

A revision of *Sinaspideretes wimani* Young & Chow, 1953 (Testudines: Cryptodira: Trionychoidea) from the Jurassic of the Sichuan Basin, China

HAIYAN TONG*†‡, LU LI‡ & HUI OUYANG§

*Palaeontological Research and Education Centre, Mahasarakham University, Kantarawichai,
Mahasarakham 44150, Thailand

‡Key Laboratory of Vertebrate Evolution and Human Origin of Chinese Academy of Sciences, Institute of Vertebrate
Palaeontology and Palaeoanthropology, Chinese Academy of Sciences, Beijing 100044, China

§Chongqing Museum of Natural History, 74 Pipashanzhengjie, Yuzhong District, Chongqing 400013, China

(Received 8 May 2013; accepted 24 June 2013; first published online 4 September 2013)

Abstract – *Sinaspideretes wimani* Young & Chow, 1953 was based on a single shell from the Jurassic red beds of the Sichuan Basin. Originally referred to Trionychoidea but later tentatively assigned to Carettochelyidae, it was long thought to be the oldest representative of those families. The re-examination of the carapace and further preparation of the plastron of the holotype of *S. wimani* revealed a number of important characters which clearly exclude this taxon from both Trionychoidea and Carettochelyidae, but unite it with the primitive trionychoid *Yehguia tatsuensis* (Ye, 1963). *S. wimani* is therefore considered as the basalmost member of Trionychoidea. Our study adds to the evidence from the fossil record for the antiquity of Trionychoidea, thus is in agreement with the early split of Trionychia (Trionychoidea and Carettochelyidae) among the crown Testudines suggested by the molecular phylogeny of turtles.

Keywords: Testudines, Trionychoidea, *Sinaspideretes wimani*, Jurassic, Sichuan Basin, China.

1. Introduction

The Jurassic deposits of the Sichuan Basin have yielded abundant turtle remains, which consist predominantly of archaic turtles (sichuanchelyids and bashuchelyids) in the Middle Jurassic and primitive eucryptodiran turtles (xinjiangchelyids) in the Upper Jurassic (Tong *et al.* 2012a,b), while trionychoid remains are scarce. Two trionychoid taxa have been hitherto described from that basin: *Sinaspideretes wimani* Young & Chow, 1953 and *Yehguia tatsuensis* (Ye, 1963). Both of them are based on a single specimen and both have a rather complex story. In 1953, Young and Chow studied a series of turtle specimens collected along the railway between Chengdu and Chongqing (Chengyu Railway) during its construction and the clearing away of building foundations in Datianwan, in the suburbs of Chongqing. The specimens from the Chengyu Railway are presumably of Middle or Late Jurassic age, but the exact location and horizon are unknown. One incomplete shell was named *Sinaspideretes wimani* and placed in the family Trionychoidea based on the morphology of the neurals and the ornamentation on the shell surface (Young & Chow, 1953). This was long considered as the oldest member of that family (Young & Chow, 1953; Ye, 1963; Mlynarsky, 1976; Pritchard, 1979; Ernst & Barbour, 1989; Ye, 1994; Zhang, Zong & Ma, 1998; Lucas, 2001). Alternatively, *S. wimani* was placed in a separate family, Sinaspideretidae, and considered

as intermediate between Adocidae and Trionychoidea (Chkhikvadze, 1987). It was also thought to be intermediate between Trionychoidea and Carettochelyidae, or even a primitive carettochelyid (de Broin, 1977). More than 30 years after the first description, Meylan and Gaffney examined a cast and the photographs of *S. wimani* and concluded that the specimen had been interpreted in an incorrect orientation, with the posterior end at the front. The new interpretation led to *S. wimani* being tentatively placed in the family Carettochelyidae (Meylan & Gaffney, 1992), a conclusion generally accepted (Sukhanov, 2000; Brinkman, Li & Ye, 2008), but contested recently (Tong, Zhang & Li, 2010).

The second trionychoid turtle from the Jurassic of the Sichuan Basin, *Yehguia tatsuensis* (Ye, 1963), was originally described as *Plesiochelys tatsuensis* Ye, 1963 (Plesiochelyidae), based on a shell with a poorly preserved carapace, complete plastron and other appendicular elements from the Upper Jurassic deposits of Dazu, between Chongqing and Chengdu (Ye, 1963). The systematic position of *P. tatsuensis* was first questioned by Nessonov, who considered it as a member of Adocidae (Nessonov & Julinen, 1977). It was even included in the adocid subfamily Shachemydinae, because a primitive hinge was supposed to be present between the epiplastron and entoplastron/hyoplastra (de Lapparent de Broin, 2004). Danilov & Parham (2006) re-studied *P. tatsuensis*. Their phylogenetic analysis placed it in a group of basal Trionychoidea named Adocusia, which comprised also Adocidae and Nanhsiungchelyidae, but a subsequent analysis placed this taxon within Adocidae,

†Author for correspondence: htong09@yahoo.fr



Figure 1. Map showing the Sichuan Basin, Chengyu Railway and Jurassic turtle localities. Dazu (IVPP V996) and Suining (CQMNH C.1000) are indicated by stars; other Jurassic turtle localities are marked by dots.

in the basalmost position within that family (Danilov & Syromyatnikova, 2009).

The type and only specimen of *S. wimani* (CQMNH C.994) consists of an incomplete carapace with articulated plastron. The plastron, being only slightly exposed, had attracted little attention in the previous studies (Young & Chow, 1953; Meylan & Gaffney, 1992) and a comparison between *S. wimani* and *Y. tatsuenensis* had never been attempted because of the lack of overlapping parts. For the present study, the left half of the plastron of *S. wimani* was prepared. In addition, we have found recently in the Chongqing Museum of Natural History collections a new specimen of Trionychidae from the Upper Jurassic of the Sichuan Basin which consists of a nearly complete carapace. The detailed description of the type specimen of *S. wimani* (CQMNH C.994) and the new specimen (CQMNH C.1000) are presented herein. They are compared with the type specimen of *Y. tatsuenensis* (IVPP V996), based on the revision by Danilov & Parham (2006) and first-hand observations by one of us (H. Tong). Our study reveals that *S. wimani* Young & Chow, 1953 and *Y. tatsuenensis* (Ye, 1963) belong to a single taxon.

Institutional abbreviations. CQMNH – Chongqing Museum of Natural History, Chongqing; IVPP – Insti-

tute of Vertebrate Palaeontology and Palaeoanthropology, Chinese Academy of Sciences, Beijing.

2. Geological and geographical settings

The geology of the Sichuan Basin was summarized in Tong *et al.* (2012a). Figure 1 shows the path of the Chengyu Railway and places which yielded Jurassic turtles in the Sichuan Basin. The holotype of *S. wimani* Young & Chow, 1953 (CQMNH C.994) was collected along the Chengyu Railway, without record of an exact location and horizon. It was considered as (?) Late Jurassic by Young & Chow (1953). The series of turtle specimens originally described by Young & Chow (1953) consists of six shells. Except for CQMNH C.994, all belong to Xinjiangchelyidae and based on their morphology, they are likely to be from the Upper Jurassic Shangshaximiao Formation (Tong *et al.* 2012a,b).

The type specimen of *Y. tatsuenensis* (Ye, 1963), IVPP V996, was collected from the Upper Jurassic beds at Gaofeng Mountain, Daan road, Dazu, Sichuan Province and sent to the IVPP by Mr Deng Yuncong in 1956 (Ye, 1963).

According to the registration documents in the Chongqing Museum of Natural History, CQMNH

C.1000 was collected in June 1977 from the Upper Jurassic Shangshaximiao Formation of Suining, Sichuan Province, some 80 km north of Dazu where the type specimen of *Y. tatsuensis* comes from.

3. Description

3.a. Type specimen of *Sinaspideretes wimani* (CQMNH C. 994; V. 709 in Young & Chow, 1953; Fig. 2)

The shell is incomplete, lacking all the peripheral region of the carapace. The specimen is dorsoventrally crushed, with some plates of the carapace disarticulated and part of the shell surface damaged (see Fig. 2). The plastron is pushed dorsally and the left half is disarticulated from the right one along the midline. To avoid damaging the specimen, only the left half of the plastron was prepared; it is almost complete, lacking only the left epiplastron and entoplastron.

Our orientation of the shell agrees with that of Meylan & Gaffney (1992), which is further confirmed by the prepared plastron (see Fig. 2). The close examination of the specimen reveals more details on the carapace, in comparison with previous studies (Young & Chow, 1953; Meylan & Gaffney, 1992). Although the carapace surface is worn, an ornamentation is clearly present and comparable to that of *Y. tatsuensis* (IVPP V996) and CQMNH C.1000 (Fig. 2e). On the carapace, most sutures are preserved, except those of the nuchal. The first to third neurals are missing, and the seventh and eighth neurals are incomplete, but their outline can partly be reconstructed from the imprint on the internal mould. The complete series of eight neurals reaches the suprapygal, with the neural formula of $6 < 4 > 6 > 6 > 6 > 6 > 6 > 6$. All neurals are longer than wide. The first neural appears to be hexagonal with short posterolateral sides. The second neural is rectangular and shorter than the third neural. The third to eighth neurals are all hexagonal with short anterolateral sides. The eighth neural appears, however, to be shorter than the seventh. The first suprapygal is complete, triangular and quite large. A transversal and anteriorly convex suture on the posterior end of the carapace indicates the presence of a large second suprapygal plate. The costal plates, eight in number, have almost parallel anterior and posterior margins. The rib head of the left second costal is visible on the internal mould; it is unreduced as in *Y. tatsuensis* (Danilov & Parham, 2006). No peripherals are preserved.

The scute sulci are visible on the carapace where the surface is not damaged. Nearly complete third and fourth vertebrae and part of the second and fifth vertebrae are preserved. The second and third vertebrae are narrow, the third vertebral being slightly longer than wide. The fourth vertebral is more elongate and narrower than the third, being clearly longer than wide. The fifth vertebral is wider than the fourth at its anterior margin. The unusual shape of the fifth vertebral scute is likely an anomaly of development. The intervertebral sulci pass through the third, the fifth and the eighth

neurals, respectively. There are four pleural scutes, with the interpleural sulci running parallel to the intercostal sutures. At the lateral end of the right second costal, an anteroposteriorly directed short sulcus is visible, indicating that the fifth marginal extends onto the costal plate.

On the plastron, the left hyoplastron, hypoplastron and xiphoplastron were exposed after the preparation; they are almost complete, with the bridge and the lateral margin of the posterior lobe damaged. The hyoplastron and hypoplastron are disarticulated and the hyoplastron has its posterior end hidden by the hypoplastron. Although the bridge region is damaged, enough is preserved on the left side to show that the plastron is sutured to the carapace. The surface of the plastron is rough as in *Y. tatsuensis*. The anterior lobe is wide. The bridge is relatively long, being roughly as long as the posterior lobe as in *Y. tatsuensis*. The posterior lobe is relatively narrow, with rather straight lateral margins. The axillary buttress, even though incomplete, is long, in contrast to the very short buttress in carettochelyids such as *Anosteira maomingensis* (Tong, Zhang & Li, 2010). The axillary notch is narrow and the inguinal notch is wider than the axillary notch. The anal notch is absent. Although the entoplastron is not preserved, the preserved entoplastron/hyoplastron suture indicates that the entoplastron is a large element, which is likely wider than long.

The scute sulci are clearly visible on the plastron. The humeropectoral sulcus is slightly convex anteriorly in the middle with the lateral end turned anteriorly. It is located at the base of the anterior lobe and far posterior to the entoplastron. The pectoral scute is shorter than the abdominal scute. The pectoroabdominal sulcus is almost straight and transverse. The abdominofemoral sulcus is convex anteriorly. The femoroanal sulcus is convex anteriorly but does not reach the hypoplastron/xiphoplastron suture. Two anterior inframarginals are preserved on the hyoplastron. The midline sulcus is sinuous.

3.b. IVPP V996 (holotype of *Yehguia tatsuensis* (Ye, 1963), Fig. 3)

Danilov & Parham (2006) provided a detailed redescription of IVPP V996. Only additional observations are provided here. Although the posterolateral portion of the carapace margin is damaged on both sides, the better preserved left margin indicates that the carapace is slightly expanded posteriorly. The lateral margin of the carapace is not upturned on the peripherals 3–4 and the anterior part of the peripheral 5; a very slightly upturned lateral margin is observed from the posterior part of the peripheral 5 to peripheral 7. Two large suprapygals of similar width are distinguishable on the internal mould. Although the posterior margin is damaged, the pygal is certainly wider than long, with the lateral margins convergent forward. The marginals 4–7 extend onto the costals, from the posterior part of costal 1 to the anterolateral tip of costal 5; the marginal

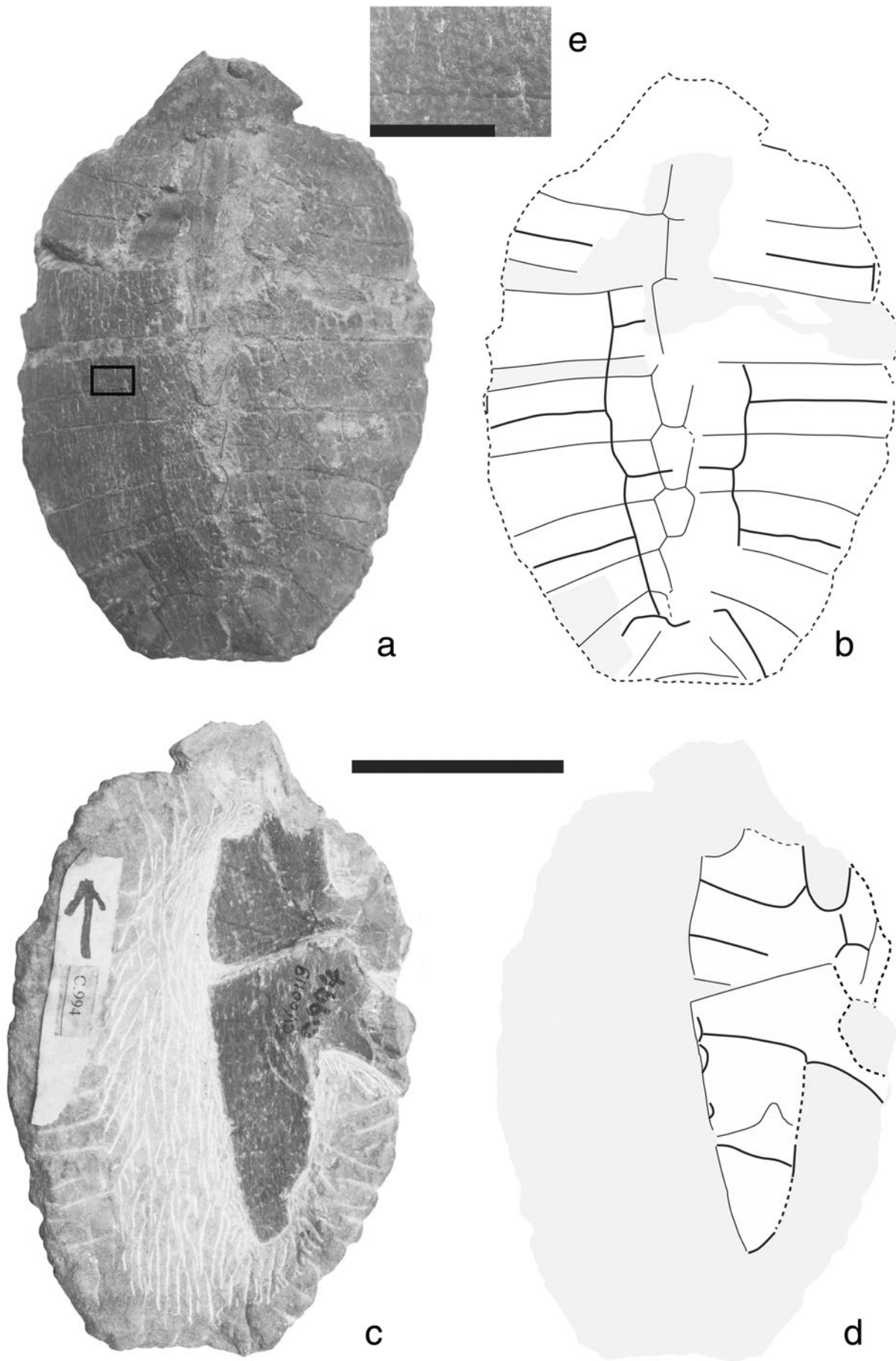


Figure 2. Holotype of *Sinaspideretes wimani* Young & Chow, 1953 (CQMNH C.994) from the Jurassic of the Sichuan Basin in dorsal (a, b) and ventral (c, d) views and detail of ornamentation (e). Scale bar represents 5 cm for (a–d) and 1 cm for (e).

8 is restricted to the peripheral. Our interpretation of the carapace and plastron of IVPP V996 is shown in Figure 3.

3.c. New specimen (CQMNH C.1000; Fig. 4)

CQMNH C.1000 is an almost complete carapace without a plastron. The specimen is well preserved without deformation, although the margin area is damaged (see Fig. 4).

The shell is low. The carapace has an oval outline which is slightly expanded posteriorly, with a wide and rather deep cervical notch. The anterolateral edge is slightly upturned, but not forming a clear gutter. The surface of the shell is covered with a pitted ornamentation (Fig. 4c). The nuchal is damaged, but the outline can be made out; it is trapezoidal in shape. The complete neural series reaches the suprapygal, with a neural formula of 6<4>6>6>6>6>6>6. The first neural is hexagonal, with short posterolateral sides. The second neural is rectangular and clearly shorter than the third neural. The third to eighth neurals are hexagonal, with short anterolateral sides. The first to seventh neurals are longer than wide, while the eighth one is short and roughly as long as wide. There are two large triangular suprapygals of roughly equal size. The pygal is slightly wider than long. The peripherals from the fourth to the sixth are narrow, while the seventh to eleventh are greatly expanded mesiolaterally.

The scute sulci are clearly visible. The cervical is not preserved. All vertebrals are relatively narrow. The second and third vertebrals are roughly as wide as long, though the fourth vertebral is longer than wide. The intervertebral sulci pass through the first, the third, the fifth and the eighth neurals, respectively. The first costal scute is longer than wide and the second to the third costal scutes are roughly as long as wide. The marginals 4–7 extend onto the second to fifth costal plates, and the eleventh and twelfth marginals are mesiolaterally expanded, overlapping the suprapygals.

4. Comparisons (Table 2)

The shells of CQMNH C.994, CQMNH C.1000 and IVPP V996 are similar in their small size and in their sculptured carapace surface. The general shape of the carapace is also comparable, with a low dome and oval outline. Both CQMNH C.1000 and IVPP V996 have a slightly upturned anterolateral carapace margin. The carapaces of CQMNH C.1000 and IVPP V996 are slightly expanded posteriorly, although the posterolateral carapacial margins of IVPP V996 are damaged (see Section 3).

The carapaces of CQMNH C.994 and CQMNH C.1000 have a similar shape and proportion of the neurals, with a neural formula of 6<4>6>6>6>6>6>6, neural 2 being clearly smaller than neural 3, and neural 7 larger than neural 6. There are two large suprapygals of similar size. The vertebral scutes are narrow, with vertebral 3 as wide as long and an elongate vertebral 4.

Although the carapace of IVPP V996 is mostly missing, the morphology of the preserved peripherals and lateral portion of the costals perfectly matches those of CQMNH C.1000: the anterior peripherals, from the third to the sixth, are mesiolaterally narrow, and the seventh to eleventh peripherals are mesiolaterally expanded; the fourth marginal scute is restricted to the peripheral plate anteriorly, but extends onto the second costal plate posteriorly; the fifth to seventh marginals extend onto the costals, and the eighth to tenth marginals are again restricted to the peripherals. In CQMNH C.994, the pleuromarginal sulcus is visible on the right second costal.

The plastron of CQMNH C.994, as exposed, is similar to that of IVPP V996 in the following features: plastron sutured to the carapace; relatively long and narrow bridge; long axillary buttress; broad entoplastron; humeropectoral sulcus located at the base of the anterior lobe; pectoral shorter than abdominal; femoroanal sulcus not reaching hypoplastron/xiphoplastron suture; sinuous midline sulcus of plastron; and presence of inframarginals. However, compared with IVPP V996, CQMNH C.994 seems to have a slightly narrower posterior lobe of the plastron, with straighter lateral margins.

5. Systematic palaeontology

Order TESTUDINES Linnaeus, 1758

Infraorder CRYPTODIRA Cope, 1868

Superfamily TRIONYCHOIDAE Fitzinger, 1826

Genus *Sinaspideretes* Young & Chow, 1953

1963 *Plesiochelys tatsuensis* Ye, p. 9, fig. 7, pl. I, 3–4.

1994 *Plesiochelys tatsuensis* Ye, p. 21, fig. 8.

2006 *Yehguia tatsuensis* Danilov & Parham, p. 573, figs 2–3.

2008 *Yehguia tatsuensis* Brinkman, Li & Ye, p. 62, fig. 64.

Type species. *Sinaspideretes wimani* Young & Chow, 1953.

Type locality and horizon. Along Chengyu Railway, exact location and horizon unknown.

Emended diagnosis. Trionychoid of small size, with a carapace length of about 165 mm; carapace low, with a shallow cervical notch and an oval outline which is slightly expanded posteriorly; characterized by the following combination of features: carapace surface with pitted ornamentation, plastron surface rough; complete neural series reaching suprapygal, with a neural formula of 6<4>6>6>6>6>6>6; two suprapygals of equal size; vertebral scutes narrow, with the second and third vertebrals roughly as long as wide; plastron sutured to carapace; relatively large epiplastron; large entoplastron which is roughly as wide as long; pair of intergulars present, extending slightly onto entoplastron; pectoral shorter than abdominal; anal scute

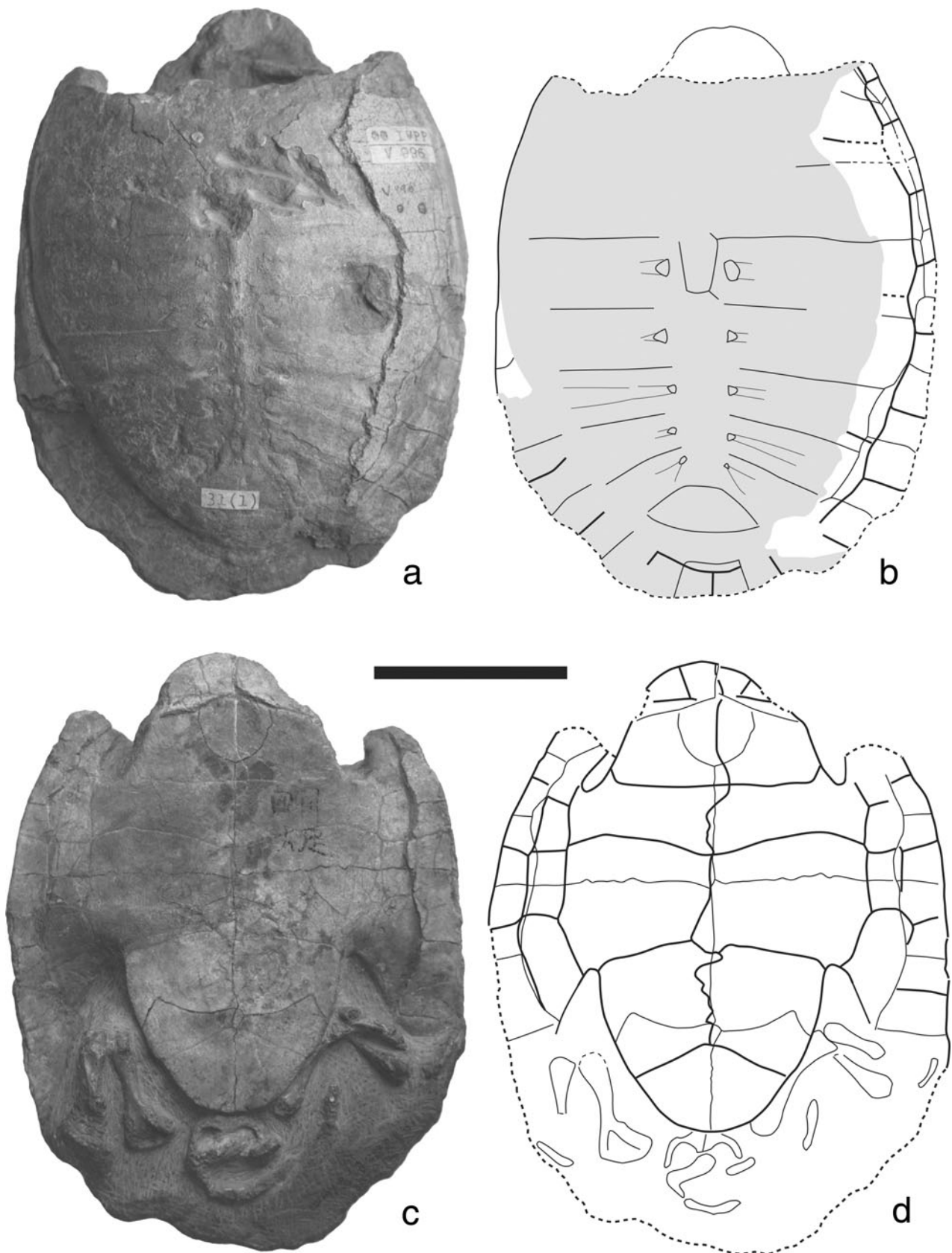


Figure 3. *Sinaspideretes wimani* Young & Chow, 1953 (IVPP V996, holotype of *Yehguia tatsuensis* (Ye, 1963)) from the Upper Jurassic of Dazu, Sichuan Basin in dorsal (a, b) and ventral (c, d) views. Scale bar represents 5 cm.

Table 1. Measurements of *Sinaspideretes wimani* Young & Chow, 1953

	Carapace		Plastron	
	Preserved	Estimated	Preserved	Estimated
CQMNH C.994	(146 × 96)	155 × 120	97 × 45	112 × 88
CQMNH C.1000	165 × 128	–	–	–
IVPP V996	(138 × 120)	160 × 123	116 × 89	–

Length × width, in millimetres.

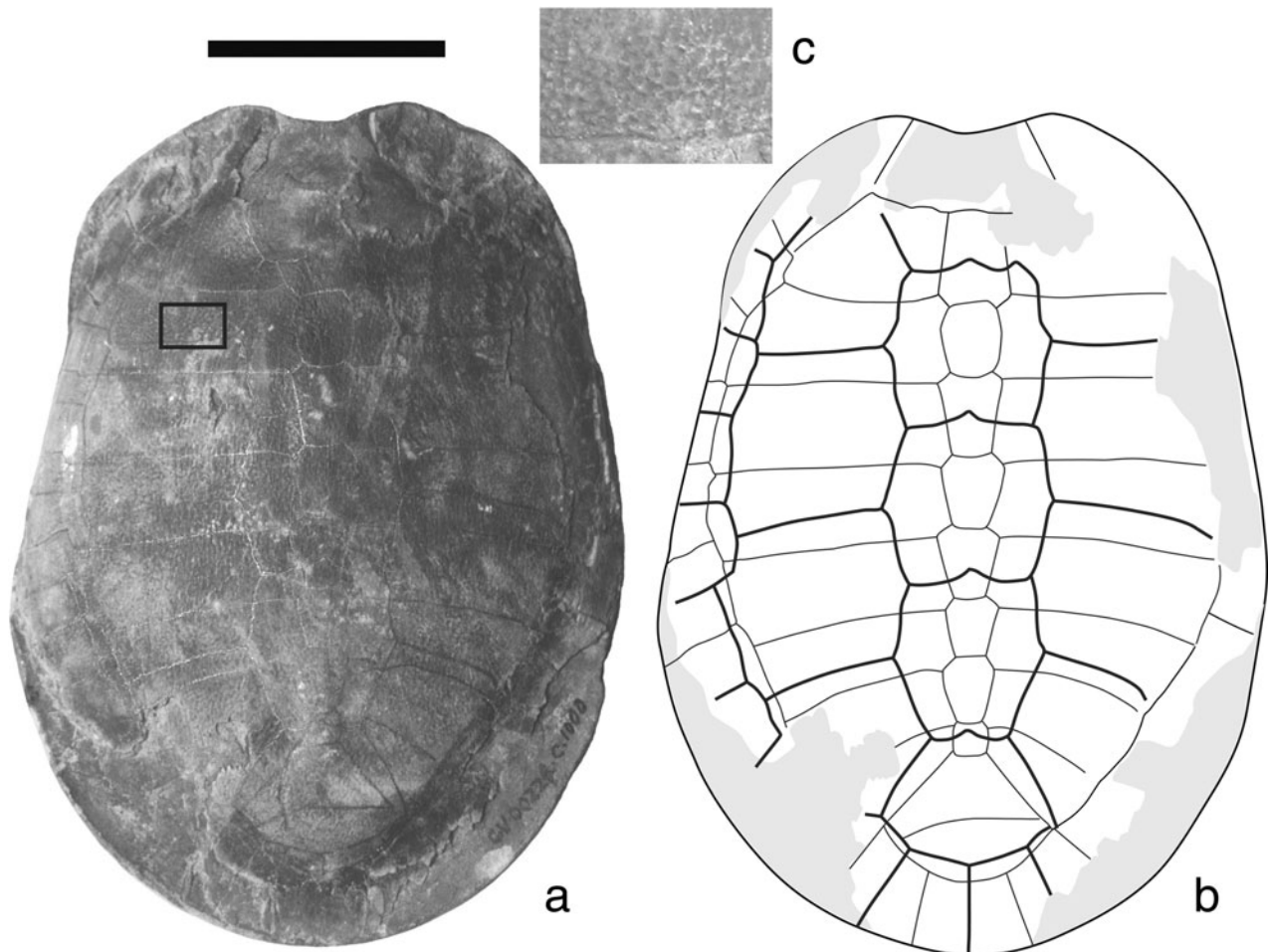


Figure 4. *Sinaspideretes wimani* Young & Chow, 1953 (CQMNH C. 1000) from the Upper Jurassic of Suining, Sichuan Basin in dorsal view (a, b) and detail of ornamentation (c). Scale bar represents 5 cm.

restricted to xiphiplastron; four pairs of inframarginal scutes; midline sulcus of plastron sinuous.

Measurements. See Table 1.

Distribution. Upper Jurassic Shangshaximiao Formation; Sichuan Basin, China.

6. Discussion

Based on the comparisons above, *Y. tatsuensis* (Ye, 1963) is synonymized with *S. wimani* Young & Chow, 1953. Slight differences, such as the narrower posterior plastral lobe of CQMNH C.994 relative to IVPP V996 are probably owing to individual variation or might also reflect sexual dimorphism.

The species *S. wimani* now includes three specimens which provide an almost complete aspect of the

shell. A reconstruction is shown in Figure 5. In agreement with previous opinions (Young & Chow, 1953; Meylan & Gaffney, 1992; Danilov & Parham, 2006), *S. wimani* is a member of Trionychoidea. The trionychoid synapomorphies observed in *S. wimani* include the carapace surface covered with a pitted sculpture, the neural formula of 6<4>6>6>6>6>6>6 and a broad entoplastron. The pitted ornamentation of *S. wimani* is reminiscent of the adocids *Ferganemys* spp., *Adocus* spp. and *Isanemys srisuki* (Tong, Buffet & Suteethorn, 2006; Syromyatnikova & Danilov, 2009; Danilov, Sukhanov & Syromyatnikova, 2011; Syromyatnikova, 2011). The neural pattern with a hexagonal first neural with short posterolateral sides followed by a rectangular second neural is present in nearly all Adocidae (with one exception: *Isanemys*) and Nanhsiungchelyidae. It is also observed in some

Table 2. Comparisons between CQMNH C.994, IVPP V996 and CQMNH C.1000

Characters/specimen	CQMNH C.994 Holotype of <i>Sinaspideretes wimani</i>	IVPP V996 Holotype of <i>Yehguia tatsuensis</i>	CQMNH C.1000
Shell height	Low	Low	Low
Shell outline	?	Long oval, enlarged posteriorly	Long oval, enlarged posteriorly
Carapace surface ornamentation	Pitted	Pitted	Pitted
Neural series	Complete, reaching suprapygal	?	Complete, reaching suprapygal
Neural formula	6<4>6>6>6>6>6>6	?	6<4>6>6>6>6>6>6
Suprapygals	2 large suprapygals of similar size	2 large suprapygals of similar size	2 large suprapygals of similar size
Peripheral number	?	11	11
Peripherals 8 to 11 mesiolaterally expanded	?	Yes	Yes
Vertebral scutes	Narrow	?	Narrow
Lateral marginals	Extending onto costal 2 at least	Extending onto costals 2 to 5	Extending onto costals 2 to 5
Marginals 11 and 12	?	?	Mesiolaterally expanded, extending onto suprapygal 2
Plastron/carapace attachment	Sutured	Sutured	?
Plastron surface	Rough	Rough	?
Anterior lobe	Large and wide	Large and wide	?
Bridge	Long and narrow	Long and narrow	?
Posterior lobe	Long, but narrower than in C996	Long and wide, with rounded lateral margins	?
Axillary buttress	Long	Long	?
Axillary notch	Narrower than inguinal notch	Narrower than inguinal notch	?
Inguinal buttress	Long	Long	?
Entoplastron	Broad	Broad	?
Midline sulcus	Sinuuous	Sinuuous	?
Pectoral shorter than abdominal	Yes	Yes	?
Humeropectoral sulcus position	Posterior to entoplastron, at the base of the anterior lobe	Posterior to entoplastron, at the base of the anterior lobe	?
Femoroanal sulcus	Not reaching hypoplastron	Not reaching hypoplastron	?
Inframarginals (number)	Present, total number unknown	Present (4)	?

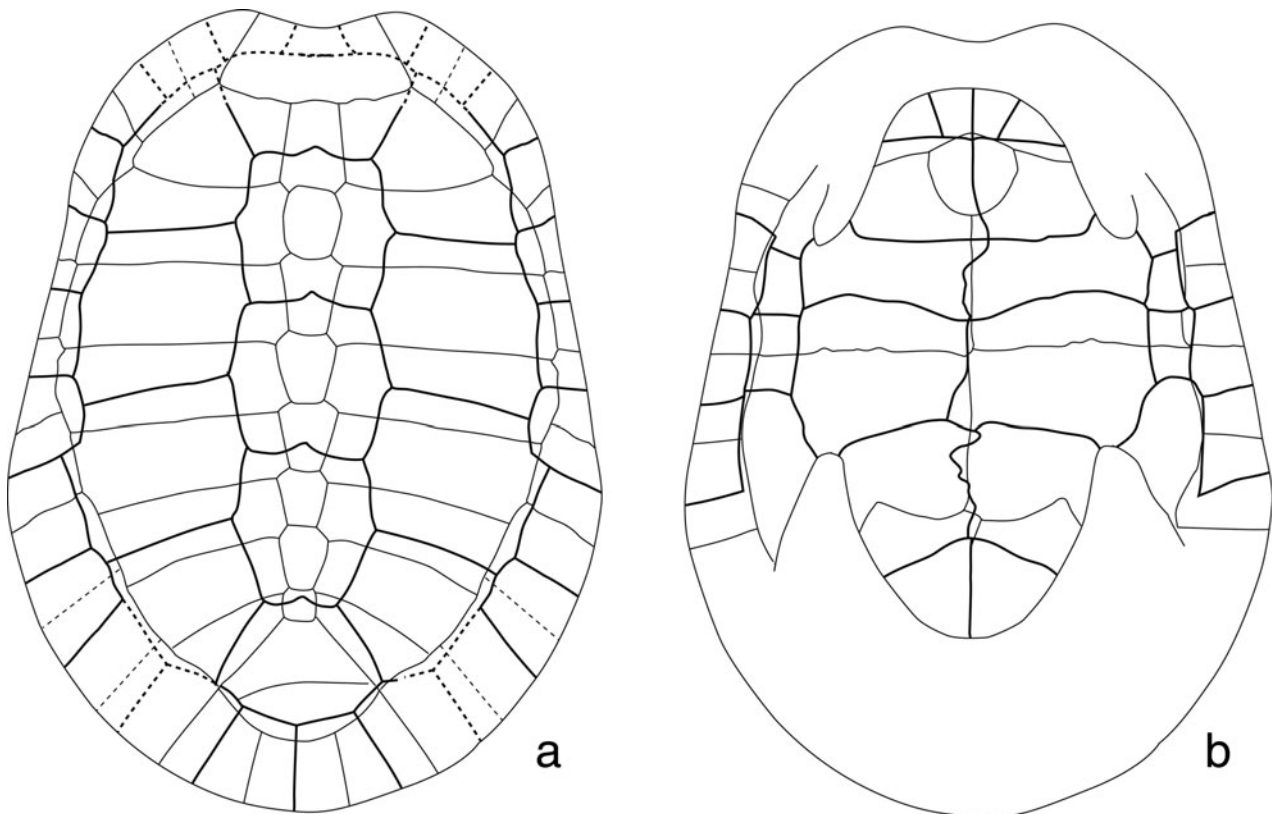
Figure 5. Reconstruction of *Sinaspideretes wimani* Young & Chow, 1953, in dorsal (a) and ventral (b) views.

Table 3. Data matrix of *Sinaspideretes wimani* Young & Chow, 1953

10	20	30	40	50	60	70	
?????????	?????????	?????????	?????????	?????1212	10001000?0	0011100000	0001

xinjiangchelyids as intraspecific variation, such as *Chengyuchelys latimarginalis* (Young & Chow, 1953) from the Upper Jurassic of the Sichuan Basin and *Xinjiangchelys* from the Upper Jurassic of Pinfengshan, Junggar Basin, China (Peng & Brinkman, 1993; Tong *et al.* 2012b). A broad entoplastron is present in Trionychoidea, and also in Testudinoidea (Tong *et al.* 2009). The entoplastron is oval in Xinjiangchelyidae and triangular in 'Macrobaenidae'; in both cases it is clearly longer than wide. In addition, the pectoral being shorter than the abdominal and the anal scute being restricted onto the xiphiplastron are also characters shared with basal trionychoids but distinct from xinjiangchelyids.

S. wimani was originally included in Trionychidae but was later tentatively placed in Carettochelyidae by Meylan & Gaffney (1992), where it was the oldest member of that family. Contrary to the opinion of Meylan & Gaffney (1992), we exclude *S. wimani* from Carettochelyidae. The relatively wide neurals, complete series of neurals reaching the suprapygal, two large suprapygals, 11 pairs of peripherals, unreduced scutes, plastron sutured to the carapace with a long and narrow bridge and long axillary and inguinal buttresses, broad epiplastron and a diamond-shaped entoplastron which is located clearly anterior to the base of the anterior lobe seen in *S. wimani* are all inconsistent with Carettochelyidae. The family Carettochelyidae, known since the mid Cretaceous of SE Asia (de Lapparent de Broin, 2004; Tong *et al.* 2004, 2005), represents a relatively homogenous group. In this family, the neurals are slender, the neural series is reduced, with the posterior costal plates meeting at the midline; a single large suprapygal is present; there are ten pairs of peripherals; the plastron is attached to the carapace by ligaments; the bridge is short with reduced axillary and inguinal buttresses; the epiplastron is elongate; and the entoplastron is triangular and located at the base of the anterior lobe. The scutes are extremely reduced in Carettochelyidae; they are greatly modified in Anosterinae and totally lost in adults of Carettochelyinae.

The recent revision of *Y. tatsuensis* placed this taxon at first in a group of basal Trionychoidea named Adocusia, which includes also Adocidae and Nanhsiungchelyidae (Danilov & Parham, 2006), while subsequent phylogenetic analyses placed it in a basalmost position among Adocidae because of the presence of three synapomorphies: a longer than wide pygal, shell surface sculpture consisting of small and regular pits or dots, and shallow and narrow scute sulci (Danilov & Syromyatnikova, 2009). Although *S. wimani* has a pitted shell surface ornamentation like adocids, a series of primitive characters seems to support its more basal

position relative to Adocidae and Nanhsiungchelyidae within Trionychoidea: two large suprapygals of similar size; a roughly as wide as long entoplastron which is located anteriorly; and the humeropectoral sulcus located at the base of the anterior lobe. Adocidae and Nanhsiungchelyidae share a number of derived characters such as a reduced first suprapygal, an entoplastron clearly wider than long and located posteriorly, and the humeropectoral sulcus posterior to the anterior lobe.

We performed a phylogenetic analysis adding in the data from *S. wimani* (Table 3) to the data matrix used in Tong *et al.* (2009). Twenty-seven of 74 characters were coded in *S. wimani*. Based on the recent works on Xinjiangchelyidae (Tong *et al.* 2012a,b), one character coding in *Xinjiangchelys* (character 50: marginal scutes reaching costal plates) was changed to 2. Ten most parsimonious trees were produced using Paup 4.0b10, with a tree length of 183 steps, consistency index of 0.45 and retention index of 0.73. The general topography of the strict consensus tree remains comparable to that of Tong *et al.* (2009), except that the position of *Adocus*, nanhsiungchelyids and *Basilochelys* relative to Trionychia within Trionychoidea is unresolved. *S. wimani* is placed in the basalmost position among Trionychoidea (Fig. 6) in contrast to the recent phylogenetic analysis by Danilov & Syromyatnikova (2009), which placed *Y. tatsuensis* within the family Adocidae.

7. Conclusion

S. wimani Young & Chow, 1953 is the only trionychoid turtle in the Jurassic of the Sichuan Basin. Although the original information about the exact stratigraphical level and geographical origin of the holotype (CQMNH C.994) is missing, given that two other referred specimens (IVPP V996 and CQMNH C.1000) are both from the Upper Jurassic Shangshaximiao Formation, CQMNH C.994 is likely from the same stratigraphical unit.

S. wimani is excluded here from Carettochelyidae since it lacks all synapomorphic features of that group. The family Carettochelyidae, as currently documented, first occurs in the mid Cretaceous, with the oldest representatives being from the Lower Cretaceous Sao Khua Formation (Barremian) of Thailand (Tong *et al.* 2004). *S. wimani* is considered as the most basal member of Trionychoidea. The presence of trionychoids in the Upper Jurassic adds to the evidence from the fossil record for the antiquity of the group, thus is in agreement with the early split of Trionychoidea among the crown Testudines suggested by the phylogeny of turtles based on the molecular data, which places

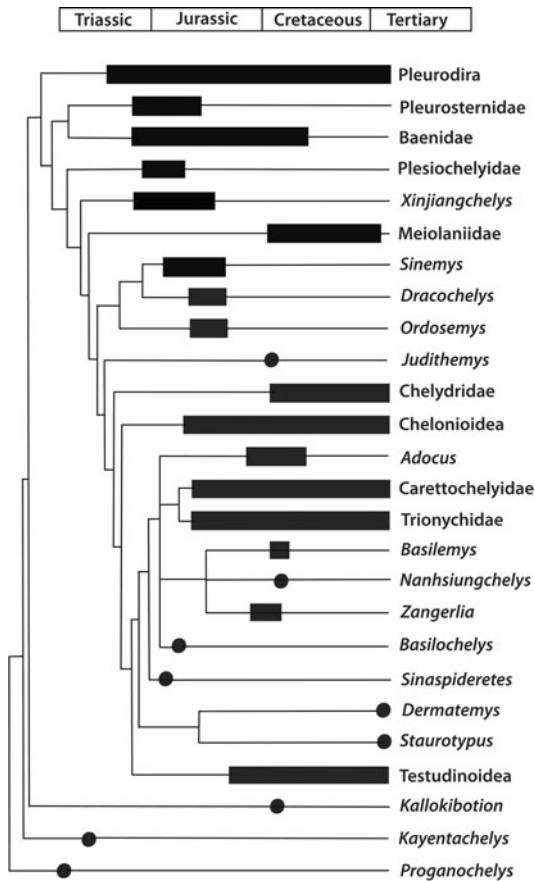


Figure 6. Strict consensus tree produced using data matrix of Tong *et al.* (2009) with *S. wimani* included.

Trionychia (Carettochelyiidae and Trionychidae) in the basalmost position among Cryptodira (Krenz *et al.* 2005; Near, Meylan & Shaffer, 2005; Lourenço *et al.* 2012), although the analysis using morphological characters alone does not suggest the same scenario.

Acknowledgements. We thank Fang Zheng and Yuan Wang (IVPP, Beijing), Songlin Zhu and Jiangbo Tong (CQMNH, Chongqing) for access to the specimens in their care; Julien Claude (Montpellier) and Donald Brinkman (Drumheller) for review and Eric Buffetaut (Paris) for improving the manuscript. This work is supported by a National Natural Science Foundation of China (Grant 41172017) to H. T. and L. L.

References

BRINKMAN, D., LI, J.-L. & YE, X.-K. 2008. Order Testudines. In *The Chinese Fossil Reptiles and their Kin* (eds J.-L. Li, X.-C. Wu & F.-C. Zhang), pp. 35–102. Beijing: Science Press.

DE BROIN, F. 1977. Contribution à l'étude des Chéloniens. Chéloniens continentaux du Crétacé et du Tertiaire de France. *Mémoires du Muséum National d'Histoires naturelles, Paris C*, **38**, 1–366.

CHKHIKVDZE, V. M. 1987. Sur la classification et caractères de certaines tortues fossiles d'Asie, rares et peu étudiées. *Studia Geologica Salamanticensia, Studia Palaeocheloniologica* **2**, 55–86.

COPE, E. D. 1868. On the origin of genera. *Proceedings of the Academy of Natural Sciences of Philadelphia* **20**, 242–300.

DANILOV, I. G. & PARHAM, J. F. 2006. A redescription of *Plesiochelys tatsuensis* from the Late Jurassic of China, with comments on the antiquity of the crown clade Cryptodira. *Journal of Vertebrate Paleontology* **26**, 573–80.

DANILOV, I. G., SUKHANOV, V. B. & SYROMYATNIKOVA, E. V. 2011. New Asiatic materials on turtles of the family Adocidae with a review of the adocid record in Asia. *Proceedings of the Zoological Institute RAS* **315**, 101–32.

DANILOV, I. & SYROMYATNIKOVA, E. V. 2009. Phylogeny of the extinct turtle clade Adocusia. In *Gaffney Turtle Symposium, 17–18 October 2009*, Drumheller, Canada, pp. 44–51.

ERNST, C. H. & BARBOUR, R. W. 1989. *Turtles of the World*. Washington D.C.: Smithsonian Institution Press.

FITZINGER, L. 1826. *Neue Classification der Reptilien nach ihren natürlichen Verwandtschaften*. Wien: J. G. Heubner.

HAY, O. P. 1908. The fossil turtles of North America. *Carnegie Institute of Washington* **75**, 1–568.

KRENZ, J. G., NAYLOR, G. J., SHAFFER, H. B. & JANZEN, F. J. 2005. Molecular phylogenetics and evolution of turtles. *Molecular Phylogenetics and Evolution* **37**, 178–91.

DE LAPPARENT DE BROIN, F. 2004. A new Shachemydinae (Chelonii, Cryptodira) from the Lower Cretaceous of Laos: preliminary data. *Comptes Rendus Palevol* **3**, 387–96.

LINNAEUS, C. 1758. *Systema Naturae*. Stockholm, 824 pp.

LOURENÇO, J. M., CLAUDE, J., GALTIER, N. & CHIARI, Y. 2012. Dating cryptodiran nodes: origin and diversification of the turtle superfamily Testudinoidea. *Molecular Phylogenetics and Evolution* **62**, 496–507.

LUCAS, S. G. 2001. *Chinese Fossil Vertebrates*. New York: Columbia University Press.

MEYLAN, P. A. & GAFFNEY, E. S. 1992. *Sinaspideretes* is not the oldest trionychid turtle. *Journal of Vertebrate Paleontology* **12**, 257–9.

MLYNARSKY, M. 1976. *Testudines*. Handbuch der Paläoherpetologie Teil 7. Stuttgart: Gustav Fischer Verlag.

NEAR, T. J., MEYLAN, P. A. & SHAFFER, H. B. 2005. Assessing concordance of fossil calibration points in molecular clock studies: an example using turtles. *The American Naturalist* **165**, 137–46.

NESSOV, L. A. & JULINEN, V. A. 1977. On phylogenetic relationships and history of distribution of some families of continental turtles. In *Life on Ancient Continents, its Establishment and Development. Trudy Vsesoyuznogo Paleontologicheskogo Obshchestva* **1977**, 54–6.

PENG, J.-H. & BRINKMAN, D. 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.

PRITCHARD, P. C. H. 1979. *Encyclopedia of Turtles*. T. F. H. Publications.

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 & E. N. Kurochkin), pp. 309–67. Cambridge: Cambridge University Press.

SYROMYATNIKOVA, E. V. 2011. Turtles of the genus *Ferganemys* Nessov et Khosatzky, 1977 (Adocidae): shell morphology and phylogenetic position. *Proceedings of the Zoological Institute RAS* **315**, 38–52.

- SYROMYATNIKOVA, E. V. & DANILOV, I. G. 2009. New material and a revision of turtles of the genus *Adocus* (Adocidae) from the Late Cretaceous of Middle Asia and Kazakhstan. *Proceedings of the Zoological Institute RAS* **313**, 74–94.
- TONG, H., BUFFETAUT, E. & SUTEETHORN, V. 2006. *Isanemys*, a new adocid turtle from the Sao Khua Formation (Early Cretaceous) of the Khorat Plateau, northeastern Thailand. In *Fossil Turtle Research, Vol. 1, Russian Journal of Herpetology* (eds I. Danilov & J. F. Parham), pp. 128–37.
- TONG, H., BUFFETAUT, E., SUTEETHORN, V. & SRISUK, P. 2004. First carettochelyid turtle from the Lower Cretaceous of Thailand. Abstract. In *2nd EAVP Meeting* (eds O. Ostal, R. Gregorova & M. Ivanov), p. 44. Brno: Moravian Museum.
- TONG, H., CLAUDE, J., NAKSRI, W., SUTEETHORN, V., BUFFETAUT, E., KHANSUBHA, S., WONGKO, K. & YUANGDETKLA, P. 2009. *Basilochelys macrobios* n. gen. and n. sp., a large cryptodiran turtle from the Phu Kradung Formation (latest Jurassic–earliest Cretaceous) of the Khorat Plateau, NE Thailand. In *Late Palaeozoic and Mesozoic Continental Ecosystems in SE Asia* (eds E. Buffetaut, G. Cuny, J. Le Loeuff & V. Suteethorn), pp. 153–74. Geological Society of London, Special Publication no. 315.
- TONG, H., DANILOV, I., YE, Y., OUYANG, H. & PENG, G.-Z. 2012a. Middle Jurassic turtles from the Sichuan Basin, China: a review. *Geological Magazine* **149**, 675–95.
- TONG, H., DANILOV, I., YE, Y., OUYANG, H., PENG, G.-Z. & LI, K. 2012b. A revision of xinjingchelyid turtles from the Late Jurassic of Sichuan Basin, China. *Annales de Paléontologie* **98**, 73–114.
- TONG, H., SUTEETHORN, V., CLAUDE, J., BUFFETAUT, E. & JINTASAKUL, P. 2005. The turtle fauna from the Khok Kruat Formation (Early Cretaceous) of Thailand. In *Proceedings of the International Conference on Geology, Geotechnology and Mineral Resources of Indochina (GEOINDO 2005)* (eds L. Wannakao, W. Youngme, K. Srisuk & R. Lertsirivorakul), pp. 610–14. Khon Kaen, Thailand: Khon Kaen University.
- TONG, H., ZHANG, J.-Y. & LI, J.-J. 2010. *Anosteira maomingensis* (Testudines: Carettochelyidae) from the Late Eocene of Maoming, Guangdong, southern China: new material and redescription. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **256**, 279–90.
- YE, X.-K. 1963. Fossil turtles of China. *Palaeontologia Sinica* **150** (new series C 18), 1–112.
- YE, X.-K. 1994. *Fossil and Recent Turtles of China*. Beijing: Science Press.
- YOUNG, C.-C. & CHOW, M.-C. 1953. New fossil reptiles from Szechuan, China. *Acta Scientia Sinica* **2**, 216–43.
- ZHANG, M., ZONG, Y. & MA, J. 1998. *Fauna Sinica. Reptilia 1. General Accounts of Reptilia, Testudoformes and Crocodyliformes*. Beijing: Science Press.