Geol. Mag. **152** (*1*), *2015, pp. 166–175. © Cambridge University Press 2014*
doi:10.1017/S0016756814000223

A new primitive eucryptodiran turtle from the Upper Jurassic Phu Kradung Formation of the Khorat Plateau, NE Thailand

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(*Received* 17 February 2014; *accepted* 3 May 2014; *first published online* 19 June 2014)

Abstract – A new genus and new species of primitive eucryptodiran turtle, *Phunoichelys thirakhupti* gen. et sp. nov., is described on the basis of shell remains from the lower part of the Phu Kradung Formation, at Phu Noi locality, Kalasin Province, NE Thailand. It is assigned to Xinjiangchelyidae on the basis of the marginals covering the lateral end of the costals and the anal scutes invading the hypoplastra. The new taxon is further characterized by a low and rounded carapace without a cervical notch; the whole carapace and plastron covered with a clear ornamentation consisting of tiny irregular vermiculated furrows; a complete neural series that reaches the suprapygal; a very wide and short cervical scute; relatively wide vertebral scutes; and a long first thoracic rib that extends along the full width of the first costal. The sutured plastron/carapace connection and the marginals covering the lateral end of the second to seventh costals suggest that the turtles from Phu Noi may be related to some primitive xinjiangchelyids from the Sichuan Basin. The discovery of a xinjiangchelyid turtle in the lower part of the Phu Kradung Formation supports a Late Jurassic age for that part of the formation.

Keywords: Testudines, Eucryptodira, Xinjiangchelyidae, *Phunoichelys thirakhupti*, Late Jurassic, Phu Kradung Formation, NE Thailand.

1. Introduction

Our knowledge of the Mesozoic turtle faunas of Thailand has increased during the last two decades, but is still scanty compared with the other regions of Asia (China and Central Asia). The Mesozoic non-marine deposits of the Khorat Group in NE Thailand have yielded carettochelyids and adocids in the Sao Khua and Khok Kruat formations, and the large turtle *Basilochelys* in the upper part of the Phu Kradung Formation (Tong *et al.* 2004, 2005; Tong, Buffetaut & Suteethorn, 2006; Tong *et al.* 2009*a*). Here we report on new turtle remains from the lower part of the Phu Kradung Formation, which consist of shell remains of a primitive eucryptodiran turtle.

2. Geological setting

The Phu Noi locality is located on the flank of a small hill near the village (Ban) Dinji, Kham Muang District, Kalasin Province. Stratigraphically, the locality is in the lower part of the Phu Kradung Formation, which is the oldest formation of the Khorat Group. The Phu Kradung Formation is over 1000 m in thickness at the type locality (Ward & Bunnag, 1964). It is composed of sandstones, siltstones and mudstones with intermittent calcretes, deposited in a mainly lake-dominated floodplain cut by meandering and occasionally braided river channels (Racey & Goodall, 2009). At Phu Noi, the extensive excavations since 2008 have unearthed abundant vertebrate remains, including sharks, bony fishes, turtles, crocodiles, pterosaurs, and ornithopod, sauropod and theropod dinosaurs (Chanthasit, 2011; Cuny *et al.* 2011; Deesri *et al.* 2012). Three fossiliferous layers are recognized at the Phu Noi locality; the material described in the present work comes from a series of siltstones and mudstones of the palaeochannel, referred to as PNB by Cuny *et al.* (2013), approximately 10 m above the basal conglomeratic sandstone. Stratigraphically, Phu Noi is approximately 500 m below all the localities that yielded the large *Basilochelys* turtles (Kham Phok, Dan Luang, Huai Sai and Dan Kaeng;

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Tong *et al.* 2009*a*); the four sites mentioned above are situated closer to the boundary with the overlying Phra Wihan Formation (Cuny *et al.* 2013).

The age of the Phu Kradung Formation is still debated. The studies on dinosaur remains suggested a Late Jurassic age (Buffetaut, Suteethorn & Tong, 2006; Buffetaut & Suteethorn, 2007), while the recent studies on palynology supported a basal Cretaceous age for that formation, although a latest Jurassic age cannot be ruled out for its lowermost part (Racey & Goodall, 2009).

3. Systematic palaeontology

Order TESTUDINES Linnaeus, 1758
Suborder CRYPTODIRA Cope, 1868
Infraorder EUCRYPTODIRA Gaffney, 1975
Family XINJIANGCHELYIDAE Nessov *in* Kaznyshkin, Nalbandyan & Nessov, 1990 (fide Tong *et al.* 2012*b*)
Phunoichelys thirakhupti gen. et sp. nov.
Figures 1–3

Etymology. The genus name comes from the Phu Noi locality where the turtle specimens come from; the species name is in honour of Dr Kumthorn Thirakupt, a Thai expert on turtles who brought together the remarkable living turtle collection at Chulalongkorn University, Bangkok, Thailand.

Holotype. PRC 230, an almost complete shell with articulated carapace and plastron. The carapace is nearly complete, lacking the posterior peripheral region. The plastron lacks most of the posterior lobe, and the anterior end of the anterior lobe and the left bridge are damaged. The shell is slightly crushed dorsoventrally and the carapace surface is somewhat damaged.

Referred material. PRC 231, a posterior portion of carapace associated with a nearly complete plastron. The carapace is visible in dorsal view, with the fifth to eighth neurals, part of the first suprapygal, the incomplete right fourth costal and the paired fifth to eighth costals in articulation. The plastron is almost complete but disarticulated along the hyoplastron/hypoplastron suture, lacking the anterior end. PRC 232, disarticulated costals of comparable size, which are preserved together, including the right first to third costals (PRC 232-1 to 3), and the left third, fourth and sixth costals (PRC 232-4 to 6). PRC 233, an isolated scapula. PRC 234, a left seventh peripheral. PRC 235, two bridge peripherals in articulation with one another. PRC 236, a partial carapace, lacking all peripheral regions. PRC 237, a plastron disarticulated along the hyoplastron/hypoplastron suture, with the anterior lobe and both bridges damaged.

Locality and horizon. Phu Noi locality, Ban Dinji, Kham Muang District, Kalasin Province, NE Thailand; lower part of the Phu Kradung Formation, Late Jurassic.

Diagnosis. Xinjiangchelyid turtle (*sensu* Tong *et al.* 2012*b*) of small size (carapace length about 25 cm); characterized by the following combination of characters: (1) low shell with rounded outline; (2) shell surface with clear ornamentation consisting of tiny irregular vermiculated furrows; (3) cervical notch absent; (4) complete neural series reaching suprapygal; (5) relatively wide neurals, most regularly hexagonal in shape with short anterolateral sides; (6) very short and wide cervical scute; (7) anterior sulcus of vertebral 1 strongly convex forward, almost reaching the anterior margin of the carapace; (8) second to fourth vertebrals wider than long; (9) first marginal triangular; (10) lateral marginals extending onto the second to seventh costals; (11) plastron sutured to the carapace; (12) long axillary buttress extending anteriorly, reaching the second peripheral; (13) anterior lobe of plastron elongate, with the front margin reaching the level of the anterior margin of the carapace; (14) posterior lobe triangular, with the lateral margins tapering backward; (15) entoplastron elongate; (16) long first thoracic rib extending along the full width of the first costal; (17) strong swelling on the visceral surface of the fifth costal. Differs from all other Xinjiangchelyidae by characters 2, 6–7; similar to *Chengyuchelys*, *Tienfuchelys*, *Yanduchelys* and *Protoxinjiangchelys* but differs from *Xinjiangchelys* and *Annemys* by character 11; similar to *Yanduchelys* and *X. chowi* but differs from other xinjiangchelyids by character 10.

Measurements. See Table 1.

3.a. Description

Carapace. As preserved in the holotype, the carapace has a rounded outline and is flat, with the length only slightly greater than the width when reconstructed. The anterior rim of the carapace is straight, without a cervical notch. The carapace margin is smooth and sharp. The anterolateral margin of the carapace is slightly upturned from the second peripheral to about the fifth peripheral. A light midline ridge is present on the posterior end of the carapace, located on the eighth neural in the holotype, PRC 231 and PRC 236. Narrow lateral carapacial fontanelles are present between the costals and peripherals, extending from the second to fifth costals in the holotype. The free rib ends on the costals in PRC 231 and PRC 236 indicate that the carapacial fontanelles are also present in these specimens. The carapace is very thin in the small specimens (holotype and PRC 236), but becomes thicker in the larger specimens (PRC 231 and PRC 232). The entire carapace surface is covered with a clear ornamentation consisting of tiny irregular vermiculated furrows (Fig. 1c).

The nuchal, preserved only in the holotype, is trapezoidal in shape and wider than long, with the posterior border slightly wider than the anterior margin. The neural series is complete in the holotype. It is incompletely preserved in PRC 236, and the fifth to eighth neurals are preserved in PRC 231. The neurals are relatively wide in all specimens. The neural formula is 5<4>6>6>6>6>6–4 in the holotype. In this specimen, the first to fifth neurals and the eighth neural are longer than wide, the sixth neural is as long as wide and the seventh neural is wider than long. In PRC

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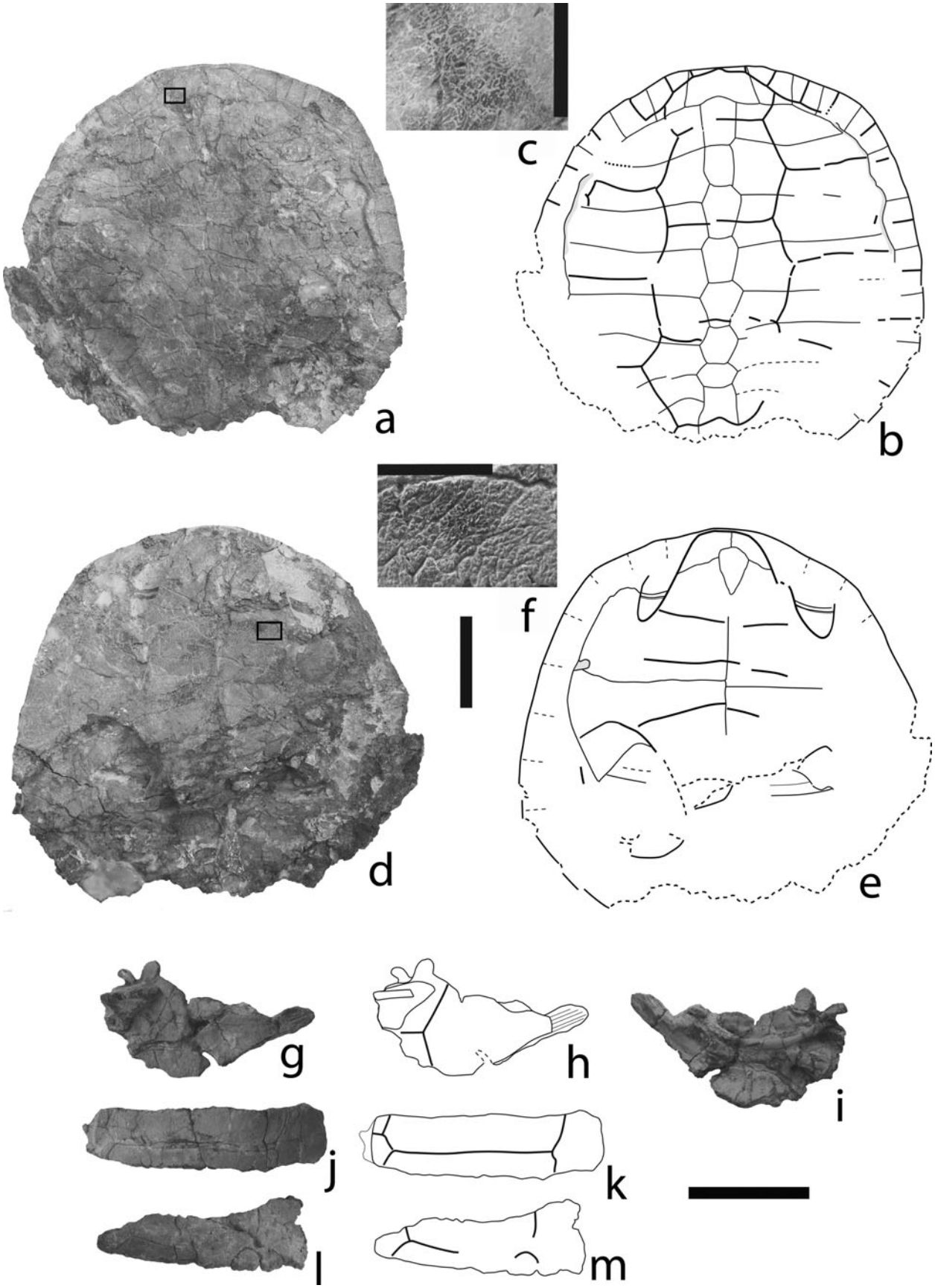

Figure 1. *Phunoichelys thirakhupti* gen. et sp. nov. from the Phu Kradung Formation (latest Jurassic) of Phu Noi Locality, NE Thailand. (a–f) PRC 230 (holotype), shell in dorsal (a, b) and ventral (d, e) views, and detail of ornamentation on carapace (c) and plastron (f); (g–m) PRC 232, (g–i) right costal 1 (PRC232-1) in dorsal (g, h) and ventral (i) views; (j, k) left costal 4 (PRC232-5), (l, m) left costal 6 (PRC232-6). Scale bar = 5 cm for (a), (b), (d), (e) and (g–m), 1 cm for (c) and (f).

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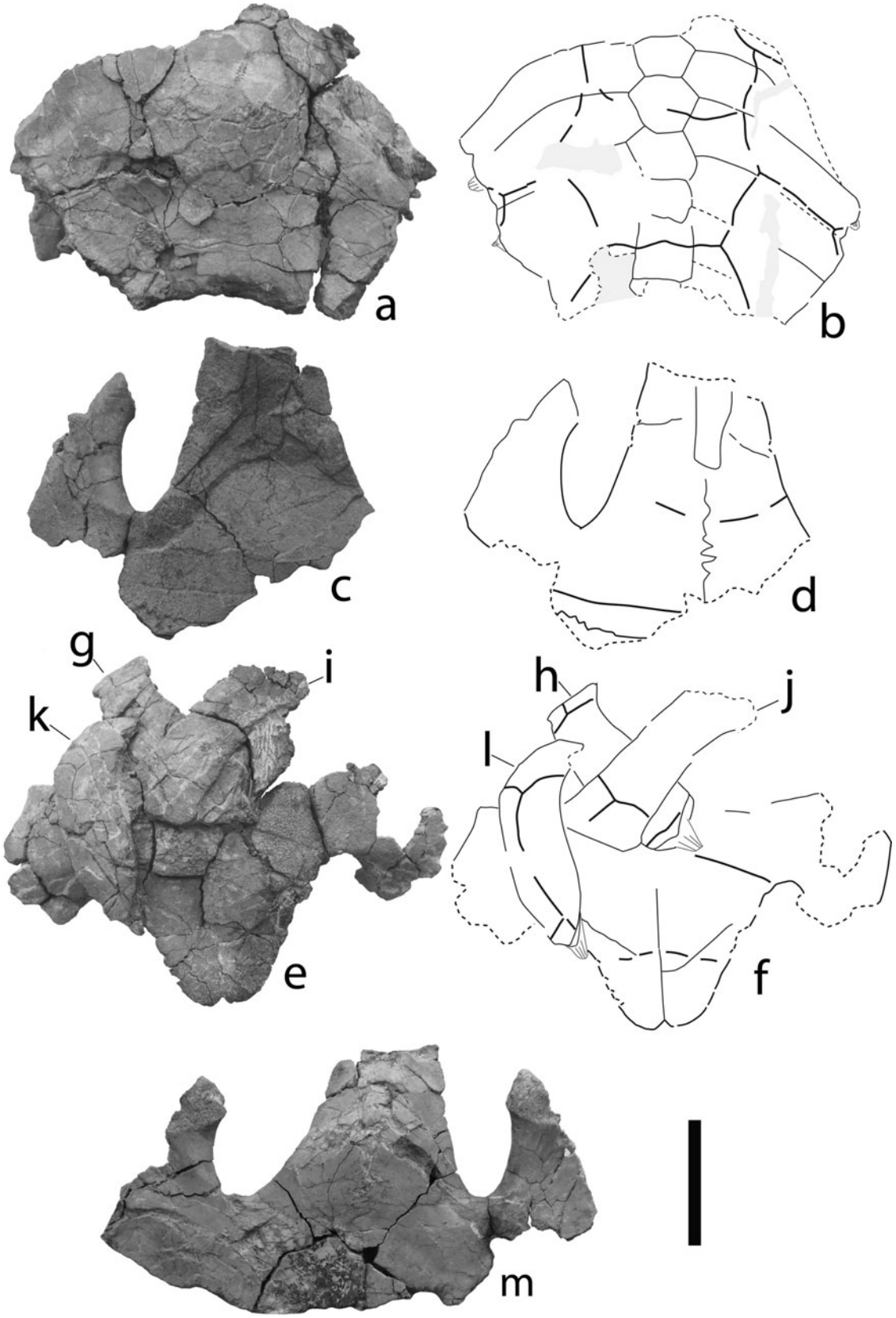

Figure 2. *Phunoichelys thirakhupti* gen. et sp. nov. from the Phu Kradung Formation (latest Jurassic) of Phu Noi Locality, NE Thailand. (a–f, m) PRC 231, posterior portion of carapace in dorsal view (a, b), anterior half of plastron in ventral (c, d) and dorsal (m) views, posterior half of plastron in ventral view (e, f); (g–l) PRC 232, disarticulated costals: (g, h) left costal 3 (PRC 232-4), (i, j) right costal 3 (PRC232-3), (k, l) right costal 2 (PRC232-2). Scale bar = 5 cm.

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Table 1. Measurements of *Phunoichelys thirakhupti* gen. et sp. nov. from the Phu Kradung Formation (Latest Jurassic) of Phu Noi Locality, NE Thailand (in mm)

Specimen		PRC 230 (Holotype)	PRC 231	PRC 236	PRC 237
Carapace	Preserved	(180)/195	(100)/(165)	(135)/(95)	–
(length/width)	Estimated	205/200	240/235	145/140	–
Plastron	Preserved	(130)/150	85/165	–	(115)/(100)
(length/width)	Estimated	170/150	180/170	–	120/110
Anterior lobe (length/width at the base)	48/77	(48)/73	–		
Bridge	64 Right, 68 Left	75 Right	–		
Posterior lobe (length/width at the base)	–/78	50/82	–	37/45	

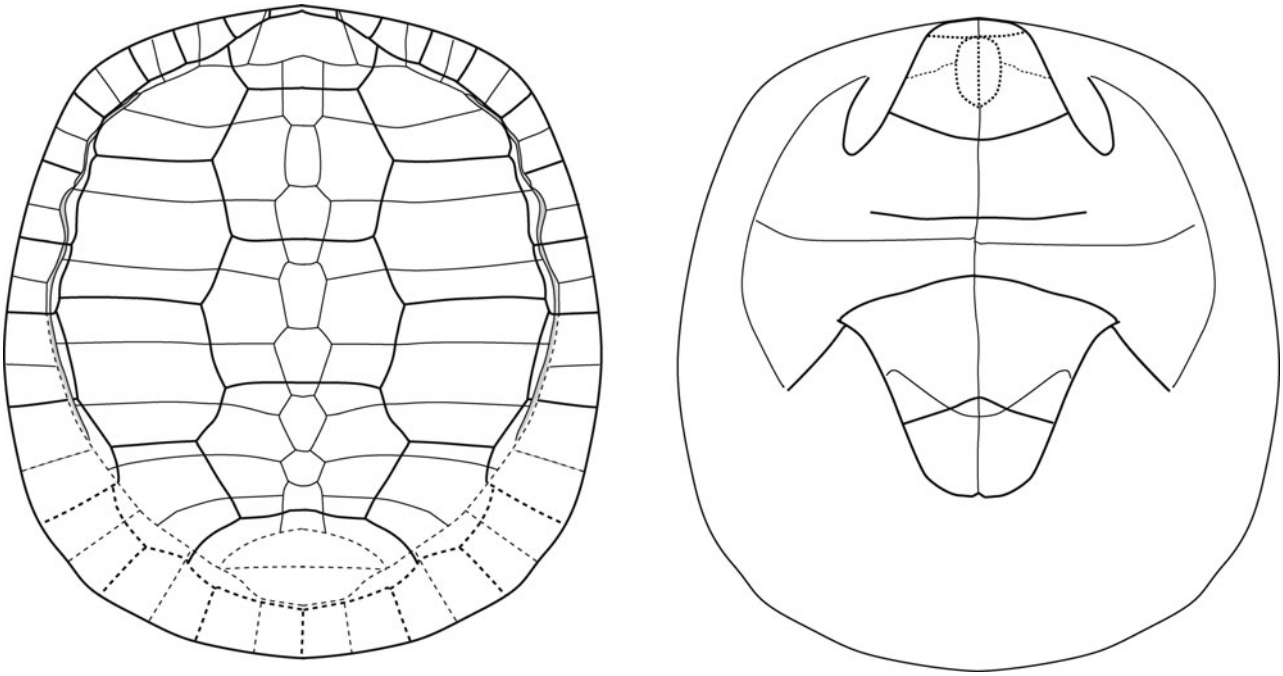

Figure 3. Reconstruction of the shell of *Phunoichelys thirakhupti* gen. et sp. nov. from the Phu Kradung Formation (latest Jurassic) of Phu Noi Locality, NE Thailand. (a) Carapace in dorsal view; (b) plastron in ventral view.

231, the fifth to seventh neurals are all wider than long and the eighth neural is subdivided and unusually long (Fig. 2b). In PRC 236, the fourth to sixth and the eighth neurals are longer than wide, while the seventh neural is short. Only a small portion of the first suprapygal is preserved in PRC 231, which indicates that this plate is wider than the eighth neural. The pygal (and the second suprapygal if present) are not preserved in any specimen. The complete series of eight pairs of costals is preserved in the holotype. In this specimen, the first costal is shorter and narrower than the second costal and contacts the nuchal though the anteromedial end of the fourth peripheral. In PRC 232, the first costal is as long as the second costal. The peripheral series is incompletely preserved in the holotype. The first and second peripherals are roughly square. The third to seventh peripherals are wider than long. The shape of the eighth and ninth peripherals is unclear since the costoperipheral suture is not discernible.

The first costal of PRC 232, fully prepared on both sides, shows a nicely preserved visceral structure. This plate bears a strong and sharp ridge and a large flat rib head on the visceral surface. A long and curved first thoracic rib is sutured to this ridge, extending along the full width of the plate up to the axillary buttress of the plastron (Fig. 1i). This structure is also partly visible on both sides of the holotype. In addition, a prominent swelling is present on the inner surface of the fifth costal, which begins close to the rib head and becomes more prominent laterally up to the lateral end of the plate. This structure is preserved on both right and left sides of the holotype, and also visible in PRC 236. A clear ridge is also present on the visceral surface of the eighth costal of PRC 236, which is completely preserved on the right side, but damaged on the left side.

The cervical scute, preserved only in the holotype, is very short and wide. The first to fourth vertebrals are preserved in the holotype and the third to fifth vertebrals are preserved in PRC 231, while the scute sulci are mostly obliterated in PRC 236. In the holotype, the first vertebral is the narrowest; it is slightly narrower than the second vertebral, with its anterior sulcus strongly convex forward, lying close to the anterior margin of the carapace. The width of the vertebrals increases slightly from the first to the fourth vertebral. The intervertebral sulci pass through the first, third, fifth and eighth neurals, respectively. In PRC 231, the intervertebral sulci

https://doi.org/10.1017/S0016756814000223 Published online by Cambridge University Press

pass through the sixth and eighth neurals, respectively. As preserved in the holotype, the first to third marginals are restricted to the peripherals. The first marginal is triangular and much smaller than the second marginal, with a short contact with the cervical scute. The following marginals are not well preserved in the holotype. PRC 231 and PRC 236 show that the lateral marginals extend onto the costals (as preserved, from the second costal through the seventh in PRC 231 and the second costal through the fourth in PRC 236).

Plastron. The plastron is documented by the holotype (PRC 230), PRC 231 and PRC 237. The plastron is narrow, with a short and relatively broad bridge. The axillary notch is narrow and deep. The inguinal notch is wider than the axillary notch. The contact with the carapace is better preserved on the right side in the holotype, which shows that the plastron is tightly sutured to the carapace. The lateral margins of the plastron in PRC 231 are straight, without a series of pegs along the margin as seen in 'macrobaenids' or *Xinjiangchelys*. The axillary buttresses are long and extend anteriorly and medially, reaching the second peripheral and the lateral end of the first costal. The inguinal buttress reaches the eighth peripheral and the lateral end of the fifth costal. Both axillary and inguinal buttresses are also directed dorsally and end with a large process, which likely fitted into a socket on the carapace. Fontanelles are absent on the plastron in all three specimens (holotype, PRC 231 and PRC 237). A tiny hole, however, is present on the right side of the holotype, between the hyoplastron, hypoplastron and peripherals. The entire plastron surface is covered with a clear ornamentation which matches that of the carapace, but stronger. This is better preserved in the holotype (Fig. 1f).

The anterior lobe is damaged in the holotype, lacking the anterior end, but the outline is preserved as an imprint, showing that the anterior margin of the plastron almost reached the level of the anterior margin of the carapace. The anterior lobe is nearly complete in PRC 231, but deformed and lacks the anterior end. In both specimens, the anterior lobe is long and narrow. It is almost as long as the posterior lobe, but shorter than the bridge. Its anterior border is rounded and the lateral margins are convergent forward. The narrower anterior lobe of PRC 231 relative to the holotype is likely due to the deformation. The posterior lobe is complete in PRC 231. It is triangular, wide at the base and tapers posteriorly, with a small anal notch.

The entoplastron is almost complete in PRC 231, but mostly missing in the holotype. It is an anteroposteriorly elongate element. The epiplastron/hyoplastron suture is not clearly visible in the holotype and it is obscured by the cracks in PRC 231, thus rendering the interpretation tentative. The epiplastron is quite large, with the epiplastron/hyoplastron suture running posterolaterally. Although the anterior end of the plastron is damaged, the epiplastron probably has a short suture with its counterpart in front of the entoplastron. Posterior to the entoplastron, the hyoplastron contacts its counterpart with an interfingered suture, which is well preserved in PRC 231. The mesoplastron is absent. The midline length of the hyoplastron is shorter than that of the hypoplastron. The hypoplastron/xiphiplastron suture, preserved in PRC 231 and PRC 237, is strongly convex posteriorly.

The scute sulci are weakly impressed on the plastron. The gulars and intergulars are not preserved in any specimen, but they would have been short since there is no trace of their sulci on the anterior part of the entoplastron or epiplastra. As preserved in the holotype and PRC 231, the humeropectoral sulcus is convex posteriorly and located clearly anterior to the base of the anterior lobe, but far posterior to the entoplastron. The pectoroabdominal sulcus is almost straight and the abdominofemoral sulcus is convex anteriorly. The femoroanal sulcus, preserved in PRC 231, is slightly convex forward and cuts the hypoplastron/xiphiplastron suture. The inframarginals are not visible in any specimen.

Scapula. The scapula has a long neck. The scapular process and acromion process form an angle of about 90°.

4. Discussion

The turtle remains from the Phu Noi locality described above include at least five individuals. They are considered to belong to the same taxon on the basis of the morphology of the shell. Characters in common include the ornamentation of the shell surface, the complete neural series of eight relatively wide neurals which separate all costals, a weak but clear midline ridge on the eighth neural, a strong and sharp ridge on the visceral surface of the first costal extending across the full width of the plate, a prominent ridge on the inner surface of the fifth costal which extends to the lateral end of the plate, an unreduced first thoracic rib, a long and relatively narrow anterior lobe of the plastron, a relatively short and triangular posterior lobe, and well-developed axillary and inguinal buttresses which are somewhat dorsally directed. The differences in shell thickness are likely due to the different growth stages since the small specimens have a thinner shell compared to larger specimens. Individual variations occur in the shape and size of the neurals, as well as in the position of the intervertebral sulcus between the third and fourth vertebrals (see Section 3.a).

These turtles from Phu Noi belong to Eucryptodira since the pelvic girdle is not sutured to the carapace and plastron, and the mesoplastron is absent (Gaffney & Meylan, 1988). The shell morphology of the Phu Noi turtles generally resembles that of the primitive eucryptodirans Xinjiangchelyidae, Sinemydidae and 'Macrobaenidae' in the low domed carapace and the relatively narrow plastron with a broad bridge. The Phu Noi turtles have a sutured plastron/carapace connection; the peg-like processes on the lateral margins of the bridge, an indication of the ligamentous connection between the carapace and plastron seen in sinemydids,

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'macrobaenids' and some xinjiangchelyids, are absent, even in the relatively small specimens (holotype). This character separates our specimens from all sinemydids (*sensu* Tong & Brinkman, 2013) and 'macrobaenids' (*sensu* Brinkman *et al.* 2013*b*). Both sutured and ligamentous plastron/carapace connections are present in Xinjiangchelyidae. *Xinjiangchelys* spp. and *Annemys* spp. have a ligamentous plastron/carapace connection, with a series of pegs on the lateral margin of the plastron fitting into the sockets on the peripherals, while the primitive xinjiangchelyids from the Middle and Upper Jurassic of the Sichuan Basin (*Protoxinjiangchelys*, *Chengyuchelys*, *Tienfuchelys* and *Yanduchelys*) have the plastron sutured to the carapace (Peng & Brinkman, 1993; Nessov, 1995; Sukhanov & Narmandakh, 2006; Tong *et al.* 2012*a*, *b*; Wings *et al.* 2012; Brinkman *et al.* 2013*a*). The disarticulated PRC 231 shows the strong axillary and inguinal buttresses ending with a large process that seems to fit into a socket on the carapace. The details of plastral buttress morphology in xinjiangchelyids with a sutured plastron/carapace connection are unknown since the inner structure is usually invisible in the articulated shell.

The turtles from Phu Noi share several characters with xinjiangchelyids, including the lateral marginals extending onto the costals and the anal scutes invading the hypoplastra. The combination of these synapomorphic features are diagnostic of the family Xinjiangchelyidae, and are distinct from plesiochelyids, sinemydids and 'macrobaenids' (Tong *et al.* 2012*b*). One prominent feature of the Phu Noi turtles is the lateral marginals extending onto the costal plates. In most xinjiangchelyids, the lateral marginals generally cover the lateral end of the second to fourth costals (e.g. *Chenguchelys latimarginalis*, *Tienfuchelys* spp., *Xinjiangchelys junggarensis*). In our specimens, the marginals extend onto the first to seventh costals. This particular morphology is reminiscent of the xinjiangchelyid *Yanduchelys delicatus* from the Upper Jurassic of the Sichuan Basin and *X. chowi* from the Jurassic of Shishugou, Junggar Basin, Xinjiang, China, in which not only do the lateral marginals extend onto the second to fourth costals, but the posterolateral marginals also cover the lateral end of the sixth and seventh costals in *Yanduchelys* and the sixth to eighth costals in *X. chowi* (Tong *et al.* 2012*b*; Brinkman *et al.* 2013*a*). In other Eucryptodira, the lateral marginals extend onto the costals in the basal trionychoid *Adocus*, but it may be the result of convergent evolution.

The femoroanal sulcus cuts the hypoplastron/xiphiplastron suture in the Phu Noi turtles as in other xinjiangchelyids. However, this slightly anteriorly convex sulcus is different from the omega-shaped femoroanal sulcus seen in most xinjiangchelyids (e.g. *Chengyuchelys* spp. *Tienfuchelys tzuyangensis*, *Xinjiangchelys* spp., *Annemys* spp.; Peng & Brinkman, 1993; Sukhanov, 2000; Sukhanov & Narmandakh, 2006; Tong *et al.* 2012*b*; Wings *et al.* 2012; Brinkman *et al.* 2013*b*; Rabi *et al.* 2013). Tong *et al.* (2012*b*) recognized three morphotypes of the shape of the femoroanal sulcus among xinjiangchelyids from the Upper Jurassic of the Sichuan Basin: (1) femoroanal sulcus clearly omega-shaped, intersecting hypoplastron; (2) femoroanal sulcus slightly convex forward, intersecting hypoplastron or barely reaching hypoplastron; and (3) femoroanal sulcus almost straight, not reaching hypoplastron. The morphology of the specimens from Thailand corresponds to the morphotype 2.

The entoplastron of the Phu Noi turtles is anteroposteriorly elongate as in xinjiangchelyids and 'macrobaenids', but different to the broad entoplastron of basal trionychoids (Nanhsiungchelyidae and Adocidae), testudinoids and Sinochelyidae. The epiplastron in our specimens has a posterolaterally directed contact with the hyoplastron. This morphology differs from that of most xinjiangchelyids in which the epiplastron/hyoplastron suture runs transversally, but more resembles the condition of macrobaenids, such as *Kirgizemys* spp. or *Ordosemys* spp. (Sukhanov, 2000; Tong, Ji & Ji, 2004; Danilov *et al.* 2006; Danilov & Parham, 2007). A similar morphology is nevertheless also present in a few xinjiangchelyids, such as *Tienfuchelys chungkingensis* Young & Chow, 1953 from the Jurassic of the Sichuan Basin, *Xinjiangchelys* sp. from the Lower Cretaceous Tugulu Group of Xinjiang and *X. tianshanensis* from the Middle Jurassic of Kirgizstan (Nessov, 1995; Danilov & Parham, 2007; Tong *et al.* 2012*b*).

The Phu Noi turtles have a long first thoracic rib that is sutured to a sharp ridge on the ventral surface of the first costal, which extends along the full width of that plate. A long first thoracic rib has been reported in the 'macrobaenid' *Ordosemys leios* and sinemydid *Sinemys brevispinus* (Brinkman & Peng, 1993*a*; Tong & Brinkman, 2013). A reduced first thoracic rib that extends only across half the width of the first costal is known in some xinjiangchelyids (*X. qiguensis* and *X. chowi*) and their close relatives the bashuchelyids (*Bashuchelys* sp.), and was previously considered as a diagnostic feature of Xinjiangchelyidae (Matzke *et al.* 2004, 2005; Tong *et al.* 2012*a*). Peng & Brinkman (1993) originally reported a reduced first thoracic rib in *Xinjiangchelys junggarensis* from the Upper Jurassic of Pinfengshan, Junggar Basin in Xinjiang, but Rabi *et al.* (2013) noted a long first thoracic rib in this species. An unreduced first thoracic rib has been reported recently in *Xinjiangchelys radiplicatoides* from the Middle–Upper Jurassic of the Junggar Basin (Brinkman *et al.* 2013*a*), while a partly reduced first thoracic rib that extends to the distal fifth of the first costal width is reported in *Annemys levensis* (but coded as 'long first thoracic rib' by Rabi *et al.* 2014). An unreduced first thoracic rib is considered a plesiomorphic feature, being present in primitive turtles such as *Proganochelys* and *Heckerochelys* (Gaffney, 1990; Sukhanov, 2006). This character appears to be variable among xinjiangchelyids, and

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its systematic significance among the group remains unclear.

The ornamentation of tiny irregular vermiculated furrows seen in the Phu Noi turtles is particular and distinct from the smooth shell surface, or the radiating ridges known in other xinjiangchelyid members. Such an ornamentation is somewhat reminiscent of that of *Sinemys gamera* and *S. brevispinus* (Brinkman & Peng, 1993*b*; Tong & Brinkman, 2013).

Based on the comparisons above, the turtle remains from Phu Noi appear to be different from all other primitive Eucryptodira, and therefore a new genus and new species are erected: *Phunoichelys thirakhupti* gen. et sp. nov. The new taxon is assigned to the family Xinjiangchelyidae (*sensu* Tong *et al.* 2012*b*), a diverse group of basal eucryptodiran turtles known mainly from the Middle and Upper Jurassic of China and Central Asia. The taxonomic content of Xinjiangchelyidae is still unstable, depending on phylogenetic datasets and phylogenetic methods, and is also subjective to authors. Rabi *et al.* (2014) proposed a phylogenetic definition for Xinjiangchelyidae as being 'the most inclusive clade containing *Xinjiangchelys junggarensis* Ye, 1986, but not *Sinemys lens*, *Macrobaena mongolica* Tatarinov, 1959, or any species of recent turtle'. Although this definition should bring some stability, being not character based it does not favour any current phylogenetic hypotheses. The study of Anquetin (2012) proposed a restricted and alternative content for the Xinjiangchelyidae of Tong *et al.* (2012*b*) including *Xinjiangchelys qiguensis*, *C. latimarginalis*, *Annemys levensis* and *Siamochelys peninsularis* Tong, Buffetaut & Suteethorn, 2002 on the basis of the morphology of the anterior plastral lobe and sinuous midline contact between the plastral scales. As these features are not preserved in our fossils, we followed the study of Tong *et al.* (2012*b*) and estimate that the discovery of new material in the future (including skull, the anterior part of the plastron and posterior part of the carapace) may help to better understand its systematic relationships. As defined in Tong *et al.* (2012*b*), Xinjiangchelyidae contains six genera and more than a dozen species in Asia. Based on the plastron/carapace connection, two groups can be recognized in that family. A primitive group with a sutured plastron/carapace connection is known from the Middle and Upper Jurassic of the Sichuan Basin, China; it includes *Chengyuchelys* Young & Chow, 1953 (*C. baenoides* Young & Chow, 1953; *C. latimarginalis* (Young & Chow, 1953); *C. radiplicatus* (Young & Chow, 1953)); *Tienfuchelys* Young & Chow, 1953 (*T. tzuyangensis* Young & Chow, 1953; *T. chungkingensis* (Young & Chow, 1953) and *T. zigongensis* (Peng, Ye, Gao, Shu & Jiang, 2005)); *Yanduchelys delicatus* Peng, Ye, Gao, Shu & Jiang, 2005; and *Protoxinjiangchelys salis* Tong, Danilov, Ye, Ouyang & Peng, 2012*a*. A more derived group with a ligamentous plastron/carapace connection is known from the Jurassic of China and Central Asia; it includes *Xinjiangchelys* Ye, 1986 (*X. junggarensis* Ye, 1986; *X. oshanensis* (Ye, 1973); *X. tianshanensis* Nessov, 1995; *X. qiguensis* Matzke, Maisch, Sun, Pfretzschner & Stöhr, 2004; *X. chowi* Matzke, Maisch, Sun, Pfretzschner & Stöhr, 2005; *X. rediplicatoides* Brinkman, Eberth, Xu & Wu, 2013*a*; *X. wusu* Rabi, Zhou, Wings, Sun & Joyce, 2013; and *Annemys* Sukhanov & Narmandakh, 2006 (*A. latiens* and *A. levensis*). In addition, *Siamochelys peninsularis* Tong, Buffetaut & Suteethorn, 2002 from the Jurassic of Southern Thailand has been placed within Xinjiangchelyidae according to the phylogenetic analysis; but the same analysis failed to resolve the relationships of this taxon with other members of the family (Anquetin, 2012). In some works, *Annemys* has been included in *Xinjiangchelys* based on the phylogenetic analyses (Matzke *et al.* 2004; Tong *et al.* 2012*b*), but subsequent studies considered it as a separate genus (Wings *et al.* 2012; Rabi *et al.* 2013, 2014), an opinion that we follow here since the skull morphology of *Annemys* is very different from that of *Xinjiangchelys*. *Phunoichelys* appears to be closer to the primitive xinjiangchelyids from the Sichuan Basin than to *Xinjiangchelys* and *Annemys* in having a sutured plastron/carapace connection, and particularly to *Yanduchelys* in that the marginals extend onto the second to seventh costals.

5. Conclusion

As currently documented, the turtle assemblages of the Khorat Group (latest Jurassic to mid-Cretaceous) in NE Thailand are composed predominantly of trionychoids (Tong *et al.* 2009*b*). The oldest formation, the Phu Kradung Formation, where the new turtle remains come from, has yielded the large basal trionychoid *Basilochelys macrobios* in its upper part (Tong *et al.* 2009). Although a recent phylogenetic analysis placed *Basilochelys* in a more basal position among Eucryptodira, between xinjiangchelyids and sinemydids/'macrobaenids', because of the presence of a pair of large basipterygoid processes (Rabi *et al.* 2013), its derived features (broad entoplastron and strong ornamentation of vermiculated ridges on the shell surface that are comparable to those of nanhsiungchelyids) clearly separate this taxon from the basal Eucryptodira. The discovery of a xinjiangchelyid turtle in Thailand adds to the still poorly known turtle fauna of the Phu Kradung Formation and extends the geographical distribution of that family to SE Asia. Lapparent de Broin (2004) reported *Xinjiangchelys* sp. from the Lower Cretaceous Grès Supérieurs Formation of Laos, but subsequent observations revealed that the specimen belongs to the adocid *Shachemys* (Syromyatnikova, pers. comm.).

The presence of xinjiangchelyid turtles in the Phu Kradung Formation is of stratigraphical importance. The age of the Phu Kradung Formation is still controversial. It was previously considered as Late Jurassic based on the studies of dinosaur remains (Buffetaut, Suteethorn & Tong, 2006; Buffetaut & Suteethorn, 2007). However, recent palynological studies suggested an Early Cretaceous age for the Phu Kradung

https://doi.org/10.1017/S0016756814000223 Published online by Cambridge University Press

Formation, but a latest Jurassic age cannot be excluded for its lowermost part because of the absence of the key Early Cretaceous marker taxa (Racey & Goodall, 2009). Xinjiangchelyids are dominant components in the turtle faunas of the Upper Jurassic of China and Central Asia, while the Early Cretaceous turtle fauna is mainly composed of sinemydids and 'macrobaenids'. Only a few xinjiangchelyids have been hitherto recorded from the Early Cretaceous: a shell of *Xinjiangchelys* sp. from the Tugulu Group, Xinjiang, China and an undescribed specimen from the Okurodani Formation, in central Japan (Hirayama, 2006). The presence of the xinjiangchelyid *Phunoichelys* in the lower part of the Phu Kradung Formation is in favour of a Late Jurassic age for that part of the formation, although admittedly turtles from the lowermost Cretaceous are still poorly documented in Asia.

Acknowledgements. The excavations and research at the Phu Noi locality are supported by Mahasarakham University fiscal year 2014 grant. E. Buffetaut's visits to Thailand have been supported by grants from the Centre National de la Recherch Scientifique, Paris. We thank all colleagues who took part the field work at Phu Noi and two anonymous reviewers for improving the manuscript.

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