosauria: 10, 20, 109, 133, 214, 347, 417, 463
8) Ornithomimosauria: 9, 18, 24, 86, 234, 235, 349, 407, 419, 420, 564, 565, 567
9) *Pelecanimimus* + (*Shenzhousaurus* + (*Hapymimus* + (Deinocheiridae + Ornithomimidae))): 277, 356, 363, 370, 385
10) *Shenzhousaurus* + (*Hapymimus* + (Deinocheiridae + Ornithomimidae)): 14, 218, 225, 236
11) *Hapymimus* + (Deinocheiridae + Ornithomimidae): 74, 188
12) Deinocheiridae + Ornithomimidae: 179, 207, 236, 265, 300, 376, 419, 556, 559
13) Deinocheiridae (including *Kinnareemimus*): 508, 524

4.1.2 Discussion

Ornithomimosauria

The flatten ventral surface of the pedal unguals (char. 567) nests *Kinnareemimus* within the Ornithomimosauria.

Deinocheiridae + Ornithomimidae

The expanded medial side of the anterior surface of distal end of Mt III (Char. 556) and the length of the Mt IV which is markedly longer than the Mt II (char. 559) unite Deinocheiridae and Ornithomimidae together.

Deinocheiridae

The cnemial crest projects strongly proximal to posterior condyles (char. 508) and the anterior portion fibular proximal dimensions in proximal view is mediolaterally wider than the posterior portion (char. 524) unite *Kinareemimus*, *Garudimimus*, and *Beishanlong* within Deinocheiridae.
The char 567 (ventral surface of pedal unguals flexor fossa) is present in all ornithomimosaurs except *Ornithomimus edmontonicus*. The char 508 (cnemial crest project strongly proximally in deinocheirids), char 529 (oval fossa fibula in deinocheirids and ornithomimids (including

Kinnareemimus)), char 556 (mt III distal medial expanded in deinocheirids and ornithomimids (including *Kinnareemimus*)), and char 524 (fibular proximal dimensions in proximal view is anterior portion mediolaterally wider than the posterior portion) are present in the Deinocheiridae including *Kinnareemimus*.

4.2 After McFeeters et al., 2016

Follow the method and matrix of McFeeters et al. (2016) which was modified from Sues & Averianov (2016) which is the modified version of Choiniere et al (2012) with 568 characters,
104 taxa. It produced 6 MPTs (New Tech Search), 2932 steps, CI = 0.229, RI = 0.613 (fig. 5B).

4.2.1 Synapomorphy list

1) Ornithomimosaurian synapomorphies: 18, 24, 84, 234, 268, 349, 351, 407, 410, 420, 564, 567

4.2.2 Discussion

Possible Ornithomimidae + Deinocheiridae synapomorphies (after included *Kinnareemimus* in McFeeters et al 2016):

The possible Onithomimidae + Deinocheiridae synapomorphies recovered from present study including 1) maxillary antorbital fossa in front of the internal antorbital fenestra is more than 40% of the length of the external antorbital fenestra (char. 34:1), 2) ventral edge of maxillary body and ventral ramus is ventrally convex (44:1), 3) dorsoventral thickness of maxillary ramus of lacrimal is moderate, less than or subequal to anteroposterior thickness of jugal ramus (74:1), 4) frontals are narrow anteriorly as a wedge between nasals (84:0), 5) dentary anterior end in lateral view is deflected ventrally (188:1), 6) edentulous dentary (236:2), 7) shaft of cervical ribs is broad and shorter than vertebra (328:1), and 8) transverse width of distal humerus is less than twice shaft width (371:2).

Possible Deinocheiridae synapomorphies:

1) Anterior end of jugal is excluded from the internal antorbital fenestra (char. 56:1), 2) form of anterior end of jugal is without anterior process underneath antorbital fenestra (57:0), 3) jugal antorbital fossa is absent or developed as a slight depression (58:0), 4) supratemporal fenestra is bounded laterally and posteriorly by the squamosal (111:0), 5) pubic apron is with medial opening distally above the pubic boot (463:1), and 6) metatarsal III shape of shaft in cross section is rectangular (557:0).

5. DISCUSSION

5.1 Character evolution

1) A cnemial crest is synapomorphic for dinosauromorphs, and a slightly laterally curved crest is a dinosaur synapomorphy (Nesbitt 2011; Langer et al., 2014). 2) Theropod tibiae differ from those of other archosaurs in the presence of a ridge/crest for the attachment of the fibula on the lateral side of the proximal part of the shaft. This is developed as a strong crest in theropods (Langer et al., 2014). 3) Most theropods have the facet for the ascending process of the astragalus restricted to the cranial part of a craniocaudally narrow distal articulation of the tibia (Langer et al., 2014). 4) In most theropods, the outer malleolus reaches further distally than the inner malleolus and this line forms an oblique angle to the long axis of the shaft (Langer et al., 2014). 5) The presence of a posterolateral process (=lateral malleolus) of the distal tibia that is set off laterally from the tibial shaft is a synapomorphy of neotheropods (Rauhut, 2003; 2012; Nesbitt et al., 2007). 6) In averostrans, the distal tibia is further expanded transversely, completely backs the fibula posteriorly and forms a broad contact with the calcaneum distally (Rauhut, 2012). 7) Two tetanuran synapomorphies (Rauhut, 2005; 2012): 7.1) a fibular condyle that is offset from the cnemial crest by a strongly developed incisura tibialis; and 7.2) a strongly developed fibular crest that is offset from the proximal end (Rauhut, 2005; 2012). 8) Metatarsal III, midshaft cross-sectional shape: wedge-shaped, plantar surface pinched. In avetheropods, the cross-section of metatarsal III is trapezoidal as a consequence of the relatively narrow ventral (plantar) surface (Carrano et al, 2012).

Key synapomorphies of Coelurosauria: 1) tibial length more than 12 times its anteroposterior width at mid-length (Novas et al. 2013; Porfiri et al., 2014). 2) the distal end of tibia anteriorly flat (Novas et al. 2013; Cau 2018); 3) distal half of metatarsal IV shaft contacting metatarsal III (Cau 2018); 4) the fibular crest does not reach the proximal end of the tibia (Cau 2018).

Synapomorphies of Ornithomimosauria: 1) pedal unguals ventrally flattened, with a semicircular depression instead of a flexor tubercle (Rauhut 2003). 2) medial expansion of mt III. (Choiniere et al. 2012; Averianov et al. 2017).

Synapomorphies of Ornithomimidae: 1) a reduced proximal metatarsal III forming and arctometatarsalian foot (Holtz et al. 2004); 2) loss of the first pedal digit (Holtz et al. 2004).

From Averianov et al. (2017) (focus on materials that found in *Kinnareemimus*): 1) Shafts of metatarsals II-IV closely appressed throughout most of the length of the metatarsus, adjacent surfaces flattened for contact (Choiniere et al., 2012, character 543(1)), a common condition for Coelurosauria and outgroup taxa, reversed in

Therizinosauria. 2) Distal end of metatarsal III: smooth, not ginglymoid (Choiniere et al., 2012, character 553(0)), a ginglymoid distal end of metatarsal III is characteristic for Paraves. 3) Medial side of the anterior surface of the distal end of metatarsal III expanded (Choiniere et al., 2012, character 556(1)), a synapomorphy for Ornithomimosauria more derived than *Nqwebasaurus thwazi*. 4) Metatarsal III shape of shaft wedge-shaped in cross-section, plantar surface pinched (Choiniere et al., 2012, character 557(1)). This derived state is found in all ornithomimosaurs except *Harpymimus okladnikovi*, *Garudimimus brevipes*, and *Deinocheirus mirificus*, a synapomorphy for Ornithomimidae according to Brusatte et al. (2014, character 200(2)). 5) Shaft of metatarsal IV round or thicker dorsoventrally than wide in cross-section (Choiniere et al., 2012, character 558(0)). This is a plesiomorphic character present in all ornithomimosaurs. The derived state, with a transversely wide metatarsal IV, is present in Dromaeosauridae and a few other taxa. 6) Shape of the ventral surface of the pedal unguals: straight in lateral view (Choiniere et al., 2012, character 565(1)). This condition is characteristic for all ornithomimosaurs with some variation. 7) Ventral surfaces of the pedal unguals with pronounced flexor fossa on the ventral surface of the proximal end (Choiniere et al., 2012, character 567(1)), a synapomorphy for Ornithomimosauria, reversed in *Qiupalong henanensis* and *Ornithomimus edmontonicus*. 8) Form of the flexor fossa on the pedal unguals: small flexor tubercle presents within the flexor fossa (Choiniere et al., 2012, character 568(1)). Ornithomimosaurs have a low longitudinal ridge rather than a tubercle in the flexor fossa. The ridge in the flexor fossa is absent in derived ornithomimids.

However, the shafts of metatarsals II-IV are not closely appressed throughout most of the length of the metatarsus in *Kinnareemimus*, *Nedcolbertia*, *Arkansaurus*, *Qiupalong*, *Ornithomimus velox*, and *Archaeornithomimus*.

5.2 Paleobiogeography

During the Early Cretaceous, the ornithomimosaurs were widespread, they were present in Asia, Eastern Asia, Southeast Asia, Europe, South Africa, and North America. Whereas during the Late Cretaceous, they were restricted to central Asia and western North America (fig. 6).

5.3 Theropod arctometatarsalia evolution

Four types of metatarsus are present in theropods. They consist of 1) underived metatarsus, 2) subarctometatarsus, 3) arctometatarsus (White 2009), and 4) antarctometatarsus (e.g. Rauhut and Carrano 2016). The arctometatarsus shows tree features including 1) a proximally narrow metatarsal III that is almost completely excluded from articulation with the tarsus and is excluded by expansion of metatarsals II and IV in anterior view, 2) a medial section, in which the metatarsal III is a simple solid splint of bone between the more columnary and hollow II and IV, and 3) a distal section, in which metatarsal III forms a wedge that abuts facets on the interior regions of metatarsals II and IV (White 2009; Holtz 1994).

Anterior views of metatarsi showing: 1) third metatarsal unpinched; 2) the third metatarsal pinched proximally only; 3) the third metatarsal pinched proximally and at midshaft (Senter 2007). Posterior view of metatarsi showing (metatarsal III shapes of the shaft in cross section): 1) rectangular; and 2) wedge-shaped, plantar surface pinched (Choiniere et al 2012).

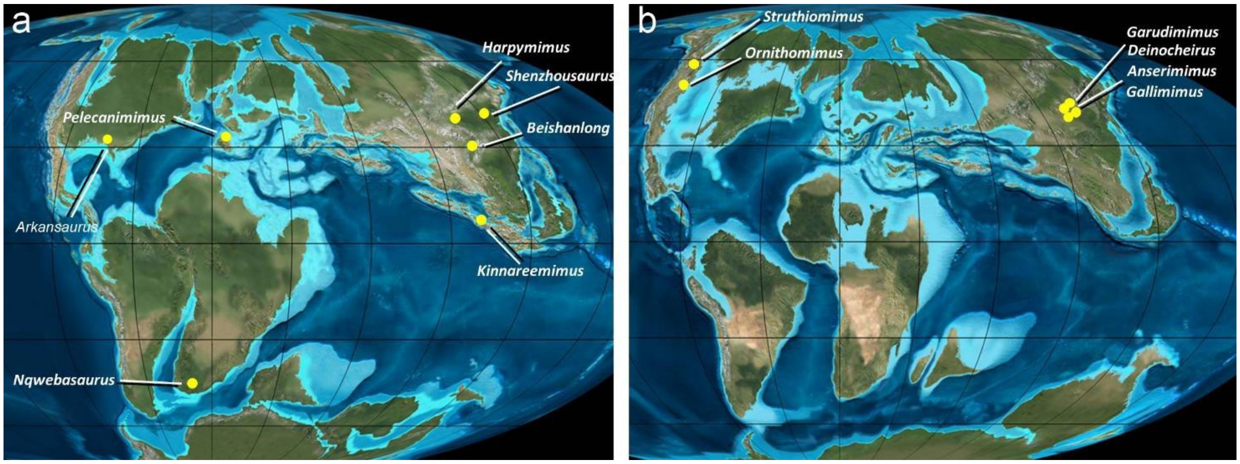


Fig. 6. Paleobiogeography of ornithomimosaurs, a) Early Cretaceous, b) Late Cretaceous. Paleogeographic maps from Ron Blakey (http://deeptimemaps.com/).

In *Kinnareemimus*, the subarctometatarsalian metatarsus with a triangular cross-section of the distal mt III is not found in any known theropods with subarctometatarsus (see White 2009). This unique character of *Kinnareemimus* might be a ‘transition’ condition between the ‘normal’ subarctometatarsus and arctometatarsus as suggested by Buffetaut et al. 2009. This should be tested in the further study.

6. CONCLUSION

Kinnareemimus is a basal ornithomimosaur. Whether it is one of the most basal ornithomimosaurs or belongs to the subclade Deinocheiridae, cannot be determined in the present study and must await further discovery. The ontogeny and fragmentary nature of the specimens is a main factor. Furthermore, during the Early Cretaceous, the ornithomimosaurs were more widespread than the Late Cretaceous, where they were restricted to central Asia and western North America.

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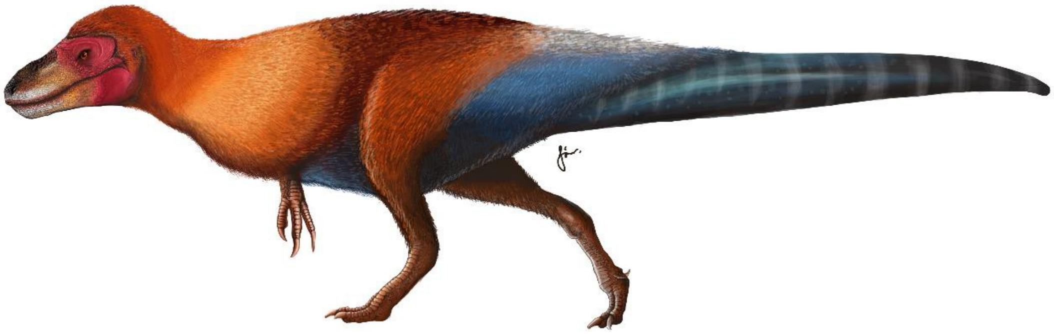
CHAPTER 5

Revision of *Siamotyrannus isanensis* from the Early Cretaceous of Thailand



CHAPTER 5

A REVISION AND PHYLOGENY OF *SIAMOTYRANNUS ISANENSIS* (DINOSAURIA; THEROPODA) FROM THE EARLY CRETACEOUS OF THAILAND

Abstract:

Siamotyrannus isanensis Buffetaut, Suteethorn, and Tong 1996 from the Early Cretaceous Sao Khua Formation (≈ Barremian) of northeastern Thailand is a large theropod dinosaur. It was first interpreted as a basal member of the tyrannosaur lineage. Since then, this conclusion has been questioned by various authors, for example, some found it belongs to the Allosauroidea or Metriacanthosauridae (= Sinraptoridae).

Here we re-describe this taxon in detail based on the holotypic material plus the additional information on the dorsal vertebrae which were only briefly described in the original publication. Phylogenetic analyses found *Siamotyrannus* to nest within the Coelurosauria, outside Tyrannoraptora, based on 1) the medial shelf of the brevis fossa being completely hidden in lateral view and falling short of its lower margin; 2) vertical pubis; 3) straight or slightly curved chevrons; 4) relatively long pubic peduncle of the ilium. Within Coelurosauria, *Siamotyrannus* is diagnosed by autapomorphies including 1) double, low and broad vertical ridges on the central part of the lateral iliac blade and 2) a notch on the dorso-posterodorsal part of the postacetabular blade of the ilium.

The *Siamotyrannus* material indicates that some basal coelurosaurs, more basal than Tyrannosauroidea plus 'derived' coelurosaurs, were large-bodied. Coelurosaurs probably first evolved as large-sized theropods, like their relatives, basal tetanurans, before becoming small in the stem of the clade Tyrannoraptora. The other possible explanation is that the basal coelurosaurs first were represented by small forms and only later evolved into large-bodied forms in several lineages convergently.

Keywords: Early Cretaceous, Sao Khua Formation, Thailand, *Siamotyrannus*, Coelurosauria, Theropoda

1. INTRODUCTION

Non-avian theropods were carnivorous, saurischian dinosaurs found from the Late Triassic (ca. 228 million years ago) until the end of the Cretaceous (ca. 65 million years ago) (Rowe and Tykoski 2004). The origin of birds lies within theropod dinosaurs. The size range of theropods is wide, most of the theropods were medium to large in size (O'Gorman and Hone 2012). Some theropods were among the largest land-living animals, the gigantic forms such as *Tyrannosaurus*, *Spinosaurus* and *Giganotosaurus* attained a length of 14 m and weighed an estimated six tons or more (Coria and Salgado 1995; Holtz and Osmólska 2004; Brusatte et al. 2010a). Theropods were found on all continents including Antarctica (Hammer and Hickerson 1994). Large-bodied theropod fossils from the Early Cretaceous (ca. 145 – 99 million years ago) of Asia are rare (Brusatte et al. 2010b), but relatively complete and informative specimens are known from China, Japan, Laos, and Thailand (Buffetaut and Suteethorn 1999; Azuma and Currie 2000; Brusatte et al. 2010b; Allain et al. 2012).

The first dinosaur bone from Thailand was found in 1976 by a geologist from the Department of Mineral Resources, Bangkok, during a uranium survey at Phu Wiang District, Khon Kaen Province. It was a fragment of a sauropod femur from the Sao Khua Formation (Buffetaut 1982). Since then, a collaboration led by the Department of Mineral Resources, Thailand and the Centre National de la Recherche Scientifique, France has led to the discovery of many other dinosaurs including ornithischians, sauropods, and theropods (Buffetaut and Suteethorn 1992; Martin et al. 1994; Suteethorn et al. 2009). The latter include the large theropod *Siamotyrannus*, the topic of this contribution.

The Sao Khua Formation is one of the most fossil-rich formations of the Khorat Group of northeastern Thailand (fig. 1). It consists of red clays, sandstones, and conglomerates, indicating deposition in a floodplain with meandering rivers. The formation has yielded freshwater hybodont sharks, actinopterygian fishes, turtles, crocodilians, and dinosaurs (Buffetaut and Suteethorn 1998). The formation was originally considered Jurassic in age, but it was later shown to be in the Early Cretaceous. Buffetaut and Suteethorn (1999) were the first to suggest an Early Cretaceous age based on the vertebrate fossils. Most recently, the age was constrained to the late Barremian based on non-marine bivalves (Tumpeesawan et al. 2010). Thus, we follow this age assignment.

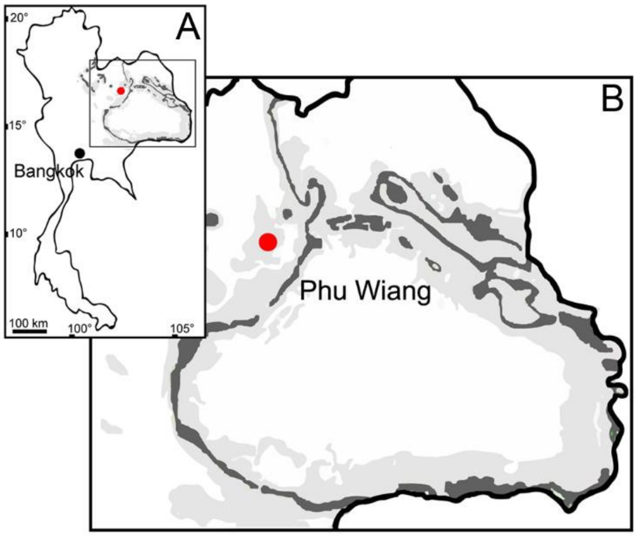


Fig.1. A map of northeastern Thailand showing outcrops of the Sao Khua Formation (dark grey) and the Phu Wiang Locality, Khon Kaen Province (circle).

Seven distinct theropods have been reported from the Sao Khua Formation (Samathi et al. 2019), including a probable small-bodied compsognathid (Buffetaut and Ingavat 1984), several teeth of a spinosaurid *Siamosaurus suteethorni* (Buffetaut and Ingavat 1986), a theropod *Siamotyrannus isanensis* (Buffetaut et al. 1996), an ornithomimosaur (ostrich-mimic dinosaur) *Kinnareemimus khonkaenensis* (Buffetaut et al. 2009), a partial skull of a carcharodontosaurid (PRC 61, Buffetaut and Suteethorn 2012), and two basal coelurosaurs (Samathi et al. 2019a). The Phuwiang carcharodontosaurid (PRC 61) might belong to same animal as *Siamotyrannus*.

In 1993, Mr. Somchai Triamwichanon from the Department of Mineral Resources, Bangkok found a fossil skeleton of a theropod dinosaur in red sandstones of the Sao Khua Formation, Phu Wiang District, Khon Kaen Province, northeastern Thailand. This partial skeleton (SM-PW9-1) consists of the left half of the pelvis, the sacrum, the 13 anterior tail vertebrae with several chevron bones and five dorsal vertebrae (Fig. 2). It was three years later named *Siamotyrannus isanensis* by Buffetaut, Suteethorn, and Tong (1996). The name *Siamotyrannus* came from 'Siam', the old name of Thailand, plus the Greek *tyrannos* for the tyrant, and the specific name *isanensis* came from 'Isan', the local name for the northeastern part of Thailand, where the specimen was discovered (Buffetaut et al. 1996).

Siamotyrannus isanensis was first interpreted as a basal member of the Tyrannosauridae which includes such famous members as *Tyrannosaurus rex* from North America and *Tarbosaurus bataar* from central Asia (Buffetaut et al. 1996). This conclusion has been debated since then because of the new information and new interpretation of theropod dinosaurs that have been continually discovered from around the world in the last two decades (e.g. Rauhut 2003a, b; Brusatte and Sereno 2008; Carrano et al. 2012).

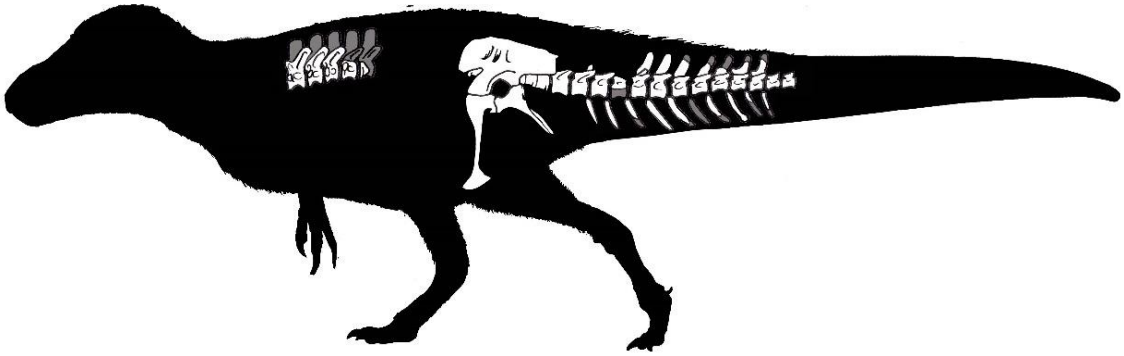


Fig.2. *Siamotyrannus isanensis*, Skeleton reconstruction based on the holotype (SM-PW9-1). Restored areas of the bones are indicated with grey tone.

Previous cladistic analyses

Holtz (1998) did not include *Siamotyrannus* in his analysis because, at that time, the dorsal vertebrae were just briefly reported and not fully prepared. Holtz (2001) concluded that *Siamotyrannus* might be an ancestral member of the tyrannosaur lineage, but lacking additional material, especially the skull, such a proposal remains uncertain. Rauhut (2003a) found this theropod to be a primitive allosauroid rather than a basal tyrannosauroid. Holtz et al. (2004) also found *Siamotyrannus* to be a primitive allosauroid, but closely related to *Fukuiraptor* from the Aptian - Albian of Japan. Brusatte and Sereno (2008) suggested that *Siamotyrannus* may be a carcharodontosaurid closely related to *Acrocanthosaurus* from North America based on the character of the ischium, but they suggested that a careful reexamination of the type material is needed before the phylogenetic relationships of this theropod can be assessed. Carrano et al. (2012) found *Siamotyrannus* to belong to the Metriacanthosauridae (= Sinraptoridae) and to be closely related to *Sinraptor* from China and *Metriacanthosaurus* from England (both from the Late Jurassic) based on the left pelvis, whereas Buffetaut and Suteethorn (2012) suggested that the discovery of a carcharodontosaurid from Thailand should be used to reconsider the phylogenetic position of *Siamotyrannus*, but they stated that the comparison of *Siamotyrannus* with new a tyrannosauroid from China, *Yutyrannus*, is also needed (Fig. 3).

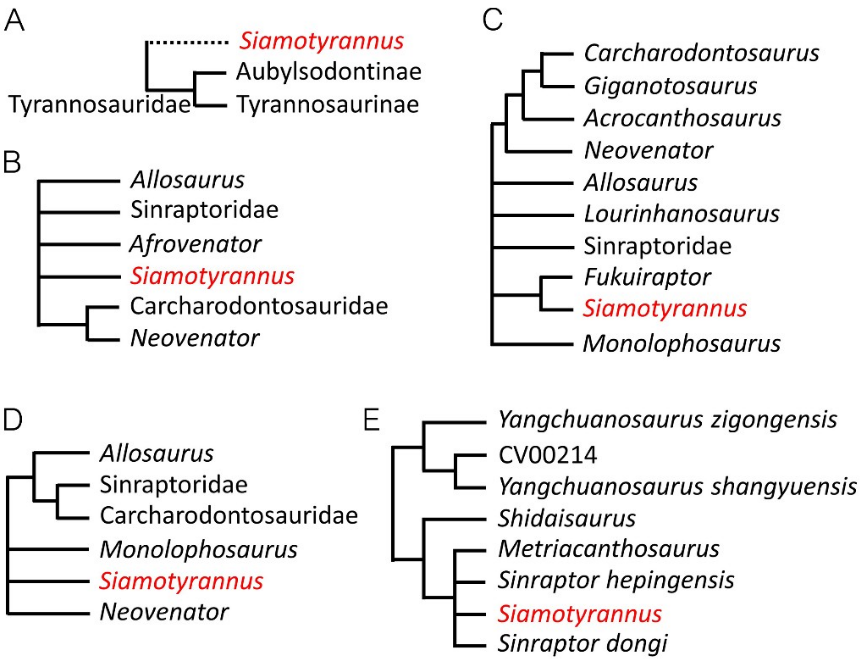


Fig.3. Phylogenetic reconstruction after Holtz, 2001 (A) which based on Buffetaut *et al.*, 1996 suggested *Siamotyrannus* might be a basal most Tyrannosauridae; B) from Rauhut, 2003a found *Siamotyrannus* to nest within Allosauroidea; C) from Holtz *et al.*, 2004 found *Siamotyrannus* to nest within Allosauroidea; D) from Rauhut *et al.*, 2009 found *Siamotyrannus* to nest within basal Allosauroidea; and E) from Carrano *et al.*, 2012., found *Siamotyrannus* to nest within Metriacanthosauridae (= Sinraptoridae).

Institutional abbreviation

BSP: Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich; **CV**, Municipal Museum of Chongqing, Chongqing; **FPDM**: Fukui Prefectural Dinosaur Museum, Katsuyama, Japan; **MB**: Museum für Naturkunde, Berlin, Germany; **MCNA**: Museo de Ciencias Naturales y Antropológicas "Cornelio Moyano", Mendoza, Argentina; **NMV**: National Museum of Victoria, Melbourne, Australia; **PRC**: Paleontological Research and Education Center, Maha Sarakham University, Maha Sarakham, Thailand; **SM**: Sirindhorn Museum, Department of Mineral Resources, Kalasin, Thailand; **UMNH**: Natural History Museum of Utah**,** Salt Lake City, Utah, USA.

Materials and methods

Materials

This research is based on the study of the partial skeleton (SM-PW9-1) housed at the public and permanent repository of the paleontological collection of Sirindhon Museum, Kalasin Province and from the dinosaur site 9, locally known as 'Lan Hin Lad Yao', Phuwiang Fossil Research Center and Dinosaur Museum, Khon Kaen Province, which are under the Department of Mineral Resources, Ministry of Natural Resources and Environment, The Royal Thai Government, Bangkok, Thailand.

Phylogenetic Methods

For the phylogenetic analyses, the characters were re-scored and edited in the program Mesquite (Maddison and Maddison 2015). The resulting matrices were imported into TNT 1.1 (Goloboff et al. 2008). We employed the methods and data matrices of Carrano et al. (2012) as well as Apesteguía et al. (2016) for an independent test of affinities of *Siamotyrannus*.

We used the data matrix of Carrano et al. (2012) since this matrix is the most up to date version of a theropod data matrix focused mainly on the basal (= non-coelurosaurian) tetanuran theropods. *Eoraptor* and *Herrerasaurus* serve as the outgroup taxa. All 351 characters were used and set to unordered and equally weighted. There were 61 terminal taxa. We used 'New Technology' search option, these included the default setting for sectorial, ratchet, tree drift, and tree fusion (see Carrano et al. 2012). We subjected the resulting most parsimonious trees (MPTs) to tree bisection and reconnection (TBR) branch swapping. We modified the character scoring for *Siamotyrannus* according to this study

We used the data matrix of Apesteguía et al. (2016), modified from Novas et al. (2013), because this data matrix focused primarily on Allosauroidea and basal Coelurosauria. *Ceratosaurus* serves as the outgroup. All 288 characters were used and set to unordered and equally weighted. There were 45 terminal taxa. We used the 'New Technology' search option which included the default settings for sectorial, ratchet, tree drift, and tree fusion as in Apesteguía et al. (2016). We added *Siamotyrannus* with our scoring to the dataset and excluded *Neovenator* and *Santanaraptor* from the analysis for a better result. and avoid polytomy.

Systematic paleontology

Dinosauria Owen, 1842

Theropoda March, 1881

Tatanurae Gauthier, 1986

Coelurosauria von Huene, 1914

Siamotyrannus isanensis Beuffetaut, Suteethorn, and Tong, 1996

***Holotype*:** SM-PW9-1**,** paleontological collection of Sirindhorn Museum, Kalasin Province, Thailand. The skeleton consists of five dorsal vertebrae, the sacrum, the 13 anterior to mid caudal vertebrae with chevrons, and the left half of the pelvis. Some of the caudal vertebrae are still in the digging site (dinosaur site number 9 'Lan Hin Lad Yao') in the Phu Wiang National Park, Khon Kaen Province.

***Locality and horizon*:** Sao Khua Formation (Barremian), Early Cretaceous, at Phu Wiang Site 9 Locality, Phu Wiang District, Khon Kaen Province, northeastern Thailand.

***Original diagnosis*:** A large theropod (total length ~ 6.5 m) with a long and relatively low ilium, the anterior blade of which forms an incipient subhorizontal medioventral shelf. Pubis with a long, straight shaft terminating in a massive distal boot, which is more developed anteriorly than posteriorly. No proximolateral crest on the pubis. Obturator foramen of pubis open ventrally, but largely encircled by the proximal bony hook. Ischium slender, curved, with a small but well defined scar on its proximodorsal edge for the insertion of the Musculus flexor tibialis internus part 3. Anterior caudal vertebrae with tall, slender neural spines. More posterior caudals with the small dorsal process on the neural arch anterior to the main neural spine. Anterior chevrons long, straight and slender (all from Buffetaut et al. 1996).

***Revised diagnosis*:** *Siamotyrannus* is diagnosed by the following unique autapomorphies: 1) double, low and broad vertical ridges on the central part of the lateral iliac blade, and 2) a notch on the dorso-posterior part of the postacetabular blade of the ilium.

***Discussion*:** The characters suggested in the original diagnosis were more widespread among theropod dinosaurs, so we revised it by using unique autapomorphies that clearly observed from *Siamotyrannus*.

2. RESULT

Description

Axial skeleton

Dorsal vertebrae

The dorsal vertebral column is represented by five dorsal vertebrae that are in articulation (fig. 4, 5). The position of the dorsals in present work will be given by the number of the preserved series, not the exact position in the vertebral column. The neural arches are fused to the centra. The centra are amphiplatyan and lack pleurocoels. The specimen is probably an adult because of the fusion of the dorsal neural arch to the centrum. The dorsal vertebrae are incomplete, lacking the neural spines and the left transverse processes. The dorsal 4 in the preserved series has an incomplete right transverse process and only the parapophysis is preserved. Only half of the centrum of dorsal 5 is preserved. The centra have no hypapophyses, and they are hourglass shape so that the articular faces have nearly double the cross-sectional diameter of the middle of the centra (see supplementary table 1).

In anterior view, only the right prezygapophysis and a part of left prezygapophysis of dorsal 1 are preserved. There is possibly hypantrum in the dorsal 1 (fig. 4B, 5B). In lateral view, the postzygapophyses do not project posteriorly beyond the level of the posterior articular surface of the centra of dorsal 1 and 2. The dorsal transverse processes are long and posterodorsally inclined (sloping backward), especially in dorsal 2 and 3. The centrum is gently amphiplatyan (based on the preserved part of dorsal 1). Because of centra are preserved in articulation, this character, however, must be confirmed in other specimens. In dorsal view, the dorsal transverse processes are strongly back-turned caudally and triangular (fig. 4E, 5E).

The dorsal vertebrae have well developed transverse processes; these processes bear both parapophyses and diapophyses. They are horizontally directed. The diapophyses slope backward (extending laterally, posteriorly, and dorsally) and the slope is greater in dorsal 3 than in dorsal 1. Each process is triangular in cross-section distally. The parapophyses are long in dorsal 2 – 4 and short in dorsal 1. They are positioned high in dorsal 2 – 4 at the base of the transverse process (anterodorsal of the centra). Whereas in dorsal 1, the parapophysis is in a low position. The parapophysis is situated at mid-height on the centrum of dorsal 1 and tends to rise up onto the arch in dorsal 2, 3, and 4 so that eventually it is located just ventrolateral to the prezygapophysis (at the base of diapophysis). The parapophyseal articular surface on the dorsal 1 is smaller than those of dorsal 2 – 4, and has a square shape in outline. However, in dorsal 2 – 4, the surfaces have an oval outline. In dorsal 2, 3, and 4, the parapophyses become pedunculate (the articular surface is supported by a stalk that projects outward and downward). Dorsal 1 lacks this stalk. The stalk of the dorsal 2 is 60 mm long, in dorsal 3 it is 48 mm, and in dorsal 4 it is 53 mm in length.

The length of the parapophyses projects far laterally. In Abelisauroids, the parapophyses extend nearly twice as far laterally as in, whereas they are reduced in allosauroids so that they are nearly flush with the arch (Carrano and Sampson 2008). In *Siamotyrannus*, the elevation of the parapophyses is projected far laterally but not more than half the diapophyseal length. The prezygapophyses of dorsal 1 are inclined dorsally. The orientation of the hyposphene laminae is parallel and sheet-like (narrow), as seen in the hypantrum of dorsal vertebra 1. Centrum length relative to height is less than 2.

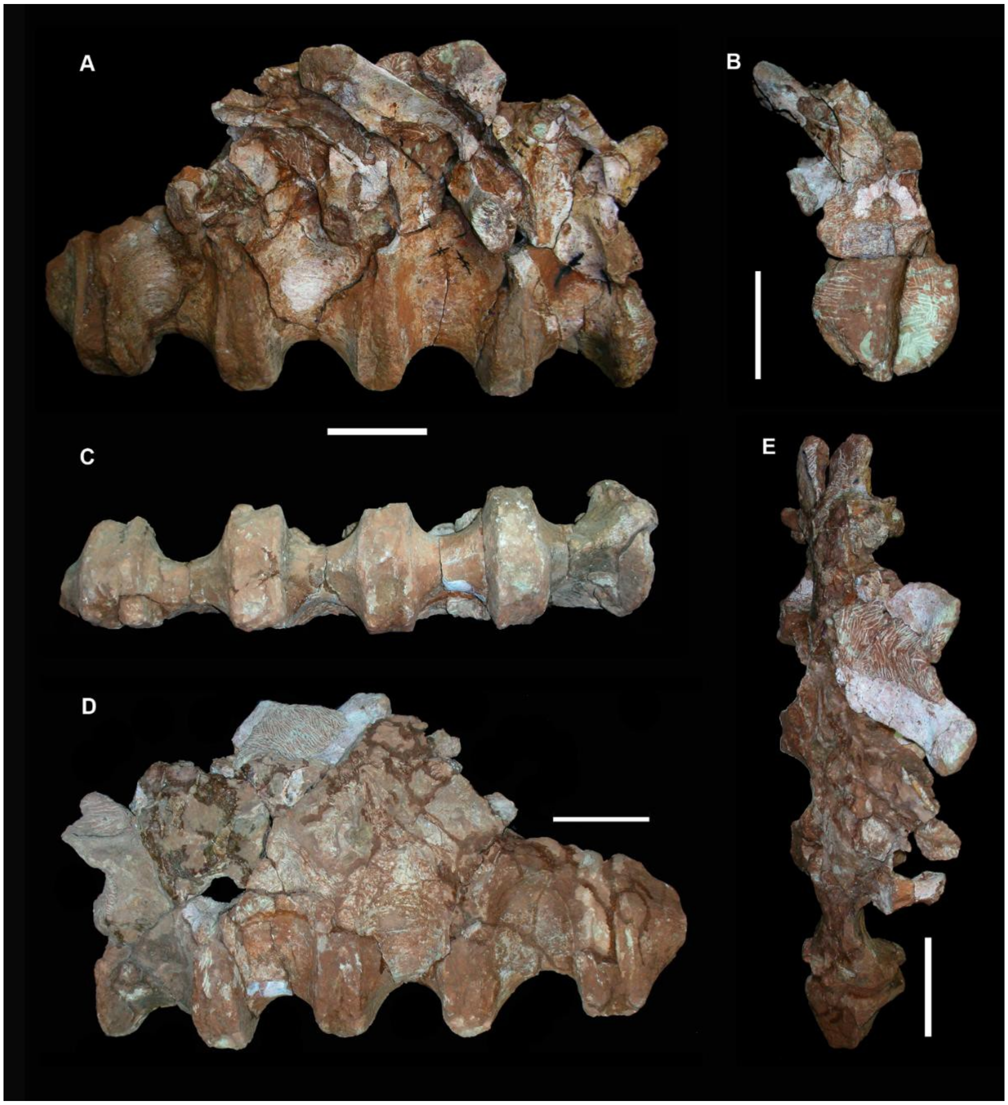


Fig.4. *Siamotyrannus isanensis*, SM-PW9-1. Middle dorsal vertebrae in right lateral (A), anterior (B), ventral (C), left lateral (D), and dorsal (E) views. Scale bar = 10 cm.

Laminae

We follow the terminology of Wilson (1999) in identifying the laminae on the dorsal vertebrae. The laminae are quite complex in *Siamotyrannus* compared to other theropods. The parapophysis is linked to the centrum by the anterior centroparapophyseal lamina (acpl, in dorsal 2, 3, and 4, absent in dorsal 1) and the posterior centroparapophyseal lamina (pcpl, in dorsal 2, and 3, absent in dorsal 1 and 4).

The parapophysis of dorsal 1 is supported by prezygoparapophyseal lamina (prpl) and an unidentified ridge or lamina. The parapophysis of dorsal 2 is supported by the paradiapophyseal lamina (ppdl), posterior centroparapophyseal lamina (pcpl), and anterior centroparapophyseal lamina (acpl). The parapophysis of dorsal 3 is supported by the paradiapophyseal lamina (ppdl), posterior centroparapophyseal lamina (pcpl), anterior centroparapophyseal lamina (acpl), and prezygoparapophyseal lamina (prpl). Finally, the parapophysis of dorsal 4 is supported by the paradiapophyseal lamina (ppdl), prezygoparapophyseal lamina (prpl), and anterior centroparapophyseal lamina (acpl, fig. 2A, 3A). The posterior centroparapophyseal laminae (pcpl) on dorsal 2 and 3 are posterodorsally oriented and weakly developed.

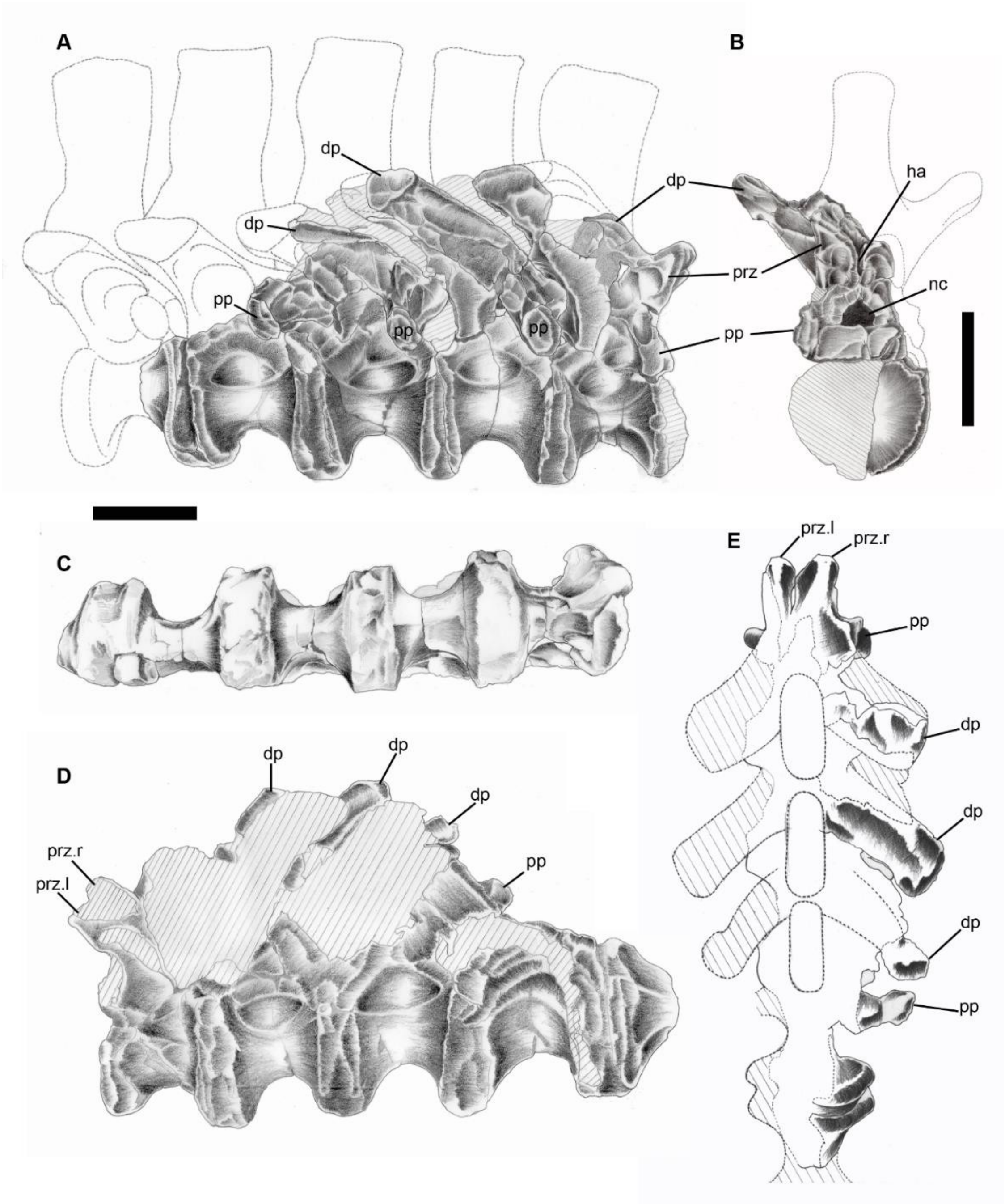


Fig.5. *Siamotyrannus isanensis*, SM-PW9-1. Middle dorsal vertebrae in right lateral (A), anterior (B), ventral (C), left lateral (D), and dorsal (E) views. **dp**, diapophysis; **ha**, hypantrum; **nc**, neural canal; **pp**, parapophysis; **prz**, prezygapophysis. Scale bar = 10 cm.

There are ridges that extend posterodorsally and posteroventrally from the prezygapophyses to the parapophyses, forming the anterior margin of the fossae (infraprezygapophyseal fossae) in dorsal 2, 3, and 4. This fossa is formed by the paradiapophyseal lamina and anterior centroparapophyseal lamina in dorsal 2, by the prezygoparapophyseal lamina and anterior centroparapophyseal lamina in dorsal 3 and 4. In the dorsal 2 and 3, there are two or more laminae that join the parapophyses to the laminae between the prezygapophyses and diapophyses. The infradiapophyseal fossae are found posteriorly to these laminae and ventrally to the transverse process. There are strong ridges that support the posterior margins of the transverse processes and form the anterolateral margins of the fossae (infrapostzygapophyseal fossae) associated with the postzygapophyses found in dorsal 1, 2, and 3. In dorsal 3, there are many ridges on the parapophysis, i.e., the prezygoparapophyseal lamina and anterior centroparapophyseal lamina that form the infraprezygapophyseal fossa, and the paradiapophyseal lamina and posterior centroparapophyseal lamina that form the infradiapophyseal fossa. There is no ventral groove on the centra.

The presence of the paradiapophyseal lamina (ppdl) on the dorsal 2, 3, and 4 but not on the dorsal 1 suggest that the dorsal 1 is most likely to be the fourth dorsal vertebra (see Wilson, 1999) The dorsal vertebra in which the parapophysis first interrupts the anterior centrodiapophyseal lamina (acdl) to form the paradiapophyseal lamina (ppdl) and anterior centroparapophyseal lamina (acpl) is usually the fifth vertebra (Wilson, 1999). The first presence of the paradiapophyseal lamina (ppdl) on the fifth dorsal vertebra is also presents in *Sinraptor dongi* (Currie and Zhao 1993, p.2059) and *Sinraptor hepingensis* (Gao 1998, p.28).

Dorsal rib

A fragment of the dorsal rib is preserved. It is about 150 mm in length and had an oval outline in cross-section. There is no rib head or pneumaticity preserved.

Sacral vertebrae

The sacrum consists of five sacral vertebrae plus the last dorsal vertebra incorporated as an additional dorsosacral into the structure (Fig. 6, 7). However, whereas the fusion of the sacrals 1–5 is complete, the last dorsal (the dorsosarcral in this study) remains more clearly differentiated but still contacted the ilium. Its centrum resembles the last dorsal of *Metriacanthosaurus* (Carrano et al. 2012) and *Allosaurus* (A.S. pers. obs.) in that the ventral surfaces of posterior dorsal centra of all these taxa are flat.

The sacrum is not complete. It lacks some of the neural arches. The quality of preservation is generally good but is better on the left side than on the right side which is eroded. The centra are generally well preserved. The transverse processes and sacral ribs are not preserved on the right side because of the erosion. The complete, articulated sacrum is 680 mm in anteroposterior length without the dorsosacral vertebra. The sacral centra are not concave laterally as opposed to the dorsal vertebrae and are all higher than long. The neural spines of sacrals 1, 2, 4, and 5 are preserved but lack the distal end, and the neural spines of sacrals 4 and 5 are fused into a single plate. The neural arches of these two sacrals are fused with the centra. The ilium covers six vertebrae, and six vertebrae contact the ilium. The sacral centra are rounded ventrally. The second sacral centrum is constricted in ventral view (fig. 6B, 7B). There is no ventral keel. The dorsosacral is flattened ventrally as mentioned above. There appear to be small foramina on the sacral vertebrae 2 and 4 on both sides, but this character needs to be verified by more preparation and careful examination.

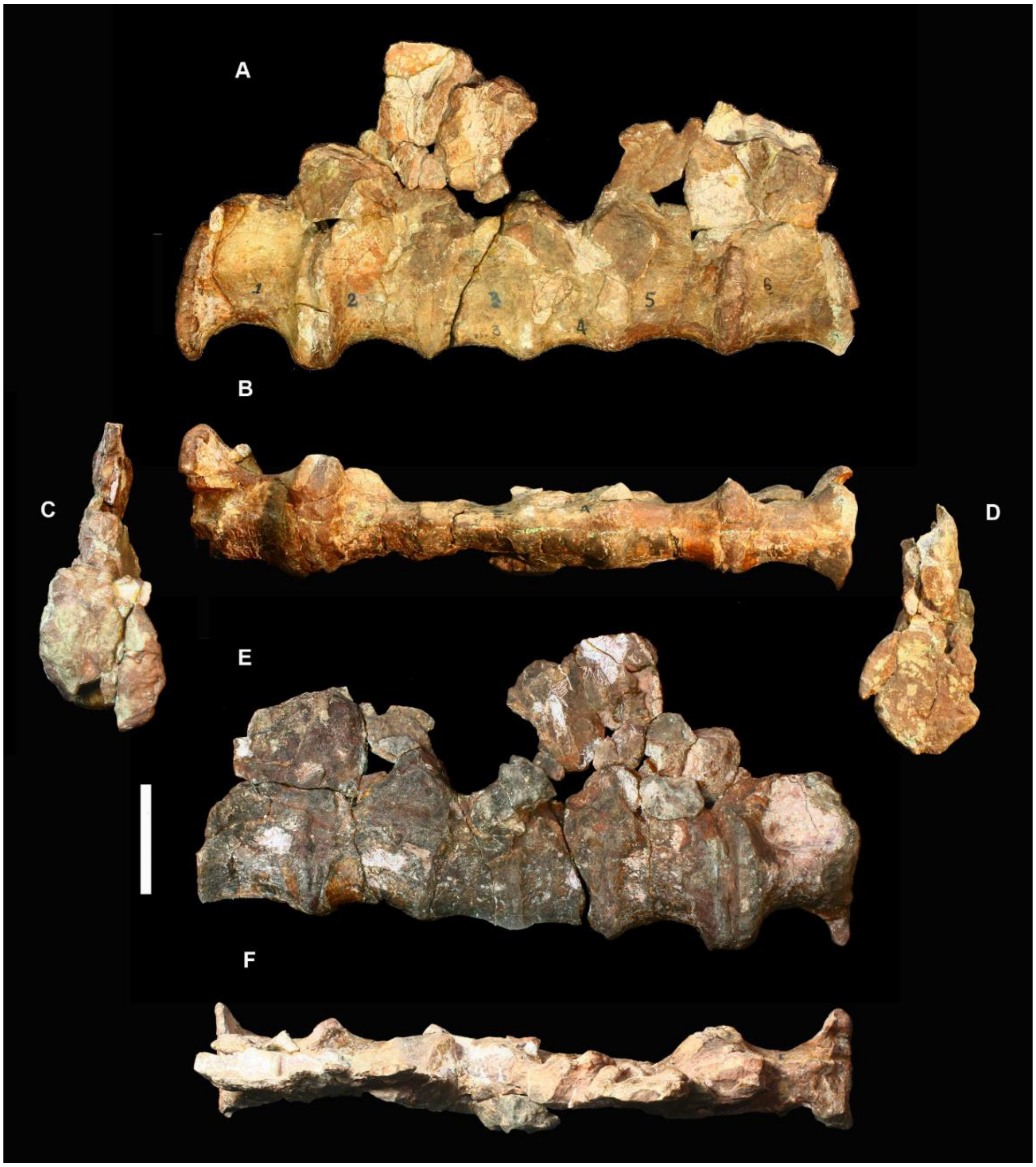


Fig.6. *Siamotyrannus isanensis*, SM-PW9-1. Sacral vertebrae in left lateral (A), ventral (B), anterior (C), posterior (D), right lateral (E), and dorsal (F) views, scale bar = 10 cm.

The anterior surface of the dorsosacral centrum and the posterior surface of the fifth sacral centrum are flat, so the sacrum might be amphiplatyan. The centra of the sacral 2 and 3 are relatively short compared to the sacral 1, the centrum of the sacral 2 is relatively narrow ventrally compare to the sacral 1. The first sacral rib had a limited contact with the centrum (as in *Allosaurus*, Currie and Zhao 1993). The sacral ribs and transverse processes are fused to the iliac blade, but we also can see the suture between them. The transverse processes are short, robust, and not fused together dorsally. The third and fourth transverse processes are long anteroposteriorly and longer than the first and second transverse processes. The first transverse process is thin anteroposteriorly and long ventrodorsally.

The orientation of the ventral margin of middle sacral centra is approximately horizontal. The position of the posterior attachment of the sacral ribs to the ilium is posterodorsal. The sacral ribs. depth relative to ilium height is less than 85%.

On the dorsosacral vertebra, the diapophysis of this vertebra is anterior in position and high above the centrum (evidence from the first transverse process on the medial side of the ilium, although the neural arch of the dorsosacral is not preserved). The centrum is flat ventrally.

On the first sacral vertebra, the neural spine is preserved and thick transversely. The spine is higher than the sacral centrum height and does not fuse to the second sacral neural spine. The neural spine becomes broader towards the distal end and is slightly inclined posteriorly. It is placed near the posterior part of the centrum. The thickness of the spine is approximately the same from base to tip. The anterior margin of the neural spine is vertical laterally. In a fracture surface, it can be seen that the spine is pneumatized. On the second sacral vertebra, the neural spine is preserved, it is inclined posteriorly and more so than the first spine. The spine is placed near the anterior part of the centrum. The centrum is higher than long. On the third sacral vertebra, the centrum is higher than long. On the right side, there is a sacral rib articulation situated on the anterodorsal side of the third sacral centrum and the posterodorsal of the second sacral centrum at the base of the neural arch. The sacral rib on the left side has the same position. On the fourth and fifth sacral vertebrae, the neural spines of the fourth and fifth vertebrae are preserved, they are fused together but lack the tips. The articulation for the sacral ribs and the transverse process is clearly defined.

The sacral ribs are well separated from each other but the sacral ribs and transverse processes are fused to each other (sacral vertebra 2, 3, and 4) and form a continuous sheet or lamina, linking sacral rib and transverse process (as in *Alioramus alti*, Brusatte et al. 2012) (see the ilium part). The transverse process – sacral rib of the second sacral vertebra (tr2/sr2) is located at the same position as the anterior vertical ridge on the lateral side of the ilium. The transverse process sacral rib of the third sacral vertebra (tr3/sr3) is located at the same position as the posterior vertical ridge on the lateral side of the ilium.

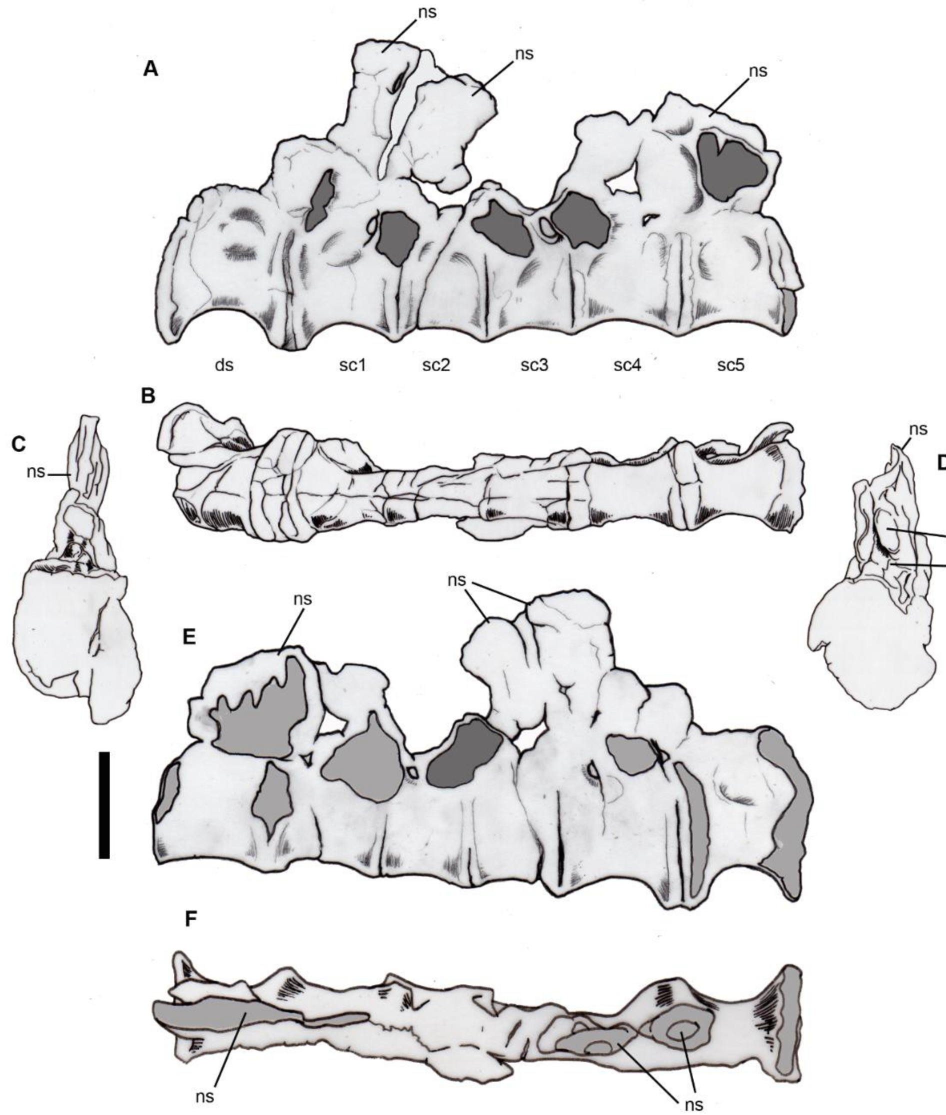


Fig.7. *Siamotyrannus isanensis*, SM-PW9-1. Sacral vertebrae in left lateral (A), ventral (B), anterior (C), posterior (D), right lateral (E), and dorsal (F) views. **ds**, dorsosacral vertebra; **nc**, neural canal; **ns**, neural spine; **poz**, postzygapophysis; **sc**, sacral vertebra. Dark grey tone indicates sacral rib articulations, light gray tone indicates broken bone surface. Scale bar = 10 cm.

Caudal vertebrae

The preserved caudal vertebrae are represented by 13 anterior-to-mid caudals that comprise a continuous series measuring approximately 1600 mm long (fig. 8, 9, 10).

On the first caudal vertebra, the centrum is complete and well preserved. The neural arch lacks prezygapophyses, the neural spine, and the right transverse process. Only the left transverse process, left postzygapophysis, and the hyposphene are preserved (fig. 8A). There is no centrodiapophyseal lamina or infradiapophyseal fossa on the neural arch as opposed to the dorsal vertebrae. The centrum is slightly concave anteriorly and flat posteriorly. The centrum is higher than long. The transverse process is long, emerges posterolaterally from the neural arch and is nearly horizontal in lateral view. It becomes broader towards the distal end. The transverse process is inclined caudally and triangular in dorsal view. It is placed near the middle of the centrum but slightly posteriorly. The hyposphene is present. It is a thin, vertical sheet of bone at the base, and its ventral end is expanded transversely. There is a ventral sulcus or small groove located in the middle of the ventral surface of the centrum. The sulcus is approximately 20 mm in length. There is no pleurocoel or foramen on the centrum. The facet for chevron articulation cannot be observed due to incomplete preservation. On the second caudal vertebra, the anterior part of the centrum is concave, the posterior part is flat or slightly concave but less concave than the anterior part. The centrum is higher than long. A hyposphene-hypantrum articulation is present. The shape of the hyposphene is similar to the hyposphene of the first caudal. The ventral sulcus is present and is approximately 20 mm long. There is no pleurocoel or foramen on the centrum, but a lateral fossa is present on the dorsal part of centrum below the base of the neural arch. There is a facet for chevron articulation on the posterior margin. On the third caudal vertebra, the anterior part of the centrum is concave, the posterior part is flat. The centrum is slightly longer than high or equal in length. The hyposphene is present but its distal end is less expanded than that of the first and second caudal, maybe due to the quality of preservation. A lateral fossa is present on the centrum as in the second caudal. There is a facet for chevron articulation (fig. 8C). On the fourth caudal vertebra, only the upper part of the centrum and the base of the neural arch are preserved. The anterior of the centrum is slightly concave, the posterior one cannot be observed.

The broken bone surface reveals that there is no pleurocoel or pneumaticity inside the bone. The lateral fossae on the upper part of the centrum might be present as evidenced by the constriction of the preserved part of the centrum. On the fifth caudal vertebra, The anterior part of the centrum is slightly concave; the posterior part cannot be observed. The centrum is longer than high. The ventral sulcus is present and approximately 25 mm long. There is no pleurocoel or foramina on the centrum, but lateral fossae are present on the upper part of centrum below the base of the neural arch. On the sixth caudal vertebra, the centrum is longer than high. The ventral sulcus is present and approximately 28 mm long (fig. 9, 10A, B). On the seventh caudal vertebra, the centrum is longer than high and box-like in cross- section. The ventral side of the centrum is nearly flat and does not show a sulcus or groove (fig. 9, 10A, B). On the eighth to the eleventh caudal vertebrae (CV 8-11), their centra are all longer than high and have box-like shape except caudal 11. Its centrum is slightly oval in shape in cranial and caudal view. The ventral surface of the centra is nearly flat, lacking any sulcus or groove and less compressed laterally than dorsal vertebrae (fig. 9, 10C, D). On the twelfth and thirteenth caudal vertebra (CV 12-13), these centra are longer than high. The ventral surface is convex and lacks a ventral sulcus or groove. The centra are oval or circular in shape in cranial and caudal view (fig. 9, 10E, F). These two preserved last caudal vertebrae, however, might be from a more posterior position, for example, in the position of 14-15 or 15-16 vertebrae based on the shape and size of the centra and the much small neural spines of the caudal vertebrae compare with the preceeding caudal vertebrae.

Fig.8. *Siamotyrannus isanensis*, SM-PW9-1. Caudal vertebra 1 to 5 in anterior, left lateral, posterior, right lateral, dorsal, and ventral view respectively. (A) = caudal 1, (B) = caudal 2, (C) = caudal 3, (D) = caudal 4, and (E) = caudal 5. **chaf**, facet for chevron articulation; **hyp**, hyposphene; **nc**, neural canal; **ns**, neural spine; **prz**, prezygapophysis; **poz**, postzygapophysis; **tr**, transverse process; **arrow**, ventral sulcus. Scale bar = 10 cm.

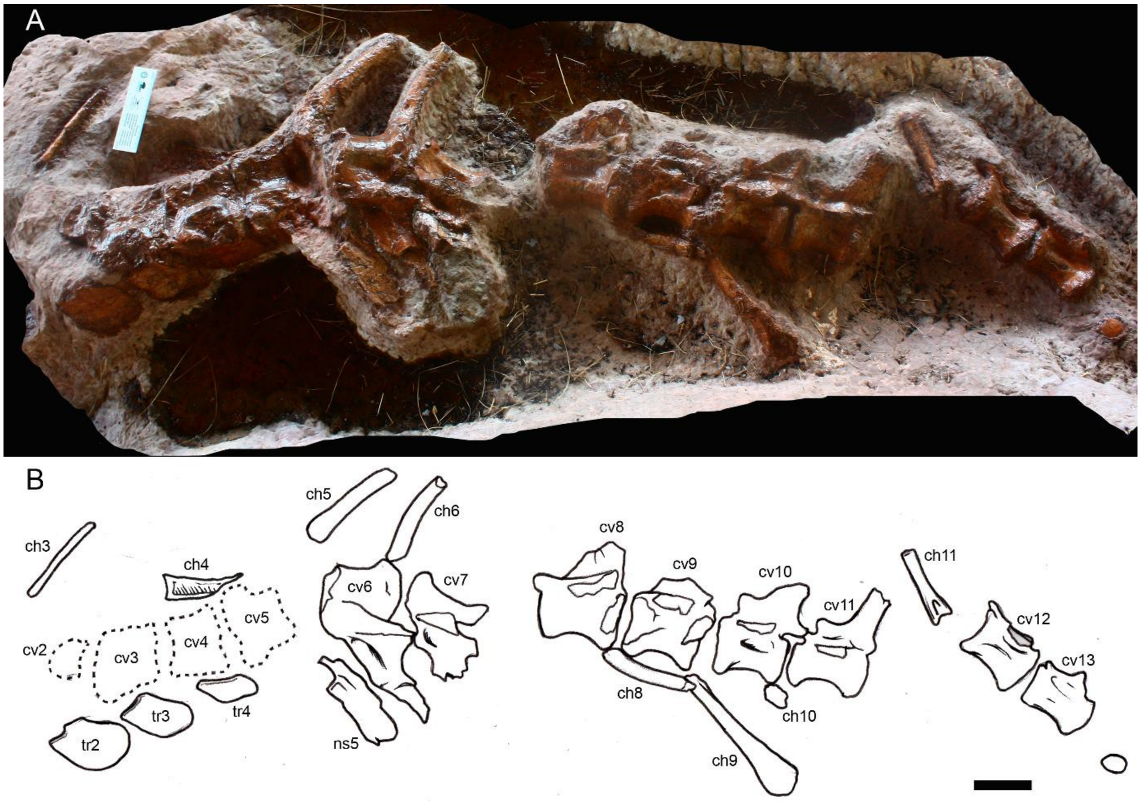


Fig.9. *Siamotyrannus isanensis*, SM-PW9-1. Caudal vertebra 2 to 13 in original posture. **ch**, chevron; **cv**, caudal vertebra; **ns**, neural spine; **tr**, transverse process. Scale bar = 10 cm.

Chevrons

Some chevrons of the anterior to mid-caudal vertebrae are preserved (chevron 2 to 6 and 8 to 11) (fig. 9, 10). Chevron 2 is nearly complete, lacking the proximal end. It is straight, and the distal part is wider than the proximal part. Chevron 3 is also nearly complete but lacks the proximal end. It has straight posterior margin and gently curved anterior margin and tapering distally. The distal end of chevron 4 is broken, so its length is uncertain. Chevron 5 is complete, rod-like, with parallel margins and gently curves posteriorly. It is proportionately long and slender. The distal part is wider than the middle part but narrower than the proximal part. Chevron 6 is gently curved and lacks the distal end. It has a small cranial process. Its middle part is narrower than the proximal and distal part. Chevron 8 is slightly curved, with the cranial process, but lacks the distal end. The bone is wider distally. Chevron 9 is gently curved with a rounded distal end. This might due to a pathology. Only the proximal part of chevron 10 is preserved. It has a cranial process, and its curvature is uncertain. Chevron 11 lacks the distal end but appears to be straight. The haemal arch canal is enclosed dorsally in chevrons 4, 9, and 11. The proximal articular surface of the chevrons is without distinct anterior and posterior facets (low mounds may be present, as evidenced by chevrons 5, 6, 8, and 9).

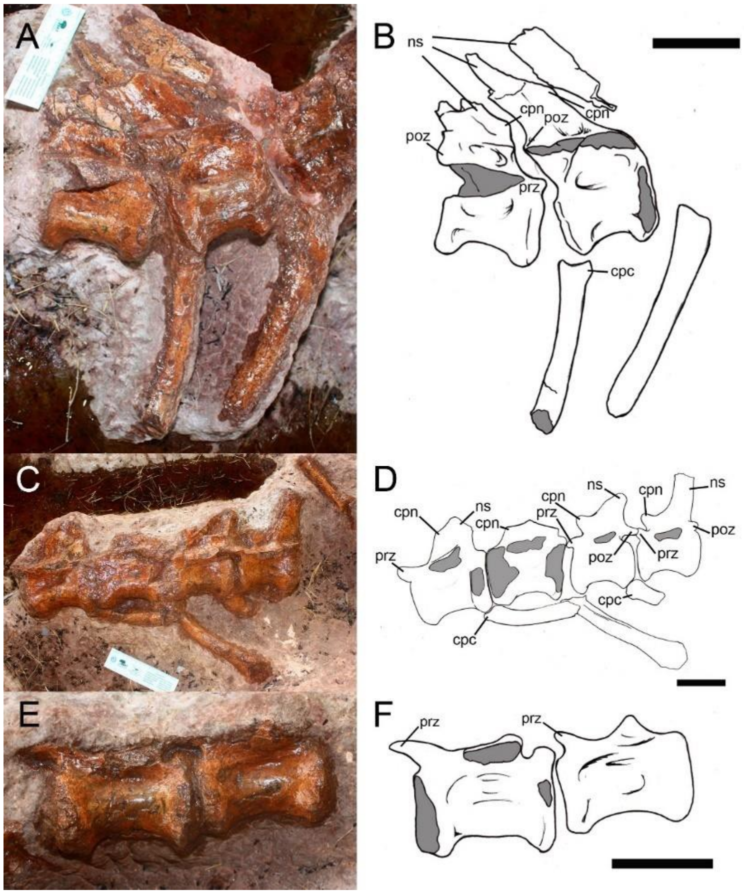


Fig.10. *Siamotyrannus isanensis*, SM-PW9-1. Caudal vertebra 5 to 7 (A, B), caudal vertebra 8 to 11 (C, B), and caudal vertebra 12, 13 (E, F). **cpc**, cranial process of the chevron; **cpn**, cranial process of the neural spine; **ns**, neural spine; **prz**, prezygapophysis; **poz**, postzygapophysis, gray tone indicates broken bone surface. Scale bar = 10 cm.

Appendicular skeleton

Pelvis

Only the left half of the pelvis is known. The ilium and pubis are almost complete, lacking only the distal part of the preacetabular blade of the ilium and posterior part of the pubic boot. The ischium is nearly complete but lacks the anterior obturator process and the distal end of the shaft (fig. 11, 12, 13). The nearly complete left ilium was found *in situ* and associated with the sacral vertebrae and the anterior caudal vertebrae. The pelvic elements are not fused. The ilium is dolichoiliacic, i.e., it has an elongated and dorsoventrally expanded, blade-like preacetabular process that overhangs the pubic peduncle anteriorly. The pelvis is propubic or triradiate which us found in basal dinosauriformes, sauropodomorphs, and many theropods. In *Siamotyrannus* the pubis is oriented almost vertically.

Ilium

The iliac blade is thin transversely (circa 13 -19 mm) and has two vertical ridges on its lateral surface above the acetabulum. The acetabular margin of the pubic peduncle is slightly mediolaterally concave. The surface of the distal part of the postacetabular blade is nearly flat, whereas the surface of the preacetabular blade is concave, forming a large fossa between the anterior margin of the preacetabular blade and the anterior of the two-vertical ridge. The open space between the preacetabular process and pubic peduncle of the ilium is narrow, but it becomes slightly broader at the distal part in lateral view. The notch is wider and expands in width as it continues anteriorly. It does not remain narrow across its entire length as opposed to *Stokesosaurus clevelandi* and *Juratyrant langhami* (Brusatte and Benson 2013).

Fig.11. *Siamotyrannus isanensis*, SM-PW9-1. Left pelvis in lateral view (A), medial view (B), and the distal end of the pubic boot (C), scale bar = 10 cm.

The ilium is sub-rectangular in shape and nearly as tall posteriorly as above the acetabulum. The semi-oval ilium of Xiongguanlong as described by Brusatte and Benson (2013) is problematic since the entire postacetabular blade and the ischial peduncle are reconstructed (Li et al. 2009 supplementary material).

There are two parallel vertical ridges on the lateral surface of the ilium as already mentioned. The ridges project straight dorsally and are slightly posterodorsally inclined (as defined by the angle between the pelvis and the vertebral column). The ridges are well defined and well developed on the lateral surface of the iliac blade. The posterior ridge is broader, slightly lower, and shorter than the anterior ridge. The two ridges are short and do not extend to the dorsal margin of the iliac blade. They divide the iliac blade into three fossae. The two ridges are narrow at the bases and the tips, not broad at the base and narrow at the tip.

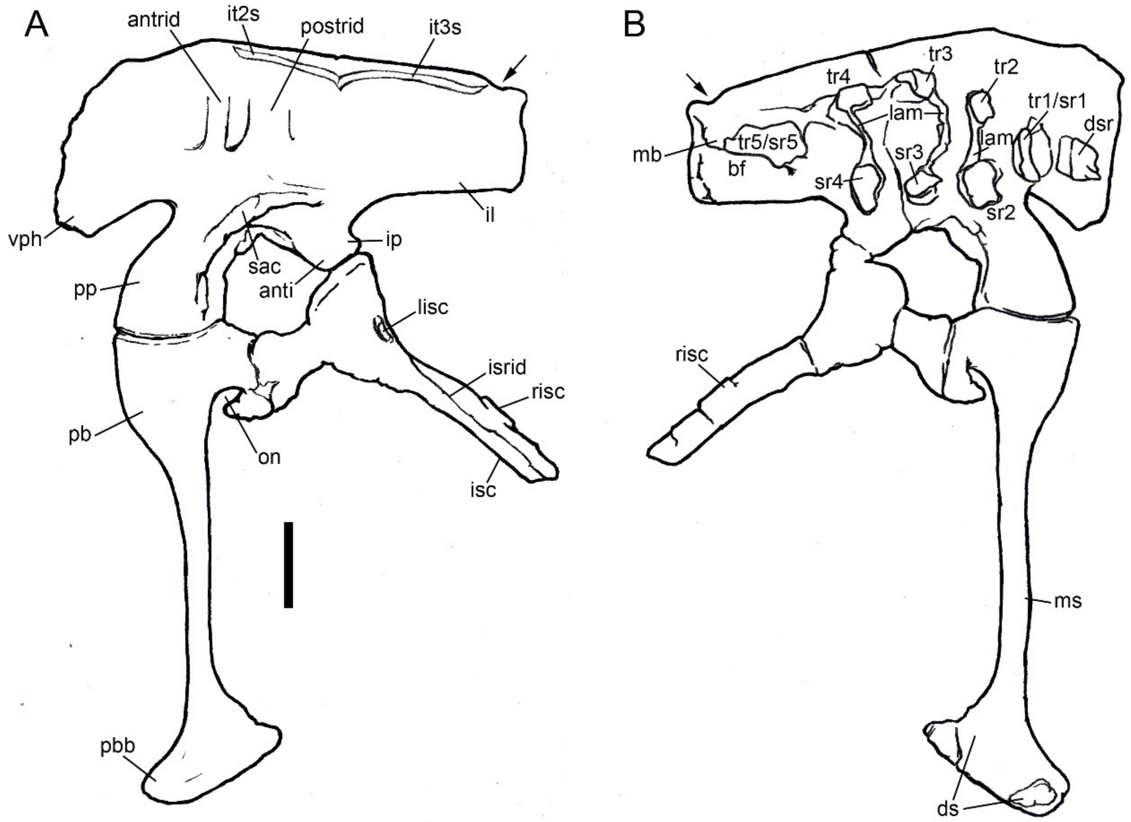


Fig.12. *Siamotyrannus isanensis*, SM-PW9-1. Line drawing of the left pelvis in lateral view (A) and medial view (B). **anti**, antitrochanter; **antrid**, anterior ridge on lateral surface; **bf**, brevis fossa; **ds**, distal symphysis; **dsr**, dorsosacral rib articulation; **il**, ilium; **ip**, ischial peduncle; **isc**, ischium; **isrid**, ischial ridge; **it2s**, M. iliotibialis 2 original scar; **it3s**, M. iliotibialis 3 original scar; **lam**, lamina linking sacral rib and transverse process; **lisc**, ligamental scar on ischium; **mb**, medial blade; **ms**, medial symphysis; **msac**, medial supraacetabular crest; **on**, obturator notch; **postrid**, posterior ridge on lateral surface; **pb**, pubis; **pbb**, pubic boot; **pp**, pubic peduncle; **risc**, small fragment of right ischium; **sac**, supraacetabular crest; **sr**, sacral rib articulation; **tr**, transverse process articulation; **vph**, ventral preacetabular hook; **arrow**, iliac notch. Scale bar = 10 cm.

The ilium is 800 mm long. The iliac blade is relatively low and robust. The height above the acetabulum is 320 mm. The dorsal margin of the iliac blade is gently straight throughout its entire length. The anterodorsal part of the iliac blade is broken off. The distal end of the ilium is robust. The preacetabular process is slightly shorter than the postacetabular process (suppl. table 6). The anterior end of the preacetabular process is ventrally expanded (down-curved dorsal margin of the preacetabulum), although the distal end of the process is broken. The anterior margin of the preacetabular process is straight. The anterodorsal part is broken, so whether it is convex/round or formed an angle cannot be assessed. The posterior end of the ilium is rectangular and the posterior margin of the postacetabular process is nearly straight. The preacetabular part of the ilium is significantly taller than the postacetabular part (excluding the ventral expansion). It is also slightly higher than the basal part of the postacetabular process (suppl. table 6).

The anterior margin of pubic peduncle of the ilium is convex in lateral view. The pubic peduncle is long anteroposteriorly and narrow. The length/width ratio of the pubic peduncle is approximately 1.9. This ratio is circa 2.0 in allosaurians, circa 3.0 in coelurosaurs, and equal to or less than 1.7 in all non-avetheropods and metriacanthosaurids (Carrano et al. 2012). The outline cross section of the pubic peduncle of the ilium is semi-oval. The posterior margin is wider than the anterior margin transversely (fig. 13C, D). The ventral part of the pubic peduncle ends is an anteroventrally directed tip, facing more ventrally than anteriorly and without a pronounced kink. There is a ridge on the ventral margin of the preacetabular process. This ridge does not continue onto the lateral surface of the base of the pubic peduncle. It ends just before the base of the pubic peduncle (mentioned in Buffetaut et al. 1996 as a sub-horizontal medioventral shelf of the anterior iliac blade). On the medial side, there is a low, medial ridge that extends from the preacetabular process onto the base of the pubic peduncle for a short distance. These two ridges just stop at the midpoint of the pubic peduncle neck, so the lower part of the neck is smooth. Between the two ridges, there is a low fossa.

The dorsal margin of the postacetabular blade is straight and meets the posterior end in a nearly right angle. The dorsal margin of the acetabulum is laterally expanded into a supraacetabular crest. The supraacetabular crest is well developed (fig. 13C, D) and its depth is 50 mm. The iliac acetabulum depth is 65mm. The brevis fossa is deep and wide (broad). There is a ligamental scar for muscle attachment (brevis tubercle) on the dorsolateral roof of the brevis fossa. The muscle inserts in a longitudinal ventral groove that is bounded by the iliac blade laterally and the brevis shelf medially (Rauhut 2003a). The lateral and medial wall of iliac brevis fossa are nearly horizontal, the lateral wall covering the medial wall of the fossa along the entire length in lateral view. The supraacetabular crest and the lateral blade of the brevis fossa are not continuous.

For the articulation of the iliac blade with the sacrum, the iliac blade is vertical, well separated above the sacrum. The medial side of the iliac blade is well separated from the sacral neural spines. The pubic peduncle is significantly longer than ischial peduncle. The ischial peduncle is tapering slightly ventrally with a well-defined articular facet. The pubic peduncle is 193 mm long, 84 mm wide anteriorly, and 100 mm wide posteriorly. The ischial peduncle is 65 mm longand 101 mm wide. The ischial peduncle length thus is less than half of the pubic peduncle length. The articular facet of the ischial peduncle of the ilium is posterodorsally inclined in ventral view, not vertical as in *Sinraptor dongi* (cast of the holotype housed at FPDM) or horizontal as in *Syntarsus* (Rauhut 2003a) (fig. 13C, D).

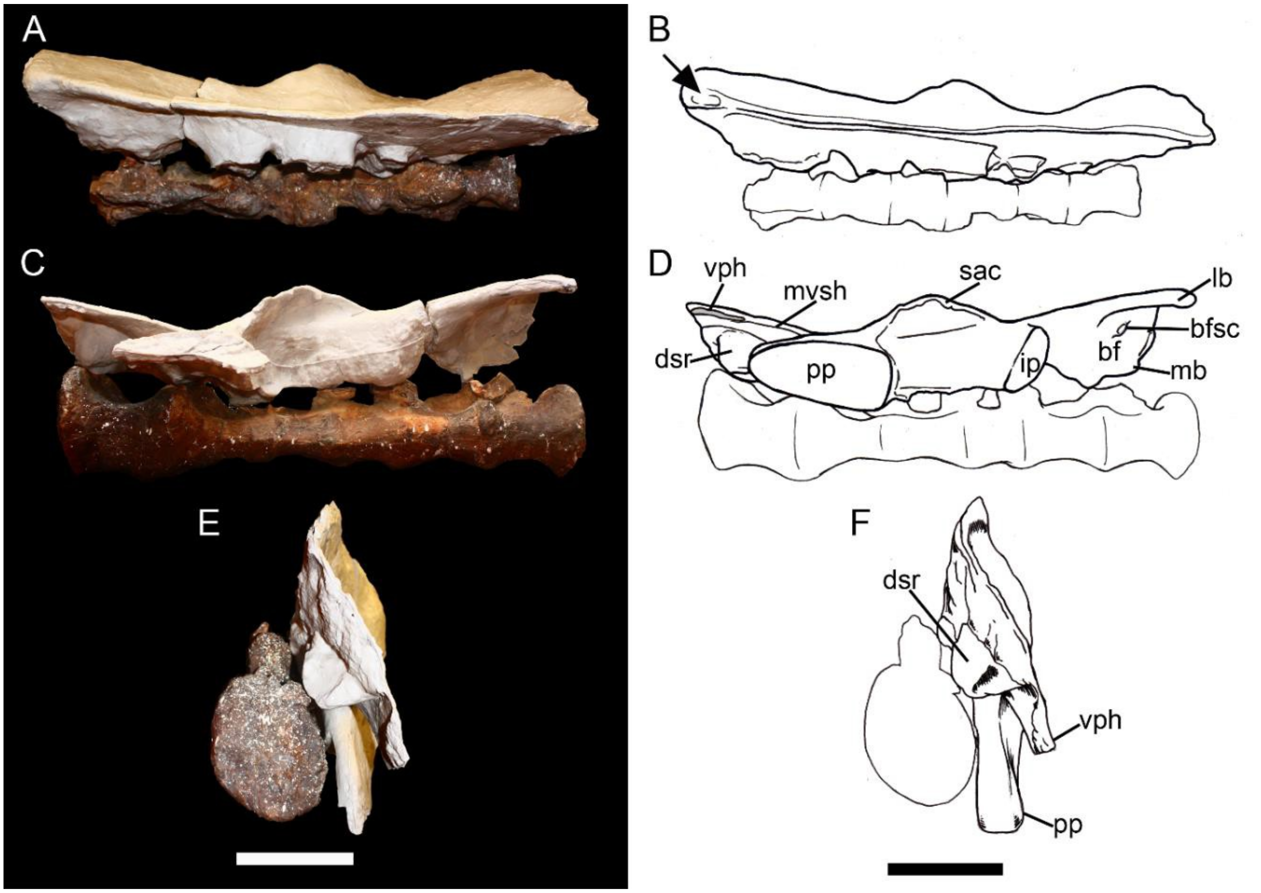


Fig.13. *Siamotyrannus isanensis*, SM-PW9-1; cast. Left ilium in dorsal (A, B), ventral (C, D), and anterior (E, F) views. **bf**, brevis fossa; **bfsc**, ligamental scar on the brevis fossa; **dsr**, dorsosacral rib articulation; **ip**, ischial peduncle; **lb**, lateral blade; **mb**, medial blade; **msac**, medial supraacetabular crest; **mvsh**, medioventral shelf or ridge of ilium; **pp**, pubic peduncle; **sac**, supraacetabular crest; **vph**, ventral preacetabular hook; **arrow**, iliac notch. Scale bar = 10 cm.

As for the medial side of the ilium and its articulation with the sacrum (fig. 11B, 12B), there are laminae linking the sacral ribs to transverse processes as in *Alioramus altai* (Brusatte et al. 2012). A lamina links transverse process 2 to sacral rib 2, transverse process 3 to sacral rib 3, and transverse process 4 to sacral rib 4. The anteriormost articular facet is for the attachment of the dorsosacral vertebra. It is located on the anterior-ventral part of the preacetabular process (fig. 11B, 12B, 13E, F). The last articular facet is located on the medial side of the medial blade of the brevis fossa. The transverse process 2 / sacral rib 2 - articulation is at the same position as the anterior vertical ridge on the lateral side of the iliac blade. The transverse process 3 / sacral rib 3 - articulation is also at the same position as the posterior vertical ridge on the lateral side of the iliac blade (see *Alioramus altai*, Brusatte et al. 2012). Furthermore, there is a notch on the dorsoposterior part of the posterior blade of the ilium which is likely to be an autapomorphy of *Siamotyrannus* (fig. 11, 12, 13A, B).

Pubis

The proximal part of the pubic shaft is large, expands anteroposteriorly. The morphology of the puboischiadic plate is open along the midline with a pubic obturator foramen that opens anteroventrally, encircled by the proximal part of the obturator process as a hook, thus forming an obturator notch. The pubic fenestra verntral to the obturator foramen is absent. In anterior view, the pubic apron has a medial opening distally above the pubic boot. Pubic shaft in lateral view is straight, long and slender, with an oval or circular shape in cross-section. There is medial symphysis in the middle part below the pelvic canal and above the medial opening of the pubic apron. The articulation between apices is fused. The pubic boot is strongly expanded and has a distinct anterior expansion. The distal end of the posterior part of the boot is broken off. The angle of the pubic boot to the pubic shaft is slightly more than 60 degrees. The length of the boot is 270 mm anteroposteriorly. The anterior part of the pubic boot is circa 120 mm long, and the posterior part of the boot is circa 135 mm or more. The boot length relative to the shaft length is approximately 31.4%. The pubic boot in ventral view is broadly triangular with the apex oriented posteriorly in ventral view as in allosauroids and not parallel as in tyrannosauroids (fig. 11C). The ventral boot maximum width is circa 80 mm. The distal end of the boot is not the same as *Sinraptor dongi* in shape. Its angle is also greater than in *Sinraptor dongi*. The angle is roughly the same as in *Acrocanthosaurus* (see Stovall and Langston 1950), *Allosaurus* (Madsen 1976; Malafaia et al. 2007), and *Aerosteon* (MCNA-PV-3137; cast The obturator foramen of the pubis is small and subcircular, whereas the obturator foramen is enlarged in metriacanthosaurids and *Lourinhanosaurus* (Carrano et al. 2012). In *Acrocanthosaurus* (Stovall and Langston 1950), the pubic shaft is elongate, straight, and slender. It is inclined ventrally and anteriorly, meeting the broadly expanded boot at an angle of 35 degrees (Stovall and Langston 1950).

Ischium

The left ischium is generally well preserved but nearly complete lacks the anterior obturator process and the distal end. A small piece of the right ischium is preserved. It is fused, i.e., forms a symphsis, with the left ischium near the distal part. The obturator process of the ischium is offset from the pubic peduncle of the ischium by a distinct notch, as in *Allosaurus*, metriacanthosaurids, *Compsognathus*, *Neovenator*, carcharodontosaurids, and tyrannosaurids (Rauhut 2003a). The obturator process is located on the proximal half of the ischial shaft. The ventral notch between the obturator process or obturator flange on the ischium cannot be observed due to the incompleteness of the specimen, but the trace or mark of the obturator process on the ischial flange can be observed. The ischium is at least two thirds or more the length of the pubis (the pubic length is 860 mm; the ischial length is approximately 510 mm). A ligament scar or ischial tuberosity is present on the dorsoposterior part of the proximal part of the ischium. Brusatte and Sereno (2008) mentioned "the ischia of *Acrocanthosaurus* and *Siamotyrannus* are marked by a distinct muscle attachment scar on the posterior surface. Thus, *Siamotyrannus* may be a carcharodontosaurid". However, the positions are not the same in *Acrocanthosaurus*, in which the scar is situated just ventral the middle of the shaft (Stovall and Langston 1950), whereas in *Siamotyrannus*, it is situated on the proximodorsal part of the shaft.

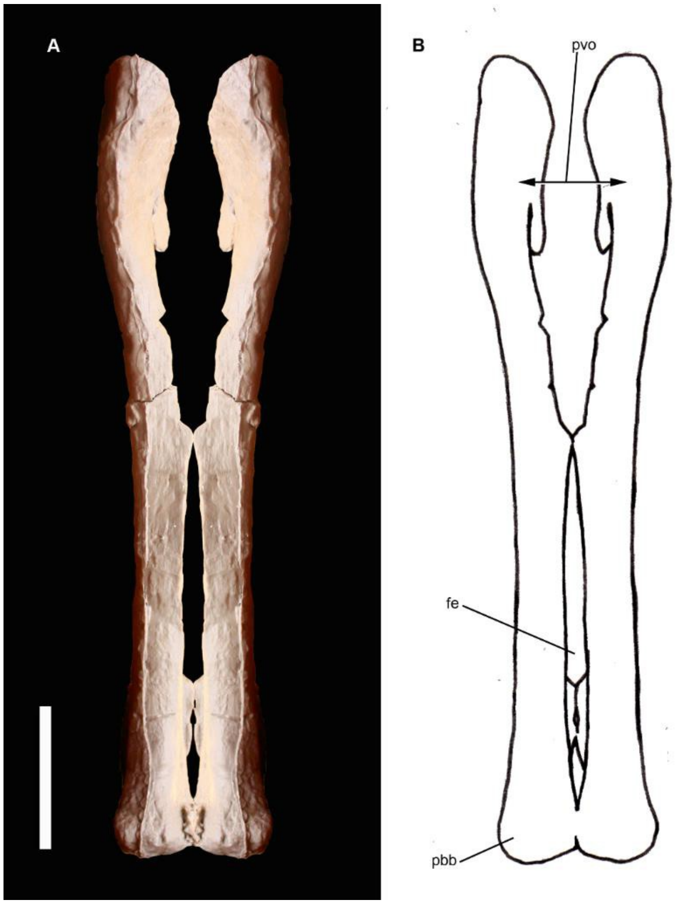


Fig.14. *Siamotyrannus isanensis*, SM-PW9-1; cast. Reconstruction of the pubes (right pubis is a mirror image of left pubis) in anterior view (A), and line drawing of the pubes in anterior view (B), **fe**, fenestra; **pbb**, pubic boot; **pvo**, pelvic outlet. Scale bar = 10 cm.

The posteriorly directed flange on the iliac peduncle of the ischium is absent (Brusatte and Sereno 2008). The ischial shaft is curved ventrally, transversely flattened, triangular in cross section at the proximal part and rectangle at the distal part. A ridge on the lateral side of the ischial shaft is present. It extends from the posterodorsal part (above the mid-shaft) of the ischium to the middle part of the lateral surface (fig. 12A).

The margins of the ischial shaft are approximately parallel in lateral view (proximal width is 100 mm, distal width is 50 mm, length of the preserved ischiam is ca. 510 mm, and the obturator process is approximately 210 mm long). The distal end of the ischium cannot be observed due to incompletene preservation but can be reconstructed from the shape of the distal shaft region which is tapering distally in anterior and posterior view.

The pubic peduncle of the ilium and iliac peduncle of the pubic articulation are elongated, narrow, and semi-oval in shape. The ischial peduncle of the ilium is a semi-oval to semicircular in section. The iliac peduncle of the ischium is circular in section. The iliac peduncle of the ischium articulation is slightly concave.

Comparison

Basesd on the phylogenetic hypotheses proposed by Buffetaut et al. (1996), Rauhut (2003a), Holtz et al. (2004), Brusatte and Sereno (2008), and Carrano et al. (2012) (see the introduction part), we compared *Siamotyrannus* with theropods in the clade Metriacanthosauridae (Carrano et al., 2012), Carcharodontosauria (Benson et al., 2010), Neovenatoridae (Benson et al., 2010), Allosauridae (Sereno, 2005), and Tyrannosauroidea (Sereno, 2005), as well as Megalosauroidea (Benson, 2010), basal tetanurans (Allain et al., 2012), and basal coelurosaurs (Sereno, 2005). The selected taxa below have anatomical overlap with the *Siamotyrannus* holotype and only specimen.

Acrocanthosaurus (Strovall and Langston 1950) is a carcharodontosaurid from the Antlers and Twin Mountains Formations, late Aptian – early Albian, Early Cretaceous of North America. Its pubis is slender with a broadly expanded boot. The ischium is straight, slender, elongate, and expanded distally. Pleurocoel fossae and pneumatic foramina are present on all presacral and sacral vertebrae (Currie and Carpenter 2000). The pubis has a caudally gently curved (i.e., convex), a rod-shaped shaft that widens proximally into a plate of bone. The obturator foramen is completely open (D'Emic et al. 2012). Harris (1998) reported the morphology of another pubis of *Acrocanthosaurus* as gently curved cranially (concave), however. In *Siamotyrannus*, there are no pleurocoel in the presacral vertebrae, and its pubis is straight.

Tyrannotitan (Novas et al. 2005) is a carcharodontosaurid from Cerro Barcino Formation, Aptian, Early Cretaceous of South America. It has pleurocoels on all preserved dorsal vertebrae (Canale et al. 2014) which absent in *Siamotyrannus*.

Concavenator is a carcharodontosaurian from Las Hoyas, Calizas de La Huérguina Formation, later Barremian, Early Cretaceous of Spain. It shows a vertical pubis, no pleurocoel in the dorsal vertebrae, and medial wall of brevis fossa is exposed (Ortega et al. 2010).

Fukuiraptor (Azuma and Currie 2000) is a megaraptoran from the Kitadani Formation (Barremian), Early Cretaceous of Japan. Its pubic peduncle of the ilium is approximately as broad anteroposteriorly as mediolaterally (Azuma and Currie 2000; Carrano et al. 2012; pers. obs.), so this character is clearly different from *Siamotyrannus* in which the pubic peduncle of the ilium is significantly longer anteroposteriorly than mediolaterally.

Giganotosaurus (Coria and Salgado 1995) is a carcharodontosaurid from the Rio Limay Formation (Albian - Cenomanian), Early Cretaceous of Argentian. Its dorsal vertebrae have deep pleurocoels which are absent in *Siamotyrannus*. Its brevis shelf is narrow but broad in *Siamotyrannus*. Its ischium is straight whereas a ventrally curved ischium is found in *Siamotyrannus*.

Lourinhanosaurus (Mateus 1998) is a basal allosauroid or basal coelurosaur from the Upper Kimmeridgian/Tithonian, Sobral Unit, Late Jurassic of Portugal. There are triangular spurs anterior to the neural spines of even the most proximal caudal vertebrae, the same as in *Siamotyrannus*. In *Lourinhanosaurus*, the medial shelf of the brevis fossa is exposed in lateral view, contrary to *Siamotyrannus*.

Megalosaurus bucklandii shares with *Torvosaurus* (both are megalosaurids) that the brevis fossa of the ilium is narrow (Benson 2010), whereas the brevis fossa of the ilium is broad and wide in *Siamotyrannus*. *Torvosaurus* also has pleurocoels on all dorsal vertebrae (Britt 1991), which is absent in *Siamotyrannus*.

Monolophosaurus is a basal tetanuran from the Lower Shishugou (= Wucaiwan) Formation, middle Bathonian – late Callovian, Middle Jurassic of China. Its pubic peduncle is large relative to the ischial peduncle. The articular surface of the pubic peduncle is composed of two facets (Zhao et al. 2010). The supracetabular crest is hood-like and hypertrophied (Benson 2010). Only one facet of the articular surface of the pubic peduncle is found in *Siamotyrannus*, and its supraacetabular crest is not hood-like and hypertrophied as in basal tetanurans.

Metriacanthosaurus is a metriacanthosaurid from the Upper Oxford Clay, early Oxfordian, Late Jurassic of England (Benson and Barret 2009). The ventral surfaces of its posterior dorsal centra are flat and their width is approximately two thirds of the posterior height of centrum (Carrano et al. 2012). The dorsosacral vertebra (the last dorsal) of *Siamotyrannus* is also flat on the ventral surface, as well as the last dorsal vertebra of *Allosaurus*.

Shidaisaurus (Wu et al. 2009 is a metriacanthosaurid from the Upper Lufeng Formation, Middle Jurassic of China. Its pubic length is almost the same as the length of the iliac blade. It lacks a ventral notch distal to the obturator process on the ischium and has a relatively long ischium. There is a shallow ventral groove along the midline of the caudal centra in *Shidaisaurus*. in *Siamotyrannus*, there are short sulci on the anterior caudals whereas the more posterior caudals have flat centra. The caudal centra of *Shidaisaurus* are slightly concave or weekly amphicoelous as in the sacrals, as in *Szechuanosaurus zigongensis* and *Yangchuanosaurus*, whereas they are platycoelous in *Siamotyrannus*. The anterior blade of the ilium does not have a pronounced anteroventral process in *Shidaisaurus*, contrary to *Siamotyrannus*. In *Shidaisaurus*, the posterior blade is not as squared off as in *Siamotyrannus*, and the lateral surface of the iliac blade is neither concave nor strongly ridged, whereas is *Siamotyrannus* there are both concavities and ridges on the iliac surface. The ischial shaft is straight and thicker than the pubic shaft in *Shidaisaurus*, and the distal half of its ischium becomes wider distally. In *Siamotyrannus*, the ischial shaft is ventrally curved and more slender than the pubis, and its ischium is parallel-sided in lateral view. The ischial boot of *Shidaisaurus* has a short, robust anterior process, not anteriorly narrower as in *Sinraptor* and *Szechuanosaurus*. This character is uncertain in *Siamotyrannus*. The medial blade of the ilium brevis fossa is hidden in lateral view as in *Siamotyrannus* and *Sinraptor hepingensis*. The presence of pleurocoels in the anterior to middle dorsals is uncertain in *Shidaisaurus* since its fourth dorsal vertebra is covered by the pubis (Wu et al. 2009).

Sinraptor dongi (Currie and Zhao 1993) is a metriacanthosaurid from the Shishugou Formation, Late Jurassic of China. The cross-section of the distal end of the pubis (pubic boot) is an inverted L shape in outline. There is a nearly straight or slightly convex pubic peduncle of the ilium in lateral view, narrow brevis fossa, the distal half of ischium becomes wider distally, and there is a straight, more robust ischial shaft than the pubic shaft. Unlike in *Siamotyrannus*, in which the pubic boot is triangular in cross-section, *Sinraptor dongi* has a strongly convex pubic peduncle of the ilium in lateral view, a broad and wide brevis fossa in which the medial wall of brevis fossa hidden in lateral view. The distal half of the ischium is parallel in lateral view, and the ischial shaft is ventrally curved and more slender than the pubic shaft.

Sinraptor hepingensis (Gao 1992) is a metriacanthosaurid from the Late Jurassic of China, specifically from the Shangshaximiao (= Upper Shaximiao) Formation of Oxfordian to early Kimmeridgian age. The characters that are similar to *Siamotyrannus* consist of the more horizontally oriented pubic boot and the boot being short and broad, a long and slender pubic shaft, a medial wall of the brevis fossa not exposed in lateral view, and constricted sacral centra. The characters that differ from *Siamotyrannus* are as follows: the fourth dorsal has a ventral ridge (no ventral ridge in *Siamotyrannus*); the ischium is slightly shorter but thicker than the pubis (shorter and slender ischium in *Siamotyrannus*); the distal half of the ischium becomes wider distally (parallel in *Siamotyrannus*); dorsal vertebral pleurocoels are present, high ilium has an anterior lobe curved ventrally; there is small obturator notch (contrary to *Siamotyrannus*); and the caudal vertebrae are amphicoelous with grooves ventrally (Gao 1992) (ventrally flat in *Siamotyrannus*).

Szechuanosaurus campi CV00214 (Dong et al. 1983) is a metriacanthosaurid from the Shangshaximiao Formation, Oxfordian – early Kimmeridgian, Late Jurassic of China. Its dorsal vertebrae are amphiplatyan, have no pleurocoels and are constricted in the center as in *Siamotyrannus*. The dorsal vertebrae have very slightly depressed posterior ends whereas in *Siamotyrannus* the dorsal vertebrae are depressed above the centra and below the neural arches centrally. The parapophyses of CV00214 lie anterodorsally as small circular depression whereas they are stalk-like in *Siamotyrannus*. A sacral centrum is amphiplatyan, convex ventrally and is not constricted medially, contrary to *Siamotyrannus* in which the sacral centra are constricted medially. The caudal centra are shallowly amphicoelous in CV00214 vs. platycoelous in *Siamotyrannus*. Caudal neural spines are gradually inclined posteriorly and lengthen anteroposteriorly corresponding with the centra in CV00214, whereas the neural spines are shorter than the centra anteroposteriorly in *Siamotyrannus*. The ilium of CV00214 is fan-shaped with a wide preacetabular notch, the ischial shaft is straight, and the pubic boot is not well developed, so the pelvic characters of CV00214 are clearly different from *Siamotyrannus*.

Szechuanosaurus zigongensis (Gao 1998) is a metriacanthosaurid from Lower Xiaximiao (Xiashaximiao) Formation, Middle Jurassic of China. The five neural spines of the sacrum are not fused in *S. zigongensis*. and the caudal vertebrae are platycoelous, whereas the last two neural spines of the sacrum are fused in *Siamotyrannus*, and its caudals are also platycoelous. The ilium of *S. zigongensis* is low. The preacetabular process curves ventrally. The preacetabular notch is narrow but not parallel. The postacetabular blade is longer and narrower than the preacetabular blade. The iliac blade is curved dorsally and fan-shaped in morphology. The pubic peduncle is slightly longer than the ischial peduncle. The preacetabular notch of *Siamotyrannus* is larger, and the ratio of the pubic to ischial peduncle is significantly higher than in *S. zigongensis*. The supracetabular crest in *S. zigongensis* is well developed as in *Siamotyrannus*. The obturator foramen of the pubis is oval in shape, whereas it is open in *Siamotyrannus*. The pubic shaft of *S. zigongensis* is long and slender and fused along its entire length with its counterpart except for the proximal end. The pubic boot is more developed posteriorly than anteriorly. In *Siamotyrannus*, the anterior boot is well developed. In *S. zigongensis*, the ischium is thicker and slightly shorter than the pubis, contrary to *Siamotyrannus* in which the ischium is more slender than the pubis.

Yangchuanosaurus shangyouensis (Dong et al. 1975, 1983) is a metriacanthosaurid from the Shangshaximiao Formation, Oxfordian – early Kimmeridgian, Late Jurassic of China. Its dorsal vertebrae are amphiplatyan. Its anterior four sacral neural spines are united to form a plate, whereas only the last two are fused in *Siamotyrannus*.This could be ontogenetic variation, however. The ilium is low and elongate anteroposteriorly, nearly fan-shaped in outline in *Y. shangyouensis*, whereas a straight dorsal margin is present in *Siamotyrannus*. In *Y. shangyouensis*, caudal vertebrae 1 – 5 are amphicoelous, whereas they are platycoelous in *Siamotyrannus*.

NMV P186046 is a possible tyrannosauroid from the Early Cretaceous of Australia (Benson et al. 2010a). Its pubic boot is transversely narrow and parallel-sided. The pubic tubercle is prominent, anterolaterally curving, and flange-like. Whereas the pubic boot in ventral view is triangular in *Siamotyrannus*.

Raptorex (Sereno et al. 2009) is a tyrannosauroid from the Early Cretaceous of northern China (see Fowler et al. 2011 and Newbrey et al. 2013 for and alternate interpretation that found *Raptorex* is from the Upper Cretaceous form Mongolia). Its ilium is elongate with a straight dorsal margin that appears to be pressed against the sacral neural spine. The straight dorsal margin of the ilium is present in *Siamotyrannus*, but it is not pressed against the sacral neural spines. The ischium of *Raptorex* exhibits a narrow tapering shaft, contrary to *Siamotyrannus* in which the ischium is not tapering but appears to be parallel-sided. In *Raptorex*, a pleurocoel is present on the sides of all presacral centra and most of the sacrals, whereas in *Siamotyannus* there is no pleurocoel on the dorsal centra.

Xiongguanlong (Li et al. 2009) is a tyrannosauroid from Xinminpu Group (Aptian - Albian), Early Cretaceous of China. Its dorsal iliac borders are highly convex and pressed against each other, indicating that a contact above the sacrum was present, as in Late Cretaceous tyrannosaurids, in contrast to the parallel, straight-edged ilia of *Guanlong* and *Siamotyrannus*. The base of the cuppedicus fossa is preserved, and the fossa is deepest just ventral to the base of the preacetabular process. This fossa is shallow in *Siamotyrannus*. A low ridge rises dorsally above the acetabulum of the ilium as in other tyrannosauroids and in *Siamotyrannus*.

Sinotyrannus is a tyrannosauroid from Jiufotang Formation (Aptian – Albian), Early Cretaceous of China (Ji et al. 2009). Its iliac preacetabular blade is comparatively short but wide and lacks the ventrally expanded anterior hook. The ilium is quite long. The postacetabular blade is much longer but slightly narrower than the preacetabular blade. *Siamotyrannus* has an anterior hook, and the preacetabular is slightly shorter than the postacetabular blade. The caudal margin of the ilium of *Sinotyrannus* is smoothly convex in lateral view but straight in *Siamotyrannus*. The anterior margin of pubic peduncle is concave in lateral view whereas it is strongly convex in *Siamotyrannus*. A well-marked, prominent median vertical ridge exists on the external side of the ilium, extending from the dorsal margin of the ilium to the dorsal border of the acetabulum in *Sinotyrannus*, whereas in *Siamotyrannus*, the two medial ridges are low and do not extend from the dorsal margin of the ilium to the dorsal border of the acetabulum. There might be a shallow pleurocoel close to the parapophysis on the dorsal vertebrae of *Sinotyrannus*, whereas there is no pleurocoel in *Siamotyrannus*.

Yutyrannus (Xu et al. 2012) is a tyrannosauroid from the Yixian Formation, Early Cretaceous of China. The character that is similar to *Siamotyrannus* is the dorsal margin of the ilium which is mostly straight. A character that differ from *Siamotyrannus* are the ventral margin of the postacetabular process of the ilium, which in *Yutyrannus* bears a prominent lobe-like flange. The *Yutyrannus* pubic boot is large and forms a distinct anterior expansion. The ischium is much more slender than the pubis, as in *Siamotyrannus*. The ischium is straight in *Yutyrannus* whereas it is ventrally curved in *Siamotyrannus*. The anterior margin of the preacetabular blade of the ilium is concave in *Yutyrannus*, which is a tyrannosauroid character (Rauhut 2003) and not found in *Siamotyrannus*.

Compare some elements of *Siamotyrannus* with other theropods, we found that: the long and stalk-liked parapophyses or pedicles on dorsal vertebrae are present in *Carnotaurus*, *Majungasaurus*, *Eoabelisaurus*, *Datanglong*, *Deinocheirus*, and *Siamotyrannus*. The parapophyses on dorsal vertebrae form low pedicles are present in *Monolophosaurus, Cryolophosaurus, Dilophosaurus*, and *Piatnitzkysaurus* (Smith et al. 2007; Zhao et al. 2009).

The ridges on the ilium of *Siamotyrannus* are much fainter, broader, and lower than in tyrannosauroids. The posterior vertical ridge is situated more anteriorly compared to tyrannosauroids, the posterior margin of the posterior vertical ridge being located just above the middle of the acetabulum. In the tyrannosauroids, the midline of the vertical ridge is situated above the acetabulum or even posteriorly, as in *Juratyant langhami* and *Stokesosaurus clevelandi* (Brusatte and Benson 2013).

The pubic shaft of *Siamotyrannus* in lateral view is straight as in *Sinraptor hepingensis*, *Sinraptor dongi*, *Shidaisaurus*, *Szechuanosaurus zigongensis*, *Yangchuanosaurus shangyouensis*, *Szechuanosaurus campi* CV00214, *Aerosteon*, *Monolophosaurus*, *Gorgosaurus*, *Dilong*, NMV P186046, *Guanlong*, *Qiupalong*, *Gallimimus*, and *Ornithomimus* (Xu et al. 2011), whereas they are convex in *Coelophysis*, *Syntarsus*, *Ceratosaurus*, and concave in *Allosaurus*, carcharodontosaurids, tyrannosaurids, and *Yutyrannus*.

The ratio of the posterior iliac blade length to the anterior iliac blade length is approximately 1.05 in *Siamotyrannus*, compared with over 1.45 in *Shidaisaurus*, 1.30 in *Sinraptor hepingensis*, 1.43 in *Szechuanosaurus zigongensis*, and 2.00 in *Sinraptor dongi* (Wu et al. 2009).

The ratio of the maximum height of the anterior iliac blade to the total length of the iliac blade is approximately 0.41 in *Siamotyrannus*, approximately 0.20 in *Szechuanosaurus*, 0.33 in *Shidaisaurus*, 0.36 in *Sinraptor dongi*, 0.39 in *Allosaurus* and *Sinraptor hepingensis*, 0.29 in *Yangchuanosaurus shangyouensis*, and 0.28 in *Yangchuanosaurus magnus* (Wu et al. 2009).

Metriacanthosauridae all have a large ischial boot (except *Metriacanthosaurus*, probably not in *Siamotyrannus*). Their pubic boots are present, but the anterior boots are not well developed as in *Siamotyrannus*. Metriacanthosauridae all have a straight or slightly ventrally curved ischium, the distal half of the ischium usually becomes wider distally, whereas *Siamotyrannus* has a ventrally curved ischium, and its shaft is parallel in lateral view. The ischium is slightly shorter than pubis in metriacanthosaurids, possibly much shorter in *Siamotyrannus*.

The ratio between the width of the pubic boot and the length of the pubis is approximately 0.31 in *Siamotyrannus* (pers. obs.), 0.34 in *Shidaisaurus* and *Szechuanosaurus zigongensis*, 0.37 in *Sinraptor hepingensis*. (Wu et al., 2009).

The ratio between the length of the ischium and the pubis is approximately 0.59 in *Siamotyrannus* (pers. obs.), 0.97 in *Shidaisaurus*, 0.93 in *Sinraptor hepingensis* and *Sinraptor dongi*, 0.88 in *Szechuanosaurus zigongensis*, and 0.94 in *Yangchuanosaurus shangyouensis*. (Wu et al., 2009).

Phylogenetic analysis

To test the phylogenetic position of *Siamotyrannus*, we added it to the cladistic data matrix of Carrano et al. (2012) and Apesteguía et al. (2016) (see materials and methods).

1. Modified from Carrano et al. 2012

The TNT analysis of 61 taxa and 351 characters. 65 characters could be scored from Siamotyrannus. The analysis produced 8 most parsimonious trees, each of 1045 steps in length. The consistency index (CI) is 0.415, the retention index (RI) is 0.689 (fig. 15A).

The Avetheropoda synapomorphies recovered from the first analysis are 1) the proximal articular facet of the chevrons is divided into anterior and posterior facets by distinct transverse ridge (215, 0), 2) ridge on medial surface adjacent to preacetabular notch of the ilium is present (273, 1), and 3) morphology and foramina/notches of the puboischiadic plate is open along midline (281, 2).

Siamotyrannus plus *Compsognathus* share with more derived coelurosaurs including 1) the height of the lateral wall of brevis fossa of the ilium relative to the medial wall is taller along the whole length (265, 0), and 2) the length-to-width ratio of the pubic peduncle of the ilium is relatively high (272, 2).

The synapomorphies that united *Siamotyrannus* and *Compsognathus* are 1) chevrons are straight or gently curved and 2) ventrally curved ischium.

2. Modified from Apesteguía et al. 2016

For the second analysis, we excluded *Santanaraptor* and *Neovenator* for a better result. The TNT analysis of 45 taxa and 288 characters produced 7 MPTs 925 steps in length, a CI of 0.370 and an RI of 0.652 (fig. 15B).

The Avetheropoda synapomorphies recovered from the second analysis are 1) ilium cuppedicus fossa is present (char. 148, 1), 2) pubis obturator foramen is a wide and well-developed opening (155, 2), and 3) dorsal vertebrae hyposphene is sheet-like (244, 1).

The Coelurosauria synapomorphies recovered from the second analysis are 1) dorsal vertebrae have no pleurocoel (106, 0), 2) caudal vertebrae are ventrally flat (113, 0), 3) ilium brevis fossa hidden by brevis shelf in lateral view (154, 1), 4) a vertical pubis (157, 1), and 5) ischium is relatively short compared to pubis (165, 1).

3. DISCUSSION

1. Systematic and taxonomic analysis

The ilium of *Siamotyrannus* clearly exhibits the theropod ilium with the dolichoiliacic morphology. Its ilium shows several tetanuran synapomorphies such as the dorsoventrally expanded anterior end of the iliac blade, the anteroposteriorly elongated pubic peduncle, and the ventrally tapering ischial peduncle with a reduced articular facet (Rauhut 2003b). *Siamotyrannus* also shows an avetheropod synapomorphy: a preacetabular fossa on the ilium, but this fossa is shallow and bounded by a low medial ridge as in allosauroids instead of a prominent ridge as in tyrannosauroids and neovenatorids (Benson and Xu 2008).

Focusing on the coelurosaurian and tyrannosauroid characters (mainly on the pelvic elements) as proposed by Rauhut (2003b), we found that *Siamotyrannus* lacks coelurosaurian and tyrannosauroid synapomorphies, the details are as follows.

Coelurosauria characters (Rauhut 2003b).

1. Preacetabular blade of the ilium as long as or longer than the postacetabular blade. In *Siamotyrannus* the preacetabular blade is slightly shorter than postacetabular blade (preacetabular length = 395 mm, postacetabular length = 415 mm, the ratio = 0.95).
2. Pubic peduncle of ilium transversely narrow and more than three times longer anteroposteriorly than wide at its middle. In *Siamotyrannus*, the length/width ratio of its pubic peduncle is approximately 2 as in *Allosaurus* and higher than in the metriacanthosaurids.
3. Anterior margin of the pubic peduncle is concave whereas the anterior margin of the pubic peduncle is straight or slightly convex in non-tetanurans and basal tetanurans. In *Siamotyrannus*, the anterior margin of the pubic peduncle is strongly convex as in *'Szechuanosaurus' zigongensis* and more convex than in *Sinraptor dongi*, *Sinraptor hepingensis*, *Shidaisaurus*, and *Allosaurus*.

4. There is a transversely narrow, parallel-sided pubic boot (Rauhut 2003a, Benson et al. 2010b). However, in *Siamotyrannus*, the pubic boot in ventral view is broadly triangular with the apex oriented posteriorly.

Tyrannosauroidea characters (Rauhut 2003b).

1. Strongly developed and the well defined vertical ridge above the acetabulum on the ilium. In tyrannosauroids, the vertical ridge is narrow, sharply defined, rounded and extends over almost the complete height of the ilium. In *Juratyrant langhami*, *Stokesosaurus clevelandi*, and *Eotyrannus langhami*, which are basal, non-tyrannosaurid tyrannosauroids, the ridges are posterodorsally inclined. In *Siamotyrannus*, there are two parallel, vertical ridges that are wide and do not extend to the dorsal margin of the iliac blade.
2. Dorsal part of the anterior margin of the preacetabular blade is concave (bilobate shape) in tyrannosaurids, *Aviatyrannis*, *Stokesosaurus*, and *Yutyrannus*. *Siamotyrannus* lacks this bilobate shape.

Siamotyrannus are clearly not carcharodontosaurian because it lacks any synapomorphies of this clade, the details are as follow.

Carcharodontosauria synapomorphies (Benson et al. 2010b):

1. Pneumatic foramina or pleurocoels present in all presacral vertebrae. A pleurocoel is absent at least in the anterior-mid dorsal vertebrae in *Siamotyrannus*.
2. Anteroposterior length of pubic distal expansion is more than 60% of pubic shaft length; this ratio is approximately 31% in *Siamotyrannus*.
3. The iliac articular surface of the ischium is deeply concave (socket-like), whereas the surface of the iliac articular surface of the ischium is slightly concave in *Siamotyrannus*.
4. Dorsal hyposphenes form transversely narrow sheets; this character is also present in *Siamotyrannus*.

Neovenatoridae synapomorphies (Benson et al. 2010b):

1. Middle-posterior dorsal vertebrae with small, flange-like lateral extensions of the postzygapophyseal facets, unknown in *Siamotyrannus*;
2. Proximal caudal vertebrae bearing ventral longitudinal ridge (independently derived in some carcharodontosaurids); there is a small ventral sulcus instead of the ridge in *Siamotyrannus*;
3. Iliac preacetabular fossa bounded dorsomedially by a prominent shelf and ilium with external foramina and internal pneumatic spaces. There is only a low ridge, not a prominent shelf on the preacetabular blade and no external foramina on the

ilium in *Siamotyrannus*;

4. The vertical ridge on the lateral surface of the ilium is absent (in *Aerosteon* and *Murusraptor*). In *Siamotyrannus*, there are two vertical ridges on the lateral surface of the ilium.

Megaraptora synapomorphies:

1. Pneumatic caudal vertebrae (Benson et al. 2010b). This character is absent in *Siamotyrannus*.
2. Pneumatic sacral vertebrae (Aranciaga Rolando et al. 2017). This character is absent in *Siamotyrannus*.

Metriacanthosaurinae synapomorphies (Carrano et al. 2012):

1. Pronounced ventral keel on anterior dorsal vertebrae, unknown in *Siamotyrannus*, but at least the fourth dorsal vertebra of *Siamotyrannus* lack a ventral keel which is present in *Sinraptor hepingensis*;
2. Straight posterior margin of the iliac postacetabular process, same as in *Siamotyrannus*, also in *Tyrannosaurus* (Brochu 2003), *Allosaurus* (UMNH VP5410), and *Gallimimus* (Osmolska et al. 1972).
3. Angle of less than 60 degrees between long axes of pubic shaft and boot. This angle is approximately 60 degrees or more in *Siamotyrannus*;
4. Ventrally curved ischial shaft. This character might be problematic since *Shidaisaurus* has a straight, robust ischial shaft and both *Sinraptor* species have straight or slightly ventrally curved, robust ischial shafts with distal half becoming wider distally (A.S. pers. obs.), whereas a ventrally curved and slender ischial shaft with a parallel in lateral view is present in *Siamotyrannus*.

Megalosauroidea synapomorphies (Benson 2010):

1. The proximal articular surface of chevrons without distinct anterior and posterior facets (low mounds may be present laterally on either side). This character is uncertain in *Siamotyrannus* since its chevrons are still in the sediment.
2. Length-to-width ratio of pubic peduncle of the ilium is 1.3 – 1.4, significantly shorter than in *Siamotyrannus* (≈ 1.9).

Megalosauria (Megalosauridae + Spinosauridae) synapomorphies (Benson 2010):

1. Length to width ratio of pubic peduncle is 1.55 – 1.75 (also present in Metriacanthosauridae), significantly shorter than in *Siamotyrannus* (≈ 1.9).

Megalosauridae synapomorphies:

1. The acetabular margin of the pubic peduncle is transversely concave (slightly convex or nearly flat in *Siamotyrannus*).
2. Ischial shaft curves anteroventrally (as in *Siamotyrannus*).
3. Ischial antitrochanter is absent (also in *Allosaurus* and Coelurosauria).
4. Ischial symphysis expanded as an apron (also in most neotetanurans).

The length/width proportion of the pubic peduncle in allosaurians is ≈ 2.0. It is approximately 3.0 in coelurosaurs. It is ≤1.7 in all non-avetheropods and metriacanthosaurids (Carrano et al. 2012). In *Siamotyrannus*, this proportion is ≈ 1.9.

The **coelurosaurian characters** of *Siamotyrannus* which we recovered in the present study are 1) the medial shelf of the brevis fossa is completely hidden in lateral view and falls short of its lower margin; 2) the pubis is vertical; 3) the chevrons are straight, or slightly curved, and 4) the pubic peduncle of the ilium is relatively long compared to basal theropods.

Non-coelurosaurian (= plesiomorphic) characters found in *Siamotyrannus* include: 1) the ilium does not contact sacral neural spines in anterior view / the ilium does not lie against the sacral neural spines, 2) the pubic boot is triangular in ventral view, 3) the anterior blade of the ilium is slightly shorter than the posterior blade, 4) the centra of the dorsal vertebrae are higher than long, 5) the anterior spurs of the neural spines on caudal vertebrae are present, and 6) there is large supraacetabular crest of the ilium in ventral view.

From this study we rewrite the diagnosis of *Siamotyrannus* by the following autapomorphies: a coelurosaurian theropod with 1) double, low and broad vertical ridges on the central part of the lateral iliac blade and 2) a notch on the dorsoposterior part of the postacetabular blade of the ilium. Furthermore, *Siamotyrannus* also shows a unique combination of the following characters: 1) long parapophyses on the middle dorsal vertebrae (stalk-like pedicels) and 2) short medial wall of the brevis fossa which is completely hidden by the lateral wall in lateral view and falls short of its lower margin. *Siamotyrannus*, *Lourinhanosaurus*, and metriacanthosaurids (e.g. *Sinraptor*, *Yangchuanosaurus*, and *Shidaisaurus*) exhibit some plesiomorphic characters which sometimes are misinterpreted as their synapomorphies and united them in an apparent clade at the base of Allosauroidea and/or Coelurosauria (e.g. Rauhut 2003a; Holtz et al. 2004; Rauhut et al. 2009; Benson 2010; Carrano et al. 2012). The similarity also might due to convergent evolution or homoplasy among these two theropod lineages. The fragmentary nature of some of these theropods should be considered. However, more detailed studies of the members of the Chinese Jurassic Metriacanthosauridae, which is beyond the scope of this study, is needed.

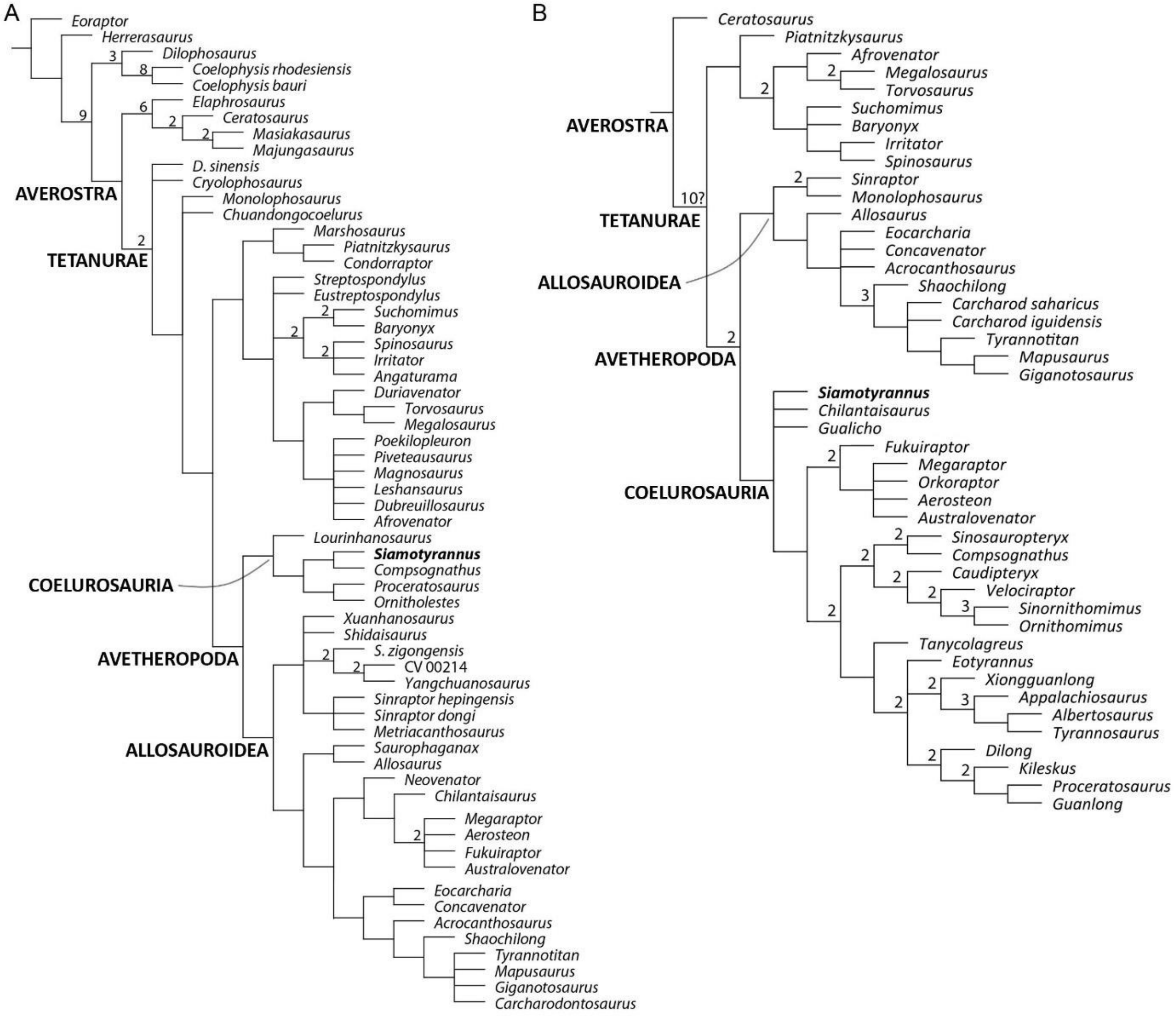


Fig.15. Cladograms showing the phylogenetic positions of *Siamotyrannus isanensis* generated by TNT 1.1. (A) The strict consensus of the 8 most parsimonious trees comprising 351 characters and 61 dinosaur taxa. Tree was rooted with *Eoraptor* and *Herrerasaurus* as the outgroup and all characters were unordered and founds *Siamotyrannus* as a basal coelurosaur. (B) The strict consensus of the 7 most parsimonious trees comprising 288 characters and 45 dinosaur taxa. Tree was rooted with *Ceratosaurus* as the outgroup and all characters were unordered and founds *Siamotyrannus* as a basal coelurosaur and forms polytomy with *Chilantaisaurus* and *Gualicho*, and they are sister taxa to the (Megaraptora (Tyrannosauroidea ('derived' Coelurosauria))). Numbers each node are Bremer values greater than 1.

2. The Phuwiang carcharodontosaurid

Based on size and occurrence, the carcharodontosaurid (PRC 61) found from the Phu Wiang Mountain might belong to same animal as *Siamotyrannus*. However, more findings and study are needed to test this hypothesis, so we did not include the PRC 61 specimen in present study.

3. Paleobiogeography through time

Assessing the paleobiogeography and size evolution in basal coelurosaurs, we needed to look at their early radiation. During the Middle Jurassic, the earliest coelurosaurs that have been recorded were the small-bodied basal tyrannosauroids *Proceratosaurus* from Europe and *Kileskus* from Asia. This suggests that the coelurosaurs which include the basal forms and the tyrannosauroids plus 'derived' coelurosaurs appeared no later than the Middle Jurassic (see Rauhut et al. 2010). During this time, metriacanthosaurids were the dominant carnivores in Asia and megalosaurids were apex predators in Europe and North America (Samathi et al., 2019b).

In the Late Jurassic, there were four, small-bodied basal tyrannosauroids including *Guanlong* from Asia, *Aviatyrannis* and *Juratyrant* from Europe, and *Stokesosaurus* form North America, as well as *Zuolong*, a small-bodied basal coelurosaur from Asia. Other small-bodied maniraptorans and compsognathids also appeared during this time (Sales et al. 2014; Foth and Rauhut 2017).

In the Early Cretaceous, *Siamotyrannus*, a basal coelurosaur from the Barremian of Southeast Asia and *Fukuiraptor*, a basal megaraptoran coelurosaur from the Barremian of East Asia were present. They had evolved into mid-to-large sized predators, as did *Yutyrannus* and *Sinotyrannus* from China. The small-bodied ornithomimosaurs, compsognathids, and maniraptorans were also already present during this time.

During the Late Cretaceous, basal coelurosaurs are represented by *Chilantaisaurus*, a large- bodied, probable basal coelurosaur from the mid-to-Late Cretaceous of East Asia, *Gualicho*, a large-bodied, probable basal coelurosaur from the Late Cretaceous of Argentina, and *Bicentenaria*, a small-sized basal coelurosaur from the Late Cretaceous of Argentina.

Large-bodied predators occupying the same or overlapping niches have been reported in various studies (e.g. Chiarenza and Cau 2016; Candeiro et al. 2018). In the Sao Khua Formation of Thailand, there were a large coelurosaur (*Siamotyrannus*), mid-sized basal coelurosaurs (*Phuwiangvenator* and *Vayuraptor*), a mid-to-large sized spinosaurid (*Siamosaurus*), a probable large carcharodontosaurid (PRC61), and small coelurosaurs including an ornithomimosaur and probable a compsognathid (*Kinnareemimus*) (see Samathi et al. 2019b for detail).

4. Evolution of body size in basal coelurosaurs

The basal coelurosaurs including *Siamotyannus, Chilantaisaurus*, *Gualicho* (Apesteguía et al., 2016), and the Megaraptora exhibit mid-to-large size. However, other basal coelurosaurs including *Zuolong*, *Bicentenaria*, compsognathids, and basal ornithomimosaurs are small-bodied. The basal tyrannosauroids including *Kileskus*, *Proceratosaurus*, *Guanlong*, *Dilong*, *Tanycolagreus*, and *Coelurus* also exhibit small-to-mid size with exception of *Yutyrannus* (Xu et al., 2012). The basal coelurosaurs *Aorun* and *Tugulusaurus* were recently found to be basal alvarezsaurs by Xu et al. (2018). This might suggest that the basal coelurosaurs were plesiomorphically large-bodied, like in other basal tetanurans (Lee et al., 2014). Then they appeared to have reduced body size in the stem tyrannosauroids plus 'derived' coelurosaurs. The other possible explanation is that the basal coelurosaurs first exhibited small forms (eg., Rauhut et al. 2010; Cau, 2018), then they evolved into large-bodied forms in many lineages separately. This has to be tested in further studies.

4. CONCLUSION

Here, *Siamotyrannus* is described anatomically in detail and compared with other theropods including recently found taxa. Then its phylogenetic status is analyzed based on the most up-to- date datasets with focused on basal theropods and basal coelurosaurs.

Siamotyrannus is found to be a basal coelurosaur, more basal than tyrannosauroids plus 'derived' coelurosaurs. The original hypothesis of tyrannosaurid affinities (Buffetaut et al. 19) remains no longer valid. The exact position, however, cannot be assessed due to the fragmentary nature of the material and a lack of consensus on basal coelurosaur relationships. Convergent evolution or homoplasy in basal allosauroids and basal coelurosaurs is also an important factor. Other basal coelurosaurs worth mentioning are *Chilantaisaurus*, *Gualicho*, and the Megaraptora.

Coelurosaurs probably first evolved as large-sized theropods, like their relatives, the basal tetanurans, before they became small in the stem of the clade Tyrannoraptora. The other possible explanation is that the basal coelurosaurs first exhibited small forms, then they evolved into large-bodied in many lineages convergently. Detailed study of the Chinese Jurassic metriacanthosaurids is needed. Broad and thorough phylogenetic analyses focusing on basal allosauroids and basal coelurosaurs are also needed to better understand the evolution of large- bodied basal coelurosaurs including *Siamotyrannus*.

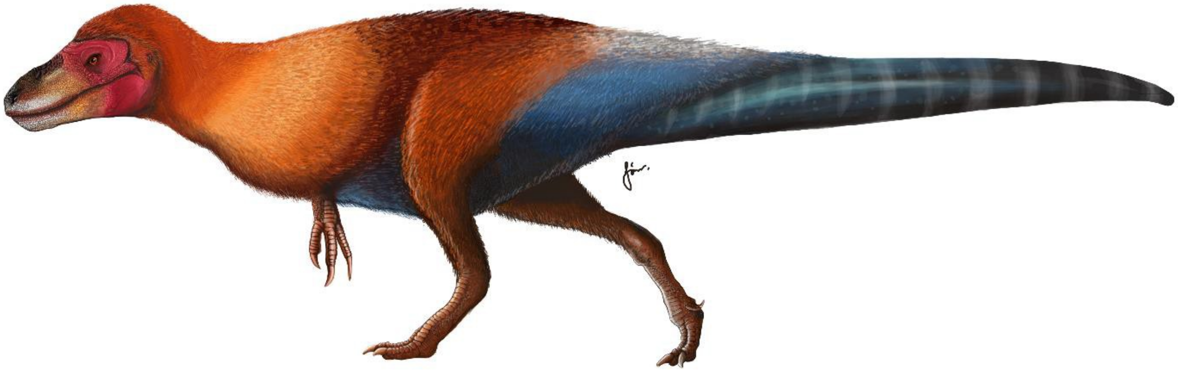


Fig. 16. Live restoration of *Siamotyrannus isanensis* illustration by ©Wijanee Sendang.

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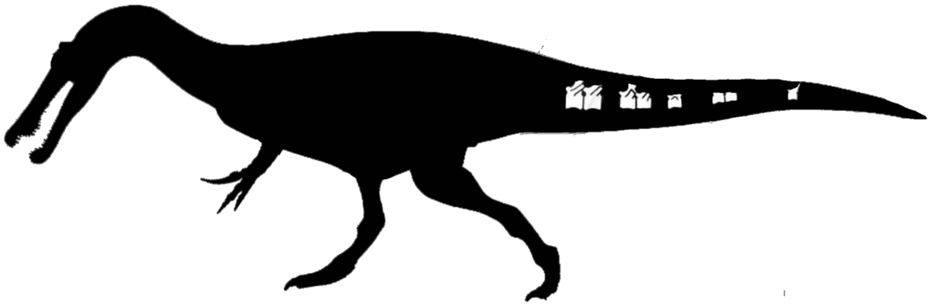
CHAPTER 6

A Spinosaurid from Thailand and the Reassessment of *Camarillasaurus* from the Early Cretaceous of Spain



CHAPTER 6

A SPINOSAURID FROM THAILAND AND THE REASSESSMENT OF *CAMARILLASAURUS* FROM THE EARLY CRETACEOUS OF SPAIN

Abstract:

Siamosaurus suteethorni Buffetaut and Ingavat, 1986 is a spinosaurid theropod from the Barremian Sao Khua Formation of northeastern Thailand. Because it was based on teeth, the status of this theropod is uncertain. Here we report the caudal vertebrae found in the Phu Wiang Mountain (called here the Phuwiang spinosaurid B) that resemble to the Portuguese *Baryonyx* and here pertain to the Spinosauridae based on (1) striation at the surface of transverse process of the caudal vertebrae, (2) well-developed double keels and long and deep groove in between on the ventral centra, (3) two buttresses and three fossae below the transverse process of the caudal vertebrae, and (4) posterior caudal vertebrae have curve, rod-like neural spines with small process at the base anteriorly. This supports the presence of spinosaurids in the Sao Khua Formation in this region. Whether the Phuwiang spinosaurid B belong to *Siamosaurus* or to another unknown spinosaurid, is beyond the objective of this study.

Furthermore, the supposed to be a ceratosaurian *Carmaillasaurus cirugedae* Sánchez-Hernández and Benton, 2014 from the Early Cretaceous of Spain is found here to be a spinosaurid based on the morphology and the resemblance of the type materials to the Phuwiang spinosaurid B described in present work. Despite its fragmentary nature and possibly ontogeny, the referral of *Camarillasaurus* to the Spinosauridae is based on the phylogenetic analysis and the similarity of the caudal vertebrae, chevrons, and tibiae to other spinosaurids.

In Europe, spinosaurids have been reported from England, Portugal, and Spain, the reassessment of *Camarillasaurus* adds the number of this group to this region. Moreover, the small size of *Camarillasaurus* (approximately 4 m long) suggested this animal is a juvenile or sub-adult. The presence of more than one spinosaurid taxon in the same region or rock formation is common and can be found in the Kem Kem Beds of Morocco, the Ararepe Basin of Brazil, and the Khorat Plateau of Southeast Asia.

Keywords: spinosaurids, *Siamosaurus*, *Camarillasaurus*, Early Cretaceous, Thailand, Spain

1. INTRODUCTION

(1) The brief overview of the Spinosauridae

Spinosauridae is a clade of carnivorous, large-bodied theropod dinosaurs from the Jurassic and Cretaceous of Gondwana and Laurasia (Holtz et al, 2004; Hone & Holtz, 2017). They were presumably, at least partially, fish-eating lifestyle (Hendrickx et al. 2016). The Spinosauridae monophyly is well supported (Holtz et al 2004; Carrano et al 2012; Hone & Holtz 2017), whereas there are currently three hypotheses of the relationship within Spinosauridae. 1) The Spinosauridae can be divided into the Spinosaurinae and Baryonychinae (e.g. Sereno et al, 1998; Hone & Holtz, 2017). 2) The polytomy Spinosauridae (Evers et al 2015). 3) Only the Spinosauinae forms a monophyletic clade, the Baryonychinae is paraphyletic (Sales & Schultz 2017).

(2) Spinosaurids from the Early Cretaceous of Thailand

In Thailand, spinosaurid theropods have been reported from two Formations, the Sao Khua and Khok Kruat Formations. The spinosaurids from the Sao Khua Formation are mainly consisting of teeth. Based on those teeth and then-novel features, the name *Siamosaurus suteethorni* was elected (Buffetaut and Ingavat, 1986) and its status has been debated since then (see Bertin 2010; Carrano et al. 2012; Arden et al. 2019). Whereas the one reported from the Khok Kruat Formation (the Khok Kruat spinosaurid) consists of teeth and postcranial elements (Buffetaut et al. 2004; 2005; Milner et al. 2007).

Here we identify the caudal vertebrae commonly found in the Phu Wiang Mountain, Khon Kaen Province in the past three decades. It essentially belongs to the Spinosauridae based on size and affinity and might support the status of *Siamosaurus*. We call the material in the present study the 'Phuwiang spinosaurid B' in avoidance the confusion with *Siamosaurus* which also found in the Phu Wiang Mountain.

Theropod dinosaurs from the Phu Wiang Mountain, Khon Kaen Province, northeastern Thailand (Samathi et al. 2019b) consist of an avetheropod *Siamotyrannus*; a spinosaurid *Siamosaurus*; an ornithomimosaur *Kinnareeminus*; a carcharodontosaurid; a probable compsognathid; a new basal coelurosaur, probably megaraptoran; and a spinosaurid (Phuwiang spinosaurid B, present study) possibly belong to *Siamosaurus*.

The PW9 Locality or 'Hin Lad Yao' Locality where theropods were found divided into the PW9, PW9A, and PW9B localities. The PW9 is where *Siamotyrannus* was found, the PW9B is where a new, probably megaraptoan and the Phuwiang spinosaurid B were found, and the PW9A is where the referred materials of theropods in PW9B were found.

It possible that these theropods came from different animals since they were, except for the case of *Siamotyrannus*, disarticulated and scattered when found.

(3) The Case of PW9B Locality

In the PW9B Locality, Phu Wiang Mountain, Khon Kaen Province, northeastern Thailand, there are at least three theropods discovered including the new coelurosaur, probably megaraptoran *Phuwiangvenator* (SM-PW9B-taxon A; see Chapter 3), the Phuwiang spinosaurid B (SM-PW9B-taxon B, present work), and the small theropod (SM-PW9B-taxon C; see Chapter 7). This conclusion came from the fact that the materials such as claws, sacral vertebrae, and hind limb elements of *Phuwiangvenator* (SM-PW9B-taxon A) look similar to other coelurosaurs and megaraptorans, whereas the caudal vertebrae of the Phuwiang spinosaurid B look similar to other spinosaurids. The small theropod found in the same area also probably belongs to Megaraptora or Spinosauridae. We note that there are some other materials such as small pedal claws and fragment phalanges which not included in this study. Further discovery will help to solve this problem, so in this case, we will treat them separately.

(4) *Camarillasaurus* from the Early Cretaceous of Spain

Camarillasaurus was described and assigned to basal Ceratosauria by Sánchez-Hernández and Benton (2014) but it shows dubious evidence of being a ceratosaur (Gianechini et al. 2015). Some characters of *Camarillasaurus* are present in some tetanurans and coelurosaurs (Wang et al. 2017). It was not included in the analysis of Rauhut and Carrano (2016) which focused on the Ceratosauria. Since some materials of *Camarillasaurus* look similar to the Phuwiang spinosaurid B which is most possibly a spinosaurid, a reassessment of the phylogenetic position of *Camarillasaurus* is needed and necessary for clarifying the status of the Phuwiang spinosaurid B.

(5) Institutional Abbreviation

FPDM: Fukui Prefectural Dinosaur Museum; **FSAC**: Faculté des Sciences Aïn Chock (University of Casablanca), Casablanca, Morocco; **MB**: Museum für Naturkunde, Humboldt- Universität zu Berlin, Germany; **MNN**: Musée National du Niger, Niamey, Republic of Niger; **MPG**, Museo Paleontológico de Galve, Galve village, Teruel Province, Spain; **SHN**: Sociedade de História Natural, Torres Vedras, Portugal; **SM**: Sirindhorn Museum, Department of Mineral Resources, Kalasin, Thailand; **UMNH**: Natural History Museum of Utah**,** Salt Lake City, Utah,USA.

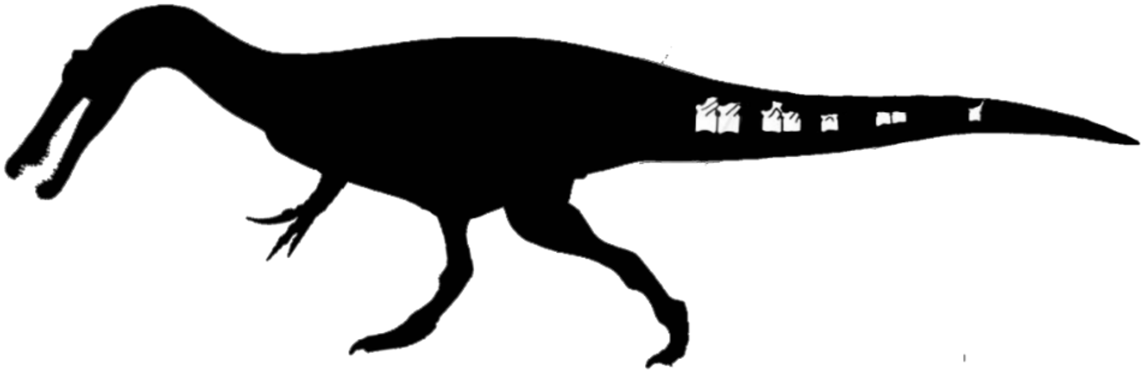


Fig.1. Skeleton reconstruction of the Phuwiang spinosaurid B. It is approximately 5 m long compare with about 4 m long in *Camarillasaurus*.

2. THE PHUWIANG SPINOSAURID B FROM THAILAND

(1) **Systematic Paleontology**

Dinosauria Owen, 1841
Theropoda Marsh, 1881
Tetanurae Gauthier, 1986
Spinosauridae Stromer, 1915
Phuwiang spinosaurid B = ? cf. *Siamosaurus suteethorni* Buffetaut and Ingavat, 1986

Material: caudal vertebrae SM-PW9B-17, SM-PW9B-13, SM-PW9B-15, SM-PW9B-14, SM-PW9B-16, SM-PW9B-11, SM-PW9B-12 (fig. 1; 2).

Referred material: SM-PW9A-unnumbered (size comparable to the SM-PW9B taxon B), SM- PW9-unnumbered, and SM 2017-1-176.

Locality and Horizon: *Type material* - PW9 'Hin Lad Yao' Locality site B, Phu Wiang District, Khon Kaen Province, northeastern Thailand. Sao Khua Formation, Late Barremian, Early Cretaceous. *Referred material* – PW9 'Hin Lad Yao' Locality site A.

Hypothesis: The Phuwiang spinosaurid B together with the spinosaurid teeth (including *Siamosaurus*) is common and can be found in many localities in the Phu Wiang Mountain, possibly due to the scavenging behavior of these animals.

Fig.2. Caudal vertebrae of the Phuwiang spinosaurid B in left laterl view, from left to right: SM-PW9B-17; SM-PW9B-13; SM-PW9B-15; SM-PW9B-14; SM-PW9A-unnumberred; SM-PW9B-16; SM-PW9B- 11; SM-PW9B-12.

(2) Description

Caudal vertebrae

CV1 SM-PW9B-17: centrum, anterior is concave, posterior is slightly concave. The centrum is longer than height. Ventral groove located on the posterior surface of the ventral side of the centrum, length of the ventral groove is 37 mm. no pleurocoel or foramina on the centrum, but lateral fossae are present. The chevron facet is well observed. The centrum is an hourglass shape, and longer than high. The centrum is a circular shape posteriorly, while the anterior part is incomplete.

CV2 SM-PW9B-13: centrum, anterior is strongly concave, posterior is slightly concave. The centrum is a circular shape in anterior view. Two prezygapophyses are preserved. No hyposphene-hypantrum articulation. Prezygapo-diapophysis lamina (prdl) and centro-diapophysis lamina (cdl) are present. No pleurocoel or foramina on the centrum, but lateral fossae are present. Bases of neural spine and right diapophysis are preserved. The ventral groove is present on the posterior half of the ventral surface of the centrum. Its length is about 34 mm and narrower than that of the CV1. The chevron facet is clearly seen. Hourglass shaped centrum. The centrum is slightly longer than high.

CV3 SM-PW9B-15: the centrum is longer and more slender than SM-PW9B-14 (the centrum central thickness is less than that of SM-PW9B-14). The ventral groove is long and wide, almost the ventral part of centrum but the anterior rim is incomplete. it is approximately 50 mm long and 15 mm wide. The centrum, anterior is circular, posterior is sub-circular shape. Amphicoelous. Slightly longer than height. Partial prezygapophyses, the base of diapophyses, and base of the neural spine are preserved. The neural spine is short anteroposteriorly, posteriorly incline, and situated on the posterior half of the neural arch. Hourglass shape centrum (Fig. 3).

CV4 SM-PW9B-14: centrum, circular (oval)/subcircular shape. Shallow lateral fossae below the neural arch. The centrum is slightly concave anteriorly and posteriorly (amphicoelous). Prezygapophyses, the base of right diapophysis, and base of the neural spine are preserved. Neural arch fuses with centrum. The chevron facet is clearly observed. The ventral groove is wide and long, starts from the posterior part and beyond the mid part of centrum but not reach the anterior rim, the length is 43.5 mm, and the width is 15 mm hourglass shape centrum. The centrum is slightly long equal to high (fig. 4).

CV5 SM-PW9A-unnumbered: its position is before SM-PW9B-16 since the SM-PW9A caudal vertebra is slightly larger than SM-PW9B-16 but clearly smaller than SM-PW9B-14. The SM- PW9A caudal vertebra would be one or two position/step before SM-PW9B-16. Centrum, posterior is flat or slightly concave, anterior is possibly concave. The centrum is longer than high. The chevron facet is present. The ventral groove situates almost the entire length of the centrum, but deep and wide posteriorly than the anterior portion (maximum 13 mm width). There is no pleurocoel, foramina, lateral fossa or depression. Neural arch is missing. The centrum is slightly anterior incline, and hourglass-shaped in ventral view.

CV6 SM-PW9B-16: the ventral groove is long and wide, almost the ventral part of centrum and nearly reach the anterior rim. It is 55 mm long and 9 mm wide. The chevron facet is clearly observed. The posterior is slightly concave. The neural arch is missing and the suture on the centrum can be observed. No lateral fossa but weak lateral depression is present on the dorsal part of centrum under the neural arch contact. The centrum is weak hourglass shape in ventral view, longer than high. It is circular shape anteriorly and subcircular posteriorly.

CV7 SM-PW9B-11: The centrum is longer than high. The ventral groove is long and wide, but not wide as of the CV4. It is 54 mm long and 11 mm wide. The ventral groove situates almost the entire length of the centrum. The chevron facet is clearly observed. Bases of diapophyses and neural spine are preserved. The neural spine is rod-liked, anteroposteriorly short, posteriorly incline, and placed on the posterior end of the neural arch. The neural arch is fused with the centrum. There is no pleurocoel, foramina, or fossae, only small depression on the dorsal part of the centrum. The centrum shape is subcircular or oval shape anteriorly and posteriorly. The two buttresses (acdl and pcdl) and three fossae below the transverse process are present.

CV8 SM-PW9B-12: the neural spine is rod-liked, posteriorly incline, and placed on the posterior end of the neural arch (fig. 5).

(3) Comparison

1) Striation at the surface of the transverse process of the caudal vertebrae, found in Phuwiang spinosaurid B and cf. *Baryonyx* from Portugal (Mateus et al. 2011; P.M.S. pers. obs.).

2) Well-developed double keels and long and deep groove in between, found in Phuwiang spinosaurid B and cf. *Baryonyx* from Portugal but the morphology of the grooves is different.

3) Two buttresses and three fossae below the transverse process of the caudal vertebrae are present in Phuwiang spinosaurid B, as well as in *Baryonyx* (Charig and Milner 1997), the Brazilian spinosaurid NM 4743-V (Bittencourt & Kellner 2004), a megalosaurid *Torvosaurus* (Bittencourt & Kellner 2004; Britt 1991), probably in a megalosaurid SHN.388/8 (Malafaia et al. 2017), and probably *Ichthyovenator* (cast of the Holotype housed at FPDM).

4) Posterior caudal vertebrae have curve, posteriorly inclined, rod-like neural spines with small process at the base anteriorly, found in Phuwiang spinosaurid B, cf. *Baryonyx* from Portugal, *Suchomimus*, and *Camarillasaurus* (fig. 6).

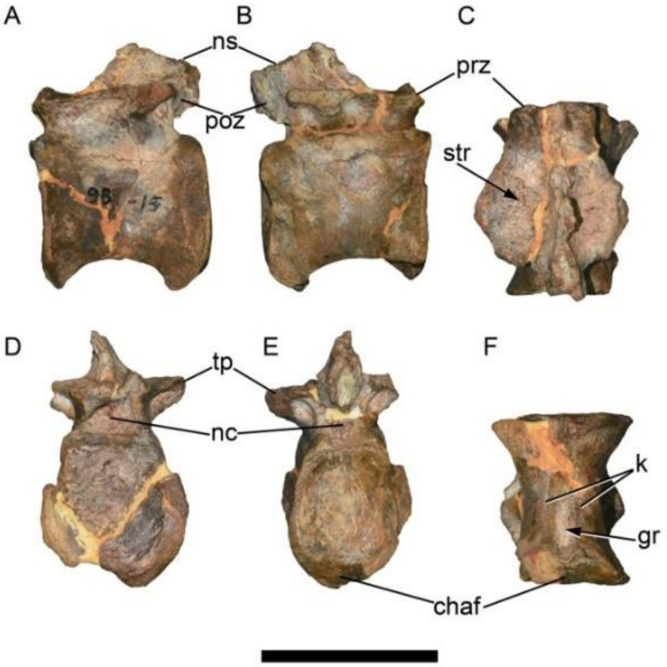


Fig. 3. Anterior-to-mid caudal vertebra (SM-PW9B-15) of the Phuwiang spinosaurid B. Abbreviations: **chaf**, facet for chevron articulation; **gr,** ventral groove; **k**, ventral keel; **nc**, neural canal; **ns**, neural spine; **prz**, prezygapophysis; **poz**, postzygapophysis; **str**, striation; **tr**, transverse process. Scale bar = 10 c

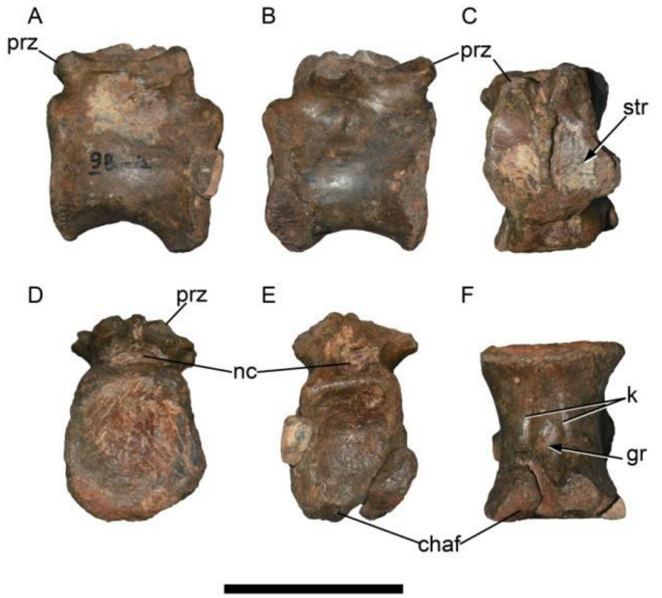


Fig. 4. Anterior-to-mid caudal vertebra (SM-PW-14) of the Phuwiang spinosaurid B. Abbreviations: **chaf**, facet for chevron articulation; **gr**, ventral groove; **k**, ventral keel; **nc**, neural canal; **prz**, prezygapophysis; str, striation. Scale bar = 10 cm.

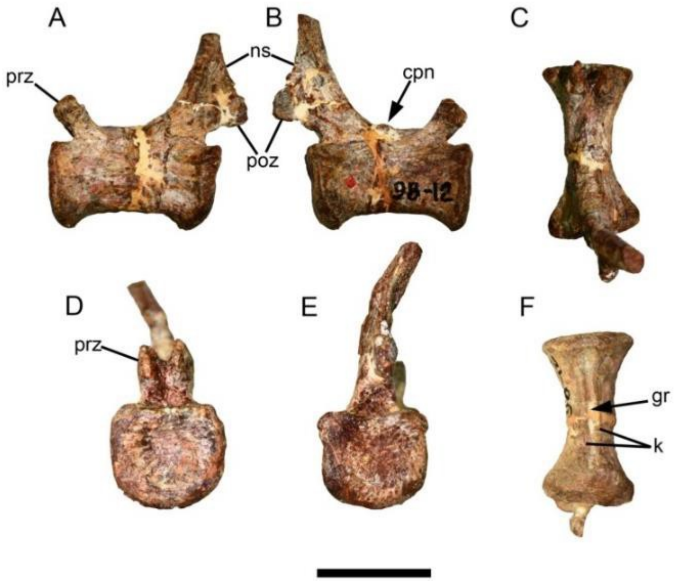


Fig. 5. Distal caudal vertebra (SM-PW9B-12) of the Phuwiang spinosaurid B. Abbreviations: **cpn,**cranial process of neural spine; **gr,** ventral groove; **k**, ventral keel; **ns**, neural spine; **prz**, prezygapophysis; **poz**, postzygapophysis. Scale bar = 5 cm.

The caudal vertebrae show amphicoelous; the anterior caudal centrum is hourglass-shaped in ventral view; sub-circular in posterior view; chevron facets are well noticeable; in the ventral view of the centrum, two parallel ridges are present with deep and wide longitudinal grooves extend along the midline. The groove is the deepest posteriorly. These look similar to the tail materials of *Camarillasaurus* and the Portuguese *Baryonyx* (Mateus et al 2011).

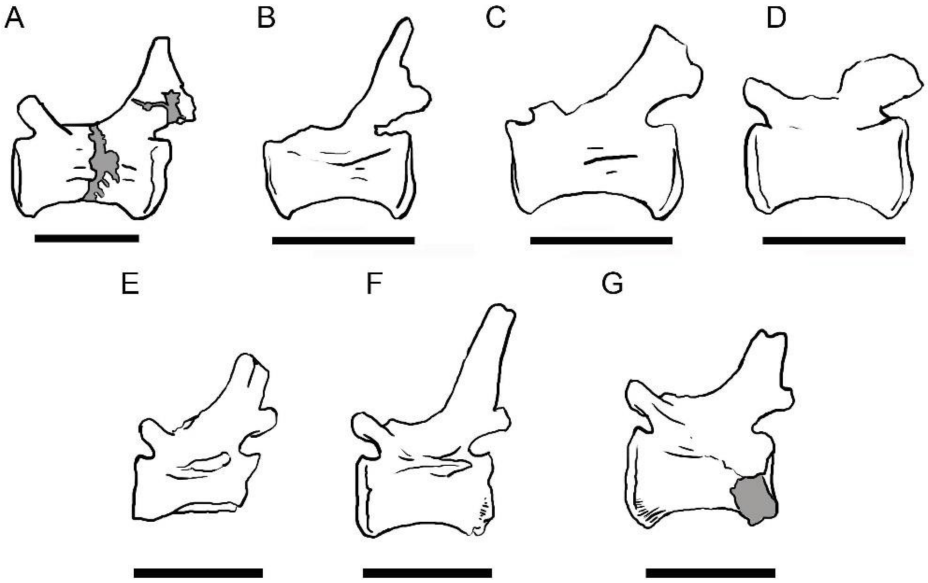


Fig. 6. Comparison of the caudal vertebrae of A) the Phuwiang spinosaurid B (SM-PW9B-12); B-C) *Camarillasaurus* (drawn from Sánchez-Hernández and Benton 2014); D) the Portuguese *Baryonyx* (Mateus); E-G) *Suchomimus* MNN GAD G94-50, MNN GAD 70, and MNN GAD 87; and F) *Ichthyovenator* cast of the holotype (FPDM-V-9533-38). Scale bar A - C = 5 cm, D - G = 10 cm.

3. THE REASSESSMENT OF *CAMARILLASAURUS* FROM SPAIN

The Phuwiang spinosaurid B looks similar to *Camarillasarus* and *Suchomimus*. *Camarillasaurus* is possibly a spinosaurid or megalosauroid by comparing the tibiae, chevrons, and caudal vertebrae with *Suchomimus*, *Spinosaurus*, and *Condorraptor*. Phylogenetic analysis found *Camarillasaurus* to nest within the Spinosauridae, together with the similarity of the caudal vertebrae, chevrons, and tibiae to other spinosaurids.

(1) Systematic Paleontology

Dinosauria Owen, 1841
Theropoda Marsh, 1881
Tetanurae Gauthier, 1986
Spinosauridae Stromer, 1915
Camarillasaurus cirugedae Sánchez-Hernández and Benton, 2014

Material: MPG-KPC1-46, a tooth, isolated vertebrae, ribs, and limb elements.

Locality and Horizon: Teruel, Aragón, Spain. Camarillas Fm, lower Barremian.

Revised diagnosis: A spinosaurid with 1) the length/width ratio of the tibia proximal end is very high and higher than any theropods; 2) g-shaped cross-section of the shaft of the tibia with a longitudinal groove on anteromedially (all information from Sánchez-Hernández and Benton, 2014).

We note that 1) the high length/width ratio can be found in other theropods such as *Suchomimus* (=2.34), *Spinosaurus* (=2.4), *Arcovenator* (=2.4), and *Majungasaurus* (=2.7) but they are not as high as *Camarillasaurus* (=2.8); and 2) the vertical groove is present on one of the tibia of *Spinosaurus* neotype, but it differs from *Camarillasaurus* in some degree and might due to preservation.

(2) Comparison

First, we compare *Camarillasaurus* with other theropods focused mainly on the spinosaurids.

Teeth

Looks similar to Spinosaurus (Stromer 1915) but also Ceratosaurus (UMNH VP 5278; pers. obs.) (fig. 7).

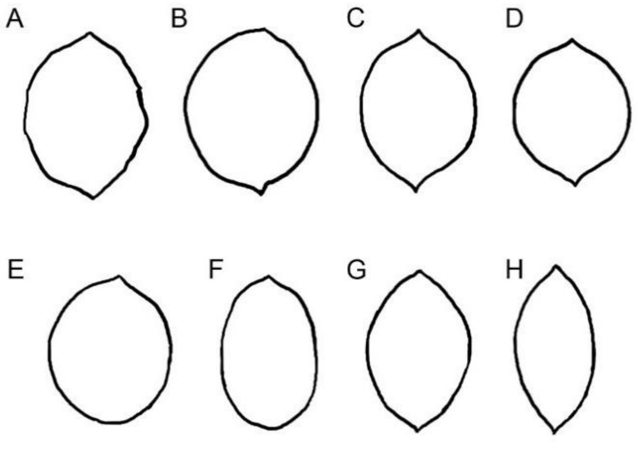


Fig.7. Teeth comparison A) *Camarillasaurus* (drawn from Sanchez-Hernandez & Benton 2014); B) *Spinosaurus* (drawn from Hasegawa et al 2010); C) *Spinosaurus* (redrawn from Stromer 1915); D) cf. *Spinosaurus* MSNM V4047; E-H) the Brazilian spinosaurids (redrawn from Medeiros 2006), not to scale.

Cervical vertebra

From Wang et al 2016 – "*A fragmentary vertebra tentatively identified as a cervical most likely represents an anterior dorsal based on the position of the parapophyses and presence of a hypapophysis.*". The supposed to be a cervical is size-problematic. It is too small to belong to the same individual or even the same taxon as *Camarillasaurus*.

Dorsal vertebra

Striations are present on the dorsal vertebrae in *Camarillasaurus*, *Suchomimus*, *Spinosaurus* Neotype, *Ceratosaurus* (UMNH VP), but not in *Majungasaurus*, *Carnotaurus*, *Elaphrosaurus* (Rauhut & Carrano 2016), and *Allosaurus*.

From Sanchez-Hernandez & Benton (2014), the ventral surface of dorsal vertebra bears a groove between two well developed hypapophyseal ridges. This is similar to caudal vertebrae of many theropods such as the Phuwiang spinosaurid B, the Portuguese Baryonyx, Torvosaurus, Megalosaurus, and Ceratosaurus there for we suggest this is a caudal vertebra, possibly anterior caudal vertebra.

Sacral vertebrae

The sacrals of Camarillasaurus are longer than high, similar to Suchomimus and Spinosaurus.

Caudal vertebrae

On the last caudal, the prezygapophyses are not project beyond the anterior rim of the centrum. The distal caudal vertebrae are look similar to that of Suchomimus and the Phuwiang spinosaurid B (SM PW9B-12), and possibly cf. Baryonyx from Portugal. Longitudinal grooves are present on ventral side of the centra in Camarillasaurus, Phuwiang spinosaurid B (SM PW9B-12), and in the Portuguese Baryonyx but not present in Suchomimus.

On the anterior caudal vertebrae, the morphology of the ventral surface is either flat, groove, or ridge. The caudals are ventrally flat can be found in: *Coelophysis*, *Concavenator*, *Elaphrosaurus*, *Herrerasaurus*, *Ichthyovenator*, *Suchomimus*, *Spinosaurus*, *Siamotyrannus* (almost flat/convex with small and short sulcus, but no keels). The caudals with groove ventrally can be found in: *Allosaurus*, *Ceratosaurus*, *Condorraptor*, *Dilophosaurus*, *Sinosaurus*, *Eustreptospondylus*, *Lourinhanosaurus*, *Majungasaurus*, *Masiakasaurus*, *Megalosaurus*, *Metriacanthosaurus*, *Monolophosaurus*, *Ornitholestes*, *Piatnitzkysaurus*, *Shidaisaurus*, *Sinraptor dongi*, *Torvosaurus*, *Sinraptor hepingensis*, *Baryonyx* Portugal, Phuwiang spinosaurid B. And the caudals with ridge can be found in: *Acrocanthosaurus*, *Aerosteon*, *Giganotosaurus*, *Mapusaurus*, and *Neovenator*.

Chevron

Chevron of *Camarillsaurus* is similar to that of *Suchomimus* (pers. obs.), *Baryonyx* (Charig & Milner 1997), the Khok Kruat spinosaurid (SM-KK14, pers. obs.), and *Ichthyovenator* in that they have large haemal canal whereas small haemal canal is present in *Majungasaurus* (O'Connor 2007), *Ceratosaurus* (Madsen & Welles 2000), *Carnotaurus* (Bonaparte et al. 1990), and *Elaphrosaurus* (Rauhut & Carrano 2016). *Camarillasaurus* is also express longitudinal grooves on both sides, these grooves are present in *Suchomimus* (pers. obs.), *Baryonyx* (Charig & Milner 1997), the Khok Kruat spinosaurid (SM-KK14, pers. obs.), and *Ichthyovenator* as well as in other theropods such as *Majungasaurus*, *Carnotaurus*, and *Torvosaurus*. The longitudinal grooves on chevrons might be widely distributed across theropod taxa, but in *Camarillasaurus*, it is clearly different from *Carnotaurus* (Bonaparte), *Majungasaurus* (O'Connor 2007), and *Ceratosaurus* (Madsen & Welles 2000). In *Ceratosaurus* and *Majungasarus*, their chevrons exhibit anterior process whereas this character is not present in *Camarillasaurus*, *Suchomimus*, the Khok Kruat spinosaurid, and *Baryonyx* (Fig. 8). The spinosaurid character in *Camarillasaurus* is: no anterior process on the chevron. Non-ceratosaurian characters in *Camarillasaurus* is: no ridge on the proximal articular surface of the chevron.

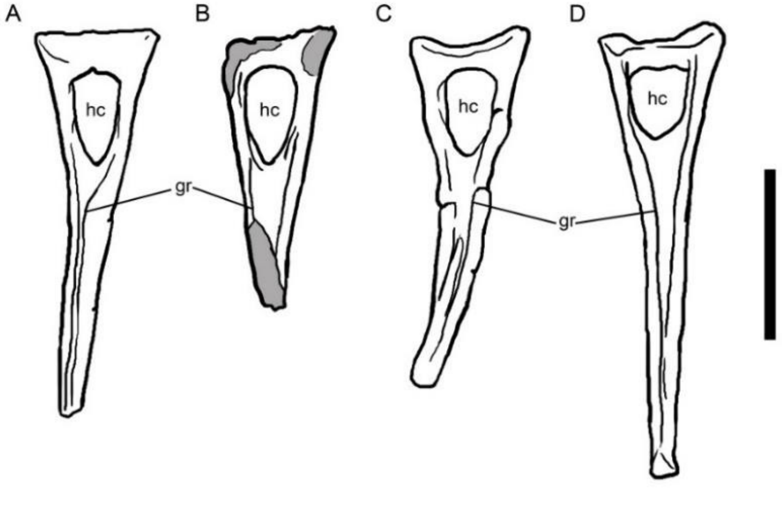


Fig. 8. Chevrons in posterior view of A) *Camarillasaurus* (drawn from Sánchez-Hernández and Benton 2014); B) *Suchomimus* MNN GAD G94-52; C) the Khok Kruat spinosaurid (SM-KK14); D) *Baryonyx* BMNH R9951 (redrawn from Charig & Milner 1997). Abbreviations: **gr**, groove; **hc**, heamal canal. Scale bar = 10 cm (the chevrons have no anterior process; the heamal canals are large; there are grooves on anterior and posterior).

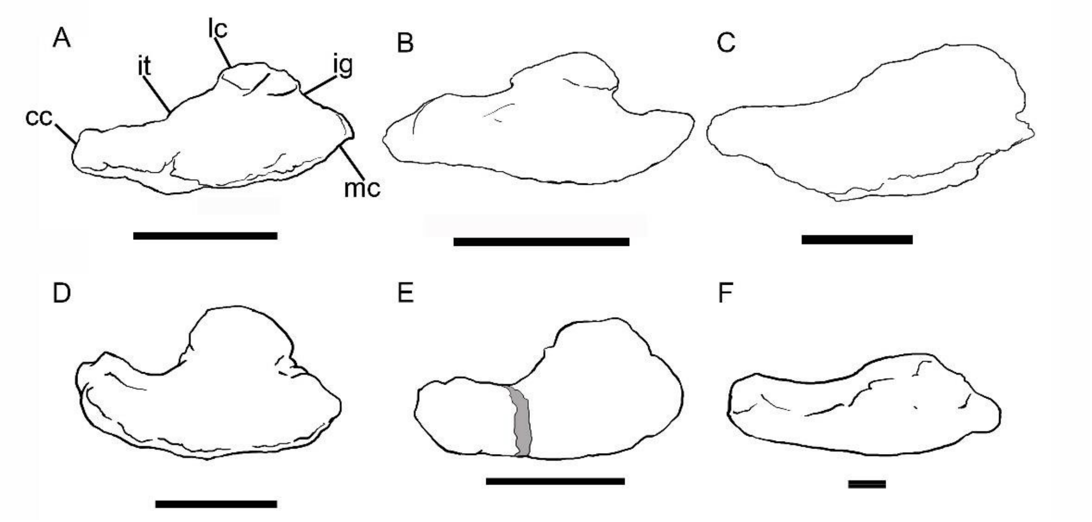


Fig. 9. Proximal tibia of A) *Camarillasaurus* (MPG-KPC8; B) *Spinosaurus* cast of neotype FSAC-KK 11888; C) *Suchomimus* MNN GAD 500; D) *Ceratosaurus* UMNH VP 5278; E) an abelisaurid MB.R. 3626; F) *Majungasaurus* (drawn from Carrano 2007). Abbreviations: **cc**, cnemial crest; ig, intercondylar groove; **it**, incisura tibialis; **lc**, lateral condyle; **mc**, medial condyle. Scale bar A – E = 10 cm, F = 1 cm.

Tibia

Extreme depth of tibia proximal end in *Camarillasaurus* (2.8), this can be found in *Suchomimus* (2.34), *Spinosaurus* (2.4), *Arcovenator* (2.4) (Tortosa et al. 2013), and *Majungasaurus* (2.7). Deep longitudinal groove on tibia in *Camarillasaurus* also found in *Spinosaurus* Neotype (might due to preservation), a longitudinal groove can be found in one tibia of *Suchomimus*. Tibia of *Camarillasaurus* is similar to *Suchomimus* and *Spinosaurus* in proximal view, in which they exhibit low length/width ratio. It is also tapering toward the distal end of the cnemial crest as in *Suchomimus* and *Spinosaurus*, whereas it is parallel and square off towards distal end in Ceratosaurs e.g. *Majungasaurus*, *Pycnomymosaurus* (Kellner & Campos 2002; Delcourt 2017), *Elaphrosaurus*, and *Masiakasaurus*. The shape of the tibia of *Camarillasaurus* is similar to Spinosaurus in having fan-shape, unlike the ratchet-shape as in ceratosaurs (fig. 9). The fibular crest of *Camarillasaurus* is not making a contact with the proximal tibia and located lower than in other ceratosaurs, differs from ceratosaurs, basal averostrans, and basal theropods (fig. 10). The fibular crest of *Camarillasaurus* is possibly reduced and if this is the case, it will be similar to *Spinosaurus*. The groove, which consists of a cnemial crest and fibular crest, on the tibia is also present in *Spinosaurus* Neotype, in case of *Spinosaurus* the groove might present due to the crash or preservation. The tibia cross-section shows high bone compactness or pachyostosis which can be referred to the Spinosaurinae (Aureliano et al 2018; Arden et al. 2019). *Camarillasaurus* also shows non-ceratosaurian characters – the development of the fibular crest of the tibia does not extend to the proximal end.

From Sanchez-Hernandez & Benson (2014), *Camarillasaurus* differs from all other theropods in possessing three autapomorphies: 1) "*the ratio of minimum to maximum diameter of the proximal end of the tibia is very high, measuring 2.8*", this is present in *Suchomimus*, *Spinosaurus*, and *Majungasarusu* but the ratios are not as high as *Camarillasaurus*; 2) "*g-shaped cross-section of the shaft of the tibia produced by the central narrow deep longitudinal groove on the medial surface, placed anteriorly to the fibular crest*", this might present on the left tibia of *Spinosaurus* Neotype, but also might due to preservation and its morphology is slightly different (pers. obs.); 3) "*chevron with a deep longitudinal groove along the length of the shaft on the anterior and posterior sides*", this is present in other spinosaurids such as *Suchomimus* and the Khok Kruat spinosaurid (pers. obs.).

Due to lack of material, we here tentative assign it into Megalosauroidea, and possibly Spinosauridae based on similarity.

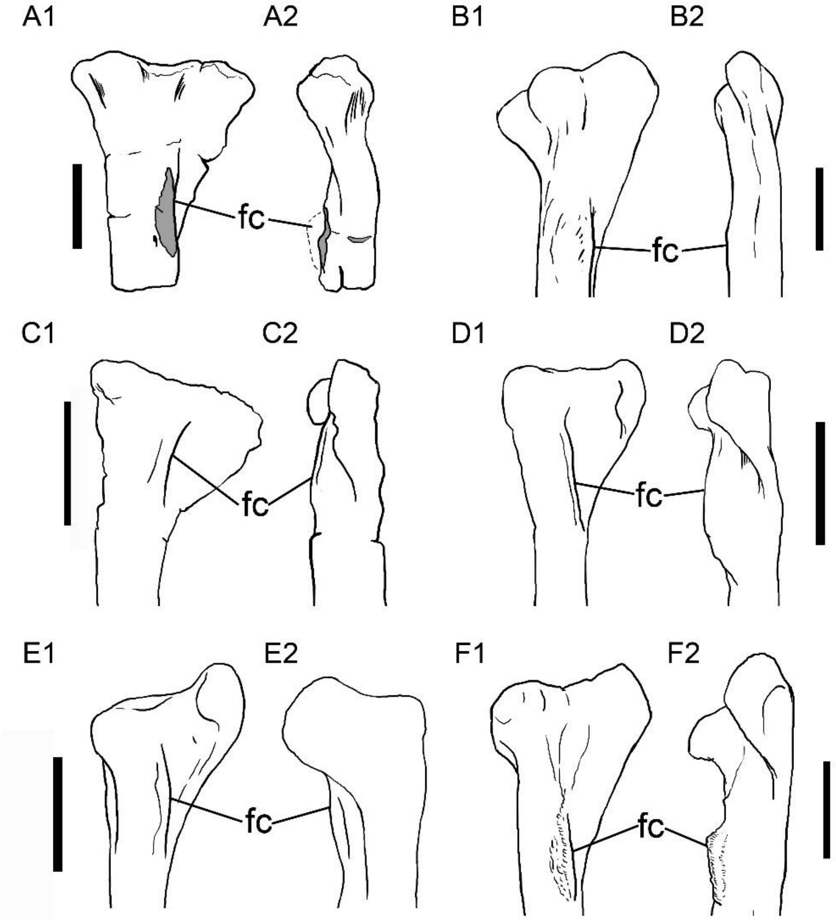


Fig. 10. Tibia of A) a spinosaurid *Camarillasaurus* in lateral and anterior view (MPG-KPC8); B) a spinosaurid *Spinosaurus* cast of neotype FSAC-KK 11888; C) an abelisaurid *Arcovenator* (drawn from Tortosa et al 2013); D) a ceratosaurian *Elaphrosaurus* MB R 4960 (drawn from Rauhut & Carrano 2016, reversed); E) a ceratosaurid *Ceratosaurus* UMNH VP 5278 (reversed); F) an allosaurid *Allosaurus* UMNH VP 7936. Abbreviations: fc, fibular crest. Scale bar = 10 cm.

(3) Spinosaurids by chronological order

The Early Cretaceous spinosaurids including:

Early Barremian: the Portuguese *Baryonyx* and *Camarillasaurus*.

Barremian: the British *Baryonyx*, *Siamosaurus*, and the Phuwiang spinosaurid B.

Aptian-Albian: *Ichthyovenator*, *Suchomimus*, *Irritator*, and SM-KK 14.

(4) The systematic relationships of *Camarillasaurus*

Camarillasaurus was not included in the analysis by Gianechini et al (2015) because it shows dubious evidence of being a ceratosaur (Gianechini et al 2015). It was found that some characters are present in some tetanurans and coelurosaurs by Wang et al (2016). It was not included in the analysis of Rauhut and Carrano (2016).

Phylogenetic analysis (added to the matrix of Carrano et al 2012)

Camarillasaurus – modified version
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Phylogenetic Analysis

Data matrix from Carrano et al 2012, 59 taxa (excluded *Streptospondylus* & *Eustreptospondylus*), 351 char, using traditional search with 1000 random seed, strict consensus, the TNT (Goloboff et al. 2008) produces 7 MPTs, each of 1014 steps, CI = 0.426, RI = 0.698. It found *Camarillasaurus* to nest within Megalosauroidea possibly Spinosauridae, we, therefore, prefer the Spinosauridae hypothesis and suggest this unclear solution is due to the incompleteness of the material.

Synapomorphy recovered from present analysis:

Tetanurae: 5 sacral vertebrae (197:0); sacral vertebrae are not constricted (198:0); sacral vertebrae orientation is horizontal (199:0); sacral dorsal neural spine as thin as dorsal edge (200:0); chevron proximal articular surface has no ridge (215:1); tibia cnemial crest is round (319:0) (contra to Ceratosauria).

Megalosauroidea: anterior dorsal vertebrae with ventral keel (184:1), uncertain in *Camarillasaurus.*

Megalosauria: distal end of chevron is expanded (218:0), not present in *Camarillasaurus.*

Spinosauridae: anterior process of the chevron is absent (217:0); Coracoid, development of posteroventral process is pronounced, posteroventrally tapering process (226:1), convergent in Allosauria; tibia fibular crest does not extend to the proximal end (324:2), convergent in *Torvosaurus* and allosaurians.
Possibly Spinosaurinae: pachyostosis (see Fig. S4 cross section of the tibia) and limb reduction.

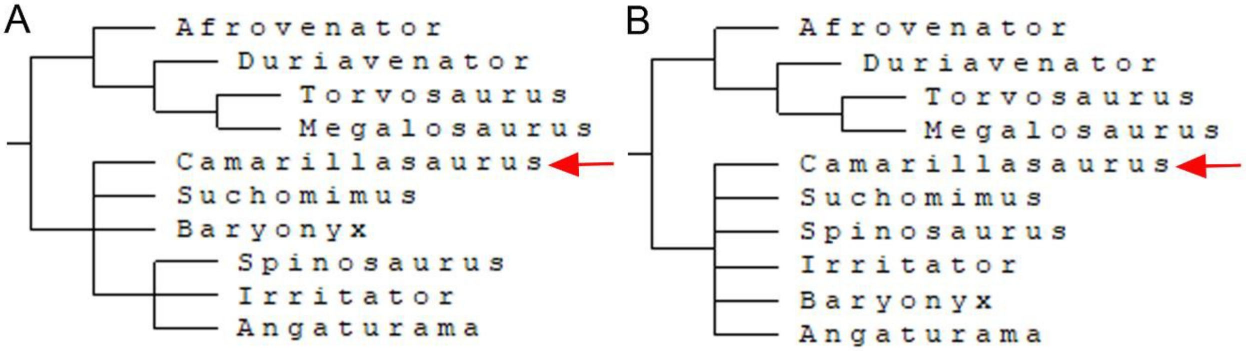

Fig. 11. Phylogenetic analysis of *Camarillasaurus*. (A) Modified from Carrano et al 2012, 351 characters, 59 taxa (excluded *Streptospondylus* & *Eustreptospondylus*) produced 7 MPTs each of 1014 steps, CI = 0.426, RI = 0.698. (B) After TBR 50000 trees (follow method of Carrano et al. 2012) recovered 1350 MPTs.

4. DISCUSSION

Phylogenetic analysis of *Camarillasaurus* from the Early Cretaceous of Spain found it to nest within the Spinosauridae. Agreed with the evidence that it exhibits some characters similar to *Suchomimus* and *Spinosaurus*, therefore we assign *Camarillasaurus* to the Spinosauridae. From the phylogenetic analysis, the non-ceratosaurian characters in *Camarillasaurus* consist of 1) no ridge on the proximal articular surface of the chevron (char. 215); 2) the development of the fibular crest of the tibia does not extend to proximal end (char. 324); 3) tibia cnemial crest is round, not hatchet-shaped (char. 319). The spinosaurid character in *Camarillasaurus* is no anterior process on the chevron (char. 217). The spinosaurine character in Camarillasaurus is pachyostosis tibia and limb reduction. The Phuwiang spinosaurid B from the Early Cretaceous Sao Khua Formation of Thailand shows great similarity to the Portuguese *Baryonyx* and *Camarillasaurus*, as well as the Brazilian spinosaurid, as mention above, therefor we referred it to the Spinosauridae and possibly cf. *Siamosaurus*. Whether the Phuwiang spinosaurid B is the same taxon as *Siamosaurus* or not is beyond the objective of this study.

The Iberian spinosaurids

A possible *Baryonyx* (Mateus et al. 2005) has been reported from the Early Cretaceous of Portugal. The spinosaurids in Spain including: a manual ungual (Gasca et al. 2018). A possible baryonychine (CMP-3b/42; CMP-3b/211; CMP-MS-0/22; CMP-3c/188) (Malafaia et al. 2018). Teeth collected from the Early Barremian Camarillas Formation in Galve, Teruel Province were tentatively assigned to Spinosaurinae based on the lack of serrated carinae and the conical shape of the crowns (Sánchez-Hernández et al., 2007; Malafaia et al. 2018). More than one spinosaurid taxon might present which suggested by the appearance of different tooth morphotypes (Malafaia et al. 2018).

Comparison of the Spinosauridae in Southeast Asia and Europe

In Southeast Asia, the spinosaurids have been reported from the Early Cretaceous of Thailand, Laos, and Malaysia (see Chapter 2) as well as in Europe where the spinosaurids have been reported from the Early Cretaceous of England, Portugal, and Spain.

The occurrence of more than one spinosaurid in the same locality

Two spinosaurids presented in the Kem Kem beds of Morocco are based on two morphotypes of vertebrae (Evers et al. 2015), two morphotypes of quadrates (Hendrickx et al. 2016), two morphotypes of rostra (Arden et al. 2019; see dal Sasso et al. 2005; Cuff & Rayfield 2013), and two morphotypes of frontals (Arden et al. 2019). The presence of at least two spinosaurids from the Romualdo Formation of northeastern Brazil consists of *Irritator* and *Angaturama* (Sales & Schultz 2017; Aureliano et al. 2018). The presence of at least two spinosaurids from the Aptian of Southeast Asia, the Khok Kruat Formation of Thailand (the Khok Kruat spinosaurid) (Buffetaut et al. 2004; 2005; Milner et al. 2007) and the Grès supérieurs Formation of Laos (*Ichthyovenator*) (Allain et al. 2012). Two tooth morphotypes from Pra Prong locality, Sa Kaeo Province, Thailand (possibly Sao Khua Formation) have been recently reported (Suteethorn et al. 2018), as well as the Khok Kruat Formation of northeastern Thailand (Wongko et al. 2019).

5. CONCLUSION

1) Striation on the surface of the transverse process of the caudal vertebrae, found in the Phu Wiang spinosaurid (Phuwiang spinosaurid B) and cf. *Baryonyx* from Portugal. 2) Well- developed double keels and long and deep groove in between, found in Phuwiang spinosaurid B and cf. *Baryonyx* from Portugal but the morphology of the grooves is different. 3) Two buttresses and three fossae below the transverse process of the caudal vertebrae are present in Phuwiang spinosaurid B, as well as in *Baryonyx*, the Brazilian spinosaurid NM 4743-V, a megalosaurid *Torvosaurus*, and probable *Ichthyovenator*. 4) Posterior caudal vertebrae have curve, rod-like neural spines with

small process at the base anteriorly, found in Phuwiang spinosaurid B, cf. *Baryonyx* from Portugal, *Suchomimus*, and *Camarillasaurus*. 5) The Phuwiang spinosaurid B might belong to *Siamosaurus* and possibly closely related to *Baryonyx*. The caudal vertebrae similar to the Phuwiang spinosaurid B can be found in many places in the Phu Wiang Mountain. This is same situation as the teeth of *Siamosaurus* which normally can be found in various places in the Phu Wiang Mountain. 6) The phylogenetic analysis found *Camarillasaurus* to nest within the Spinosauridae, agreed with the similarity of its caudal vertebrae, chevrons, and tibiae to other spinosaurids, including the Phuwiang spinosaurid B. 7) *Camarillasaurus* is approximately 4 m in length and probably sub-adult spinosaurid. The Phuwiang spinosaurid B is approximately 5 m long.

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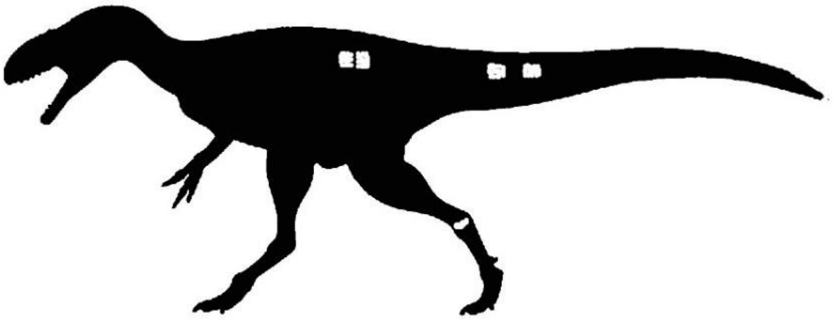
CHAPTER 7

First Record of a Juvenile Theropod Dinosaur from the Early Cretaceous of Thailand: Spinosaurid or Basal Coelurosaur?



CHAPTER 7

FIRST RECORD OF A JUVENILE THEROPOD DINOSAUR FROM THE EARLY CRETACEOUS OF THAILAND: SPINOSAURID OR BASAL COELUROSAUR?

Abstract:

We describe here the first juvenile tetanuran theropod dinosaur discovered from the Phu Wiang Mountain, Late Barremian Early Cretaceous Sao Khua Formation of northeastern Thailand. The Phu Wiang site 9B Locality in the Phu Wiang Mountain has yielded much diverse theropod faunas. This consists of atleast three theropod taxa including a megaraptoran *Phuwiangvenator*, a probable spinosaurid (SM-PW9B-taxon B), and a juvenile theropod (SM-PW9B-taxon C) which is the main objective of this work. The juvenile theropod (SM-PW9B-taxon C) consists of partial sacral vertebrae, two caudal vertebrae, almost complete astragalus lacking the ascending process, and pedal phalanges. Its vertebrae are not fused to the transverse processes and the astragalus is also not fused to other bones, so it is concluded here to be a juvenile of other theropods in that area such as a basal coelurosaur (including the megaraptoran) or spinosaurid. The morphological and phylogenetic analyses, as well as the information on the theropods discovered in this region recently suggest that this small theropod could be refer to Tetanurae, possibly Spinosauridae. Pending the discovery of more materials, we will not identify beyond this step. The 'primitive' or unclear characters is due to the fragmentary nature of this animal, as well as its ontogeny. This is the first record of juvenile theropod found in Thailand and Southeast Asia so far.

Keywords: Juvenile theropod, Spinosauridae, Early Cretaceous, Sao Khua Formation, Thailand

1. INTRODUCTION

Several juvenile specimens of non-maniraptoran theropods have been reported sofar. These include *Torvosaurus*, *Lourinhanosaurus* (Araújo et al. 2013), the Portuguese allosauroid (3-3.5 m in length, Malafaia et al. 2016), *Spinosaurus* (Maganuco and Dal Sasso 2018.), *Sciurumimus* (Rauhut et al. 2012), *Juravenator* (Göhlich and Chiappe 2006), *Allosaurus* (Carpenter 2010),*Tarbosaurus* (Tsuihiji et al. 2011), Spain spinosaurid (Malafaia et al. 2018), Moroccan spinosaurids (Lakin & Longrich 2019), *Megaraptor* (Porfiri et al. 2014).

The Phu Wiang Mountain, Khon Kaen Province of northeastern Thailand Early Cretaceous Sao Khua Formation (≈ Late Barremian) has yielded much diverse theropod faunas in Thailand and Southeast Asia (see Chapter 2). This including a compsognathid from the PW1 Locality (Buffetaut and Ingavat 1984), several teeth of a spinosaurid *Siamosaurus suteethorni* from various sites (Buffetaut and Ingavat 1986), postcranial skeleton of an ostrich-mimic dinosaur *Kinnareemimus khonkaenensis* from the PW5A Locality (Buffetaut et al. 2009; see Chapter 4), a maxilla of a carcharodontosaurid from the PW1A Locality (Buffetaut and Suteethorn 2012), and a basal tyrannosauroid *Siamotyrannus isanensis* from the PW9 Locality with the new study suggests it could be a basal coelurosaurs (Buffetaut et al 1996, Samathi 2013; see Chapter 5).

The Phu Wiang site 9B Locality which is not much far from the PW9 Locality has yielded several theropods. This consists of the theropod taxon A, B, and C. The Phuwiang theropod A (SM-PW9B-taxon A) is a basal coelurosaur, possibly a megaraptoran and recently named *Phuwiangvenator*. It consists of dorsal and sacral vertebrae and fore and hindlimbs (see Chapter 3, Samathi et al. 2019). The Phuwiang theropod B (SM-PW9B-taxon B) is probably a spinosaurid and so-called here the 'Phuwiang spinosaurid' (see Chapter 6), and the Phuwiang theropod C (SM-PW9B-taxon C), so-called here the 'Phuwiang juvenile', is the main objective of this work.

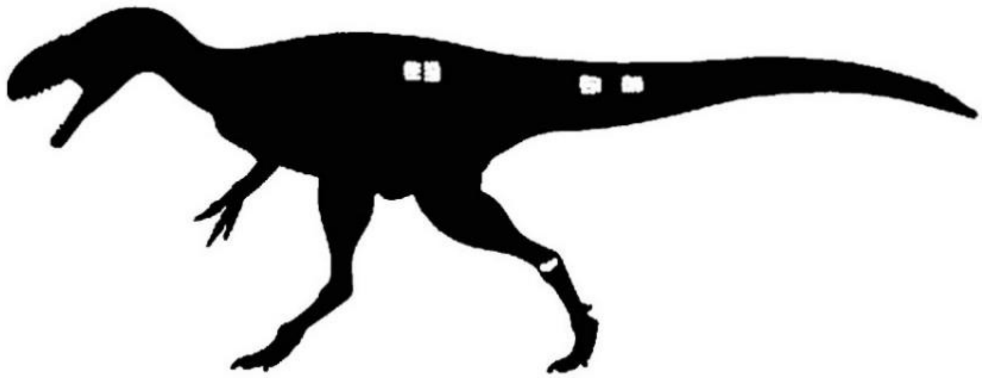


Fig. 1. Skeleton reconstruction of the Phuwiang juvenile (SM-PW9B- taxon C). It is approximately 3 m long.

The main questions are:

1) is the Phuwiang juvenile (SM-PW9B-taxon C) the same taxon as *Phuwiangvenator* or not?
2) is the Phuwiang juvenile (SM-PW9B-taxon C) a coelurosaur, spinosaurid or tetanuran indet.?

Materials

This study is based on the material number SM-PW9B housed at Sirindhorn Museum, Department of Mineral Resources, Kalasin Province, Thailand.

Institutional abbreviations

SM: Sirindhorn Museum, Department of Mineral Resources, Kalasin, Thailand; **FPDM**: Fukui Prefectural Dinosaur Museum, Katsuyama, Japan; **MB**: Museum für Naturkunde, Humboldt- Universität zu Berlin, Germany; **MCNA**: Museo de Ciencias Naturales y Antropológicas "Cornelio Moyano", Mendoza, Argentina; **MNN**: Musée National du Niger, Niamey, Republic of Niger; **UMNH**: Natural History Museum of Utah**,** Salt Lake City, Utah, USA. **NMV**: Museum Victoria, Melbourne, Australia.

2. SYSTEMATIC PALEONTOLOGY

Dinosauria Owen, 1842
Theropoda March, 1881
Tetanurae Gauthier, 1986
?Spinosauridae Stromer 1915
Gen. et sp. indet.

Materials: astragalus (SM-PW9B-38); sacral vertebrae (SM-PW9B-unnumbered); caudal vertebrae (SM-PW9B-35 and SM-PW9B-37); pedal phalanges (SM-PW9B-8 and SM-PW9B-9) and some pedal unguals (fig. 1).

Geological setting: Early Cretaceous Sao Khua Formation (≈ Late Barremian).

Locality: Phu Wiang site 9B Locality, Phu Wiang District, Khon Kaen Province, Thailand.

Comment: The Phuwiang juvenile (SM-PW9B-taxon C) is about the size of subadult *Falcarius* (UMNH VP 12364) or slightly smaller based on the size of their astragali (pers. obs.). It is, therefore, approximately 3 m in length.

3. DESCRIPTION

Sacral vertebrae

One small last sacral vertebra is preserved with the small part of sacral 4 still attached to it. Centrum is slightly flat and circular in shape posteriorly. The neural arch is missing and not fused to the centrum. The rib articulation for contact to ilium is preserved on both sides. It situated anterodorsally of the centrum below the neural arch (at the base of the neural arch). It is long, about 8 mm basoapically (stalk-like) and 35 mm anteroposteriorly. There is no groove on the centrum ventrally and no pleurocoel or foramina (fig. 2).

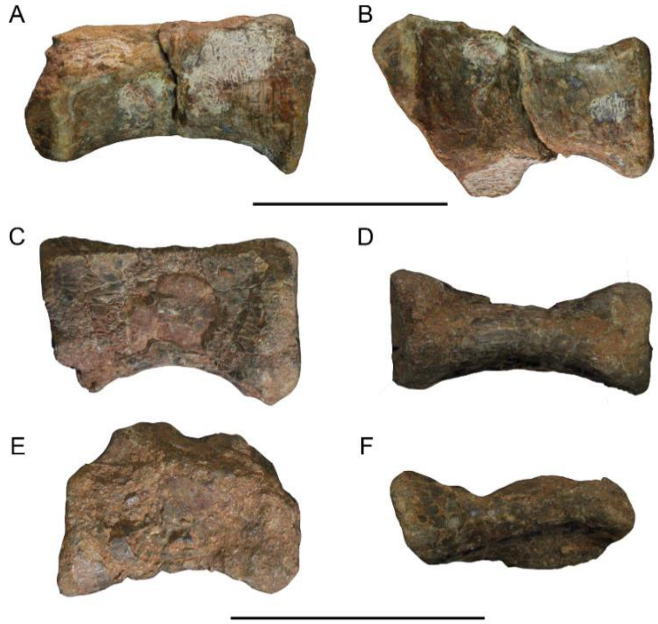


Fig. 2. Sacral (A, B) and caudal (C, D) vertebrae of the PW9B-taxon C. scale bar = 5 cm.

Caudal vertebrae

CV1 – SM-PW9B-35: The centrum is slightly concave anteriorly and posteriorly, hourglass shape and strongly constrict at the middle of the centrum. The facet for chevron articulation can be observed. The neural arch is missing and is not fused with the centrum. No pleurocoel, foramina, possibly no ventral groove, no keel (hypapophysis). The centrum is longer than high, and is elliptical or subrectangular shape anteriorly and posteriorly.

CV2 – SM-PW9B-37: the centrum is oval shape anteriorly, posterior is incomplete. It is longer than high and hourglass shape in ventral view. There is no pleurocoel, foramina, hypapophysis, ventral groove. The neural arch is fused to the centrum. The centrum is concave anteriorly (fig. 2).

Astragalus

The Phuwiang juvenile astragalus (SM-PW9B-38) looks resemble with that of *Phuwiangvenator* which is much larger (SM-PW9B-18 and SM-PW9A-unnumbered) with some degree of differences (see comparison below). This might be due to the ontogenetic, inter- or intraspecific variation that effects its phylogenetic status (fig. 3).

The horizontal groove on the anterior surface of the astragalar body is present. The bone in distal view is a trapezoidal outline and narrowing laterally. There is no proximolateral extension of the astragalar body. There is no anterior extension of the astragalar body in distal view. Calcaneal notch is not present. The ascending process of the astragalus is likely lamina and sheet-liked and more possibly parallel or sub-parallel (as evidenced from the broken base on the astragalar body). Its base extends approximately 50% of the breadth of the astragalar body, being placed on the lateral half of the astragalar body. Base on the orientation of the base of the ascending process, it is clearly indicating that the distal condyles of the astragalus were oriented anterodistally.

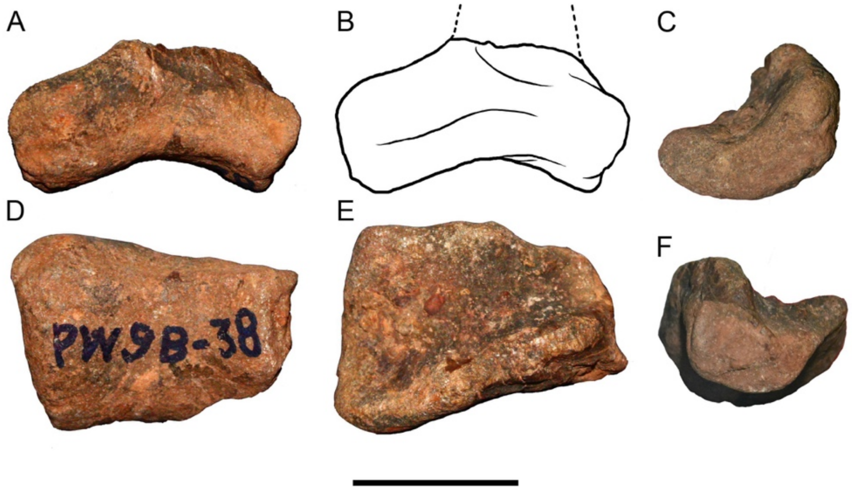


Fig. 3. The Phuwiang juvenile, left astragalus (SM-PW9B-38) and line drawing in anterior (A, B), medial (C), distal (D), proximal (E), and lateral (F) view. Scale bar = 3 cm.

The lateral side of the astragalus is considerably narrower anteroposteriorly than the medial side as in *Zupaysaurus*, *Pandoravenator*, and tetanurans (Rauhut & Pol 2017), but not in *Liliensternus* (pers. obs.) and *Elaphrosaurus* (Rauhut & Carrano 2016; Rauhut & Pol 2017). The distal articular surface of the astragalus is concavely arched in anterior view.

Pedal Phalanges

The pedal phalanges of the Phuwiang juvenile (SM-PW9B-xx) are not as dorsoventrally flattened as in those of Suchomimus and Spinosaurus. Probably pedal phalanx III-2 and III-3.

Fig. 4. PW9B-taxon C pedal phalanges. Dorsal, ventral, and ?lateral view. Scale bar = 5 cm.

4. COMPARISON

Kinnareemimus (SM-PW5A-100): the Phuwiang juvenile might be an ornithomimosaur. Since there are no overlapped materials with *Kinnareemimus*, we then compare the Phuwiang juvenile with other Early Cretaceous ornithomimosaurs (see below).

Siamotyrannus (SM-PW9-1): there is no overlapped materials.

The Phuwiang spinosaurid (SM-PW9B-taxon B): there is no overlapped materials.

Phuwiangvenator (SM-PW9B-taxon A): the astragalar body of the Phuwiang juvenile has no cranio-proximal process and its lateral side is not extended anteroposteriorly in distal view, these are contra to the condition of *Phuwiangvenator* and *Vayuraptor* (SM-NB A1-2) (fig. 5; see Chapter 3; Samathi et al. 2019a). These characters are more resemble to the condition in spinosaurids than to basal coelurosaurs. However, it might due to ontogeny or they are phylogenetically significant. These have to be tested in further studies.

Carcharodontosaurid (PRC 61): there is no overlapped materials.

Fig. 5. Astragali in ventral view, A) Phuwiang juvenile (SM-PW9B-38); B) *Phuwiangvenator* (SM-PW9B-18); C) *Vayuraptor* (SM-NB A1-2); D) *Suchomimus* adult (MNBH GAD98), not to scale.

Majungasaurus, the astragalus in ventral view is obliquely hourglass-shaped, due to the enlargement of the anteromedial corner relative to the anterolateral corner (Carrano 2007).

The spinosaurid *Suchomimus*: there is no inflexion in the anterior margin of the astragalar body in distal view as found in the Phuwiang juvenile (fig. 5; pers. obs.).

Allosaurus UMNH VP 11003 (pers. obs.): there is a slight inflexion in the anterior margin of the astragalar body in distal view.

The ornithomimosaurs *Nqwebasaurus* (Choiniere et al. 2012), *Harpymimus* (Kobayashi 2005), *Beishanlong* (Makovicky et al. 2010), *Garudimimus* (Barsbold 1981): 1) the base of the ascending process occupies complete breadth of the astragalar body, 2) there are strong inflexion in the anterior margin of the astragalar body in distal view. These are completely different from the Phuwiang juvenile.

The megaraptorans *Phuwiangvenator*, *Fukuiraptor* (pers. obs.), *Australovenator* (White et al. 2013), and *Aerosteon* (pers. obs.): there are strong inflection in the anterior margin of the astragalar body in distal view (fig. 5). This condition is different from the Phuwiang juvenile.

5. PHYLOGENETIC ANALYSES

The anatomical characters and synapomorphies allow us to identify the Phuwiang juvenile as members of Averostra, potentially Tetanurae, as outlined in the descriptive section above. To further test these identifications, we included the Phuwiang juvenile in the phylogenetic analyses of Carrano et al. (2012) and Coria and Currie (2016), which focused on the relationships of basal Tetanurae and Avetheropoda, respectively.
Our phylogenetic analyses modified from Carrano et al. 2012 and Coria & Currie 2016 found the Phuwiang juvenile is an averostran, possibly belongs to the Ceratosauria, Spinosauridae, or basal Coelurosauria.

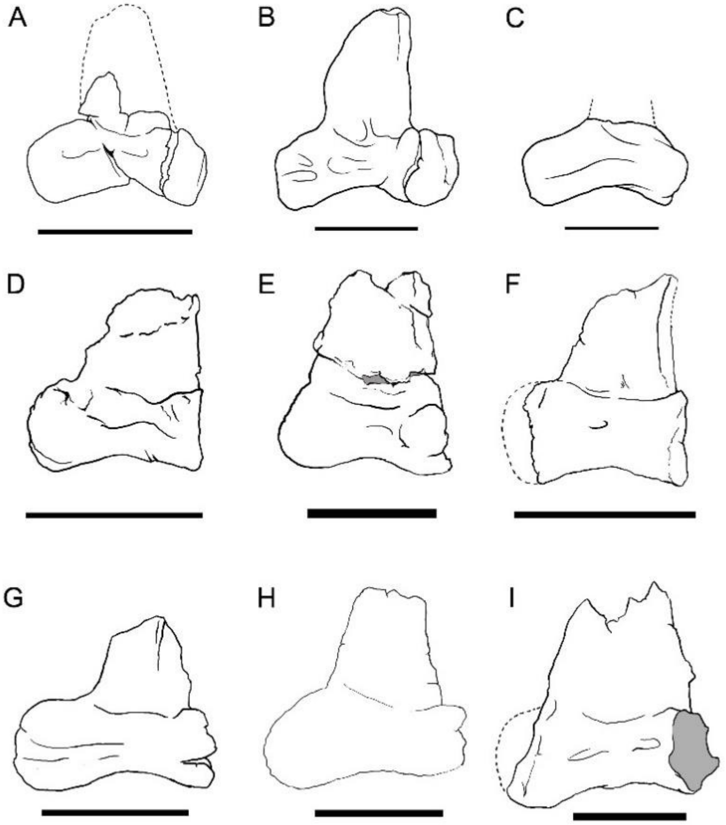


Fig. 6. Astragali of A) *Phuwiangvenator* (SM-PW9B); B) *Vayuraptor* (SM-NB A1-2); C) the Phuwiang Juvenile (SM-PW9B-taxon C); D) *Australovenator*; E) *Aerosteon*; F) *Fukuiraptor*; G) *Allosaurus*; H) *Suchomimus* subadult; I) *Suchomimus* adult. Scale bar (A-B, D-I) = 10 cm, (C) = 3 cm.

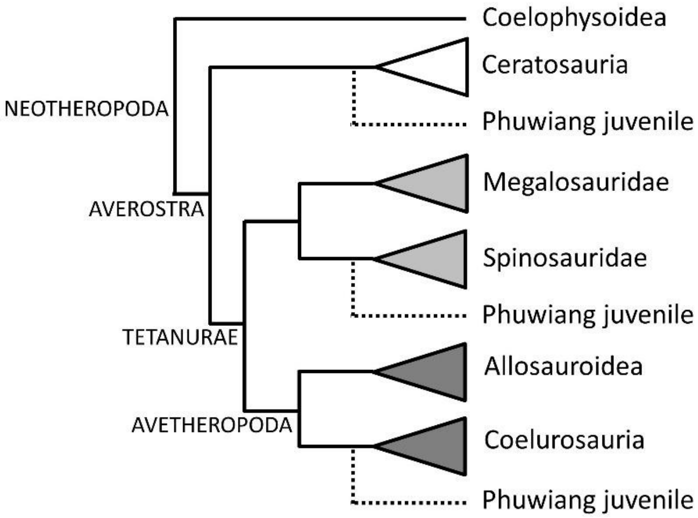


Fig.7. The consensus tree collapsing major clades of theropods result using dataset of Coria & Currie 2016 and Carrano et al 2012 found the Phuwiang juvenile is an averostran, possibly belongs to the Ceratosauria, Spinosauridae, or basal Coelurosauria (for full phylogenetic analyses, see suppl. file).

Character analysis

The Phuwiang juvenile shows following characters, including:

Theropod character (Theropoda *sensu* Marsh 1882)

1. the astragalus with an anterior horizontal groove (Cau 2018).

Averostran characters (Averostra *sensu* Paul 2002)

1. A semilunate fossa at the base of the astragalar ascending process (Cau 2018).
2. An anteriorly-restricted fibular face of astragalus (Cau 2018).
3. Anterodistally oriented distal condyles of the astragalus (Carrano et al. 2012; Rauhut 2003).
4. Laminar ascending process of the astragalus (Carrano et al. 2012; Rauhut 2003).

Tetanuran characters (Tetanurae *sensu* Gauthier 1986)

1. Ascending process of the astragalus is higher than the astragalar body (Rauhut 2003). – unknown in Phuwiang juvenile.
2. Astragalar condyles are expanded proximally on the anterior side of the distal end of the tibia and face anterodistally (Rauhut 2003).

Neotetanuran characters (Neotetanurae *sensu* Sereno et al. 1994)

1. The distal end of fibular placed anterior of the tibia (Cau 2018).
2. More anterodistally-oriented condyle of astragalus (Cau 2018).
3. Proximodistally longer ascending process of astragalus (Cau 2018). – unknown in Phuwiang juvenile.

The Phuwiang juvenile was excluded from Coelurosauria and Megaraptora by:

1. Astragalar body, no cranio-proximal process.

2. Astragalar body, no inflection in the anterior margin of the astragalar body in distal view (in some coelurosaurs).

The Phuwiang juvenile was excluded from Ceratosauria by:

1. the distal end of fibula placed anterior to the tibia, and more anterodistallyoriented condyles of astragalus are neotetanuran synapomorphies (Cau 2018).

By morphology, the astragalus of Phuwiang juvenile (SM-PW9B-18) resembles that of *Suchomimus* (MNBH GAD98) and here tentatively referred to Spinosauridae.

6. DISCUSSION AND CONCLUSION

Phylogenetic analyses and comparison with other theropods found the Phuwiang juvenile (SM- PW9B-taxon C) to nest within Averostra, possibly Ceratosauria, Spinosauridae, or basal Coelurosauria. This is agreed with the morphology of the dinosaur since these three groups exhibit some similar features on their lower legs (e.g. shape of astragalus and ascending process, the vertical medial ridge on the tibia). Since the Ceratosauria is more unlikely to be found in this region but the basal coelurosaurs and spinosaurids have been reported sofar. Furthermore, the distal end of fibula placed anterior to the tibia, and more anterodistallyoriented condyles of astragalus (Cau 2018) are neotetanuran synapomorphies, so we can exclude the Ceratosauria possibility. We suggest that the Phuwiang juvenile belongs to Tetanurae, either basal Coelurosauria or Spinosauridae. Comparison with *Suchomimus*, the Phuwiang juvenile shows great resemblance with the astragalus of this theropod than to basal coelurosaurs. We note that the caudal vertebrae (SM-PW9B-35, SM-PW9B-37) of the juvenile theropod described here are different from the Spinosaurid caudals (the SM-PW9B-taxon B) found from the same locally (i.e. caudal centra ventrally flat vs ventrally with two keels and deep groove). With the above reasons, we here tentatively referred the Phuwiang juvenile to Spinosauridae. Pending the discovery of more materials, we will not identify beyond this step. The 'primitive' or unclear characters is due to the fragmentary nature of this animal. The ontogeny also plays an important role.

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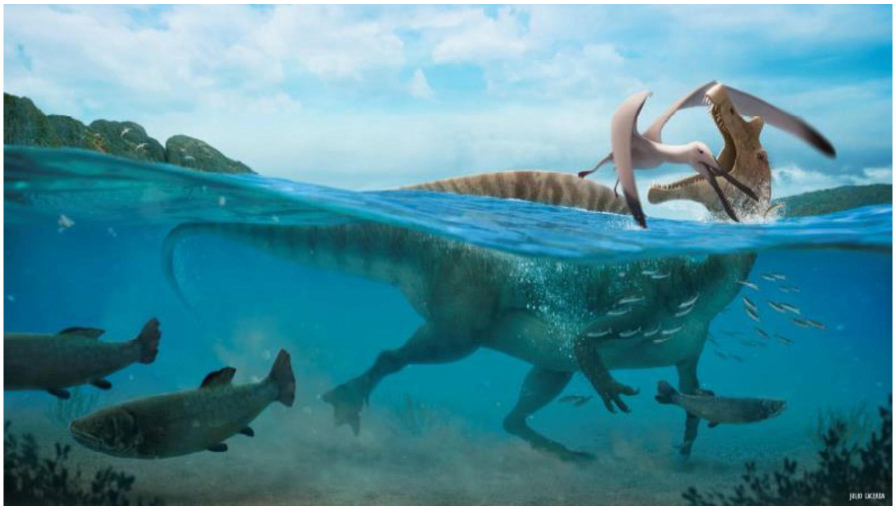
CHAPTER 8

Semi-aquatic Adaptation in a Spinosaur from the Early Cretaceous of Brazil



CHAPTER 8

SEMI-AQUATIC ADAPTATIONS IN A SPINOSAUR FROM THE LOWER CRETACEOUS OF BRAZIL

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ABSTRACT

Spinosaurinae are known to have a strong relationship with aquatic environments, involving several anatomical adaptations. Nonetheless, this group of theropods remains enigmatic, due to the relative incompleteness of its fossil record. A large partial tibia from the Aptian-Albian Romualdo Formation, Northeast Brazil, is herein described through anatomical comparisons and paleohistological analyzes. It features characteristics previously only observed in *Spinosaurus aegyptiacus*, which includes a reduced fibular crest and an osteosclerotic condition. The later, a character supported as correlated with semi-aquatic habits in many limbed vertebrates. The results presented here support high bone compactness being already present in Brazilian Spinosaurinae millions of years before the Moroccan *Spinosaurus*. Furthermore, histological analyses demonstrate the Romualdo Formation specimen was a young subadult still growing fast by the time of its death and suggests Araripe Basin Spinosaurinae could have grown larger than previously thought. This work contributes to a better paleobiological and ecological understanding of South American spinosaurs and helps fill a gap in the macroevolutionary comprehension of Spinosaurinae. Ultimately, it also contributes to further advancing the paleoecological characterization of the Romualdo Formation.

Keywords: Paleohistology, Araripe Basin, Theropoda, Megalosauroidea, Spinosaurinae.

INTRODUCTION

Spinosauridae remains a poorly known group due to the incompleteness of its fossil record. However, in recent years, new specimens and different approaches have provided a wider understanding of the clade (e.g., Amiot *et al.*, 2010a; Kellner et al., 2011; Allain et al., 2012; Cuff & Rayfield, 2013; Ibrahim et al., 2014; Hendrickx et al., 2016; Sales & Schultz, 2017). Most of the knowledge on Spinosauridae comes from North African (mostly from Morocco and Niger) and west European taxa (Spain, Portugal and England; eg. Canudo et al., 2008), and comparatively little information has been published about South-American representatives. The South- American records are mostly restricted to the Cenomanian Alcântara Formation (São Luís-Grajaú Basin) (Medeiros & Schultz, 2002; Medeiros, 2006; Kellner et al., 2011) and the Aptian-Albian Romualdo Formation (Araripe Basin) (Kellner & Campos, 1996; Sues et al., 2002) of Northeast Brazil. However, there is also a single tooth attributed to Spinosauridae recently found in Feliz Deserto Formation, Sergipe Alagoas Basin, also in NE Brazil, in Berriasian–Valanginian strata (Sales et al., 2017), which would represent the oldest Spinosauridae record in South America. Spinosaur theropods have been associated with coastal environments (Rayfield et al., 2007; Ibrahim et al., 2014; Sales et al., 2016) and by presenting a semi-aquatic life style (Charig & Milner, 1997; Sereno et al., 1998; Dal Sasso et al., 2005; Amiot et al., 2010; Ibrahim et al. 2014). In a recent work, Ibrahim and colleges (2014) described new materials from Morocco (including the neotype) belonging to *Spinosaurus aegyptiacus* with several semi-aquatic adaptations including retraction of the fleshy nostrils to a position near the mid-region of the skull; an elongate neck and trunk shifting the center of mass to the knee joint; short pelvic girdle and hindlimbs; and high density of the limb bones. The bone density in *Spinosaurus* suggests that this species could have a buoyancy control in water (Ibrahim et al., 2014). However, this feature is only found in *S. aegyptiacus* so far, and other species (e.g., *Suchomimus tenerensis*) should have had a more terrestrial lifestyle (Ibrahim et al., 2014). Histological analyses are important to obtain information on extinct animals including developmental stages, growth rates, and physiological details (Chinsamy, 2005; Sander et al., 2011; Padian & Lamm, 2013; Ibrahim et al., 2014; Ghilardi et al., 2016; Cerda et al., 2017), allowing a comprehensive biological and ecological understanding.

Therefore, in this contribution we described a new material attributed to an indeterminate spinosaur from Araripe Basin, and performed a histological examination in order to interpret its lifestyle and to compare with terrestrial and semi-aquatic animals.

GEOLOGICAL SETTINGS

The Araripe Basin is located in the northeastern-most portion of South America, in Brazil, between longitudes 38°30' to 40°55' W and latitudes 7°07' to 7°49' S (WGS- 84), comprising parts of Ceará, Pernambuco, and Piauí states (Neumann & Cabrera, 1999) (Fig. 1). The Santana Group is part of the post-rift basin sequence, and comprises (from bottom to top) lacustrine carbonate sediments, coastal and transitional evaporites, and shallow marine/saline lagoon shales of the Crato, Ipubi, and Romualdo formations, respectively (Neumann & Cabrera, 1999). The Romualdo Formation (upper Aptian-lower Albian; Ponte, 1992) encompasses interbedded shales, marls, and limestones with abundant calcareous concretions containing fossils (Valença et al., 2003). These concretions often enclose fossils with exceptional three dimensional and soft tissue preservation (Martill, 1988; Maisey, 1991).

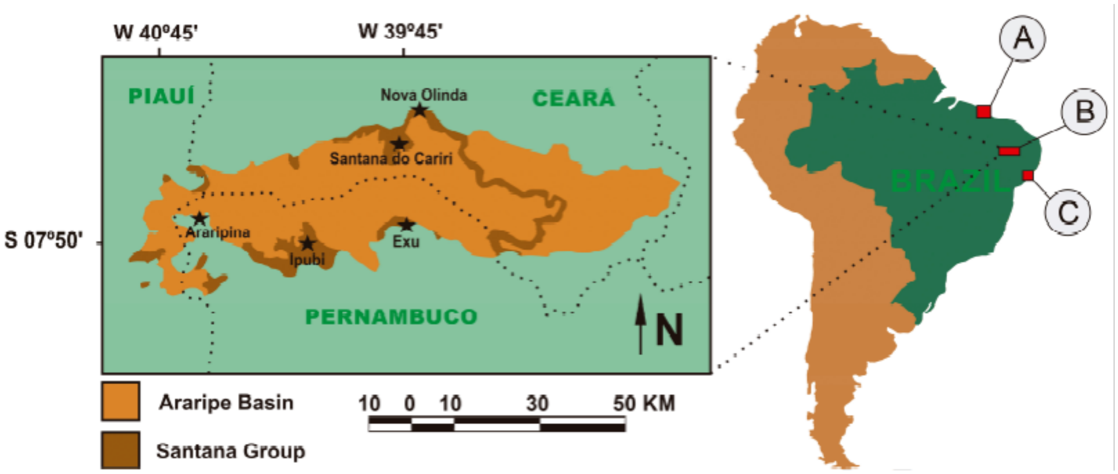

Figure 1. On the left, detail of the Araripe Basin with the Santana Group and the main fossil localities of this unit highlighted (modified from Neumann & Cabrera, 1999). On the right, South American context with geographical location of all geological units that yielded Spinosauridae fossils to date: **A**, Cenomanian Alcântara Formation (São Luís-Grajaú Basin) in coastal Maranhão state; **B**, Aptian-Albian Romualdo Formation (Araripe Basin) on the outback in the frontier between Ceará, Pernambuco and Piauí states; **C**, Berriasian-Valanginian Feliz Deserto Formation (Sergipe-Alagoas Basin) in eastern Sergipe state, all Brazil.

The Romualdo Formation is particularly well known for the great variety and quantity of fossil fishes (Maisey, 1991; Fara et al., 2005). Nevertheless, it also yielded fossil plants and invertebrates (e.g., Coimbra et al., 2002; Lima et al., 2012; Pinheiro et al., 2014), besides crocodyliform, chelonian and pterosaur remains (e.g., Price, 1959; Wellnhofer, 1991; Oliveira & Kellner, 2007; Kellner et al., 2013). Dinosaur fossils are rare (Kellner, 1996; Bittencourt & Langer, 2010), and only theropod material has been recovered so far (Bittencourt & Kellner, 2010). The Romualdo Formation dinosaurs include: two Spinosaurinae, *Irritator challenger* Martill et al., 1996 and *Angaturama limai* Kellner & Campos, 1996; an indeterminate coelurosaur, *Santanaraptor placidus* Kellner, 1999; a large compsognathid, *Mirischia asymmetrica* Naish et al., 2004; and a megaraptoran (Rolando et al., 2017). Spinosaurinae fossils are unequivocally the most common dinosaur remains found in this geological context to date (Bittencourt & Kellner, 2010). Spinosauridae fossils include two partial skulls (Martill et al., 1996; Kellner & Campos, 1996; Sues et al., 2002); a sacro-caudal vertebral sequence associated with chevrons 98 (Bittencourt & Kellner, 2004); a rib tentatively assigned to the clade (Machado & Kellner, 2007); a pelvis, parts of anterior and posterior limbs, and further sacral and caudal vertebrae still undescribed (Campos & Kellner, 1991; Kellner, 1996; Kellner, 2001; Machado & Kellner, 2005; Machado, 2010). The two Romualdo Formation spinosaurids were erected on the recovered cranial material. The *I. challengeri* consists on an incomplete articulated skull with associated mandibles, lacking the anterior portion of the rostrum and the anterior part of both mandibles, and *A. limai* consists of the tip of a rostrum, comprising both pre-maxillae and the anterior-most portions of both maxillae. Several authors consider *A. limai* to be a junior synonym of *I. Challenger* (Charig et al., 1997; Sereno et al., 1998; Buffetaut & Ouaja, 2002; Sues et al., 2002, Dal Sasso et al., 2005; Ibrahim et al., 2014). However, Kellner & Campos (2000), Machado & Kellner (2005), and Sales & Schultz (2017) assume this as a premature conclusion because, although both species have a minimal overlapping features, and therefore are considered different individuals, further information on skulls are need to suggest the synonymy (Sales & Schultz, 2017).. Thus, the question will remain open until more complete cranial material is found (Hone & Holtz, 2017; Sales & Schultz, 2017).

MATERIALS AND METHODS

Institutional abbreviations: AODF, Australian Age of Dinosaurs Museum, Queensland, Australia; **DGM/MCT**, Museu de Ciências da Terra/Departamento Nacional de Produção Mineral, Rio de Janeiro, Brazil; **LPP**, Laboratório de Paleoecologia e Paleoicnologia, Universidade Federal de São Carlos, Brazil; **MCNA**, Museo de Ciencias Naturales de Álava/Arabako Natur Zietzien Museoa, Vitoria- Gasteiz, Spain; **ML**, Museu da Lourinhã, Portugal; **MN**, Museu Nacional, Universidade Federal do Rio de Janeiro, Brazil; **MNFSAC**, Faculté des Sciences Aïn Chock, Casablanca, Morocco; **MNN**, Museé National du Niger, Niamey, Niger; **MPEF**, Museo Paleontológico Egidio Feruglio, Trelew, Argentina; **MSNM**, Museo di Storia Naturale di Milano, Italy; **OUM**, Oxford University Museum, England; **PVL**, Fundación Miguel Lillo, Tucumán, Argentina; **SMNS**, Staatliches Museum für Naturkunde Stuttgart, Germany; **UCMP**, Museum of Paleontology, University of California, Berkeley, USA; **UMNH**, Utah Museum of Natural History, Salt Lake City, USA.

The studied specimen (LPP-PV-0042; Fig. 2) corresponds to a fragmentary left tibia. The material is deposited at the Laboratório de Paleoecologia e Paleoicnologia (LPP) paleontological collection of the Universidade Federal de São Carlos (UFSCar), São Carlos, São Paulo state, Brazil.

CT-Scan

A 3D reconstruction of the specimen was obtained using a Philips Diamond Select Brilliance CT 16-slice medical scanner with more than 1000 slices and a voxel size of 1 mm at UFSCar University Hospital. The software *3D-Slicer* v4.6 was used to visualize and segment the images. Bone density analysis was conducted in *Bone Profiler* (Girondot & Laurin, 2003).

Bone histology

For the histological study we followed the standard methodology presented by Lamm (2013). The specimen was replicated in resin and CT-Scanned before being sectioned. The fossil was transversely sectioned at the distal-most point of the preserved diaphysis and then embedded in resin for polishing until the thickness of the section was variable from ca. 40 μm to 100 μm. The thin-section was observed in and photographed with the petrographic microscope Leica DM750P with camera Leica MC170HD and the imaging software LAS (Leica Application Suite) v4.4. We later corrected the images for brightness and contrast using Adobe Photoshop CC. The composite images were prepared in Corel Draw X6. The histological nomenclature used herein is in accordance with Francillion-Vieillot et al. (1990) and Padian & Lamm (2013).

SYSTEMATIC PALEONTOLOGY

Dinosauria Owen, 1842
Theropoda Marsh, 1881
Tetanurae Gauthier, 1986
Megalosauroidea Fitzinger, 1843
Spinosauridae Stromer 1915
Spinosaurinae Stromer, 1915
gen. et. sp. indet.

Referred material: LPP-PV-0042, a fragmentary tibia.

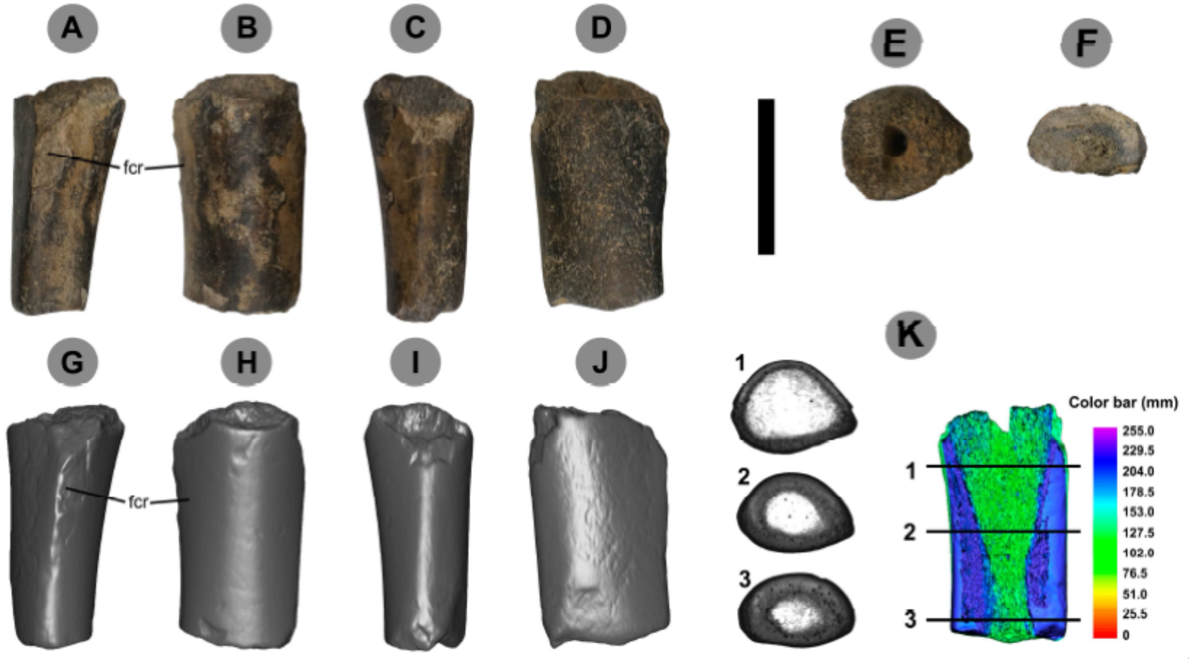

Figure 2. LPP-PV-0042, a fragmentary tibia of Spinosaurinae from the Lower Cretaceous of Brazil. **A, G**, lateral; **B, H**, posterior; **C, I**, medial; **D, J**, anterior; **E**, proximal; and **F**, distal views. **G-J** represent the three-dimensional 904 model from CT scan data. **K**, reconstructed 3D model from CT-Scan with color bar highlighting distinct bone densities in posterior view with longitudinal slices in 1, 2, and 3. Abbreviation: **fcr**, fibular crest. Scale bar = 10 cm.

Locality and horizon: Exact geological and geographical provenance is unknown, but the fossil was collected in the Araripe area, Northeast Brazil. Outcrops of the Lower Cretaceous Santana Group (Araripe Basin) are worldwide known for providing well-preserved fossils and are located in the Araripe region. In the Santana Group, three-dimensional fossils with calcite mineralization are unique to the Romualdo Formation (Aptian-Albian), whereas Crato Formation (Aptian) is well known to provide fossils in laminated limestone. The specimen here described is attributed to the Romualdo Formation due to its three-dimensional preservation condition and typical calcite infilling of this unit. It was prepared from concretion by original owner. Also, the lack of crushing suggests that the specimen is not from the Crato Fm.

RESULTS

Morphological description

The fossil consists of partial diaphysis and metaphysis of a left tibia (Fig.2). The shaft becomes wider while the internal density decreases toward the proximal end (Fig.2K). In cross-section, the bone is anteriorly flat or slightly convex near the diaphysis, but it gets distinctively drop-shaped as the shaft expands through the metaphysis. The anterior surface is broad, flat and rugose, suggesting muscular attachment (*tibialis anterior* muscle). The fibular crest is almost straight and only slightly curved proximally towards the posterior side of the specimen. The fibular crest is somewhat reduced and low. Distinct osteosclerosis, or thickening of the cortical bone, can be recognized in distal cross-section. The preserved total length of the specimen is 150 mm. The proximal-most cross section has 84 mm in length and 66 mm in width; while the distal-most extremity has a transverse section of 76 X 46 mm. The reconstructed maximum length of the tibia is 60 ± 3 cm, based on *Spinosaurus aegyptiacus* Stromer, 1915 (FSAC-KK 11888; Ibrahim et al., 2014) and *Suchomimus tenerensis* Sereno et al., 1998 (MNN GDF500).

Petrography

Electron microscopy was conducted with an Oxford X-act EDS attached to a Fei Quanta 250 SEM. The analysis of LPP-PV-0042 indicates the abundance of calcium and absence of silicon in the bone matrix, a condition commonly observed in the Romualdo Formation fossils (e.g., Aureliano et al., 2014; see Fig.S1, in Supplementary material). Thin sections also demonstrate calcite infilling of the vascular spaces typical of this geological unit (Fig.3).

Histological analyses

There are no preparation marks on surface, but there are truncated osteons in one region of the bone surface. Other regions appear uncompromised. Truncation was caused either by pre-burial transport, by post-exhumation transport or by preparation.

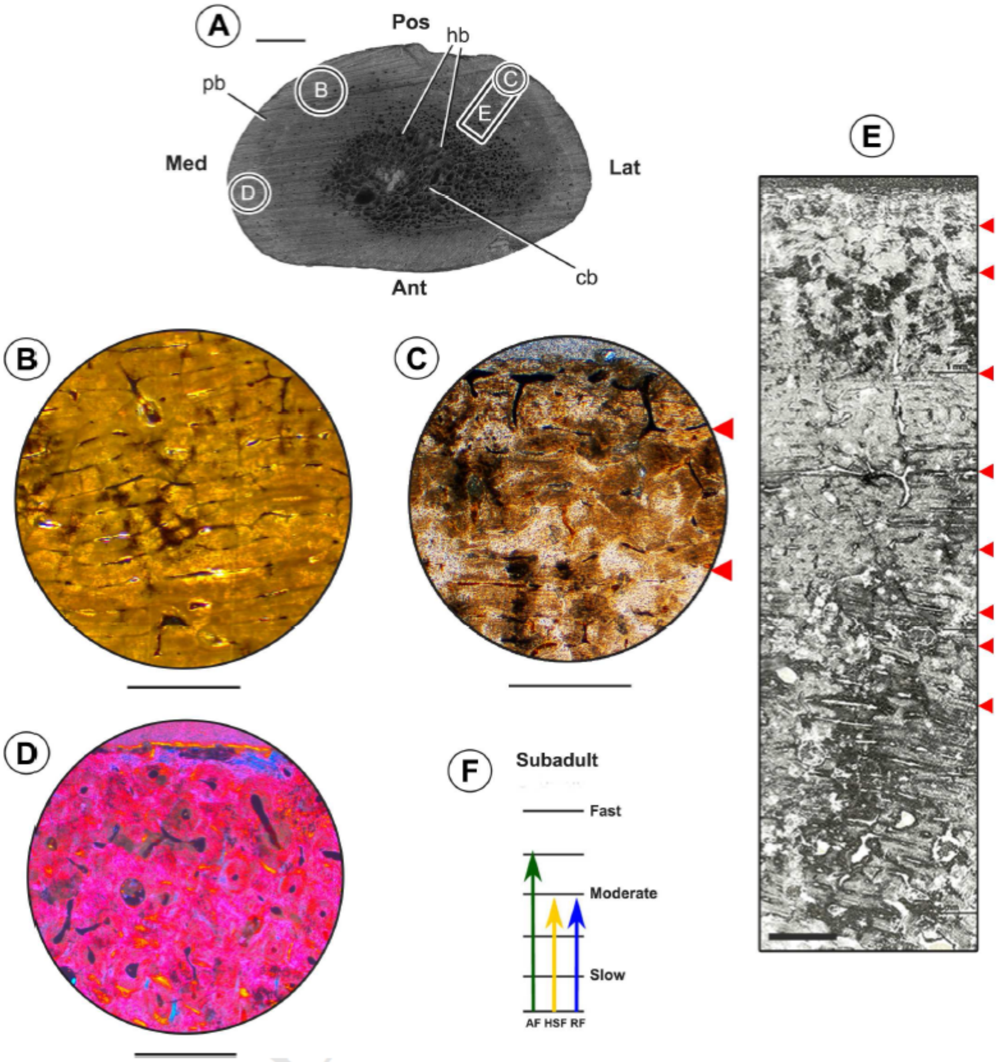

Figure 3. Transverse thin section and bone histology of LPP-PV-0042. **A**, External cortex from the posteromedial part of the bone showing typical fibro-lamellar bone with a plexiform arrangement of the vascularization. **B**, reticular organization of the vascularization and two growth marks in the outermost layer of cortex in the posterolateral area of cross-section. **C**, external cortex from the medial part of the bone showing secondary remodeling with Haversian channels and the absence of an EFS. **D**, polished transverse section showing the thick cortex (CT/CaM = 0.097; *sensu* Mitchell & Sander, 2014). **E**, external cortex showing the decreasing spacing of four (possibly eight) LAGs (arrows). **F**, a three-front model from E, indicating a subadult ontogenetic status to the specimen. Photographs taken under polarized light in A, B, C and E. A filter was applied in C to increase birefringence in 560 λ. Abbreviations: **AF**, apposition front; **Ant**, anterior; **cb**, cancelous bone; **hb**, Haversian bone; **HSF**, Haversian substitution front; **Lat**, lateral; **Med**, medial; **pb**, p bone; **Pos**, posterior; **RF**, resorption front. Scale bar in A = 1 cm, in B-E = 1 mm.

The medullary cavity of the bone is reduced and filled with spongiosa (Fig.3D). The cortical thickness ratio is very high (CT/CaM = 0.097 *sensu* Mitchell & Sander, 2014; global bone compactness from tomography = 0.872; Fig.2.F, K). The extent and type of vascularization vary considerably across thin sections. In the posterior half of the bone, the cortex is predominantly primary in nature with a laminar to plexiform arrangement of the vascularization in fibrolamellar bone tissue (Fig.3A). Reticular organization of the vascularization can be found at the posterolateral outer cortex of the bone (Fig.3B), also in fibrolamellar bone tissue. Curiously, the anteromedial area of the internal bone wall is composed of tissue not formed in laminae, and a predominance of longitudinally oriented vascular canals within a woven matrix with numerous secondary osteons extending outwards to the cortex surface (Fig.3C). The tissue in this area is probably due to the insertion of the *tibialis anterior* muscle. The transition between the medullary cavity and the cortex is gradual, due to the presence of many resorption cavities in the inner cortex. Resorption cavities tend to decrease in density and size towards the external surface of the cortex, and they are more abundant in the anteromedial area of the cross section. Their outline changes from irregular to rounded or elliptical. In the fibrolamellar bone, primary vascular canals are only partially filled by lamellar bone. In the region with laminar to plexiform fibrolamellar bone, zonation can be observed but not every cycle is clearly distinguishable, however. Between four and eight lines of arrested growth (LAGs) are identified (Fig.3.E). The spacing between LAGs decreases towards the surface of the bone. It is clear that no external fundamental system (EFS) is present despite the surface damage in some regions. Horner & Padian (2004) similarly observed that large *Tyrannosaurus rex* Osborn, 1905 specimens presented several LAGs but did not show an outer avascular layer (EFS) that would indicate effective cessation of growth. These concluded that those large bodied, seemingly mature individuals were still growing, although at a lower rate. Similarly, LPP-PV-0042 shows no EFS, but was still growing moderately fast by the time of its death, as suggested by the prevalence of primary tissue at the apposition front.

In sum, the increasing organization of vascular canals toward the outer surface in LPP-PV-0042, the presence of some Haversian systems, the decreasing spacing between LAGs and the absence of an EFS observed in the thin sections of the tibia suggest this individual was subadult at the moment of its death. The subadult status is here interpreted as an ontogenetic stage which the individual has not yet reached full sized and sexual maturity (Mitchell & Sander, 2014). Furthermore, by applying the three-front model of Mitchell & Sander (2014) to the posterior area of the bone, the subadult status is reinforced (Fig.3.F). Although this model was developed for sauropod dinosaurs, it can be applied to other dinosaurs and large mammals (Mitchell & Sander 2014). The balance between the Haversian front and the esorption front, both of which are slower than the apposition front is typical for subadult dinosaurs (Fig.3.F, Mitchell & Sander 2014, fig. 15).

Taphonomy

The specimen, besides fragmentary, also exhibits signs of abrasion. Both features, however, can be interpreted as modern artifacts, since fractures are obtuse, never sharp, and the abraded area is porous and brittle (Reif, 1971). It is common for large

Romualdo concretions to break into several pieces and these become loose on the surface, undergoing erosion (e.g., Kellner et al., 2013). This could have happened with the referred material. Besides, sedimentological characteristics of the Romualdo Formation do not support a high energy transportation model.

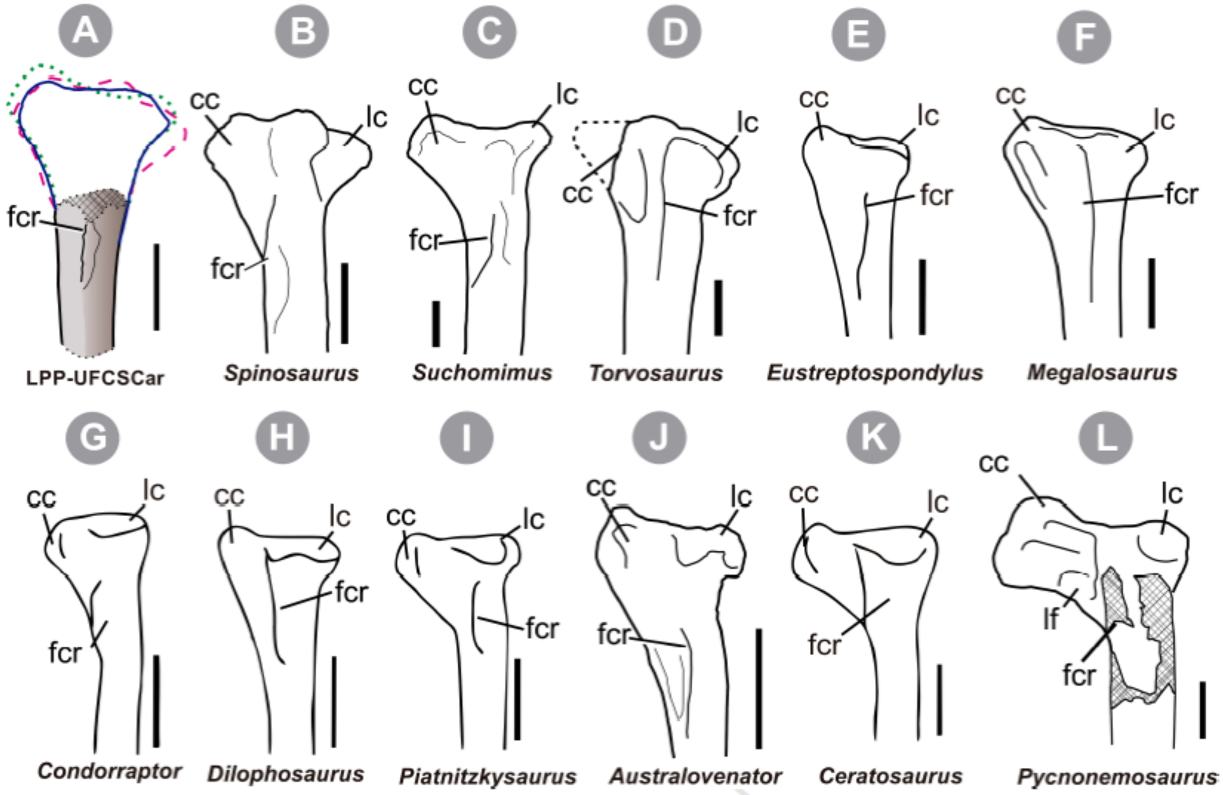

Figure 4. Comparison of the proximal ends of left theropod tibiae in lateral view. **A,** Spinosaurinae indet. LPP-PV-0042. The blue solid line is the epiphysis reconstruction based on Spinosaurinae indet. MN4819-V (from Machado, 2010). The pink dashed line is the epiphysis reconstruction based on *Spinosaurus*. In green, epiphysis reconstruction based on *Suchomimus*. **B,** *Spinosaurus aegyptiacus* (FSAC KK 11888; reversed) (Ibrahim et al., 2014). **C,** *Suchomimus tenerensis* (MNN GDF500) (Sereno et al., 1998). **D,** *Torvosaurus gurneyi* (ML 430) (Hendrickx & Mateus, 2016). **E,** *Eustreptospondylus oxoniensis* (OUMNHJ. 13558) (Sadleir et al., 2008). **F,** *Megalosaurus bucklandii* Mantel, 1827 (OUMNHJ.13505) (Carrano et al., 2012). **G,** *Condorraptor currumili* Rauhut, 2005 (MPEF-PV 1672). **H,** *Dilophosaurus* Welles, 1970 (UCMP V 4214) (Rauhut, 2005). **I,** *Piatnitzkysaurus* (PVL 4073) (Rauhut, 2005). **J,** *Australovenator* (AODF 604) (White et al., 2013). **K,** *Ceratosaurus* Marsh 1884 (UMNH VP 5278) (Rauhut, 2005). **L,** *Pycnonemosaurus* (DGM 8D9-R) (Delcourt, 2017). Abbreviations: **cc**, cnemial crest; **fcr**, fibular crest; **lc**, lateral condyle; **lf**, lateral fossa. Scale bar = 10 cm.

DISCUSSION

Taxonomy and comparisons

The anatomical features of LPP-PV-0042 support the presence of a large Spinosaurinae in the Romualdo Formation, expanding the fossil record of this group in this geological unit.

The transverse diaphysis section of the analyzed specimen differs from most theropods. In taxa including *Pycnonemosaurus nevesi* Kellner & Campos, 2002, *Allosaurus fragilis* Marsh, 1887, and *Tyrannosaurus rex* (e.g., Horner & Padian, 2004; Delcourt, 2017; see Fig.5), for example, the tibiae have an oval or subcircular in mid-shaft cross-section. LPP-PV-0042, however, is anteriorly flat (slightly convex), similar to what is observed in *S. aegyptiacus*, some megaraptorans (*Australovenator wintonensis* Hocknull et al., 2009, and *Aerosteon riocoloradensis* Sereno et al., 2008) and a few other theropods like *Neovenator salerii* Hutt et al., 1996 and *Chilantaisaurus tashuikouensis* Hu, 1964 (e.g., White et al., 2013; Brusatte et al., 2008; see Table S1).
The sharp-ridged fibular crest present in LPP-PV-0042 is considered an unambiguous synapomorphy of Tetanurae theropods (Holtz, 1994). This feature is not present in abelisaurids and other ceratosaurians as well as in basal theropods, sauropods, and ornithischians (e.g., Holz, 1994; Naish, 1999; Rauhut, 2005; Carrano et al., 2012). The fibular crest of the Romualdo Formation specimen differs from allosauroids (e.g., *Allosaurus fragilis*, *Aerosteon* and *Giganotosaurus carolinii* Coria & Salgado, 1995), as well as from that of the megalosauroids *Torvosaurus gurneyi* Hendrickx & Mateus, 2014, *Piatnitzkysaurus floresi* Bonaparte, 1986, and *Eustreptospondylus oxoniensis* Walker, 1964 (Sadleir et al., 2008), because it is not well developed as in those taxa. In the spinosaurid *S. tenerensis* (MNN GDF500; Sereno et al., 1998), the fibular crest is large and bulbous (see Fig.4.C), differing from LPP-PV-0042, in which it is much smaller. Nevertheless, the reduced fibular crest of LPP-PV-0042 resembles that of *Spinosaurus* (FSAC-KK 11888), which is low and distally broad (Fig.4.B and Fig.S2). The reduced fibular crest might have been associated with the reduction of the knee joint for the vertical limb support as seen in *Spinosaurus* (Ibrahim et al., 2014) and probably also in this Romualdo taxon. Regarding bone density, the extremely thick-walled cortical bone observed in the referred specimen is a feature currently only shared with *S. aegyptiacus* (Ibrahim et al., 2014) among other non-avian theropods (see further discussion in the next topic). Although the robust appendicular bone proportion has been considered a typical feature of megalosauroids (Carrano et al., 2012), here we prefer not to take this into consideration for the taxonomic identification of LPP-PV-0042. As shown by Grillo & Delcourt (2017), the apparent robustness of abelisauroid tibiae was misinterpreted based just in a qualitative examination, and there is a strong correlation among the tibia length, tibia shaft anteroposterior diameter and tibia shaft width. Thus, statistical analyses of megalosauroid allometry should be done before including robustness as a taxonomic character.

Even though several spinosaurid specimens have been recovered from the Romualdo Formation beds, most of them remain undescribed (Machado & Kellner, 2005; Machado, 2010). No appendicular elements have been formally published so far, and the unpublished specimens (see Machado & Kellner, 2005; Machado et al., 2008; Machado & Kellner, 2009) could not be directly assessed for comparison. A proximal epiphysis of a right tibia attributable to Spinosaurinae described in Elaine Machado's Msc thesis (Machado, 2010; Fig.3.B, MN4819-V). However, this specimen was not useful, because the preserved portion did not overlap with LPP PV-0042 anatomically because it is missing the fibular crest (contrary to Machado, 2010).

Lastly, it is worth considering that LPP-PV-0042 differs from crocodylian tibiae in its straight shaft, as well as because it displays an anterolateral sharp ridge, and the cross-section near the diaphysis is not circular (see Snyder, 2007; Woodward et al., 2014). The specimen described here cannot be considered a pterosaur or a bird either, because its shaft lacks the well expressed medullary cavity and extremely thin compact bone typical of these groups (e.g., Kellner et al., 2013; Aureliano et al., 2014). Moreover, even in the largest birds, the fibular crest is not as apparent (i.e. robust) as it is in this specimen (see Naish, 1999).

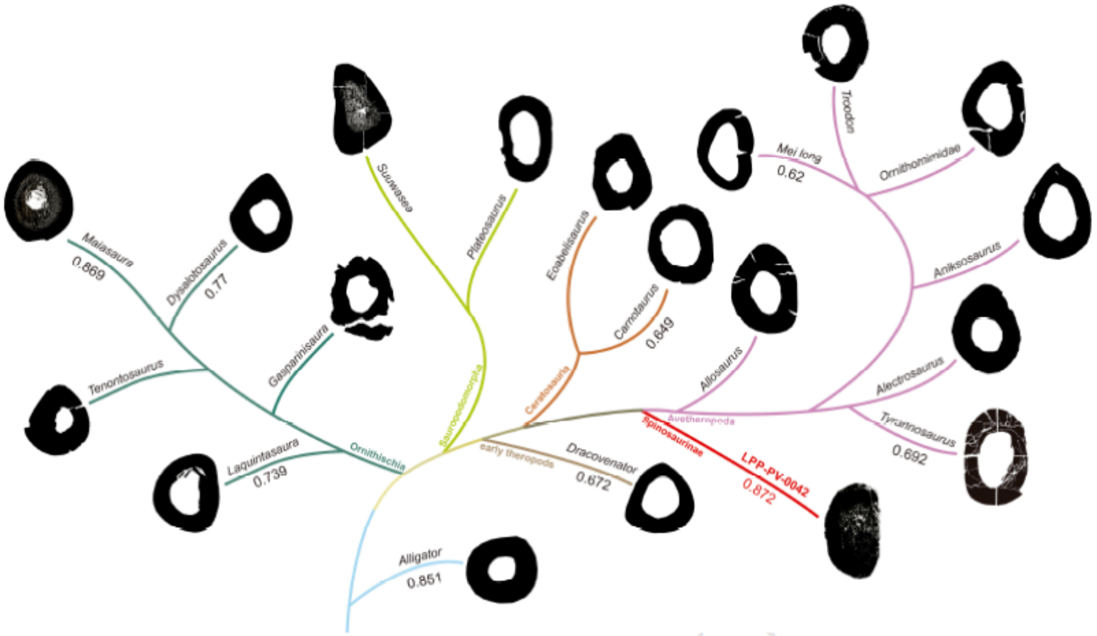

Figure 5. Different tibial cross-sections in non-avian dinosaurs and *Alligator*. The reported values are global compactness obtained with **Bone Profiler**. Specimen numbers and references are in Tables S2-S3 (Supplementary material). Cross sections not to scale.

Bone histology and evolutionary implications for the group

Spinosauridae had a strong relationship to aquatic environments involving several adaptations in the cranial and axial skeleton (Holtz, 1998; Bertin, 2010; Ibrahim et al., 2014; Hone & Holtz, 2017). Some of these adaptations include conical teeth with sub-circular transverse sections; concave anterior portion of the upper jaw; laterally expanded anterior portion of upper and lower jaws; and elongated snout usually associated with piscivory (Charig & Milner, 1986; Taylor, 1987; Kellner & Campos, 1996). Other features including size and position of nares and high bone compactness have also been pointed out as associated with the evolution of a semi-aquatic lifestyle in this group (Dal Sasso et al., 2005; Ibrahim et al., 2014; Sales & Schultz, 2017). High bone compactness is a feature strongly correlated with semi-aquatic and aquatic habits in limbed vertebrates (Kriloff et al. 2008; Houssaye, 2009; Quemeneur et al., 2013; Houssaye et al. 2016). It occurs in different degrees and varies among different parts of the skeleton (Fish & Stein, 1991; Kriloff et al. 2008; Houssaye, 2009; Houssaye et al. 2016). Bone ballast is a primary function of this specialization, which means that dense bones are used for reducing buoyancy by compensating for the air filled lung (Taylor, 2000). Similar evolutionary pathways involving independent acquisition of this character are independently observed in several mammal groups (Wall, 1983; Madar, 2007; Amson et al., 2014), some birds (Ksepka et al., 2015), and some marine reptiles (Hugi & Sánchez-Villagra, 2012; Houssaye, 2013). In all of them, bone compactness clearly increases in taxa adapted to life in shallow water. In theropods, the large open medullary cavity in long bones apparently is a plesiomorphic feature (Ibrahim et al., 2014). Theropods are known to have 'hollow bones' since the early divergence of the bird branch (Ibrahim et al., 2014). Among non-avian theropods, semi-aquatic adaptations based on anatomical and osteohistological characters have previouslyonly been observed in *S. Aegyptiacus* (Ibrahim et al., 2014). However, the high bone compactness value observed in the specimendescribed here (0.872) is strikingly similar to the one observed in FSAC 11888 (0.968, based on a femur; Ibrahim et al., 2014), suggesting a similar adaptation. Although variations in bone compactness are known between appendicular elements (Fish & Stein, 1991; Kriloff et al. 2008; Houssaye, 2009; Houssaye et al. 2016), this does not invalidate the direct comparison made here, nor does the fact that those two former taxa (FSAC-KK 11888 and LPP-PV-0042) have much higher bone compactness than other theropods and most dinosaurs (see Fig.5). The osteosclerotic condition in LPP-PV-0042 shows that this feature was already present in Brazilian Spinosaurinae during the early Albian, at least 10 myr before the Moroccan *Spinosaurus* (Cenomanian in age). This observation expands the occurrence of high bone compactness in Spinosaurinae as well as the suggested link to a semi-aquatic lifestyle in this group. Using the principle of phylogenetic bracketing (Bryant & Russell, 1992), osteosclerosis may be present in the entire Spinosaurinae clade, a hypothesis that must be empirically tested by observing more material related to the clade. Baryonychinae (*sensu* Sereno et al., 1998) appears to have a plesiomorphic condition regarding this state, as noted by Ibrahim et al. (2014) based on the analysis of *Suchomimus* (femur global compactness =0.670), but sampling inside this group also needs to be expanded. Finally, the evolution of large sizes (10-15 m length) in Spinosaurinae may also have been reinforced by the evolution of semi-aquatic preferences, which should be tested elsewhere using biomechanical and statistical analyses and it is beyond the scope of this paper.

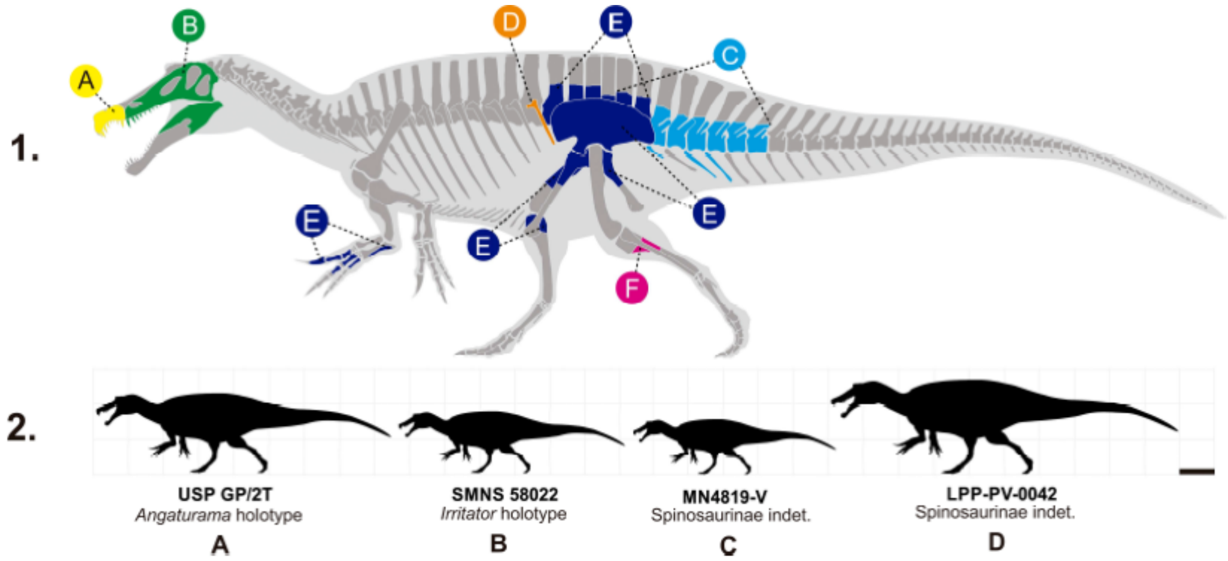

Figure 6. 1. Spinosaurinae remains currently recovered from the Romualdo Formation, Araripe Basin, Brazil. Not to scale. **A**, USP GP/2T-5, holotype of *A. limai* (Kellner & Campos, 1996), fragmentary anterior tip of skull. **B**, SMNS 58022, holotype of *I.challengeri* (Sues et al., 2002) (originally mistakenly identified as a maniraptor by Martill et al., 1996), partial posterior portion of skull and mandible. **C,** MN 4743-V, incomplete indeterminate spinosaur sacral and caudal vertebrae series (S3, S4, S5, C1, C2. C3, C4, C4, C6) (Bittencourt & Kellner, 2004). **D**, MN 7021-V, indeterminate spinosaur rib (Machado & Kellner, 2007). **E**, MN 4819-V, incomplete indeterminate spinosaur pubis, pelvis, dorsal, sacral and caudal vertebrae (d, S1, S2, S3, S4, S5,C1), incomplete indeterminate spinosaur right manus, fragmentary right tibia and femur (Machado & Kellner, 2008; Machado & Kellner, 2009; Machado, 2010)**.** **F**, LPP-PV-0042, Spinosaurinae indet. metaphysis of left tibia described in this work. Skeletal reconstruction made by Tito Aureliano, based on the work by Scott Hartman and Marcos Sales. **2.**, Romualdo Spinosaurinae specimens to scale. **A**, *Angaturama* USP GP/2T (~8.3 m, on the reconstruction by Sales & Schultz, 2017). **B**, *Irritator* SMNS 58022 (~6.5 m, from the reconstruction by Sales & Schultz, 2017). **C**, Spinosaurinae indet. MN4819-V (~5.9 m; Machado et al., 2008). **D**, Spinosaurinae indet. LPP-PV-0042 (~10 m; this work). Scale bar in 7.2 is 1 m.

Comments on the Araripe Basin Spinosaurinae

Figure 6.1.1 summarizes all Spinosauridae specimens recovered from the Romualdo Formation to date. A notable feature is the variation in size among sampled individuals. The total length (TL) of the reconstruction of LPP-PV-0042 is estimated to be 10 ± 3 m, based on the TL of *Spinosaurus* (~15 m, Ibrahim et al. 2014) and *Suchomimus* (~11 m, Sereno et al. 1998). The new specimen represented a much larger individual than MN4819-V (TL ~5.9 m, Machado et al., 2008), which can be easily observed by comparing both tibiae. LPP-PV-0042 was also probably larger than *I. challengeri* holotype (TL ~6.5 m, on Sales & Schultz, 2017; despite Paul, 2010, and Holz, 2011, proposition of 7.5-8 m TL) at the time of death and of roughly comparable size to the *A. limai* type specimen (TL ~8.3 m, from Sales & Schultz, 2017, scaling) (Fig.6.1.2).

As already mentioned, histological evidence indicates that LPP-PV-0042 was a subadult at the time of death. Thus, the specimen suggests that the Romualdo Formation Spinosaurinae could have reached larger sizes than previously thought. It is not possible to estimate how much the referred individual could still have grown, since the ontogeny and growth dynamics of spinosaurs are currently unknown. However, histological analyses of other Araripe specimens have the potential to clarify Spinosauridae ontogeny parameters and also to shed light on controversial aspects in Brazilian Spinosaurinae taxonomy.

Sales and Schultz (2017) suggested that Brazilian Spinosauridae apparently demonstrate several intermediate conditions between Baryonychinae and Spinosaurinae. The link between this information and the osteohistological condition described here add relevance to the study of the Araripe Basin forms. Both anatomical and osteohistological adaptations favorable to the interaction with the aquatic environment may have extended amphibious habits in Romualdo Formation spinosaurs. This has great evolutionary relevance and means local and chrono correlated regional ecological contingencies (in both northeast Brazil and northwest Africa), which may have favored this evolutionary pathway, need to be further explored.

The potential of the Araripe Basin to provide more Spinosaurinae remains is great. Almost yearly, new exceptional vertebrate and invertebrate fossils are discovered and described from the basin (e.g., Kellner et al., 2013, Bantim et al., 2014, Pinheiro et al., 2014, Maldanis et al., 2016, Freitas et al., 2016). Including a possible Megalosauroidea with affinities to Spinosauridae from the Ipubi Formation (which underlies the Romualdo Formation) which is still undescribed (see Silva et al., 2013). Controlled excavations carried out in recent years (Fara et al., 2005; Vila Nova et al., 2011; Lima, 2013) probably will lead to important discoveries due proper stratigraphic control.

Unfortunately, all known Spinosaurinae material of the Araripe Basin came from uncontrolled collecting, the primary purpose of which was (and still is) illegal trade. Illegal because the trade of Brazilian fossils is prohibited by federal laws. Most of the specimens mentioned were part of private collections and were fortuitously donated, as is also the case of the specimen herein described. Illegal trade is still a problem in the Araripe region, and the negative implications related to this activity (e.g., loss of field data, alteration of specimens, loss to inaccessible private collections, etc.) need to be strongly curtailed as they delay the advancement of paleontological knowledge. The Romualdo Formation, in particular, offers a unique opportunity for the study of Spinosaurinae paleobiology and paleoecology. Unlike other deposits where these dinosaurs occur, the differential preservation of Santana Group fossils allows access to many details about the ecosystem in which these dinosaurs lived, including improved knowledge about the trophic web. In addition, the potential for soft tissue preservation is great, which raises the possibility of unveiling rare details about the biology, ecology and evolution of this fossil group.

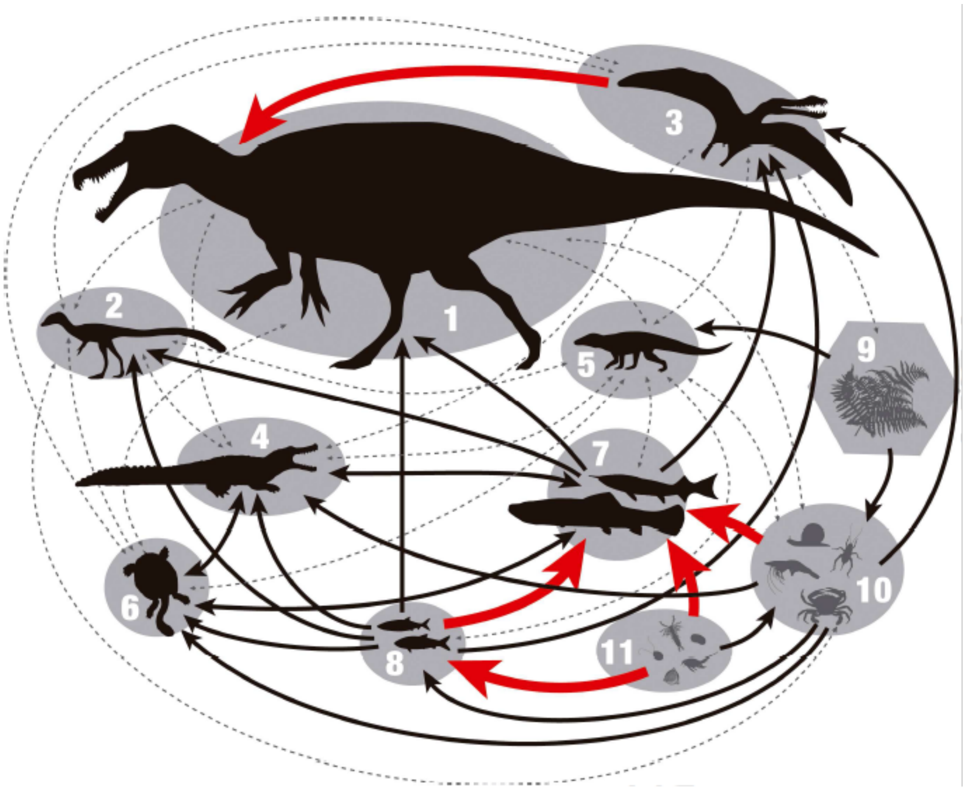

Figure 7. Inferred food web of the Aptian-Albian Romualdo Formation, Northeast Brazil. Vertebrate silhouettes are highlighted in black. Trophic relations are represented by arrows, of which solid bold red represent ecological interactions with direct fossil evidence from Romualdo Formation; solid black indicate putative trophic interactions with general theoretical support; and dashed grey represent weak or uncertain but plausible trophic links. **1,** Spinosaurinae; **2,** small to medium sized terrestrial theropods; **3,** pterosaurs; **4,** semi-aquatic crocodyliforms; **5,** terrestrial omnivorous crocodyliforms; **6,** semi-aquatic chelonians; **7,** large fishes; **8,** small fishes; **9,** plants; **10,** macroinvertebrates; **11,** plankton. See Text S1 in the Supplementary material for list of references. Spinosaurinae silhouette by Tito Aureliano. Other silhouettes from Phylopic (http://phylopic.org/), courtesy of Almandine (vectorized by T. Michael Keesey), FunkMonk (adapted), Hans Hillewaert, John Conway, Melissa Broussard, Nobu Tamura (vectorized by T. Michael Keesey), Olegivvit, Robert Gay and Sergio A. Muñoz-Gómez. See Supplementary material (Text S1) for references and further information.

Romualdo Formation paleoecological inferences

The articulated skull with mandibles of a Spinosaurinae found in the Romualdo Formation (Kellner & Campos, 1996; Sues et al., 2002) suggests an autochthonous or parautochthonous burial (see Voorhies, 1969). A floating carcass model, as already suggested for some tetrapods of the Santana Group (Elgin and Frey, 2012), is not plausible in this case. First, because the jaws were found tightly articulated to the skull, which is unusual for floating carcasses (Liebig et al., 2003). Second, because the osteosclerotic histological condition of the skeleton would cause the carcass to rapidly sink. This leads us to conclude that most probably these organisms were buried in their living environment and must be interpreted as part of the local ecosystem.

The Romualdo Formation was deposited in a coastal lagoon influenced by transgressive-regressive marine cycles (Custódio et al., 2017) and variable freshwater influence (Antonietto et al., 2012). The terrestrial environment around the Romualdo Formation is interpreted as arid to semi-arid, which is supported by the occurrence of fossil plants with xeromorphic adaptations (Lima, 2013). The absence of herbivorous dinosaurs in this geological context led Naish et al. (2004) to infer a possible low productivity for the surrounding area, which probably would not sustain a resident mega-herbivore fauna. Therefore, the main source of food for local large tetrapod carnivores would have been the abundant aquatic fauna of the Romualdo paleolagoon (e.g., Russell, 1996; Läng et al., 2013). Therefore, the Romualdo Formation Spinosaurinae most likely have exploited the local diversity of fishes and other aquatic organisms (see Maisey, 1991; Wenz et al., 1993).

This would imply in a shortening of the trophic web, similar to what was proposed by Benyoucef et al. (2015), for the Grès Rouges Formation, Algeria. Figure 8 shows an inferred trophic web for the Romualdo Formation. The presence of several piscivorous organisms in the same community, (crocodylomorphs, large fishes and various pterosaurs), could hypothetically have caused overexploitation of the food resource, leading to high levels of competition (see Begon et al., 2009). Nonetheless, the large size of the Spinosaurinae as well as their unique physiological and morphological adaptations must have allowed them to explore a different range of food items (see Cuff and Rayfield, 2013). Despite the possible overlap of fundamental niches of local carnivores, the way the resources were exploited (i.e. realized niche) must have differed significantly. Smaller-sized species, for example, would not have been able to exploit larger food items. Moreover, they may have explored different areas or even different depths of the paleolagoon. The absence of large crocodylomorphs and other large aquatic predators that could compete directly with spinosaurs in the Romualdo Formation paleoecosystem must have facilitated the occupation of this niche by these dinosaurs (e.g., Holtz, 1998; Amiot et al., 2010a; Hone and Holtz, 2017).

A sequence of cervical vertebrae of a large pterosaur from the Romualdo Formation associated with a spinosaur tooth described by Buffetaut et al. (2004), indicate a direct case of interaction between those organisms, and a possible case of consumption. Thus, even with a diet interpreted mainly as piscivorous, predation on pterosaurs could occasionally have occurred (see also Kellner, 2004). Beyond that, small to medium-sized terrestrial dinosaurs, juveniles of the same species, crocodyliforms (both semi-aquatic and terrestrial), and turtles could also have been preyed on, placing Spinosaurinae as the top predators of the local environment. Figure 8 shows an artistic reconstruction of the Romualdo Formation paleoenvironment highlighting the semi-aquatic habit inferred for the local Spinosaurinae.

Coexistence of other large theropod groups such carcharodontosaurids and abelisaurids in sympatry with spinosaurs is known from other fossil deposits (Benton et al., 2000; Martill, 2007; Sereno & Brusatte, 2008; Amiot et al., 2010b; Ibrahim et al., 2014). However, no other large theropod has been found in the Romualdo Formation apart from spinosaurids so far, even after more than 40 years of geological exploration of the area. The preference for a coastal environment in Spinosauridae (Benyoucef et al., 2015; Sales et al., 2016) and the semi-aquatic lifestyle observed in the Cenomanian *Spinosaurus* (Ibrahim et al., 2014) probably occurred due to the clade's strong link to a piscivorous diet, and likely was reinforced by the presence of other large sympatric theropods in some contexts (see Amiot et al., 2010a; Benyoucef et al., 2015 and Sales et al., 2016 discussion). Since we do not yet have evidence of the later in the Araripe context, it is not possible to extend this explanatory hypothesis to the Brazilian paleoscenario.

CONCLUSION

The Romualdo Formation specimen LPP-PV-0042 comprises a fragmentary tibia with a reduced fibular crest and osteosclerotic histology previously only observed in *S. aegyptiacus,* supporting that this unique feature was already present in Brazilian Spinosaurinae (basal Spinosaurinae) during the Aptian-Albian time, at least 10 myr before the Moroccan *Spinosaurus*.
Histological analyses suggest LPP-PV-0042 was a young, fast growing subadult and also that the bone microstructure varies a lot across the cross-section, probably due to areas of muscle insertion. The latter observation suggests that caution is needed when describing bone histology of dinosaurs, since only one slice from the shaft is not always representative of the entire histology of the bone.

Furthermore, the current specimen represents one of the largest spinosaurs from this unit so far (~10 m in reconstructed TL). It was larger than the *Irritator* holotype and possibly larger than *Angaturama* holotype as well. Considering the subadult status inferred from its histology, the referred individual would have grown even larger. The Romualdo paleoenvironment could support large predators with semi-aquatic habits due to its high productivity and diversity of aquatic species as an ecotone. Spinosaurinae from Romualdo Formation probable occupied the position of apex predators different.

Thus, the skeletal element LPP-PV-0042 from the Romualdo Formation, although fragmentary, has provided much information about Brazilian Spinosaurinae paleobiology and ecology. Moreover, it gives new insight into the evolution of semi aquatic adaptations in this group, revealing the need to investigate other taxa within the clade and expand the search for more spinosaur fossils.

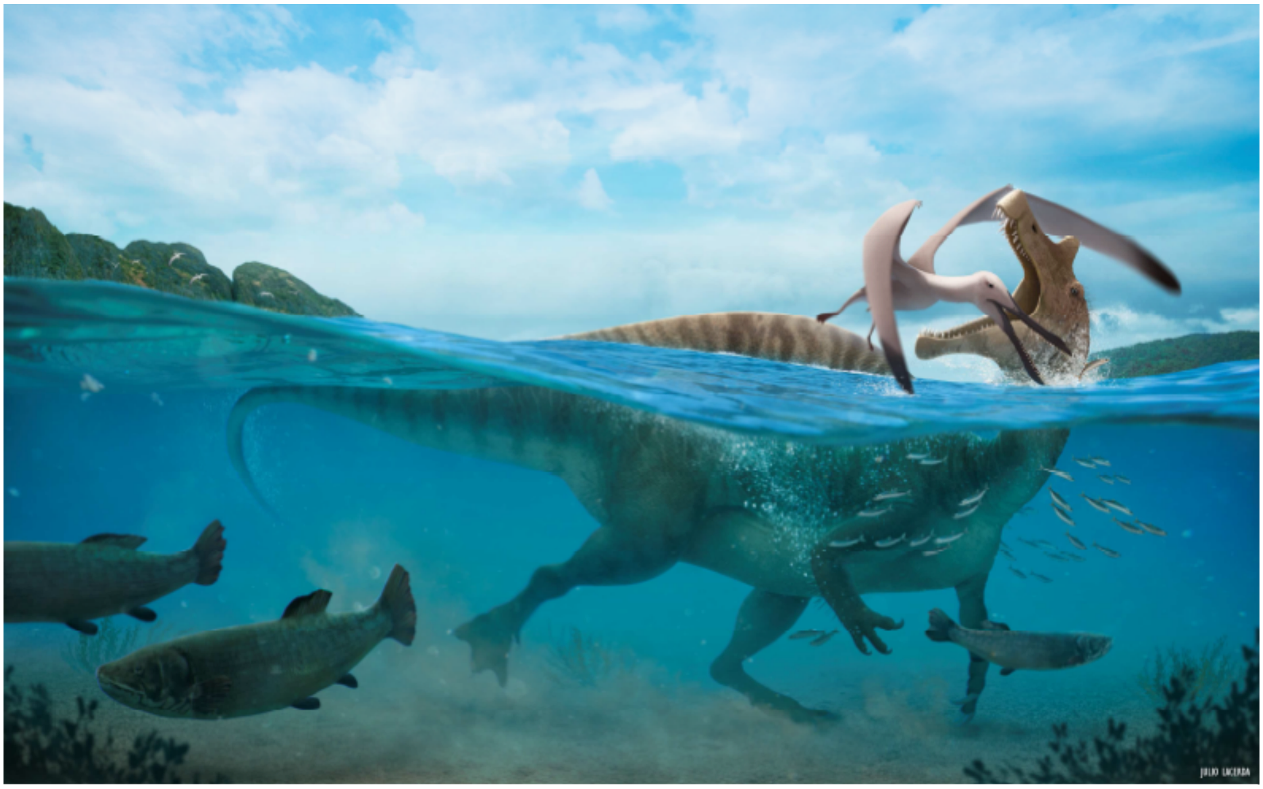

Figure 8. Reconstruction of a Spinosaurinae at the Aptian-Albian lagunar/shallow marine environment of the Romualdo Formation, Araripe Basin, NE Brazil. Illustration by Julio Lacerda.

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APPENDICES

Supplementary information Chapter 3

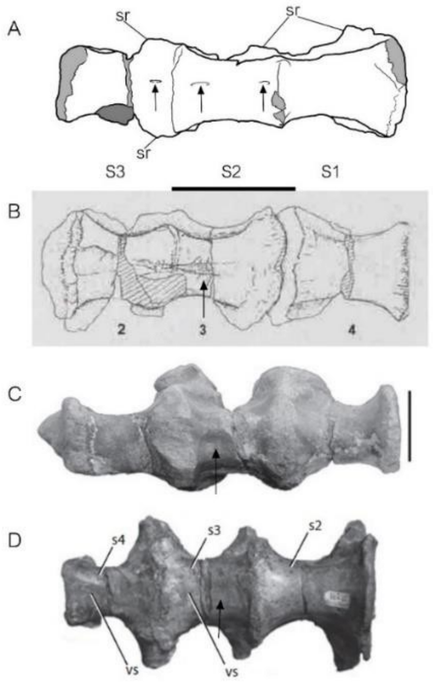
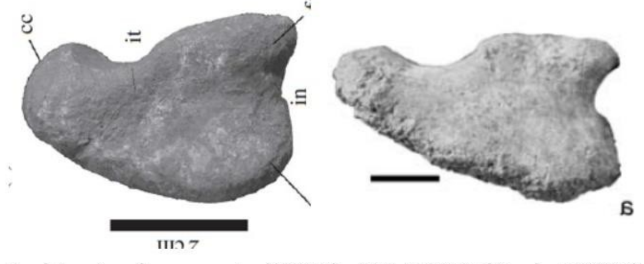


Fig. S1. Sacral vertebrae in ventral view in various theropods showing ventral groove (arrow). A, *Phuwiangvenator yaemniyomi* gen. et sp. nov; B, *Neovenator* (Brusatte et al. 2008); C, *Condorraptor* (Rauhut 2005); D) *Falcarius* (Zanno 2010).

Fig. S2. Right astragalus of *Fukuiraptor* and left astragalus of NMV P150070 in posterior view showing accessory posterolateral ascending process (plap – arrow).

We note that the autapomorphy of *Tachiraptor* "the caudolateral corner of the fibular condyle forms a sharp angle in proximal view and extends slightly more caudally than the medial condyle" in Langer et al. (2014) is also present in a small abelisauroid from Tanzania (MB.R.1751; Rauhut 2005; pers. obs.).



Tachiraptor (Langer et al 2014); MB.R.1751 (Rauhut 2005)
scale bar=20 mm scale bar=10 mm

Fig. S3. Tibiae in proximal view of *Tachiraptor* (left) and MB.R.1751 (right).

Table 1. *Phuwiangvenator yaemniyomi* gen. et sp. nov. measurements of sacral vertebrae (SM-PW9B-unnumbered) (in mm). * = incomplete

Sacral vertebrae (SM-PW9B-unnumbered)	S1	S2	S3
Centrum length at midheight	89	73	92
Posterior centrum height	54	75	63
Anterior centrum height	67	53	68
Posterior centrum width	54*	64	54*
Centrum central thickness	46*	48*	48*
Neural spine height	?	?	?
Neural spine width maximum	?	?	?
Neural spine apical length	?	?	?
Neural spine basal length	?	?	?
Anterior centrum width	74	55*	69

Table 2. *Phuwiangvenator yaemniyomi* gen. et sp. nov. measurements of manual phalanges (SM- PW9B-3, 4, 5, 8, and 9) (in mm).

	SM-PW9B-3	SM-PW9B-4	SM-PW9B-5
Length	107	50	49
Transverse width (middle)	24	18	12
Prox. height	35	24	19
Prox. width	37	22	17

Table 3. *Phuwiangvenator yaemniyomi* gen. et sp. nov. measurements of manual unguals (SM- PW9B-19, 21, and 23) (in mm). * = incomplete.

	SM-PW9B-19	SM-PW9B-21	SM-PW9B-23
Length	55*	39*	35*
Length at base (prox. height)	41	25	32
Width at middle (prox. width)	19.5	11	12
Proximal height/ width ratio	2.1	2.27	2.67

Table 4. *Phuwiangvenator yaemniyomi* gen. et sp. nov. measurements of right tibia (SM-PW9B- unnumbered) (in mm).

Total length	615
Proximal mediolateral width	58
Proximal craniocaudal width	83
Craniocaudal length of proximal articular end	142
Mediolateral width of proximal articular end	104
Circumference at midshaft	190
Midshaft mediolateral width	60.5
Midshaft craniocaudal width	44.5
Distal mediolateral width	120
Distal craniocaudal width	60
Height of facet for ascending process	89

Table 5. *Phuwiangvenator yaemniyomi* gen. et sp. nov. measurements of left tibia (SM-PW9B- unnumbered) (in mm). * = incomplete.

Total length	?
Proximal mediolateral width	55
Proximal craniocaudal width	84.5
Craniocaudal length of proximal articular end	132*
Mediolateral width of proximal articular end	76*
Circumference at midshaft	?
Midshaft mediolateral width	?
Midshaft craniocaudal width	?
Distal mediolateral width	132
Distal craniocaudal width	68
Height of facet for ascending process	91*

Table 6. *Phuwiangvenator yaemniyomi* gen. et sp. nov. measurement of left astragalus (SM- PW9B-18) (in mm) * = incomplete.

Ascending process height	?
Ascending process width at base	59*
Craniocaudal width at mid	53
Mediolateral width	94
Maximum width at medial/ craniocaudal width at medial condyle	66
Cranial height at the middle	32
Total height (ascending process + base)	?
Total breadth (maximum/ mediolaterally)	103

Table 7. *Phuwiangvenator yaemniyomi* gen. et sp. nov. measurement of left calcaneum (SM- PW9B-18) (in mm).

Width craniocaudally	66
Width mediolaterally	25
Height	39
Total width of astragalocalcaneum	123.5

Table 8. *Phuwiangvenator yaemniyomi* gen. et sp. nov. measurement of right astragalus (SM- PW9A-B17) (in mm).

Ascending process height	?
Ascending process width at base	63.5
Craniocaudal width at mid	49
Mediolateral width	90.5
Maximum width at medial/ craniocaudal width at medial condyle	70.5
Cranial height at the middle	30
Total height (ascending process + base)	?
Total breadth (maximum/ mediolaterally)	103

Table 9. *Phuwiangvenator yaemniyomi* gen. et sp. nov. measurement of right calcaneum (SM- PW9A-B17) (in mm).

Width craniocaudally	62
Width mediolaterally	24
Height	45
Total width of astragalocalcaneum	122

Table10. *Phuwiangvenator yaemniyomi* gen. et sp. nov. measurements of selected pedal unguals (SM-PW9B-10, 22) (in mm).

	SM-PW9B-10	SM-PW9B-22
Length	68	43*
Height at base	26	37
Width at base	21	22

Table 11. *Vayuraptor nongbualamphuensis* gen. et sp. nov. measurements of left tibia (SM-NB A1-2) (in mm).

Total length	515
Proximal mediolateral width	44.5
Proximal craniocaudal width	52
Craniocaudal length of proximal articular end	112
Mediolateral width of proximal articular end	71
Circumference at midshaft	140
Midshaft mediolateral width	48
Midshaft craniocaudal width	37
Distal mediolateral width	90
Distal craniocaudal width	43
Height of facet for ascending process	73

Table 12. *Vayuraptor nongbualamphuensis* gen. et sp. nov. measurements of left Astragalus (SM-NB A1-2) (in mm).

Ascending process height	70
Ascending process width at base	42
Craniocaudal width at mid	38.5
Mediolateral width	62.5
Maximum width at medial/craniocaudal width at medial condyle	49
Cranial height at the middle	19.5
Total height (ascending process + base):	105
Total breadth (maximum)	70

Table 13. *Vayuraptor nongbualamphuensis* gen. et sp. nov. measurements of left calcaneum (SM-NB A1-2) (in mm)

Width craniocaudally	41.5
Width mediolateraly	18
Height	42
Total width of astragalocalcaneum	82

Table 14. Morphological comparison of sacral vertebrae in various theropods (Y=yes; N=no).

	Proportion	constriction	Pleurocoel	Camerate/ Camellate	ventral view
Phuwiangvenator	Longer than high	N	N		Flat
SMNS 58023	Longer than high	N	Y	Y	Convex
Siamotyrannus		Y	N	N	Convex
Megaraptor			Y	Y	Flat
Aoniraptor		?	Y	Y	Flat
Datanglong		Y	N		Convex
Suchomimus	Longer than high	N			Convex
Spinosaurus		?	?		Convex
Baryonyx		?	?		Flat

Table 15. Morphological comparison of sacral vertebrae in various theropods.

	Centra anteriorposteriorl	Ventral view/ ventral ridge	Ventral in lateral view
Ichthyovenator	possibly long?	?	
Baryonyx holotype	Long	convex/flat, NA?	
Suchomimus	Long	Convex, no ridge?	
Spinosaurus	Long	Convex, no ridge?	
Phuwiangvenator	Long	Flat, no ridge, sulci	Less concave
Aoniraptor	Short	Flat, no ridge?	Less concave
Datanglong	Short	Convex, no ridge	Less concave except the last sacral
Megaraptor	Short	Flat?, no ridge	Less concave
SMNS 58023	Long	Convex, no ridge	
MPMA 08-003-94	Long	Flat	
CPPLIP 1324	Long	Flat	
Neovenator		?Convex, groove	
Falcarius		?flat, groove	
Condorraptor		Flat, groove	

Table 16. Manual ungual I-2, the ratio of proximal height/ width

Torvosaurus (Benson et al. 2010)	1.95
Suchomimus MNBH GAD 500	1.78
Baryonyx cast of BMNH R9951	1.9
Allosaurus UMNH VP5676	1.9
Chilantaisaurus (Benson and Xu 2008)	2.7
Fukuiraptor FPDM-V43-11	2.7
Phuwiangvenator SM-PW9B-19	2.4
Australovenator (Benson et al. 2010)	2.4
Megaraptor (Benson et al. 2010)	2.75

Table 17. Measurement of the tibiae of some megaraptorans and other theropods (in mm) showing tibial height and the length/width at mid-length ratio of the tibia in various theropods. * = incomplete.

Theropod tibia	Length in mm	Length/width ratio
Phuwiangvenator gen. et sp. nov.	615	13.82
Vayuraptor gen. et sp. nov.	515	13.9
Australovenator	569 (left), 564 (right)	12.53
Fukuiraptor	App. 507*	≈14.3-14.5
Murusraptor	690	11.9
Chilantaisaurus	954	
Aerosteon referred material	635	14
Neovenator	680 (left), 685 (right)	
Orkoraptor	700* or 600* (Coria and Currie 2016)	
Qianzhousaurus	760	
Spinosaurus Neotype	668	12.09
Suchomimus MNBH GAD 500 Holotype	960 (pers. obs.); 945 (Sereno et al. 1998)	9.6
Suchomimus MNBH GAD97 'subadult'	760	10.86
Suchomimus MNBH GAD72 'juvenile'	700	11.67
Allosaurus	690	
Sinraptor	769 (left); 776 (right)	

Table 18. Cross-section of tibia at mid-length in various theropods.

Theropod tibia	Shape in cross-section
Vayuraptor gen. et sp. nov.	anteriorly flat (pers. obs.)
Phuwiangvenator gen. et sp. nov.	anteriorly flat (pers. obs.)
Abelisauroid (MCT 1783-R)	oval (Machado et al. 2013)
Abelisaurid (MB.R.3625)	anteriorly convex (pers. obs.)
Abelisaurid (MB.R.3626)	anteriorly convex (pers. obs.)
Majungasaurus	anteriorly flat? (Carrano 2007)
Pycnonemosaurus	subcircular (Delcourt 2017)
Megalosaurus	oval (Benson 2010)
Suchomimus (MNBH GAD 500)	anteriorly convex (pers. obs.)
Spinosaurus (FSAC-KK 11888; cast)	anteriorly flat/ slightly convex (pers. obs.)
Spinosaurine (LPP-VP-42)	anteriorly flat/ slightly convex (pers. obs.)
Sinraptorid (SM10)	Slightly flat (pers. obs.)
Sinraptor dongi (cast of Holotype housed at FPDM)	convex at mid-length and flatten distally (pers. obs.)
Allosaurus	oval/ anteriorly convex (pers. obs.; Bybee et al. 2006)
Neovenator	anteriorly flat, posteriorly convex (Brusatte et al. 2008)
Chilantaisaurus	slightly flat anteriorly proximally (Benson and Xu 2008)
Australovenator	anteriorly flat (White et al. 2013)
Aerosteon (MCNA-PV-3139; cast)	anteriorly flat (pers. obs.)
Orkoraptor	oval cross-section (Novas et al. 2008)
Gualicho	"anterolaterally-posteromedially elongate ellipse in cross section" (Apesteguia et al. 2016)

Alioramus	anteriorly convex (Brusatte et al. 2012)
Teratophoneus (UMNH VP 16690)	anteriorly convex (pers. obs.)
Tyrannosaurus	oval cross-section (Horner and Padian 2004)
Acrocanthosaurus	anteriorly flat (Stovall et al. 1950)
Murusraptor	anteriorly flat (Coria and Currie 2016)

Table 19. Proportion of the ascending process of the astragalus; * = estimated. asc.proc. = ascending process of the astragalus; ast.body = astragalar body.

Theropod taxa	asc.proc. height/ asc.proc. width	asc.proc. height/ ast.body height	asc.proc. width at base/ ast.body width
Phuwiangvenator gen. et sp. nov.	1.39*	1.73*	65%
Vayuraptor gen. et sp. nov.	1.66	1.7	63%
Fukuiraptor	1.1	1.7	63%*
NMV P150070	1.3	1.43	55%
Australovenator	1	1.4	70%
Aerosteon cast of referred material	1	1.9	83%
Suchomimus MNBH GAD97	0.88	1.3	56%
Suchomimus MNBH GAD98	0.8	1.25	72%
Allosaurus UMNH VP11003	1	1.14	50%
Falcarius	1.1	1.3	66%
Alioramus	1.4	2.5	78%

Character quotes of Thai theropods added to the data matrix of Apesteguía et al. 2016

Phuwiangvenator

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00???????????????????????????10110000??111100???2111110?????2??
10?1?0????1????????????????????????1????????????????????????????????????0????0

Vayuraptor

??
???121100???2111111??????2??
1?????????1????????????????????????0???

Siamotyrannus

???0??1?
00100?00??????????????????????????????101?0011110101000???01??0??????????????????????????????????????0??
0???0???????????0?????0?????????2?10?????????????????????????????????????01????

Supplementary information Chapter 5

The dorsal margin of the ilium is straight in *Siamotyrannus*, *Spinosaurus*, *Ichthyovenator*, *Masiakasaurus*, and *Avimimus*, but curved or convex in *Allosaurus*, *Torvosaurus*, *Stokesosaurus*, *Sinraptor*, *Shidaisaurus*, *Aerosteon*, *Suchomimus*, *Yangchuanosaurus*, and *Monolophosaurus*.

The pubic boot in ventral view is broadly triangular in *Siamotyrannus*, *Dilophosaurus*, metriacanthosaurids, carcharodontosaurids, abelisaurids, *Aerosteon*, and *Allosaurus*, whereas it is narrow with subparallel margin in *Herrerasaurus*, birds, dromaeosaurids, ornithomimosaurs, and tyrannosaurids (Rauhut 2003a). The triangular boot is mentioned as a primitive character state in dinosaurs by Rauhut (2003a).

Pleurocoels on dorsal vertebrae are present on the dorsals 1-2 in *Eoabelisaurus* (Pol and Rauhut 2012), on the dorsal vertebrae 1-3 in the basal tetanuran *Monolophosaurus* (Zhao et al. 2010) and coelophysoids (usually 1-2 or 1-3, Tykoski 2005). They are present on the dorsal vertebrae 1-4 in *Allosaurus* and *Sinraptor dongi*, on the dorsal vertebrae 1-5 in *Sinraptor hepingensis*, *Baryonyx* (Charig and Milner 1997), and probable *Dilophosaurus* (Welles 1984). Pleurocoels are present in all dorsal vertebrae in abelisaurids, *Torvosaurus*, carcharodontosaurids, *Neovenator*, megaraptorids (*Tratayenia*, *Megaraptor*, and *Aerosteon*), *Fukuivenator* (Azuma et al. 2016). The pleurocoels are absent in *Elaphrosaurus*, *Concavenator*, *Avimimus*, *Coelurus*, *Scipionyx* (Dal Sasso and Maganuco 2011), *Compsognathus*, *Dilong* (Xu et al. 2004), *Guanlong* (Xu et al. 2006), ?*Eustreptospondylus* (Sadleir et al. 2008), uncertain in *Siamotyrannus* (but we note that its fourth dorsal vertebra has no pleurocoel), and uncertain in *Shidaisaurus* since its fourth dorsal vertebra is covered by the pubis (Wu et al. 2009).

The dorsal vertebrae are opisthocoelous from dorsal 1-4 in *Sinraptor dongi*, *Allosaurus*, and probably spinosaurids, from dorsal 1-5 in *Monolophosaurus*, *Acrocanthosaurus*, and *Torvosaurus*. In *Siamotyrannus* and *Sinraptor hepingensis*, their fourth dorsal vertebra is amphiplatyan.

The anterior spur on the caudal vertebrae is present in *Siamotyrannus*, *Afrovenator*, *Wiehenvenator*, *Lourinhanosaurus*, *Allosaurus*, SHN.019 (Malafaia et al. 2018), *Concavenator*, *Acrocanthosaurus* (Stovall and Langston 1950; Harris 1998; Currie and Carpenter 2000), *Bicentenaria*, and *Sinraptor hepingensis*.

The mid-caudal chevrons are expanded and usually turned backward ventrally so they are roughly L-shaped in *Poekilopleuron*, *Allosaurus*, metriacanthosaurids, and tyrannosaurids (Rauhut 2003a). This character is uncertain in *Siamotyrannus* because its mid-caudal chevrons are broken distally, and some are not preserved.

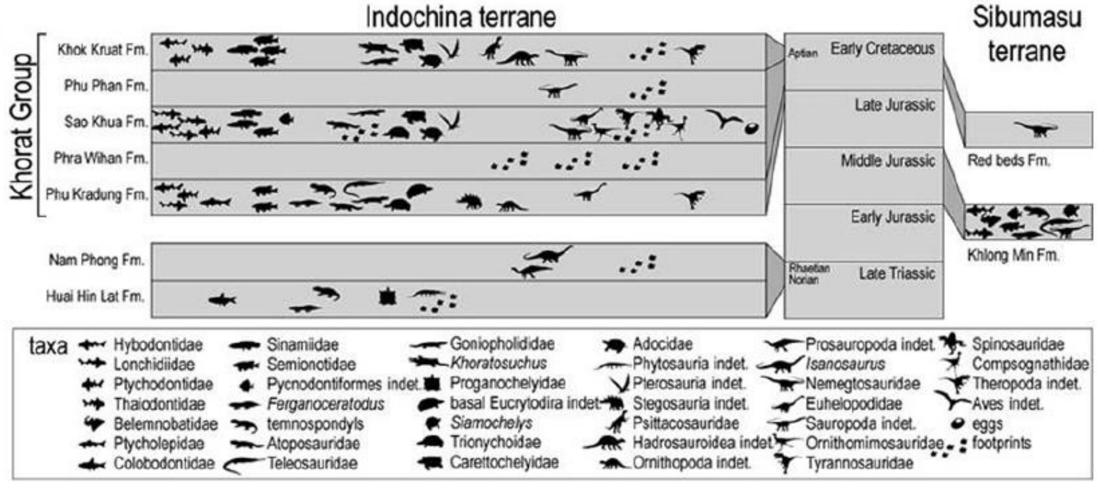

Fig.S1. Distribution of main groups of vertebrates in the non-marine formations of Thailand (from Suteethorn *et al.*, 2012).

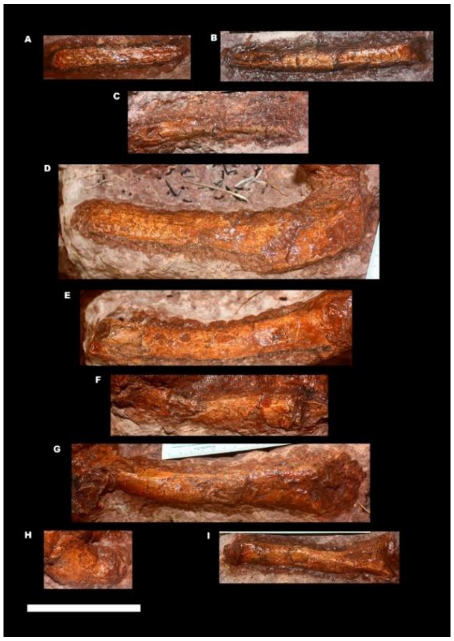

Fig.S2. *Siamotyrannus isanensis*, SM-PW9-1. Chevrons 2 to 11, A = chevron 2, B = chevron 3, C = chevron 4, D = chevron 5, E = chevron 6, F = chevron 8, G = chevron 9, H = chevron 10, and I = chevron 11, scale bar = 10 cm.

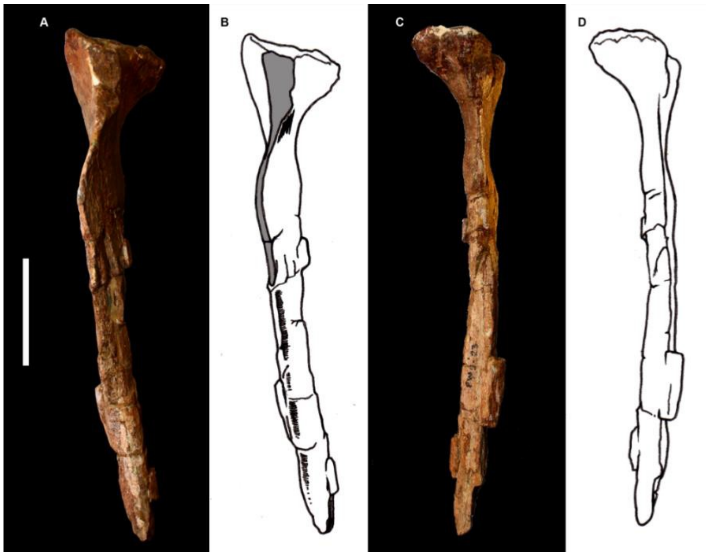

Fig.S3. *Siamotyrannus isanensis*, SM-PW9-1. Left ischium in anterior view (A), line drawing of the left ischium in anterior view (B), left ischium in posterior view (C), and line drawing of the left ischium in posterior view, gray tone indicates broken bone surface. Scale bar = 10 cm.

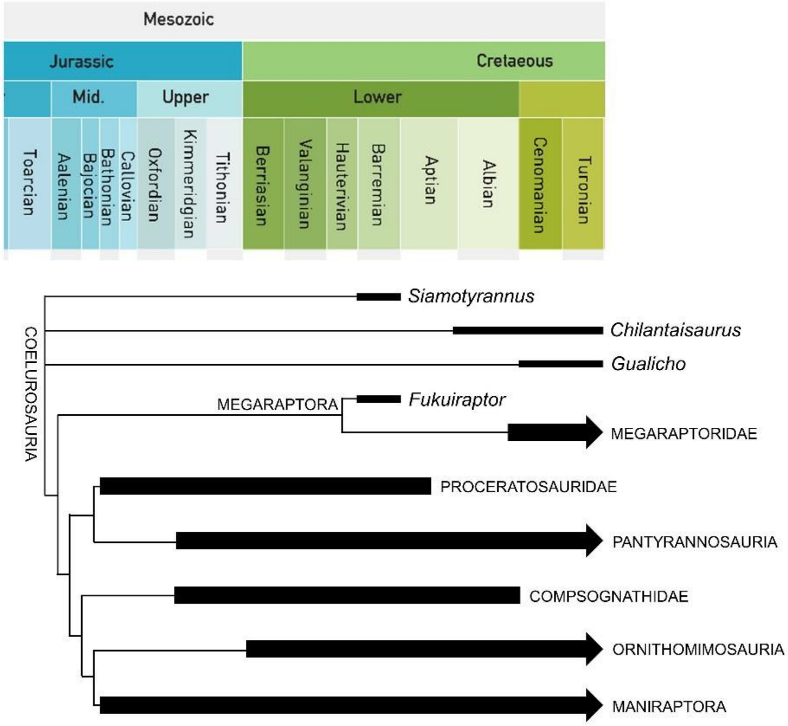

Fig.S4. Phylogenetic relationship of *Siamotyrannus isanensis* (SM-PW9-1) recovered from present analysis.

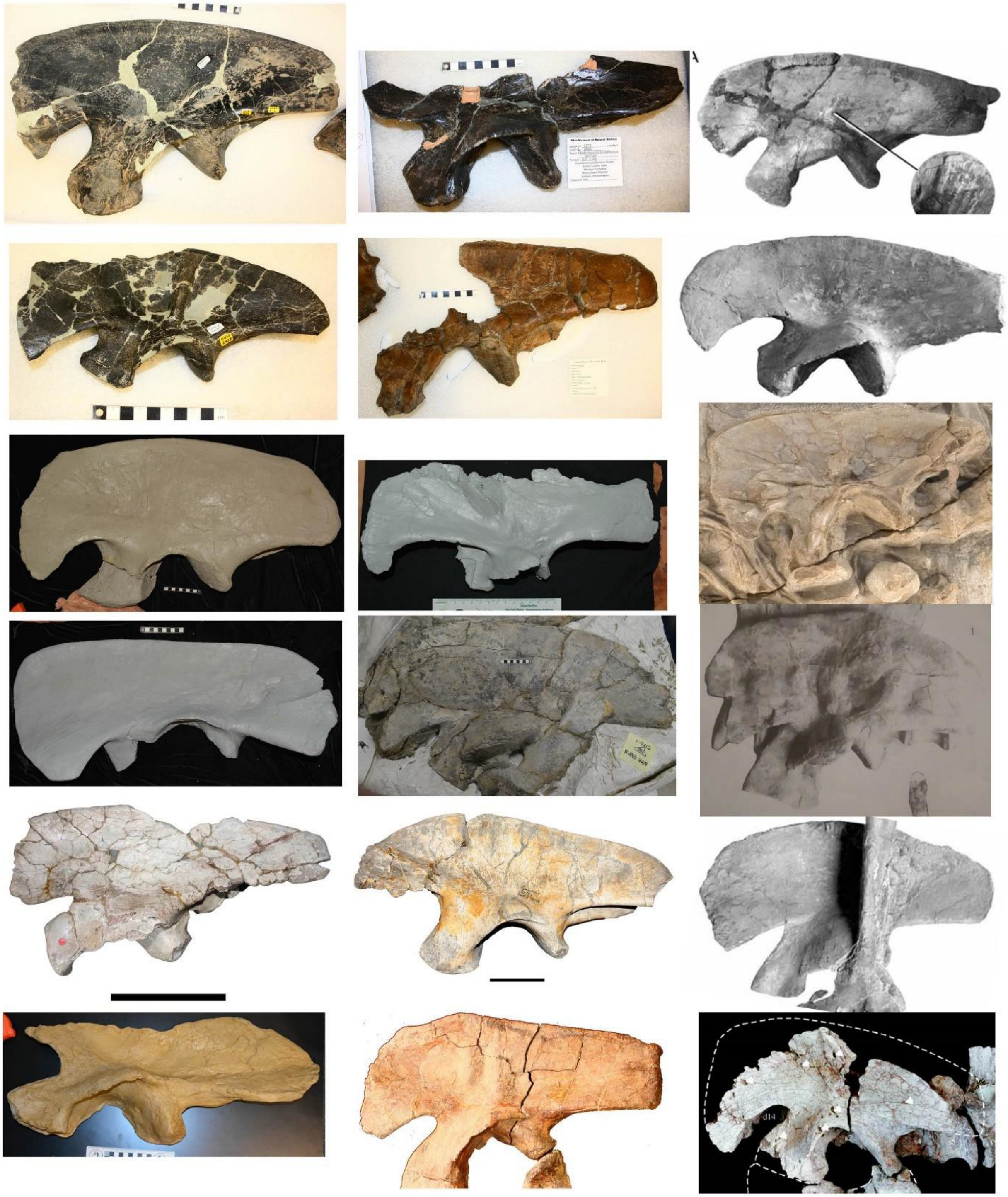

Fig. S5. Theropod ilium in lateral view, from left to right, top to bottom, *Allosaurus*, *Mashosaurus*, *Megalosaurus*, *Stokesosaurus*, *Terratophonius*, *Monolophosaurus*, *Aerosteon*, *Sinornithomimus*, *Concavenator*, *Spinosaurus*, *Suchomimus*, *Sinraptor hepingensis*, *Liliensternus*, MB.R.3628, *Shidaisaurus*, *Sinraptor dongi*, *Siamotyrannus*, *Datanglong*.

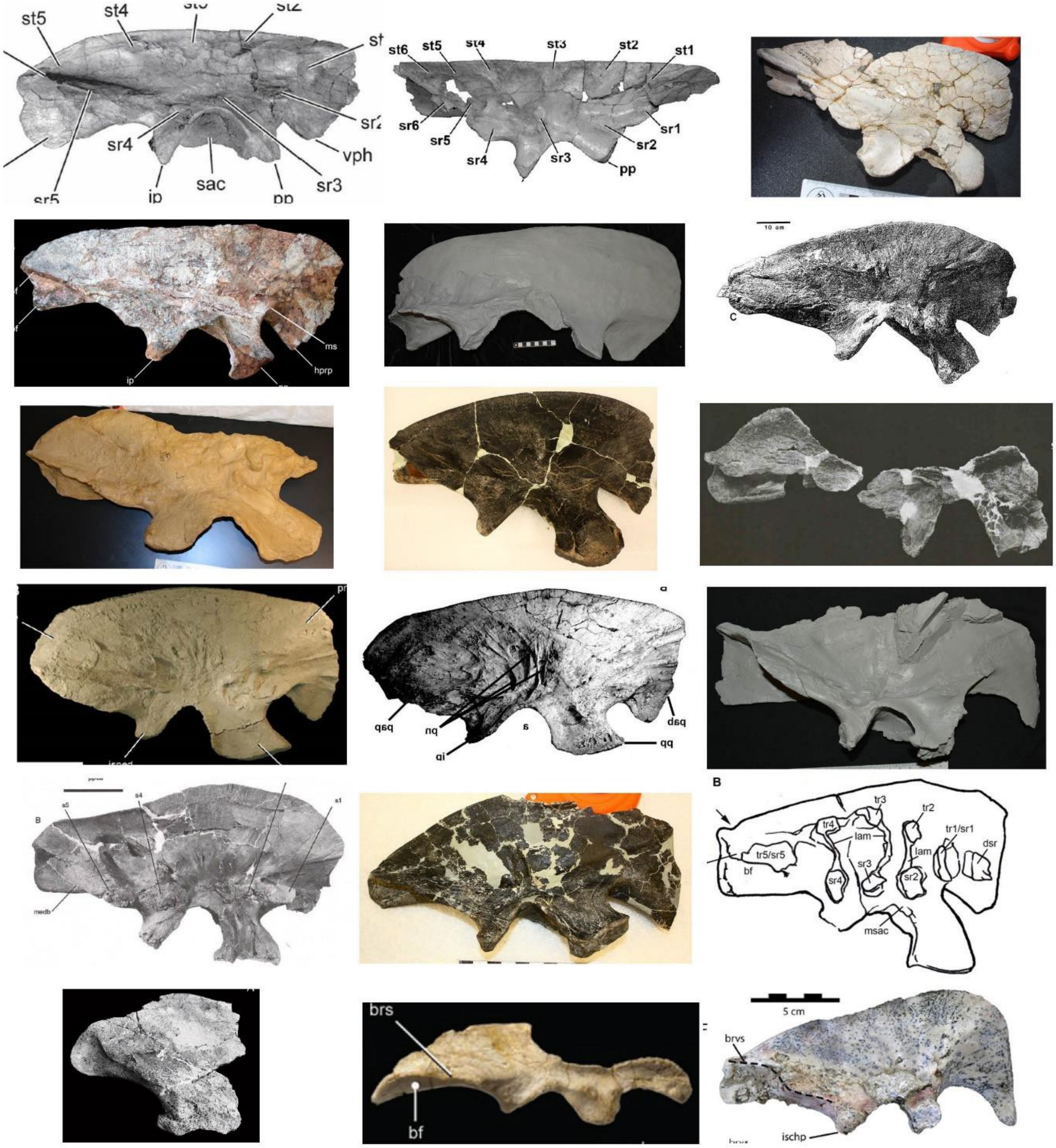

Fig. S6. Theropod ilium in medial view, from left to right, top to bottom, *Majungasaurus*, *Masiakasaurus*, *Liliensternus*, *Ichthyovenator*, *Spinosaurus*, *Torvosaurus*, *Sinraptor*, *Allosaurus*, *Neovenator*, *Aerosteon*, *Murusraptor*, *Sinornithomimus*, *Tyrannosaurus*, *Stokesosaurus*, *Siamotyrannus*, Unenlagia (Turner et al 2012), *Mahakala* (Turner et al. 2007), *Avimimus nemegtensis* (Funston et al. 2017).

TABLE 1. Measurements (in millimeters) of dorsal vertebrae; * = the bones are incomplete.

	D1	D2	D3	D4	D5
Centrum length	87	80	80	96	60*
Centrum cranial height	100	125	123	140	135
Centrum caudal height	127	130	132	139	-
Centrum cranial width	123	122	111	109*	102*
Centrum caudal width	123	116	110*	101*	-
Width of diapophysis	91	65	64	-	-
Length of diapophysis	191	204	174	-	-
Height of diapophysis	186	177	136	-	-
Central section thickness	54	51	52	41	40

TABLE 2. Measurements (in millimeters) of sacral vertebrae of *S. isanensis*. * = the bones are incomplete.

	Dorsosacral	Sacral 1	Sacral 2	Sacral 3	Sacral 4	Sacral 5
Centrum length at midheight	120	117	91	89	115	115
Anterior centrum height	161	143	140	140	130	118
Posterior centrum height	140	140	140	130	118	127
Anterior centrum width	131	113	45*	46*	85	90
Posterior centrum width	121	45*	46*	85	90	124
Centrum central thickness	84	45	32	44	54	57
Neural spine height	-	190*	150*	-	125*	
Neural spine width maximum	-	40*	50*	-	40	
Neural spine apical length	-	73*	78*	-	115*	
Neural spine basal length	-	50	55	-	130	

TABLE 3. Measurements (in millimeters) of caudal vertebrae (caudal 1 - 13) of *S. isanensis*. * = the bones are incomplete.

	C1	**C2**	**C3**	**C4**	**C5**	**C6**	**C7**	**C8**	**C9**	**C10**	**C11**	**C12**	**C13**
Centrum length	110	115	120	112	130	122	130	123	133	126	134	122	114
Centrum cranial height	130	124	116	-	105	113	76	78	96	84	67	71	70
Centrum caudal height	130	126	118	-	100	103	65	80	92	81	85	85	66
Centrum cranial width	120	100	87	90	98	77	91	71	45*	51*	65	53	44
Centrum caudal width	110*	70*	72*	-	88	78	83	48*	50*	57*	66	50	41
Width of transverse process proximal	53	70	72	60	-	-	-	-	-	-	-	-	-
Width of transverse process distal	62	100	96	78	-	-	-	-	-	-	-	-	-
Length of transverse process	125*	105	120	110	-	-	-	-	-	-	-	-	-
Central section thickness	82	74	32*	-	82	68	55	-	-	-	-	-	-
Neural spine height	-	-	-	-	240	170	90*	70*	42*	77*	97*	-	-
Neural spine width maximum	-	-	-	-	52	66	91	87	82	95	60	-	-
Neural spine apical length	-	-	-	-	52	44*	70	50	52	54	42	-	-
Neural spine basal length	-	-	-	-	43	84	91	87	82	95	60	-	-
Neural arch length at base	90	90	93	78	94	120	90	122	103	80	97	95	92

TABLE 4. Measurements (in millimeters) of chevrons of *S. isanensis*. * = the bones are incomplete.

	Ch2	Ch3	Ch4	Ch5	Ch6	Ch8	Ch9	Ch10	Ch11
Length	116*	175*	150*	275	210*	170*	235*	80*	148*
Width proximal	11	17	10	45	34	22	22	31	-
Width middle	-	-	-	30	28	-	29	-	-
Width distal	17	13	14	34	34	25	53	34	20

TABLE 5. Measurements (in millimeters) of the left pelvis of *S. isanensis*. * = the bones are incomplete.

Ilium length	800
Pubis length	860
Ischium length	510*
Ilium/pubis	800/860 = 0.93
Pubis/ischium	860/510* = 1.69*

TABLE 6. Measurements (in millimeters) of the ilium of *S. isanensis*. * = the bones are incomplete.

Iliac blade, maximum length	800
Iliac blade, height above acetabulum	320
Preacetabular process length	395
Preacetabular process, height at base	295
Preacetabular process, height at distal end	330*
Postacetabular process length	415
Postacetabular process, height at base	270
Postacetabular process, height at mid length	220
Pubic peduncle, anteroposterior length	193
Pubic peduncle, maximum transverse width	100
Ischial peduncle, maximum transverse width	101
Acetabulum, maximum width	200
Acetabulum, maximum depth	140
Supraacetabular crest depth	50
Medial supraacetabular crest depth	25

TABLE 7. Measurements (in millimeters) of pubis of *S. isanensis*. * = the bones are incomplete.

Pubic length	860
Maximum length of the proximal end	245
Length of the iliac peduncle	195
Width of the iliac peduncle	73
Width of the distal end	80
Length of the distal end	270*
Maximum width of the pubic blade	52
Length of the ischial peduncle	132

TABLE 8. Measurements (in millimeters) of the ischium of *S. isanensis*. * = the bones are incomplete.

Ischial length	510*
Maximum length of the proximal end	245
Length of the pubic peduncle	132
Width of the pubic peduncle	68
Length of the iliac peduncle	65
Width of the iliac peduncle	70
Minimum width of the ischial blade	24
Width of the distal end	-

TABLE 9. Compare pelvis, dorsal and caudal vertebrae with some theropods.

	Siamotyrannus	*Sinraptor dongi*	*Sin. hepingensis*	*Concavenator*
Medial shelf of brevis fossa	Short	High	High	High
Pubis	Vertical	Anterior	Anterior	vertical
Ant-mid dorsal pleurocoels	No	Yes	Yes	No
Ant-mid dorsal	Amphiplatyan	Opithocoelus	Amphiplatyan	?
Anterior caudals	Almost flat (with small sulci)	Convex & double keel (groove)	Groove	Flat & groove
Mid caudals	Flat	?	Groove	

TABLE 10. The differences among the anterior/ mid/ posterior caudal vertebrae.

	Anterior caudals	**Mid-caudals**	**Posterior caudals**
Siamotyrannus	Almost flat with sulci	Flat	?flat
Sinraptor dongi	Convex & double keel (groove)	?	?
Sin. Hepingensis	Groove (Gao 1992)	Groove (shallow)	no groove
Concavenator	Flat & groove		
Ichthyovenator	flat (pers. obs.; Evers et al 2015)	Flat	?
***Baryonyx* holotype**	NA (Charig & Milner	NA?	NA?
cf. *Baryonyx* Portugal	groove (Mateus et al	Groove	Groove
Suchomimus	flat (pers. obs.)	Flat	Flat
Spinosaurus	flat (pers. obs.)	Flat	Flat
cf. *Baryonyx* Thailand (SM-PW9B-taxon B)	Double keel/groove (pers. obs.)	Groove	Groove
Camarillasarus	?	?	groove (Sanchez-Hernandez et al 2014)

TABLE 11. Pelvic elements length in mm.

Taxa	Ilium length	Pubis length
Siamotyrannus	800	
Allosaurus		
Datanglong	590 (incomplete)	
Aerosteon	768	
Suchomimus		
Concavenator		
Yutyrannus	710 (estimated)	
Ichthyovenator	920(L), 910(R)	
Shidaisaurus	620	
Sz. Zigongensis	550	
Y. shangyuensis	747	
Sinraptor dongi	680	
Sin. Hepingensis	760	

PHYLOGENETIC ANALYSES

I. Character quote of Siamotyrannus added to Carrano et al., 2012.

Siamotyrannus

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110210?0110001???0100?01[01]??
0 0 2 0 0 0 1 0 0 1 0 2 1 1 1 1 1 1 1 [0 1] 2 0 1 2 0 0 0 1 1 0 0 ? 1 0 1 ?
01???

II. Character quote of Siamotyrannus added to Apesteguía et al., 2016

Siamotyrannus

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0????????????????????????????????????0??0???0???????????0?????0?????????2?
10?????????????????????????????????????01????

Supplementary information Chapter 6

Supplementary figures

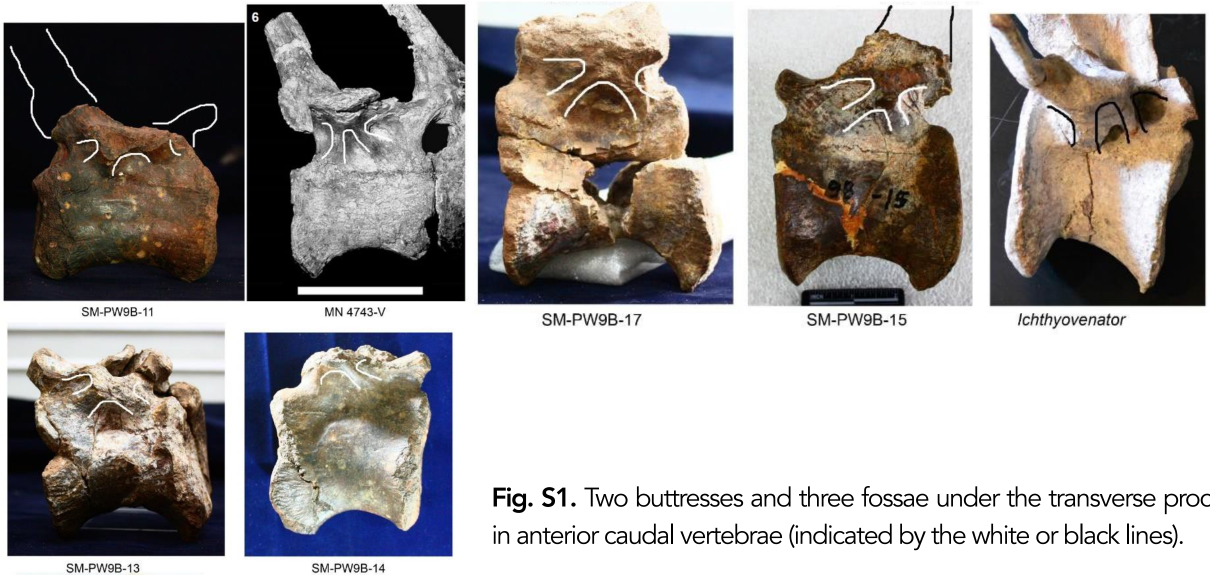

Fig. S1. Two buttresses and three fossae under the transverse process in anterior caudal vertebrae (indicated by the white or black lines).

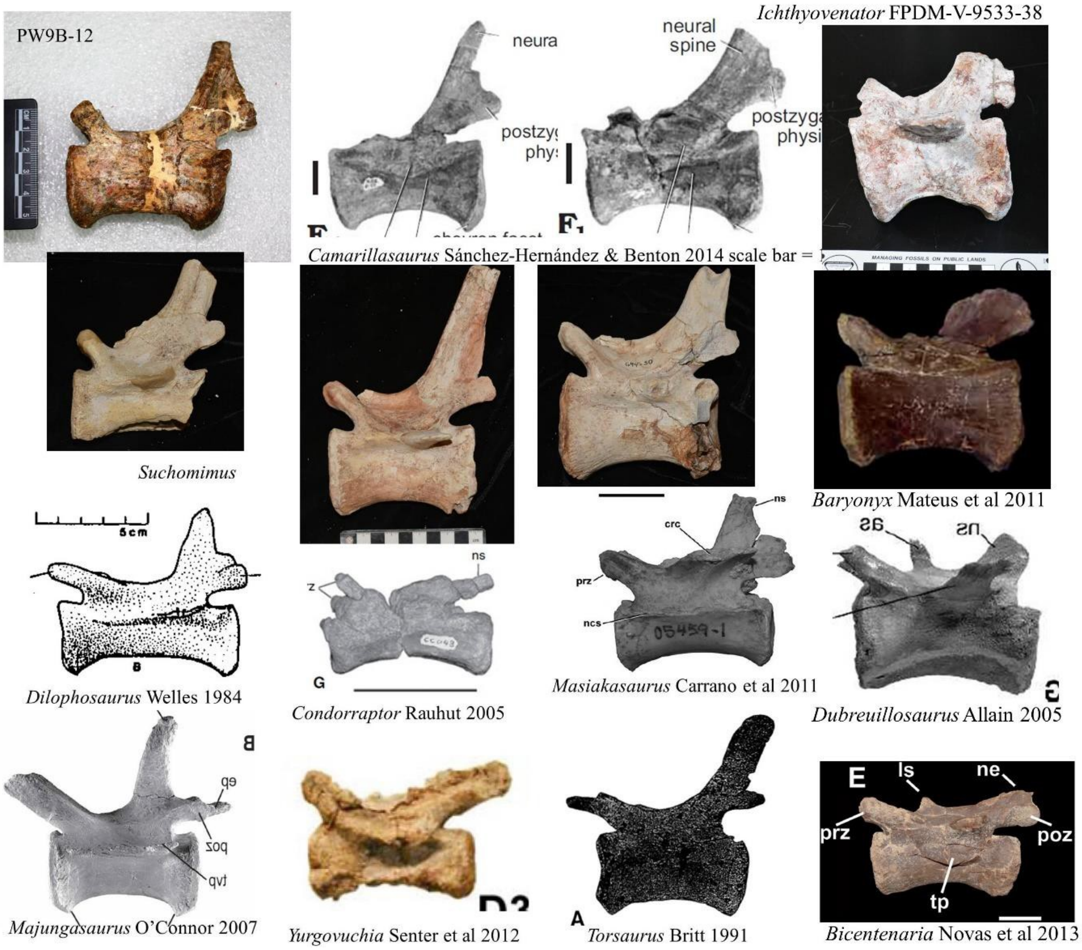

Fig. S2. Distal caudal vertebrae comparison

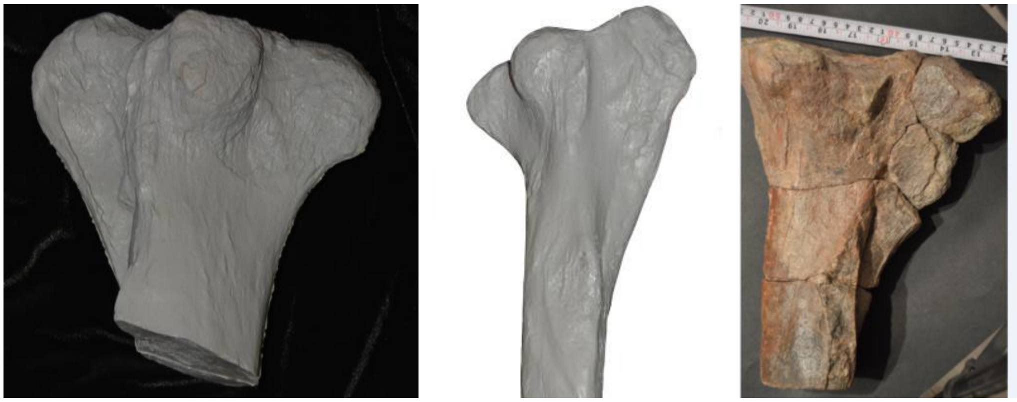

Fig. S3. Tibia. Left and middle: *Spinosaursu* Neotype cast housed at Uni Chicago. Right: *Camarillasaurus* picture provided by the Galve Museum, Spain.

Fig. S4. Tibia cross-section of *Camarillasaurus* picture provided by the Galve Museum, Spain.

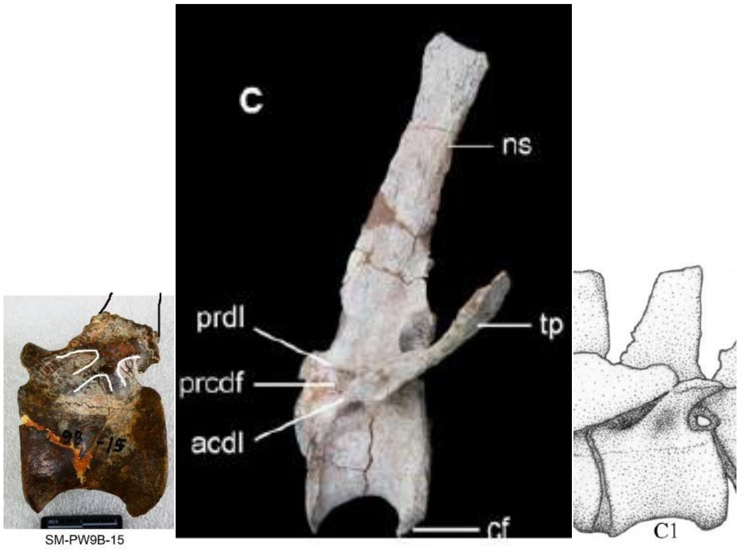

Fig. S5. Anterior caudal vertebra of (A) the Phuwiang spinosaurid B; (B) *Ichthyovenator*; (C) the Brazilian spinosaurid MN 4743-V.

Fig. S6. phylogenetic analysis of *Camarillasaurus*. Modified from Carrano et al 2012, 351 characters, 59 taxa (excluded *Streptospondylus* & *Eustreptospondylus*) produced **7** MPTs each of **1014** steps, CI = 0.**426**, RI = 0.**698**.

Table 1. Measurement of caudal vertebrae (in mm), * = incomplete.

	C1 SM-PW9B-17	C2 SM-9B-13	C3 SM-9B-15	C4 SM-9B-14	C5 SM-PW9A	C6 SM-9B-16	C7 SM-9B-11	C8 SM-9B-12
Centrum length	96	88.5	90	82	88	88	83	71.5
Centrum cranial height	89.5	84.5	80	80	69	56	56	37
Centrum caudal height	88	88	80	83	58*	62	54	38
Centrum cranial width	74*	97	76.5	71	61	54.5	46	40
Centrum caudal width	96.5	94*	60*	71	52*	52	39*	39
Width of transverse process proximal	?	?	37 R&L	?	?	?	?	-
Width of transverse process distal	?	?	?	?	?	?	?	-
Length of transverse process Central	?	?	?	?	?	?	?	-
Central section thickness	60*	63.5	40	50	35	27	28	21
Neural spine width maximum	?	?	15	?	?	?	?	12
Neural spine apical length	?	?	?	?	?	?	?	11
Neural spine basal length	?	?	53	?	?	?	?	25
Neural arch length base	61.5	67.5	69	69	69	68	60	59
Neural spine height	?	?	?	?	?	?	?	57*
Ventral groove length	37	34	50 along centrum length	43.5	53 along centrum length	55 along centrum length	54 along centrum length	49 Long & narrow

Table 2. the differences among: anterior/ mid/ posterior caudal vertebrae. NA = not applicable.

	Anterior caudals	Mid-caudals	Posterior caudals
Ichthyovenator	flat (per.obs.; Evers et al 2015)	Flat	? NA?
Baryonyx holotype	NA (Charig & Milner 1997)	NA?	NA?
cf. Baryonyx Portugal	groove (Mateus et al 2011)	Groove	Groove
Suchomimus	flat (per.obs.)	Flat	Flat
Spinosaurus	flat (per.obs.)	Flat	Flat
Phuwiang spinosaurid B	groove? (per.obs.)	Groove	Groove
Camarillasarus	?	?	Groove(Sanchez- Hernandez et al 2014)
SNSB-BSPG 2008 I 67	flat (Lex 2017, per.com.)	?	?

Table 3. Sacral Vertebrae in ventral view

	Centra anteriorposteriorly	Ventral view/ventral ridge
Camarillasaurus	Long	Convex/ no ridge
Ichthyovenator	possibly long?	NA
Baryonyx holotype	Long	convex/flat, NA?
Suchomimus	Long	Convex/ no ridge?
Spinosaurus	Long	Convex/ no ridge?
PW9B-taxon A	Short	Flat, no ridge?
PW9B-taxon C	Long	Slightly flat
Aoniraptor	Short	Flat, no ridge?

Datanglong	Equal/short	Convex/ no ridge
Megaraptor	Short	Flat?, no ridge
SMNS 58023	Long	Convex/ no ridge
MPMA 08-003-94	Long	Flat
CPPLIP 1324	Long	Flat
Majungasaurus		
Ceratosaurus		
Elaphrosaurus		

Supplementary information Chapter 7

Table 1. Measurement of juvenile sacral vertebrae (in mm).

	S4	S5
Centrum length at midheight	?	65
Anterior centrum height	?	33
Posterior centrum height	?	33.5
Anterior centrum width	?	?
Centrum central thickness	?	24
Neural spine height	?	?
Neural spine width maximum	?	?
Neural spine apical length	?	?
Neural spine basal length	?	?
Posterior centrum width	?	36

Table 2. Measurement of juvenile caudal vertebrae (in mm).

	C1	C2
Centrum length	48	46
Centrum cranial height	30	27
Centrum caudal height	33	21*
Centrum cranial width	23	18
Centrum caudal width	21	12*
Width of transverse process proximal	?	?
Width of transverse process distal	?	?
Length of transverse process	?	?
Central section thickness	8	7
Neural spine width maximum	?	?
Neural spine apical length	?	?
Neural spine basal length	?	?
Neural arch length at base	43	33
Neural spine height	?	?
Ventral groove length	-	-

Table 3. Comparison of the sacral vertebrae of PW9B-taxon C to Ceratosauria, Spinosauridae, and Megaraptora.

	Centra anteriorposteriorly	S5 Ventral view/ventral ridge
SM-PW9B taxon C	Long	Slightly flat
Ichthyovenator	possibly long?	NA
***Baryonyx* holotype**	Long	convex/flat, NA?
Suchomimus	Long	Convex, no ridge?
Spinosaurus	Long	Convex, no ridge?
SM-PW9B-taxon A	Short	Flat, no ridge, with short & shallow sulci
Aoniraptor	Short	Flat, no ridge?
Datanglong	Equal/short	Convex, no ridge?
Megaraptor	Short	Flat?, no ridge
SMNS 58023	Long	Convex, no ridge
MPMA 08-003-94	Long	Flat
CPPLIP 1324	Long	Flat
Majungasaurus		Flat
Elaphrosaurus		Flat

Table 4. Comparison of the caudal vertebrae of PW9B-taxon C to Ceratosauria, Spinosauridae, and Megaraptora.

	Anterior caudals	Mid-caudals	Posterior caudals
PW9B-taxon C	flat	?	?
cf. *Baryonyx* Thailand (PW9B-taxon B)	groove? (pers. obs.)	Groove	Groove
Ichthyovenator	flat (pers. obs.; Evers et al 2015)	Flat	?
***Baryonyx* holotype**	NA (Charig & Milner 1997)	NA?	NA?
cf. *Baryonyx* Portugal	groove (Mateus et al 2011; pers. obs.)	Groove	Groove
Suchomimus	flat (pers. obs.)	Flat	Flat
Spinosaurus	flat (pers. obs.)	Flat	Flat
Camarillasarus	?	?	Groove(Sanchez- Hernandez et al 2014)
SNSB-BSPG 2008 I 67	flat (Lex 2017, per.com.)		?
Majungasaurus			
Elaphrosaurus			

Table 5. measurements of pedal phalanges (SM-PW9B-8 and 9) (in mm)

	SM-PW9B-8	SM-PW9B-9
Length	37	51
Transverse width (middle)	17	18
Prox. Height	20	24
Prox. Width	22	23

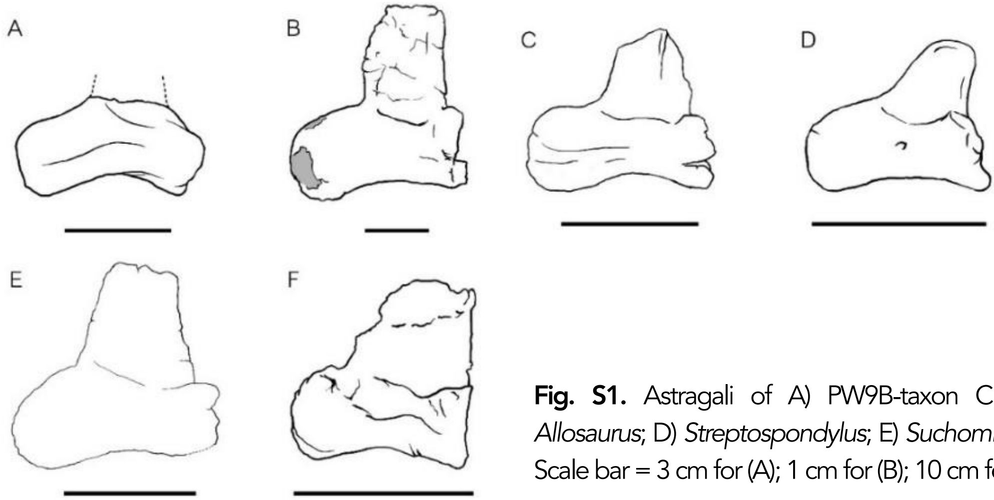

Fig. S1. Astragali of A) PW9B-taxon C; B) *Masiakasaurus*; C) *Allosaurus*; D) *Streptospondylus*; E) *Suchomimus*; F) *Australovenator*. Scale bar = 3 cm for (A); 1 cm for (B); 10 cm for (C) – (F).

Fig.S2. The consensus trees of theropods result using dataset of Coria & Currie 2016 (left) found the Phuwiang juvenile belongs to the **basal Coelurosauria** and dataset of Carrano et al. 2012 (right) found the Phuwiang juvenile is an averostran, possibly belongs to the **Ceratosauria** or **Spinosauridae**.

1. Characters from Coria & Currie 2016

Phuwiang Juvenile

???00?
00??0001???????????1??
1???

2. Characters from Carrano et al 2012

196. Sacral vertebrae, centrum pneumaticity: absent (0)
197. Sacral vertebrae, number: 5 (?)*
202. Caudal vertebrae, anterior, morphology of ventral surface: flat (0)
204. Caudal vertebrae, pleurocoels (large pneumatic foramina in centrum): absent (0)
317. Tibia, lateral malleolus: overlaps calcaneum (1)
322. Tibia, anteromedial buttress for astragalus: absent (0), ventral (1), marked oblique step-like ridge (2), reduced oblique ridge (3), bluntly rounded vertical ridge on medial side (4).
329 astragalus & ascending process: fused (1)
330. Astragalus, orientation of distal condyles: 30-45° anterior (1).
331. Astragalus, ascending process morphology: laminar (2).
332. Astragalus, angle of dorsal margin of ascending process: high and oblique (**?**).
333. Astragalus, ascending process height relative to depth of astragalar body: **?**
334. Astragalus, prominent proximolateral extension: absent (0)
335. Astragalus, round fossa at base of ascending process: large (2).
336. Astragalus, development of articular surface for distal end of fibula: reduced, lateral (1).
337. Astragalus, posterolateral crest: absent (0).
338. Astragalus, posteromedial crest: absent (0).
339. Astragalus, articulation with calcaneum in adults: separate (**?**).

The PW9B-38 can be coded for 17 characters from 351 characters = 4.84% (The file name: PW9B-3B in Carrano et al 2012)

Phuwiang juvenile

???
??0?????0?
0??1????
4??????112??02100?????????????

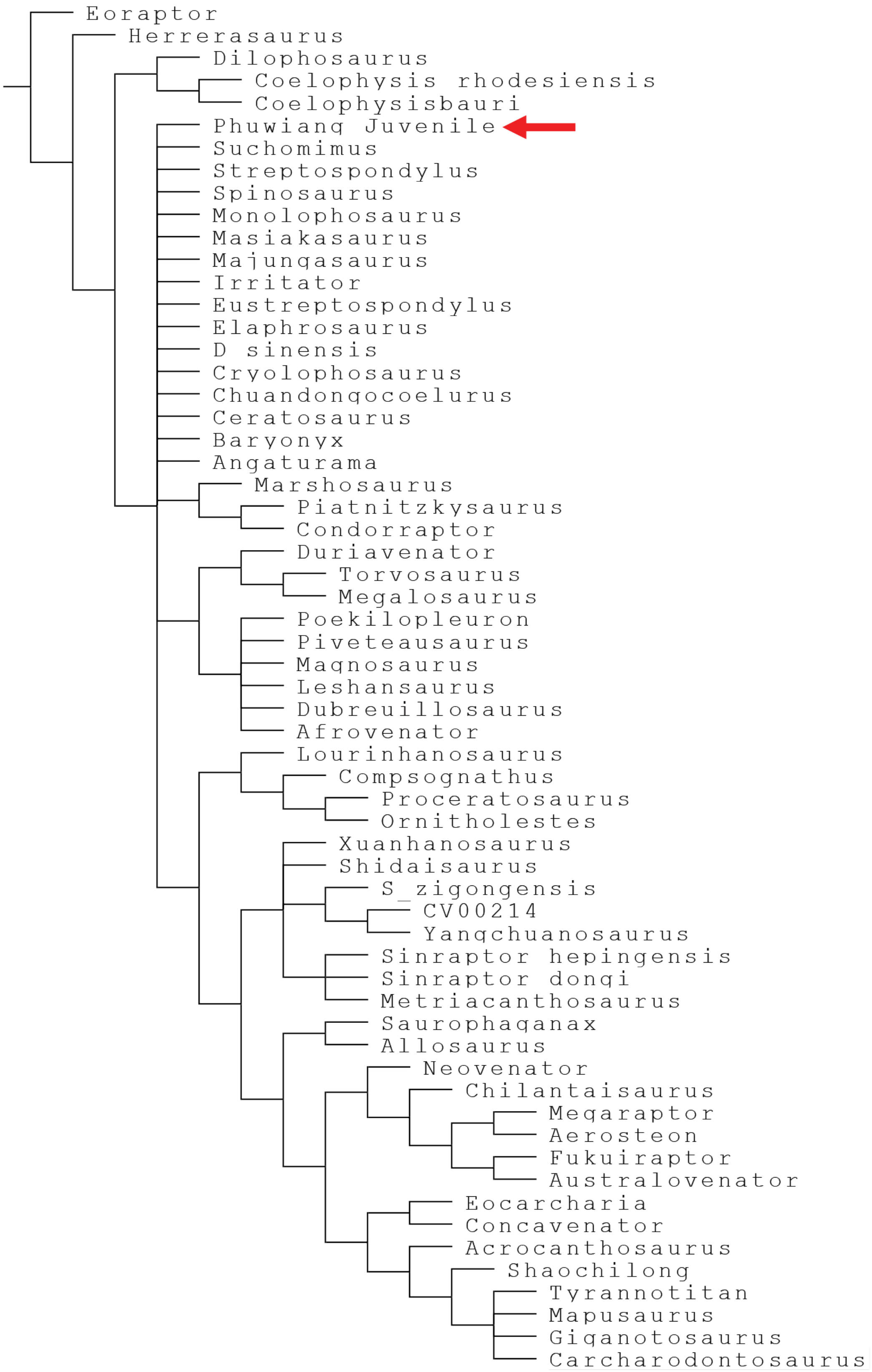

Fig. S3: Strict consensus tree of 351 characters, 66 taxa modified from Carrano et al 2012, found the PW9B-taxon B to nest within **Averostra**

Fig. S4. a selected tree found PW9B-taxon B is a **Ceratosauria**

Fig. S5. a selected tree found PW9B-taxon B is a **Spinosauridae**

Fig. S6. a selected tree found PW9B-taxon B is a **basal coelurosaur**.

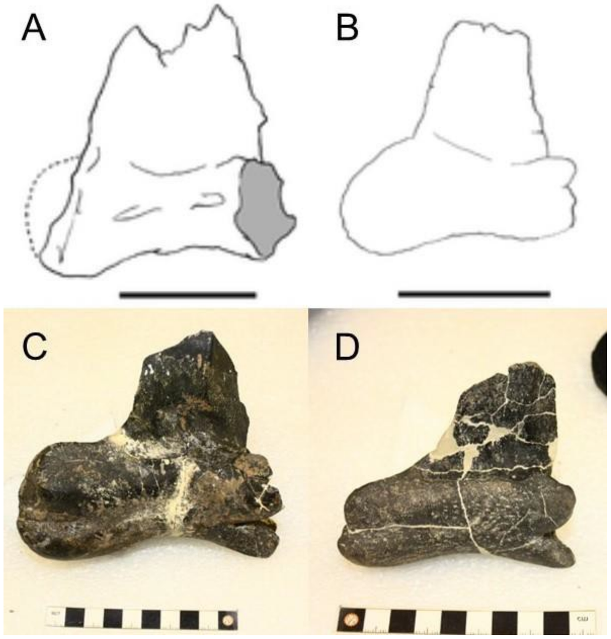

Fig. S7. *Suchomimus* adult MNBH GAD97 (A); *Suchomimus* sub-adult/juvenile MNBH GAD97 (B); *Allosaurus* adult UMNH VP 11003 (C); *Allosaurus* sub-adult/juvenile UMNH VP 9409 (D). Scale bar = 10 cm.

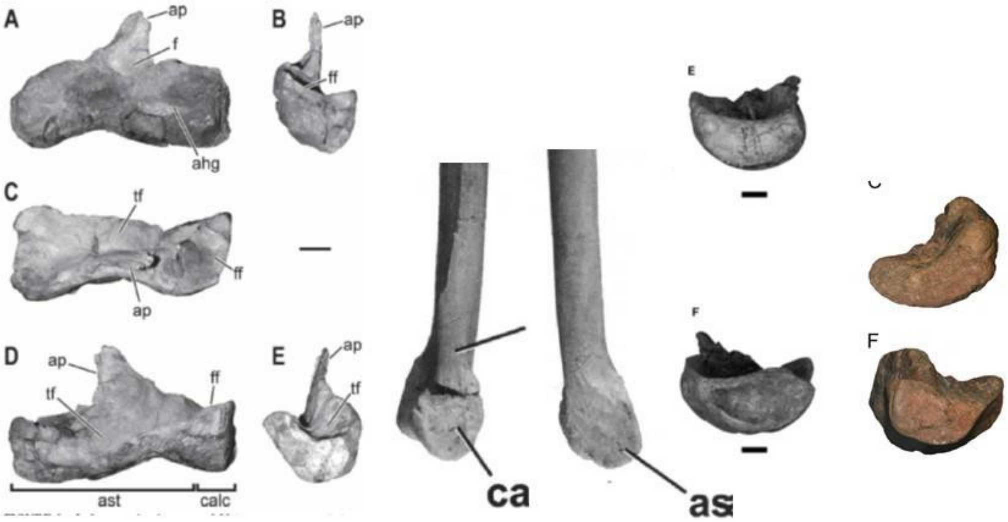

Fig. S8. Tasus in medial and lateral view. *Majungasaurus*, *Masiakasaurus*, *Elaphrosaurus*, Phuwiang juvenile.

Fig. S9. Phuwiang juvenile, *Suchomimus*, Phuwiang theropod A, and *Australovenator* astragalus in proximal view.

Fig. S10. Comparison of vertebrae of Phuwiang juvenile and Suchomimus.

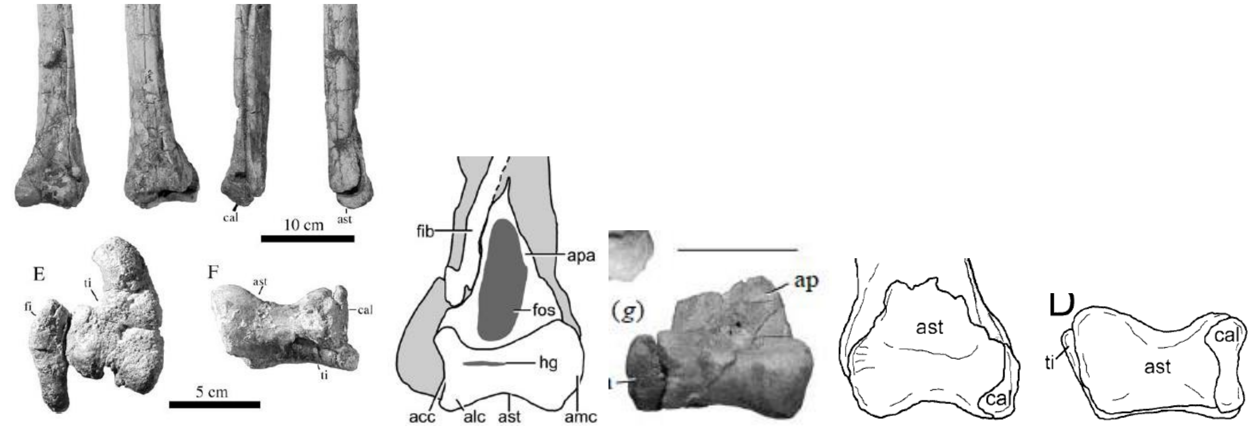

Fig. S11. Astragalus of ornithomimosaurs: *Garudimimus*, *Nqwebasaurus*, *Beishanlong*, *Harpymimus*.

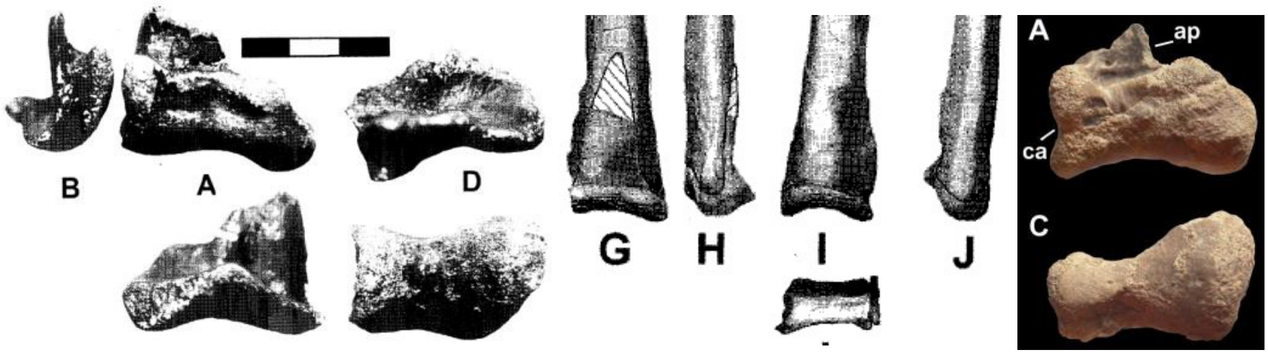

Fig. S12. Astragalus of *Coelurus*, *Tanycolagreus*, *Bicentenaria*.

CURRICULUM VITAE

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EDUCATION

2014-Present PhD student in evolutionary biology and paleontology, Division of Paleontology, Institute of Geosciences, Rheinische Friedrich-Wilhelms-Universität Bonn, Germany.
PhD Thesis: "Theropod Dinosaurs from Thailand and Southeast Asia: Phylogeny, Evolution, and Paleobiogeography".
Supervisor: Prof Dr P. Martin Sander. Division of Paleontology, Institute of Geosciences, Rheinische Friedrich-Wilhelms-Universität Bonn, Germany.

2011-2014 M.Sc. in Evolution, Ecology, and Systematics, Munich Graduate Program for Evolution, Ecology and Systematics, Ludwig-Maximilians-Universität München (LMU), Munich, Germany.
Master Thesis: "Osteology and Phylogenetic Position of *Siamotyrannus isanensis* (Dinosauria; Theropoda) from the Lower Cretaceous of Thailand".
Supervisor: Dr Richard J. Butler, GeoBio-Center LMU, Munich, Germany and School of Geography, Earth and Environmental Sciences, Burmingham University, Burmingham, UK.
Co-supervisor: PD Dr Oliver W. M. Rauhut, Bavarian State Collection of Paleontology and Geology, LMU Munich, Germany.

2004-2008 B.Sc. major in Biology (Honor), Faculty of Science, Mahidol University, Bangkok, Thailand.
Bachelor Project: "Additional preserved vertebrae of *Siamotyrannus isanensis* (Dinosauria; Theropoda) from the Type Locality" (original in English).
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RESEARCH INTERESTS

Taxonomy, paleobiogeography, and evolution of theropods. Evolution of basal rhynchosaurs and ichthyopterygians. Ecology, biodiversity, museum study, and comparative anatomy in general.

PUBLICATIONS

Samathi, A., Chanthasit, P., and Sander, P.M. 2019a. Two new basal coelurosaurian theropod dinosaurs from the Lower Cretaceous Sao Khua Formation of Thailand. *Acta Palaeontologica Polonica* 64 (2): 239–260.

Samathi, A., Chanthasit, P., and Sander, P.M. 2019b. A review of theropod dinosaurs from the Late Jurassic to mid-Cretaceous of Southeast Asia. *Annales de Paléontologie* (*in press.*), https://doi.org/10.1016/j.annpal.2019.03.003

Yang, T-R., Engler, T., Lallensack, J.N., **Samathi, A.,** Makowska, M., and Schillinger, B. (*in revision*). Hatching asynchrony in oviraptorid dinosaurs sheds light on their unique nesting biology. *Integrative Organismal Biology*.

Samathi, A., Chanthasit, P., and Sander, P.M. (*in prep*). A revision of *Siamotyrannus isanensis* (Dinosauria: Theropoda) from the Early Cretaceous of Thailand.

Aureliano, T., Ghilardi, A. M., Buck, P. V., Fabbri, M., **Samathi, A.,** Delcourt, R., Fernandes, M.A., Sander, P.M. 2018. Semi-aquatic adaptations in a spinosaur from the Early Cretaceous of Brazil. *Cretaceous Research*. 90: 283-295.

Butler, R. J., Ezcurra, M. D., Montefeltro, F. C., **Samathi, A.,** and Sobral, G. 2015. A new species of basal rhynchosaur (Diapsida: Archosauromorpha) from the early Middle Triassic of South Africa, and the early evolution of Rhynchosauria. *Zoological Journal of the Linnean Society.* 174: 571-588.

RESEARCH EXPERIENCE (SELECTED)

2013-Present Study on theropods dinosaurs from Thailand, Laos, Japan, Africa, South and North America. Focus on their anatomy, taxonomy, and paleobiogeography.

2012 Individual Research Training 2: study on a new basal rhynchosaur from South Africa, supervisor: Dr Rischard J. Butler, GeoBio-Center, LMU Munich.

2011-2012 Individual Research Training 1: Comparative Histology and Fine Structure of Bivalve Mantle Edges, supervisor: PD Dr Martin Heß, Faculty of Biology, LMU Munich.

2009 Volunteer, Animal skeleton preparation and restoration, Zoological Museum, Faculty of Science, Kasetsart University, Bangkok, Thailand and fossil expedition in Loei Province, Thailand.

2007-2008 Volunteer in dinosaur research at Dinosaur Museum, Sawannakhet Province, Lao People's Democratic Republic. Volunteer in Fossil preparation at Sirindhorn Museum and Phu Kum Khao Dinosaur research center, Kalasin Province.

2006 Summer course in Marine Ecology, Marine Biological Institute, Phuket Province and Walailak University, Nakorn Sri Thammarat Province, Thailand.

2006 Trained in capturing, marking and measuring of birds at Lam Pak Bia research center, Samut Sakorn, Thailand.

TEACHING EXPERIENCE

2015, 2017, 2018 Teaching assistant in Phylogenetic analysis using TNT for post-graduate students, Rheinische Friedrich-Wilhelms-Universität Bonn, Germany

2009 Teaching assistant in Ecology for undergraduate students, Department of Biology, Faculty of Science, Mahidol University and in Animal stuff, Department of Zoology, Faculty of Science, Kasetsart University.

CONFERENCES (SELECTED)

Samathi, A. 2018. Biodiversity of non-maniraptoran theropod dinosaurs during the Mesozoic in Asia. *GeoBonn 2018 Bonn* (poster)

Samathi, A., Chanthasit, P., and Sander, P. M. 2018. Non-avian Theropod dinosaurs in Thailand and Southeast Asia: Evolution and Paleobiogeography. *5th International Palaeontological Congress 2018* Paris (talk) and *13th Symposium on Mesozoic Terrestrial Ecosystems and Biota* Bonn (talk).

Samathi, A. 2018. Phylogenetic Position of the Ornithomimosaur *Kinnareemimus khonkaenensis* from the Early Cretaceous of Thailand. *5th International Palaeontological Congress 2018* Paris and *15th Annual Meeting of the European Association of Vertebrate Palaeontologists 2017* Munich(poster).

Samathi, A., Chanthasit, P. 2017. Two New Basal Megaraptora (Dinosauria: Theropoda) from the Early Cretaceous of Thailand with Comment on the Phylogenetic Position of *Siamotyrannus* and *Datanglong*. *Journal of Vertebrate Paleontology 37, Program and Abstracts: 188* (talk).

Samathi, A., Butler, R. J., & Chanthasit, P. 2015. A Revision of *Siamotyrannus isanensis* (Dinosauria: Theropoda) from the Early Cretaceous of Thailand. *2nd International Symposium on Asian Dinosaurs 2015 Bangkok* (talk).

GRANT AND AWARD

2017 Patterson Memorial Grant, Society of Vertebrate Paleontology, Calgary, Canada.

2009-2018 Full-time Scholarship to study abroad, Royal Thai Government Ministry of Science and Technology, Kingdom of Thailand.

2008 Outstanding Presentation, 9th Science Exhibition, Faculty of Science, Mahidol University on the Topic of "Additional Preserved Vertebrae of *Siamotyrannus isanensis* (Dinosauria; Theropoda) from the Type Locality".

TECHNICAL SKILLS

- Program TNT, Mesquite, Agisoft Photoscan, mrBayes, R, and Perl.
- Fossil excavation and preparation. Bone histology and microtome techniques.
- Animal stuff and skeleton restoration. Scientific illustration (drawing and photography). Watching, capturing, marking and measuring of birds. Plant tissue culture technique.