A new skeleton of *Phuwiangosaurus sirindhornae* (Dinosauria, Sauropoda) from NE Thailand

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Abstract: A new skeleton of a sauropod dinosaur has been discovered in the Early Cretaceous Sao Khua Formation at Ban Na Khrai in Changwat Kalasin (NE Thailand). All sauropod bones from Ban Na Khrai share all their characteristics with the type specimen of *Phuwiangosaurus sirindhornae* Martin, Buffetaut & Suteethorn 1994. The 60% complete skeleton is very well preserved and includes cranial elements (a tooth, a frontal, a postorbital, a squamosal, both quadrates, and the braincase), whereas the type specimen is only 10% complete and consists of postcranial bones only. The material from Ban Na Khrai belongs to a single subadult individual of *Phuwiangosaurus*, as attested by the unfused neurocentral sutures of the vertebrae, which are firmly fused and larger in size in the holotypic specimen.

Supplementary material: Catalogue numbers of Ban Na Khrai specimens are available at http://www.geolsoc.org.uk/SUP18348.

Thailand has an especially good record of sauropods, with Triassic, Jurassic and Cretaceous fossils from many localities across the country. The first sauropod identified in Thailand was *Phuwiangosaurus sirindhornae* Martin, Buffetaut & Suteethorn 1994 from the Sao Khua Formation (Early Cretaceous). The holotype consists of postcranial elements only and the species was not assigned to a precise sauropod family by Martin et al. (1994). According to cladistic analyses, based on the post-cranial skeleton only, *P. sirindhornae* represents one of the most basal titanosaurs (Upchurch 1998; Upchurch et al. 2004; Curry Rogers 2005). Slender teeth and jaw elements were subsequently discovered associated with *P. sirindhornae* skeletons at Phu Kum Khao (Suteethorn et al. 1995; K4 or ‘Wat Sak Kawan’ locality; see below for details), and were tentatively assigned to this form. They closely resemble those of *Nemegtosaurus mongoliensis* Nowinski 1971, a Late Cretaceous sauropod from Mongolia, thus Buffetaut & Suteethorn (1999) suggested that *P. sirindhornae* belongs to the family Nemegtosauridae. However, more evidence is needed to confirm that this cranial material does belong to *P. sirindhornae* and that this form belongs to the Nemegtosauridae, as it is clear that two different sauropod species are present at Phu Kum Khao (Buffetaut et al. 2002; Buffetaut & Suteethorn 2004). The discovery of a partly articulated skeleton at Ban Na Khrai, representing about 60% of a complete skeleton and including a braincase and cranial elements, provides the first opportunity to confirm the link between cranial and post-cranial elements suggested by Buffetaut & Suteethorn (1999). The objective of this paper is to briefly describe the new sauropod skeleton from Ban Na Khrai and to compare it with the holotype of *P. sirindhornae*.
Abbreviations and Thai vocabulary
CNRS, Centre National de la Recherche Scientifique, France; DMR, Department of Mineral Resources, Bangkok, Thailand; K1–K16, localities in Changwat Kalasin; PW1–PW5, localities in Phu Wiang area, Changwat Khon Kaen; SM, Sirindhorn Museum, Changwat Kalasin, Thailand (the specimens housed at the Sirindhorn Museum are identified by the acronym SM).

In the present paper, the appellations of the localities are in Thai; they consist of specific Thai names and prefixes, including ‘Amphoe’, ‘Changwat’, ‘Wat’, ‘Phu’ and ‘Ban’. The meanings of these words are as follows: ‘Amphoe’ means district (e.g. Amphoe Phu Wiang refers to the district of Phu Wiang); ‘Changwat’ means province (e.g. Changwat Kalasin refers to Kalasin province); ‘Wat’ means temple or monastery (e.g. Wat Sak Kawan refers to the temple named Sak Kawan); ‘Phu’ means mountain or hill (e.g. Phu Kum Khao refers to Kum Khao hill); ‘Ban’ means village (e.g. Ban Na Khrai refers to Na Khrai village).

Historical review of sauropod discoveries in the Sao Khua Formation of Thailand
The first dinosaur bone from Thailand was found in 1976 by S. Yaemniyom, a geologist from the DMR in the course of a uranium survey at Phu Wiang (Amphoe Phu Wiang, Changwat Khon Kaen). It is a fragment of a sauropod femur from the Sao Khua Formation (Ingavat & Taquet 1978; Ingavat et al. 1978). 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 sauropod remains (see Buffetaut et al. 2002, for a recent summary). The Sao Khua Formation has yielded more dinosaur remains than any other formation on the Khorat Plateau, and most of them belong to sauropods. Sauropod remains occur both as more or less complete articulated skeletons in Phu Wiang 1 (PW1), Phu Kum Khao (K4) and Ban Na Khrai (K11) and as accumulations of disarticulated bones (Phu Wiang 5 (PW5), Phu Pha Ngo (K1), Phu Peng (K16)) (Fig. 1).

Changwat Khon Kaen
In 1981, an incomplete sauropod femur was discovered on Phu Wiang (PW1A). The year after, a partly articulated sauropod skeleton associated with theropod teeth was found at PW1 (Fig. 1), a few metres from the first locality (Buffetaut & Suteethorn 1989). This partial skeleton became the type of Phuwiangosaurus sirindhornae Martin, Buffetaut & Suteethorn 1994.

In 1989, seven cervical vertebrae of a sauropod were found in connection at another site on Phu Wiang (PW2). An attempt was made to preserve them in situ, but unfortunately an efficient protection proved impossible and the specimen was almost completely destroyed before it could be studied (Martin et al. 1999).

Fig. 1. (a) Fossil sites that have yielded Phuwiangosaurus sirindhornae plotted on a map of the Cretaceous formations (black areas) of Thailand. (b) Map of Changwat Kalasin, showing the localities that have yielded material of P. sirindhornae. PW1, Phu Wiang 1; K1, Phu Pha Ngo; K2, Ban Nong Mek; K4, Phu Kum Khao; K5, pond at Phu Pha Ngo; K11, Ban Na Khrai; K16, Phu Peng.
In 1990, many small bones were found in a forest on Phu Wiang (PW4) by schoolboys, and given to the Department of Mineral Resources by their teacher. These small bones were the first remains of juvenile sauropods to be found in Thailand (Martin et al. 1993, 1999). Then in 1991 and 1992, more sauropod remains were discovered, including many bones of juveniles (PW5, PW5A). The juvenile sauropods belonged to the same species as the adult remains they were associated with, *P. sirindhornae* (Martin 1994).

**Changwat Kalasin**

In 1980, a sauropod humerus was discovered at Wat Sak Kawan in Amphoe Sahat Sakhan. The monks used to collect archaeological objects and pottery, and they thought that this bone was petrified wood (Martin et al. 1993, and see below).

The first important finds in the Kalasin region were made at Phu Pha Ngo and Phu Kum Khao localities (K1 and K4, respectively). In January 1991, 200 km west of Phu Wiang, the Thai–French team discovered about 40 bones and many other bone fragments at K1 locality near the temple of Wat Pha Sawan, which is located at the foot of Phu Pha Ngo in Amphoe Kuchi Narai. Most of the bones were damaged and broken into small pieces. These bones had been placed there by local workers during the erection of the temple and were thought to be elephant bones. The Thai–French team excavated 60 m² from March to April 1991, and found only 10 more bones, including bone fragments, as well as two crocodile teeth, fish scales, and turtle shell elements. The material from K1 can be assigned to at least three individuals of *P. sirindhornae*, on the basis of identifiable specimens, such as three right pubes (Martin et al. 1999).

In the same year, 10 km south of Phu Pha Ngo, the Thai–French team found a few vertebræ and ribs at Ban Nong Mek locality (K2). Martin et al. (1999) referred these specimens to *P. sirindhornae*. In 2005 the villagers at Ban Nong Mek found more bones, which are kept at Wat Nong Mek. These specimens, including a femur, sacral and caudal vertebræ, belong to *P. sirindhornae*.

In September 1994, geologists from the Department of Mineral Resources discovered a remarkable locality at Phu Kum Khao where fossil bones had first been found by P. V. Sahashkunthe, the head of the monks in Wat Sak Kawan, many years before (see above). The bone-bed is located at the base of Phu Kum Khao. The excavation started on 19 November 1994. More than 600 specimens were discovered in one year. They consist of well-preserved, partly articulated remains of several individuals; jaw elements were found for the first time in association with skeletons of *P. sirindhornae* (Suteethorn et al. 1995; Martin et al. 1999) and a second undescribed sauropod species was also recognized (Buffetaut et al. 2002).

The ‘Phu Kum Khao’ locality (K4) was mentioned as the ‘Wat Sakawan’ or ‘Wat Sak Kawan’ locality according to the transliteration system used, both names referring to the temple name ‘Sak KaWan’ where the fossils were found and placed (Suteethorn et al. 1995; Buffetaut & Suteethorn 1999; Martin et al. 1999). In 1998–1999, the ‘Phu Kum Khao Dinosaur Research Centre’ was established, 200 m from the excavation site (K4), and the name of this site was changed to ‘Phu Kum Khao’, which is the name of the mountain where the excavation site is located (Buffetaut et al. 2002, 2003; Buffetaut & Suteethorn 2004). Since 2002, the Department of Mineral Resources has built a palaeontological museum near the Phu Kum Khao Dinosaur Centre, which houses most of the palaeontological collections of Thailand. The museum opened in 2007 under the name of ‘Sirindhorn Museum’, in honour of Her Royal Highness Princess Maha Chakri Sirindhorn, Princess of Thailand. The material described in the present paper is housed at the Sirindhorn Museum.

Several years after the excavation at K1 locality (Fig. 1), S. Suwantri and villagers at Ban Na Khrai (300 m from K1 on the same hillside and in the same bone-bed layer of the Sao Khua Formation) discovered some bones while digging a pond. At that time a team from the DMR surveyed the site (K5) and found only a few bones. Later, the villagers enlarged the pond to the north of K5 site. They found many bones on the opposite side of the pond 50 m from K5. This new site is referred to as K11. Students brought one of the large bones, a part of a left femur (SM K11-0151), to Wat Pha Sawan. Then in 1998, the Thai–French expedition team went to Wat Pha Sawan and surveyed this site. They found more than 10 bones (one femur, one fibula, one ischium, one rib, and several vertebrae). A 17 day excavation was then begun on 13 March 1998 under the direction of one of us (V. S.), yielding about 100 bones. Remaining bones were collected on 14–17 May 1998, and all the remains were brought to the Dinosaur Research Centre in Phu Kum Khao. This material is described for the first time in the present paper.

Finally, on 15 February 2001, villagers in Ban Na Sombun found some bone fragments on an outcrop of the Sao Khua Formation at the bottom of Phu Peng (K16) and brought them to Wat Phu Peng (Amphoe Sahat Sakhan, Changwat Kalasin). An excavation was undertaken over 10 m² and more than 25 bones were recovered. Most of them belong to one or several adult sauropods and some to a juvenile or small sauropod (Buffetaut et al. 2002). These bones show some differences from *P. sirindhornae* and will be described later.
Geological setting

The specimens from K11 were collected over a 25 m$^2$ excavation area (Fig. 2). The bone-bed layer is 2 m below the ground level. The fossil-bearing layer consists of brownish red sandstone, siltstone and claystone. The layer is interbedded with lime nodule conglomerate. The sediments are characteristic of the Sao Khua Formation of the Khorat Group, which is composed of various cycles of reddish brown silty claystones interbedded with siltstones, fine- to medium-grained sandstones and conglomerates, and caliches, calcrete nodules, and thin-bedded and nodular silcretes (Meesook

Fig. 2. Excavation map of Ban Na Khrai Phuwiangosaurus sirindhornae skeleton (drawing by A. Kumchu). Scale bar: 1 m.
Based on palynological data, Racey & Goodall (2009) gave an Early Cretaceous (Barremian–Aptian) age for the Sao Khua Formation. The red siltstones are floodplain deposits; the area can be interpreted as a wide floodplain environment with low-energy meandering rivers and semi-arid climate with two distinct seasons. This is confirmed by the co-occurrence of articulated dinosaur skeletons or parts of skeletons together with remains of aquatic animals, such as fish scales and fish vertebrae (Buffetaut & Suteethorn 1998; Martin et al. 1999).

Taphonomy

Of 167 labelled specimens from K11, 129 are elements of the axial skeleton that fit in size. Most of them are unfused elements, such as centra, neural arches, and ribs. There are only five cervical vertebrae with fused neural arch and centrum, although their ribs are sometimes unfused. The presence of 11 right cervical ribs, 11 right dorsal ribs and five sacral centra show that this sauropod possessed at least 13 cervical (including atlas and axis), 12 dorsal and five sacral vertebrae (see details below). The K11 specimen has 34 caudal vertebrae (out of a total of more than 54 present in an articulated Phuwiangosaurus skeleton from K4, Phu Kum Khao). There is an important variation in the shape of sauropod vertebrae and it can be demonstrated that there is no overlapping in the vertebrae of K11. Furthermore, the vertebral and pelvic remains were found partly in articulation. There are 11 right dorsal ribs that were still in situ, in the same position as when the sauropod carcass was buried (Fig. 2). The posterior dorsal and sacral centra were connected and the right pelvic girdle (pubis, ischium and ilium) lay below the sacral vertebrae. Most cervical vertebrae and eight skull bones were discovered in the same area but they were not articulated as the sacral vertebrae were. The tail elements were dispersed all over the 25 m² of the excavation, with two concentrations east and west of the sacrum.

In K11 there are two fibulae (one right and one left), two femora (one right and one left), and two ischia (one right and one left) but no extra paired bone (i.e. a third femur, for example). Moreover, all left and right paired bones have the same length, and in all likelihood belonged to the same individual. The preserved parts of the left ribs also fit very well in size and shape with the well-preserved right ribs.

The skeleton from K11 is about 60% complete (167 labelled specimens out of a total evaluated at 284 pieces) (Fig. 3). Based on the absence of extra paired bones, the identical measurements of paired bones, the partial articulation of the dorsal and sacral regions, the limited scattering of the cervical and caudal regions, and the consistency in size of all elements, all the bones most probably belong to a single individual that was lying on its right side.

Scavenging by a theropod dinosaur is attested by the discovery of one theropod tooth (SM K11-0168), which was probably broken when the meat-eater was defleshing the corpse, and also by the presence of tooth marks on specimen SM K11-0092 (Fig. 4). Buffetaut & Suteethorn (1989, p. 80) reported a similar example of theropod teeth associated with a sauropod skeleton at PW1. They suggested ‘the sauropod carcass was exposed for some time on a floodplain surface before it was eventually buried under fine sediment, presumably during a flood. The theropod teeth found among the sauropod bones can safely be interpreted as those of one or several carnosaurs which fed on the carcass (probably contributing to its partial disarticulation) before it was buried. Whether the sauropod was killed by carnosaurs before it was eaten by them, or whether they merely acted as scavengers on the carcass of a sauropod which had died

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Fig. 3. Reconstruction of Phuwiangosaurus sirindhornae Martin, Buffetaut & Suteethorn 1994. Shaded bones represent the material from Ban Na Khrai locality.
from other causes, cannot be determined on the basis of the available data.’ Scavenging and running water possibly were the primary causes of the dispersion of the skeleton from K11. These phenomena could have led to the disappearance of some parts of the skeleton before its burial.

**Systematic palaeontology**

Sauropodomorpha Huene
Sauropoda Marsh
Titanosauria Bonaparte & Coria
*Phuwiangosaurus* Martin, Buffetaut & Suteethorn
**Type species.** Phuwiangosaurus sirindhornae Martin, Buffetaut & Suteethorn 1994

*Phuwiangosaurus sirindhornae* Martin, Buffetaut & Suteethorn

**Holotype.** SM PW1-0001 to SM PW1-0022; partly articulated skeleton including three cervical vertebrae, three dorsal vertebrae, scapulae, left humerus, left ulna, ilia, pubes, ischia, femora, left fibula, coracoid, chevron and rib.

**Referred material.** Most of the abundant sauropod bones found in the Phu Wiang and Kalasin areas, including the baby and juvenile material described by Martin (1994) and Martin et al. (1999). All sauropod specimens from K11 (SM K11-0001 to SM K11-0167) as follows. Cranial elements including SM K11-0001, right frontal; SM K11-0002, right postorbital; SM K11-0003, right squamosal; SM K11-0004, left quadrate; SM K11-0005, right quadrate; SM K11-0006, co-ossified braincase consisting of supraoccipital, exoccipital–opisthotic, prootic, basioccipital and basisphenoid–parasphenoid; SM K11-0007, laterosphenoid–orbitosphenoid; SM K11-0008, an isolated tooth. Postcranial skeleton with partly articulated caudal dorsal and sacral centra lacking two or three cervical vertebrae, cranial dorsal vertebrae, most of cranial and middle caudal vertebrae, forelimbs and distal hind limbs. The catalogue numbers of specimens are available as supplementary material.

**Type locality.** Phu Wiang Site PW1, Sao Khua Formation, northeastern Thailand.

**Age.** Early Cretaceous, Barremian–Aptian (Racey & Goodall 2009).

**Emended diagnosis.** Middle-sized sauropod (15–20 m long); postorbital with short and acute caudal process; hook-shaped squamosal with vertical flat rostral process and L-shaped caudal process; robust quadrate condyle with deep quadrate fossa that faces caudolaterally and a prominent bulge on medial margin; exoccipital with a foot-like structure that participates to the occipital condyle; heart-shaped occipital condyle; paroccipital process extended caudolaterally with rounded distal end; triangular basal tubula flattened with lateral rugose surface; basipterygoid process directed rostroventrally; anterior cervical vertebrae with a very low and wide neural arch; diapophyses and parapophyses very developed lateroventrally; large synapophyses situated low and far from each other, firmly diverging laterally from the centrum; neural spine of the posterior cervical vertebrae widely bifurcated with no median spine; cervical vertebrae with a well-developed system of laminae and cavities; centra of the dorsal vertebrae opisthocoelous with deep pleurocoels; posterior dorsal vertebrae with unforked neural spine; neural spine elongated craniocaudally; long diapophyses directed more dorsally than laterally, nearly reaching the level of the spine; hyposphene–hypantrum system present; elongated scapula with lateral ridge on the proximal extremity at right angle with the shaft, and slight distal expansion; humerus similarly expanded at both ends; anterior blade of the ilium well developed; pubic peduncle of the ilium straight, long and directed at right angle to the direction of the blade; ischiatic peduncle of the ilium faintly marked; pubis with very open angle between the axis of the shaft and the ischiatic border; well-marked curvature of the caudal border of the shaft of the ischium; femur flattened anteroposteriorly with the head situated slightly above the level of the great trochanter; fourth trochanter crest-shaped, located medially above the midlength of the shaft; very large lateral epicondyle at the distal end of the femur; slight lateral bending of the shaft of the fibula.

**Description**

We describe below in some detail the skeletal elements from Ban Na Khrai that provide new information about the osteology of *Phuwiangosaurus sirindhornae*; namely, the skull bones and the vertebral column. Other elements, which do not differ significantly from those already described for *Phuwiangosaurus sirindhornae* on the basis of the type and referred specimens (Martin et al. 1999), such as girdles and limb bones, are alluded to more briefly in the ‘comparison’ section. The nomenclature for vertebral laminae used herein follows Wilson (1999) and Apesteguia (2005).

There are 167 catalogue entries for Ban Na Khrai specimens, including one theropod tooth. Each isolated specimen has received a separate number, for example one disarticulated cervical vertebra consists of four specimens: one centrum, one neural arch and two cervical ribs, and each of them received a separate number. The total number of catalogue entries is different from the field number (156), as some more bones were found during preparation of the plaster jackets. (See online supplementary data.)

**Description of the skull elements from Ban Na Khrai**

**Frontal.** The right frontal SM K11-0001 is well preserved and shows a straight suture line for the left frontal (Fig. 5). The bone is flat and rectangular in shape. In dorsal view its rostral edge is concave and acute rostrolaterally. Its lateral margin is
slightly oblique caudolaterally with its greatest breadth at the caudal end and forms the dorsal rim of the orbit. Its lateral surface is smooth along the frontal and postorbital.

The frontal–nasal contact is obscured by matrix. The prefrontal–frontal contact is an embayment, indicating that the caudal part of the prefrontal is embraced by the frontal as in *Nemegtosaurus* (Nowinski 1971, p. 66; Wilson 2005, p. 298, fig. 7). The caudal part of the frontal contacts the parietal and postorbital. It seems that the frontal does not participate in the supratemporal fossa (see ‘postorbital’ below).

In ventral view the suture with the orbitosphenoid is located in the middle of the frontal. A strong ridge extends rostrolaterally from the rostral part of the frontal–orbitosphenoid suture, separating the orbit from the nasal cavity. The frontal–laterosphenoid suture slopes caudolaterally and interdigitates with the frontal–postorbital suture.

A small convexity is present on the dorsal surface of the frontal caudomedially, corresponding to the rostral part of the endocranial cavity. This condition differs from the doming on the frontal of *Rapetosaurus* (Curry Rogers & Forster 2004, fig. 13), which is more prominent and situated more rostrally than in K11-68A.

Postorbital. The right postorbital SM K11-0002 is a triradiate, T-shaped bone in lateral view, with an elongate ventral process and relatively short rostral and caudal processes (Fig. 6). The lateral surface of the postorbital that forms the margin of the orbit and infratemporal openings is smooth along its length. It differs from that of *Nemegtosaurus*, which is heavily ornamented (Wilson 2005, fig. 7).

The rostral process of the postorbital is flattened dorsoventrally and expands transversely towards its distal end. The distal end of the rostral process contacts the frontal rostrally, the parietal medially and the laterosphenoid ventrally. This interdigitating process separates the orbit from the supratemporal fenestra. Medially, the rostral process has a shallow depression, forming the lateral margin of the supratemporal opening. It appears that the postorbital contacted both ends of the parietal, enclosing the supratemporal opening without the frontal and squamosal.

The caudal process of the postorbital is extremely short and tapers distally to a pointed end, where it contacts the rostral process of the squamosal on its lateral surface. The postorbital–squamosal contact is flat vertically and oriented rostrocaudally (see ‘squamosal’ below). The caudal process of the postorbital separates the supratemporal fenestra from the infratemporal fenestra.

The ventral process of the postorbital is long and thin, compressed rostrocaudally and widened transversely towards its proximal end. The ventral

![Fig. 5. Right frontal (SM K11-0001) of *Phuwiangosaurus sirindhornae* in (a) ventral view and (b) dorsal view.
enc, endocranial cavity; ls, laterosphenoid facet; ns, nasal facet; nsc, nasal cavity; obs, orbitosphenoid facet; orb, orbit; p, parietal facet; po, postorbital facet; prf, prefrontal facet. Scale bar: 5 cm.](image-url)
process is bent toward the orbit and its rostral surface is concave transversely and faces rostrolateral. The postorbital–jugal contact is a socket on the distal portion of the ventral process (Fig. 6). The socket opening faces caudolaterally and occupies one-third of the length of the ventral process. As the lacrimal is not preserved in K11; its contact with the postorbital is unknown.

**Squamosal.** The right squamosal SM K11-0003 is a triradiate element in lateral view, with a hook-shaped rostral process and broad ventral and caudal processes (Fig. 7). The squamosal shaft is plate-like, flat and thin transversely. The smooth rostral margin of the squamosal forms the margin of the infratemporal opening. The rostral process of the squamosal is hook-shaped and projects rostrally. The rostral process bears two facets on its medial surface. A small triangular facet is located on the most rostral part of the medial surface. It is oriented vertically in sagittal plane, contacting the caudal process of the postorbital. This contact differs from the transverse orientation of the postorbital–squamosal contact in *Nemegtosaurus* as noted by Wilson (2005, p. 297). The postorbital–squamosal contact separates the squamosal from the supratemporal opening. The second facet is a large one occupying the dorsal part of the squamosal. It is separated from the squamosal shaft by a ridge that extends from the rostral facet, contacting the caudal process of the parietal.

The ventral process of the squamosal expands distally. The distal end of the ventral process bears a faint articulation, which contacts the quadratojugal. Although the quadratojugal is not preserved in K11, the presence of the quadrate–quadratojugal articulation along the lateral margin of the quadrate fossa (see ‘quadrate’ below) confirms that the quadratojugal reaches the squamosal. SM K11-0003 presents a ‘spur’ on the caudal surface of the ventral process (Fig. 7), a character considered as an autapomorphy of *Nemegtosaurus* by Wilson (2005, p. 297).

The caudal process of the squamosal is separated from the caudal margin of the squamosal shaft by a notch on the lateral surface. Medially, a horizontal ridge originates from the squamosal–quadratojugal contact to the mid-length of the squamosal shaft and bends backwards, forming the lower floor of the caudal process. The caudal process is L-shaped in caudal view, receiving the paroccipital process. Below the ridge where it bends backward, there is a shallow depression or socket that received the dorsal head of the quadrate. This ridge separates the paroccipital process from the quadrate.

**Quadrate.** Both left and right quadrates (SM K11-0004, -0005, respectively) are preserved (Fig. 8). The dorsal head of the quadrate is long.
and thin dorsoventrally. The dorsal head bends backward, perpendicular to the long axis of the quadrate condyle, and forms the articulation at its distal end to attach the squamosal socket (see ‘squamosal’ above).

The quadrate fossa is large, deep and has a triangular shape in caudal view. The quadrate fossa faces caudolaterally relative to the pterygoid flange which was oriented rostrocaudally and look like those of *Nemegtosaurus* and *Quaesitosaurus* (Wilson 2005, figs 9 and 18). A sutural scar is present along the lateral surface of the quadrate from the ventral condyle to the dorsal articulation. This suture contacts the squamosal dorsolaterally and the quadratojugal ventrolaterally.

The pterygoid flange of the quadrate is plate-like, flattened transversely and blunt distally. It is rectangular in lateral view, oriented vertically and rostrocaudally. Medially, the middle portion of the pterygoid flange is depressed and presents a rugose surface. This depression received the palate (pterygoid), which can be seen as a medial bulge in caudal view.

The quadrate condyle is robust and oriented ventrally. In ventral view the articular condyle is kidney-shaped, with a convex caudal margin and slightly concave rostral margin. In caudal view the quadrate condyle is sloped so its facet faces ventrolaterally. The quadrate condyle of K11 is similar to that of *Nemegtosaurus* (Wilson 2005, fig. 11). The shape of the quadrate is similar to that of *Malawisaurus dixeyi* (Gomani 2005, fig. 5), but the quadrate fossa of *Malawisaurus* is oval-shaped and wider transversely.

**Braincase.** The braincase is well preserved and nearly complete, lacking the left laterosphenoid–orbitosphenoid, and the distal end of the parasphe-noid rostrum (Figs 9 and 10). The right laterosphenoid–orbitosphenoid unit (SM K11-0007) is preserved separately from the main body of braincase (SM K11-0006), which is co-ossified and consists of the following elements: supraoccipital, exoccipital opisthotic, prootic, basioccipital, basiophenoid and paraphenoid. These elements can be distinguished by the sutures, except the exoc-cipital–opisthotic, basiophenoid–paraphenoid and laterosphenoid–orbitosphenoid sutures, which cannot be traced.

**Supraoccipital.** The supraoccipital is the most dorsal part of the braincase and forms the dorsal margin of the foramen magnum (Fig. 9). In occipital view the supraoccipital is triangular in shape. The sutures that connect the supraoccipital with the exoccipital–opisthotic complex ventrally and the prootic rostrally are very clear. The parietal contact is marked by a rostromedial groove on the dorsal surface of the supraoccipital.

A vertical median ridge, which is high and prominent dorsally, extended from the dorsal margin of the foramen magnum across the occipital surface of the supraoccipital. As in *Nemegtosaurus*, this supraoccipital ridge can be seen as a small,
Fig. 8. Quadrates of *Phuwiangosaurus sirindhornae*. (a, c, e, g) Left quadrate (SM K11-0004); (b, d, f) right quadrate (SM K11-0005). (a, b) lateral view; (c, d) caudal view; (e, f) medial view; (g) ventral view. dsp, dorsal process; pt, pterygoid facet; ptf, pterygoid flange; qc, quadrate condyle; qf, quadrate fossa; qj, quadratojugal facet; sq, squamosal facet. Scale bar: 5 cm.
triangular process in dorsal view (Wilson 2005, p. 300, fig. 7).

Exoccipital–opisthotic. The exoccipital–opisthotic suture cannot be determined. The exoccipital–opisthotic complex is united with the supraoccipital dorsally, prootic rostrally, basioccipital ventrally, and squamosal laterally (Fig. 9). The ventral footlike structure of the exoccipital forms the lateral and ventral margin of the foramen magnum, which is enclosed by the supraoccipital dorsally. This structure extends backward, participating in the
dorsolateral part of the occipital condyle. The caudal surface of the exoccipital shows the opening for the exit of the hypoglossal nerve (cranial nerve XII) lateral to the occipital condyle.

In lateral view, the exoccipital–opisthotic, basioccipital, basisphenoid, and prootic form the otic region (Fig. 9). The otic region shows two distinctive fenestrae, although covered by matrix; a rostral one, which is rounded and oval-shaped; and a caudal one, which is more expanded dorsoventrally. The rostral one is the fenestra ovalis for the reception of the footplate of the stapes and the caudal one is the metotic foramen through which the glossopharyngeal, vagus and spinal accessory nerves (cranial nerves IX–XI), and the caudal branch of the jugular vein are transmitted (see Chatterjee & Zheng 2005).

The opisthotic forms part of the paroccipital process, which is flattened transversely and expands caudolaterally. The concavity on the

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**Fig. 10.** Right laterosphenoid–orbitosphenoid (SM K11-0007) of *Phuwiangosaurus sirindhornae* in (a) craniolateral view and (b) dorsal view. can, crista antotica; enc, endocranial cavity; f, frontal facet; obs, orbitosphenoid facet; po, postorbital facet; pr, prootic facet; I, foramen for olfactory nerve; II, foramen for optic nerve; III, foramen for oculomotor nerve; IV, foramen for trochlear nerve. Scale bar: 5cm.
dorsal margin of the paroccipital process forms the ventral margin of the post-temporal opening. The distal end of the paroccipital process is rounded, flattened transversely and expands slightly caudoventrally.

**Prootic.** The prootic is a plate-like element (Fig. 9). It faces rostrolaterally and forms the lateral wall of the temporal region. The prootic contacts the supraoccipital caudodorsally, the exoccipital–opisthotic caudally, the basisphenoid and the basisphenoid caudoventrally, and the laterosphenoid rostrally.

The rostral surface presents two foramina nearly parallel to each other, which are referred to the trigeminal nerve (cranial nerve V). The foramina are directed ventrolaterally and enclosed rostrally by the laterosphenoid. The dorsal foramen marks the passage for the maxillary branch of the trigeminal nerve, and the ventral foramen marks the passage for the mandibular branch (Chatterjee & Zheng 2005). The caudal edge of the prootic is sharp and forms the rostral margin of the otic region (see 'exoccipital–opisthotic' above). This edge extends caudally along the opisthotic to the mid-length of the paroccipital process. The prootic expands ventrally, forming a plate-like element, the crista prootica.

**Basioccipital.** The basioccipital forms most of the occipital condyle except the dorsolateral part made by the exoccipitals (see 'exoccipital–opisthotic' above). The occipital condyle projects and faces caudoventrally when the occipital surface of the supraoccipital is oriented vertically (Fig. 9). The articular surface of the occipital condyle is heart-shaped in occipital view, slightly concave dorsally and hemispherical in lateral view. The width of the occipital condyle is twice that of the foramen magnum.

The basal tubera are formed by the basisphenoid rostrally and the basioccipital caudally. The plate-like basal tubera are triangular in shape and project ventrally. The right basal tubera is larger and more prominent than the left one. Although the right basal tubera seems to have an articulation on its lateral margin, it does not contact the quadrat. This condition differs from *Nemegtosaurus* and *Quaesitosaurus*, where the basal tubera articulate with the quadrates (Wilson 2005, figs 9 and 18). The lateral margins of the basal tubera are slightly rugose, particularly on their basisphenoid portion. This irregular surface expands ventrally on the midline down to the posterior face of the basipterygoid processes and may represent an extension for muscle attachment (Curry Rogers & Forster 2004). Four small openings are oriented vertically in sequence between the basal tubera. This is different from *Rapetosaurus*, *Nemegtosaurus* and *Quaesitosaurus*, which have a unique small foramen between the basal tubera (Curry Rogers & Forster 2004, figs 23 and 24; Wilson 2005, fig. 11), and from *Suuwassea*, where the small foramen is referred to the median subcondylar foramen (Harris & Dodson 2004).

**Basisphenoid–parasphenoid.** The basisphenoid–parasphenoid suture cannot be determined. The basisphenoid forms a rostral portion of the basal tubera and the basipterygoid processes (Fig. 9). The basipterygoid processes direct rostrolaterally when the occipital surface is vertically oriented and diverge ventrolaterally at approximately a 30° angle from one another. The basipterygoid processes are subtriangular in cross-section with a prominent ridge along the rostral margin. The length of the basipterygoid process is 3.8 times its basal width. The distal ends of these processes are gently rounded. A smooth, slightly concave, triangular surface occupies the area between the bases of basipterygoid processes and the parasphenoid rostrum. The internal carotid artery opens at the lateral base of the basipterygoid process.

The parasphenoid is represented by the parasphenoid rostrum. The parasphenoid rostrum is flattened transversely and expanded rostrocaudally from the bases of basipterygoid processes. Its distal end is incomplete. At the base of the rostrum, a vertical wall, the *dorsum sella*, extends from the basisphenoid on either sides of the large circular opening (pituitary fossa) to articulate with the orbitosphenoid. The *dorsum sella* is pierced by the opening for the *abducens nerve* (cranial nerve VI) and is similar to that of *Camarasaurus lentus* and *Rapetosaurus* (Curry Rogers & Forster 2004; Chatterjee & Zheng 2005).

**Laterosphenoid–orbitosphenoid.** The laterosphenoid–orbitosphenoid suture cannot be determined. The laterosphenoid–orbitosphenoid unit forms the rostral and lateral wall of the endocranial cavity and the medial wall of the orbit (Fig. 10).

The orbitosphenoid is a plate-like element on the rostral portion of the unit. A median suture separates the orbitosphenoids from one another. A large V-shaped opening of the olfactory nerve (cranial nerve I) passes through the orbitosphenoids rostrally, between the contacts of the frontals and orbitosphenoids. Farther ventrally, a large foramen for the optic nerve (cranial nerve II) exits through the orbitosphenoid just rostral to that of the oculomotor nerve (cranial nerve III). Slightly above the oculomotor foramen, a small foramen for the trochlear nerve (cranial nerve VI) oriented transversely through the laterosphenoid–orbitosphenoid.
The laterosphenoid expands outward and upward, forming a wing-like structure, the crista antotica. The crista antotica interdigitates with the frontal and postorbital, separating the temporal region of the skull from the orbital region (see ‘frontal’ above). Caudally, a rugose surface of the laterosphenoid contacts the prootic, enclosing the parallel foramina for cranial nerve V.

Tooth. A single peg-like tooth SM K11-0008 is preserved (Fig. 11). This tooth was half broken. The upper part of the tooth crown lost some enamel, especially at the wear facet. The lower part of the crown with root is embedded in matrix.

The tooth crown is narrow and tapers toward a blunt apex. There are two wear facets (apical and mesial–distal). The apical wear facet is diagonal and set on the distal end of the crown. The mesial–distal facet is nearly vertical. The ridges on both mesial and distal edges are not prominent. The enamel surface is finely wrinkled throughout the crown.

The tooth crown is slightly D-shaped in cross-section and the apical wear facet on the flattened side (lingual side) of the crown suggests that this crown is an upper tooth, by comparison with the teeth of \textit{Nemegtosaurus mongoliensis} (see details given by Nowinski 1971, p. 71; Wilson 2005, p. 305). In this case, the tooth is lingually curved.

![Fig. 11. Tooth (SM K11-0008) of \textit{Phuwiangosaurus sirindhornae} in (a) lingual view and (b) distal view. awf, apical wear facet; wf, wear facet. Scale bar: 1 cm.](image)

\textbf{Description of the axial skeleton from Ban Na Khrai}

\textit{Cervical vertebrae}. Ten cervical vertebrae have been recovered from K11 (Fig. 12). Their original positions were determined using the relative sizes of the neural arches and/or articulation of the centra (Table 1). The K11 sauropod had probably 13 cervical vertebrae. Eight of the 10 preserved cervical are referable to the cervical C2–C9 and the other two, which are represented by their centra only, are more posterior ones. C5–C9 have fused centra and neural arches. Eleven right cervical ribs are preserved separately from the vertebrae. A comparison with the fused left ribs of C5 and C7 suggests that these ribs belonged to C3–C13. The last cervical rib (C13) presents a distinctive character from the preceding one and from dorsal ribs, the rib shaft being reduced to a short and small, pencil-like process.

The axis (C2, SM K11-0009) preserved only the neural arch and the prezygapophyses are incomplete. The neural arch is low and wide. The diapophysis is directed laterally. The transversal width of the diapophysis is equal to that of the postzygapophyses. A shallow depression is present on the lateral surface of the neural spine dorsal to the diapophyses. In lateral view the prespinal lamina is straight and directed dorso-posteriorly to its greatest height. The postzygapophyses overhang the posterior end of the neural arch. The postzygapophyseal facets are oval, horizontal and flat. The spinopostzygapophyseal lamina diverges and is directed ventroposteriorly to support the postzygapophyses dorsally with a posterior extension, the epiophysis (¼ ‘torus dorsalis’, Ksepka & Norell 2006). The prominent epiophysis projects posteriorly beyond the postzygapophyseal facets.

All the cervical centra are strongly opisthocoelous (Fig. 12). The vertebrae are relatively low and elongate. The centra lengthen from C3 to C8. C8 is the longest centrum, C9 becoming shorter. The articulations of the anterior centra are oval-shaped, flat dorsoventrally, and became more spherical in the succeeding vertebrae. There are two pleurocoels on the lateral surface of the centrum. A shallow depression is present on the ventral surface of the centra between the parapophyses. The ventral keel is not present in cervical centra.

The elongated neural spines are extended anteroposteriorly so that the prezygapophyses overhang the anterior end of the centra whereas the postzygapophyses overhang their posterior ends. The neural spine begins to divide in C7 and the distance between the two neural spines becomes larger in the succeeding vertebrae with no median spine.
Fig. 12. Cervical vertebrae of Phuwiangosaurus sirindhornae. (a, i) Axis (SM K11-0009); (b, c, j, k) cervical 4 (SM K11-0012 and SM K11-0011); (d, l) cervical 5 (SM K11-0013); (e, m) cervical 6 (SM K11-0014); (f, n) cervical 7 (SM K11-0015); (g, o) cervical 8 (SM K11-0016); (h, p, q) cervical 9 (SM K11-0017). (a–h) anterior view; (i–p) lateral view; (q) dorsal view. aap, anterior accessory process; acdl, anterior centrodiapophyseal lamina; cap, capitulum; cprl, centroprezygapophyseal lamina; cpol, centropostzygapophyseal lamina; di, diapophysis; epp, epipophyses; ns, neural spine; pa, parapophysis; pc, pleurocoel; pcdr, posterior centrodiapophyseal lamina; podl, postzygodiapophyseal lamina; poz, postzygapophysis; prdl, prezygodiapophyseal lamina; prz, prezygapophysis; r, rib; spol, spinopostzygapophyseal lamina; sprl, spinoprezygapophyseal lamina; tu, tuberculum. Scale bar: 10 cm.
The dorsal heads of the bifid spines are blunt and thick. The prezygapophyseal facets are oblique relative to the sagittal plane and face anterodorsally in lateral view. The facets of the prezygapophyses and postzygapophyses are flat and oval in outline, wider transversally.

The diapophyses are compressed dorsoventrally and expand anteroposteriorly, supported by the prezygodiapophyseal, posterior centrodiapophyseal and postzygodiapophyseal laminae. The prezygodiapophyseal lamina extends anteriorly beyond the prezygapophyseal facet, forming the accessory anterior process. The prominent plate-like epipophysis extends posteriorly and overhangs the postzygapophyseal facet.

The cervical ribs are longer than the posterior end of the centrum. The capitulum process presents a strong depression on its dorsal surface. A vertical lamina is present between the tuberculum and capitulum processes. The tuberculum–capitulum angle of the rib is acute, so that the rib is hanging lateroventrally to the centrum. The caudal process of the rib is slightly V-shaped in cross-section. The ventral surface of the rib presents a shallow depression and a faint ridge lateroventrally.

Dorsal vertebrae. All dorsal centra and neural arches are unfused (Fig. 13). The K11 sauropod had twelve dorsal vertebrae (Table 2). Eleven of them are preserved. Five of the 11 dorsal (D8–D12) were found articulated with four sacral centra (S1–S4). Three others are anterior dorsals D1, D3 and D4, considering the position of the parapophysis that is located on the centrum and moved dorsally at the level of neural canal in D4, and considering the length of the centrum relative to its width (McIntosh 1990). Twelve dorsal neural spines are preserved. Six anterior dorsal neural arches (D1–D6) were found articulated; the other six posterior dorsal neural arches (D7–D12) were disarticulated. Eleven right dorsal ribs were preserved in situ.

All centra are opisthocoelous. The articulations of the centra are semispherical in the anterior vertebrae and became less prominent, more flattened anteroposteriorly in the succeeding elements. The pleurocoel is a simple large pit. It is circular in D1 and D3, and becomes spindle-shaped in D4–D7; it gradually extends dorsally and becomes drop-shaped in D8–D12. A ventral keel is present on the ventral surface of the centra D3–D7.

The neural arches D1–D5 are relatively low and wide transversally, and the neural spines are divided by a U-shaped cleft. The posterior neural arches are short anteroposteriorly and uniform in height. The first undivided neural spine is D6. The undivided neural spines are short related to the neural arches. The spine is directed dorsally in D12 and slightly inclined dorsoposteriorly in the preceding vertebrae. These spines were supported anteriorly by the prespinal and spinoprezygapophyseal laminae, and posteriorly by the postspinal, spinodiapophyseal and spinopostzygapophyseal laminae. The prespinal and postspinal laminae are present as roughened ridges for interspinous ligaments. In dorsal view, the distal end of the spine D6–D12 expands laterally where the spinopostzygapophyseal lamina joins with the spinodiapophyseal lamina, forming the triangular process (Fig. 13).

The prezygapophyses of the anterior dorsals D1–D4 are situated at the base of the diapophyses and above the level of the diapophyses. Their facets are large, flat horizontally and diverge from each other. The prezygapophyses of the succeeding dorsals D5–D12 move downward and inward and are close to one another, just below the base of the diapophyses. The prezygapophyses and

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**Table 1. Measurements of cervical vertebrae of Ban Na Khrai Phuwiangosaurus sirindhornae**

|   | 1   | 2   | 3   | 4   | 5   | 6   | 7   | 8   | 9   | 10  | 11  | 12  | 13  |
|---|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| C |     |     |     |     |     |     |     |     |     |     |     |     |     |
| GLC | – | – | – | 200 | 215 | 240 | 235 | 270 | 220 | 180* | – | – | 200 |
| HA | – | – | – | 30  | 35  | 40  | 50  | 56  | 65  | – | – | – | 85 |
| WA | – | – | – | 45  | 70  | 70  | 90  | 89  | 95  | – | – | – | 140 |
| HC | – | – | – | 40  | 45  | 60  | 70  | 70  | 90  | 100 | – | – | 95* |
| WC | – | – | – | 60  | 80  | 90  | 110 | 100 | 125 | 145 | – | – | 145 |
| LPRZ | – | – | – | 55  | 80  | 80  | 100 | 90  | 120 | – | – | – | – |
| LPOZ | – | – | – | 66  | 80  | 90  | 100 | 100 | 155 | – | – | – | – |
| LNS | – | 115 | * | 240 | 290 | 308 | 315 | 340 | 270 | – | – | * | * |
| TH | – | 60* | * | * | 130 | 140 | 160 | 180 | 200 | * | * | – | – |

Measurements in millimetres. C, cervical; GLC, greatest length of centrum; HA, height of articulation; WA, width of articulation; HC, height of centrum at posterior; WC, width of centrum at posterior; LPRZ, length between prezygapophyses; LPOZ, length between postzygapophyses; LNS, length of neural spine; TH, total height.

*Incomplete.
Table 2. Measurements of dorsal vertebrae of Ban Na Khrai Phuwiangosaurus sirindhornae

|   | 1     | 2     | 3     | 4     | 5     | 6     | 7     | 8     | 9     | 10    | 11    | 12    |
|---|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| GLC | 185   |       | 105   | 160   | 160   | 130   | 160   | 150   | 140   | 145   | 135   | 130   |
| WC  | 135   | –     | 140   | 90    | 105   | 110   | 115   | 120   | 120   | 135   | 120   | 130   |
| LNS |       | –     | –     | –     | –     | –     | –     | –     | –     | –     | –     | *     |
| HNS |       | –     | –     | –     | –     | *     | *     | 160   | 150   | 150   | 160   | 150   |

Measurements in millimetres. D, dorsal; GLC, greatest length of centrum; WC, width of centrum at posterior; LNS, length of neural spine; HNS, height of neural spine.
*Incomplete.
postzygapophyses are oriented obliquely in D7 and gradually inclined to horizontal in D12.

The hyposphene–hypantrum system is present on D7–D12. It cannot be observed on the articulated specimen and the posterior part of D6 is incomplete. The hypantrum is limited by the closely placed prezygapophyses and centroprezygapophyseal laminae. The hyposphenes of D7–D10 are developed at the connection of the postzygapophyses and are buttressed ventrally by the paired medial centropostzygapophyseal laminae. Those of D11 and D12 are buttressed by a single medial centropostzygapophyseal lamina (Apesteguía 2005).

The diapophyses are flattened dorsoventrally and directed laterally in the anterior dorsals. They became rounded and directed dorsolaterally in the posterior dorsals. The diapophyses of the posterior dorsals are buttressed by five laminae, the prezygodiapophyseal, spinodiapophyseal, postzygodiapophyseal, paradiapophyseal and posterior centrodiaipophyseal laminae (Fig. 13).

The parapophyses of D7 are situated at the level of the prezygapophyses, anteroventral to the diapophyses, which migrate to a more ventral position in the succeeding dorsals. The articular facets of the parapophyses are subcircular to oval-shaped from D7 to D12; they are elongated dorsally and smaller in the last vertebrae. The parapophyses of the posterior dorsal are buttressed by four laminae, the prezygaparapophyseal, paradiapophyseal, anterior and posterior centroparapophyseal laminae.

Eleven right dorsal ribs were preserved in situ. The proximal head of the anterior ribs is large and flat. It is smaller and rounder in the posterior ribs. The capitulum processes project at right angles to the long axis of the rib in D2–D7; then they are slightly curved along their axis in D8–D12. The tuberculum processes are short and blunt with a depression on the lateral surface of the processes.

**Sacral vertebrae.** Four articulated sacral centra and four co-ossified neural arches are considered as the sacrals S1–S4 (Table 3, Fig. 14). An unfused centrum and neural spine present characteristics of both sacrals and caudals, and we regard them as a caudosacral or last sacral S5. Six sacral ribs are preserved, including four right ribs and two left (Fig. 15). The numbers of preserved centra and neural arches and the shapes of sacral ribs, especially the distal part that contact the ilium, suggest that K11 sauropod had five sacral vertebrae, as noted by Martin et al. (1999, p. 65) for *Phuwiangosaurus sirindhornae*.

All sacral centra are amphiplatyan. A small pneumatic fossa is present on the lateral surface of S1–S4 just anterior to the parapophyses and vanishes in S5. The anterior articulations of the centra are rounded; trapezoid-shaped in S2 and S3; rectangular in S4; slightly oval, wider dorsoventrally in S5. The posterior articulation of S5 is flat and circular, which is similar to that of the caudal centrum.

The co-ossified neural spines of S1–S4 are compressed laterally. The heights of the spines are nearly the same as those of the posterior dorsals (Table 2). The neural spines of S1–S4 are well-developed laminae, very thin transversely and blunt at the distal end. That of S5 thickens transversely through the spine without the blunt end. The diapophyses of S1 and S2 are directed laterally. The parapophyses move down to the centrum, inserting both on the centrum and neural arch.

The sacral ribs are triradiate elements in S1–S4; S5 sacral rib is rectangular (Fig. 15). The proximal parts that contact the vertebrae are plate-like and thin transversely. The distal parts are robust and oriented horizontally in S1–S3, vertically in S4 and S5. The distal ends of S1–S5 connect to each other, forming the sacrocostal yoke that contacts the acetabulum. The attachment scar for the sacrocostal yoke can be seen on the medial side of the ilium, and is restricted to the distal part of the acetabulum.

**Caudal vertebrae.** A few poorly preserved proximal caudal vertebrae were recovered. Most of the preserved centra and neural arches are unfused (Table 4, Fig. 16). The amphicoelous centra are short anteroposteriorly relative to their height. The anterior and posterior articulations of the centra are circular in shape. The lateral surface of the centrum is strongly concave anteroposteriorly. The chevron facet is not present on the most proximal caudal CA1 and CA2. The neural arch of CA1 is flattened anteroposteriorly and its spine is flattened transversely. The spine of CA1 presents roughened ridges on its anterior and posterior surfaces. The neural spines of proximal caudal are slightly curved posteriorly. The prezygapophyseal facets are nearly vertical, corresponding to the postzygapophyses. The transverse processes are situated at the level of the neural canal and directed lateroposteriorly.

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**Table 3. Measurements of sacral vertebrae of Ban Na Khrai Phuwiangosaurus sirindhornae**

|   | S   | 1   | 2   | 3   | 4   | 5   |
|---|-----|-----|-----|-----|-----|-----|
| S | GLC | 110 | 125 | 115 | 125 | 90  |
|   | WC  | 170 | 135 | 125 | 100 | 135 |
|   | HNS | 275 | 280 | 280 | *   | 140 |

Measurements in millimetres. S, sacral; GLC, greatest length of centrum; WC, width of centrum at posterior; HNS, height of neural spine.

*Incomplete.*
The middle caudal centra are amphiplatyan, nearly rectangular in lateral view. The ventral surfaces are flat and present a faint longitudinal ridge. The chevron facets are marked posteriorly and triangular in shape. The neural spines are very thin transversely and extended posteriorly; the postzygapophyses overhang the posterior margin of its centrum.

The distal caudal centra become amphiplatyan and biconvex in the most distal caudals (Fig. 17). Their centra are elongated anteroposteriorly. In anterior view the articular face of the centrum is sub-rectangular in outline.

Sixteen chevrons are preserved. The proximal facets are not confluent. The chevron blades are flat transversely and curved caudoventrally. The chevron blades are shorter in the posterior elements. The most posterior chevron blades are L-shaped in lateral view.

Comparison with the holotype of *Phuwiangosaurus sirindhornae* Martin, Buffetaut & Suteethorn 1994

The holotype of *Phuwiangosaurus sirindhornae* from Phu Wiang (PW1) is a partly articulated skeleton consisting of cervical vertebrae, dorsal vertebrae, pelvic girdle, left scapula, coracoid, left humerus, left ulna, both femora, left fibula, chevrons and ribs. Two more bones were found later: a posterior dorsal vertebra and an anterior caudal vertebra (Suteethorn et al. 2009).
Martin et al. (1999) emended the diagnosis of the type as follows: (1) middle-sized sauropod (15–20 m long); (2) anterior cervical vertebrae with a very low and wide neural arch; (3) diapophyses and parapophyses very developed lateroventrally; (4) large zygapophyses situated low and far from each other, firmly diverging laterally from the centrum; (5) neural spine of the posterior cervical vertebrae widely bifurcated with no median spine; (6) cervical vertebrae with a well-developed system of laminae and cavities; (7) centra of the dorsal vertebrae opisthocoelous with deep pleurocoels; (8) posterior dorsal vertebrae with unforked neural spine; (9) neural spine elongated craniocaudally; (10) long diapophyses directed more...
dorsally than laterally, nearly reaching the level of the spine; (11) hypophyse–hypaptrum system present; (12) elongated scapula with lateral ridge of the proximal extremity at right angle with the shaft, and slight distal expansion; (13) humerus similarly expanded at both ends; (14) anterior blade of the ilium well developed; (15) pubic peduncle of the ilium straight, long and directed at right angles to the direction of the blade; (16) ischiatic peduncle of the ilium faintly marked; (17) pubis with very open angle between the axis of the shaft and the ischiatic border; (18) well-marked curvature of the caudal border of the shaft of the ischium; (19) femur flattened anteroposteriorly with the head situated slightly above the level of the great trochanter; (20) fourth trochanter crest-shaped, located medially above the mid-length of the shaft; (21) very large lateral epicondyle at the distal end of the femur; (22) slight lateral bending of the shaft of the fibula.

Among these characters, important apomorphies of the taxon are: (3) diapophyses and parapophyses very developed lateroventrally; (5) neural spine of the posterior cervical vertebrae widely bifurcated with no median spine; (8) posterior dorsal vertebrae with unforked neural spine; (15) pubic peduncle of the ilium straight, long and directed at right angles to the direction of the blade; (16) ischiatic peduncle of the ilium faintly marked; (18) well-marked curvature of the caudal border of the shaft of the ischium; (21) very large lateral epicondyle at the distal end of the femur. Upchurch et al. (2004), however, retained only two diagnostic characters for *P. sirindhorneae*: cranial cervicals with low, wide neural arches and transverse widths of the proximal and distal ends of the humerus subequal. Those
workers mentioned that the other ‘diagnostic’ characters listed by Martin et al. (1994, 1999) have a wider phylogenetic distribution among sauropods. The holotype skeleton is only 10% complete whereas the skeleton from K11 is about 60% complete and much better preserved. However, the skeleton from K11 is a small individual compared with the type; for example, the femur of the type specimen (SM PW1-0016) is 25% longer than that of the K11 specimen (SM K11-0152).

**Skull**

PW1 and K11 have both yielded a single sauropod tooth. The specimen from PW1 is a half tooth preserved in longitudinal section and embedded in matrix. It is long and slender. The tooth from K11 is better preserved. Its shape is similar to that of the tooth from PW1.

**Axial skeleton**

The cervical vertebrae of the sauropod from K11 are very well preserved. SM K11-0013 and SM K11-0014 are very similar to each other, SM K11-0014 being larger than SM K11-0013. These cervical vertebrae share their characteristics with SM PW1-0001 (Fig. 18). The centra are strongly opisthocoelous and elongated craniocaudally. The hemispherical articular surface of the centrum of SM K11-0013 is similar to that of SM PW1-0001, which is more flattened dorsoventrally than in SM K11-0014. The neural arches are low and wide. Diapophyses and parapophyses are very developed lateroventrally. The prezygapophyses and postzygapophyses of the K11 vertebrae are more complete than in the type and show additional developed spines; one is below the prezygapophyseal facet (the accessory anterior process) and another is above the postzygapophyseal facet (the epipophysis). These elements cannot be observed on the holotype because of breaks but can be observed on the juvenile specimen SM PW5A-0042 (Martin 1994).

The shape of the middle cervical vertebra SM K11-0017 is similar to that of the type SM PW1-0002 (Fig. 19). The centrum is elongated and strongly opisthocoelous with a hemispherical cranial articular surface. The neural spine is relatively high. The neural spine of SM K11-0017 is divided in the same way as in SM PW1-0002, but the latter is situated lower than the postzygapophyses. The postzygapophyseal facet of SM PW1-0002 is larger than in SM K11-0017 and more oblique dorsally. The position of the neural spine and the orientation of postzygapophyses in SM PW1-0002 suggest that it is located more caudally in the vertebral column than SM K11-0017.

The centrum SM K11-0020 and neural arch SM K11-0021 share several characteristics with SM PW1-0003, which can be considered as a posterior cervical or an anterior dorsal. The anterior articular surface of the centrum is hemispherical. The centrum is compressed dorsoventrally in lateral view. On the right lateral surface the parapophyses are situated cranially in the ventral half of the lateral surface of the centrum. The neural spine is divided, with a U-shaped cleft in anterior view. The blade of the neural spine is swollen, thin

![Fig. 18. Comparison of cervical vertebrae of Phuwiangosaurus sirindhornae between the type and Ban Na Khrai specimens. (a, b) Cervical 5 of the type specimen (SM PW1-0001); (c, d) cervical 5 of Ban Na Khrai specimen (SM K11-0013). (a, c) Anterior view; (b, d) left lateral view. Scale bar: 10 cm.](image-url)
cranially and becomes thicker posteriorly with a posterolateral curve. The spine is higher than the postzygapophyses. The neural spine of SM K11-0021 is close to that of SM PW1-0003. SM PW1-0003 is characterized by a very tall neural spine and a deep bifurcation of this spine, which differs from SM K11-0021 and the more posterior spines from K11. This difference probably results from the different position in the vertebral column and from a differential compression (dorsoventral in SM K11-0021 and transversal in SM PW1-0003).

The posterior dorsal neural arches SM K11-0038 and SM K11-0042 present the same characters as the neural arches SM PW1-0006 and SM PW1-0023 (topotype) (Suteethorn et al. 2009), respectively (Fig. 20). The spine is unforked. The prezygapophyses are flat and close to each other. Parapophyses are at the same level as the prezygapophyses. The long diapophyses are flattened craniocaudally. The dorsal vertebrae from K11 are well preserved but all neural arches and centra are unfused, which is probably linked to the fact that the sauropod from K11 is a young individual.

Pelvic girdle and appendicular skeleton

The pelvic girdle and the appendicular skeleton of the specimen from K11 present the same shape as the homologous bones from the type of Phuwiangosaurus sirindhornae (PW1).

The right ilium SM K11-0147 is well preserved. The preacetabular process tapers and projects laterally. The pubic peduncle of the ilium is straight, long and directed at right angles to the direction of the blade. The ischiatic peduncle of the ilium is faintly marked. SM K11-0147 shares these characteristics with SM PW1-0011 but it is smaller.

The right pubis SM K11-0148 is well preserved. The iliac peduncle is broadly expanded into a large blade. The ischiatic peduncle is elongated and tapers

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**Fig. 19.** Comparison of cervical vertebrae of *Phuwiangosaurus sirindhornae* between the type and Ban Na Khrai specimens. (a, b) Cervical 10 (?) of the type specimen (SM PW1-0002); (c, d) cervical 9 of Ban Na Khrai specimen (SM K11-0017). (a, c) Right lateral view; (b, d) anterior view. Scale bar: 10 cm.
caudally. The obturator foramen is completely enclosed in the bone. SM K11-0148 has exactly the same characteristics as the right pubis SM PW1-0013.

Both ischia, SM K11-0149 (left) and SM K11-0150 (right), are well preserved. The pubic peduncle of the left ischium is incomplete. They have the same characteristics as SM PW1-0014 (left) and SM PW1-0015 (right), with a well-marked curvature of the caudal border of the shaft. The right femur SM K11-0151 is damaged whereas the left one (SM K11-0152) is very well preserved. The head is situated above the level of the greater trochanter. The shaft of the femur is flattened craniocaudally. The fourth trochanter, directed medially, is situated on the medial edge of the shaft above mid-length of the femur. Two developed epicondyles are separated by a wide groove. The medial condyle is larger transversally than the lateral one and very prominent. Both femora from K11 share these characteristics with SM PW1-0016 (left) and SM PW1-0017 (right).

Both fibulae, SM K11-0153 (left) and SM K11-0154 (right), are well preserved. In proximal view the proximal end of the fibula is expanded craniocaudally. The medial edge presents a sigmoid curvature, concave cranially and convex caudally. The cranial ridge is thin and expanded to the middle of the fibula, forming a shaft. The distal end is triangular in distal view, flat caudally and points cranially. Both fibulae from K11 present the same characteristics as SM PW1-0018.

Discussion and conclusion

In all characters observable in both specimens, the skeleton from K11 matches the type specimen of Phuwiangosaurus sirindhornae. We thus conclude that this sauropod does belong to the species P. sirindhornae. The difference in size is linked to a difference in age. Klein & Sander (2009) have suggested that there is a general correlation between bone size (body size) and ontogenetic stage (age) in P. sirindhornae. Based on the unfused vertebrae and the structure of the bone tissue, those workers interpreted the P. sirindhornae skeleton from K11 as a young or subadult (ontogenetic stage 7 out of 13 of Klein & Sander) whereas the type is nearly a fully grown adult (ontogenetic stage 12 out of 13). We can also conclude that the skull elements from K11 do belong to P. sirindhornae.
as all the described bones belong to a single individual.

The skeleton of *P. sirindhornae* from K11 is very well preserved and the bones represent almost 60% of this sauropod skeleton. The cranial elements of *P. sirindhornae* show close resemblances to those of the Late Cretaceous *Nemegtosaurus* (Nowinski 1971) from Mongolia. They share a postorbital–squamosal contact vertically oriented, a squamosal with spur, quadrate condyle facing ventrolaterally, and peg-like teeth with high-angled apical wear facet. Unfortunately, the postcranial skeleton of *Nemegtosaurus* is unknown. The postcranial skeleton of *P. sirindhornae* represents that of a basal titanosaur, more derived than *Brachiosaurus* but more primitive than Malawisaurus, following Upchurch *et al.* (2004) and Curry Rogers (2005).

In the near future a phylogenetic analysis of *P. sirindhornae* will thus be complemented with new information drawn from the skeleton from K11 and information from the nearly complete skeleton of the derived titanosaur *Ampelesaurus atacis* (Le Loeuff 1995) from southern France. This should shed light on the early stages of the evolutionary history of the group of Cretaceous Asian sauropods to which *Phuwiangosaurus* belongs.

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