First Evidence of a Mamenchisaurid Dinosaur from the Upper Jurassic-Lower Cretaceous Phu Kradung Formation of Thailand

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First evidence of a mamenchisaurid dinosaur from the Upper Jurassic–Lower Cretaceous Phu Kradung Formation of Thailand

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An isolated posterior cervical vertebra of a sauropod discovered at Phu Dan Ma (Kalasin Province, northeastern Thailand) is the first informative postcranial specimen from the Phu Kradung Formation, a Upper Jurassic to Lower Cretaceous continental unit. The vertebra is referred to the family Mamenchisauridae, otherwise mainly known from China. In addition, spatulate teeth from the same formation and a mid-dorsal vertebra from the Upper Jurassic Khlong Min Formation of southern Thailand are reassigned to this family. The occurrence of mamenchisaurids in the earliest Cretaceous of Thailand supports a hypothesis of geographical isolation of Central, Eastern, and Southeast Asia during the Late Jurassic. It also suggests that the main changes in their dinosaur assemblages occurred during the Early Cretaceous, rather than at the Jurassic–Cretaceous boundary.

Key words: Dinosauria, Mamenchisauridae, Jurassic, Cretaceous, Thailand.

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Introduction

The vertebrate assemblages of Thailand in the Late Jurassic–Early Cretaceous were diverse and widespread through the northeastern and northern regions, and only a few elements have been found in the southern peninsula (Buffetaut and Suteethorn 1998b; Buffetaut et al. 2003; Cavin et al. 2007; Cuny et al. 2007). Fossils are known from the Phu Kradung Formation on the Khorat Plateau of the Indochina Block (Buffetaut and Ingavat 1980; Buffetaut and Suteethorn 1998a, 2007; Buffetaut et al. 2001; Tong et al. 2006) and the Khlong Min Formation on the Shan-Thai Block (Buffetaut et al. 1994, 2005; Tong et al. 2002). Although the age of the Phu Kradung Formation is controversial, its vertebrate fauna is similar to those from the Late Jurassic of China (Buffetaut et al. 2006). Previously known informative sauropod material consists of isolated teeth from the Phu Kradung Formation (Buffetaut and Suteethorn 1998a) and a vertebra from the Khlong Min Formation (Buffetaut et al. 2005). They were interpreted as euhelopodids, but the validity of this family has recently been challenged (Wilson and Sereno 1998; Wilson 2002; Canudo et al. 2002; Wilson and Upchurch 2009).

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In 2004, Pha Kru Pariyatti Thummarakkit, the head of the monks at the temple Sum Nak Song Rakkit Thumma Wiwek, discovered some dinosaur bones on the hill of Phu Dan Ma (locality KS26) in Kuchi Narai District (Kalasin Province; northeastern Thailand) and reported this discovery to the Department of Mineral Resources (DMR) in Bangkok. In August 2004, a DMR team examined several dinosaur bones and bone fragments that had been collected by the monks. These bones included theropod teeth, fragments of sauropod limb bones, teeth and osteoderms of crocodiles, and turtle shells. A complete vertebra of a sauropod dinosaur was kept in situ. It was excavated and is now housed in the Sirindhorn Museum collections in Sahat Sakhan District, Kalasin Province. We report here the discovery of a well-preserved sauropod vertebra from the Phu Kradung Formation and provide some biogeographical hypotheses.

Institutional abbreviations.—C, National History Museum of Chongqing, Chongqing, China; CCG V, "Chengdu College of Geology" now "Chengdu University of Technology", Sichuan Province, Chengdu, China; DMR, Department of Mineral Resources, Bangkok, Thailand; PUM.R, Paleontological Museum of Uppsala University, Uppsala, Sweden; SM MD, Sirindhorn Museum, Kalasin Province, Kalasin, Thaialnd; SDRC KB, Sahatsakhan Dinosaur Research Centre, Kalasin Province, Kalasin, Thailand; SM KS, Sirindhorn Museum, Kalasin Province, Kalasin, Thailand; T, Zigong Dinosaur Museum, Sichuan Province, Zigong, China; ZDM, Zigong Dinosaur Museum, Sichuan Province, Zigong, China.

Other abbreviations.—EI, Elongation Index.

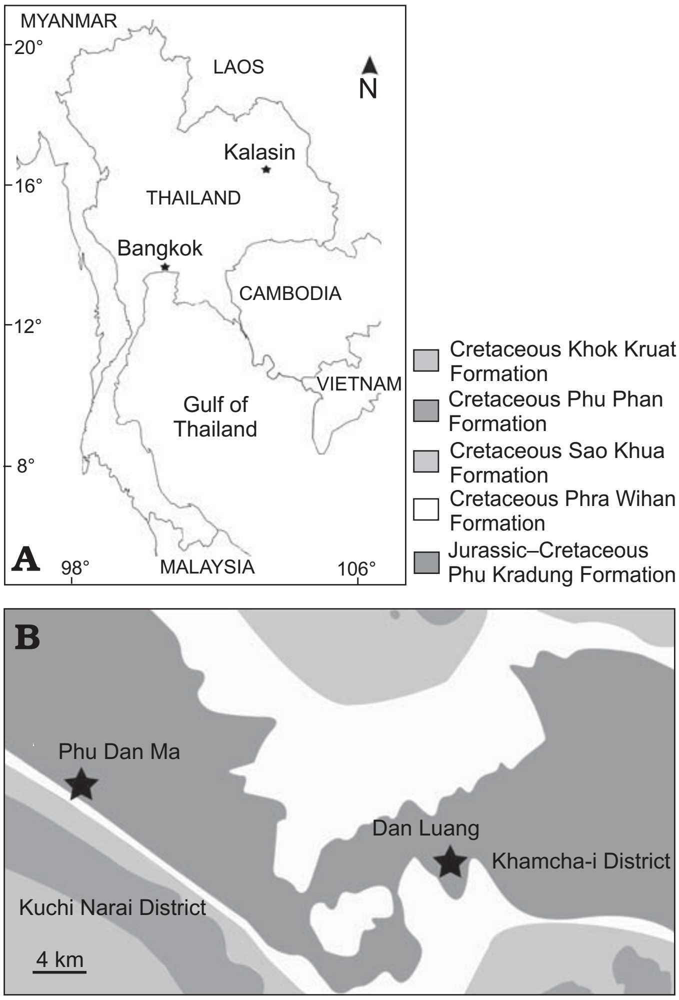

Fig. 1. **A**. Location of the study area on the map of Thailand. **B**. A map of sauropod distribution in the Late Jurassic–Early Cretaceous, Phu Kradung Formation of the Kalasin-Mukdahan region, northeastern Thailand; Phu Dan Ma in Kuchi Narai District, Kalasin Province and Dan Luang in Khamcha-i District, Mukdahan Province.

Geological setting

The Phu Dan Ma locality is in the uppermost part of the Phu Kradung Formation near a conformable contact with the overlying Phra Wihan Formation (Fig. 1). Racey et al. (1996) noted that the contact between the Phu Kradung and Phra Wihan formations is fairly gradational and that it is not easy to define this limit in the field. It is thus not unlikely that the bone beds of the Phu Kradung Formation can be considered as belonging to the basalmost part of the Phra Wihan Formation. The Phu Kradung Formation is a unit of the non-marine Mesozoic Khorat Group. Its thickness varies from 800 to 1200 m. This unit is composed of brown siltstone, claystone, sandstone, and conglomerate beds. In its upper part claystone and calcrete nodules, caliches and nodular silcretes are found (Meesook et al. 2002). The uppermost part contains cycles of fining-upward sequences: cross-bedded sandstone, fine-laminated sandstone, and massive mudstone (Horiuchi et al. 2008); the cycles suggest deposition in a meandering river system. Meesook (2000) noted that the vertebrate remains are usually found in channel conglomerate intercalated in massive mudstone units, considered as floodplain deposits (Racey et al. 1996; Meesook 2000). The specimen from Phu Dan Ma was found in greenish to grey conglomeratic sandstone with calcretes (indicating a subhumid to arid climate) overlying the sequence of mudstone and claystone interbedded with siltstones where dinosaur teeth and turtle shells were found.

The age of the Phu Kradung Formation is controversial. It has yielded abundant vertebrates, including the crocodilian *Sunosuchus thailandicus* Buffetaut and Ingavat, 1980, temnospondyl amphibians (Buffetaut et al. 1994), cryptodiran turtles (Tong et al. 2006), including the large trionychoid *Basilochelys macrobios* (Tong et al. 2009), and the tibia of a sinraptorid theropod (Buffetaut and Suteethorn 2007); the fauna is generally similar to those from the Late Jurassic of Sichuan and Xinjiang, China (Buffetaut and Suteethorn 1998b; Buffetaut et al. 2003, 2006). Le Loeuff et al. (2002) noted that many of the vertebrate sites are located at the top of the thick Phu Kradung Formation and that its vertebrate assemblages show resemblance to the ichnological faunas of the overlying Lower Cretaceous (?Neocomian) Phra Wihan Formation. These authors suggested that the uppermost part of the Phu

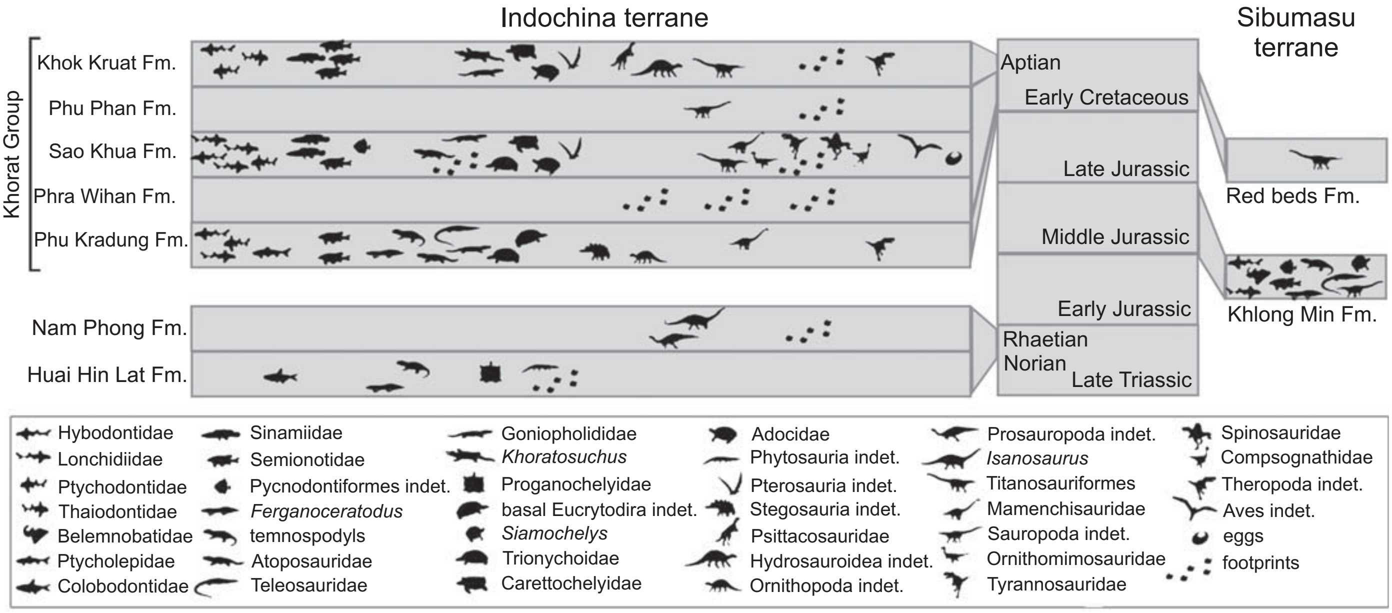

Fig. 2. Distribution of main groups of vertebrates in the non-marine formations of Thailand (courtesy of Lionel Cavin, Muséum d'Histoire Naturelle, Geneva). Fm., Formation.

Kradung Formation might be basal Cretaceous rather than Late Jurassic in age, a hypothesis supported by Racey and Goodall (2009) on the basis of palynological evidence (see Buffetaut and Suteethorn 2007 for discussion). New studies of the stratigraphy of dinosaur beds in the Khorat Group are needed to clearly understand the Phu Kradung-Phra Wihan contact and correlate the vertebrate assemblage and palynological evidence. In the present stage of knowledge a latest Jurassic or earliest Cretaceous age is likely for the Phu Kradung Formation.

Systematic palaeontology

Dinosauria Owen, 1942

Sauropoda Marsh, 1878

Mamenchisauridae Young and Zhao, 1972

Diagnosis.—Posterior cervical vertebrae of mamenchisaurids can be diagnosed by their bifid neural spine with a U-shaped cleft and no median tubercle; the centrum and neural spine are entirely filled with numerous small pneumatic camellae (cancellous inner structure); the centra show large pleurocoels with successive generations of smaller chambers.

Remarks.—The family Mamenchisauridae was erected by Young and Zhao (1972) to include the genus *Mamenchisaurus*. It was generally considered as a junior synonym of the family Euhelopodidae Romer, 1956 (= Helopodidae Wiman, 1929), which included most of the Middle Jurassic to Early Cretaceous Chinese sauropod taxa, such as *Euhelopus*, *Omeisaurus*, and *Mamenchisaurus* (He et al. 1988; Upchurch 1995, 1998; Buffetaut et al. 2005). A recent phylogenetic analysis by Wilson and Upchurch (2009) concludes that *Euhelopus* belongs to the Titanosauriformes (see also Wilson and Sereno 1998 and Wilson 2002). According to this interpretation, the family Euhelopodidae may include Asian and European Early Cretaceous sauropods (Canudo et al. 2002; Wilson and Upchurch 2009) but does not include *Mamenchisaurus* and *Omeisaurus*.

After denying the validity of a monophyletic Asian sauropod clade uniting *Euhelopus*, *Mamenchisaurus*, and *Omeisaurus* in the family Euhelopodidae (cf. Dong et al. 1983; He et al. 1988; Upchurch 1995, 1998; Martin-Rolland 1999; Buffetaut et al. 2002, 2005; Upchurch et al. 2004a), Wilson (2002) erected the family Omeisauridae to name a node including *Omeisaurus* and *Mamenchisaurus.* We consider Omeisauridae (Wilson 2002) as a junior synonym of Mamenchisauridae Young and Zhao, 1972. Lü et al. (2008) later assigned *Eomamenchisaurus yuanmouensis* from the Middle Jurassic of Yunnan Province, China to the Mamenchisauridae, although its synapomorphic characters are ambiguous. *Eomamenchisaurus* shares some characters with *Omeisaurus*, such as: slightly opisthocoelous to amphicoelous dorsal centra; pubic peduncle situated at middle part of ilium; length ratio of tibia to femur about two-thirds. The family Mamenchisauridae (= Omeisauridae Wilson 2002) is a member of Eusauropoda, and comprises Asian sauropod taxa from the Middle Jurassic to the earliest Cretaceous such as *Omeisaurus*, *Eomamenchisaurus, Mamenchisaurus*, and Thai specimens (He et al. 1988; Ouyang and Ye 2002; Lü et al. 2008). The group of Somphospondyli comprising *Euhelopus zdanskyi* Wiman, 1929; *Erketu ellisoni* Ksepka and Norell, 2006; *Dongbeititan dongi* Wang, You, Meng, Gao, Cheng, and Liu, 2007; cf. *Euhelopus* sp. Barrett and Wang, 2007; *Daxiatitan binglingi* You, Li, Zhou, and Ji, 2008 from the Early Cretaceous of China and Mongolia, and probably some

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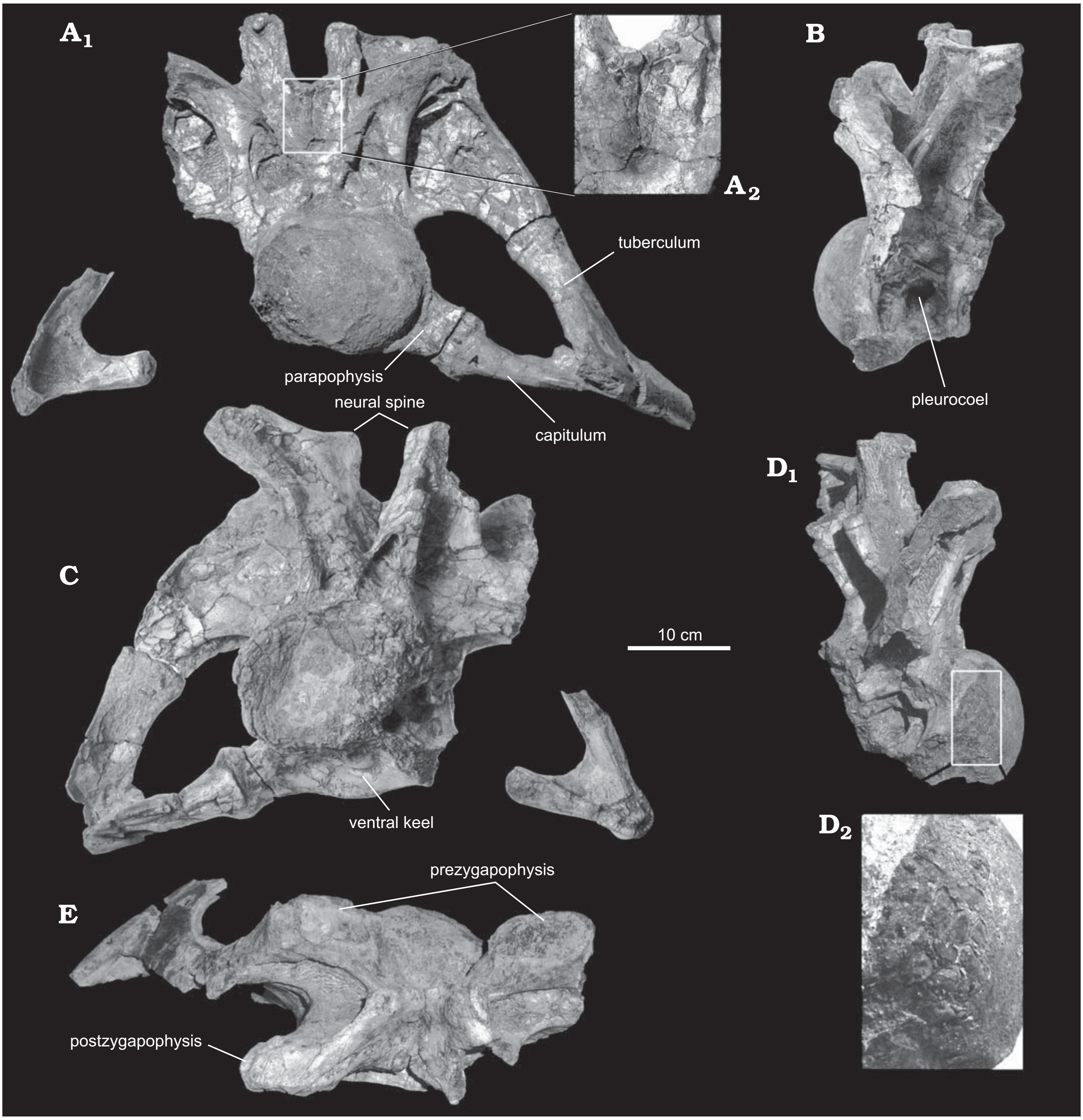

Fig. 3. Posterior cervical vertebra of *Mamenchisaurus* sp. from Phu Dan Ma, Kalasin Province, Thailand, Phu Kradung Formation, Late Jurassic–Early Cretaceous. Vertebra (SM KS26-4), right rib (SM KS26-2), and left rib (SM KS26-3) in anterior (**A**; A_2, close-up view of neural spine showing attachment scar for interspinal elastic ligament), left lateral (**B**), posterior (**C**), right lateral (**D**; D_2, close-up view of articular condyle showing a cancellous internal structure), and dorsal (**E**) views.

unnamed taxa from Spain and Russia (Canudo et al. 2002; Averianov et al. 2003) might be a monophyletic group (= Euhelopodidae sensu Canudo et al. 2002). However, Wilson and Upchurch (2009) suggested that detailed phylogenetic analyses supporting the group are needed to resurrect the term Euhelopodidae.

Genus *Mamenchisaurus* Young, 1954

Type species: *Mamenchisaurus constructus* from the Upper Jurassic Shangshximiao Formation, Yibin, Sichuan Province, China.

Mamenchisaurus sp.

Figs. 3–5.

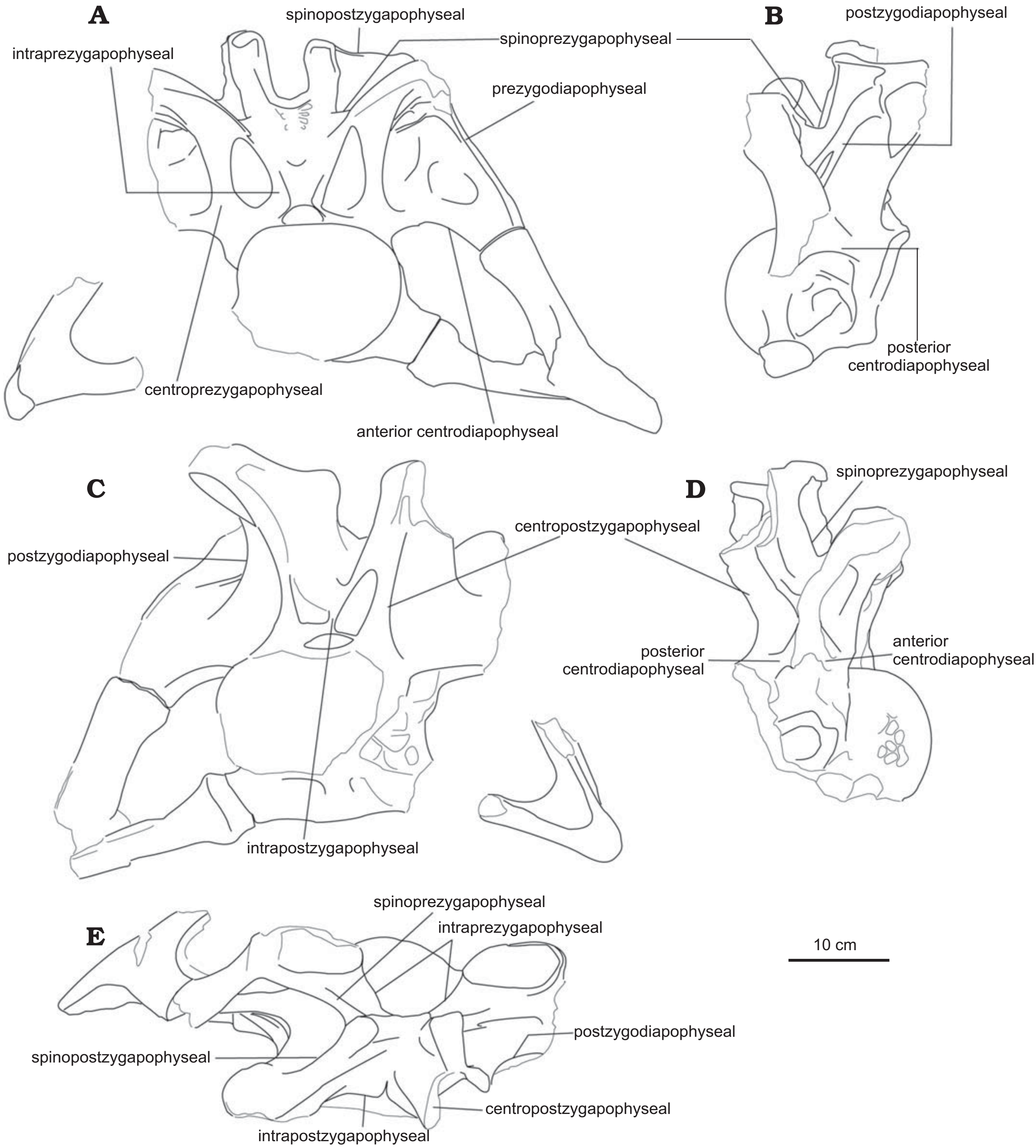

Fig. 4. Schematic drawing of mamenchisaurid posterior cervical vertebra from Phu Dan Ma, Kalasin Province, Thailand, Phu Kradung Formation, Late Jurassic–Early Cretaceous. Vertebra (SM KS26-4), right rib (SM KS26-2), and left rib (SM KS26-3), in anterior (**A**), left lateral (**B**), posterior (**C**), right lateral (**D**), and dorsal (**E**) views.

Material.—SM KS26-4, nearly complete posterior cervical vertebra; SM KS26-2, SM KS26-3, fragmentary ribs from Phu Dan Ma, Phu Kradung Formation (Upper Jurassic–?Lower Cretaceous), northeastern Thailand.

Description.—The vertebra SM KS26-4 is nearly complete and well preserved, except the right parapophysis, diapophysis, and postzygapophysis, and the posterior portion of the centrum which are damaged (Figs. 3, 4). The vertebra is

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Table 1. Measurements (in mm) of cervical vertebra (SM KS26-4) from Phu Dan Ma, Phu Kradung Formation, Thailand. Asterisks indicate approximate values.

Height of articulation	125
Width of articulation	165
Height of centrum at posterior	125*
Width of centrum at posterior	180*
Greatest length of centrum	170
Centrum length without articular condyle	145
Total height	340

Table 2. Comparative measurements (in mm) of cervical and dorsal vertebrae from various sauropods. Applied from Wiman (1929), Young and Zhao (1972), He et al. (1988), and Ouyang and Ye (2002).

Taxon	Vertebra number	Centrum length	Centrum height	Elongation
Phu Dan Ma (SM KS26-4)	?	170	125	1.4
Euhelopus zdanskyi (PMU.R-233)	C17	180	142	1.3
	C18	142	142	1.0
	C19	128	132	0.9
Mamenchisaurus hochuanensis (CCG V 20401)	C17	550	375	1.5
	C18	400	380	1.1
	C19	325	350	0.9
Mamenchisaurus youngi (ZDM0083)	C17	316	175	1.8
	C18	260	165	1.6
Omeisaurus tianfuensis (T5704)	C16	500	310	1.6
	C17	335	290	1.2

distorted and slightly compressed anteroposteriorly and laterally and the postzygapophysis is bent forward. The ribs were found articulated to the vertebra. The capitulum and tuberculum processes of the right rib (SM KS26-2) are missing. The parapophyses are located on the centrum ventrolaterally and the rib shaft is bent outward oblique to the long axis of the centrum. This feature indicates an intermediate position between cervical and dorsal vertebrae. In addition, the position of the parapophyses is as low as the ventral surface of the centrum and the shape of the rib is reminiscent of cervical ribs. Thus, SM KS26-4 is identified as one of the most posterior cervical vertebrae.

The vertebra is relatively high and short anteroposteriorly (Table 1). The centrum is strongly opisthocoelous with an Elongation Index (EI) about of 1.4 (EI = anteroposterior length/height of posterior face; sensu Upchurch 1998; Wilson 2002). The ventral surface of the centrum is concave and has a stout median keel. The centrum and neural arch are pneumatised (Wedel 2009). The breaks of the anterior articular surface show pneumatic camellate structures, circular cells separated by thin bone laminae (Wedel et al. 2000). Laterally, the pneumatic fossa occupies most of the lateral surface of the centrum. A horizontal lamina (or "supracentral lamina"; Osborn and Mook 1921) divides the pneumatic fossa into upper and lower parts.

The parapophysis is robust and projects ventrolaterally. Its dorsal surface is excavated by a pneumatic fossa. The parapophyseal facet is sub-circular.

The neural canal is triangular in anterior view and spindle-shaped in posterior view. The neural spine is relatively low. The U-shaped cleft between the bifid spines is shallow and has no median spine. Ventral to the cleft, a prominent scar is marked at the base of the neural spine in anterior view. It probably represents the mineralised attachment area for the elastic ligament (Schwarz et al. 2007).

The prezygapophyseal facets are large, subrectangular and convex transversely. Triangular pneumatic fossae excavate below the prezygapophysis and postzygapophysis and are limited medially by the intraprezygapophyseal and intrapostzygapophyseal laminae, respectively.

The diapophysis projects outward from the neural arch and curves ventrally toward its distal end. The diapophysis is flattened anteroposteriorly, with internal pneumatic cavities extending both anteriorly and posteriorly. A large pneumatic fossa excavates the diapophysis ventrally between the anterior and posterior centrodiapophyseal laminae.

Both ribs (SM KS26-2 and SM KS26-3) are preserved but not complete (Fig. 5). They show a sharp angle (45°) between the capitulum and tuberculum with a median ridge. The tuberculum is transversely wide and has a rectangular facet, while the capitulum is a peduncle-like structure with a circular facet.

Discussion.—The EI of the centrum of SM KS26-4 is reminiscent of the long-necked Chinese sauropods: it is close to that of the 17th cervical vertebra of *Omeisaurus tienfuensis* and that of the 18th cervical vertebra of *Mamenchisaurus hochuanensis* and is between those of the 17th and 18th cervical vertebrae of *Euhelopus zdanskyi* (Table 2). The large pleurocoel with successive generations of smaller chambers of SM KS26-4 is similar to that of *Camarasaurus* (Osborn and Mook 1921: pl. 69) and differs from *Euhelopus*, in which the pleurocoel is a simple and shallow concavity. Ouyang and Ye (2002) noted that there is no pleurocoel in the cervical vertebrae of *M. youngi*, but in fact the lateral surface of the centrum of *Mamenchisaurus* is excavated by a large concavity (Young and Zhao 1972: pl. 14; Ouyang and Ye 2002: pl. 8). Moreover, the centrum and neural arch of SM KS26-4 are entirely filled with numerous small pneumatic camellae like those of *Mamenchisaurus* (Russell and Zhang 1993; Ouyang and Ye 2002), *Omeisaurus* (He et al. 1988), and a vertebra from the Jurassic of Southern Thailand (Buffetaut et al. 2005). This cancellous inner structure differs from the spongy bones of somphospondylans such as *Euhelopus* and the saltasaurid *Ampelosaurus* Le Loeuff, 1995, the latter having more irregularly shaped and relatively smaller camellate cells. The camellate structure of SM KS26-4 is different from the solid bone of *Phuwiangosaurus*, from the overlying Sao Khua Formation (Martin 1994). Wedel et al. (2000) proposed that the pneumatic camellate structure in vertebrae (in both the centrum and neural spine) evolved independently at least twice in the Sauropoda: in *Mamenchisaurus* and in the Somphospondyli, a group defined as titanosauriforms more

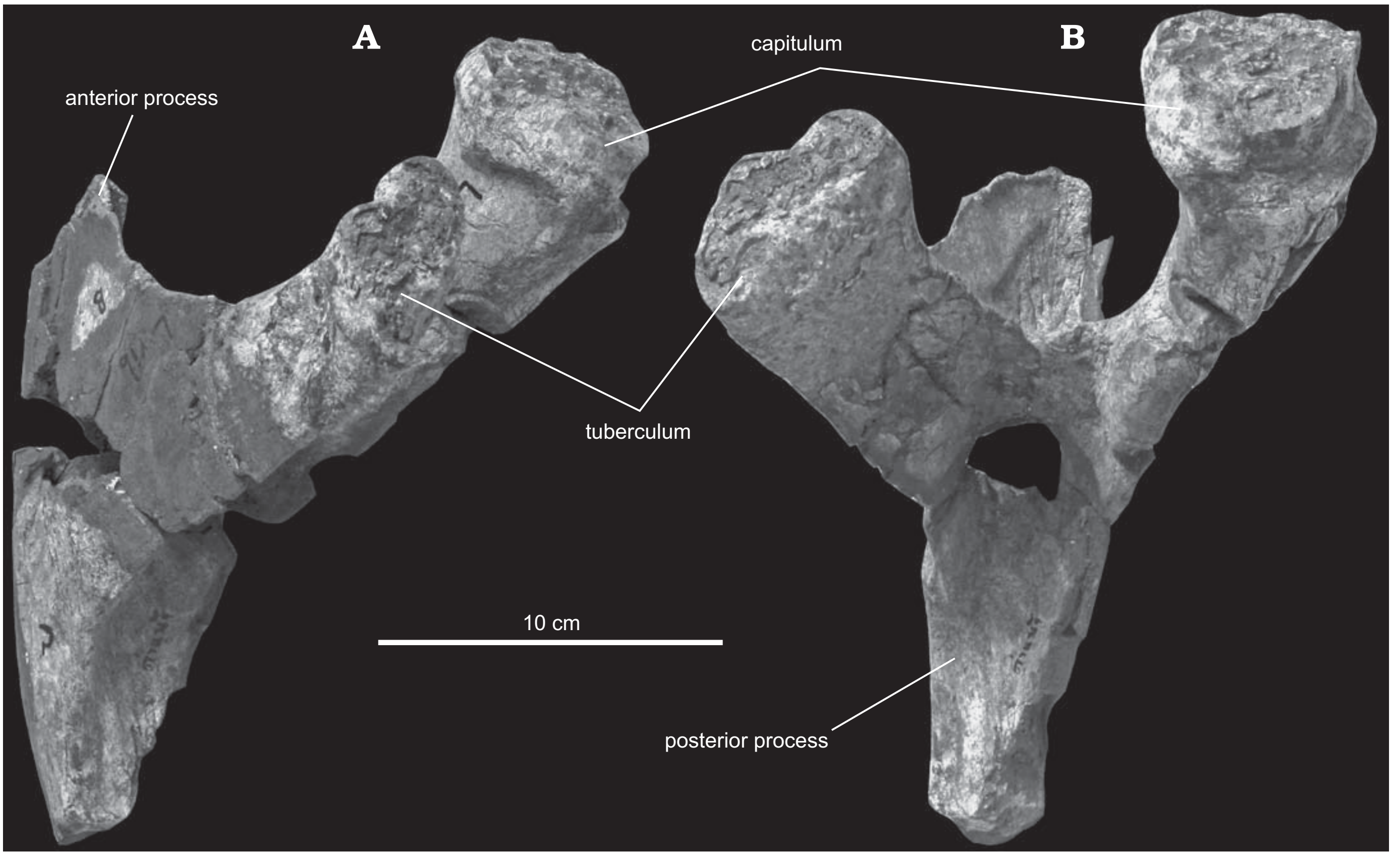

Fig. 5. Posterior cervical rib of *Mamenchisaurus* sp. from Phu Dan Ma, Kalasin Province, Thailand, Phu Kradung Formation, Late Jurassic–Early Cretaceous. Left rib (SM KS26-3) in posterior (**A**) and medial (**B**) views.

closely related to *Saltasaurus* than to *Brachiosaurus* (Wilson and Sereno 1998).

The neural spine of SM KS26-4 is reminiscent of the bifid spine of *Mamenchisaurus hochuanensis* and *M. youngi* (Young and Zhao 1972; Ouyang and Ye 2002). The cleft is broader with a U-shape in *Opisthocoelicaudia* Borsuk-Białynicka, 1977 and a V-shape in *Apatosaurus ajax* (Upchurch et al. 2004b), whereas it is deep and steep in *Camarasaurus* (Osborn and Mook 1921: pl. 69: 13) and *Phuwiangosaurus* Martin, Buffetaut, and Suteethorn, 1994. The bifid spine of *Euhelopus* has a median tubercle, which is an autapomorphy of the genus (Wilson 2002). *Omeisaurus* differs from the others as its spine is undivided (He et al. 1988). The short neural spine in the posterior cervical vertebra with a shallow U-shaped cleft is considered as an autapomorphy of *Mamenchisaurus*.

Mamenchisauridae indet. A

Fig. 6A–C.

Material.—SM MD3-53, SM MD3-54, SM MD3-62, isolated teeth from Dan Luang, Phu Kradung Formation, northeastern Thailand.

Remarks.—Buffetaut and Suteethorn (1998a, 2004) described spatulate teeth from the Dan Luang locality in the Phu Kradung Formation (Fig. 6), and recognized the resemblances between the Thai specimens and *Omeisaurus* based on the presence of denticles on unworn teeth (Buffetaut and Suteethorn 2004: figs. 1, 3). However, denticles are also present in *Mamenchisaurus* (Russell and Zheng 1993). Teeth from Thailand are similar to those of *Mamenchisaurus fuxiensis* (= *Zigongosaurus fuxiensis* Hou, Chao, and Chen, 1976) from the Wujiaba locality in the lower part of the Upper Shaximiao Formation of Zigong, China (Haiyan Tong and Hui Ouyang, personal communication 2009). Although Ouyang and Ye (2002) regarded the latter as indeterminate, because of the presence of a mosaic of characters found in *Omeisaurus* and *Mamenchisaurus*, these teeth belong to the family Mamenchisauridae as shown below.

The presence of a lingual boss has been recognized in various sauropods such as *Mamenchisaurus* (Russell and Zheng 1993: pl. 2; Ouyang and Ye 2002: figs. 9–12), *Omeisaurus* (He et al. 1988: fig. 16), *Euhelopus* (Wiman 1929: pl. 2), *Camarasaurus* (Osborn and Mook 1921: pl. 60) and isolated teeth from Thailand (Buffetaut and Suteethorn 2004: fig. 1) and Spain (Canudo et al. 2002: fig. 2). It seems that among these sauropods, those from younger formations, namely *Euhelopus* and the Spanish specimen (Wiman 1929; Canudo et al. 2002; Barrett and Wang 2007), show a complex pattern of cingular structure. Some of their teeth (Wiman 1929: pl. 2: 12, 15, 17, 18, 23) have a lingual boss associated with a cingulum, a horizontal ridge and some (Wiman 1929: pl. 2: 14, 16,19, 21; Canudo et al. 2002: figs. 2, 3) have two lingual

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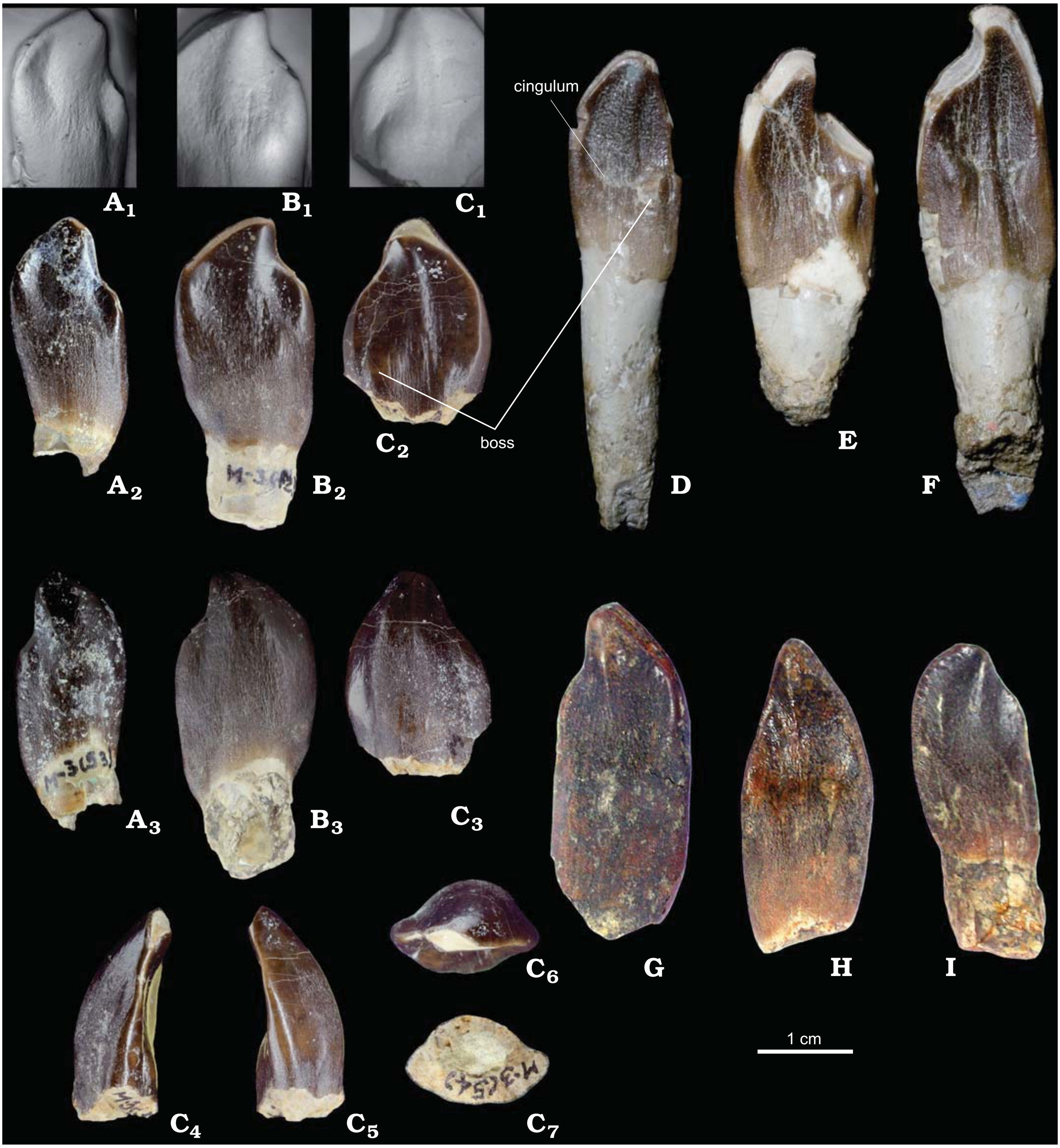

Fig. 6. Teeth of mamenchisaurids and the titanosauriform *Euhelopus zdanskyi*. **A**–**C**. Mamenchisauridae indet. A teeth (SM MD3-53, -62, -54, respectively) from Dan Luang, Mukdahan Province, northeastern Thailand, Phu Kradung Formation, Late Jurassic–Early Cretaceous, in cast showing a lingual boss (A_1–C_1), and in lingual (A_2–C_2), labial (A_3–C_3), distal (C_4), mesial (C_5), dorsal (C_6), and ventral (C_7) views. **D**–**F**. *Euhelopus zdanskyi* Wiman, 1929 teeth (PMU.R-182i, -182g, -182b, respectively) from central Shandong Province, China, Mengyin Formation, Early Cretaceous, in lingual view showing cingulum and boss. **G**–**I**. *Mamenchisaurus fuxiensis* Hou, Zhao and Chu, 1976 teeth (C.1042) from Wujiaba, Zigong Perfecture, China, Upper Shaximiao Formation, Late Jurassic, in lingual view.

bosses, mesially and distally, associated with a medial ridge or (third) boss forming a pseudo-cingulum. These differences possibly result from their positions in the tooth row such as anterior-posterior or upper-lower teeth. Teeth of sauropods from older formations, namely *Mamenchisaurus, Omeisaurus*, and Thai specimens (Russell and Zheng 1993:

fig. 4; Zhang et al. 1998: pl. 1; Ouyang and Ye 2002: figs. 11, 12; He et al. 1988: pl. 2; Buffetaut and Suteethorn 2004: fig. 1), show a single distal boss with a smoothly curved lingual concavity. We agree with Canudo et al. (2002) that the complexity of the cingular structures (a cingulum and boss) possibly represents a derived state (Fig. 6). Regardless, it should be stated that this feature is not present in all preserved specimens and is sometimes present in more primitive sauropods such as *Camarasaurus* (Osborn and Mook 1921: pl. 60: 6a). The spatulate teeth from Dan Luang are thus similar to those of *Mamenchisaurus* and *Omeisaurus* on the basis of primitive characters: presence of tooth denticles, single boss on lingual surface.

Mamenchisauridae indet. B

Material.—SDRC KB1-1, a dorsal vertebra from Khlong Thorn District, Krabi, Khlong Min Formation, southern Thailand.

Remarks.—A sauropod vertebra from the Upper Jurassic Khlong Min Formation of southern Thailand was described by Buffetaut et al. (2005). The shape of the centrum and the position of the parapophysis indicate a position midway through the dorsal vertebral series and its pneumatic camellate structure resembles that of the mamenchisaurids and Titanosauriformes (Wedel 2003). Buffetaut et al. (2005) noted the difference between these groups using pleurocoel shape, the pleurocoels of Titanosauriformes tending to have a tapering, acute caudal margin. They considered the vertebra from southern Thailand as a mid-dorsal vertebra of a euhelopodid (sensu Upchurch 1995, 1998) on the basis of camellate structure and the shape of the pleurocoel. This vertebra can be excluded from the genus *Euhelopus* because of the lack of a "K"-lamina, an autapomorphic character of *Euhelopus* recognized by Wilson and Upchurch (2009). It resembles *Mamenchisaurus* and *Omeisaurus* in several respects and accordingly can be placed in the family Mamenchisauridae.

Conclusions

The posterior cervical vertebra (SM KS26-2 to KS26-4) from Phu Dan Ma is assigned to *Mamenchisaurus* sp. in the family Mamenchisauridae, based on the following characters: short posterior cervical vertebra (EI = 1.4) with camellate internal structure; bifurcated neural spine with shallow U-shaped cleft. Because of the lack of unambiguous characters of the isolated teeth from the Dan Luang locality and the dorsal vertebra from southern Thailand, a generic attribution cannot be confirmed. However, they share several characters with the Mamenchisauridae and we assign these remains to the family Mamenchisauridae.

Sauropod remains from the Phu Kradung Formation of Thailand thus belong to a family of Jurassic sauropods first described from China, and their occurrence in Thailand can be interpreted as evidence of faunal links between the Indochina Block and mainland Asia during the Late Jurassic–Early Cretaceous. This is in agreement with Buffetaut et al. (2006) and Buffetaut and Suteethorn (2007) who mentioned resemblances between the vertebrates from the Phu Kradung Formation, such as the crocodilian *Sunosuchus* and a sinraptorid theropod, and those from the Upper Shaximiao and Shishugou formations of China, which are dated to the Middle Jurassic (Chen et al. 2006) to the Late Jurassic (Dong et al. 1983; Eberth et al. 2001; Lucas 2001; Weishampel et al. 2004). Wang et al. (2003) described *Mamenchisaurus* sp. from the Penglaizhen Formation, which overlies the Upper Shaximiao Formation. They suggested that *Mamenchisaurus* was present in China until the latest Jurassic; however, the age of the *Mamenchisaurus* strata in Sichuan and the neighbouring areas need to be reconsidered (Wang et al. 2003). The age of the Phu Kradung Formation is also controversial: on the basis of vertebrate evidence, Buffetaut et al. (2006) suggested a Upper Jurassic series, whereas palynological evidence suggests a Upper Jurassic to Lower Cretaceous series (Racey and Goodall 2009), based on the occurrence of *Dicheiropollis etruscus*, which suggests that the Phu Kradung Formation and the overlying Phra Wihan Formation may have been deposited during the Berriasian to Hauterivian stages. Le Loeuff et al. (2002) suggested that the ichnological record of the Phra Wihan Formation shows more similarities with the vertebrate assemblage of the Phu Kradung Formation than with that of the younger Sao Khua Formation. The vertebrate assemblages from the Sao Khua Formation and Phu Kradung Formation are indeed very different (Buffetaut and Suteethorn 2004; Buffetaut et al. 2002, 2003, 2006; Cavin et al. 2007; Suteethorn et al. 2010).

Le Loeuff et al. (2002) hypothesized that the main changes in southeast Asian dinosaur assemblages occurred during the Early Cretaceous, after the deposition of the Phra Wihan Formation and before the deposition of the Sao Khua Formation, rather than at the Jurassic–Cretaceous boundary. This might be true for all dinosaur assemblages of Central and Eastern Asia. It seems that the Mamenchisauridae occurred through central, eastern and southeast Asia from the Middle Jurassic to Early Cretaceous (Young and Zhao 1972; Russell and Zhang 1993; Ouyang and Ye 2002; Buffetaut et al. 2005); they would have evolved during a period of geographical isolation caused by the formation of the Turgai Sea between Europe and Asia from the Late Jurassic to the Early Cretaceous (Russell 1993; Barrett et al. 2002; Upchurch et al. 2002). Wilson and Upchurch (2009) hypothesized that Titanosauriformes might have invaded mainland Asia before its isolation since these groups had already appeared in the Middle Jurassic. However, the age of the Mengyin Formation, which has yielded the somphospondylan *Euhelopus zdanskyi*, is uncertain (Late Jurassic or Early Cretaceous). New informative fossils from the Late Jurassic–Early Cretaceous as well as better correlations between southeast Asian and Chinese localities are needed to better understand the biogeography and evolution of Asian sauropods.

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