

A REASSESSMENT OF SOME POORLY KNOWN TURTLES FROM THE MIDDLE JURASSIC OF CHINA, WITH COMMENTS ON THE ANTIQUITY OF EXTANT TURTLES

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ABSTRACT—Recent studies have shown that the Middle Jurassic is a key time for understanding the origin and early evolution of crown group turtles, but few turtle-bearing localities from this epoch are known. This study adds to our knowledge by providing a detailed description of two poorly characterized specimens (IVPP-V6507 and IVPP-V8805) from the Middle Jurassic of China that previously were both assigned to the poorly known species *Chengyuchelys baenoides*. This reappraisal allows us to present new observations, images, and taxonomic conclusions about these specimens and others from the same locality (Dashanpu, Zigong Prefecture, Sichuan Province, China). With at least four species, Dashanpu is the most diverse locality from the Middle Jurassic; all other turtle localities from this time have only one species each. We place *Chengyuchelys* into a cladistic analysis of turtle relationships for the first time. Our analysis places *Chengyuchelys* as sister to *Xinjiangchelys latimarginalis* and solidly on the stem of Cryptodira. This result is surprising because *Chengyuchelys* retains mesoplastra. Nevertheless, derived osteological and scalation characters of this taxon drive its phylogenetic position as a relatively advanced stem cryptodire. This finding, combined with a reappraisal of other Middle Jurassic turtles from Asia, shows that the crown group Testudines had evolved by the Middle Jurassic. Unfortunately, many key specimens from Sichuan Province are still poorly characterized morphologically and stratigraphically. This lack of phylogenetic and temporal resolution hinders our understanding of the origins of extant turtle clades, but also highlights the importance of Jurassic Asian turtles for ultimately resolving these issues.

INTRODUCTION

The Jurassic is a key time for understanding the origin and early evolution of the major turtle lineages. Although the oldest turtles (Testudinata) evolved as early as the Late Triassic, new evidence suggests that the origin of extant turtles (Testudines) did not occur until the Late Jurassic (Joyce, 2007; all suprageneric clade names follow Joyce et al. [2004] unless otherwise noted). Danilov and Parham (2006) showed that the origin of Testudines was quickly followed by evidence for the first cryptodires in the Late Jurassic of China. Cryptodira is the most diverse of the two crown clades that include all extant turtles (the other, Pleurodira, did not originate until the Early Cretaceous; reviewed in Joyce et al. [2004]). Given the rarity of pre-Late Jurassic turtles (Fig. 1), fossils from previous epochs are important for understanding the origin of the crown groups Testudines and Cryptodira. In an effort to provide new insights into these events, we provide new data derived from our study of two Middle Jurassic specimens from the Dashanpu locality (Fig. 1H), which is in the Xiashaximiao (= Lower Shaximiao) Formation in Zigong Prefecture, Sichuan Province, China (see Peng et al. [2005] for the latest review of vertebrate faunas and stratigraphy of the Zigong region). Our study of these specimens reveals previously unknown and misunderstood characters. These new observations also allow us to include a taxon from Dashanpu into an analysis of turtle relationships for the first time in an attempt to better constrain the origination times of turtle clades.

Middle Jurassic Turtles of Dashanpu

Just eight species of turtle have been reported from the Middle Jurassic worldwide (Fig. 1) and four of those are from Dashanpu (Young and Chow, 1953; Yeh, 1982; Fang, 1987; Ye and Pi, 1997). Dashanpu also is the only Middle Jurassic turtle locality characterized by more than a single species. The turtles of Dashanpu differ from most later Asian taxa by the presence of mesoplastra, which is a primitive character for turtles (Gaffney and Meylan, 1988; Joyce, 2007). Mesoplastra are a pair of bones that occur between the hyoplastra and hypoplastra in the plastron of turtles. Mesoplastra are known in stem Testudines, as well as some Pleurodira (including all stem pleurodires). At present, mesoplastra are not definitively known in stem or extant cryptodires (Pancryptodira). According to Joyce (2007), all previously reported stem cryptodires with mesoplastra instead can be assigned to the stem of Testudines. Another Middle Jurassic Asian turtle, *Siamochelys peninsularis* Tong, Buffetaut, and Suteethorn, 2002, from Thailand (Fig. 1I), was reported to have mesoplastra and considered by Tong et al. (2002) as primitive Cryptodira sensu Gaffney and Meylan (1988; = stem Cryptodira sensu Joyce et al. [2004]). However observations by one of us (Danilov, pers. obs.) show that in fact this species seems to have no mesoplastra.

The four species of turtles from Dashanpu are referred to two genera: *Chengyuchelys* Young and Chow, 1953, and *Sichuanchelys* Ye and Pi, 1997. *Chengyuchelys* contains three named species (*C. baenoides* Young and Chow, 1953; *C. zigongensis* Yeh, 1982; and *C. dashanpuensis* Fang, 1987) whereas *Sichuanchelys* is monotypic (*Sic. chowi* Ye and Pi, 1997). The

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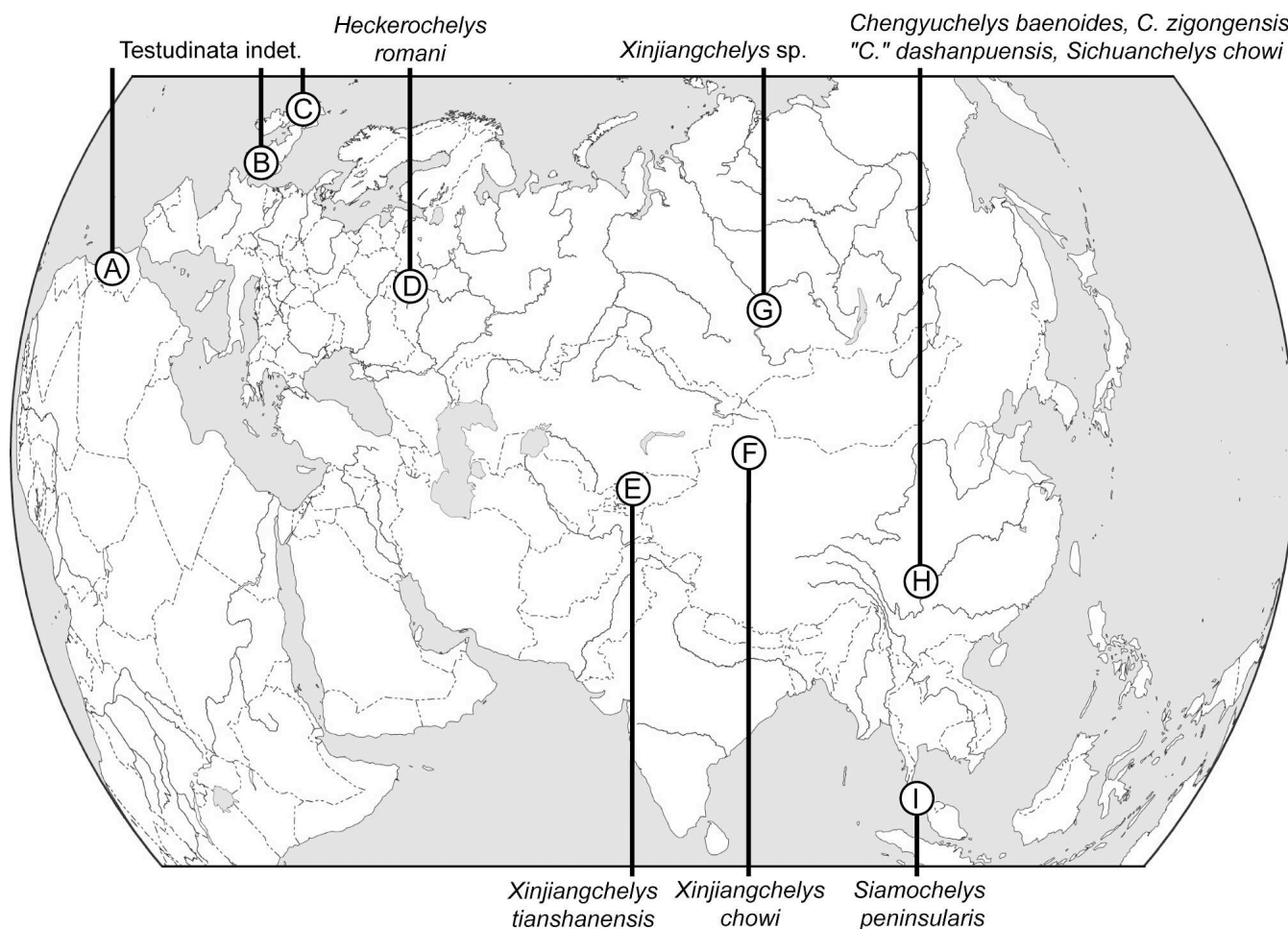


FIGURE 1. Map showing all known occurrences of Middle Jurassic turtles. **A**, unreported formation, El Kelaa des Sraghna Province, Morocco (Termier et al., 1940). **B**, multiple formations, England, United Kingdom (reviewed by Evans and Milner, 1994). **C**, Great Estuarine Series, Skye, Scotland, United Kingdom (reviewed by Evans and Milner, 1994). **D**, unreported formation, Moskovskaya Oblast, Russia (reviewed by Sukhanov, 2006). **E**, Balabansai Formation, Dzhatal-Abadskaya Oblast, Kyrgyzstan (Nessov, 1995). **F**, Toutunhe Formation, Xinjiang Province, China (Matzke et al., 2005). **G**, Itak Formation, Krasnoyarsk Krai, Russia (Danilov et al., 2005). **H**, Xiashaximiao Formation (where known), Sichuan and Chongqing provinces, China (reviewed by Yeh, 1994; Lucas, 2001). **I**, unreported formation, Changwat Nakhon Si Thammarat, Thailand (reviewed by Tong et al., 2002).

type species of *Chengyuchelys*, *C. baenoides*, was based on two specimens (an incomplete shell and a fractured plastron) from a “locality near the Chengyu Railway (between Chengdu and Chongqing, Sichuan province) . . .” (Yeh, 1994:5) and not Dashanpu. Since that time, Dashanpu (Fig. 1H) has been the source of all Middle Jurassic Sichuan specimens including the type material of the two other species of *Chengyuchelys* (*C. dashanpuensis* and *C. zigongensis*) and *Sic. chowi*. Additional specimens from Dashanpu have been referred to *C. baenoides*, *C. zigongensis*, *C. cf. zigongensis*, *Chengyuchelys* sp., and *Chengyuchelyidae* indet. (Yeh, 1982; Fang, 1987; Yeh, 1990a, b, 1994; Peng et al., 2005).

DESCRIPTIONS

We examined two specimens from the Dashanpu locality that were previously assigned to *Chengyuchelys baenoides* (Yeh, 1982, 1990b, 1994; Peng et al., 2005): IVPP-V6507, the anterior third of a shell (Yeh, 1982:fig. 2, Pl. II, figs. a–c; Peng et al., 2005:fig. 23) and IVPP-V8805, a previously unfigured, incomplete shell consisting of the posterior two-thirds of a carapace and an almost complete plastron. Mainly for comparison we also

examined a cast of the holotype of *Chengyuchelys baenoides* (IVPP-V708). Other IVPP specimens from this locality were not made available for our study.

Institutional Abbreviations—**C.V.**, vertebrate fossil collection of the Chongqing Natural History Museum, Chongqing, China; **I-L**, **I-T**, **I-Z**, **KI**, and **ZDM**, fossil collections of the Zigong Dinosaur Museum, Sichuan, China; **IVPP-V**, vertebrate fossil collection of the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China.

IVPP-V6507

Description—IVPP-V6507 (Fig. 2) includes the following elements: nuchal; complete neurals 1 and 2 and anterior portion of neural 3; complete right costals 1 and 2, lateral portions of right costals 3 and 4, and medial portions of left costals 1 and 2; right peripherals 1 through 7 and left peripherals 1 through 3; complete left epiplastron and most of right epiplastron; complete entoplastron; both hyoplastra, each missing most of their lateral (bridge) parts; almost complete right mesoplastron and medial piece of left mesoplastron; and anterior part of right hypoplastron. Besides these shell elements, fragments of the left pectoral

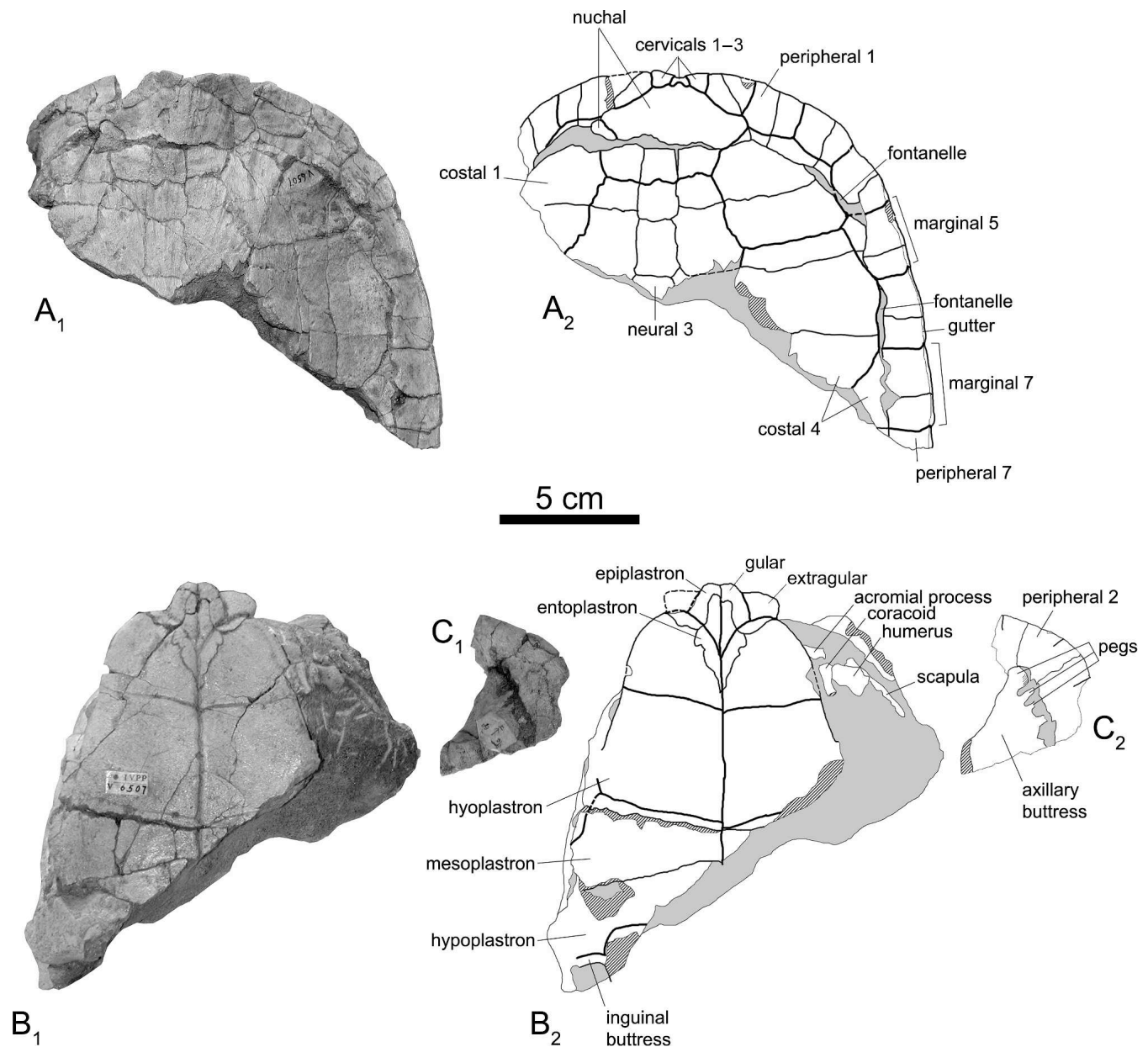


FIGURE 2. *Chengyuchelys baenoides*, IVPP-V6507, anterior part of shell; Dashanpu, Zigong Prefecture, Sichuan Province, China; Xiashaximiao Formation, Middle Jurassic. **A**, dorsal view, photograph (A₁) and explanatory drawing of same (A₂). **B**, ventral view, photograph (B₁) and explanatory drawing of same (B₂). **C**, fragment with left axillary buttness and anterior peripherals in ventral view, photograph (C₁) and explanatory drawing of same (C₂). In drawings matrix is filled with grey and broken bone is hatched.

girdle and humerus are visible inside the specimen where part of the shell has been removed (Fig. 2B). The estimated midline length of the shell is about 25 cm. The anterior edge of the carapace is rounded and bears a small nuchal emargination, smaller than in *Xinjiangchelys latimarginalis* (Young and Chow, 1953) sensu Peng and Brinkman (1993). *Chengyuchelys baenoides* was reported to have a sutural plastron/carapace connection (Yeh, 1990a; Sukhanov, 2000; Tong et al., 2002), but IVPP-V6507 shows that the plastron/carapace connection is loose (ligamentous) via peripherals 2 through 8, with pegs on the plastron fitting in sockets on the peripherals (Fig. 2C) similar to the condition in *X. latimarginalis* and other basal stem cryptodires. The anterior lobe of the plastron is relatively narrow and elongate, projecting slightly beyond the anterior margin of the carapace. In

comparison, *X. latimarginalis* seems to have a comparatively shorter and wider anterior lobe (see Peng and Brinkman, 1993, figs. 3, 4B).

The nuchal is a wide trapezoid with a free (anterior) margin that is two times narrower than the posterior margin. The posterior border of the nuchal has a sinuous contact with neural 1 and the first pair of costals. The shape of the nuchal in IVPP-V6507 is similar to *Xinjiangchelys latimarginalis*. The anterior neurals are narrow and similar in shape to *X. latimarginalis*. Neurals 1 and 2 are almost rectangular. Neural 1 has a small contact with the second pair of costals and neural 2 widens posteriorly and has a small contact with the right third costal. The shape of neural 3 is unclear. Costal 1 is very short antero-posteriorly and narrower than the rest of the visible costals,

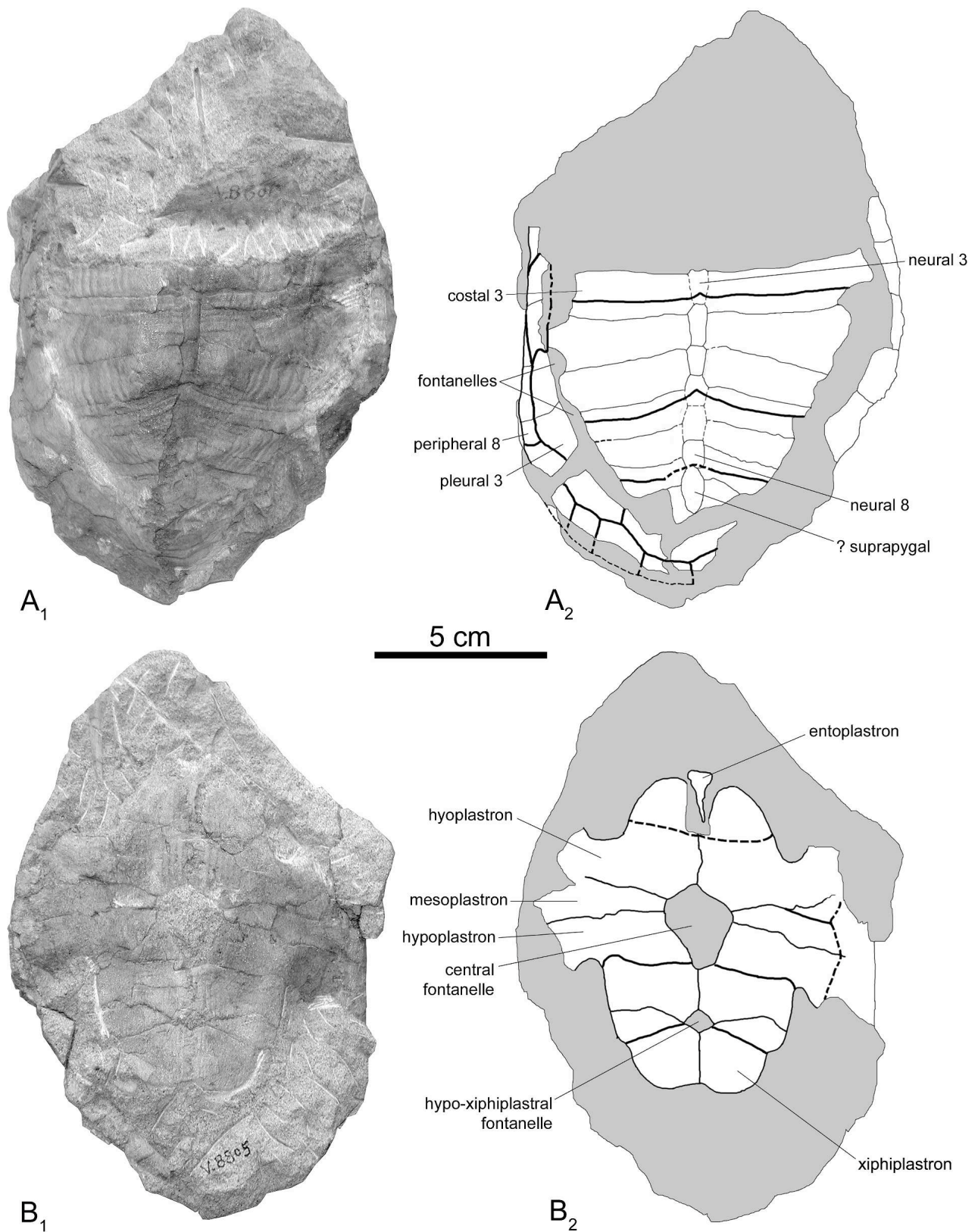


FIGURE 3. *Sichuanchelys* sp. indet., IVPP-V8805, incomplete shell; Dashanpu, Zigong Prefecture, Sichuan Province, China; Xiashaximiao Formation, Middle Jurassic. **A**, dorsal view, photograph (A₁) and explanatory drawing of same (A₂). **B**, ventral view, photograph (B₁) and explanatory drawing of same (B₂). In drawings matrix is filled with grey.

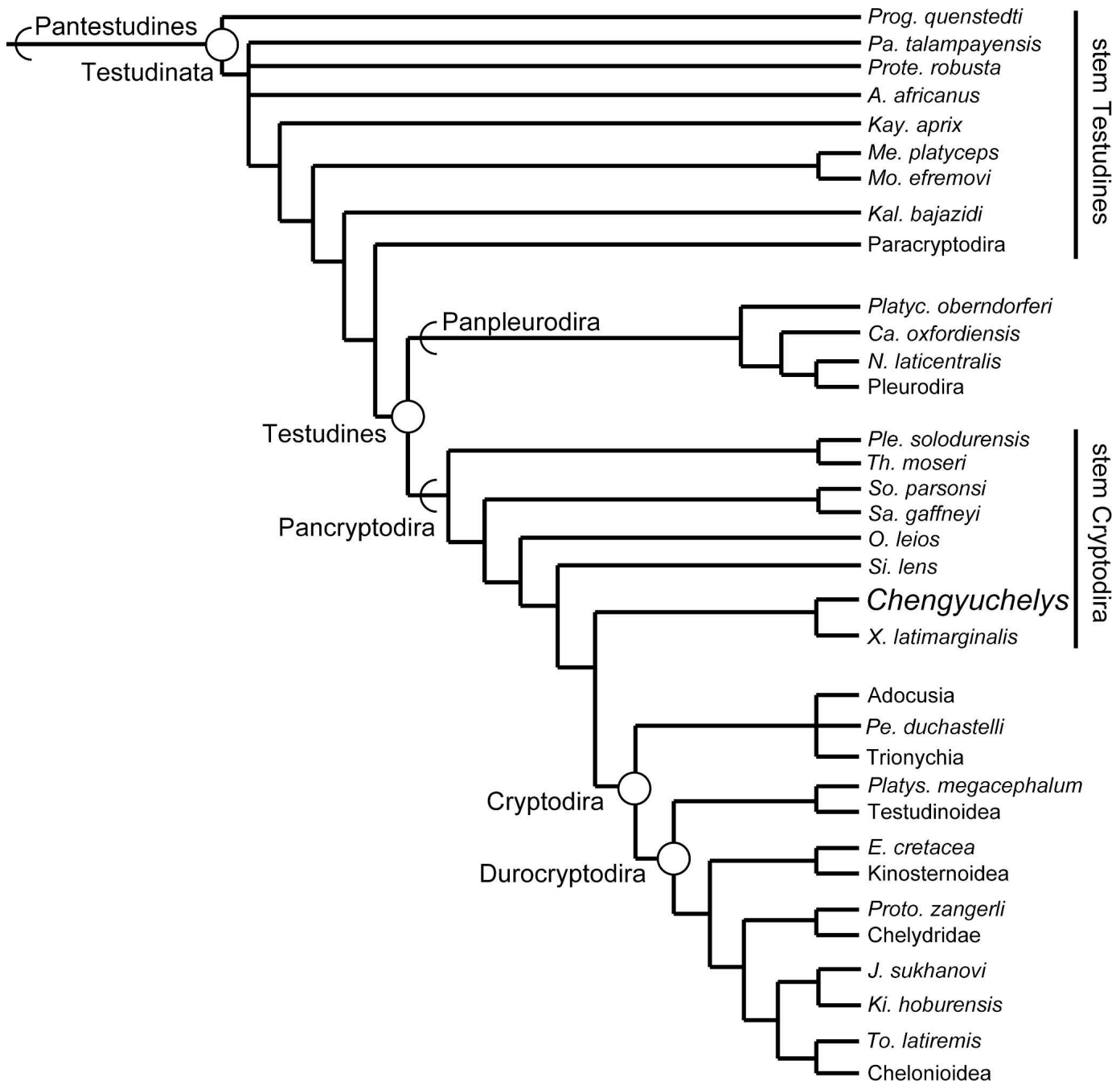


FIGURE 4. Strict consensus of ten most parsimonious trees showing the phylogenetic position of *Chengyuchelys* (sensu this study) recovered by our cladistic analysis. The following taxa have been condensed for space reasons and simplicity: Adocusia, Chelonioida, Chelydridae, Kinosternoidea, Testudinoidea, Trionychia, Pleurodira, and Paracryptodira. Other suprageneric taxa shown are either stem based (open semi-circle) or node based (circle). **Abbreviations:** **A.**, *Australochelys*; **Ca.**, *Caribemys*; **E.**, *Emarginachelys*; **J.**, *Judithemys*; **Kal.**, *Kallokiboton*; **Kay.**, *Kayentachelys*; **Ki.**, *Kirgizemys*; **Me.**, *Meiolania*; **Mo.**, *Mongolochelys*; **N.**, *Notoemys*; **O.**, *Ordosemys*; **Pa.**, *Palaeochersis*; **Pe.**, *Peltochelys*; **Platyc.**, *Platychelys*; **Platys.**, *Platysternon*; **Ple.**, *Plesiochelys*; **Prog.**, *Proganochelys*; **Prote.**, *Proterochersis*; **Proto.**, *Protochelydra*; **Sa.**, *Santanachelys*; **Si.**, *Sinemys*; **So.**, *Solnhofia*; **Th.**, *Thalassemys*; **To.**, *Toxochelys*; **X.**, *Xinjiangchelys*.

which is common for many primitive turtles. Costals 2 and 3 also are longer laterally than medially. Narrow costal-peripheral fontanelles are present between costals 2 and 3 and their corresponding peripherals. Peripheral 1 is almost triangular, with its length along the free edge about three times longer than at its border with the first costal. Peripheral 2 is quadrangular. Other costals are rectangular and longer than wide. The peripherals are upturned, forming a gutter near the free edge that is especially

visible on the bridge peripherals (Fig. 2A). Upturned peripherals are characteristic of most basal pancryptodires (Peng and Brinkman, 1993; Parham and Hutchison, 2003).

There are three small cervicals, lying along the anterior border of the nuchal. Among basal eucryptodires, three cervicals are known in *Plesiochelys* Rüttimeyer, 1873, and *Palaeomedusa testa* Meyer, 1860, both from the Late Jurassic of Europe (Bräm, 1965; Joyce, 2003). Three cervicals were also reported, probably as an

aberration, in the 'macrobaenid' *Kirgizemys dmitrievi* Nessov and Khosatzky, 1981 (Danilov et al., 2006). Vertebral 1 is wide and hexagonal, reaching the second marginals laterally. Vertebral 2 is also hexagonal, but its exact shape and proportions remain unknown because it is incomplete. Pleural 1 is peculiar in that it extends to the posterolateral corner of the nuchal and also covers medial margins of peripherals 1 through 3. In *Xinjiangchelys latimarginalis*, pleural 1 is, as a rule, excluded from the nuchal. Marginals 1 through 3 are restricted to the peripherals, whereas marginals four and six reach the costal-peripheral suture and marginals five and seven strongly overlap onto the corresponding costals (at least 2–4). The overlap of marginals onto the anterior costals is also observable in IVPP-V708, although only costals 1 and 2 are visible on that specimen. In this character, IVPP-V6507 and IVPP-V708 resemble *X. latimarginalis*, in which the medial tips of the marginals extend onto costals 2 through five (Peng and Brinkman, 1993). The extension of the marginals onto the anterior costals is also recorded in *Yehguia tatsuensis* Yeh, 1963 (Danilov and Parham, 2006).

The epiplastra are relatively small and well separated by a waist from the rest of the plastron. The epiplastral symphysis is short. The free edge of the epiplastron has two projections, corresponding to its gular and extragular parts (terminology of plastral scales is after Hutchison and Bramble, 1981). The posterolateral extension of the epiplastron, which is common in many stem cryptodires, is absent. The dorsal surface of the epiplastron does not reveal the presence of dorsal epiplastral processes, which are known in many primitive turtles (reviewed in Joyce et al., 2006). Joyce et al. (2006) recently demonstrated that in *Kayentachelys aprix* Gaffney, Hutchison, Jenkins, and Meeker, 1987, dorsal epiplastral processes may be easily detached or broken. Thus the condition of the dorsal epiplastral processes in IVPP-V6507 should be considered unclear. The entoplastron is leaf-shaped, having a blunt anterior process that extends between the epiplastra. The ento-hyoplastral suture is zigzag-shaped. In general, the shape of the epiplastra and entoplastron in IVPP-V6507 is most similar to *K. aprix*, but differs in that in *K. aprix* the entoplastron completely separates the epiplastra. In IVPP-V708

the entoplastron also seems to be more elongate and not diamond-shaped as previously reported (Young and Chow, 1953; Yeh, 1994). The hyoplastra and preserved part of the hypoplastron exhibit no peculiar features. The mesoplastra are wedge-shaped, twice longer laterally than medially, and contact one another across the midline.

The following scales of the plastron are visible in ventral view: gulars, extragulars, humerals, pectorals, a small part of the right femoral, and the right inframarginal 2 or 3. The gulars are long, covering the entire anterior half of the entoplastron. This condition is similar to *Kayentachelys aprix*, but differs from basal pancryptodires that all have a weak or nonexistent overlap of the gulars onto the entoplastron. The extragulars are smaller triangular scales restricted to the epiplastra. The humeral-pectoral sulcus is straight and situated posterior to the entoplastron and distant from the axillary notches. In this respect, IVPP-V6507 is more similar to *K. aprix*, than to *Xinjiangchelys latimarginalis*. In *X. latimarginalis*, this sulcus is set closer to the axillary notches. As a result, the pectorals in IVPP-V6507 are relatively larger and longer medially than in *X. latimarginalis*. The pectoral-abdominal sulcus is also straight and situated just anterior and along the hyo-mesoplastral suture. In *X. latimarginalis*, this sulcus is usually convex anteriorly. The abdominal-femoral sulcus is situated just anterior to the posterior plastral lobe, as in most turtles. The number and shape of inframarginals is unclear.

The shell surface is not sculptured in either IVPP-V6507 or IVPP-V708 (contra Young and Chow, 1953). Within the vertebral scales, there are well developed radiating folds or plications; this ornament is typical in juvenile or subadult individuals of many turtle species and in primitive Testudines (see Młynarski, 1976).

Preserved portions of the non-shell postcrania include parts of the dorsal and acromial processes of the scapula, coracoid, and proximal part of the humerus. The preservation of these fragments is poor and no important characters can be observed. Measurements for this specimen are given in Table 1.

Remarks—We support Yeh (1982, 1990b, 1994) in assigning IVPP-V6507 to *Chengyuchelys baenoides* (see below, Systematic

TABLE 1. Shell measurements (in mm) for *Chengyuchelys baenoides*, IVPP-V6507.

Nuchal (length/width anterior/width maximal)	26/27/56
Neural 1 (length/width)	27/13.5
Neural 2 (length/width)	21/14.5
Costal 1 (length medially/width at posterior margin)	21.5/54.5
Costal 2 (length medially/width at posterior margin)	23/-73
Peripheral 1 (length at free edge/width at the middle)*	22.5/22
Peripheral 2 (length at free edge/width at the middle)*	23/24.5
Peripheral 3 (length at free edge/width at the middle)*	25.5/20.5
Peripheral 4 (length at free edge/width at the middle)*	27/15.5
Peripheral 5 (length at free edge/width at the middle)*	26/15.5
Peripheral 6 (length at free edge/width at the middle)*	27.5/19
Middle cervical (length/width anterior/width posterior)	3/3.2/7.2
Vertebral 1 (length/width)	36.5/51.5
Vertebral 2 (width anterior/width maximal)	35.5/58.5
Marginal 1 (length at free edge/width at the middle)*	20/13
Marginal 2 (length at free edge/width at the middle)*	20/17
Marginal 3 (length at free edge/width at the middle)*	23.5/18
Marginal 4 (length at free edge/width at the middle)*	23.5/21
Marginal 5 (length at free edge/width at the middle)*	25/25
Marginal 6 (length at free edge/width at the middle)*	27.5/19.5
Marginal 7 (length at free edge/width at the middle)*	29.5/31
Anterior lobe (length/width at the base/width at humeral-pectoral sulcus/width at extragular-humeral sulcus)	-64/-82/66.5/-38
Epiplastron (length/width at free edge)	4.5/22
Entoplastron (length/width)	32.5/-18
Hyoplastron (length)	46.7
Mesoplastron length (medial/lateral)	10/25.6
Gular (length)	25
Humeral (length)	19
Pectoral (length)	36.5

*Designate measurements from the right side.

Paleontology section) based on the shared presence of mesoplastra and extension of the anterior marginals onto the costals. However, we note that other *C. baenoides* specimens differ from IVPP-V6507 in the degree of the extension of marginals onto the costals and in having a mesoplastron that is more distant from the pectoral-abdominal sulcus.

IVPP-V8805

Description—IVPP-V8805 (Fig. 3) includes the following elements: neurals 3 through 8; a questionable suprapygal; costals 3 through 8 on both sides; and parts of the bridge and posterior peripherals. The plastron is missing the epiplastra and preserves the entoplastron, hyo-, meso-, hypo- and xiphiplastra. The estimated midline length of the shell is about 15 cm. The type of plastron/carapace connection is unclear. Costal-peripheral fontanelles are present in the carapace and central and hypoxiphiplastral fontanelles are present in the plastron. The surface of the carapace bears up to seven growth lines within the vertebral scales, which might indicate a subadult or adult individual.

The neurals are relatively narrow, more so than in IVPP V6507. The shape of neural 3 is unclear. Neurals 4 and 5 are hexagonal and short-sided anteriorly, whereas neural 6 is hexagonal with equal anterolateral and posterolateral sides. Neurals 7 and 8 are of unclear shape. The known neural elements of *Sichuanchelys chowi* (neurals 3–6; Ye and Pi, 1997:fig. 1) are also hexagonal and short-sided anteriorly. Posterior to the neural series in IVPP-V8805 there is an elongate oval element that could be a suprapygal. All the preserved costals, except costal 4, have almost equal lengths medially and laterally. Costal 4 is much longer laterally than medially. The costal-peripheral fontanelles are visible on the left side between costals 4 and 5 and their respective peripherals. The peripherals are poorly preserved and exhibit no peculiar features.

The following carapace scales are present, either completely or partially: vertebrales 2–5, pleurals 2–4; and an uncertain number of marginals. The vertebrales are very wide and completely cover the costals. Although their lateral borders are not discernable, they could be within the costal-peripheral fontanelles. The sulcus between vertebrales 2 and 3 passes through the posterior half of neural 3 and the sulcus between vertebrales 3 and 4 crosses neural 6. The posterior border of vertebral 4 seems to cross the posteriormost portion of neural 8. Medially, the intervertebral sulci form anteriorly directed points. The pleurals are narrow and cover only parts of the peripherals. The marginals, represented by an uncertain number, are also rather narrow, especially on the bridge. A similar scalation pattern (i.e., wide vertebrales, narrow pleurals, narrow marginals, and neural 6 crossed by an intervertebral sulcus) is known in *Sichuanchelys chowi* and *Kayentachelys aprix*.

The entoplastron is triangular with a long posterior process. The hyoplastra and hypoplastra have no peculiar features. The mesoplastra are similar to *Sichuanchelys chowi* in being wedge-shaped and about three times longer laterally than medially. The xiphiplastra are short and have a small anal notch. In *S. chowi*, the xiphiplastra are not short and the anal notch is absent.

The position of the humeral-pectoral sulcus is unclear, but it certainly lies posterior to the entoplastron. Part of the pectoral abdominal sulcus is visible on the lateral part of the left mesoplastron. The medial part of this sulcus is not discernable, but it may pass along the hyo-mesoplastral suture as in *Sichuanchelys chowi*. The abdominal-femoral sulcus lies just anterior to the posterior plastral lobe as in most other turtles. The femoral-anal sulcus medially reaches the hypoplastron at the hypoxiphiplastral fontanelle. In *S. chowi*, the anal scales do not reach the hypoplastra. The positions and number of inframarginals are unclear.

Measurements of this specimen are not given due to its poor preservation.

Remarks—IVPP-V8805 is removed from *Chengyuchelys* based on its extremely wide vertebral scales and narrow mesoplastra. In these respects, it matches *Sichuanchelys chowi*. However, we note that IVPP-V8805 differs from *S. chowi* in important characters such as the presence of fontanelles in the carapace and plastron and the anal scales reaching the hypoplastra. IVPP-V8805 might represent a new species of *Sichuanchelys*, but we conservatively refer it to *Sichuanchelys* sp. indet. pending further study of other Dashanpu turtles.

PHYLOGENETIC ANALYSIS

Our new observations of *Chengyuchelys baenoides*, combined with previously published data on *C. zigongensis*, allow us to include the genus in a computer assisted cladistic analysis for the first time. We score *Chengyuchelys* for characters from the global turtle matrix of Joyce (2007) according to the parameters used therein (15 ordered characters and three excluded ‘rogue’ taxa) and modified by Danilov and Parham (2006). The latter modifications include a DNA-based constraint tree for living taxa (Danilov and Parham, 2006:577, fig. 4) and the addition of *Yehguia tatsuensis* (Yeh, 1963). In addition, we add one new character “Marginal B” (see Appendix 1). Of the 136 characters used by Joyce (2007), we could score *Chengyuchelys* for 38 of them (Appendix 2). The taxon *Hangaiemys hoburensis* is changed to *Kirgizemys hoburensis* based on Danilov et al. (2006).

Our analysis resulted in 124 trees of 375 steps (CI: .453; HI: .547; RI: .803). The strict consensus of these trees resulted in a polytomy that includes most extant cryptodire lineages, some stem cryptodires, and *Chengyuchelys*. To facilitate further inspection of these 124 trees, we examined the agreement subtree and were able to identify three taxa that showed varying phylogenetic positions in equally parsimonious trees (*Australochelys africanus* Gaffney and Kitching, 1994; *Dracochelys bicuspis* Gaffney and Ye, 1992; and *Peltochelys duchastelli* Dollo, 1884). Only one of these, *D. bicuspis* from the Early Cretaceous of China, was responsible for the polytomy involving *Chengyuchelys*. The placement of *D. bicuspis* on either the stem of Cryptodira or the stem of Cheloniodea (extant sea turtles) is equally parsimonious, so a strict consensus collapses the extant cryptodire lineage into a polytomy. After pruning *D. bicuspis*, the 124 equally parsimonious trees could be collapsed to just ten. It is important to note that the phylogenetic signal for the deleted *D. bicuspis* is still included in the pruned trees. Analyzing agreement subtrees merely simplifies the inspection of recovered trees and does not alter the parameters and assumptions of the cladistic analysis. Removing *D. bicuspis* from the analysis beforehand results in the same ten trees (Fig. 4; 374 steps; CI: .455; HI: .545; RI: .804) showing that the exclusion of *D. bicuspis* has no effect on the overall topology. Attempts at bootstrap analyses recovered so many trees on their first replicate that it was deemed computationally infeasible, but a search of trees one step longer collapsed all stem cryptodire nodes into a polytomy. This result is likely the result of the incomplete coding for *Chengyuchelys* (< 28% of characters), although overall low support for this part of the turtle tree has been found by others (e.g., Joyce, 2007).

In every most parsimonious tree, *Chengyuchelys* was placed as a stem cryptodire and sister to a species from the Late Jurassic of China, *Xinjiangchelys latimarginalis*. Danilov and Parham (2006) were unable to resolve whether *X. latimarginalis* was a member of the crown clade Cryptodira or not (see Danilov and Parham, 2006:fig. 5), but the strict consensus of the ten agreement subtrees from the present analysis (Fig. 4) consistently placed *X. latimarginalis* outside of Cryptodira.

An examination of the character reconstructions on the most parsimonious trees shows that *Chengyuchelys* is placed as a

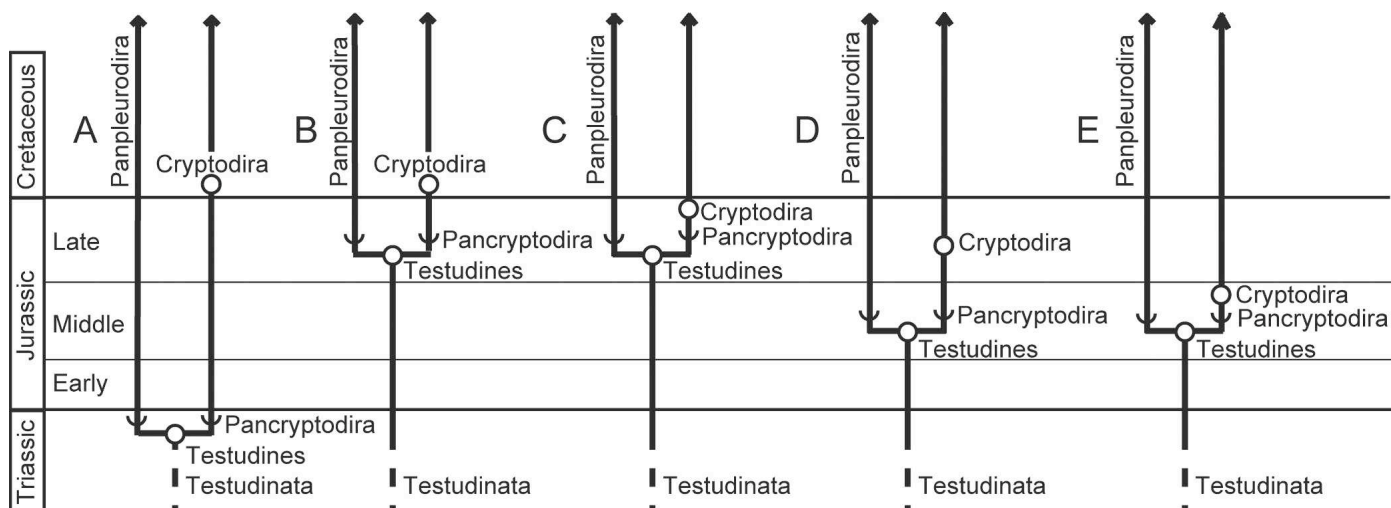


FIGURE 5. Diagram illustrating changing ideas about the origins of Testudines and Cryptodira: **A**, traditional hypothesis (e.g., Gaffney and Meylan, 1988; Shaffer et al., 1997); **B**, hypothesis of Joyce (2004, 2007); **C**, hypothesis of Danilov and Parham (2006); **D**, preferred hypothesis of this study. **E**, pattern if *Sinaspideretes wimani* is a Middle Jurassic Cryptodire. Taxa are either stem based (open semi-circle) or node based (circle).

relatively advanced stem cryptodire, because it has narrow vertebral scales and a plastron that has a ligamentous connection with the peripherals (Characters: Hypoplastron A, Hypoplastron A, Plastron A, Plastron B, and Vertebral B). The sister relationship to *Xinjiangchely latimarginalis* is supported by two scalation characters: the overlapping of the anal scales onto the hypoplastron and the overlap of the marginal scales onto the costals (characters: Anal A and Marginal B, respectively).

The placement of *Chengyuchelys* as a stem cryptodire is interesting because, unlike any other Pancryptodire, it retains mesoplastra. Because *Chengyuchelys* is not the most basal stem cryptodire, our result suggests that mesoplastra may have been lost independently early on in several pancryptodire lineages. Joyce (2007) hypothesized that the reduction and loss of mesoplastra has occurred in other turtle lineages such as *Kallokibotium bajaizidi* Nopsca, 1923, *Baena arenosa* Leidy, 1870, and Chelidae Lindholm, 1929. Determining how many times should prove challenging because the relationships of stem cryptodires to the crown is in a state of flux.

DISCUSSION

According to our cladistic analysis, the Middle Jurassic *Chengyuchelys* is hypothesized to be one of the oldest stem cryptodires and, therefore, one of the oldest members of the crown group Testudines (Figs. 4, 5). But we caution that our result should be considered tentative because of the fragmentary nature of the material available for study. We conservatively refrain from proposing any recommendation for the suprageneric taxa *Chengyuchelyidae* Yeh, 1990b, and *Xinjiangchelyidae* Nessov, 1990 [in Kaznyshkin et al. (1990)], except to note that the utility, definition, and content of both taxa are presently questionable. Both *Chengyuchelys* and *Xinjiangchelys*-like taxa share a suite of characters associated with the scalation and osteology of the shell (see Phylogenetic Analysis) and also might be found in the same locality (see below). In our opinion, their close phenetic similarity combined with their co-occurrence in time and space lends plausibility to the hypothesis that these taxa may be closely related.

The evidence for a Middle Jurassic origin for the crown group Testudines (extant turtles) is not based solely on the phylogenetic placement of *Chengyuchelys* presented here. During the course of our study, it became apparent that there are other

possible Testudines from the Middle Jurassic of Asia. For example, Middle Jurassic species of *Xinjiangchelys*, namely *X. chowi* Matzke, Maisch, Sun, Pfretzschner, and Stöhr, 2005, from Xinjiang Province, China, and *X. tianshanensis* Nessov, 1995, from Kyrgyzstan, are potential stem cryptodires. So far, only the Late Jurassic *X. latimarginalis* has been studied in the context of basal turtle phylogenetic relationships. If *X. chowi* and *X. tianshanensis* are phylogenetically close to *X. latimarginalis*, as their congeneric status implies, these species could also be considered among the oldest known crown Testudines.

Beyond the unresolved phylogenetic relationships of Middle Jurassic Asian turtles, the poorly constrained ages of many Chinese specimens prevents us from better establishing the origination times of extant turtle clades. For example, *Sinaspideretes wimani* Young and Chow, 1953, is often cited as a potential Late Jurassic crown group Cryptodire (e.g., Meylan and Gaffney, 1992; Yeh, 1994), but in fact its precise age is unknown. The type specimen of *Sin. wimani* was found “along with” *Chengyuchelys baenoides* and *Xinjiangchelys radiplicatus* (Young and Chow, 1953) during construction of the Chengyu Railway (Yeh, 1994: 89). All three species were originally considered Late Jurassic or Early Cretaceous in age (Young and Chow, 1953). Yeh (1994) only later assigned a Middle Jurassic age for *C. baenoides* based on the presence of abundant material of *C. baenoides* and other *Chengyuchelys* specimens at the Middle Jurassic site of Dashanpu in the Xiashaximiao Formation. It is not clear why he still considered *Sin. wimani* and *X. radiplicatus* to be Late Jurassic in age. Matzke et al. (2004) claimed that *X. radiplicatus* is from the Shangshaximiao (= Upper Shaximiao) Formation, which would be Late Jurassic in age, but we are not sure what this claim is based on and if it should also apply to the holotypes of *C. baenoides* and *Sin. wimani*. Assuming the locality data are still available, a detailed stratigraphic study of the Chengyu Railway localities could determine if *C. baenoides* occurs in the Late Jurassic or if some or all of the Chengyu Railway specimens are of Middle Jurassic age like at Dashanpu.

This uncertainty about the precise age of Chinese Jurassic species also applies to *Yanduchelys delicatus* Peng, Ye, Gao, Shu, and Jiang, 2005, *Xinjiangchelys latimarginalis* (Young and Chow, 1953), and *Xinjiangchelys chungkingensis* (Young and Chow, 1953), which are all from unknown horizons and localities in Sichuan. Matzke et al. (2004) removed *X. latimarginalis* and

Table 2. Comparison of shell characters of well known Middle Jurassic turtles, plus *Kayentachelys aprix* and *Xinjiangchelys latimarginalis*.

Characters	<i>Chengyuchelys baenoides</i>	" <i>Chengyuchelys</i> " <i>dashanpuensis</i>	<i>Chengyuchelys zigongensis</i>
Shell surface ornamentation	Smooth	?	?
Carapace-plastron attachment	Ligamentous	?	?
Nuchal emargination	Small	Small	?
Number of neurals	8	8	8
Thickening of anterolateral edge forming a gutter on carapace	Present	?	Present
Number of cervical scales	3	1	?
Vertebral scales	Narrow	Broad	Narrow to broad
Intervertebral sulcus crosses neural 6	Yes	Yes	Yes
Marginal scales overlapping onto anterior costals	Yes	?	?
Epiplastron with posterolateral process	No	?	Yes
Dorsal process of epiplastron	?	?	?
Entoplastron separating epiplastra	Yes, partially	No	?
Mesoplastra	Present, posterior to pectoral-abdominal sulcus, narrowed medially	Present, posterior to pectoral-abdominal sulcus, extremely narrow	Present, crossed by pectoral-abdominal sulcus, not narrowed medially
Midline sulcus of plastron	Straight	Slightly sinusoidal	Straight
Extension of gulars onto entoplastron	Strong	Absent	?
Anal overlapping onto hypoplastron	Yes	Yes	Yes

Data for *Chengyuchelys baenoides* are from this study. Data for *Siamochelys peninsularis* are based on Danilov (pers. obs.).

X. chungkingensis from *Xinjiangchelys* based on a cladistic analysis of best-represented *Xinjiangchelys* species. However, since their data matrix lacked any non-*Xinjiangchelys* taxa, their removal of those two species from *Xinjiangchelys*, while potentially correct, has no basis at this time. We tentatively retain both species in *Xinjiangchelys* (sensu Peng and Brinkman, 1993) pending further study. The phylogenetic position and taxonomic affinities of *Ya. delicatus* are even less certain. Peng et al. (2005) placed this species in the Plesiochelyidae Baur, 1888, an antiquated convention applied to many Mesozoic Chinese fossils that has been rejected by all recent authors since the work of Peng and Brinkman (1993). From the published description it is impossible to place the type, and only known, specimen into a cladistic analysis. In fact, the only known figure of *Ya. delicatus* (Peng et al., 2005:fig.92) demonstrates that this specimen is in sore need of reappraisal. Based on the relation of the plastral scales to the underlying bones, the morphology of this specimen appears to be completely misinterpreted. We submit that the anterior-posterior orientation of the shell should be reversed and that the figured entoplastron is fictitious. Reversing the orientation of the shell would change the scalation pattern from strange and unique to utterly typical. It would also explain the enigmatic "hyoplastral horns" as they would actually be part of the broken hypoplastra-xiphiplastra suture, a feature that tends to be highly sinuous. If our supposition is correct, then the outline of the shell widens posteriorly. In this respect, this species resembles members of *Sinemys* Wiman, 1930, known from the Late Jurassic–Early Cretaceous interval in China (Brinkman and Peng, 1993). In addition to its uncertain taxonomic status, the temporal position of this taxon is also poorly characterized because it is known only from an unspecified locality in Zigong. As a result, "*Ya. delicatus*" joins the growing list of crucial Jurassic Chinese specimens that require reassessment.

Until Middle and Late Jurassic turtles from Asia are better characterized morphologically and stratigraphically, the ages of the crown clades Testudines and Cryptodira will remain inherently unstable. Despite this confusion, some general statements about the origination times of extant turtle clades can be made. For one, based on *Chengyuchelys* from the Xiashaximiao Formation (Fig. 1H), *Xinjiangchelys chowi* from the Toutunhe Formation (Fig. 1F), and *X. tianshanensis* from the Balabansai Formation (Fig. 1E), we can be relatively certain that the crown group Testudines had originated by the end of the Middle Ju-

rassic (-161 ± 4 million years ago; Gradstein et al., 2004), although the clade is potentially much older. Other taxa that may represent Middle Jurassic Testudines, but are poorly constrained temporally and phylogenetically, are *Sinaspideretes wimani*, *X. chungkingensis*, *X. latimarginalis*, and *X. radiplicatus*. Meanwhile, the oldest known cryptodire is *Yehguia tatsuensis* (Danilov and Parham, 2006) which is from the Late Jurassic (-161 ± 4 to 146 ± 4 mya; Gradstein et al., 2004). A comparison of this and other recent hypotheses on the origination times of Testudines and Cryptodira is shown in Fig. 5A–D. Besides *Ye. tatsuensis*, the next oldest, reliably dated, stem cryptodire is *Peltochelys duchastelli* from the Early Cretaceous of Europe or possibly *Dracochelys bicuspis* from the Early Cretaceous of China. Meanwhile, the phylogenetic position and age of the problematic *Sin. wimani* remains unresolved. If *Sin. wimani* is from the Middle Jurassic (as suggested by its co-occurrence with *C. baenoides* in the Chengyu Railway horizon; Yeh, 1994) and a cryptodire (as suggested by Meylan and Gaffney, 1992), then it could be the oldest cryptodire. In this scenario, the oldest Testudines and the oldest Cryptodira appeared simultaneously in the Middle Jurassic of China (Fig. 5E). Whatever the case, the Middle and Late Jurassic of Asia is a very important time and place for studying the origin of extant turtle lineages.

SYSTEMATIC PALEONTOLOGY

TESTUDINATA Klein, 1760 sensu Joyce et al. (2004)

PANTESTUDINES Joyce, Parham, and Gauthier, 2004

SICHUANCHELYS Ye and Pi, 1997

Sichuanchelys Ye and Pi, 1997:182; Peng et al., 2005:43, 208.

Chengyuchelys Young and Chow (in part): Yeh, 1990b:305; Yeh, 1994:5; Peng et al., 2005:37, 207.

Etymology—*Sichuan-* for Sichuan Province, where the Dashanpu locality is located; *chelys-* Greek for turtle.

Content—One species: *Sichuanchelys chowi* Ye and Pi, 1997.

Material—As for type species (see species account, below) plus a specifically indeterminate shell IVPP-V8805.

Diagnosis—As for type and only species, but see Remarks.

Remarks—We place IVPP-V8805 into *Sichuanchelys* based on its narrow mesoplastra and extremely wide vertebral scales. However, the presence of fontanelles and anal scales that contact the hypoplastron prevent us from placing the specimen in *S. chowi*.

Table 2. (Extended)

<i>Heckerochelys romani</i>	<i>Kayentachelys aprix</i>	<i>Siamochelys peninsularis</i>	<i>Sichuanchelys chowi</i>	<i>Xinjiangchelys latimarginalis</i>
Smooth	?	Light ridges and tubercles	Smooth	Smooth
Ligamentous	Sutured	Ligamentous	?	Ligamentous
Small	Well developed	Small	Well developed	Small
8 or 9	9	8	?	8
Absent	Absent	Present	?	Present
1	1	1	1	1
Broad	Broad	Narrow	Broad	Narrow
No	Yes	No	Yes	No
No	No	?	?	Yes
Yes	No	Yes	?	Yes
Present	Present	Present, but small	?	Present
No	Yes, completely	No	No	No
Present, crossed by pectoral-abdominal sulcus, narrowed medially	Present, crossed by pectoral-abdominal sulcus, narrowed medially	Absent	Present, probably crossed by pectoral-abdominal sulcus, narrowed medially	Absent
?	Straight	Sinusoidal	Straight	Sinusoidal
Weak	Strong	Absent	Absent	Weak or absent
No	No	Yes or no	No	Yes

SICHUANCHELYS CHOWI Ye and Pi, 1997

Chengyuchelyidae indet.: Yeh, 1990b:307; Yeh, 1994:12.
Sichuanchelys chowi Ye and Pi, 1997:182, fig. 1, pl. 1; Peng et al., 2005:43, 208, fig. 28.

Etymology—*Chow-* for Dr. Zhou (= Chow) Ming-zheng of the IVPP.

Holotype—ZDM 3014, an almost complete shell.

Referred Material—Two incomplete shells: ZDM 3001 and ZDM 3017.

Locality, Horizon, and Age—Dashanpu locality (Xiashaximiao Formation), Zigong Prefecture, Sichuan Province, China, Middle Jurassic.

Diagnosis—A basal turtle (stem-testudine) characterized by the following unique combination of characters: 1) one pair of mesoplastra; 2) mesoplastra contact at midline; 3) mesoplastra narrow medially and crossed by pectoral-abdominal sulcus only laterally; 4) anterior (nuchal) emargination of carapace well developed; 5) one cervical scale; 6) extremely wide vertebral and narrow pleural scales; 7) extremely narrow marginal scales on the bridge; 8) sulcus between vertebrals 3 and 4 crosses neural 6; 9) entoplastron without anterior process separating epiplastra; 10) extragulars present; 11) gulars do not extend onto entoplastron; 12) anals do not reach hypoplastra; 13) four pairs of inframarginals; 14) midline sulcus of plastron straight; and 15) shell surface without ornamentation. *Sichuanchelys* can be differentiated from most Pancryptodira (except *Chengyuchelys baenoides*) and *Proterochersis robusta* Fraas, 1913, by character 1, from Panpleurodira and the basal turtles *Kallokibotion bajazidi* and *Baena arenosa* by character 2, from other basal turtles by characters 3 (except some Baenidae) and 6 (except some Pleurosternidae), and from *Chengyuchelys baenoides* by characters 3–6, 9, 11, and 12. A more detailed comparison of *Sichuanchelys* with well known Middle Jurassic turtles, *Kayentachelys aprix*, and *Xinjiangchelys latimarginalis* is given in Table 2. Note that for all diagnoses in this section we have refrained from trying to identify polarities, because those are unclear for most of the diagnostic characters we employ.

Remarks—The supposed phylogenetic affinities of *Sichuanchelys* to *Chengyuchelys* (Ye and Pi, 1997) were based on the presence of mesoplastra and a similar geological age (Middle Jurassic). Among stem Testudines, *Sichuanchelys* is most similar to *Kayentachelys aprix* in the shell outline and scalation pattern, although it differs in the shape of the neurals and in that the

entoplastron does not separate the epiplastra. A more certain phylogenetic and systematic position of *Sichuanchelys* will require detailed study of new material.

TESTUDINES Batsch, 1788 sensu Joyce et al. (2004)
 PANCRYPTODIRA Joyce, Parham, and Gauthier, 2004
CHENGYUCHELYS Young and Chow, 1953

Chengyuchelys Young and Chow, 1953:217; Yeh, 1963:83; Yeh, 1982:282; Yeh, 1990a:34; Yeh, 1990b:305; Yeh, 1994:5; Sun et al., 1992:18; Peng et al., 2005:37, 207.

Etymology—*Chengyu-* for the locality of the first specimens found near the Chengyu Railway (a major railway connecting Chengdu in Sichuan Province and the Chongqing Provincial Municipality); *chelys-* Greek for turtle.

Content—Two species: *Chengyuchelys baenoides* Young and Chow, 1953 (type species) and *Chengyuchelys zigongensis* Yeh, 1982.

Material—As for each species (see species accounts, below) plus five specifically indeterminate incomplete shells: C.V. 00679, I-L1, ZDM 3019 (= I-L2), ZDM 3005 (= KI-7), and ZDM 3004 (see Fang, 1987; Yeh, 1982, 1990b, 1994; Peng et al., 2005).

Diagnosis—A stem cryptodire diagnosed by the following unique combination of characters: 1) one pair of mesoplastra; 2) mesoplastra contact at midline; 3) mesoplastra narrow medially or not and crossed by pectoral-abdominal sulcus or not; 4) ligamentous connection between plastron and carapace, via peripherals 2 and 8; 5) anterior (nuchal) emargination of carapace small; 6) eight neurals; 7) thickening of anterolateral edge forming a gutter on carapace; 8) three pairs of cervical scales; 9) vertebrals relatively narrow; 10) sulcus between vertebral scales 3 and 4 crosses neural 6; 11) marginal scales overlapping onto anterior costals; 12) epiplastron without posterolateral process; 13) entoplastron with a well developed anterior process, partially separating the epiplastra; 14) gular scales strongly extend onto entoplastron; 15) extragular scales present; 16) anal scales extend onto hypoplastra; 17) probably four pairs of inframarginal scales; 18) midline sulcus straight; and 19) shell surface without ornamentation. *Chengyuchelys* can be differentiated from all stem cryptodires by character 1, from stem and crown Pleurodira (Panpleurodira) by character 2, from most basal turtles by character 4 (except *Heckerochelys romani* Sukhanov, 2006), and from *H. romani* by characters 7–14, and 16. A more detailed compari-

son of *Chengyuchelys* with well known Middle Jurassic turtles, such as *Kayentachelys aprix* and *Xinjiangchelys latimarginalis*, is given in Table 2.

Remarks—The leaf-shaped entoplastron with a zigzag-shaped posterior suture is a synapomorphy for *Chengyuchelys* that unites *C. baenoides* with *C. zigongensis*. The problematic “*C.*” *dashanpuensis* differs from the two unequivocal *Chengyuchelys* species in possessing transversely oriented and relatively large epiplastra with posterolateral extensions, a rounded entoplastron lacking an anterior process, a single cervical scale, wide vertebrals, and very narrow mesoplastra. Conversely, “*C.*” *dashanpuensis* shares many plesiomorphic characters with *Sichuanchelys chowi* (e.g., wide vertebrals and single cervical scale), but lacks the plastral synapomorphy identified above for *Chengyuchelys* (see also Tong et al., 2002). Therefore we consider the retention of this species in the genus *Chengyuchelys* to be untenable and we recommend it be called “*C.*” *dashanpuensis*. We refrain from erecting a new genus until re-examination of the type material of this species can better determine its characters and phylogenetic affinities.

Although *Chengyuchelys* and *Sichuanchelys* are often united into the Chengyuchelyidae, this is based entirely on their antiquity, close geographic proximity, and plesiomorphic retention of mesoplastra. In fact, there are no shared derived characters uniting these taxa, and from a rank-free perspective, no need to use the name Chengyuchelyidae for now.

CHENGYUCHELYS BAENOIDES Young and Chow, 1953

Chengyuchelys baenoides Young and Chow, 1953:217, figs. 1, 2, Pl. 1; Yeh, 1963:83; Yeh, 1982:285, fig. 2, pl. II, figs. a–c; Yeh, 1990a:34, fig. 1; Yeh, 1990b:305; Yeh, 1994:5, fig. 2; Sun et al., 1992:18, fig. 20; Peng et al., 2005:37, 207, fig. 23.

Etymology—*Baen-* refers to the North American stem Testudines clade Baenidae Cope, 1882, to which this species was originally assigned; *oides-* Latin for “like” or “resembles.”

Holotype—IVPP-V708, two-thirds of a carapace and plastron.

Referred Material—Five incomplete shells: IVPP-V710 (paratype), IVPP-V6507, ZDM 3003, ZDM 3007 (= ZDM 1), and ZDM 3008 (= ZDM 3) (see Young and Chow, 1953; Yeh, 1982, 1990b, 1994; Peng et al., 2005).

Locality, Horizon, and Age—“near Chongqing by the Chengyu Railway that was then under construction” (Yeh, 1994: 5) and Dashanpu locality (Xiashaximiao Formation), Zigong Prefecture, Sichuan Province, China. Middle Jurassic.

Diagnosis—*Chengyuchelys baenoides* can be differentiated from *C. zigongensis* by its relatively narrow fourth vertebral scale and mesoplastra that do narrow medially.

Remarks—The list of referred material is taken from Yeh (1994) and Peng et al. (2005), excluding IVPP V8805, which we consider to be *Sichuanchelys* sp. (see above account for *Sichuanchelys*).

CHENGYUCHELYS ZIGONGENSIS Yeh, 1982

Chengyuchelys zigongensis Yeh, 1982:286, fig. 1, pl. I; Fang, 1987:67, pl. VI, two figures on the upper left; Yeh, 1990a:34, fig. 2; Yeh, 1990b:305; Yeh, 1994:8, fig. 3; Sun et al., 1992:19, fig. 21; Peng et al., 2005:38, 207, figs. 24, 25.

Chengyuchelys cf. *zigongensis*: Yeh, 1990b:305; Yeh, 1994:9.

Etymology—*Zigong-* for Zigong Prefecture, Sichuan Province, home of the Dashanpu locality; *ensis-* Latin for “belong to” or “from.”

Holotype—C.V. 0067, a nearly complete shell.

Referred Material—Three incomplete shells: ZDM 3012 (= I-Z1), ZDM 3006 (= ZDM 7), and ZDM 3009 (see Fang, 1987; Yeh, 1994; Peng et al., 2005).

Locality, Horizon, and Age—Dashanpu locality (Xiashaximiao Formation), Zigong Prefecture, Sichuan Province, China. Middle Jurassic.

Diagnosis—*Chengyuchelys zigongensis* can be differentiated from *C. baenoides* by its relatively wide fourth vertebral scale and mesoplastra that do not narrow medially.

“CHENGYUCHELYS” DASHANPUENSIS Fang, 1987

Chengyuchelys dashanpuensis Fang, 1987:67, figs., pl. VI, two figures on the lower left; Yeh, 1990b:306; Yeh, 1994:10, fig. 4; Sun et al., 1992:20, fig. 22; Peng et al., 2005:41, 208, fig. 26.

Etymology—*Dashanpu-* for the famous fossil locality, Dashanpu, which has yielded many dinosaurs, but even more interesting turtles; *ensis-* Latin for “belong to” or “from.”

Holotype—ZDM 3011 (= I-T19), a nearly complete shell (see Fang, 1987; Peng et al., 2005).

Referred Material—None.

Locality, Horizon, and Age—Dashanpu locality (Xiashaximiao Formation), Zigong Prefecture, Sichuan Province, China. Middle Jurassic.

Diagnosis—“*Chengyuchelys*” *dashanpuensis* can be differentiated from *Chengyuchelys* by its single cervical scale, wide vertebrals, shape of entoplastron, extremely narrow mesoplastra, sinusoidal midline sulcus of the plastron, and gulars not extending onto entoplastron. It can be differentiated from *Sichuanchelys* by narrower mesoplastra, sinusoidal midline sulcus, and anal scales that overlap the hypoplastra.

CONCLUSIONS

Recent studies of Jurassic turtles from Asia (Tong et al., 2002; Matzke et al., 2005; Danilov and Parham, 2006; this study) allow us to better understand the origination time of modern turtle lineages (Testudines). Before the end of the Middle Jurassic, the first Testudines (the stem cryptodires *Chengyuchelys* and *Xinjiangchelys*) appeared in Asia. By the Late Jurassic, the replacement of stem Testudines by stem cryptodires had begun in earnest in Europe and Asia (Joyce, 2007). At that time, we also see the oldest evidence of the crown clade Cryptodira, *Yehguia tatsuensis*, in China (Danilov and Parham, 2006). This emerging picture may be fleeting, however, as the bulk of Jurassic turtles from Asia remain unstudied.

Dashanpu is the most diverse Middle Jurassic turtle fauna anywhere, but many questions remain to be answered about the basal turtles found at this locality. Some specimens (e.g., IVPP-V8805 and the holotype of “*Chengyuchelys*” *dashanpuensis*) have uncertain taxonomic affinities that can only be resolved by a thorough revision of more material. We predict that such work will be fruitful, because even having access to just three specimens (one of them a cast) for our study, we were able to discover new characters and make new taxonomic assignments.

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APPENDIX 1. Details about new character added to matrix of Joyce (2004, 2007).

Character name: Marginal B. **Character definition:** Marginal scales overlap onto costals: 0 = absent, marginal scales restricted to peripherals; 1 = present. **Morphology and distribution:** In some taxa the marginal scales are not restricted to the peripherals, but overlap the dorsal surface of the costals. The primitive state is thought to be no overlap, although the scoring for basal turtles is incomplete. The derived condition is found in some paracryptodires, *Xinjiangchelys latimarginalis*, *Chengyuchelys*, *Adocus beatus*, and *Yehguia tatsuensis*. **Character evolution:** Marginals overlapping the costals evolved at least three times within turtles: once in the common ancestor of *X. latimarginalis* and *Chengyuchelys* and once in the common ancestor of *Ad. beatus*, and *Y.*

tatsuensis. Within Paracryptodira the evolution is more complex. It may have evolved in the common ancestor of Paracryptodira, only to be lost in *Plesiochelys antiqua*, *Baena arenosa*, *Chisternon undatum*, and *Boremys pulchra*. Alternatively, marginal overlap may have evolved independently in *Neurankylus eximus* and the pleurosternids (*Pleurosternon bullocki*, *Glyptops plicatulus*, *Dinochelys whitei*). **Codings:** Hypothetical ancestor, 0; *Proganochelys quenstedtii*, ?; *Proterochersis robusta*, ?; *Palaeochersis talampayensis*, ?; *Australochelys africanus*, ?; *Kayentachelys aprix*, 0; *Meiolania platyceps*, ?; *Mongolochelys efremoni*, 0; *Kallokibotian bajazidi*, ?; *Platychelys oberndorferi*, 0; *Caribemys oxfordiensis*, ?; *Notoemys laticentralis*, 0; *Elsya dentata*, 0; *Chelodina oblonga*, 0; *Phrynops geoffroanus*, 0; *Erymnochelys madagascariensis*, 0; *Pelomedusa subrufa*, 0; *Podocnemis expansa*, 0; *Dorsetochelys delairi*, ?; *Pleurosternon bullockii*, 1; *Glyptops plicatulus*, 1; *Dinochelys whitei*, 1; *Neurankylus eximus*, 1; *Trinitichelys hiati*, ?; *Plesiobaena antiqua*, 0; *Boremys pulchra*, 0; *Baena arenosa*, 0; *Chisternon undatum*, ?; *Portlandachelys mcdowelli*, ?; *Plesiochelys solodurensis*, 0; *Solnhofia parsonsi*, ?; *Thalassemys moseri*, ?; *Santanachelys gaffneyi*, ?; *Xinjiangchelys latimarginalis*, 1; *Chengyuchelys*, 1; *Kirgizemys hoburensis*, 0; *Judithemys sukhanovi*, 0; *Dracochelys bicuspis*, ?; *Sinemys lens*, 0; *Ordosemys leios*, 0; *Toxochelys latiremis*, ?; *Caretta caretta*, 0; *Chelonia mydas*, 0; *Mesodermodochelys undulatus*, -; *Dermochelys coriacea*, -; *Protochelydra zangerli*, 0; *Macrochelys temminckii*, 0; *Chelydra serpentina*, 0; *Platysternon megacephalum*, 0; *Mongolemys elegans*, 0; *Gopherus polyphemus*, 0; *Chrysemys picta*, 0; *Geoclemys hamiltonii*, 0; *Emarginachelys cretacea*, 0; *Baptemys wyomingensis*, 0; *Dermatemys mawii*, 0; *Hoplochelys crassa*, 0; *Staurotypus triporcatus*, 0; *Sternotherus odoratus*, 0; *Kinosternon flavescens*, 0; *Zangerlia neimongolensis*, ?; *Basilemys variolosa*, 0; *Adocus beatus*, 1; *Yehguia tatsuensis*, 1; *Peltochelys duchastelli*, 0; *Sandownia harrisi*, ?; *Apalone spinifera*, -; *Lissemys punctata*, -; *Anosteira ornata*, -; *Carettochelys insculpta*, -.

APPENDIX 2. Characters coded for *Chengyuchelys* and added to the matrix of Joyce (2004, 2007): Carapace A, 0; Carapace B, 0; Nuchal B, 0; Peripheral B, 0; Costal A, 0; Costal B, 0; Costal C, 0; Cervical A, 2; Supramarginal A, 2; Vertebral A, 1; Vertebral B, 1; Vertebral C, 0; Plastron A, 1; Plastron B, 0; Plastron C, 0; Entoplastron A, 1; Entoplastron B, 1; Entoplastron C, 1; Entoplastron D, 0; Entoplastron E, 0; Epiplastron A, 0; Hyoplastron A, 0; Mesoplastron A, 0; Hypoplastron A, 0; Xiphoplastron A, 0; Xiphoplastron B, 0; Plastral scutes A, 0; Plastral scutes B, 0; Gular A, 0; Extragular A, 0; Extragular B, 0; Extragular C, 0; Intergular A, 0; Humeral A, 0; Pectoral A, 0; Abdominal A, 0; Anal A, 1; Inframarginal A, 0.