

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

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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 coelurosaurians from the Lower Cretaceous Sao Khua Formation of Thailand are described and named as *Phuwiangvenator yaemmyomi* 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* (Sereni 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 astragalocalca-

neum (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 Tyrannosauroidae 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 Allosauroidae (Benson et al. 2010; Carrano et al. 2012); (ii) nested within Tyrannosauroidae (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 postcra-

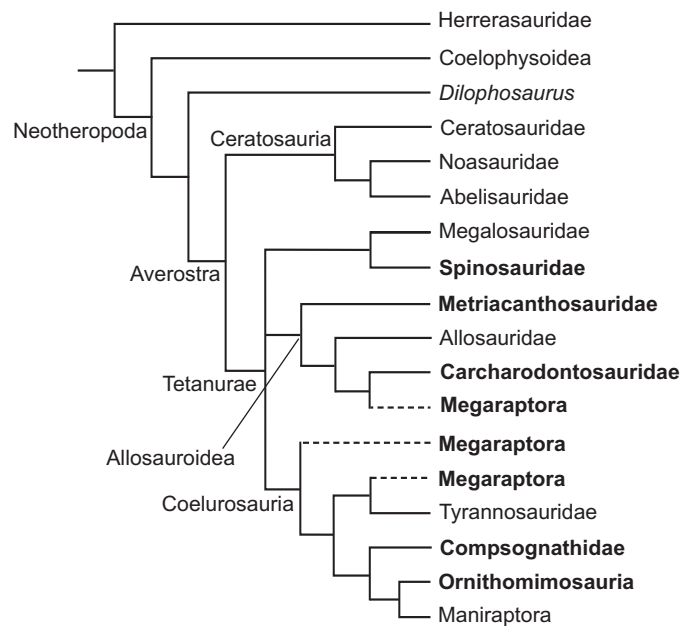


Fig. 1. Three hypotheses of the phylogenetic position of Megaraptora. Megaraptora as derived Carcharodontosauria (Benson et al. 2010; Carrano et al. 2012); basal Coelurosauria (Novas et al. 2015; Apesteguía et al. 2016; Delcourt and Grillo 2018); and basal Tyrannosauroidae (Novas et al. 2012a, 2013;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

nial 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.

*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 Ain 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-F2D-D2CCA1A7B.

## 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\\_et\\_al\\_SOM.pdf](http://app.pan.pl/SOM/app64-Samathi_et_al_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.

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, crocodylians, 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. These consists of a possible compsognathid (Buffetaut and Ingavat 1984), teeth of the spinosaurid *Siamosaurus suteethorni* (Buffetaut and Ingavat

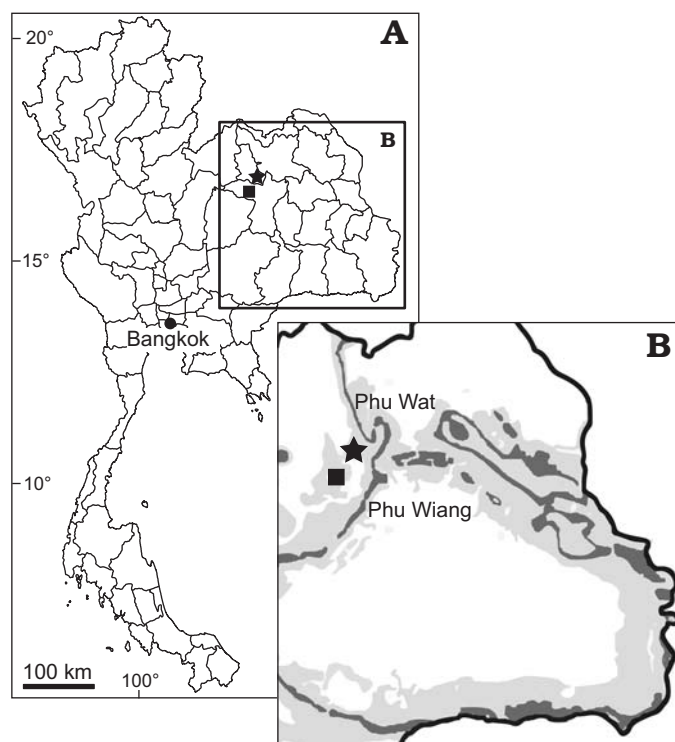


Fig. 2. Map of Thailand (A) and close-up of northeastern Thailand (B) showing the location of Phu Wiang locality, Khon Kaen Province (square) and Phu Wat locality, Nong Bua Lamphu Province (star). Dark gray, Sao Khua Formation outcrops, light gray, Phu Kradung and Khok Kruat formations.



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

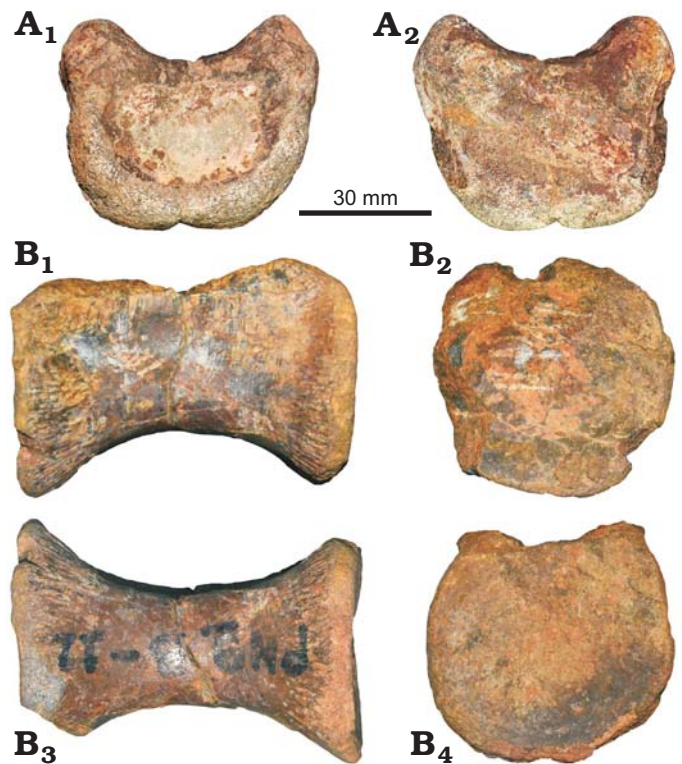


Fig. 3. Coelurosaurian theropod *Phuwiangvenator yaemniyomi* gen. et sp. nov. from the Early Cretaceous Sao Khua Formation of Phu Wiang, Khon Kaen Province, Thailand. A. SM-PW9A-1, atlantal intercentrum in anterior (A<sub>1</sub>) and posterior (A<sub>2</sub>) views. B. SM-PW9B-12, dorsal vertebra in left lateral (B<sub>1</sub>), anterior (B<sub>2</sub>), ventral (B<sub>3</sub>), and posterior (B<sub>4</sub>) views.

of 6 m. The skeletal proportions are shared by other theropods of corresponding size such as *Australovenator*.

*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 con-

cave 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

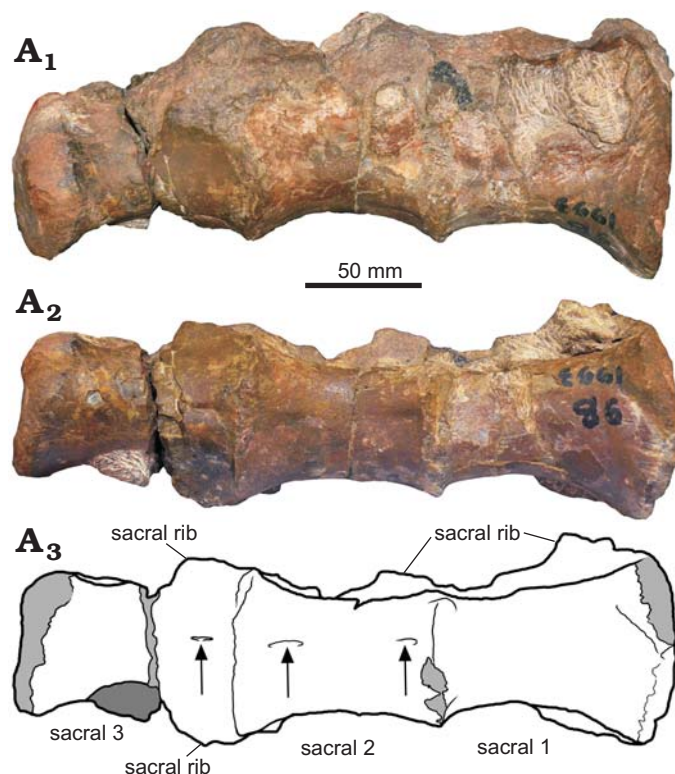


Fig. 4. Coelurosaurian theropod *Phuwiangvenator yaemniyomi* gen. et sp. nov. from the Early Cretaceous Sao Khua Formation of Phu Wiang, Khon Kaen Province, Thailand. SM-PW9B-39, anterior sacral vertebrae in right lateral (A<sub>1</sub>) and ventral (A<sub>2</sub>) views; line drawing in ventral view (A<sub>3</sub>). Arrows indicate ventral sulci, light grey, broken part; dark grey, matrix.

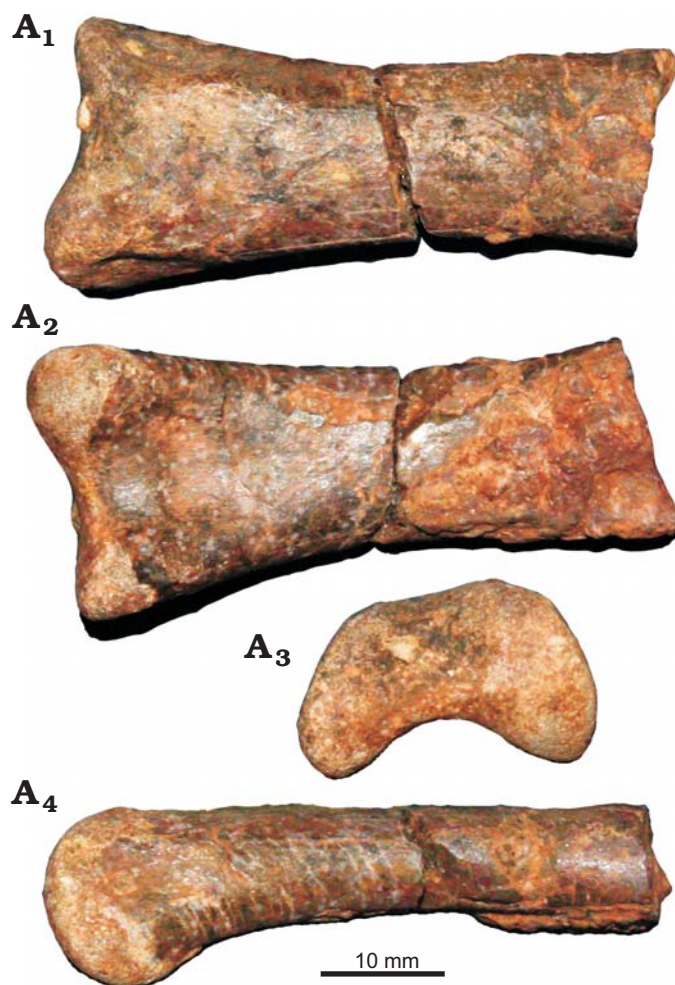


Fig. 5. Coelurosaurian theropod *Phuwiangvenator yaemniyomi* gen. et sp. nov. from the Early Cretaceous Sao Khua Formation of Phu Wiang, Khon Kaen Province, Thailand. SM-PW9B-6, right metacarpal II in dorsal (A<sub>1</sub>), ventral (A<sub>2</sub>), distal (A<sub>3</sub>), and medial (A<sub>4</sub>) views.

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 sacral 2.

**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



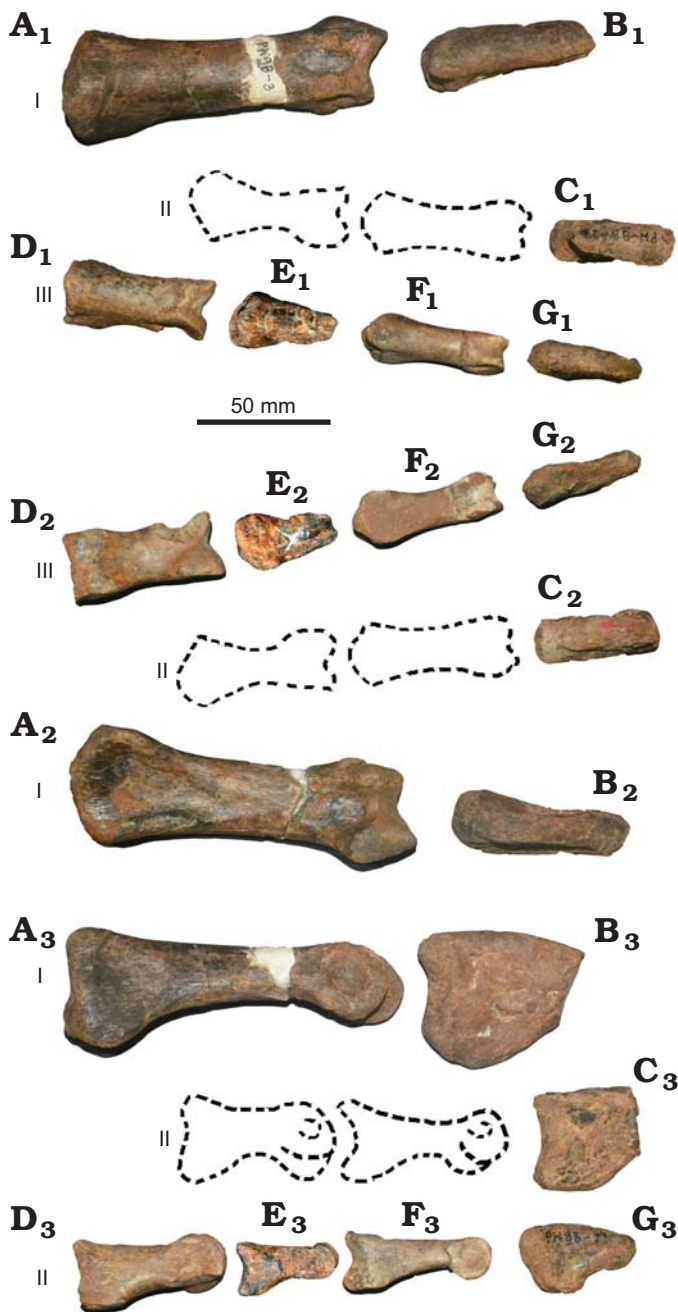


Fig. 6. Coelurosaurian theropod *Phuwiangvenator yaemniyomi* gen. et sp. nov. from the Early Cretaceous Sao Khua Formation of Phu Wiang, Khon Kaen Province, Thailand. SM-PW9B-3 (A), SM-PW9B-19 (B), SM-PW9B-23 (C), SM-PW9B-4 (D), SM-PW9B-7 (E), SM-PW9B-5 (F), SM-PW9B-21 (G); manual phalanges I–III (A, D, E, F) and unguals I–III (B, C, G), in dorsal (A<sub>1</sub>–G<sub>1</sub>), ventral (A<sub>2</sub>–G<sub>2</sub>), and lateral (A<sub>3</sub>–G<sub>3</sub>) 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 mediolaterally. 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* (Apesteguía et al. 2016). The manual phalanx 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 mediolaterally. 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 ligament 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

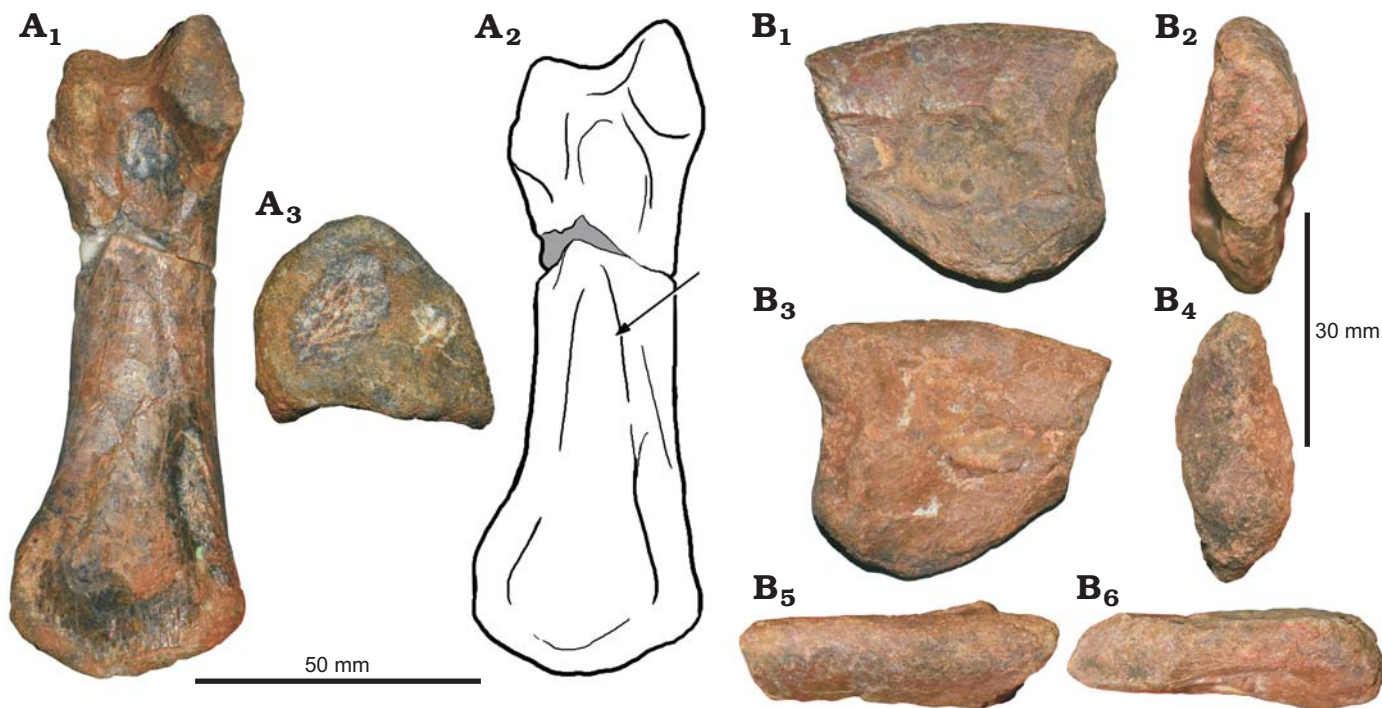


Fig. 7. Coelurosaurian theropod *Phuwiangvenator yaemniyomi* gen. et sp. nov. from the Early Cretaceous Sao Khua Formation of Phu Wiang, Khon Kaen Province, Thailand. **A.** SM-PW9B-3, manual phalanx I-1 in ventral ( $A_1$ ) and proximal ( $A_3$ ) views; line drawing in ventral view ( $A_2$ ). **B.** 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 phalanx 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 is 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



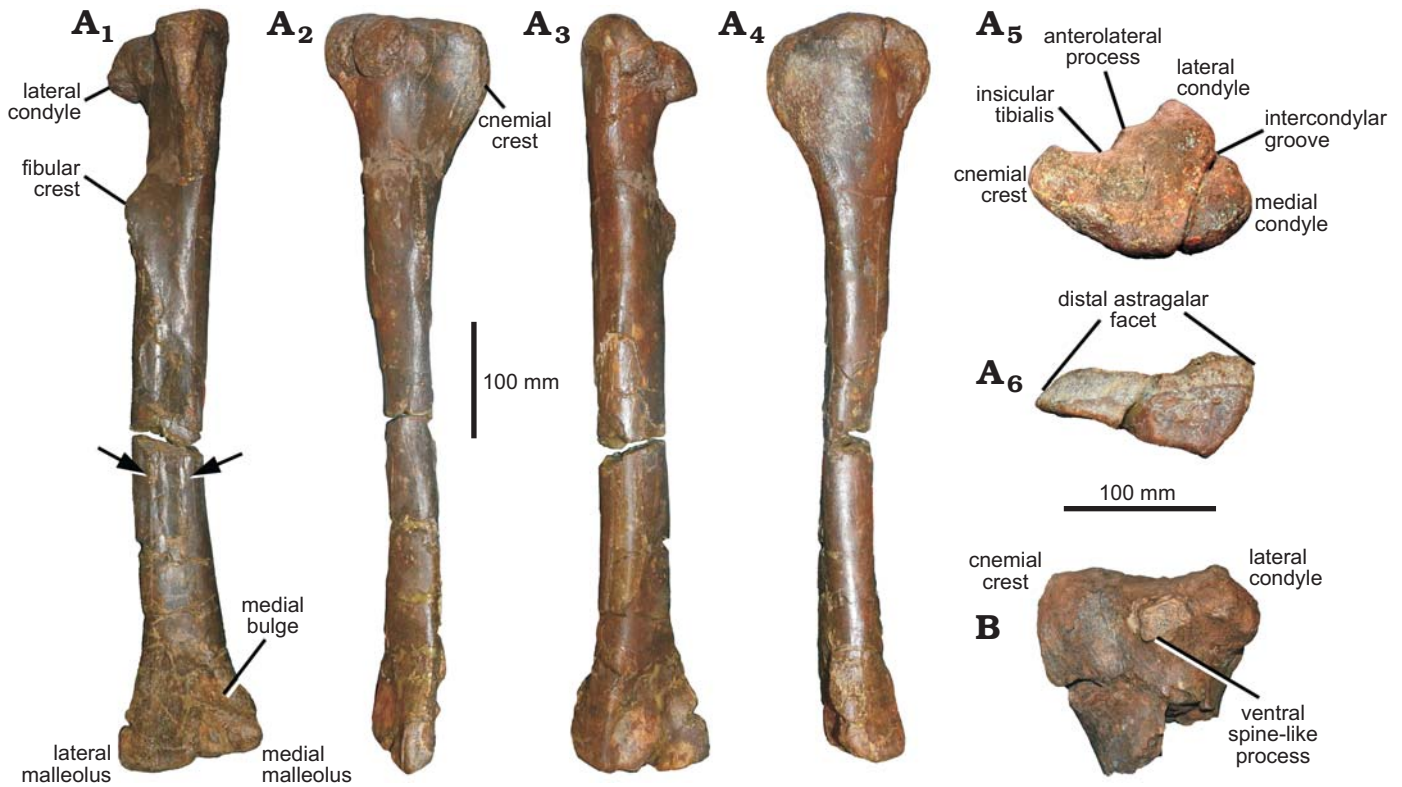


Fig. 8. Coelurosaurian theropod *Phuwiangvenator yaemniyomi* gen. et sp. nov. from the Early Cretaceous Sao Khua Formation of Phu Wiang, Khon Kaen Province, Thailand. **A.** SM-PW9B-41, right tibia in anterior (A<sub>1</sub>), lateral (A<sub>2</sub>), posterior (A<sub>3</sub>), medial (A<sub>4</sub>), proximal (A<sub>5</sub>), and distal (A<sub>6</sub>) views. **B.** SM-PW9B-40, proximal left tibia in lateral view. Arrow indicates vertical ridge on the tibia.

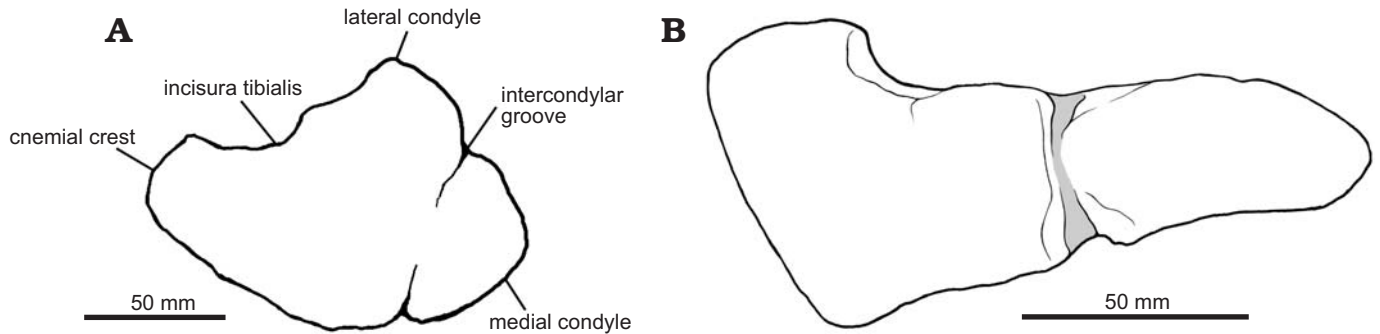


Fig. 9. Coelurosaurian theropod *Phuwiangvenator yaemniyomi* gen. et sp. nov. from the Early Cretaceous Sao Khua Formation of Phu Wiang, Khon Kaen Province, Thailand. **A.** SM-PW9B-41, right tibia in proximal view. **B.** SM-PW9B-40, left tibia in distal view. Light grey indicates broken bone.

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 astrag-

alus is 103 mm wide, the calcaneum is 25 mm wide. The astragal 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 astragal body by a shallow groove. The ascending process height relative to the depth of the astragal 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).



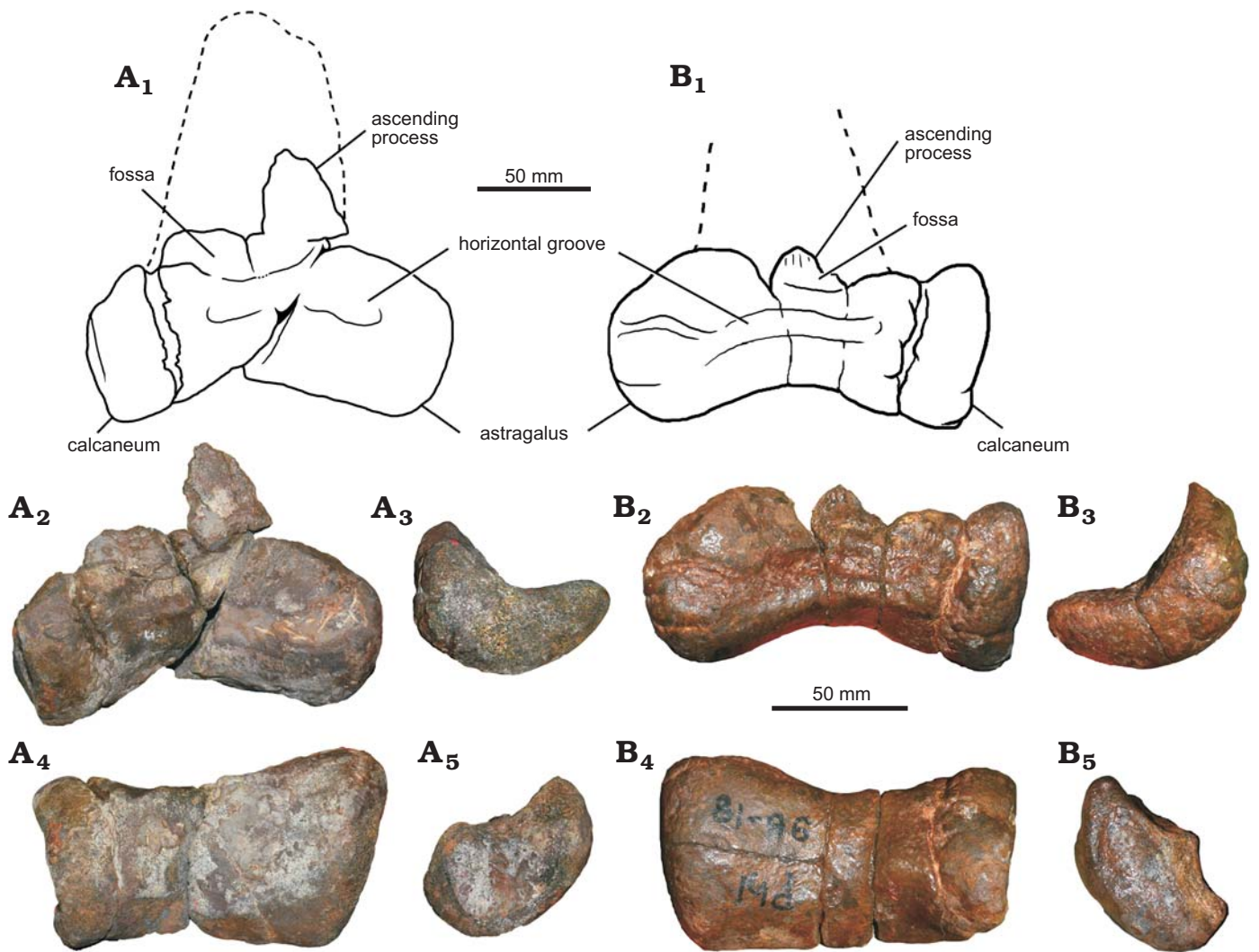


Fig. 10. *Phuwiangvenator yaemniyomi* gen. et sp. nov. from the Early Cretaceous Sao Khua Formation of Phu Wiang, Khon Kaen Province, Thailand. SM-PW9A-B17, right (A) and SM-PW9B-18, left (B); astragalocalcaneum in anterior (A<sub>2</sub>, B<sub>2</sub>), medial (A<sub>3</sub>, B<sub>3</sub>), distal (A<sub>4</sub>, B<sub>4</sub>), and lateral (A<sub>5</sub>, B<sub>5</sub>) views; line drawings in anterior view (A<sub>1</sub>, B<sub>1</sub>). 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 breadth 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).

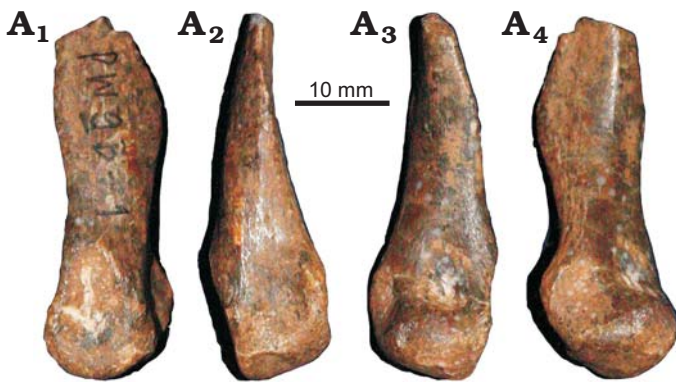


Fig. 11. Coelurosaurian theropod *Phuwiangvenator yaemniyomi* gen. et sp. nov. from the Early Cretaceous Sao Khua Formation of Phu Wiang, Khon Kaen Province, Thailand. SM-PW9B-1, left metatarsal I in lateral (A<sub>1</sub>), posterior (A<sub>2</sub>), anterior (A<sub>3</sub>), and medial (A<sub>4</sub>) views.

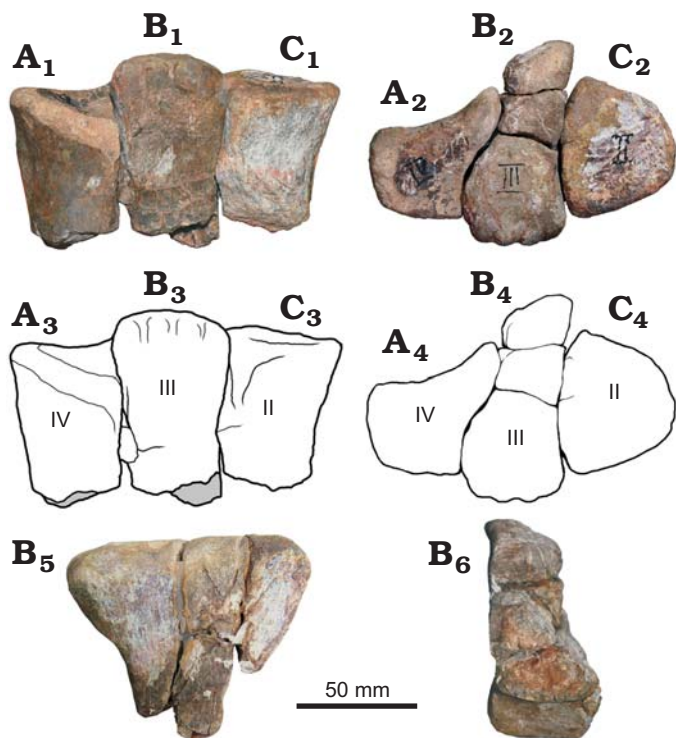


Fig. 12. Coelurosaurian theropod *Phuwiangvenator yaemniyomi* gen. et sp. nov. from the Early Cretaceous Sao Khua Formation of Phu Wiang, Khon Kaen Province, Thailand. SM-PW9B-44 (A), SM-PW9B-43 (B), SM-PW9B-42 (C); metatarsals in anterior (A<sub>1</sub>–C<sub>1</sub>) and proximal (A<sub>2</sub>–C<sub>2</sub>) views; line drawings in anterior (A<sub>3</sub>–C<sub>3</sub>) and proximal (A<sub>4</sub>–C<sub>4</sub>) views; metatarsal III in medial (B<sub>5</sub>) and distal (B<sub>6</sub>) 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 proxi-

mal 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 IV-4 (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.



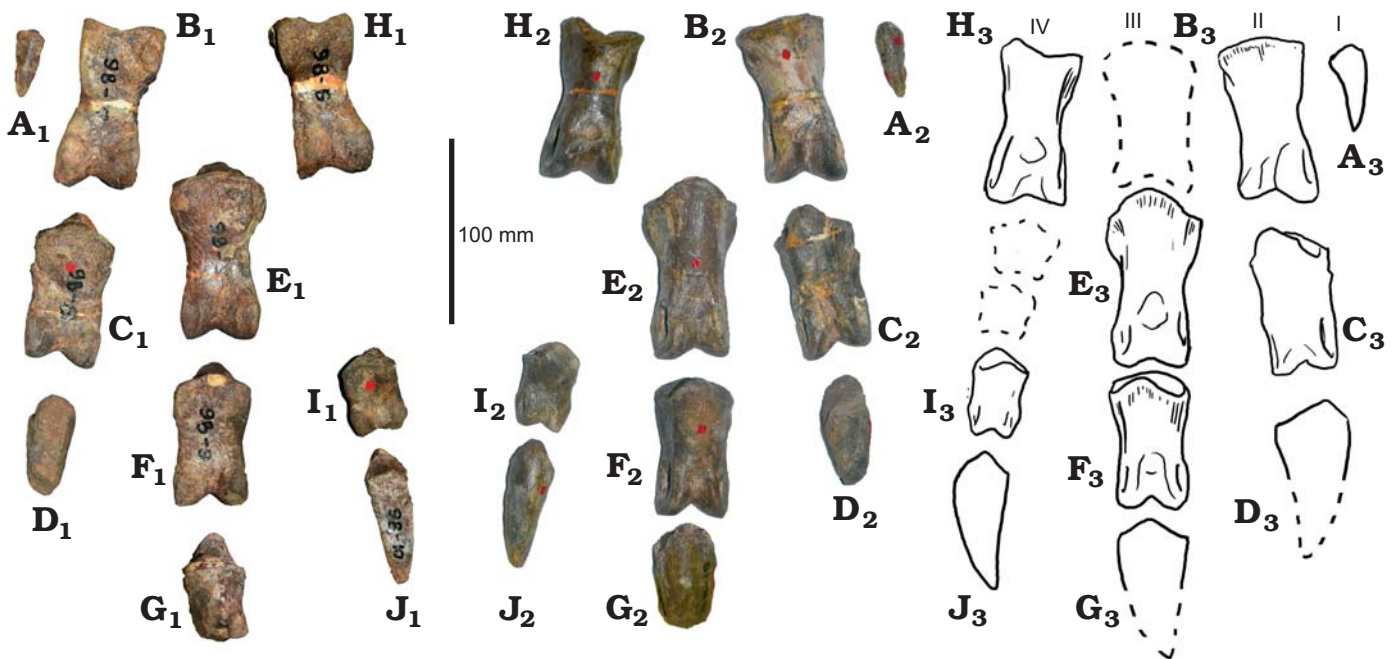


Fig. 13. Coelurosaurian theropod *Phuwiangvenator yaemniyomi* gen. et sp. nov. from the Early Cretaceous Sao Khua Formation of Phu Wiang, Khon Kaen Province, Thailand. SM-PW9B-11 (A), SM-PW9B-7 (B), SM-PW9B-8 (C), SM-PW9B-22 (D), SM-PW9B-5 (E), SM-PW9B-9 (F), SM-PW9B-19 (G), SM-PW9B-6 (H), SM-PW9B-45 (I), SM-PW9B-10 (J); right pedal phalanges (B, C, E, F, H, I) and unguals (A, D, G, J), in ventral (A<sub>1</sub>–J<sub>1</sub>) and dorsal (A<sub>2</sub>–J<sub>2</sub>) views; line drawings in dorsal view (A<sub>3</sub>–J<sub>3</sub>). 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 astragal

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.

**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. 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 unguis IV-5 in lateral (A<sub>1</sub>) and ventral (A<sub>2</sub>) views.

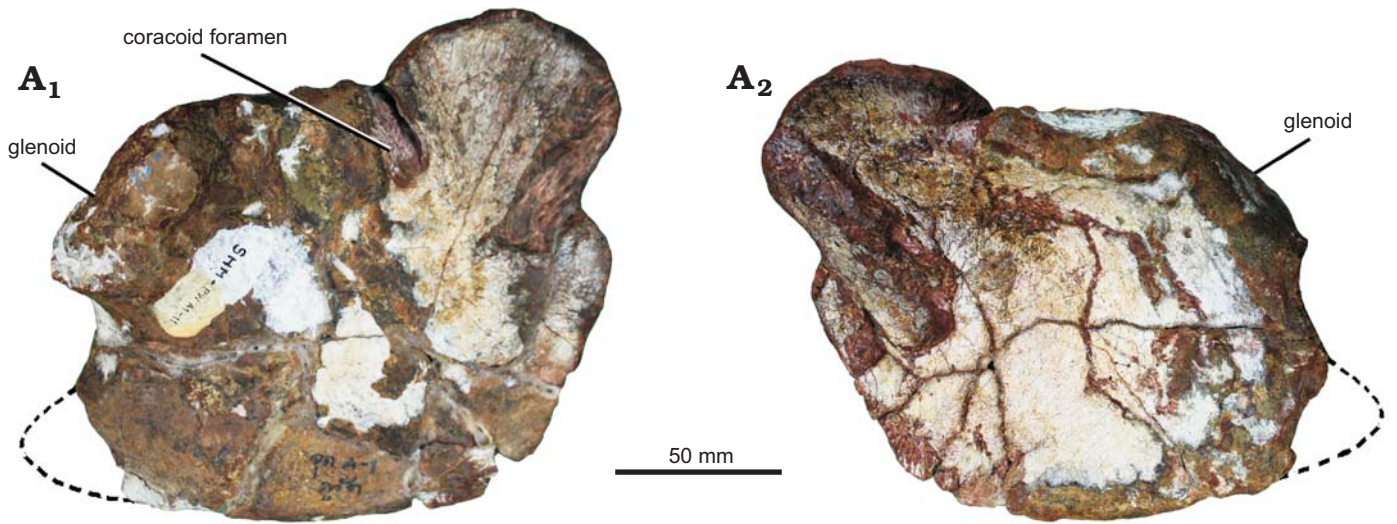


Fig. 15. Coelurosaurian theropod *Vayuraptor nongbualamphuensis* gen. et sp. nov. from the Early Cretaceous Sao Khua Formation of Phu Wat, Nong Bua Lamphu Province, Thailand. PRC-NB A1-11, right coracoid in lateral (A<sub>1</sub>) and medial (A<sub>2</sub>) views. Dashed lines are the reconstruction of the posterioventral process of the coracoid.

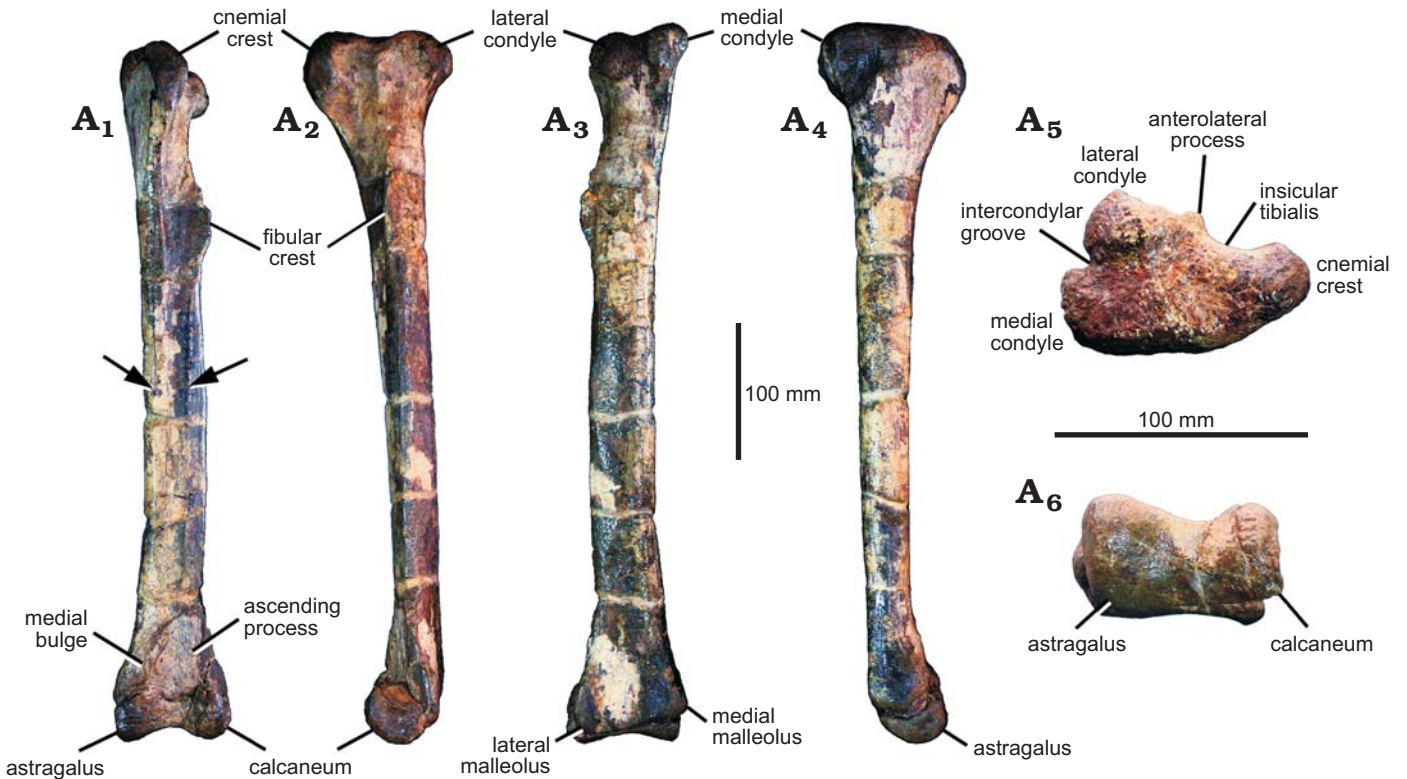


Fig. 16. Coelurosaurian theropod *Vayuraptor nongbualamphuensis* gen. et sp. nov. from the Early Cretaceous Sao Khua Formation of Phu Wat, Nong Bua Lamphu Province, Thailand. SM-NB A1-2, left tibia with associated astragalocalcaneum in anterior (A<sub>1</sub>), lateral (A<sub>2</sub>), posterior (A<sub>3</sub>), medial (A<sub>4</sub>), proximal (A<sub>5</sub>), and distal (A<sub>6</sub>) view. Arrow indicates vertical ridge on the tibia.

(PRC-NB A1-3) preserves a portion of the medial lamina 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



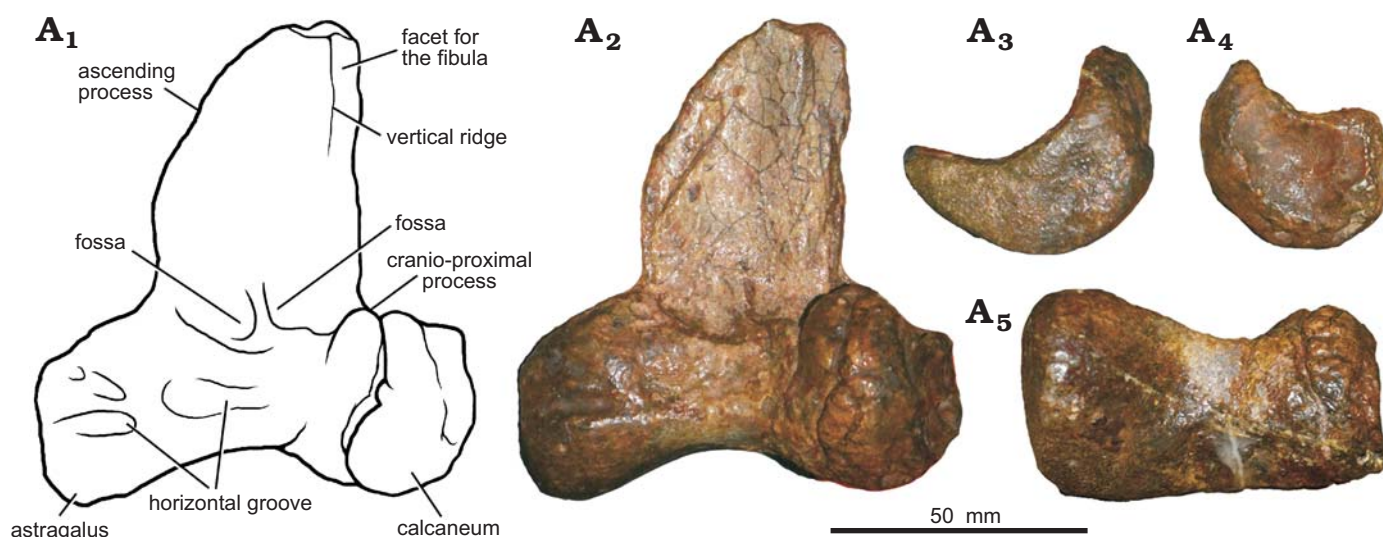


Fig. 17. Coelurosaurian theropod *Vayuraptor nongbualamphuensis* gen. et sp. nov. from the Early Cretaceous Sao Khua Formation of Phu Wat, Nong Bua Lamphu Province, Thailand. SM-NB A1-2, left astragalocalcaneum in anterior (A<sub>2</sub>), medial (A<sub>3</sub>), lateral (A<sub>4</sub>), and distal (A<sub>5</sub>) views; line drawing in anterior view (A<sub>1</sub>).

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 *Juratyran* (Benson 2008; Rauhut 2012; Brusatte 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 astragal 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 astragal 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 horizontal grooves and two foramina at the base of the astragal 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 astragal 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 breadth of the astragal body, and it is more than twice the height of the astragal body (7:2.5). The astragal 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 astragal ascending process looks similar to that of *Australovenator*, *Fukuiraptor*, *Aerosteon*, *Qianzhousaurus* (Lü et al. 2014), *Raptorex* (Sereni et al. 2009), and *Alioram* (Brusatte et al. 2012). Two fossae at the base of the ascending process are present. There is an anteroproximal (= proximolateral) expansion of the astragal 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 observations) than to *Sinraptor* (Currie and Zhao 1993), *Aerosteon* (cast of MCNA-PV-3137; AS personal observations), 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 *Yutyranus* (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* (Apestigueva 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*, *Megaraptor*, 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), *Chuangdongocoelurus* (Rauhut 2012), *Juratyran* (Benson 2008; Rauhut 2012; Brusatte 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), *Erliaensaurus* (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 coelurosaurs (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 astragalus 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 astragalus body and a strong inflection in the anterior margin of the astragalus 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/astragal body height is high in *Vayuraptor* (1.7), *Fukuiraptor* (1.7), *Aerosteon* (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 astragal body (not from its complete width) in *Phuwiangvenator*, *Vayuraptor*, *Australovenator*, *Fukuiraptor*, *Tugulusaurus*, *Bicentenaria*, and *Coelurus*. It arises from the complete width of the astragal body in *Tanycolagreus* and *Aerosteon*. The ratio of the ascending process width at base/astragal body width is low and the ascending process is restricted to the lateral side of the astragal 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 astragal 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 astragal notch for a process from the calcaneum is present in *Aerosteon*, *Phuwiangvenator*, but not *Vayuraptor*. The astragalus has a distinct socket that embraced the mediolateral end of the fibula (Azuma and Currie 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-like 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* (Serenó 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*, *Tugulusaurus*, 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 mediolateral side of the calcaneum. In the evolution from basal theropods to moderately derived coelurosaurs, there is a trend of en-



largement 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* (Serenó 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

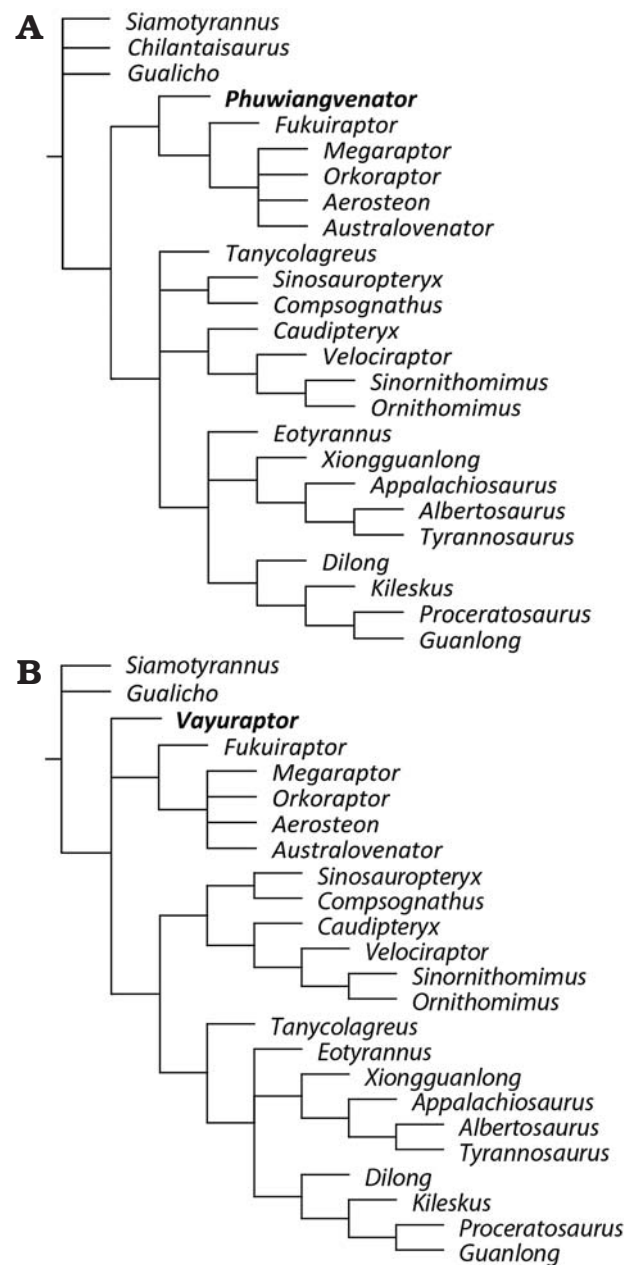


Fig. 18. Strict consensus trees of all the recovered MPTs of the phylogenetic analyses from the present study (modified from Apesteguía et al. 2016). **A.** Data matrix including *Phuwiangvenator yaemniyomi* gen. et sp. nov. **B.** Data matrix including *Vayuraptor nongbualamphuensis* gen. et sp. nov.

is much lower than metatarsal III, does not slope proximolaterally to distomedially.

**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 ornithomimosaurids. 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 astragalus 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 astragalus 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 astragalus 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 astragalus body is present, strong inflexion of the anterior margin of the astragalus 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) astragalus 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 astragal body is present and there is a strong inflexion in the anterior margin of the astragal 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 astragal 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 astragal 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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