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A new species of *Cuora* (Testudines: Geoemydidae) from the Miocene of Thailand and its evolutionary significance

WILAILUCK NAKSRI*†‡, HAIYAN TONG‡, KOMSORN LAUPRASERT*,
VARAVUDH SUTEETHORN‡ & JULIEN CLAUDE§

*Department of Biology, Faculty of Science, Mahasarakham University,
Kantarawichai, Maha Sarakham, Thailand 44150
‡Palaeontological Research and Education Centre, Mahasarakham University,
Khamriang, Kantarawichai, Maha Sarakham, Thailand 44150
§Institut des Sciences de l'évolution de Montpellier, UMR 5554 CNRS, Université de Montpellier 2,
cc064, 2, place Eugène Bataillon, 34095, Montpellier, France

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Abstract – A new species of *Cuora*, *Cuora chiangmuanensis* sp. nov., is described on the basis of a nearly complete shell with limb bones from the late Middle – early Late Miocene Chiang Muan Mine, Phayao Province (Northern Thailand). *C. chiangmuanensis* is distinguished from other fossil and living *Cuora* species mainly on the basis of its plastral morphology. Among fossil and extant *Cuora* taxa, the new species appears to be a missing link between the taxa from Southeast Asia and those from East Asia. It represents the earliest record of the genus and demonstrates that by 11–12 Ma, Asian box turtles were already present in Southeast Asia.

Keywords: *Cuora*, Geoemydidae, Miocene, Thailand, evolution, Southeast Asia.

1. Introduction

Cuora Gray, 1855 is a living and fossil genus of Geoemydidae, which is geographically restricted to Asia. Living species of *Cuora* are found in both continental areas and insular regions of Southeast and East Asia (Iverson, 1992; Parham *et al.* 2001) as shown in Figure 1. During the last three decades, the genus has received scientific interest in terms of systematics and taxonomy (Parham *et al.* 2004; Stuart & Parham, 2004; Blanck, McCord & Le, 2006; Spinks, Thomson & Shaffer, 2009; Spinks *et al.* 2012). Hypotheses regarding phylogenetic relationships within the genus are diverse (Yasukawa, Hirayama & Kikida, 2001; Honda *et al.* 2002; Stuart & Parham, 2004; Spinks & Shaffer, 2007; Zhang *et al.* 2008; Spinks, Thomson & Shaffer, 2009; Spinks *et al.* 2012). Among major findings, recent phylogenetic studies (Spinks, Thomson & Shaffer, 2009) suggest that the genera *Pyxidea* Gray, 1863 and *Cistoclemmys* Gray, 1863 should be included in *Cuora* for the genus to be monophyletic, a position that we adopt here. In addition to uncertainties regarding the phylogeny of the genus, species delimitation hardly reaches a consensus: the number of recognized species within the genus *Cuora* still varies from author to author from 10 living species (Fritz & Havas, 2006) to 12 or 13 living species (Iverson, 2008; Spinks, Thomson & Shaffer, 2009; Turtle Taxonomy Working Group, 2011). Taxonomy and systematics is rendered difficult for at least three reasons:

(1) Some species have a small geographical range or are unknown in the wild. For instance, *Cuora yunnanensis* was considered extinct until it was recently rediscovered (Zhou & Zhao, 2004; Blanck, 2005; He *et al.* 2007); species such as *C. mccordi* were for a long time unknown in the wild (Zhou *et al.* 2008).

(2) The presence of nuclear mitochondrial pseudogenes has led to misinterpretations in molecular-based phylogenies (Spinks, Thomson & Shaffer, 2009).

(3) Incomplete lineage sorting and introgression seems common between species of *Cuora* and between *Cuora* and other geoemydid genera (Stuart & Parham, 2007; Spinks, Thomson & Shaffer, 2009). This complexity is well illustrated by the species *C. serrata* Iverson & McCord, 1992. This species was thought to result from hybridization in a turtle farm for the pet trade since it was not known in the wild (Parham *et al.* 2001; Stuart & Parham, 2004, 2007). This taxon was later discovered in the wild and analysed showing that the hybridization was not necessarily driven by farming practices only (Shi *et al.* 2005; Spinks, Thomson & Shaffer, 2009).

Thanks to an increasing number of studies, the systematics of *Cuora* has nevertheless progressed, but problems in species delimitation still impact the way we understand it. Different genes provide different signals, possibly owing to introgression and hybridization (Spinks, Thomson & Shaffer, 2009). Recently, Spinks *et al.* (2012) provided one of the most detailed molecular studies, which resulted in much clearer and better supported nodes within the *Cuora* genus.

On the other hand, the fossil record of the genus is poorly documented, especially for pre-Neolithic times. A better knowledge of fossil *Cuora* can certainly help form a better understanding of the systematics and

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†Author for correspondence: nwilailuck@gmail.com

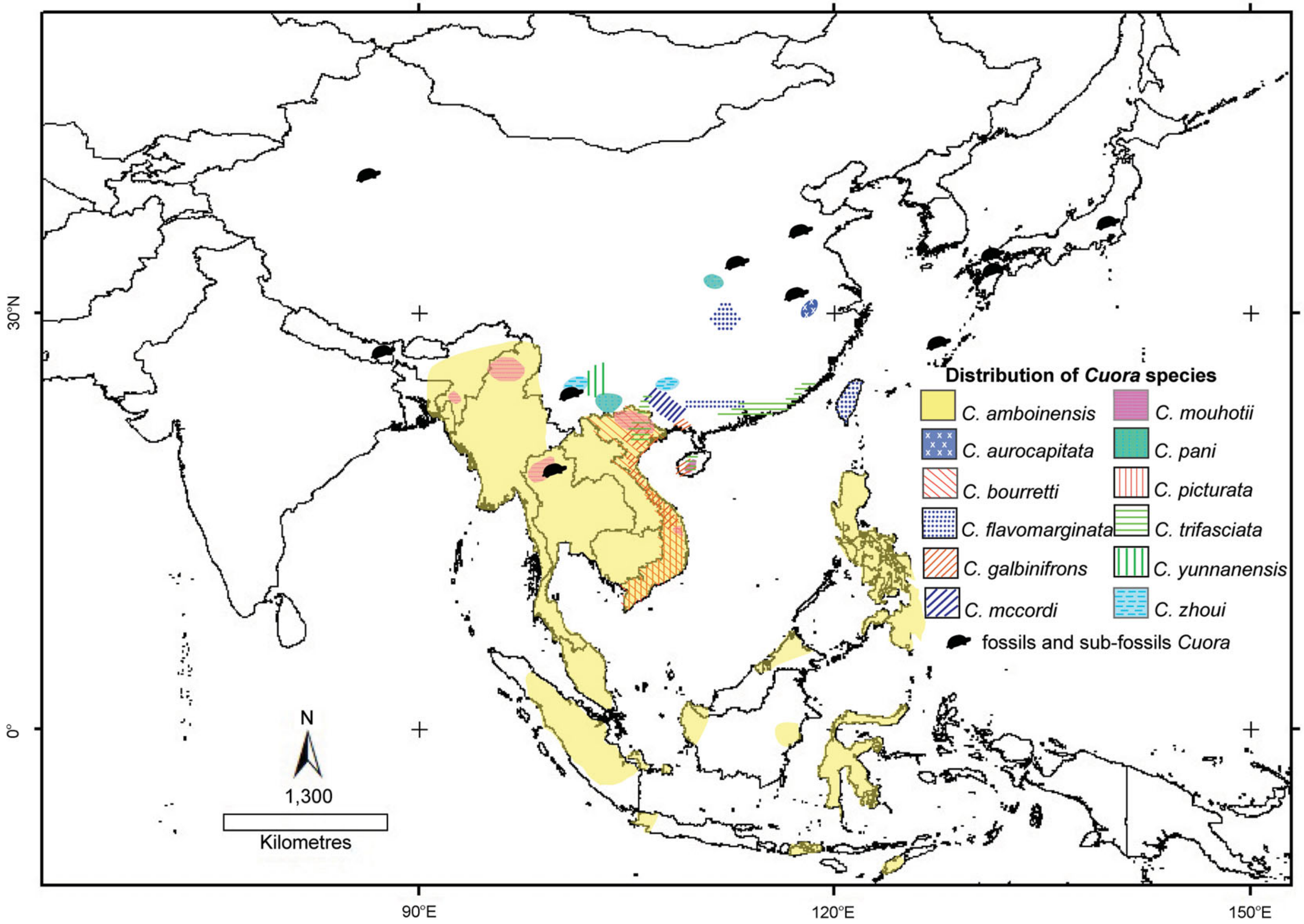

Figure 1. (Colour online) Distribution of living, sub-fossil and fossil *Cuora* species (the living distribution was compiled from Nutaphand, 1979; McCord & Iverson, 1991; Fong, Parham & Fu, 2002; Bonin, Devaux & Dupre, 2006; Turtle Taxonomy Working Group, 2011; Spinks *et al*. 2012).

evolution of the genus. Fossil *Cuora* have been recorded (see Fig. 1) from the Late Miocene to the Neolithic of China and Japan (Yeh, 1994*b*; Takahashi, Otsuka & Ota, 2008), including *Cuora pitheca* Yeh, 1981 from the Late Miocene of Lufeng, Yunnan, China; *C. miyatai* (Shikama, 1949) from the Middle Pleistocene of Oita Prefecture in Kyushu, and Tochigi and Yamaguchi prefectures in Honshu, Japan (Hirayama, 2007); *Cuora* sp. from the Pliocene of Anhui, China (Yeh, 1994*a*); and *C. flavomarginata* from the Late Pleistocene and Neolithic of China (Zhejiang, Shandong, Henan; Yeh, 1961, 1983, 1985*a,b*; Yeh & Zhang, 1994) and the Late Pleistocene of the Ryukyu Archipelago, Japan (Takahashi, Otsuka & Ota, 2008).

In this paper, we report on a recently discovered specimen of *Cuora* from the late Middle – early Late Miocene of the Chiang Muan coal mine in Northern Thailand. The detailed description and systematic study of that specimen is presented here. It is assigned to a new species, *Cuora chiangmuanensis* sp. nov. Its morphology and phylogenetic relationships with modern taxa shed new light on the origin and evolutionary history of Asian box turtles.

2. Geological setting

Chiang Muan coal mine is located in the Chiang Muan Basin, Tambon Ban Sra, Chiang Muan District, Phayao Province, Northern Thailand (Fig. 2). The Tertiary sedimentary rocks of the Chiang Muan coal mine consist of alternating beds of conglomerates, sandstones, mudstones, claystones and coal, which have yielded a rich vertebrate fauna. The palaeomagnetic study and mammalian fossils indicate a late Middle Miocene to an early Late Miocene age for this sequence (about 11–12 Ma, Kunimatsu *et al.* 2004; Pickford *et al.* 2004; Silaratana *et al.* 2004 or 9.8–13 Ma, Suganuma *et al.* 2006). The vertebrate assemblage from Chiang Muan Mine includes fishes, crocodiles, birds, mammals, snakes and turtles (Nakaya *et al.* 2002; Silaratana *et al.* 2004). Most turtle remains are shell elements which belong to geoemydid turtles. There are at least two geoemydid turtles based on the morphology of the xiphiplastron. In addition, Nakaya *et al.* (2002) reported Testudines, fam., gen. et sp. indet. Most specimens are represented by isolated plates. The specimen of *Cuora* studied in this work is one of the most complete geoemydid turtle specimens. It was collected by Mr Nikorn Wongchai, a geologist of the mine at that time, from the CMu 6 level, a ligneous claystone level under the lower massive coal seam (LM).

3. Material analysed and fossil preparation

The studied specimen (Cme-1/1) is housed at the Chiang Muan Mine museum, Phayao Province, Thailand. It comprises an articulated shell and a humerus and femur as disarticulated elements, all belonging to one individual. The material is fragile and was partly embedded within lignite. The material was first prepared using a needle to remove the matrix, then cleaned using 10 % sodium hydroxide (NaOH) to allow more details of sulci and sutures to be visible. It was then rinsed in water and the surface was cleaned using a soft brush and finally dried.

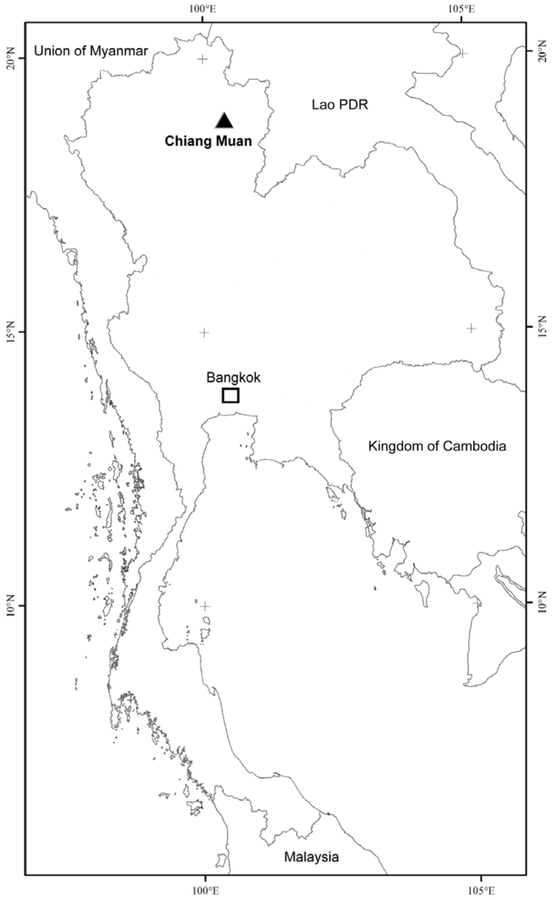

Figure 2. Map showing the location of Chiang Muan coal mine in Phayao Province, Northern Thailand (indicated by black triangle).

The specimens consulted for the comparison section of this study are listed in Table 1.

Institutional abbreviations. CIB – Chengdu Institute of Biology, Chinese Academy of Sciences, China; Cme – Chiang Muan Mine museum; CUMZ(R) – Chulalongkorn University Museum Zoology (Reptile), Bangkok, Thailand; IVPP – Institute of Vertebrate Palaeontology and Palaeoanthropology, Chinese Academy of Sciences, Beijing, China; PRC – Palaeontological Research and Education Centre, Mahasarakham, Thailand; RH – Ren Hirayama's Collection; THUb – Teikyo Heisei University, Japan; YY – Yuichiro Yasukawa's Collection, Japan.

Anatomical abbreviations. Ab – abdominal; An – anal; C – costal; Cv – cervical; Fe – femoral; H – humerus; hyp – hypoplastron; m – marginal; n – neural; N – nuchal; p – peripheral; Pl – pleural; sp – suprapygal; V – vertebral; xi – xiphiplastron.

Table 1. List of *Cuora* specimens in the comparison section of this study

Species	Specimen number and/or references
Cuora chiangmuanensis	Cme-1/1
C. pitheca Yeh, 1981	IVPP V.6178; IVPP V.6178.1; IVPP V.6178.2
C. miyatai (Shikama, 1949)	IGPS Reg. 65667; Hagesawa & Ota,1980
C. amboinensis (Riche, 1801)	CUMZ(R) 1996-01-08(1); CUMZ(R) 1997-12-25(2); CUMZ(R) 1997-12-25(3); CUMZ(R) 2008-08-06(7); RH 149; RH 838
C. aurocapitata Luo & Zong, 1988	RH 915; THUb 13; THUb 14
C. bourreti Obst & Reimann, 1994	Shi, 2008; Stuart & Parham, 2004
C. flavomarginata (Gray, 1863)	ICB 639084; ICB 64 III 088; IVPP V. 2520; RH 65; RH 104; RH 105; RH 106; RH 208; RH 429; RH 431; RH 432; RH 433; RH 435; RH 436; RH 438; RH 446; RH 629; RH 697; RH 928; RH 942
C. galbinifrons Bourret, 1939	ICB 64 III 088; RH 773; RH895; RH 900; RH 916
C. mccordi Ernst, 1988	RH 934; RH 950; RH 989; RH 1078
C. mouhotii (Gray, 1862)	CUMZ(R)-unnumbered; Stuart & Parham, 2004
C. pani Song, 1984	RH 903; RH 951; RH 989; RH 1079; Parham & Li, 1999
C. picturata Lehr, Fritz & Obst, 1998	Shi, 2008; Stuart & Parham, 2004
C. trifasciata (Bell, 1825)	RH 250; YY1; YY2
C. yunnanensis (Boulenger, 1906)	Shi, 2008
C. zhoui Zhao, 1990	RH 1157; Shi, 2008

4. Systematic palaeontology

Order TESTUDINES Linnaeus, 1758
Suborder CRYPTODIRA Cope, 1868
Superfamily TESTUDINOIDEA Batsch, 1788
Family GEOEMYDIDAE Theobald, 1868
Genus *Cuora* Gray, 1855
Cuora chiangmuanensis sp. nov.
Figure 3

Etymology. The species name refers to the type locality.

Holotype. An articulated carapace and a complete posterior lobe of a plastron, a humerus and a femur (Cme-1/1).

Type locality and horizon. Chiang Muan coal mine, Tambon Ban Sra, Chiang Muan District, Phayao Province, Northern Thailand; CMu 6, ligneous claystone under lower massive coal seam (LM), late Middle or early Late Miocene.

Diagnosis. A species of *Cuora* of moderate size (carapace length around 20 cm); carapace oval in shape with smooth margin. It is diagnosed by the following combination of characters: absence of vertebral keel extending anteriorly; first vertebral wide anteriorly nearly reaching the second marginal; smooth posterior margin (differs from *C. mouhotii* and *C. serrata*); fully divided anal scutes (unlike *C. bourreti*, *C. flavomargianata*, *C. galbinifrons* and *C. picturata*); very small anal notch present but smaller than that of *C. pitheca*, *C. mccordi*, *C. pani*, *C. mouhotii*, *C. trifasciata* and *C. zhoui*; well-developed lips on the posterior lobe of the plastron.

Measurements. See Table 2.

4.a. Description

Preservation. The holotype (Cme-1/1) consists of a nearly complete carapace, the posterior half of a plastron, a left humerus and a femur. The carapace is broken into two parts along the midline and the left part of the carapace is turned over to lie on the ventral surface of the plastron. The posterior lobe of the plastron is turned 90° to the right (see Fig. 3).

The shell is flattened dorso-ventrally and the anterior margin of the carapace is damaged. Sulci and sutures are well preserved except for the fifth vertebral sulcus, which cannot be observed. The preserved part of the carapace consists of the nuchal plate, the first to eleventh left and right peripheral plates, the first to fifth and distal part of the sixth to eighth left costal plates and the first to eighth right costals. The medial portions of the fifth to eighth costal plates of the right side are broken. The first and second neural plates are preserved in their original position and presented in dorsal view, while four other neural plates are disarticulated from the carapace and scattered on the visceral side of the left costal plates, presented on the internal view. Other neural plates are not preserved. The first suprapygal and pygal are missing. The second suprapygal is preserved but the anterior and left parts are missing. On the plastron, only the hypoplastra and xiphiplastra are preserved.

Table 2. Shell measurements (in millimetres) of the holotype of *Cuora chiangmuanensis* sp. nov.

Length of carapace (estimated)	200
Length of posterior lobe	125
Midline length of abdominal	45
Midline length of femoral	12
Midline length of anal	60
Midline length of hypoplastron	60
Width of hypoplastron	125
Midline length of xiphiplastron	52
Width of xiphiplastron	118
Length of nuchal	30
Greatest width of nuchal	43
Anterior width of nuchal	30
Posterior width of nuchal	18
Length of neural I	20
Greatest width of neural I	25
Length of neural II	24
Greatest width of neural II	28

Carapace. (Fig. 3a, b) The shell has an oval outline. The carapace outer surface is smooth without ornamentation or growth annuli. There are no fontanelles on the carapace (Fig. 3a, b). The carapace is not sutured to the plastron. The anterior and posterior carapace margins are smooth. The vertebral keel is indistinct.

The nuchal plate is hexagonal in shape with a narrow posterior end. The anterior rim of this plate is damaged. The first and second neural plates, preserved *in situ*, are hexagonal with short postero-lateral sides. The first neural is as wide as it is long. The second neural is slightly wider than long and longer than the first neural. The outline of the medial margin of the costal plates suggests that the third to fifth neural plates are also wider than long and hexagonal with short postero-lateral sides (see Fig. 3a1, b1). The four scattered neurals, presented in internal view, are interpreted as the third to sixth neurals. The neural formula

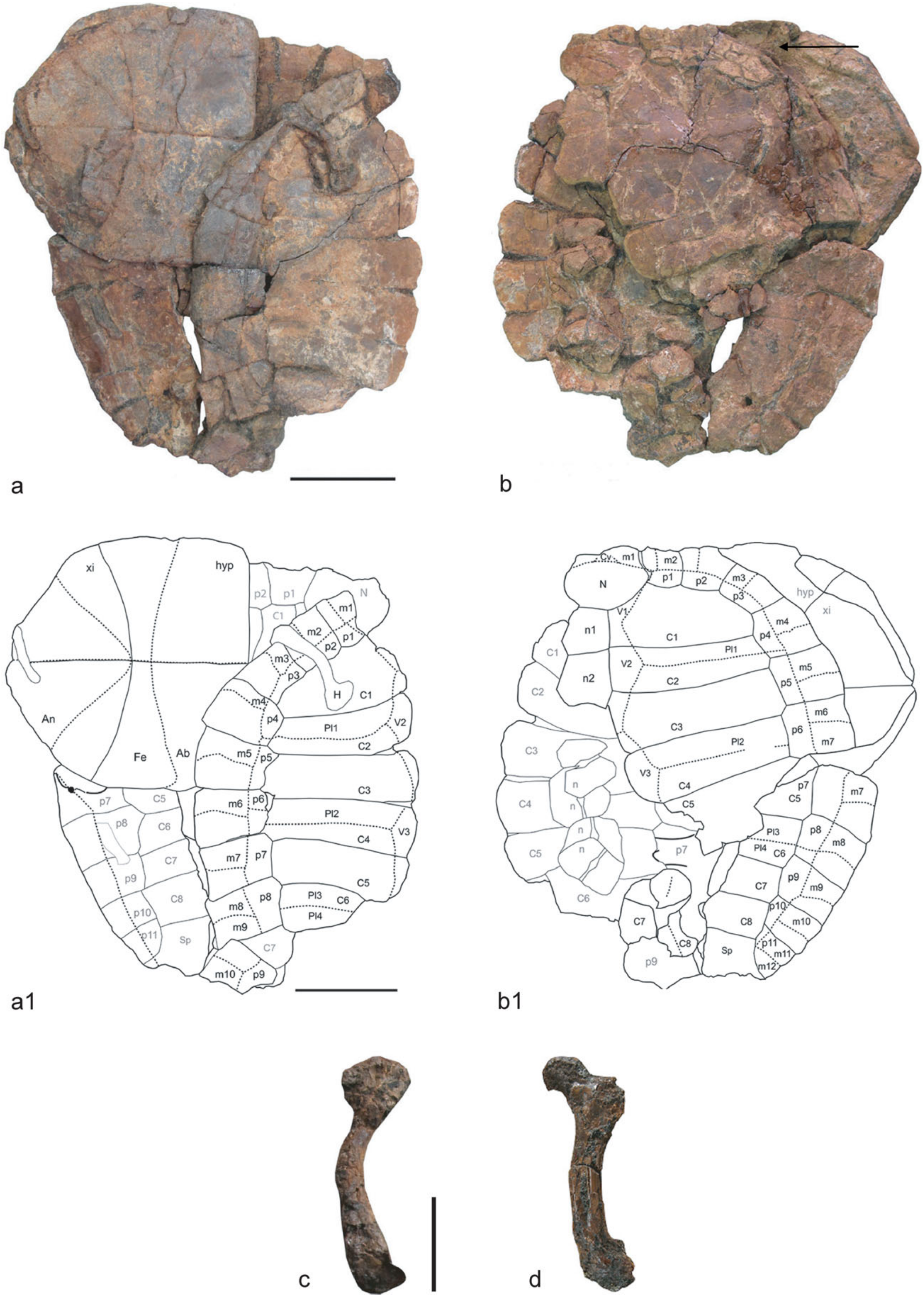

Figure 3. (Colour online) Shell and limb bones of *Cuora chiangmuanensis* sp. nov. from Chiang Muan Mine, Phayao Province. Holotype (Cme-1/1): (a, b) carapace and plastron; (c) humerus; (d) femur. Inguinal buttress is indicated by arrow. Scale bar of shell is 5 cm and that of limb bones is 2 cm.

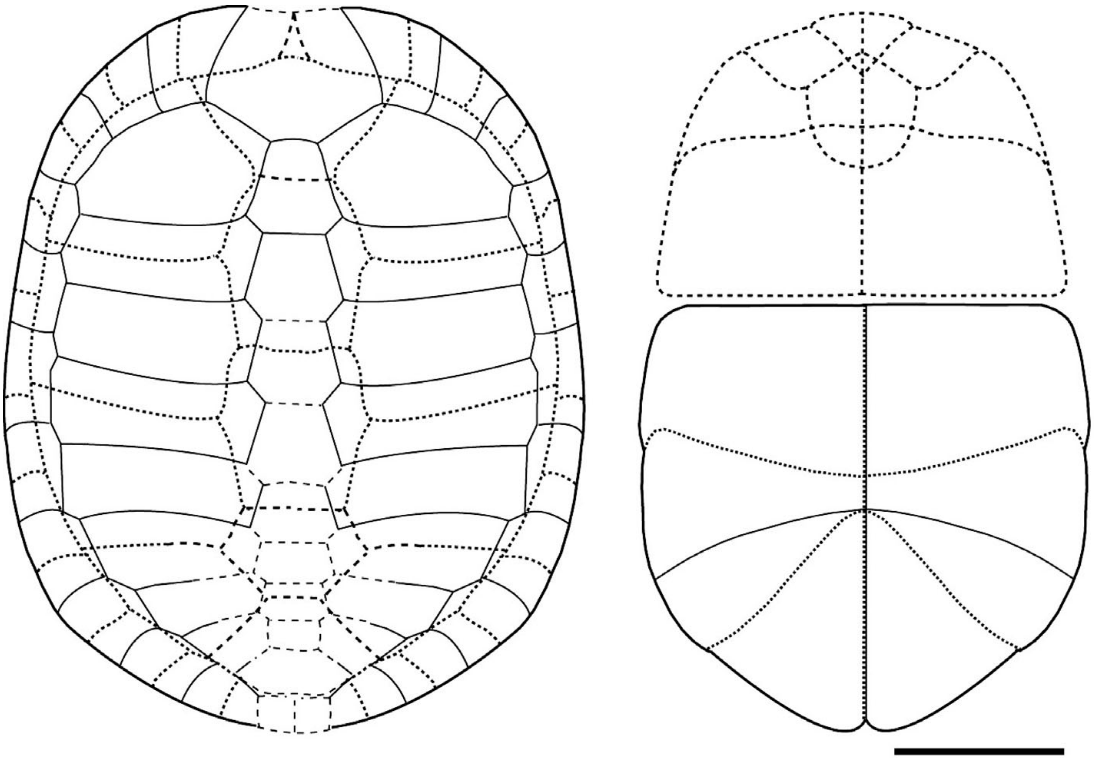

Figure 4. Reconstruction of the shell of *Cuora chiangmuanensis* sp. nov. Scale bar is 5 cm.

is, therefore, 6P,6P,6P,6P,6P,6P,?,?. The wide sixth neural with a long posterior margin indicates the presence of the seventh neural, but whether the eighth neural is present or absent is indeterminate. The presence and shape of the first suprapygal cannot be determined. As indicated by the outline of the peripherals, the eighth costals and by its preserved portions, the second suprapygal plate is probably hexagonal in shape. The pygal plate is not preserved. The first costal plate is the longest. It contacts the first peripheral plate to the anterior half of the fourth peripheral plate. The second to fourth costal plates are relatively short, slightly decreasing in length backwards. The fifth costal plate is curved posteriorly and reaches the eighth peripheral plate. There is a very short inguinal scar on the inner surface of the lateral end of the left sixth costal and seventh peripheral (see in Fig. 3a). The sixth and seventh costal plates are smaller and narrower; they are also curved posteriorly. The sixth costal plate contacts the eighth and ninth peripheral plates. The seventh costal plate contacts the ninth and tenth peripheral plates. The eighth costal plate contacts the tenth and eleventh peripheral plates. The first peripheral plate is longer than wide. The second to eleventh peripheral plates are more slender, mesio-laterally expanded and reduced in size posteriorly. The right seventh peripheral plate exhibits a distinct musk duct foramen on the ventral surface (see Fig. 3a1).

The cervical scute is incomplete. Its posterior part is rather wide. The first vertebral scute is as wide as the nuchal. It is wider anteriorly with the anterior margin more than twice its posterior margin, and nearly reaches the second marginal scute. The second and third vertebral scutes are rather narrow and hexagonal in shape with the posterior half narrower than their anterior half. The first pleural scute is long and extends posteriorly until the anterior half of the second costal plate, and contacts the anterior half of the fifth marginal scute. The second and third pleural scutes are shorter. The second pleural scute contacts the fifth and the sixth marginals, which can be observed clearly on the left side. The third pleural scute reaches the sixth to eighth marginal scutes. The fourth pleural scute is the smallest of all. It is slightly longer than wide. The pleuro-marginal sulcus is situated below the costo-peripheral suture.

Plastron. (Fig. 3a, b) Only the posterior half of the plastron is preserved. The plastral surface is smooth. The posterior border of the posterior plastral lobe is rounded. A very small anal notch is present. The hypoplastron is as long as the xiphiplatron in the midline. The anterior border of the hypoplastron corresponding to the pectoro-abdominal sulcus is straight and clearly rounded, indicating a hinge between the hyoplastra and hypoplastra. The hypo-xiphiplastral suture is slightly convex anteriorly. The abdomino-femoral sulcus is convex posteriorly. There is no constriction on the lateral borders of the xiphiplastra at the femoro-anal sulcus. The maximum length of the anal scutes is longer than the midline length of the abdominal scutes, which are both much longer than the midline length of the femoral scutes. The partial scute formula for the plastron is An > Ab > Fe. The maximum length of the anal scutes is 5.8 times greater than that of the femoral scutes. The femoro-anal sulci form a right angle between each other and oblique to the midline. This sulcus reaches the hypo-xiphiplastral suture at the midline.

On the inner surface of the plastron, a weak inguinal buttress is preserved on the left side (see Fig. 3b). The lip is well developed; it is very wide and flat on the anterior part, and becomes narrower posteriorly. The anal lip is rather wide and thick. The reconstruction of the shell is shown in Figure 4.

Humerus. (Fig. 3c) The left humerus was preserved as an isolated element on the left side of the carapace (Fig. 3a). It is 4.5 cm in length. It is nearly complete but flattened, especially the proximal and distal parts. The shaft is slender and slightly curved. The caput humerus is compressed. The lateral process is not preserved. The ectepicondyle foramen is damaged; its distal part is an open groove.

Femur. (Fig. 3d) A disarticulated femur was preserved above the left side of carapace before it was removed for preparation. It is 3.5 cm in length. It is complete but compressed laterally. The shaft is slender and slightly curved. Both the trochanter minor and trochanter major are damaged. The intertrochanter fossa is deep, narrow and open.

4.b. Comparison and discussion

4.b.1. *Systematic assignment*

The specimen from Chiang Muan displays geoemydid synapomorphies as indicated by the presence of inguinal musk duct foramina on the seventh peripheral (Hirayama, 1985; Gaffney & Meylan, 1988; Yasukawa, Hirayama & Kikida, 2001; Claude & Tong, 2004). The presence of a distinct hinge between the hyoplastron and hypoplastron and the absence of a distinct bony bridge are known in several independent geoemydid lineages (*Cuora*, *Cyclemys*, *Ptychogaster*). The reduced anal notch and the regular and wide hexagonal neural plates with short postero-lateral sides seen in Cme-1/1 are diagnostic of the genus *Cuora*. The large size and absence of the carapacial fontanelles between the costals and peripherals indicates that this specimen belongs to an adult individual. Following Spinks, Thomson & Shaffer (2009) and Spinks *et al.* (2012), we consider that the genus *Cuora* includes 12 evolving units that could be considered as extant species: *C. mccordi*, *C. galbinifrons*, *C. picturata*, *C. bourreti*, *C. trifasciata*, *C. amboinensis*, *C. mouhotii*, *C. yunnanensis*, *C. flavomarginata*, *C. zhoui*, *C. pani*, *C. aurocapitata*, plus the hybrid *C. serrata*.

In comparison with extant species of *Cuora* (see Table 3), the specimen from Chiang Muan clearly differs from *C. mouhotii* and *C. serrata* by its smooth carapacial margin and its smaller anal notch. It differs from *C. bourreti*, *C. picturata*, *C. flavomarginata* and *C. galbinifrons* in the presence of an anal notch and in lacking a vertebral keel. In *Cuora amboinensis*, *C. flavomarginata*, *C. bourreti* and *C. galbinifrons* the anal notch is absent, while *C. mccordi* and *C. pani* have a larger anal notch in comparison with our specimen. The specimen from Chiang Muan differs from *C. aurocapitata*, *C. pani*, *C. trifasciata*, *C. mouhotii*, *C. yunnanensis* and *C. zhoui* in the absence of the vertebral keel; this character, however, can vary during ontogeny. In addition, *C. chiangmuanensis* shares with *C. amboinensis*, *C. aurocapitata*, *C. galbinifrons* and *C. mccordi* the presence of a musk duct that is a closed foramen located in the middle of the seventh peripheral plate. In other species of *Cuora*, the musk duct is incised in the ligamentous area. *Cuora chiangmuanensis* differs from *C. bourreti*, *C. flavomarginata*, *C. galbinifrons* and *C. picturata* by having fully divided anal scutes as seen in other members of Geoemydidae. It differs from *C. amboinensis*, *C. bourreti*, *C. flavomarginata*, *C. galbinifrons* and *C. picturata* by the presence of a very small anal notch which is, however, smaller than in *C. mccordi*, *C. pani*, *C. trifasciata* and *C. zhoui*. *C. chiangmuanensis* has a flat lateral lip on the posterior lobe, which is still wide on the xiphiplastral part. This is similar to *C. mouhotii* but different from all other *Cuora* species. Furthermore, the femoral scute has a very short midline length in *C. chiangmuanensis* as in *C. amboinensis*, *C. flavomarginata* and *C. picturata*, while other *Cuora* species have a longer femoral midline length.

In addition to living taxa, a few fossil *Cuora* species have been reported: *C. pitheca* Yeh, 1981 from the Late Miocene of Lufeng, Yunnan and *C. miyatai* (Shikama, 1949) from the middle Pleistocene of Japan (Hasegawa & Ota, 1980; Yeh, 1981, 1985). *Cuora chiangmuanensis* differs from *C. pitheca* in having a trapezoid first vertebral scute which is much wider anteriorly than posteriorly, nearly reaching the second marginal scute, and in having the clearly longer than wide second vertebral. In *C. pitheca*, the first vertebral scute is roughly rectangular in shape, with the anterior border only slightly wider than the posterior one and reaching laterally to the mid-width of the first marginal scute; the second vertebral scute is slightly wider than long (Yeh, 1981, 1985). *Cuora miyatai* is similar to *C. chiangmuanensis* in the first vertebral scute reaching the second marginal scute. These two species differ from one another in the shape of the first vertebral scute: the anterior border of that scute is much longer than the posterior one in *C. chiangmuanensis*, while the anterior border is only slightly longer than the posterior one in *C. miyatai*. Furthermore, *C. miyatai* differs from *C. chiangmuanensis* in the second and third vertebral scutes, which are wider than long.

Concerning the plastron, *Cuora chiangmuanensis* and *C. miyatai* are similar in having a slightly wider than long posterior lobe, while the posterior lobe of *C. pitheca* is longer than wide. The abdominal is shorter than the anal scute in *C. chiangmuanensis*, differing from *C. pitheca* and *C. miyatai* in which the abdominal is longer than the anal scute. The ratio of anal/femoral midline length is less than three in *C. pitheca*, while this ratio is greater in *C. chiangmuanensis* and *C. miyatai*. In addition, *C. chiangmuanensis* shares with *C. pitheca* a wide lateral lip on the visceral surface of the posterior lobe; but the lip is flat in our specimen, while *C. pitheca* has a more prominent lip (IVPP V6718.2 and Yeh, 1985, fig. 1). Furthermore, *Cuora chiangmuanensis* differs from *C. pitheca* and *C. miyatai* in having a very small anal notch. The anal notch is clearly deeper in *C. pitheca*, and it is absent in *C. miyatai* (see Table 3; Figs 5, 6).

On the basis of the comparisons given above, *Cuora* from Chiang Muan differs from all other *Cuora* species by a combination of characters (see diagnosis), particularly in the posterior half of the plastron. It is, therefore, assigned to a new species, *Cuora chiangmuanensis* sp. nov. Among the extant and fossil *Cuora*, the new species from Thailand is most similar to *C. amboinensis* and *C. miyatai* with 9.66/13 and 8.66/12 shared characters, respectively. Similarities and differences between the living and fossil taxa are summarized in Table 3 (see the method of computation in the footnote ‖ of the table).

Table 3. Comparison of *Cuora chiangmuanensis* sp. nov. with extinct and living species of *Cuora*

Characters/species of *Cuora*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
The first vertebral scute reaches the second marginal scute	yes	no	yes	no	yes	no	no	no	no	no	yes	no	yes	yes	yes
Medial carapace carina extending anteriorly	no	no	yes	no	yes	no	yes	no	yes	yes	yes	no	yes	no/yes	yes
Lip on the visceral side of hypoplastron	flat	elevated	flat	flat	elevated	?	flat	flat	elevated	flat	flat	?	elevated	?	elevated
Lateral anal lip on the visceral side of xiphiplastron	wide	wide	narrow	narrow	narrow	?	narrow	narrow	wide	wide	narrow	?	wide	?	wide
Fully divided anal scute	yes	yes	yes	yes	yes	no	no/partial	no	yes	yes	yes	no	yes	yes	yes
Anal notch	small	deep	absent	absent	small	absent	absent	absent	small	deep	small & deep	absent	small	small or deep	small
Width to length ratio for the posterior plastral lobe (behind the hinge)[*]	A	C	A	B	C	A	B	C	A	A	B	A	C	C	A
Abdominal/anal midline length[†]	F	F	D	E	E	D	E	E	E	D	E	D	D	D	E
Abdomino-femoral sulcus[‡]	G	G	G	G	H	I	H	G	H	H	H	I	H	I	I
Musk duct foramina enclosed in seventh peripheral plate	present	?	?	present	present	?	present	absent	present	absent	absent	?	absent	?	absent
Anal to femoral midline length ratio[§]	J	K	J	J	K	K	J	K	K	K	K	J	K	K	K
Contact between the tenth marginal scute and the fifth vertebral scute	no	no	no	no	no	no	no	no	yes	yes	no	?	no	no	no
Plastral hinge	present	present	present	present	present	present	present	present	present	present	present	present	present	present	present
Characters shared with *C. chiangmuanensis*[‖]	–	7.33/12	8.66/12	9.66/13	7/13	4.66/10	6.66/13	7.16/13	8/13	5.83/13	7.16/13	4.99/9	6.5/13	5.16/10	5.16/10

1 – *C. chiangmuanensis*; 2 – *C. pitheca*; 3 – *C. miyatai*; 4 – *C. amboinensis*; 5 – *C. aurocapitata*; 6 – *C. bourreti*; 7 – *C. flavomarginata*; 8 – *C. galbinifrons*; 9 – *C. mccordi*; 10 – *C. mouhotii*; 11 – *C. pani*; 12 – *C. picturata*; 13 – *C. trifasciata*; 14 – *C. yunnanensis*; 15 – *C. zhoui*.

[*] A – wider than long; B – wider than long or longer than wide; C – longer than wide;

[†] D – abdominal longer than anal scute; E – abdominal longer, equal to, or shorter than anal scute; F – abdominal shorter than anal scute;

[‡] G – convex posteriorly; H – convex posteriorly or straight; I – straight;

[§] J – more than 3; K – less than 3.

[‖] We computed a ratio quantifying similarity between *C. chiangmuanensis* and other *Cuora* species. The denominator indicates the number of available characters, while the numerator indicates the number of similar characters. Since intermediate character states exist for multistate and ordered characters, they were given an inferior weight than if taxa differed by extreme states. Resemblance was therefore calculated so that closer states would proportionally account for more resemblances than distant states on a unit scale.

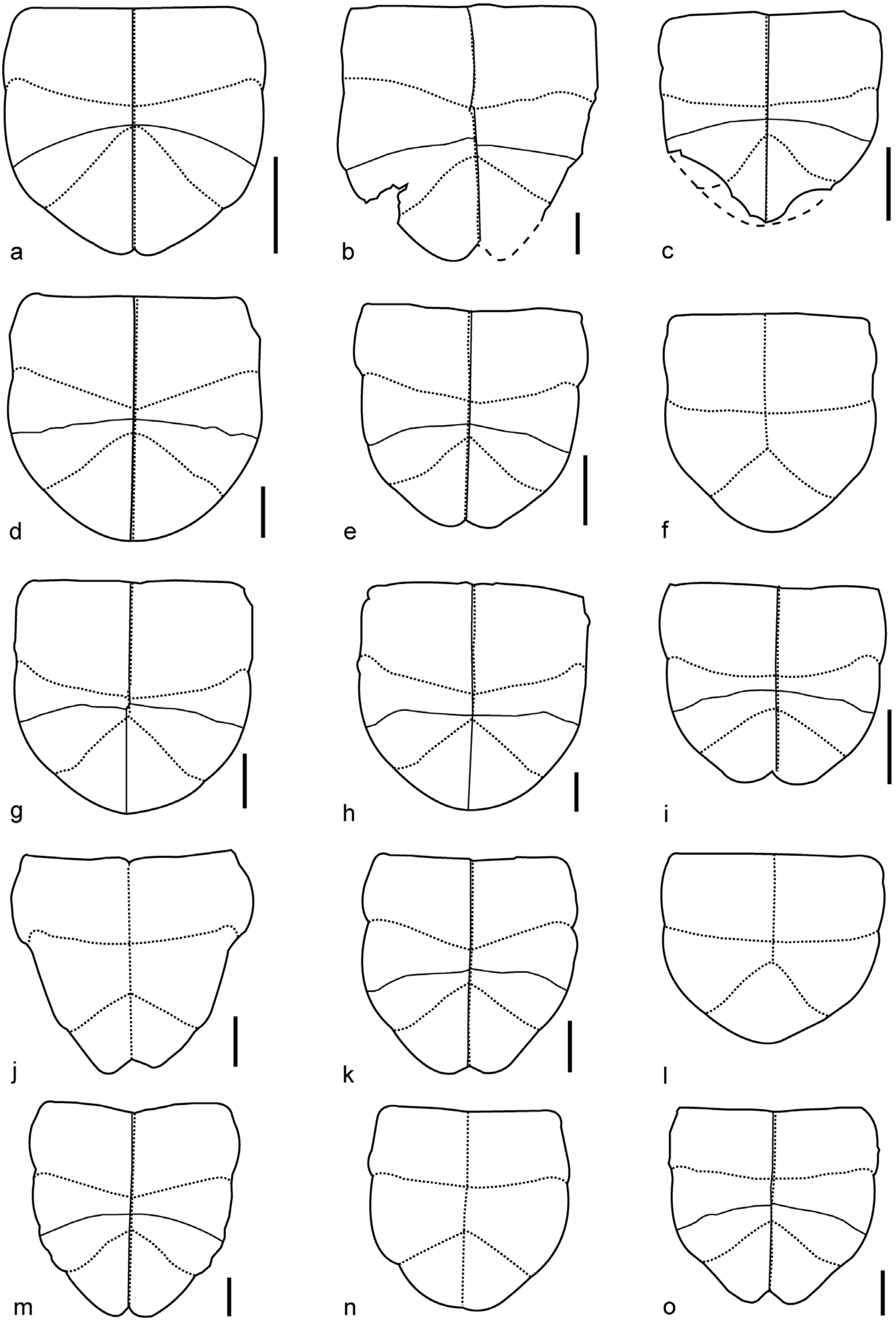

Figure 5. Posterior half of plastrons of *Cuora* in ventral view. (a) *C. chiangmuanensis* (Cme-1/1), (b) *C. pitheca* (IVPP, V.6178.2), (c) *C. miyatai* (IGPS Reg. 65667), (d) *C. amboinensis* (CUMZ(R) 1997–12–25(2)), (e) *C. aurocapitata* (RH 905), (f) *C. bourreti* (after Shi, 2008), (g) *C. flavomarginata* (RH9 82), (h) *C. galbinifrons* (RH 916), (i) *C. mccordi* (RH 950), (j) *C. mouhotii* (CUMZ(R)-unnumbered), (k) *C. pani* (RH 1079), (l) *C. picturata* (after Shi, 2008), (m) *C. trifasciata* (YY1), (n) *C. yunnanensis* (after Shi, 2008) and (o) *C. zhoui* (RH 1157). Scale bars are 2 cm.

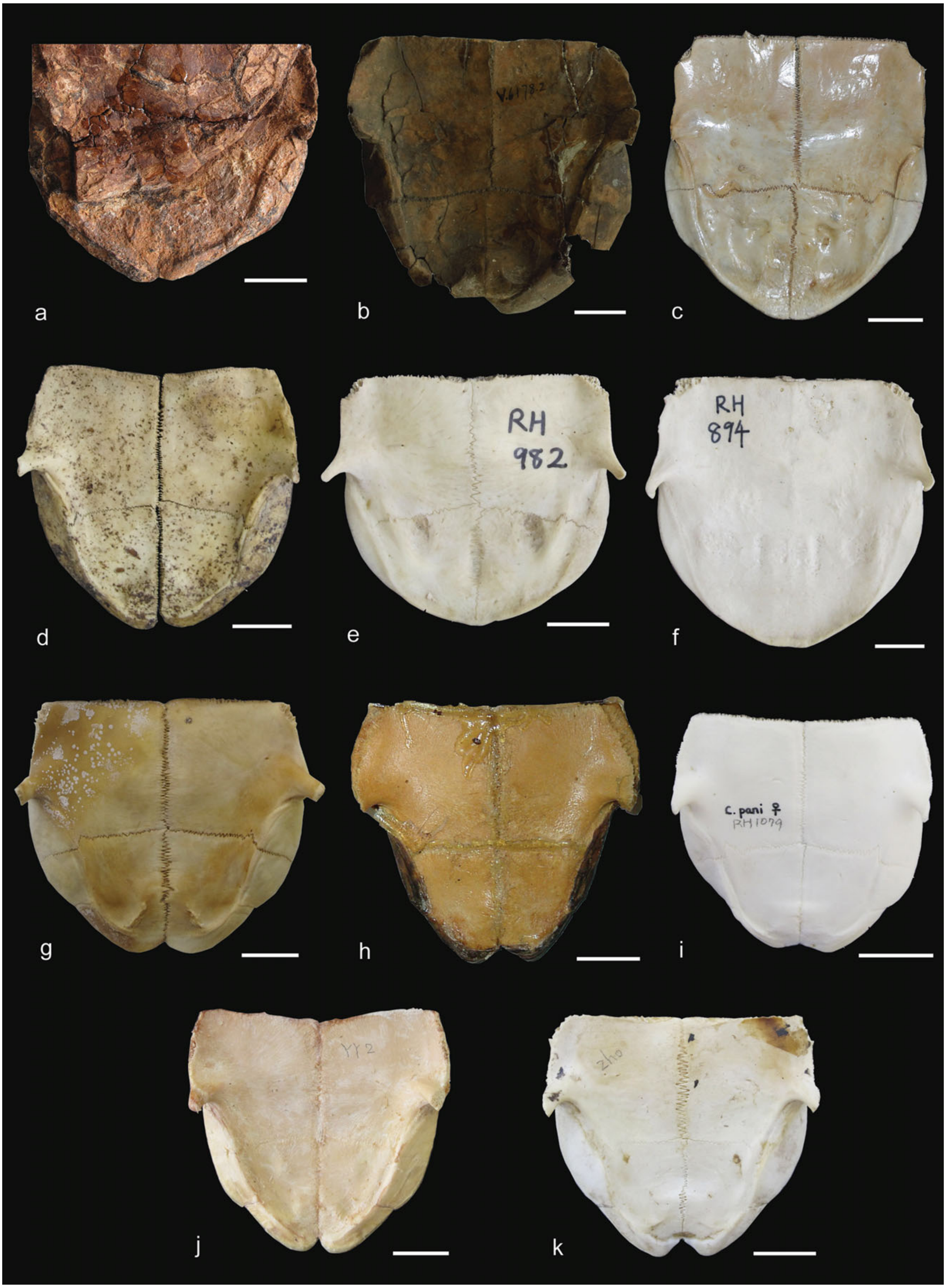

Figure 6. (Colour online) Posterior half of plastrons of *Cuora* in visceral view. (a) *C. chiangmuanensis* (Cme-1/1), (b) *C. pitheca* (IVPP, V.6178.2), (c) *C. amboinensis* (CUMZ(R)-1997–2–25(2)), (d) *C. aurocapitata* (TUTb14), (e) *C. flavomarginata* (RH982), (f) *C. galbinifrons* (RH894), (g) *C. mccordi* (RH989), (h) *C. mouhotii* (CUMZ(R)-unnumbered), (i) *C. pani* (RH1079), (j) *C. trifasciata* (YY2) and (k) *C. zhoui* (RH 1157). Scale bars are 2 cm.

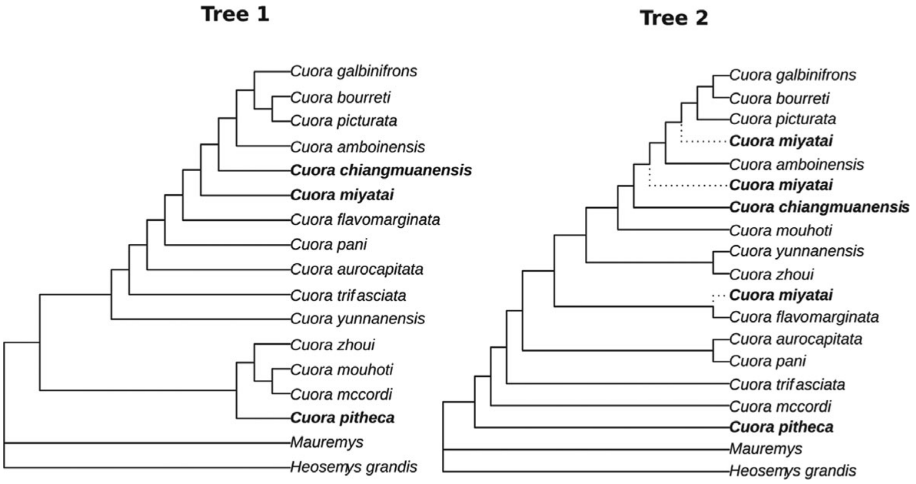

Figure 7. Most parsimonious phylogenetic hypotheses resulting from our study. Tree 1 is based only on morphological characters, while tree 2 presents the three most parsimonious hypotheses, constrained by the molecular scaffold following Spinks *et al.* (2012).

4.b.2. *Phylogenetic relationships*

Although the phylogenetic relationships among *Cuora* species are not completely congruent among authors, the most recent molecular phylogenies (Honda *et al.* 2002; Parham *et al.* 2004; Stuart & Parham, 2004; Blanck, McCord & Le, 2006; He *et al.* 2007; Iverson *et al.* 2007; Spinks & Shaffer, 2007; Spinks, Thomson & Shaffer, 2009) show that: (i) *C. bourreti*, *C. galbinifrons* and *C. picturata* form a monophyletic clade (characterized by absence of anal notch, absence of vertebral keel and fused anal scutes); (ii) *C. pani and C. aurocapitata* form a monophyletic clade (characterized by relatively flat shell, presence of vertebral keel and presence of small anal notch); and (iii) *C. amboinensis*, *C. mouhotii*, *C. bourreti*, *C. galbinifrons* and *C. picturata* tend to branch closer to each other (but not all phylogenies demonstrate this; see Spinks & Shaffer, 2007). This group, the majority of which are found in the southern range of *Cuora*, is characterized by at least one feature that can be interpreted as a symplesiomorphy: the first vertebral scute does not reach the second marginal (also found in *C. mccordi*).

Using nuclear DNA, Spinks *et al.* (2012) better resolved the phylogenetic relationships within *Cuora*. In this study, only the phylogenetic relationship of *Cuora mouhotii* with other southeastern *Cuora* was not well supported.

In order to determine the phylogenetic relationships of *C. chiangmuanensis*, a data matrix of 13 informative characters was gathered on the 12 living species and three fossil species. The tree was rooted with the help of two outgroups: *Heosemys grandis* (Gray, 1860) and *Mauremys sensu lato*. *Mauremys mutica* (Cantor, 1842), *Mauremys reevesi* (Gray, 1831) and *Mauremys leprosa* (Schweigger, 1812) were scored for determining the states of the *Mauremys sensu lato* tip.

Two analyses were run, the first one using only morphological characters and the second one constraining the relationships among living taxa using a molecular scaffold based on the phylogeny obtained from the nuclear data of Spinks *et al.* (2012). In that scaffold, only nodes that received bootstrap support above 95 % were considered; therefore, *Cuora mouhotii* formed a polytomy with Southeast Asian *Cuora* (*C. amboinensis*, *C. bourreti*, *C. picturata* and *C. galbinifrons*) and the group formed by other East Asian *Cuora*. Character descriptions and distributions are given in Appendix 1. Polymorphic characters were interpreted as intermediate characters. Characters were ordered, and all ordered multi-state characters were scaled so that those characters did not have a disproportionate effect over the binary characters in phylogeny estimation.

Parsimony analyses were performed in PAUP 4.0 b10 (Swofford, 1998) using random addition sequence, and the tree bisection-reconnection branch swapping algorithm across 10 000 replicates.

While the unconstrained analysis resulted in a single tree (Fig. 7), three most parsimonious hypotheses were found in using the molecularly constrained tree, which differed in the position of *Cuora miyatai*, either nesting it within the Southeast Asian taxa *C. chiangmuanensis*, *C. galbinifrons*, *C. bourreti*, *C. picturata* and *C. amboinensis* or forming a clade with *C. flavomariginata*. *C. chiangmuanensis* always formed a clade with the living *C. galbinifrons*, *C. bourreti*, *C. picturata* and *C. amboinensis*. *Cuora pitheca* roots all other *Cuora* in the molecularly constrained tree but forms a monophyletic group with *C. zhoui*, *C. mccordi* and *C. mouhotii* in the unconstrained tree. One should keep in mind that rooting the tree differently may challenge the understanding of the evolutionary history of *Cuora,* especially regarding whether the East Asian group constitutes a plesion or a clade. Nevertheless, the major finding of our analysis is that the position of *Cuora chiangmuanensis* is close to the Southeast Asian group formed by *C. galbinifrons*, *C. bourreti*, *C. picturata* and *C. amboinensis*. Interestingly, *C. mouhotii* is sister rooting the Southeast Asian group in the molecularly constrained analysis, while it forms a basal clade with other *Cuora* in the unconstrained phylogeny.

5. Concluding remarks

An adult geoemydid turtle from the Miocene of the Chiang Muan coal mine, Northern Thailand is described as a new species of *Cuora*, *C. chiangmuanensis*, sp. nov. This is the earliest record of that genus in the Middle Miocene or early Late Miocene and it documents an important part of the evolutionary history of Asian box turtles. Based on the mammalian fauna, the age of the hitherto known oldest *Cuora*, *C. pitheca* from the Late Miocene of Lufeng, China is of 8–9 Ma (Wang & Qi, 2005; Deng, 2006) or even younger (7 Ma, Deng & Qi, 2009). *C. chiangmuanensis* is thus likely older than *C. pitheca*, even if it appears more 'derived'. This shows that the group was already diversified before the end of the Miocene.

If we consider that *C. chiangmuanensis* forms a monophyletic group with the extant Southeast Asian *Cuora* species (*C. amboniensis*, *C. galbinifrons*, *C. picturata* and *C. bourreti*) and that *C. chiangmuanensis* is also from this region, it is possible that *C. chiangmuanensis* represents the fossil link between Southeast Asian and East Asian *Cuora*. The systematic position of *Cuora miyatai* is not resolved in our study, but it is clear that it diverged from a continental group earlier than the Middle Pleistocene. While Hirayama (2007) and one of our analyses suggested it may be a close relative of *C. flavomarginata*, some equally parsimonious hypotheses suggest it may share a common ancestry with Southeast Asian *Cuora*, suggesting an alternative biogeographic origin. According to our analyses, *Cuora mouhotii* may either represent a member of this Southeast Asian group demonstrating a vicariant evolution within the genus or a more primitive member of *Cuora* (demonstrating iterative migrations). The fossil record being still scanty and molecular constraints being unavailable for the root, it would be speculative to polarize these migrations, but palaeogeography undoubtedly influenced the diversification of the genus *Cuora*.

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Appendix 1. Character definition

Characters

1. First vertebral scute:
   0. does not reach the second marginal scute
   1. polymorphic
   2. reaches the second marginal scute
2. Medial carapace carina extending on anterior neurals:
   0. absent
   1. absent in some individuals
   2. present
3. Lip on the visceral side of the hypoplastron:
   0. elevated
   1. flat
4. Lateral anal lip on the visceral side of the xiphiplastron:
   0. wide
   1. narrow
5. Fully divided anal scute:
   0. yes
   1. incomplete for some specimens
   2. no
6. Anal notch:
   0. deep
   1. small or deep
   2. small
   3. absent
7. Width to length ratio for the posterior plastral lobe (behind the hinge):
   0. wider than long
   1. wider than long or longer than wide
   2. longer than wide
8. Abdominal/anal midline length:
   0. abdominal longer than anal scute
   1. abdominal longer, equal, or shorter than anal scute
   2. abdominal shorter than anal scute
9. Abdomino-femoral sulcus:
   0. convex posteriorly
   1. polymorphic
   2. straight

10. Musk duct foramina enclosed in seventh peripheral plate:
    0. absent
    1. present
11. Ratio of anal/femoral midline length:
    0. less than 3
    1. more than 3
12. Contact between the tenth marginal scute and the fifth vertebral scute:
    0. absent
    1. present
13. Plastral hinge:
    0. absent
    1. present

Taxa/character matrix

Cuora chiangmuanensis	2010020201 101
Cuora pitheca	000000220? 001
Cuora miyatai	221103000? 101
Cuora amboinensis	0011031101 101
Cuora aurocapitata	2201022111 001
Cuora bourreti	00??23002? 001
Cuora flavomarginata	0211131110 101
Cuora galbinifrons	0011232101 001
Cuora mccordi	0200020111 011
Cuora mouhotii	0210000010 011
Cuora pani	2211011110 001
Cuora picturata	00??23002? 1?1
Cuora trifasciata	2200022010 001
Cuora yunnanensis	21??01202? 001
Cuora zhoui	2200000120 001
Mauremys	1210002021 000
Heosemys grandis	0200002001 000