A REDESCRIPTION OF 'PLESIOCHELYS' TATSUENSIS FROM THE LATE JURASSIC OF CHINA, WITH COMMENTS ON THE ANTIQUITY OF THE CROWN CLADE CRYPTODIRA

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ABSTRACT—A reexamination of the holotype of 'Plesiochelys' tatsuensis Yeh, 1963, from the Late Jurassic of China, allows us to establish previously unknown characters of this species. A phylogenetic analysis places 'P.' tatsuensis on the stem of Trionychia, near the clades Adocidae and Nanhsiungchelyidae. Given the hypothesized phylogenetic position of 'P.' tatsuensis, a new genus, Yehguia gen. nov., is erected for this species. The phylogenetic position of Y. tatsuensis pushes the origin of the crown clade Cryptodira into the Late Jurassic. This is remarkable in light of recent studies that moved the origin of crown group turtles (Testudines) from the Triassic to the Late Jurassic. This means that the establishment of basal cryptodiran lineages must have quickly followed the origin of Testudines in the Late Jurassic. The fact that the most ancient fossil Cryptodira is hypothesized to be on the stem of Trionychia is concordant with recent molecular hypotheses that place Trionychia as the most basal extant lineage of Cryptodira. Finally, our results further highlight that the Late Jurassic of China is important for understanding the earliest evolution of cryptodiran turtles.

INTRODUCTION

Plesiochelys tatsuensis Yeh, 1963, from the Late Jurassic of China (Fig. 1), was described based on a single incomplete shell (IVPP–V996; Figs. 2, 3). The species was assigned to the Late Jurassic European genus *Plesiochelys* Rütimeyer, 1873, along with a number of other species from the Late Jurassic of China (Young and Chow, 1953; Yeh, 1963; Yeh, 1973; Yeh and Fang, 1982), based on "characters of the plastron" (Yeh, 1963:84). Recent analyses have shown that Asiatic *Plesiochelys* are not closely related to 'true' *Plesiochelys* from Europe and that, at least for the Chinese species, the taxon *Plesiochelys* serves as a catch-all for many Late Jurassic Eucryptodira Gaffney 1975 (sensu Gaffney, 1984) incertae sedis. For example, the revision of some Chinese species of '*Plesiochelys*', carried out by Peng and Brinkman (1993), resulted in their assignment to the Asiatic genus *Xinjiangchelys* Yeh, 1986 of the family Xinjiangchelyidae Nessov, 1990 in Kaznyshkin et al. (1990). Two additional species, *Plesiochelys oshanensis* Yeh, 1973 and *P. jingyanensis* Yeh and Fang, 1982, also belong to *Xinjiangchelys* (Danilov and Parham, unpublished data). Understanding the phylogenetic position of Late Jurassic turtles is important in light of recent studies that move the origin of crown group turtles (Testudines Batsch, 1788; see Joyce et al. [2004] for phylogenetic definitions of higher taxa used here) from the Late Triassic to the Late Jurassic (Joyce, 2004, in press). This new idea highlights the Late Jurassic as an important time for understanding the establishment of the primary lineages of extant turtles.

The systematic position of '*Plesiochelys*' *tatsuensis* was first questioned by Nessov with coauthors (Nessov and Julinen, 1977; Nessov, 1977; Nessov, 1981; Nessov and Khosatzky, 1981), who primarily considered it a member of the Adocidae Cope, 1870 (see phylogenetic definition of Adocidae given by Joyce and Norell, 2005). Adocids are a clade on the stem of Trionychia Hummel, 1929 that, excluding '*P.*' *tatsuensis* from the Jurassic of China, range from the Early Cretaceous to Oligocene of Asia as well as the Cretaceous and Paleocene of North America (Sukhanov, 2000; Hutchison and Archibald, 1986). The hypothesized adocid affinities of '*P.*' *tatsuensis* are based on a phenetic similarity in morphology of the anterior plastral lobe and sculpturing of the shell (Nessov, 1981; Nessov and Khosatzky, 1981). Although its exact position relative to other adocids varies from author to author, there seems to be a mounting consensus on the general phylogenetic position of '*P.*' *tatsuensis* as separate from *Plesiochelys* and somewhere within Adocidae (Sukhanov, 2000; Lapparent de Broin, 2004).

Since the original description and until now, all ideas about the phylogenetic position of '*P.*' *tatsuensis* are based on entirely on morphological data taken from the short original description and figures of bad quality (Yeh, 1963). Nobody has ever reexamined the specimen or included this taxon in a computer-assisted cladistic analysis. In this paper we redescribe the holotype of '*P.*' *tatsuensis* (IVPP-V996) and demonstrate previously unknown and misunderstood aspects of its morphology. We use our morphological data to assess its phylogenetic position within Testudines by including '*P.*' *tatsuensis* in the global turtle matrix of Joyce (2004, in press).

Institutional Abbreviation—IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China.

DESCRIPTION

The holotype of '*P.*' *tatsuensis* (IVPP-V996; Figs. 2, 3) is represented by an incomplete shell, consisting of lateral parts of the carapace and a complete plastron. The internal morphology of central and posterior regions of the carapace is partially visible as impressions on the internal matrix.

The nuchal is not preserved, because anterior part of the carapace is broken off. Imprints of neurals 4 and 5 are visible on the internal matrix; they are hexagonal short-sided anteriorly. The shape of other neurals or their total number is unclear.

The number of suprapygals is unclear. The impression of a pygal is discernable on the internal matrix. The pygal was longer than wide and narrowed anteriorly.

The costals are represented by lateral parts of right costals 1–7 and by imprints of the medial parts of costals 4–8 of both sides. Costal 1 is represented only by its posterolateral part, which contacts peripheral 3 and has point contact with peripheral 4. Costal 2 is somewhat narrowed laterally and contacts peripheral
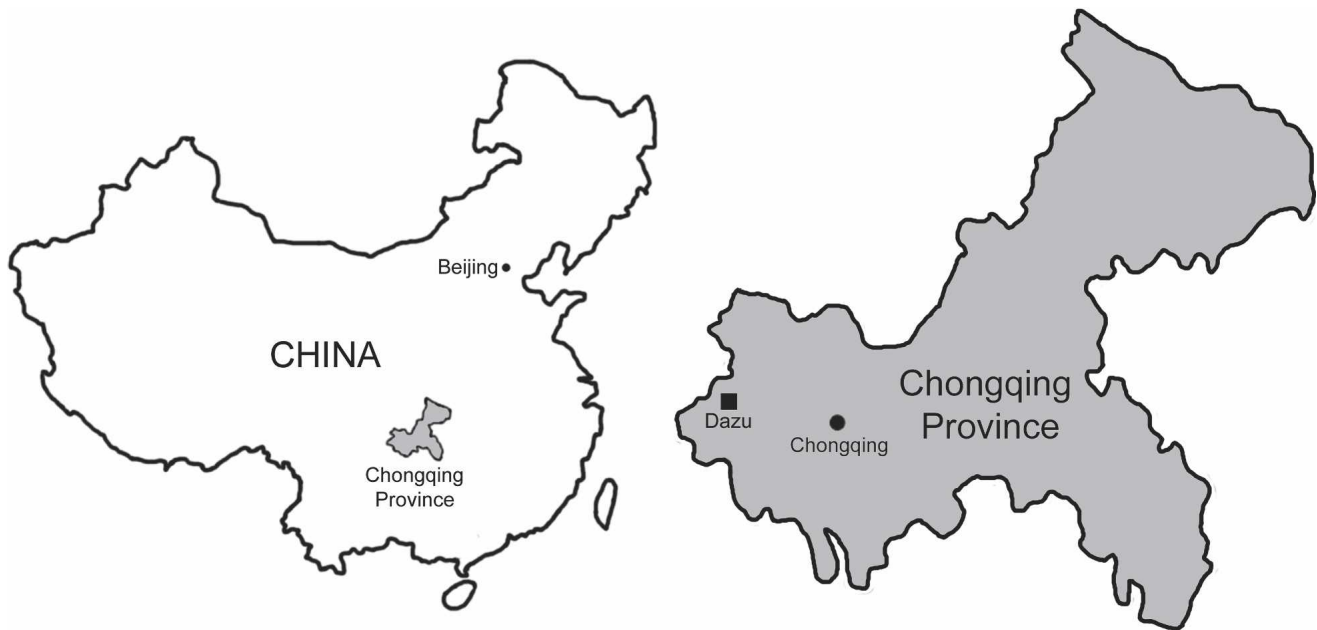
FIGURE 1.   Map showing the area where '*P.*' *tatsuensis* (IVPP-V996) was discovered marked with a square. The locality is Dazu, Chongqing Province, China (Late Jurassic Shaximiao Formation).

4. Costal 3 is widened laterally and contacts peripherals 4–6. Costals 4–8 are wider laterally than medially and contact peripherals 6–7, 7–8, 8–9, 9–10 and 10–?11 respectively. Costal ribheads are visible on imprints of costals 4–8. The ratio of the ribhead width to medial costal width for costal 4 (13 mm) is 23% (the same ratio in Asian adocids is *Ferganemys verzilini* Nessov and Khosatzky, 1977 and *"Adocus" aksary* Nessov 1984, in Nessov and Krassovskaya [1984], are 19% and 16%, respectively). The ribheads of IVPP-V996 do not show the characteristic reduction present in adocid turtles. At least one ribhead (corresponding to 9th thoracic vertebra) is discernable on the imprint of costal 8, medial to imprint of the ilial scar.

The preserved peripherals (3–10) are longer than wide. Peripheral 3 is represented by its posterior part only, whereas peripheral 10 is only shown by its anterior part. Impressions of peripheral 11 are also visible. The dorsal (carapacial) plates of the peripherals are wider than the ventral (plastral) ones. The upturned free edge of the carapace is visible on peripherals 3–6.

The plastron is suturally attached to the carapace via peripherals 2–8, although the distal ends of the posterior buttresses are covered with matrix. The anterior lobe is wider and shorter than the posterior one. The lateral borders of the posterior lobe at the femoral and anal regions are rounded in outline.

The epiplastron has a rounded free edge and an almost straight posterior border contacting the ento-and hyoplastra and forming an angle about 70° with the midline. The epi-hyoentoplastral hinge is absent (contra Nessov and Khosatzky, 1981 and Lapparent de Broin, 2004). The epiplastron is relatively big, its length along the midline makes up about 32% of the anterior lobe length. The entoplastron is slightly wider than long, its width makes up 44% of width of the anterior lobe at the epi-hyoplastral suture. Its borders with the epiplastra are straight, whereas borders with the hyoplastra are rounded. The xiphiplastron is relatively wide (its width is about 90% of length) with rounded free border.

The scalation of the carapace is poorly preserved and represented only by lateral parts of the pleurals 1–4 and marginals 4–10 on the right side of the shell. Interpleural sulci are close to the posterior borders of corresponding costals. Marginals 4–7

and probably 8 overlap the lateral parts of the costals 1–5, whereas marginals 4, 9 and 10 are restricted to peripherals. This overlapping was first noted by Nessov and Khosatzky (1981) on the basis of photo from the original description (Yeh, 1963, Pl. I: 3), but our study is first to show extent of this overlapping. Scale sulci from the ventral side of peripherals 11 and the pygal are visible as impressions on the matrix (Fig. 2A).

The plastral scales are represented by a complete set including the intergulars, gulars, humerals, pectorals, abdominals, femorals, anals and four pairs of inframarginals. The midline sulcus is strongly sinuous especially between pectorals, abdominals and femorals.The intergulars are tetragonal narrowed posteriorly, occupying about 1/3 of ventral surface of the epiplastra and slightly overlap the entoplastron. The gulars are triangular and restricted to the epiplastra. The length of the gular-intergular contact is long. The gular-intergular-humeral sulcus is straight, perpendicular to the midline, and not corresponding with the epi-entohyoplastral suture. The humeral-pectoral sulcus is curved posteriorly, reaching the line connecting centers of axillary notches. The pectoral-abdominal sulcus is curved anteriorly. Anals are restricted to the xiphiplastra. The abdominal-anal sulci are directed posterolaterally from the midline. The midline sulcus appeared to be slightly more sinuous and abdominal scutes longer along midline than on published figures (Yeh, 1963:fig. 7; 1994:fig. 8; 1996:fig. 7). Four pairs of inframarginals form complete rows that separate the rest of the plastral scales from the carapacial scales. In the original description (Yeh, 1963:fig. 7), four right and three left inframarginals were figured, whereas only three inframarginals on each side were shown in the later publications (Yeh, 1994:fig. 8; 1996:fig. 7). The inframarginals are longer than wide and are mostly restricted to the plastron lateral from the line connecting centers of axillary and inguinal notches. The lateral borders of the inframarginals generally correspond to the plastron-carapace suture although inframarginals 2–4 on the right side and 3–4 on the left side slightly overlap the peripherals. The contacts of the inframarginals are as follows: inframarginal 1 = marginals 4–5 laterally, pectoral medially, and inframarginal 2 posteriorly; inframarginal 2 = marginal 5 laterally, pectoral and abdominal medially, and inframarginal 3 pos-
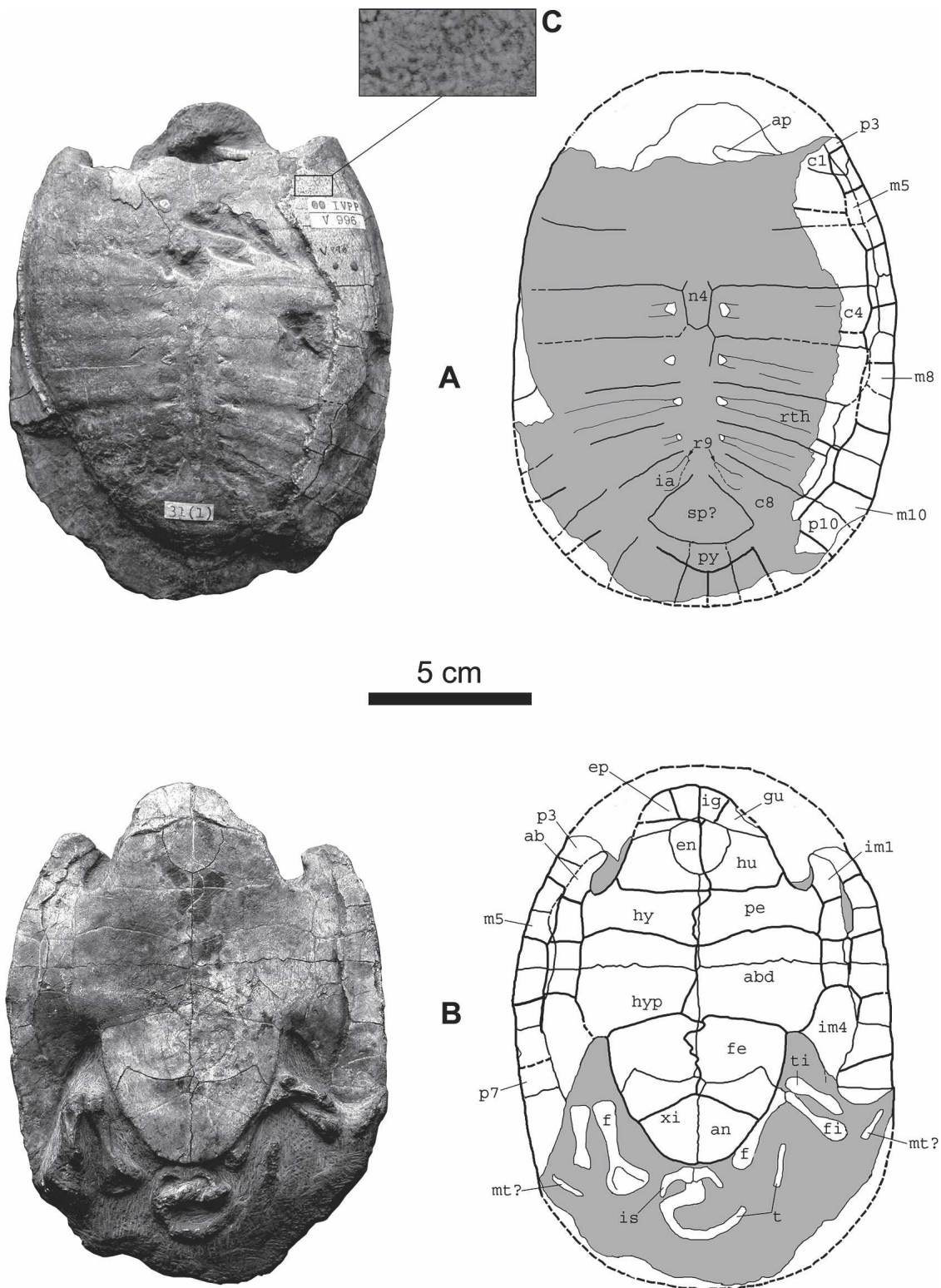
FIGURE 2. '*P.*' *tatsuensis* (IVPP-V996). **A**, dorsal view; **B**, ventral view; **C**, magnified part of the shell showing sculpturing. Matrix is filled with gray. **Abbreviations**: **ab**, axillary buttress; **abd**, abdominal; **an**, anal; **ap**, acromial process of scapula; **c1**, **c4**, **c8**, costals 1, 4, 8; **en**, entoplastron; **ep**, epiplastron; **f**, femur; **fe**, femoral; **fi**, fibula; **gu**, gular; **hu**, humeral; **hy**, hyoplastron; **hyp**, hypoplatsron; **ia**, ilial attachment; **ig**, intergular; **im1**, **im4**, inframarginals 1, 4; **is**, ischium; **m5**, **m8**, **m10**, marginals 5, 8, 10; **mt?**, unknown metatarsal; **n4**, neural 4; **p3**, **p7**, **p9**, **p10**, peripherals 3, 10; **pe**, pectoral; **py**, pygal; **sp?**, unknown suprapygal; **r9**, ribhead of 9th thoracic rib; **rth**, rib thickenning; **sc**, body of the scapula; **t**, tail; **ti**, tibia; **xi**, xiphiplastron.
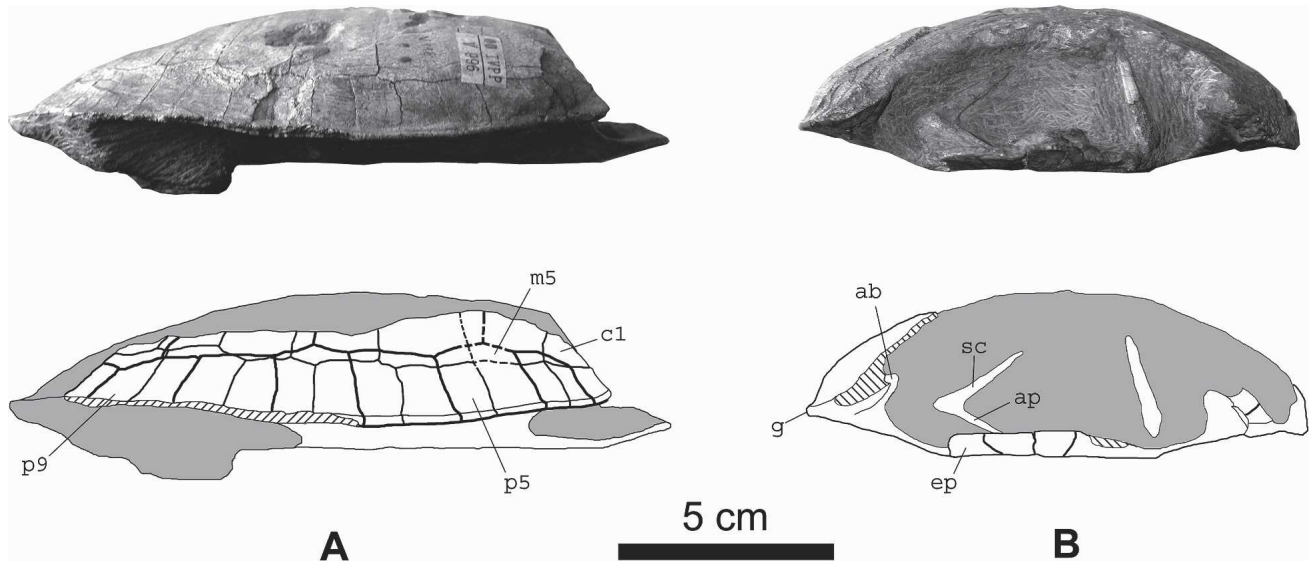
FIGURE 3. '*P.*' *tatsuensis* (IVPP-V996). **A**, right view; **B**, anterior view. Matrix is filled with gray. Broken areas are hatched. See Figure 2 for abbreviations.

teriorly; inframarginal 3 = marginal 5 and 6 laterally, abdominal medially, and inframarginal 4 posteriorly; inframarginal 4 = marginals 6–8 laterally and abdominal medially.

The surface of the shell is covered with a peculiar sculpture (Fig. 2C), consisting of small pits (about ten in 10 mm), best visible on costals. On the peripherals they arranged in longitude furrows separated by low ridges.

Parts of the pectoral girdle are visible in the anterior and dorsal views of the shell. It is represented by both scapulae. The scapular and acromial processes, preserved on the right side, form an angle about 70°. The glenoid neck is absent. The pelvic girdle is almost completely covered with matrix. Only ischia with long metischial processes are exposed in ventral view. They were never suturally connected to the plastron. The hindlimbs are poorly preserved and represented by femur, tibia, fibula and some metatarsals. The tail is visible in ventral view, but no features of its vertebrae could be determined.

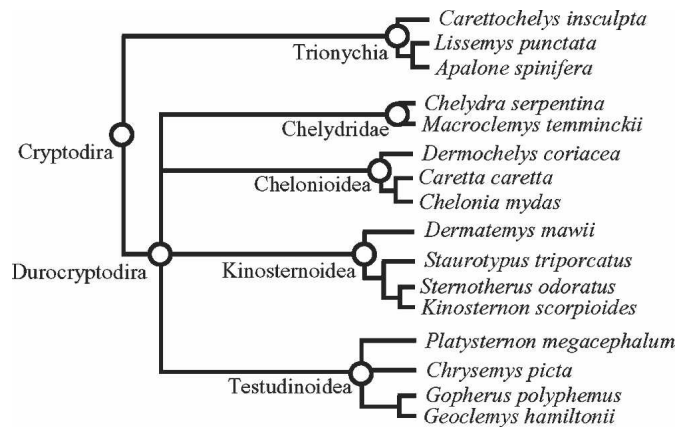For measurements of the shell elements, see Table 1.

FIGURE 4. Tree showing a conservative estimate of cryptodiran relationships based on molecular studies. These relationships were used to construct the constraint tree used in the phylogenetic analysis of '*P.*' *tatsuensis* affinities. Node based taxa are shown by a circle.

TABLE 1. Measurements (in mm) of IVPP V996.

Characters	IVPP V996
Carapace (length/width/height)	~150/~117/~35
Neural 4 (length/width)*	12.5/8.2
Peripherals (length along free edge/width of dorsal plate at the middle/width of ventral plate posteriorly)	
Peripheral 4	17.3/11.6/7.7
Peripheral 5	19.0/12.6/13.0
Peripheral 6	18.6/15.0/9.3
Peripheral 7	18.5/14.5/17.0
Peripheral 8	20.0/~20.3/?
Peripheral 9	29.0/~20.0/?
Plastron (length at the midline/width at the hyo-hypoplastral suture)	116.4/89.5
Bridge length (maximum/minimum)	~78d/44.5d
Anterior lobe (length/width at the base/width at the humeral-pectoral sulcus/width at the epi-hyoplastral suture)	~35/63.5/51.0/42.5
Posterior lobe (length/width at the abdominal-femoral sulcus/width at the hypo-xiphiplastral suture/width at the femoral-anal sulcus)	~40/55.0/47.2/36.0
Epiplastron (length at the midline)	11.3
Entoplastron (length/width)	17.5/18.9
Hyoplastron (length at the midline)	28.7d, 27.6s
Hypoplastron (length at the midline)	31.8d, 35.5s
Xiphiplastron (length at the midline)	27.0d, 25.0s
Intergular (length at the midline)	12.5
Humeral (length at the midline)	20.6
Pectoral (length at the midline)	17.4
Abdominal (length at the midline)	22.8
Femoral (length at the midline)	22.1
Anal (length at the midline)	21.1
Inframarginals (length at contact with plastral scales/width at contact with anterior scale)	
Inframarginal 1	5.2d, 6.5s/-
Inframarginal 2	11.5d, 11.4s/7.0d
Inframarginal 3	17.0d, 14.5s/11.9d, 8.8s
Inframarginal 4	14.8d, 15.5s/11.2d, 6.5s

"~" denotes estimated measurement; "*" denotes measurement based on imprint of the element; "d" and "s" designate right and left measurements.

PHYLOGENETIC ANALYSIS

Methods

Our new observations of 'P.' tatsuensis allow us to include this taxon into a computer assisted cladistic analysis for the first time. We include characters scored from IVPP-V996 into the global turtle matrix of Joyce (2004, in press) that includes one hypothetical ancestor and 64 additional species-level recent and fossil turtles covering the known spectrum of turtle diversity for a total of 66 operational taxonomic units (OTUs). Of the 136 characters used by Joyce (2004, in press), we can score IVPP-V996 for 33 of them (Appendix 1). Joyce (2004, in press) analyzed his data set in several ways and so we ordered the 15 multistate characters and excluded three rogue taxa (not counted as part of the 66 OTUs) based on his arguments. Leaving all characters unordered does not effect the placement of IVPP-V996 although it does affect other aspects of tree topology.

In order to get as accurate a phylogeny as possible, we constrain some of the relationships among living taxa based on strong molecular evidence (Krenz et al., 2005; Parham et al., 2006). The constraint tree we used was rooted with the hypothetical ancestor from Joyce (2004, in press) as well as *Proganochelys quenstedti* Baur, 1887 and a monophyletic Pleurodira Cope, 1865. The relationships we assumed for Cryptodira Cope, 1868 (Fig. 4) are well supported by molecular data and are either 1) supported by morphological data or 2) not strongly refuted by morphological data (Krenz et al., 2005; Danilov and Parham, 2005; Joyce, 2004, in press). We used the heuristic algorithm with 100 random additions employed using PAUP* 4.0b10 (Swofford, 2002).

Most of the constrained nodes have phylogenetically defined names (see Joyce et al., 2004) except for clade that includes all the non-pantrionychian cryptodires. Because this latter clade is important and worthy of discussion, we feel it needs a name. We phylogenetically define Durocryptodira tax. nov. as the crown clade arising from the last recent common ancestor of *Testudo graeca* Linnaeus, 1758, *Kinosternon* (orig. *Testudo*) *scorpioides* (Linnaeus, 1766), *Chelonia* (orig. *Testudo*) *mydas* (Linnaeus 1758), and *Chelydra* (orig. *Testudo*) *serpentina* Linnaeus, 1758, but excluding *Trionyx* (orig. *Testudo*) *triunguis* (Forskål, 1775) and *Carettochelys insculpta* Ramsay, 1887. The etymology is from *duro-*, Latin for hard, and *cryptodira-* for cryptodires; it refers to the fact that this clade includes the non-softshell cryptodires.

Results

The result of our phylogenetic analysis (Fig. 5) is 620 trees with 367 steps. In all trees, 'P.' tatsuensis is considered a stem-trionychian turtle close to adocids and nanhsiungchelyids and not near *Plesiochelys* sensu stricto from the Jurassic of Europe. If we place 'P.' tatsuensis as sister to *P. solodurensis* (the type species of *Plesiochelys* and the only member of this genus in the matrix) then we find a tree that is four steps longer (371 steps). This relatively small difference reflects the high amount of homoplasy within basal eucryptodires that results in weak support for most nodes. In fact, there are many placements for 'P.' tatsuensis that are more parsimonious than as sister to *P. solodurensis* such as on the stem of Testudinoidea or Kinosternoidea (370 steps). The most parsimonious solution is to consider 'P.' tatsuensis to be a stem trionychian as supported by its morpho-
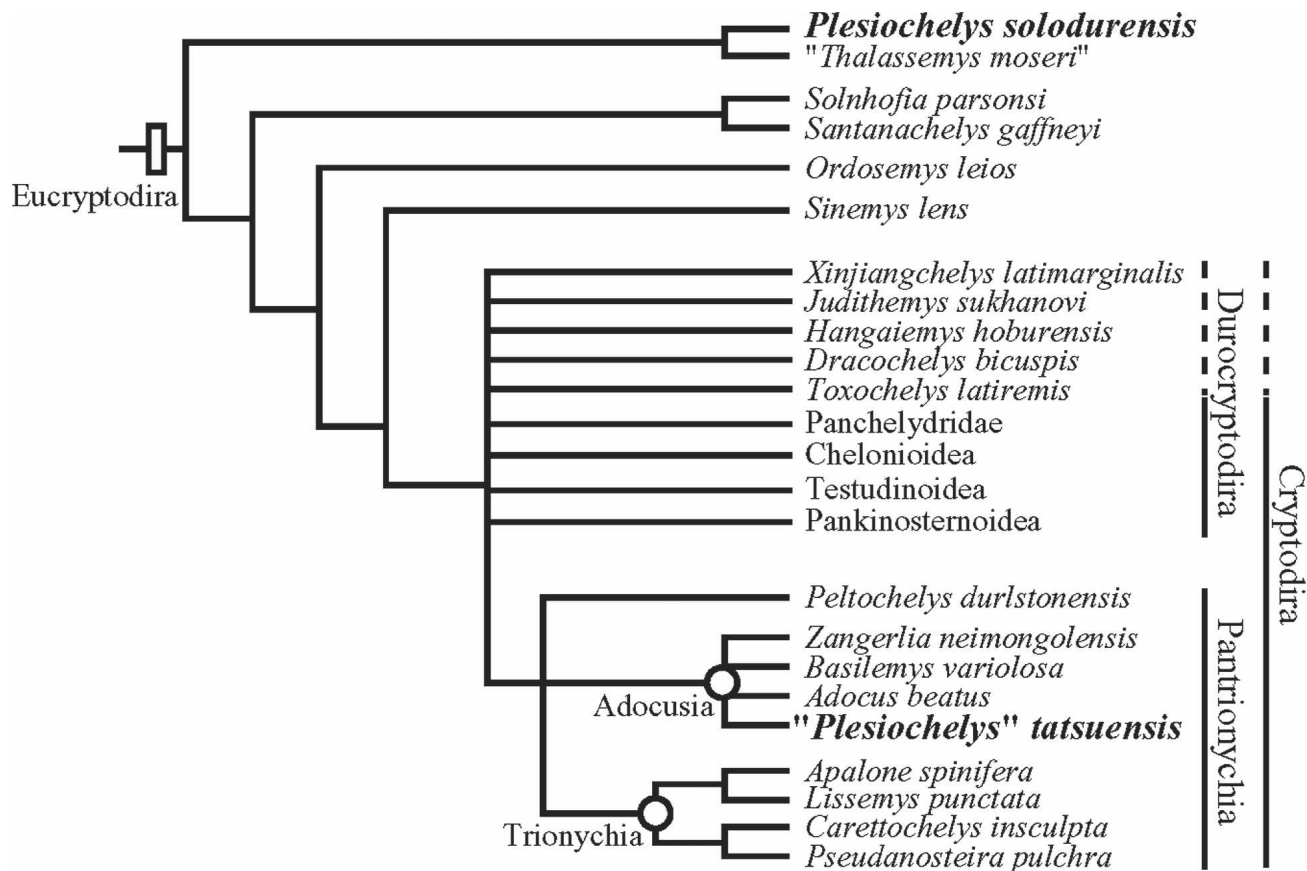

FIGURE 5. A strict consensus of 620 phylogenetic trees resulting from this study. Non-eucryptodires were eliminated from this figure. The hypothesized position of 'P.' tatsuensis (IVPP-V996) is far-removed from *Plesiochelys* sensu stricto from the Jurassic of Europe. The extent of the crown groups Cryptodira and Durocryptodira are uncertain because of the basal polytomy. All polytypic terminal taxa have been collapsed into higher taxon names for simplicity.
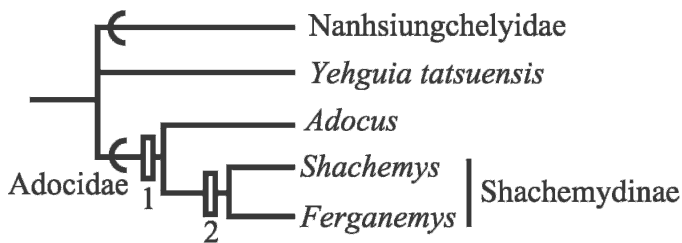
FIGURE 6. A hypothesis of the relationships of *Yehguia tatsuensis* to adocids and nanhsiungchelyids. Character 1: weak rib heads; Character 2: entoplastron is shortened and truncated anteriorly.

logical characters (see Discussion). Based on this phylogenetic hypothesis, we conclude that the continued placement of '*P.*' *tatsuensis* in the taxon *Plesiochelys* is no longer tenable and so we provide a new generic name (*Yehguia* gen. nov.) for this species.

SYSTEMATIC PALEONTOLOGY

TESTUDINES Batsch, 1788
CRYPTODIRA Cope, 1868
PANTRIONYCHIA Joyce, Parham, and Gauthier, 2004
YEHGUIA, gen. nov.

Etymology—*Yeh-* to honor Yeh Xiangkui, the China's pre-eminent paleochelonologist and the describer of *Plesiochelys tatsuensis*; *guia-* from 'gui' the Mandarin word for turtle.
Type and only known species—*Plesiochelys tatsuensis* Yeh, 1963.
Diagnosis—As for type and only species.

YEHGUIA TATSUENSIS (Yeh, 1963), comb. nov.
(Figs. 2, 3)

Plesiochelys tatsuensis Yeh, 1963:84, fig. 7, pl. 1, 3–4.
'*Plesiochelys*' *tatsuensis* (Yeh): Nessov and Julinen, 1977:55.
Ferganemys tatsuensis (Yeh): Nessov and Khosatzky, 1981:154.

Holotype—IVPP-V996, an incomplete shell with partially exposed girdles, hindlimbs and tail.
Locality and Horizon—Gaofengshan (=Kao-feng-shan) along the Danan (=Ta-an) Highway, Dazu (=Tatsu, =Longang) County, Chongqing Province (formerly Sichuan Province),

China. Probably Shaximiao Formation, Upper Jurassic (Lucas, 2001).

Diagnosis—The shell exhibits the following features typical for stem-trionychians: (1) sutural plastron-carapace connection, (2) a relatively large epiplastra, (3) both intergular and gular scutes, (4) an entoplastron that is wider than long, (5) a wide posterior plastral lobe with rounded lateral borders, (6) a sinuous midplastral sulcus, (7) anal scutes that are restricted to the xiphiplastra, (8) four pairs of inframarginal scutes, and (9) sculpturing of the shell surface with fine pits. It differs from other stem-*trionychians* by the (10) overlapping of marginal scales onto first to fifth costals. It can be separated from adocids by having (11) unreduced ribheads of the costals and from *Peltochelys* Dollo, 1884 by having (12) eleven pairs of peripherals. It can be distinguished from *Xinjiangchelys*, a common eucryptodire from the Jurassic of Asia by characters 1, 2, 4, 5, 7 and 9 and from *Plesiochelys* by characters 2, 5, 6, 9 and 10.

DISCUSSION

The Phylogenetic Position of *Yehguia tatsuensis*

In our phylogenetic analysis (Fig. 5), *Yehguia tatsuensis* is placed in a polytomy with members of the *Adocus* + nanhsiungchelyid clade. Since this latter clade is a well supported and important clade, we phylogenetically define a new clade name, Adocusia as the most inclusive clade including *Adocus* (orig. *Emys) beatus* (Leidy, 1865) and *Nanhsiungchelys wuchingensis* Yeh, 1966, but not any species of Recent turtle. The hypothesized affinity of *Y. tatsuensis* to Adocusia is supported by two characters. The first character is the shared presence of a sinuous midline plastral sulcus (Plastral scale B in Appendix 1). The second character is the osseous connection between the plastron and carapace (Plastron A in Appendix 1). Regarding the latter character, although several lineages of cryptodires have an osseous connection between the carapace and plastron, the primitive condition for Cryptodira is to have a ligamentous connection. An osseous connection evolved independently within Adocusia, Pankinosternoidea, and Pantestudinoidea.

The placement of *Y. tatsuensis* to the stem of Trionychia is also supported by the presence of sculptured shell although this character was not included in the analysis because it is difficult to homologize. For example, many lineages such as the panchelydrid *Protochelydra* Erickson, 1973 or the Trionychidae Fitzinger, 1826, show sculpturing although the morphology of this charac-
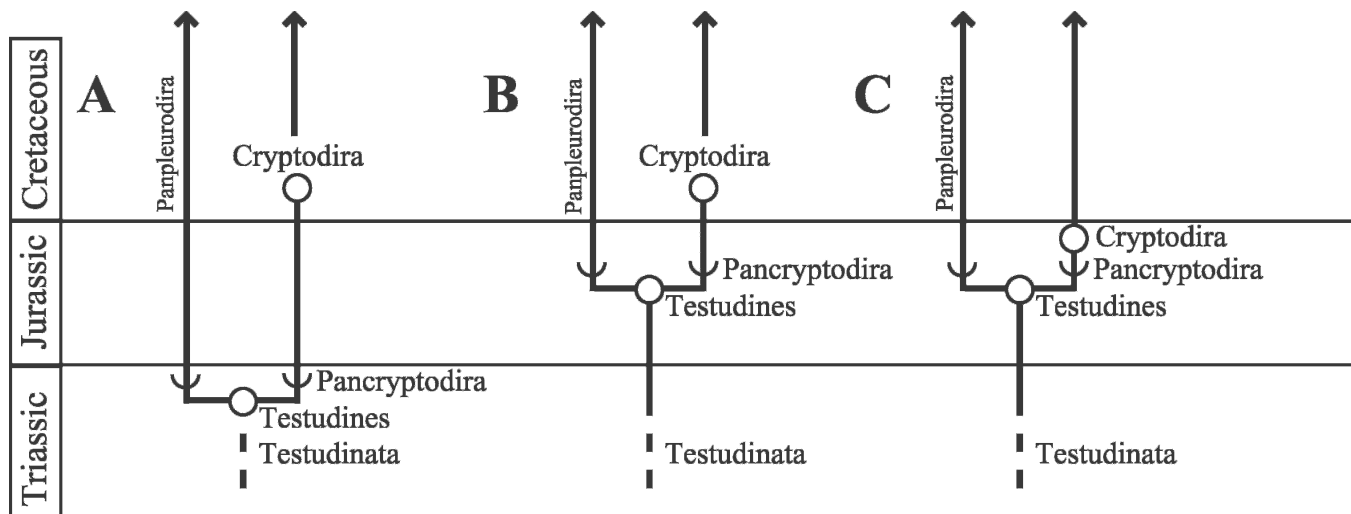

FIGURE 7. Diagram illustrating the changing ideas about the origins of Pancryptodira and Cryptodira. **A**, Traditional hypothesis (e.g., Gaffney and Meylan, 1988; Shaffer et al., 1997); **B**, Hypothesis of Joyce (2004, in press); **C**, Hypothesis of this study. Taxa are stem based (open semi-circle) or node based (circle).

ter varies considerably. However, Nessov and Khosatzky (1981) noted that the sculpturing of *Y. tatsuensis*, i.e., comprised of small pits, is similar to that seen in the adocid *Ferganemys* Nessov and Khosatzky, 1977 and we confirm that it matches the sculpturing seen in adocusians in general. Although we don't use this character in the cladistic analysis, we take it as ancillary evidence supporting the phylogenetic placement of *Y. tatsuensis* near the Adocusia clade.

A polytomy in the strict consensus is formed because of uncertainty regarding the position of *Y. tatsuensis*. Our analysis places it as either the sister taxon of Adocusia, the sister taxon of *Adocus beatus* (Leidy, 1868) (the sole adocid in this study), or else one the sister taxon of the two nanhsiungchelyids: *Zangerlia neimongolensis* Brinkman and Peng, 1996 or *Basilemys variolosa* (Cope, 1876). A detailed cladistic analysis of Adocusia could resolve this polytomy, but this is beyond the scope of this work. Nevertheless, our reexamination of IVPP-V996 provides new insights into the morphology of *Y. tatsuensis* allowing us to evaluate previous hypotheses about its phylogenetic position relative to adocids as they are based on few characters based on Yeh's (1963) low quality illustrations.

Nessov and Khosatzky (1977) and Lapparent de Broin (2004) considered *Y. tatsuensis* to be nested within Adocidae and even within the Shachemydinae Khosatzky, 1977, a group that was thought to show some degree of plastral kinesis (*Ferganemys* and *Shachemys* Kuznetsov, 1976). However, only *Shachemys* has an unambiguous epi-hyoentoplastral hinge (Kuznetsov, 1976; Nessov, 1986; Sukhanov, 2000; Lapparent de Broin, 2004), whereas the condition in *Ferganemys* is unclear (Nessov and Krassovskaya, 1984). Therefore, we consider *Ferganemys* to lack a hinge. Our study shows that *Yehguia* also lacks a hinge.

In addition to plastral kinesis, Lapparent de Broin (2004:392) used two other characters, a "more flattened shell" and "the ventral border of the marginals progressively more narrowed towards the nuchal" to unite *Y. tatsuensis* with the Shachemydinae. The former is not an obvious/discrete character, can be the result of post-mortem crushing, and is incredibly plastic among extant turtles even at the population level. Thus, we do not consider it useful for placing *Y. tatsuensis*. As for the second character, we are not sure what it means. This character needs to be clarified and then demonstrated for relevant taxa before we can address it. At the moment, Shachemydinae, excluding *Y. tatsuensis*, can be characterized by only one probable synapomorphy a shortened and anteriorly truncated entoplastron.

Beyond lacking valid, discrete characters that would link it with any known adocid, *Y. tatsuensis* lacks weakened costal rib-heads, a diagnostic feature of the Adocidae (Nessov, 1977; Nessov and Khosatzky, 1977; Meylan and Gaffney, 1989). Consequently, we take a more conservative view on the phylogenetic position of *Y. tatsuensis* and consider it to be in an unresolved polytomy with Adocidae and Nanhsiungchelyidae and possibly even sister to the Adocusia. A summary of our idea about its relationship, including the characters corrected above, is shown in Figure 6.

***Yehguia tatsuensis* and the Antiquity of Cryptodira**—*Yehguia tatsuensis* is the oldest member of the crown clade Cryptodira ever shown by a cladistic study. Another taxon from the Late Jurassic of China, *Sinaspideretes wimani* Young and Chow, 1953 is also thought to be a cryptodire (Meylan and Gaffney, 1992), but its poor state of preservation has precluded it from being included in phylogenetic data matrices. A Late Jurassic age for the origin of the Cryptodira is remarkable in light of recent studies that moved the origin of crown group turtles (Testudines) from the Triassic to the Late Jurassic (Joyce, 2004, in press; Fig. 7). If the phylogenetic position of *Y. tatsuensis* (proposed here) or *Sinaspideretes wimani* (proposed by Meylan and Gaffney, 1992) is correct, it means that the establishment of

basal cryptodiran lineages must have quickly followed the origin of Testudines in the Late Jurassic (Fig. 7).

From a temporal perspective, the fact that both of the most ancient recognizable cryptodirans are hypothesized to be on the stem of Trionychia coincides with recent molecular hypotheses that place Trionychia as the most basal extant lineage of Cryptodira; Meanwhile, the oldest taxa referable to Durocryptodira (i.e., extant lineages of non pantrionychan cryptodires, see Methods) do not appear in the Early Cretaceous. It is possible that in the Late Jurassic, pandurocryptodires had not yet evolved into the recognizable extant lineages (e.g., Panchelonioidea, Pankinosternoidea, etc.); however, we predict that stem durocryptodires should be present.

CONCLUSIONS

Our reexamination of '*P.*' *tatsuensis* from the Late Jurassic of China further confirms that it is separate from real *Plesiochelys*, from the Late Jurassic of Europe. Instead, '*P.*' *tatsuensis* is better placed on the stem of Trionychia as hypothesized by Nessov and Khosatzky (1977) and Lapparent de Broin (2004). Because it is clearly not closely related to *Plesiochelys*, we create a new genus, *Yehguia*, for '*P.*' *tatsuensis*. Our description of *Y. tatsuensis* shows that characters inferred from the original description, such as plastral kinesis, are not substantiated. Consequently, the exact affinities of *Yehguia* with adocid turtles proposed by other authors are not accepted here.

Although the exact position of *Y. tatsuensis* is uncertain, all authors agree that it is on the stem of Trionychia and so is the oldest member of Cryptodira. This requires that the origin of Cryptodira must have quickly followed the origin of Testudines and that the stem of Cryptodira should be correspondingly short. This may explain why one molecular study (Krenz et al., 2005) could not resolve the trichotomy with Pleurodira, Trionychia, and Durocryptodira. Many studies (Shaffer et al., 1997; Parham and Hutchison, 2003) have hypothesized an Early Cretaceous radiation of eucryptodires, but our results show that the Late Jurassic may be a more important time for understanding the earliest evolution of cryptodiran turtles than previously supposed.

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APPENDIX 1. Characters coded for "*P.*" *tastuensis* (IVPP-V996) from the matrix of Joyce (2004, in press): Carapace A, 0; Carapace B, 0; Peripheral A, 1; Peripheral B, 0; Costal A, 0; Costal C, 0; Supramarginal A, 2; Plastron A, 0; Plastron B, 0; Plastron C, 0; Entoplastron A, 1; Entoplastron B, 1; Entoplastron C, 1; Entoplastron D, 0; Entoplastron E, 0; Epilastron A, 0; Hyoplastron A, 0; Hypoplastron A, 0; Xiphiplastron A, 0; Xiphiplastron B, 0; Mesoplastron A, 2; Plastral scales (scutes) A, 0; Plastral scales (scutes) B, 1; Gular A, 0; Extragular A, 0; Extragular B, 0; Extragular C, 1; Intergular A, 0; Humeral A, 0; Pectoral A, 0; Abdominal A, 0; Anal A, 0; Inframarginal A, 0.