

Middle Jurassic turtles from southern Thailand

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Abstract – A new genus and species of primitive cryptodiran turtle, *Siamochelys peninsularis* n. g. n. sp., from the Middle Jurassic Mab Ching locality, in the southern peninsula of Thailand, is described on the basis of complete shells. They are characterized by a combination of primitive features (the presence of a pair of mesoplastra meeting on the midline) and a series of derived characters (loose plastron–carapace attachment, short diamond-shaped entoplastron, dorsal thickening of the lateral edge of the second to seventh peripheral plates, expanded seventh to eleventh peripheral plates, extension of the anal scute to the hyo-hypoplastral suture or onto the hypoplastron, midline sulcus sinuoidal), and thus closely resemble *Chengyuchelys*, from the Middle Jurassic of China, and more particularly *Xinjiangchelys* and its relatives from the Middle and Late Jurassic of China and Central Asia. This supports a Middle Jurassic age for the locality and suggests that the Sibumasu (Shan-Thai) block was in contact with the Asian mainland by that time.

Keywords: Chelonia, Jurassic, Thailand, palaeogeography.

1. Introduction

The Mab Ching locality was discovered by L. Raksaskulwong in 1993. Field work there in 1993, 1994 and 1996 yielded abundant vertebrate remains. The turtle remains from Mab Ching, including complete shells, girdle and limb bones, were reported in preliminary papers (Buffetaut *et al.* 1994*b*; Tong, Buffetaut & Suteethorn, 1996). The purpose of the present paper is to describe the Mab Ching turtles in detail and to examine their systematic position more accurately. In addition, we discuss the stratigraphic position of the locality and its palaeogeographical significance. The specimens studied in this paper are housed in the collection of the Geological Survey Division, Department of Mineral Resources (DMR), Bangkok, Thailand.

2. Geological setting

The turtle remains described below were found in a road cutting near Mab Ching village, west of the town of Thung Song (Amphoe Thung Song, Changwat Nakhon Si Thammarat) in the southern peninsula of Thailand (Fig. 1). There, a good section exposes alternating grey and brown clays and limestone beds. According to M. Feist (Montpellier), charophytes from that locality (including *Porochara sublaevis*) suggest a Middle Jurassic age (Buffetaut *et al.* 1994*a,b*). In addition to the turtle remains, vertebrate remains

from Mab Ching include temnospondyl intercentra (Buffetaut *et al.* 1994*a*), a spine of a large hybodont shark, scales of *Lepidotes*-like actinopterygian fish, lungfish toothplates, and vertebrae, scutes and teeth of mesosuchian crocodiles. The whole assemblage is suggestive of a lacustrine environment.

3. Systematic palaeontology

Order TESTUDINES Linnaeus, 1758
Megaorder CRYPTODIRA Cope, 1868
Capaxorder SELMACRYPTODIRA Gaffney *et al.*
1987
Siamochelys n. g.

Derivatio nominis. From *Siam*, the ancient name of Thailand, and *chelys*, Greek for turtle.

Diagnosis. Primitive Cryptodira with one pair of mesoplastra meeting on the midline and lying on both pectoral and abdominal scutes, and narrow vertebral scutes. Differing from *Chengyuchelys* in having a clear ornamentation, consisting of ridges and tubercles, on the shell surface, a pair of mesoplastra lying on the anterior part of the bridge, a nearly straight posterior sulcus of the intergulars not cutting onto the short diamond-shaped entoplastron, and a loose plastron–carapace attachment. Differing from *Xinjiangchelys* in having one pair of mesoplastra, an ornamented shell surface, no dorsal process of epiplastron, a short diamond-shaped entoplastron and musk ducts included in the plastron.

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Figure 1. Sketch map of part of southeast Asia showing the position of the Mab Ching locality and the approximate limits of the main continental blocks (broken lines).

Type species. *Siamochelys peninsularis* n. sp.

Distribution. Middle Jurassic of southern Thailand.

Siamochelys peninsularis n. sp.
Figures 2–4

Derivatio nominis. Because the specimens are from the peninsula of Thailand.

Holotype. An almost complete shell containing the carapace and plastron in connection, pelvis and limb bones, all preserved together (TF 7635, DMR, Bangkok, Thailand).

Hypodigm. A complete shell (carapace and plastron in connection) (TF 7636, DMR, Bangkok, Thailand), an incomplete shell (TF 7637, DMR, Bangkok, Thailand).

Table 1. Measurements of *Siamochelys peninsularis* n. g. n. sp. (in mm)

	TF 7635	TF 7636	TF 7637
Length of carapace	315	318	
Width of carapace	(282)	294	
Length of plastron	242	244	(212)
Length of anterior lobe	65	64	65
Width of anterior lobe at the base	134	125	108
Length of bridge	73	86	71
Length of posterior lobe	104	94	(76)
Width of posterior lobe at the base	136	115	(118)

(): estimated

Stratum typicum. Middle Jurassic.

Locus typicus. Mab Ching, Changwat Nakhon Si Thammarat, southern Thailand.

Diagnosis. same as for the genus (only known species).

Measurements. See Table 1.

3.a. Preservation

The holotype (TF 7635) is the best preserved specimen, lacking only the right fourth to tenth peripheral plates. TF 7636 is the most complete specimen but the sutures between the plates, especially those on the carapace, are not distinguishable and some plates along the midline have been pushed outside. TF 7637 is fragmentary and not complete, lacking the posterior part of both the carapace and plastron.

3.b. Description

All specimens are crushed dorso-ventrally, so the original curvature of the carapace is unknown, but it seems to have been low.

The surface of both the carapace and plastron bears a fine ornamentation. The ornamentation consists of a vermiculate pattern of light ridges and tubercles, which are less pronounced than in *Glyptops* (Gaffney, 1979). They are concentrated on the nuchal, the neurals and the medial two thirds of the costals, whereas all peripherals and the lateral margin of the costal plates are nearly smooth. On the plastron, the ornamentation is the same as on the carapace, but weaker.

The carapace has a roughly rounded outline and lacks midline or lateral keels. In spite of the dorso-ventral crushing of the shell, a shallow longitudinal depression of the neural region can be observed. This midline depression is better preserved on TF 7635 and TF 7637, which show flat neurals at the bottom of the depression and slightly dorsally convex costal plates. In TF 7636, although the neurals have been pushed

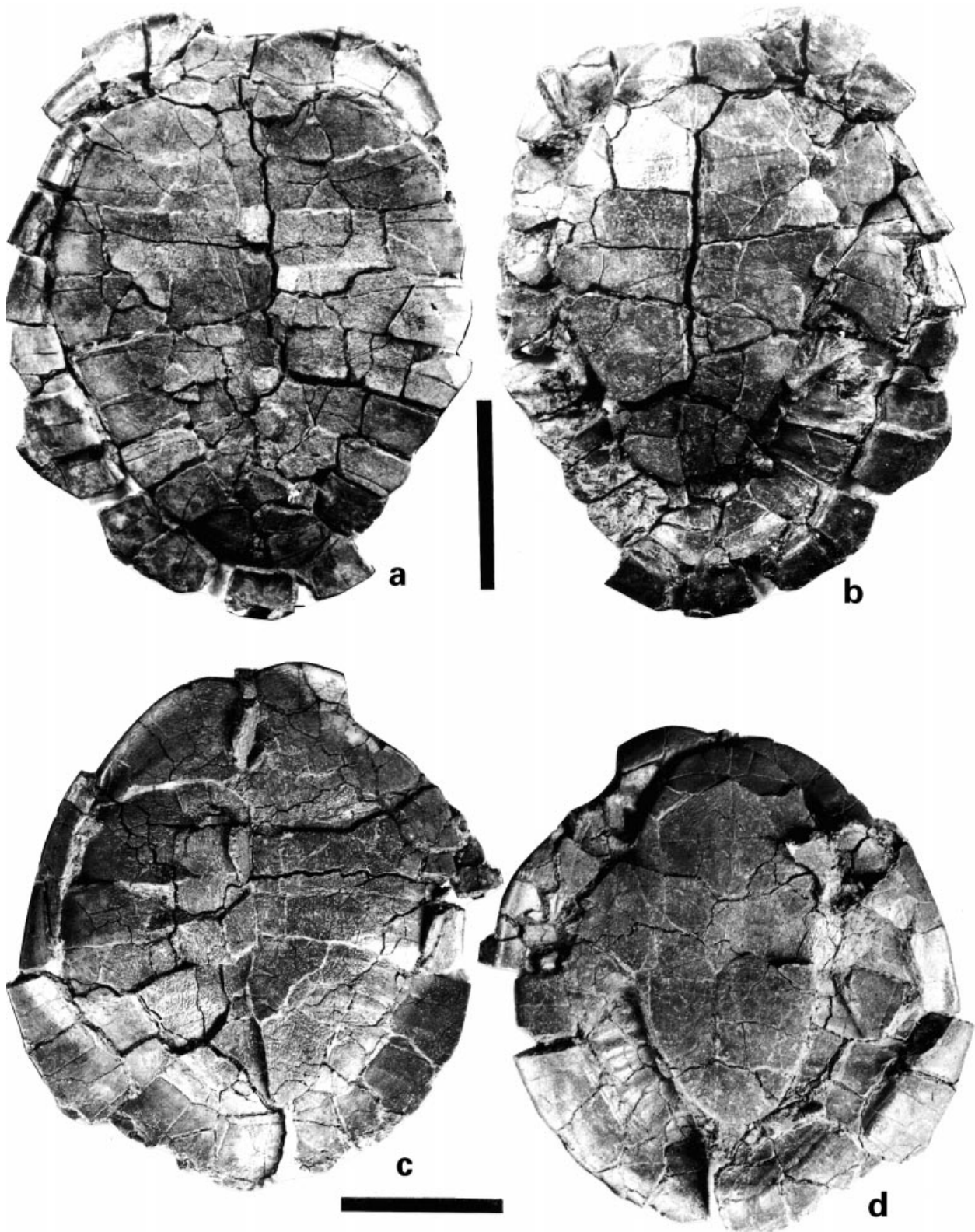


Figure 2. *Siamochelys peninsularis* n. g. n. sp. from the middle Jurassic of Mab Ching, southern Thailand. (a, b) TF 7635 (holotype); (c, d) TF 7636. (a, c) dorsal views; (b, d) ventral views. Scale bar: 10 cm (vertical scale for a, b; horizontal scale for c, d).

outside, the dorsal convexity of the costal plates is preserved. The nuchal emargination is better preserved in TF 7635, where it is large and wide. The antero-lateral margin is thickened and upturned, forming a

gutter along the antero-lateral edge of the carapace. This structure can be observed in all specimens, but its development is variable: in TF 7635 and 7636, it begins at the posterior half of the first peripheral plate

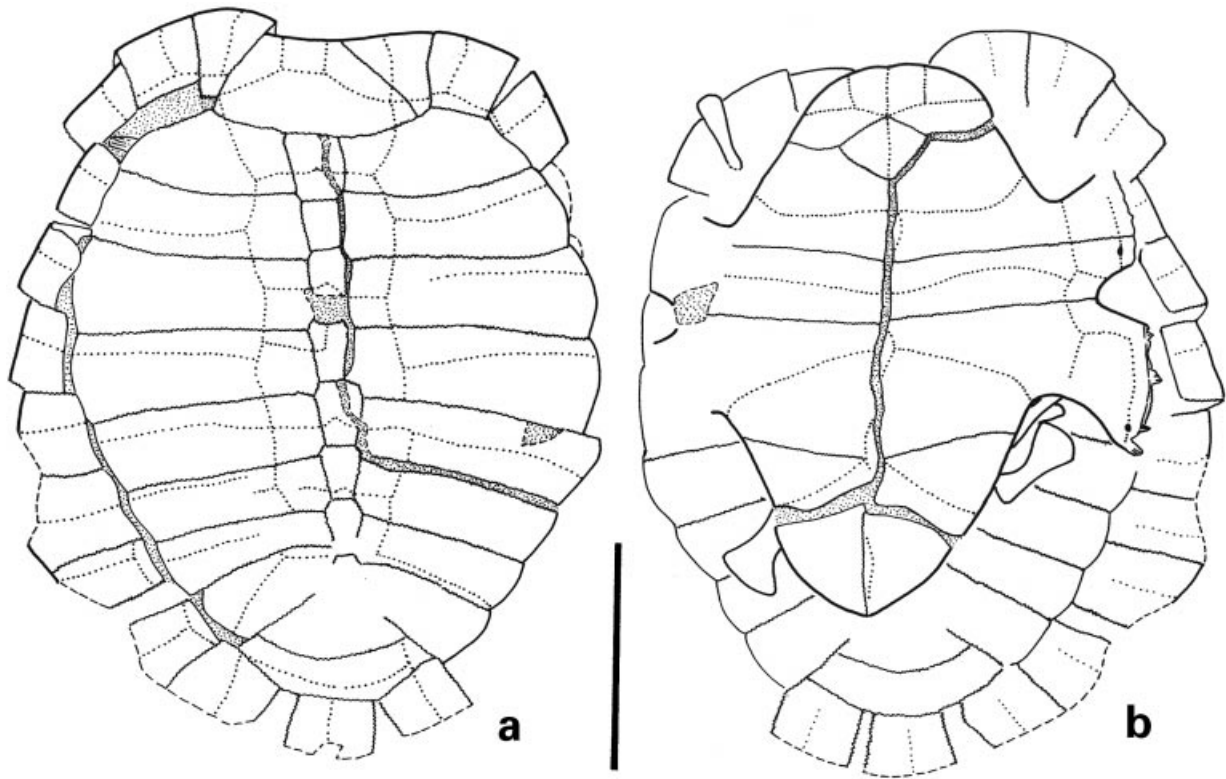


Figure 3. *Siamochelys peninsularis* n. g. n. sp., holotype (TF 7635). (a) dorsal view; (b) ventral view. Solid lines represent the free margins of plates; serrated lines represent sutures; dotted lines represent scute sulci. Scale bar: 10 cm.

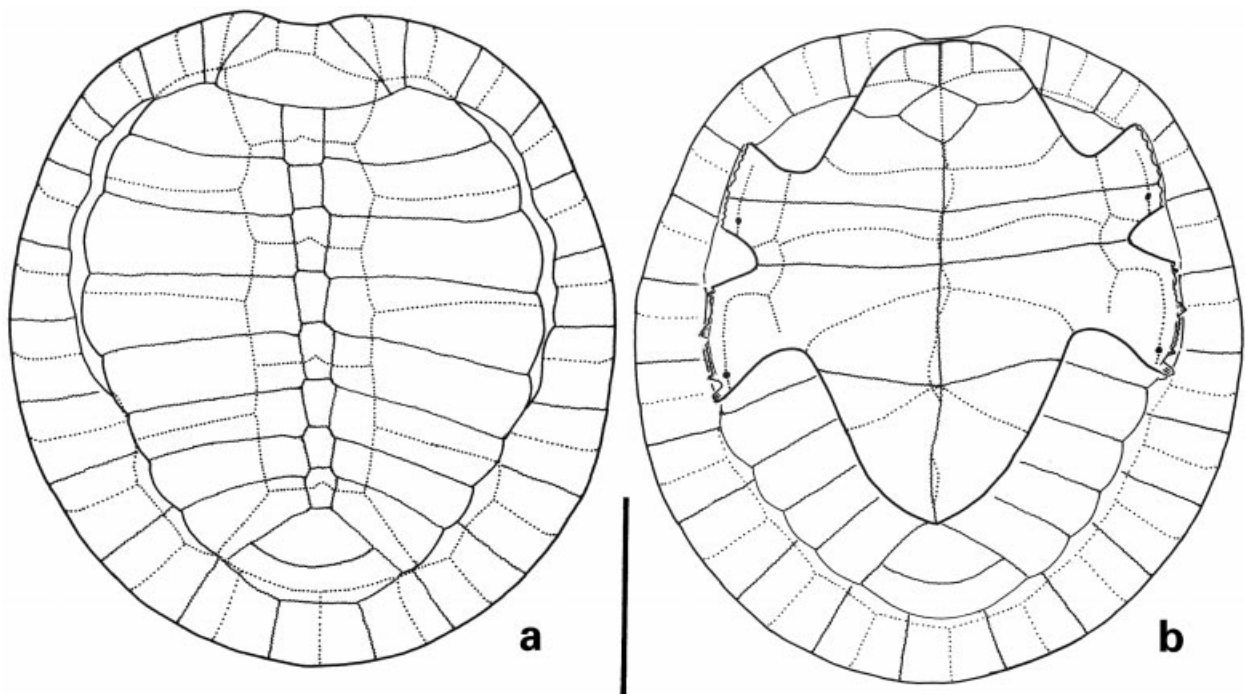


Figure 4. Restored shell of *Siamochelys peninsularis* n. g. n. sp., based on TF 7635. (a) dorsal view; (b) ventral view. Scale bar: 10 cm.

and goes on through to the seventh peripheral plate. It is more marked in TF 7635 than in TF 7636. In TF 7637, although only the anterior part of the gutter is preserved on the left side, it begins on the second

peripheral plate. It thus appears that this structure was more marked in young individuals than in adults. The postero-lateral and posterior margins of the carapace are thin, forming a sharp edge.

The nuchal plate is complete only in TF 7635. It is trapezoidal in shape and wide, with its width about 2.3 times its length.

The neural series is best preserved in TF 7635 in which seven neural bones are well visible. The eighth one is damaged, but its anterior limit can be made out by the posterior suture of the seventh neural and the medial suture of the seventh and eighth pairs of costal plates. The first neural is the largest and hexagonal in shape, with short postero-lateral sides, in TF 7635, while it is rectangular in TF 7637. The second neural is rectangular in shape and smaller than the first one. The third to sixth neurals are antero-posteriorly elongated and hexagonal, with short antero-lateral sides. The seventh and eighth neurals are not complete; their size and shape seem to be similar to those of the sixth. In TF 7635, there is a small hole between the third and fourth neurals, about 9 mm in length and 10 mm in width, which seems to be due to *post mortem* damage.

Posterior to the neural series, the suprapygal region is rather damaged in TF 7635; two or three suprapygal plates may be present. The outline of the posterior suprapygal is well visible. It is wider than the anterior one, with its anterior and posterior margins convex posteriorly; it contacts posteriorly the eleventh peripherals and the pygal. Anterior to it, there is a large and rather damaged triangular plate which does not contact the peripheral plates. A small anterior suprapygal plate may be present. The pygal is nearly complete; it is rectangular in shape and wider than long, with the posterior edge slightly upturned.

Eight pairs of costal plates are present. All the left costal plates are separated from the right ones by neurals. The first costal plate has a strong ridge on its ventral surface, extending from the medial end to the axillary buttress. The first thoracic rib is visible in TF 7637, reaching about half way to the buttress.

There are eleven pairs of peripheral plates. In TF 7635, the first and second peripheral plates are sutured to the first costal plates and the eleventh peripheral plate is sutured to the suprapygal. The medial margin of the third to tenth peripherals bears a series of small holes to receive the pegs on the lateral end of the second to eighth costal plates; both costals and peripherals have a smooth margin in this region. This suggests a long lateral fontanelle on the carapace. This lateral fontanelle is present also in TF 7636, as indicated by the smooth medial margin of the left fourth to seventh peripherals. The first to third peripherals contact the first costal plate. The first peripheral is reduced and roughly triangular in shape; its contact with the first costal plate is very short. The second peripheral plate is large and square in shape. The second to sixth peripherals are narrow medio-laterally, and the first to seventh peripherals have a thickened and upturned lateral edge forming a gutter. The seventh to eleventh peripherals are mediolaterally expanded.

The sulci are shallow but easily distinguishable, and visible on all specimens. The cervical scute is preserved

only in TF 7635. It is a single rectangular scute which is wider than long. Five vertebral scutes are present. The first vertebral scute is narrower than the nuchal plate and wider than long. The second to fifth vertebral scutes are nearly as long as wide. The anterior sulcus of the second to fourth vertebral scutes forms a forwardly directed arrow on the midline, and lies respectively on the first, third and fifth neural plates. In specimen TF 7635, there is a small additional scute on the left antero-lateral quarter of the third vertebral scute; another additional scute may be observed on the fourth vertebral scute.

Six pleural scutes are present on each side in TF 7635; they are not symmetrical, which is presumably an individual anomaly. There are twelve pairs of marginal scutes. The first to third and the ninth to tenth marginal scutes are restricted to the peripheral plates, whereas the fourth to eighth marginal scutes are not limited to the peripheral plates. In TF 7635, except for the eighth marginal scute which extends onto the fifth costal plate, most of them do not extend onto the costal plates because of the lateral carapacial fontanelle. In TF 7636, the medial tip of marginal scutes can be seen on the lateral margin of the first to third left costal plates. The twelve pairs of marginal scutes have their anterior sulcus cutting the posterior part of the posterior suprapygal.

The plastron is reduced compared to *Glyptos* and *Kayentachelys*. It is more like that of *Xinjiangchelys*, being much shorter than the carapace and well ossified. The bridge is fan-shaped and moderately developed in length; it is longer than the anterior lobe but shorter than the posterior one. A large lateral plastral fontanelle can be observed on both sides of TF 7635. It is better preserved on the left side, whereas the right one is damaged, only its medial margin being preserved. Lying on the bridge and medial to the fifth peripheral plate, the fontanelle is large and trapezoidal in shape, measuring about 25 mm in width and 12 mm in length at its medial margin, and 25 mm at its lateral margin. Although the bridge region is not well preserved in TF 7636, it appears that the plastral fontanelle is absent in this specimen. In specimen TF 7635, anterior and posterior to the fontanelle, the plastron attaches to the carapace by a series of pegs fitting into the sockets on the ventral edge of the third, fourth, and then sixth and seventh peripheral plates. In TF 7636, one peg is visible on the postero-lateral end of the right hypoplastron. Two musk ducts are included in the plastron. They are well preserved on the left side of TF 7635, lying near the lateral margin of the bridge, one on the mesoplastron and one on the hypoplastron. In TF 7636, only the posterior musk duct is preserved, on both sides.

The axillary buttress contacts the third peripheral and seems to reach the first costal plate. The inguinal buttress meets the seventh peripheral plate and does not reach the costal plates.

The anterior lobe is wider but shorter than the posterior one, with a rounded anterior margin. The posterior lobe of TF 7635 is wide at the base and strongly narrowed posteriorly, without an anal notch. The posterior lobe of TF 7636 is slightly different; it is narrower at the base but has a more rounded posterior end.

The epiplastra are large, compared to those of *Kayentachelys* and *Indochelys*. They are subrectangular in shape and have a rounded anterior edge. The two epiplastra meet each other on the midline and their suture is slightly shorter than the entoplastral length. The epiplastra contact the entoplastron with a slightly anterolaterally convex suture, and the hyoplastra posteriorly with a slightly posteriorly convex suture. The dorsal surface of the epiplastra is concave. The epiplastra do not bear a dorsal process, unlike what is seen in *Proganochelys* (Gaffney, 1990), *Kayentachelys* (Gaffney *et al.* 1987) and *Xinjiangchelys* (Peng & Brinkman, 1993), but a small and short posteriorly directed process is present, lying on the posterior margin of the epiplastron, near the midline suture. This process is visible in TF 7635 and TF 7637.

The entoplastron is a diamond-shaped plate which does not reach the anterior margin of the plastron. It is wider than long in TF 7635, but slightly longer than wide in TF 7637. The entoplastron is much smaller than the epiplastron. The hyoplastra are sutured to each other and contact the mesoplastra posteriorly. The mesoplastra are well distinguishable in specimens TF 7635 and TF 7637. Although most sutures in TF 7636 are not visible, the anterior suture of the mesoplastra is distinguishable, and is consistent with what is seen in both other specimens. The mesoplastra are large and meet each other along the midline. They lie on both the pectoral and abdominal scutes, at the anterior part of the bridge, and are not narrowed on the midline. Both the anterior and posterior sutures of the mesoplastra are slightly convex posteriorly. The hyoplastra are the largest plates of the plastron. The hypo-xiphial suture is slightly convex posteriorly in TF 7635, but much more strongly convex posteriorly in TF 7636.

Ten pairs of plastral scutes are present. The gulars and intergulars are restricted to the epiplastra. The gulars are large and triangular in shape, with a straight posterior sulcus. The pair of intergulars is large; their size is smaller than that of the gulars. The sulcus between the intergulars lies on the midline suture of the epiplastra, and their posterior sulcus is slightly convex posteriorly, and ends at the anterior suture of the entoplastron. Posterior to the gulars, the humeral scutes occupy a large part of the anterior lobe of the plastron; the humero-pectoral sulcus is placed at the level of the base of the anterior lobe, with its lateral end turned anteriorly. The pectoral scutes are shorter than the humeral scutes. The pectoro-abdominal sulcus is slightly convex posteriorly. The abdominal

scutes are even shorter than the pectoral scutes along the midline, with the abdomino-femoral sulcus strongly convex anteriorly. In TF 7635, the femoro-anal sulcus is shaped like an inverted V and reaches the hypo-xiphial suture, but does not cut it. In TF 7636, the femoro-anal sulcus is shaped like an inverted U, and extends onto the hypoplastron. From the posterior tip of the entoplastron until the posterior end of the plastron, the midline sulcus is slightly sinusoidal. Three large inframarginal scutes are present on each side of the plastron, and restricted to the bridge, the most posterior one being the largest. They are preserved in both TF 7635 and TF 7636.

No vertebra can be observed.

Some limb and girdle bones are preserved in TF 7635, including a nearly complete right ulna, a disarticulated pelvis and an incomplete left tibia and fibula. The ulna is a dorso-ventrally flattened bone with a long groove on the proximal part of the ventral side for contact with the radius. The ilium has a well-developed dorsal blade with a rugose anterior edge for muscle attachment. The posterior end of the dorsal iliac blade is rounded, and thus different from the pointed one of *Xinjiangchelys* (Peng & Brinkman, 1993).

3.c. Comparisons and discussion

The three specimens described above are assigned to the same species. Specimen TF 7635 is presumably a sub-adult individual, because of the presence of the lateral fontanelles on the carapace and plastron. The obliteration of most sutures in TF 7636 indicates that it is a fully grown adult individual, in which the plastral fontanelles are absent, but the carapacial ones, however small, remain. However, the shells of TF 7635 and 7636 are very similar in size. Thus, the presence of the lateral plastral fontanelles can be interpreted as a juvenile feature, which persisted late in sub-adult individuals. The differences between TF 7635 and 7636 in the shape of the posterior lobe of the plastron and anal scute may be interpreted as the result of sexual dimorphism or individual variation.

We follow here the systematic terminology of Gaffney & Meylan (1988) and Gaffney (1996). *Siamochelys* is clearly a cryptodire since its pelvis is not sutured to the shell. It belongs to the Capaxorder Selmacryptodira because the epiplastra are broadly in contact along the midline. The lack of a dorsal process of the epiplastron, seen in *Siamochelys*, is a synapomorphy of the Hyperorder Daiocryptodira according to these authors, but this process is considered as highly homoplastic (Gaffney, 1996) and may be present in some members of the group (e.g. *Xinjiangchelys*: Peng & Brinkman, 1993, and meiolaniids: Gaffney, 1996).

The oldest known cryptodire is *Kayentachelys aprix*, from the Early Jurassic Kayenta Formation of Arizona (Gaffney *et al.* 1987). Recently, another cryptodiran

turtle, *Indochelys spatulata*, has been described from the Early Jurassic Kota Formation of India (Datta *et al.* 2000). *Siamochelys* shares with these two Early Jurassic turtles the presence of one pair of mesoplastra meeting on the midline and lying on both pectoral and abdominal scutes. However, both *Kayentachelys* and *Indochelys* share primitive characters, which are lacking in *Siamochelys*, such as nine neural plates, very wide vertebral scutes, and a spatulate entoplastron which reaches the anterior margin of the plastron and completely separates the epiplastra. *Siamochelys* is thus more advanced than *Kayentachelys* and *Indochelys* in having only eight neurals, much narrower vertebral scutes and a shorter entoplastron which does not reach the anterior margin of the plastron. *Kayentachelys* has a dorsal process of the epiplastron which is absent in *Siamochelys*. *Kayentachelys* and *Indochelys* have been placed in two distinct families, Kayentachelyidae and Indochelyidae respectively, the former being based on both skull and shell material, while the skull is unknown in the latter.

The presence of one pair of mesoplastra meeting on the midline in *Siamochelys* is a primitive feature which leads to the exclusion of the Mab Ching turtle from the Eucryptodira (Gaffney & Meylan, 1988; Gaffney, 1996). *Siamochelys* can be compared with Middle and Late Jurassic turtles in which one pair of mesoplastra is present, such as *Glyptops* Marsh, 1890 and *Dinochelys* Gaffney, 1979, from the Late Jurassic of North America (Gaffney, 1979), *Pleurosternon* Owen, 1853, from the Late Jurassic and Early Cretaceous of western Europe (Owen, 1853; Lydekker, 1889; Gaffney, 1979), and *Chengyuchelys* from the Middle Jurassic of China. A comparison has also been attempted with the Cretaceous *Kallokibotion* Nopcsa, 1923, from Europe (Gaffney & Meylan, 1992), and *Mongolochelys* Khozatskii, 1997, from Mongolia (Khozatskii, 1997; Sukhanov, 2000). The comparison shows that the similarity between *Siamochelys*, *Glyptops plicatulus* (Cope, 1877), from the Late Jurassic Morrison Formation of North America (Gaffney, 1979), and *Chengyuchelys*, from the Middle Jurassic of China, is greater than with any other Mesozoic North American and European cryptodiran turtles. *Siamochelys*, *Glyptops* and *Chengyuchelys* all have one pair of mesoplastra meeting on the midline and relatively narrow vertebral scutes. Both *Siamochelys* and *Glyptops* have an ornamentation on the shell surface consisting of small raised ridges and tubercles, however, the surface ornamentation on the carapace of *Siamochelys* is less pronounced than that of *Glyptops*. *Siamochelys* differs from *Glyptops* by its more reduced plastron, loose carapace–plastron attachment and the presence of a sinusoidal midline sulcus on the plastron.

In having one pair of mesoplastra, a reduced plastron, a wide fan-shaped bridge and an anal scute extending to the hyo-hyoplastral suture or onto the

hypoplastron, *Siamochelys* is similar to *Chengyuchelys*, from the Middle Jurassic of China. Another character shared by *Siamochelys* and *Chengyuchelys* is the presence of a midline depression along the neural region. This feature is present on the type specimen of *Chengyuchelys baenoides* and on other taxa of chengyuchelyids (Fang, 1987; Ye, 1990; Ye & Pi, 1997). The genus *Chengyuchelys* was erected by Young & Chow in 1953 for the first Chinese turtle having one pair of mesoplastra (Young & Chow, 1953). In 1990, Ye erected the family Chengyuchelyidae, including *Chengyuchelys* and *Xinjiangchelys* (Ye, 1990). Later, Peng & Brinkman (1993) pointed out that *Xinjiangchelys* has no mesoplastron and removed it from the Chengyuchelyidae. According to Ye (1990, 1994), the genus *Chengyuchelys* includes three species: *C. baenoides* Young & Chow, 1953, *C. zigongensis* Ye, 1982 and *C. dashanpuensis* Fang, 1987, all from the Middle Jurassic of Sichuan province in southern China. Recently, a new genus and new species of chengyuchelyid, *Sichuanchelys chowi* Ye & Pi, 1997 has been described from the Middle Jurassic of Sichuan, China. *Sichuanchelys* differs from *Chengyuchelys* by its very broad vertebral scutes (Ye & Pi, 1997). It is very likely that *Chengyuchelys dashanpuensis* may be referred to *Sichuanchelys* since both have wide vertebral scutes.

Siamochelys differs from *Chengyuchelys* by the clear ornamentation consisting of ridges and tubercles on the shell surface, the pair of mesoplastra lying on the anterior half of the bridge, the short and wide diamond-shaped entoplastron and the posterior sulcus of gulars and intergulars almost straight and lying before the anterior tip of the entoplastron but not cutting it. In *Chengyuchelys*, the surface of the shell is smooth or decorated with tiny pits or light radiating folds (Young & Chow, 1953; Ye, 1982); the mesoplastra are included in the abdominal scute or lying on both pectoral and abdominal scutes as in *Siamochelys*, but on the mid-length of the bridge, and the entoplastron is antero-posteriorly elongated, and the intergulars extend deeply onto the entoplastron (Ye, 1982, 1990).

One important feature that separates *Siamochelys* from *Chengyuchelys* is the carapace–plastron attachment. In *Chengyuchelys*, the plastron is sutured to the carapace (Ye, 1982), whereas *Siamochelys* has the plastron loosely attached to the carapace, with pegs on the hyoplastron and hypoplastron fitting in sockets on the peripherals, which is typical of a ligamentous carapace–plastron attachment (Gaffney, 1990). By this character and the intergulars extending onto the entoplastron, *Chengyuchelys* is clearly more primitive than *Siamochelys*. The loose carapace–plastron attachment is considered as a derived character (Gaffney, 1996), and was used by Peng & Brinkman (1993) to suggest a close relationship between *Xinjiangchelys* and the Macrobaenidae.

Peng & Brinkman (1993) pointed out seven derived features separating *Xinjiangchelys* from the Late

Jurassic European marine turtle *Plesiochelys*: (1) presence of a loose connection between the plastron and carapace, with pegs on the plastron fitting in sockets on the peripherals; (2) extension of the marginal scutes onto the first to fifth costal plates; (3) significant dorsal thickening of the lateral edge of the second to seventh peripheral plates; (4) expanded seventh to eleventh peripheral plates; (5) extension of the anal scute to the hyo-hyoplastral suture or onto the hypoplastron; (6) reduction in length of the first thoracic rib and (7) midline sulcus sinusoidal. All these derived features are present in *Siamochelys*. Two derived characters can be added to the above-mentioned ones, shared between *Siamochelys* and *Xinjiangchelys*: narrow vertebral scutes and posterior sulcus of gulars and intergulars almost straight and not cutting the entoplastron.

The primitive eucryptodiran turtle genus *Xinjiangchelys* was erected by Ye in 1986 on the basis of a nearly complete shell with associated pectoral and pelvic girdles and limb bones from the upper Middle or lower Upper Jurassic beds of the Junggar Basin, Xinjiang province, northwestern China. Additional material of *Xinjiangchelys* has been reported from the Fergana depression, Kirgizstan (Kaznyshkin, 1988; Kaznyshkin, Nalbandyan & Nesson, 1990). In 1993, Peng & Brinkman reviewed the genus *Xinjiangchelys* and described new material including about a dozen specimens (more or less complete shells, cervical vertebrae and appendicular skeleton) from the Late Jurassic of the Junggar Basin. Some Late Jurassic turtles from Sichuan, southern China, previously assigned to *Plesiochelys*, have been synonymized with *Xinjiangchelys* by these authors. So far, *Xinjiangchelys* includes four species known from the Middle to Late Jurassic of South and North China and Kirgizstan (Peng & Brinkman, 1993). Recently, some new forms related to *Xinjiangchelys* have been reported from the Middle and Late Jurassic of Mongolia (Sukhanov, 2000).

Xinjiangchelys and related forms differ from *Siamochelys* by absence of a mesoplastron and an antero-posteriorly elongated entoplastron. Moreover, *Xinjiangchelys* has a smooth shell surface and a dorsal process of the epiplastron. One of the diagnostic features of *Xinjiangchelys* is musk ducts present between the plastron and carapace (Peng & Brinkman, 1993). In *Siamochelys*, at least two musk ducts are included in the plastron.

It thus appears that the Mab Ching turtles differ from all Jurassic turtles by their shell characters (Table 2), and the erection of a new genus and new species is therefore justified. It appears that *Siamochelys* is most closely related to *Chengyuchelys*, and, especially, *Xinjiangchelys*, from the Middle and Late Jurassic of China and Central Asia. *Siamochelys*, *Chengyuchelys* and *Xinjiangchelys* share the anal scute extending to the hyo-hyoplastral suture or onto the hypoplastron. This character is considered as derived (Peng &

Brinkman, 1993). It is worth noting that the midline depression on the neural region seen in *Siamochelys* and *Chengyuchelys* is also present in *Xinjiangchelys latimarginalis* (IVPP V7648, Ye, 1994), although it is not mentioned by Peng & Brinkman (1993). In some Macrobaenidae, such as *Ordosemys*, 'a central depression runs anteroposteriorly along the midline of the shell from the nuchal to the first suprapygal' (Brinkman & Peng, 1993), although the significance of this feature is unknown. *Siamochelys* is more derived than *Chengyuchelys* in the loose attachment of the carapace and plastron and its short diamond-shaped entoplastron. It is more primitive than *Xinjiangchelys* mainly in the presence of one pair of mesoplastra. Thus, *Siamochelys* can be considered as the sister group of the Eucryptodira. However, *Xinjiangchelys* has primitive features such as the presence of a dorsal process on the epiplastron, which is absent in *Siamochelys*. Following Gaffney (1975), the tentative interrelationships among the Cryptodira have recently been reinvestigated (Gaffney & Meylan, 1988; Gaffney, 1996; Brinkman & Wu, 1999; Hirayama, Brinkman & Danilov, 2000). *Xinjiangchelys*, which is the best studied Asian Jurassic turtle, is generally considered as the sister group of Centrocryptodira (including Sinemydidae, Chelydroidea, Chelonioida, Trionychoidea and Testudinoidea). *Chengyuchelys* has usually not been considered in these works because it is poorly known.

In a preliminary paper, these Mab Ching turtles were referred to the family Chengyuchelyidae (Buffetaut *et al.* 1994b). Chengyuchelyid material is rather abundant, but only shells are reported and they are usually poorly preserved. Thus, the descriptions are usually not detailed or informative enough for an analysis of systematic relationships. Because of the important differences between *Siamochelys* and *Chengyuchelys* and of the insufficient diagnosis of the family Chengyuchelyidae, we prefer to assign *Siamochelys* to a family *incertae sedis*, pending the discovery of more complete material.

4. Conclusions

Siamochelys is most closely related to *Chengyuchelys*, from the Middle Jurassic of southern China, and particularly to *Xinjiangchelys*, known from the Middle to Late Jurassic of China and Central Asia. It is considered as the sister group of Eucryptodira. This interpretation is solely based on shell characters. Further discovery of more complete material, especially skull and vertebrae, could lead to a revision of this tentative interpretation. The combination of primitive and derived characters seen in *Siamochelys*, as compared to Chinese and Central Asian Middle and Late Jurassic turtles, is in good agreement with a Middle Jurassic age suggested by charophytes for the vertebrate-bearing beds of Mab Ching (Buffetaut *et al.* 1994a).

Table 2. Comparison of shell features between *Siamochelys* and selected Jurassic turtles

	<i>Siamochelys</i>	<i>Xinjiangchelys</i>	<i>Chengyuchelys</i>	<i>Plesiochelys</i>	<i>Glyptops</i>	<i>Kayentachelys</i>	<i>Indochelys</i>
Shell surface ornamentation	Similar to <i>Glyptops</i> , but less pronounced	Smooth	Smooth or with tiny pits	Smooth	Raised ridges and tubercles	Ornamented	Smooth
Thickening of anterolateral edge forming a gutter on carapace	Present	Present	?	Absent	Absent	Absent	Absent
Midline depression on carapace	Present	Present and absent	Present	Absent	Absent	Absent	Present
Number of neurals	8	8	8	6–8	8	9	9
Highly expanded 7th to 11th peripherals	Present	Present	?	Absent	Absent	Absent	Absent
Vertebral scutes	Narrow	Narrow	Narrow	Narrow to broad	Narrow	Broad	Broad
Carapace–plastron attachment	Loosely attached	Loosely attached	Sutured	Sutured	Sutured	Sutured	Sutured
Mesoplastron	Present	Absent	Present	Absent	Present	Present	Present
Dorsal process of epiplastron	Absent	Present	?	Absent	Present	Present	?
Entoplastron completely separating epiplastron	No	No	No	No	No	Yes	Yes
Midline sulcus of plastron	Sinusoidal	Sinusoidal	Straight	Straight	Straight	Straight	Straight
Intergular cutting entoplastron	No	No	Yes	Yes	Yes	Yes	Yes
Femoroanal sulcus extending to hypoplastron	Present	Present	Present	Absent	Absent	Absent	Absent

The Mab Ching locality is in the southern peninsula of Thailand, which is part of the Shan–Thai, or Sibumasu, block (Buffetaut *et al.* 1994*a,b*), one of the microcontinents which make up Southeast Asia. These microcontinents have had a complex geological history, most of them having split off the northern margin of Gondwana, to drift northward and eventually collide with each other and with what was, at successive times, the southern margin of ‘mainland’ Asia (Metcalf, 1996, 1998). Palaeontological evidence can contribute to unravelling this sequence of events. Freshwater turtles such as those from Mab Ching were

in all likelihood unable to cross wide expanses of sea-water and can therefore be used as indicators of connections between land areas. As mentioned above, *Siamochelys peninsularis* is closely related to the cryptodiran turtles *Chengyuchelys* and *Xinjiangchelys*, which are known only from the Jurassic of China and Central Asia, an area consisting of several continental blocks which by Jurassic times had become accreted together. There is no evidence of close relationships between *Siamochelys* and any of the Mesozoic turtles from Gondwana, nor is there any indication that it was an endemic form, as might be expected if Sibumasu had

been an isolated land mass in the Jurassic. The logical palaeobiogeographical conclusion to be drawn from the Asian affinities of *Siamochelys peninsularis* is therefore that by Middle Jurassic times Sibumasu was connected with the Chinese blocks, which themselves had already become linked to Eurasia, possibly as early as the Late Permian (Zhao *et al.* 1996). This is in good agreement with reconstructions showing Sibumasu in contact with Indochina, itself accreted to the South China block, in the Late Triassic (Metcalf, 1996, 1998), and part of the southern margin of mainland Asia in the Late Jurassic (Besse & Courtillot, 1988; Metcalfe, 1996, 1998). Palaeobiogeographical data based on the Mab Ching turtles thus confirm the tentative suggestions previously put forward on the basis of temnospondyl remains from the same locality (Buffetaut & Suteethorn, 1998).

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References

- BESSE, J. & COURTILOT, V. 1988. Paleogeographic maps of the continents bordering the Indian Ocean since the Early Jurassic. *Journal of Geophysical Research* **93**, 11791–808.
- BRINKMAN, D. B. & PENG, J. H. 1993. *Ordosemys leios*, n. gen., n. sp., a new turtle from the Early Cretaceous of the Ordos Basin, Inner Mongolia. *Canadian Journal of Earth Sciences* **30**, 2128–38.
- BRINKMAN, D. B. & WU, X. C. 1999. The skull of *Ordosemys*, an Early Cretaceous turtle from Inner Mongolia, People's Republic of China, and the interrelationships of Eucryptodira (Chelonia, Cryptodira). *Paludicola* **2**, 134–47.
- BUFFETAUT, E., RAKSASKULWONG, L., SUTEETHORN, V. & TONG, H. 1994a. First post-Triassic temnospondyl amphibians from the Shan-Thai Block: intercentra from the Jurassic of peninsular Thailand. *Geological Magazine* **131**, 837–9.
- BUFFETAUT, E. & SUTEETHORN, V. 1998. The biogeographical significance of the Mesozoic vertebrates from Thailand. In *Biogeography and Geological Evolution of SE Asia* (eds R. Hall and J. D. Holloway), pp. 83–90. Leiden: Backhuys.
- BUFFETAUT, E., TONG, H., SUTEETHORN, V. & RAKSASKULWONG, L. 1994b. Jurassic vertebrates from the southern peninsula of Thailand and their implications. A preliminary report. *Proceedings of the International Symposium on Stratigraphic Correlation of Southeast Asia, Bangkok*, 253–6.
- COPE, E. D. 1868. On the origin of genera. *Proceedings of the Academy of Natural Sciences of Philadelphia* **20**, 242–300.
- COPE, E. D. 1877. On reptilian remains from the Dakota beds of Colorado. *Proceedings of the American Philosophical Society* **17**, 193–6.
- DATTA, P. M., MANNA, P., GHOSH, S. C. & DAS, D. P. 2000. The first Jurassic turtle from India. *Palaeontology* **43**, 99–110.
- FANG, Q. R. 1987. A new species of Middle Jurassic turtle from Sichuan. *Acta Herpetologica Sinica* **6**(1), 65–9.
- GAFFNEY, E. S. 1975. A phylogeny and classification of the higher categories of turtles. *Bulletin of the American Museum of Natural History* **155**, 387–436.
- GAFFNEY, E. S. 1979. The Jurassic turtles of North America. *Bulletin of the American Museum of Natural History* **162**, 91–135.
- GAFFNEY, E. S. 1990. The comparative osteology of the Triassic turtle *Proganochelys*. *Bulletin of the American Museum of Natural History* **194**, 1–263.
- GAFFNEY, E. S. 1996. The postcranial morphology of *Meiolania platyceps* and a review of the Meiolaniidae. *Bulletin of the American Museum of Natural History* **229**, 1–166.
- GAFFNEY, E. S., HUTCHISON, J. H., JENKINS, F. A. & MEEKER, L. J. 1987. Modern turtle origins: The oldest known Cryptodire. *Science* **237**, 289–91.
- GAFFNEY, E. S. & MEYLAN, P. 1988. A phylogeny of turtles. In *The phylogeny and classification of the tetrapods. Vol. 1, Amphibians, reptiles, birds* (ed. M. J. Benton), pp. 157–219. Systematics Association Special Volume 35A. Oxford: Clarendon Press.
- GAFFNEY, E. S. & MEYLAN, P. 1992. The Transylvanian turtle, *Kallokibotion*, a primitive Cryptodire of Cretaceous age. *American Museum Novitates* **3034**, 1–37.
- HIRAYAMA, R., BRINKMAN, D. B. & DANILOV, I. G. 2000. Distribution and biogeography of non marine Cretaceous turtles. *Russian Journal of Herpetology* **7**, 181–98.
- KAZNYSHKIN, M. N. 1988. Late Jurassic turtles of Northern Fergana (Kirghiz SSR). *Vestnik Zoologii [Herald of Zoology]* **5**, 26–32 (in Russian).
- KAZNYSHKIN, M. N., NALBANDYAN, L. A. & NESSOV, L. A. 1990. Middle and Late Jurassic turtles of Fergana (Kirghiz SSR). *Yezhegodnik Vsesoyuznogo paleontologicheskogo obshchestva [Annual of the All-union Palaeontological Society]* **32**, 185–204 (in Russian).
- KHOZATSKII, L. I. 1997. Large turtles from the Late Cretaceous of Mongolia. *Russian Journal of Herpetology* **4**, 148–54.
- LINNAEUS, C. 1758. *Systema naturae*. 10th ed., vol. 1. Stockholm, 824 pp.
- LYDEKKER, R. 1889. *Catalogue of the fossil Reptilia and Amphibia in the British Museum (Natural History). Part III. The Order Chelonia*. The British Museum (Natural History) by order of the Trustees, London, 239 pp.
- METCALFE, I. 1996. Gondwanaland dispersion, Asian accretion and evolution of eastern Tethys. *Australian Journal of Earth Sciences* **43**, 605–23.
- METCALFE, I. 1998. Palaeozoic and Mesozoic geological evolution of the SE Asian region: multidisciplinary constraints and implications for biogeography. In *Biogeography and Geological Evolution of SE Asia* (eds R. Hall and J. D. Holloway), pp. 25–41. Leiden: Backhuys.
- MARSH, O. C. 1890. Notice of some extinct Testudinata. *American Journal of Science, Ser. 3* **40**, 177–9.
- NOPCSA, F. 1923. On the geological importance of the primitive reptilian fauna of the Upper-most Cretaceous of Hungary; with a description of a new tortoise (*Kallokibotion*). *Quarterly Journal of the Geological Society of London* **79**, 100–16.

- OWEN, R. 1853. A monography of the fossil chelonian of the Wealden Clays and Purbeck Lime-stones. *Palaeontographical Society Monograph* **7**, 1–12.
- PENG, J. H. & BRINKMAN, D. B. 1993. New material of *Xinjiangchelys* (Reptilia: Testudines) from the Late Jurassic Qigu Formation (Shishugou Group) of the Pingfengshan locality, Junggar Basin, Xinjiang. *Canadian Journal of Earth Sciences* **30**, 2013–26.
- SUKHANOV, V. B. 2000. Mesozoic turtles of Middle and Central Asia. In *The Age of Dinosaurs in Russia and Mongolia* (eds M. J. Benton, M. A. Shishkin, D. M. Unwin and E. N. Kurochkin), pp. 309–67. Cambridge: Cambridge University Press.
- TONG, H., BUFFETAUT, E. & SUTEETHORN, V. 1996. Jurassic turtles from southern Thailand. Abstract. 56th Annual Meeting, Society of Vertebrate Paleontology. *Journal of Vertebrate Paleontology*, suppl. no. 3, 69A.
- YE, X. K. 1982. Middle Jurassic turtles from Sichuan, SW. China. *Vertebrata Palasiatica* **20**, 282–90.
- YE, X. K. 1986. A Jurassic turtle from Junggar, Xinjiang. *Vertebrata Palasiatica* **24**, 171–81.
- YE, X. K. 1990. Fossil turtles from Dashanpu, Zigong, Sichuan. *Vertebrata Palasiatica* **28**, 304–11.
- YE, X. K. 1994. *Fossil and recent turtles of China*. Science Press, Beijing, 112 pp.
- YE, Y. & PI, X. Z. 1997. A new genus of Chengyuchelyidae from Dashanpu, Sichuan. *Vertebrata Palasiatica* **35**, 182–8.
- YOUNG, C. C. & CHOW, M. C. 1953. New fossil reptiles from Szechuan, China. *Acta Scientia Sinica* **2**(3), 216–29.
- ZHAO, X., COE, R. S. GILDER, S. A. & FROST, G. M. 1996. Palaeomagnetic constraints on the palaeogeography of China: implications for Gondwanaland. *Australian Journal of Earth Sciences* **43**, 643–72.