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A REDESCRIPTION AND PHYLOGENETIC POSITION OF *ADOCUS PLANUS*, AN ADOCID TURTLE FROM THE LATE CRETACEOUS OF MONGOLIA

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ABSTRACT

In this paper we present a detailed description of the holotype of *Adocus* (orig. *Shineusemys*) *planus* from the Late Cretaceous of Mongolia. The holotype, originally reported to be a plastron, is actually represented by a partial shell with an almost complete plastron and few carapace fragments on the steinkern. The reexamination of the holotype of *A. planus* allows us to present new images of this specimen, improve its diagnosis and include it in a phylogenetic analysis of Adocusia (Adocidae + Nanhsiungchelyidae) for the first time. The phylogenetic analysis places *A. planus* within the *Adocus* clade in polytomy with other species of this genus. This result confirms our previous suggestion that *Shineusemys* should be considered a junior subjective synonym of *Adocus*.

Key words: Adocidae, *Adocus*, Late Cretaceous, Mongolia, *Shineusemys*, turtles

ПЕРЕОПИСАНИЕ И ФИЛОГЕНЕТИЧЕСКОЕ ПОЛОЖЕНИЕ *ADOCUS PLANUS*, АДОЦИДНОЙ ЧЕРЕПАХИ ИЗ ПОЗДНЕГО МЕЛА МОНГОЛИИ

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РЕЗЮМЕ

В этой статье мы представляем подробное описание голотипа *Adocus* (ориг. *Shineusemys*) *planus* из позднего мела Монголии. Голотип, первоначально указанный как пластрон, в действительности представлен неполным панцирем с почти целым пластроном и несколькими фрагментами карапакса на внутреннем ядре. Переизучение голотипа *A. planus* позволяет нам представить новые изображения этого экземпляра, исправить его диагноз и впервые включить его в филогенетический анализ Adocusia (Adocidae + Nanhsiungchelyidae). Филогенетический анализ помещает *A. planus* в состав клады *Adocus* в политомии с другими видами этого рода. Этот результат подтверждает высказанное нами ранее предположение о том, что *Shineusemys* следует рассматривать как младший субъективный синоним *Adocus*.

Ключевые слова: Adocidae, *Adocus*, поздний мел, Монголия, *Shineusemys*, черепахи

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INTRODUCTION

Adocus planus Sukhanov et Narmandakh, 2006 (a type and a single species of the adocid genus *Shineusemys* Sukhanov et Narmandakh, 2006) was described based on the holotype plastron and additional "numerous isolated plates" from the lower part of the Bainshire Formation (Cenomanian – early Turonian) of the Shine Us Khuduk locality of Mongolia (Sukhanov 2000; Sukhanov and Narmandakh 2006). The description was short and accompanied by a single drawing of the plastron (Sukhanov 2000, fig. 17.21). *Shineusemys plana* was distinguished from other adocids by relatively shorter ("narrower" in Sukhanov 2000) abdominals with their medial length less than that of the femorals (Sukhanov 2000). In addition, some differences of *Shineusemys plana* from *Adocus amtgai* Narmandakh, 1985 (as *Adocoides*; Sukhanov, 2000) in relative length of the plastral bridges and size of the epiplastra, were mentioned (Sukhanov 2000). Later, Danilov et al. (2011) noted that the variation of these characters is poorly studied in adocids and that they alone are not enough to diagnose the genus in this group. Because in all other characters *Shineusemys plana* corresponds well to members of *Adocus* Cope, 1868, these authors considered it to be *Adocus planus* (Danilov et al. 2011; this name is used hereinafter). In this paper we give a detailed description of the holotype of this species, which includes a partial shell with an almost complete plastron and few carapace fragments a cast of the internal cavity of the shell (referred to here as the steinkern), include it in a phylogenetic analysis of Adocusia Danilov et Parham, 2006 (a clade uniting Adocidae Cope, 1870 and Nanhsiungchelyidae Yeh, 1966) for the first time and discuss its phylogenetic position. The additional material of this species, including "numerous isolated plates", was not examined by us.

Institutional abbreviations. PIN, Borissyak Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Canada; YPM, Yale Peabody Museum, New Haven, USA.

MATERIAL AND METHODS

In addition to the specimens described below, our study relies on published data and personal observations on the following taxa of the Adocidae: *Adocus agilis* Cope, 1868 from the Late Cretaceous of USA (Hay 1908); *A. aksary* Nessov in Nessov et Krasovskaya, 1984 from the Late Cretaceous of Uzbekistan (Syromyatnikova and Danilov 2009); *A. amtgai* Narmandakh, 1985 (type species of the genus *Adocoides* Sukhanov et Narmandakh, 2006) from the Late Cretaceous of Mongolia (Narmandakh 1985; Sukhanov 2000; Danilov et al. 2011; Syromyatnikova et al. in prep.); *A. annexus* Hay, 1910 from the Paleocene of USA (Hay 1910; Gilmore 1919); *A. beatus* (Leidy, 1865) from the Late Cretaceous of USA (Hay 1908; White 1972; IGD personal observations of YPM 782); *A. bossi* Gilmore, 1919 from the Late Cretaceous of USA (Gilmore 1919); *A. hesperius* Gilmore, 1919 from the Paleocene of USA (Gilmore 1919); *A. kirtlandius* Gilmore, 1919 from the Late Cretaceous of USA (Gilmore 1919); *Adocus* sp. from the Late Cretaceous of USA (Meylan and Gaffney 1989; hereinafter *Adocus* sp. 1); *Adocus* sp. from the Late Cretaceous of Canada (EVS personal observations of RTM 99.63.1; hereinafter *Adocus* sp. 2); *A. substrictus* Hay, 1908 from the Paleocene of USA (Hay 1908); "*A.*" *kazachstanica* Chkhikvadze, 1973 from the middle Eocene of Kazakhstan (Chkhikvadze 1973; Danilov et al. 2011); "*A.*" *orientalis* Gilmore 1931 from the late Eocene of China (Gilmore 1931; Danilov et al. 2011); *Ferganemys verzilini* Nessov et Khosatzky, 1977 from the Early Cretaceous of Kyrgyzstan (Syromyatnikova 2011); species of *Shachemys* Kuznetsov, 1976: *S. ancestralis* Nessov in Nessov et Krasovskaya, 1984 from the Late Cretaceous of Uzbekistan and *S. baibolatica* Kuznetsov, 1976 from the Late Cretaceous of Tadzhikistan and Kazakhstan (Danilov et al. 2007), *S. laosiana* Lapparent de Broin, 2004 from the Early Cretaceous of Laos (Lapparent de Broin 2004); *Yehguia tatsuensis* (Yeh, 1963) from the Late Jurassic of China (Danilov and Parham 2006); Nanhsiungchelyidae: *Basilemys gaffneyi* Sullivan et al., 2012 (= *B. nobilis* Hay, 1911) from the Late Cretaceous of USA (Langston 1956; Sullivan et al. 2012); *B. praeclara* Hay, 1911 from the Late Cretaceous of USA (Brinkman and Nicholls 1993); *B. sinuosa* Riggs, 1906 from the Late Cretaceous of USA (Riggs 1906); *B. variolosa* (Cope, 1876) from the Late Cretaceous of Canada and USA (Langston 1956); *Hanbogdemys orientalis* (Sukhanov et Narmandakh, 1975) from the Late Cretaceous of Mongolia (Sukhanov and Narmandakh 1977); "*Zangerlia*" *dzamynchondi* Sukhanov et Narmandakh, 2006 from the Late Cretaceous of Mongolia (Danilov et

al. 2012); "*Z.*" *neimongolensis* Brinkman et Peng, 1996 from the Late Cretaceous of China (Brinkman and Peng 1996).

The phylogenetic analysis of the clade Adocusia was performed based on the character/taxon matrix of Danilov and Syromyatnikova (2009a, b), with additions from Syromyatnikova (2011). The character/taxon matrix was changed in the following ways: we added *Adocus planus, A. bossi* and *A. kirtlandius* to our analysis (*A. bossi* and *A. kirtlandius* were added since they are among the best-known North American members of the genus *Adocus* being represented by most parts of the shell); and we added to the analysis two additional characters: 76, width of vertebral 5: (0) as wide as or wider than more anterior vertebrals; (1) narrower than more anterior vertebrals; 77, posterior extension of the epiplastra: (0) weak, epiplastra extend posteriorly for 1/3 or less of the entoplastron length; (1) strong, epiplastra extend posteriorly for more than 1/3 of the entoplastron length. The width of vertebral 5 varies in adocids from relatively wide, as wide as or wider than more anterior vertebrals in Shachemydinae Nessov et Khosatzky, 1977 (see Danilov et al. 2007; Syromyatnikova 2011), to relatively narrow, narrower than more anterior vertebrals in most Adocinae Cope, 1870 (= *Adocus*), except *A. hesperius*. The only member of the outgroup in our analysis, in which this character is clearly observable (*Xinjiangchelys tianshanensis* Nessov, 1995), as well as nanhsiungchelyids, has vertebral 5 wider than more anterior vertebrals. The posterior extension of the epiplastra in adocusians can be weak (77(0); *Yehguia tatsuensis*, Shachemydinae) or strong (77(1) Adocinae, Nanhsiungchelyidae). The members of the outgroup which can be scored for this character (*Xinjiangchelys levensis* (Sukhanov et Narmandakh, 2006) and *X. tianshanensis*) demonstrate the weak condition. The new characters were added to the analysis to better distinguish *Adocus* from other adocids. See Appendix 1 for distribution of these new characters and Appendix 2 for characters coded for *Adocus planus, A. bossi,* and *A. kirtlandius*. The final data matrix includes 77 osteological characters for 26 taxa. Our updated matrix was assembled using NDE 0.5.0 (Page 2001) and analyzed with NONA ver. 2 and Winclada ver. 1.00.08 by Ratchet algorithm with 1000 iterations. Characters were left unordered and considered reversible and of equal weight. Bremer supports were calculated using Autodecay 4.0.1 (Eriksson 1998).

SYSTEMATICS

ADOCIDAE COPE, 1870

Adocus Cope, 1868

Adocus planus (Sukhanov et Narmandakh, 2006)

(Fig. 1)

Shineusemys plana: Sukhanov, 2000, p. 337, fig. 17.21 (unavailable name); Sukhanov and Narmandakh, 2006, p. 124.

Adocus planus: Danilov et al., 2011, p. 103, 112, 127.

Holotype. PIN 4636-1, partial shell with an almost complete plastron and few carapace fragments on the steinkern; Shine Us Khuduk (= Shine Us Khudag), Dornogov Aimag (Eastern Gobi), Mongolia; lower part of the Bainshire Formation, Cenomanian – early Turonian, Upper Cretaceous.

Material. In addition to the holotype, "numerous isolated plates" (Sukhanov 2000; see Introduction).

Diagnosis. A species of *Adocus* which can be differentiated from other species of the genus by the following characters: smaller shell size (about 300 mm); shortened plastral bridge; abdominals shorter than femorals; smaller size of inframarginals 1 (except *A. beatus*); shortened inframarginals 3 (except *A. amtgai* and "*A.*" *kazachstanica*). For more detailed comparison see Table 1.

Description. The shell is represented by an almost complete plastron and few carapace fragments on the steinkern. The estimated length of the shell was up to 300 mm, and its width, about 200 mm. The plastron made up about 80% of the carapace length and almost reached the carapace rim anteriorly. The surface of the plastron is covered by the typical adocid sculpturing, consisting of relatively small and regular grooves and pits (see Danilov et al. 2011). The scute sulci are narrow and shallow.

The carapace is almost completely missing (except for a small fragment of right costal 4 on the dorsal surface of the specimen and a small fragment of peripheral 6 visible on the ventral surface of the specimen, see below), but some of its characters can be revealed from the imprints on the steinkern of the shell. These are imprints of part of the nuchal, neural 4, suprapygal 2, part of the pygal, costals 2–5 and parts of all peripherals, except peripherals 1–3. The nuchal seems to have concave anterolateral borders. Neural 4 was hexagonal, short-sided anteriorly and relatively narrow. Suprapygal 1, presumably, was trapezoidal or

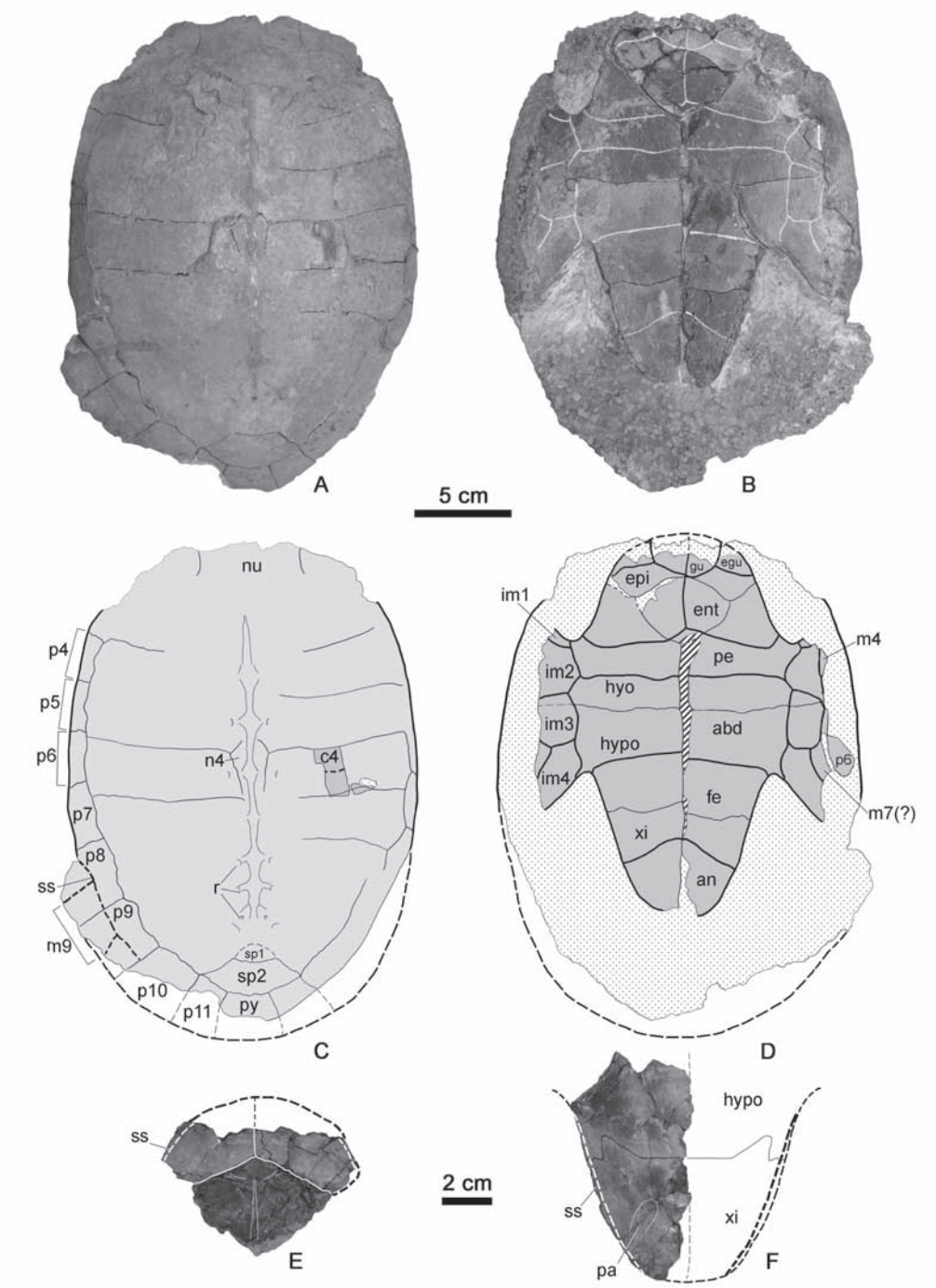

Fig. 1. *Adocus planus* (Sukhanov et Narmandakh, 2006), PIN 4636-1, holotype; Shine Us Khuduk locality (=Shine Us Khudag), Dornogov Aimag (Eastern Gobi), Mongolia; lower part of the Bainshire Formation, Cenomanian – early Turonian, Upper Cretaceous: A – dorsal view; B – ventral view; C – explanatory drawing of A; D – explanatory drawing of B; E – epiplastra + entoplastron, dorsal view; F – xiphiplastron + fragment of hypoplastron, dorsal view. Abbreviations: abd – abdominal; an – anal; c – costal; egu – extragular; ent – entoplastron; epi – epiplastron; fe – femoral; gu – gular; hyo – hyoplastron; hypo – hypoplastron; im – inframarginal; m – marginal; n – neural; nu – nuchal; p – peripheral; pa – area for pelvic attachment; pe – pectoral; py – pygal; r – ribhead; sp – suprapygal; ss – skin-scute sulcus; xi – xiphiplastron. Arabic numerals designate element numbers; tentative sutures are shown with dashed lines; matrix is shown with punctate shading, carapace core is shown with light grey, bones are shown with dark grey, broken surfaces are indicated by hatched lines.

triangular. Suprapygal 2 was wide hexagonal with concave anterior and anterolateral borders and convex posterior and posterolateral borders. Suprapygal 2 reached peripherals 10 laterally. The pygal was wider posteriorly than anteriorly, but its precise length cannot be revealed from the imprint. Costals 2, 4 and 5 were longer laterally than medially, whereas costal 3 was slightly longer medially than laterally. The small fragment of right costal 4 (from the middle part of the plate) shows the poorly visible interpleural sulcus. The ribheads of costals 3–8 were weak. The rib thickenings of the costals were also weak. Both latter characters are diagnostic for adocids (see Danilov and Syromyatnikova 2008, 2009a, b). Based on imprints of peripherals 8 and 10, the posterior peripherals probably were expanded (wider than long). A small fragment of peripheral 6 is visible on the ventral surface of the shell. Imprints of internal portions of marginals (7–10) are discernable within peripherals 8 and 9. The skin-scute sulcus is located in the middle part of the mentioned peripherals.

The plastron is almost completely preserved, except for the anterior edge of the anterior lobe. The anterior lobe of the plastron is about twice as wide as long. Presumably, the anterior lobe reached the carapace rim. The posterior lobe gradually narrows and is rounded posteriorly (the anal notch is absent). The posterior lobe is longer and narrower at the base than the anterior lobe. The length of the posterior lobe is about 34% of the plastron length, which is similar to those of *A. bossi* and *Adocus* sp. 2. Among *Adocus*, the length of the posterior lobe of the plastron varies from 28% in *Adocus* sp. 1 to 38% in *A. beatus* (see Table 1). The length of the plastral bridge is about 35% of the plastron length, which is similar to those of *Adocus amtgai*. In the other species of *Adocus*, the length of the bridge is usually greater, but does not exceed 50% of the plastron length, contrary to Nanhsiungchelyidae (see Table 1). The epiplastra are missing their anterior borders and were longer than figured by Sukhanov (2000, fig. 17.21). They strongly extend posteriorly as in other *Adocus*. The entoplastron is relatively large and tetragonal, wider than long and not shortened and/or truncated anteriorly. On its dorsal surface, there is a Y-shaped system of ridges. The hyoplastra and hypoplastra contribute equally to the bridge length. The xiphiplastra are longer than wide, narrowed posteriorly. The length of the xiphiplastra is about 76% of the posterior lobe length along the midline. A similar relative length of the xiphiplastra is known in *Adocus amtgai,* whereas in other species of the genus this value is variable (see Table 1). On the dorsal surface, the xiphiplastra bear an oval area for the pelvic attachment.

The plastral scutes are represented by a complete set including the gulars, extragulars, humerals, pectorals, abdominals, femorals, anals and four pairs of inframarginals. The gulars touch the entoplastron, but do not overlap it. The sulcus between the gular scutes coincides with the interepiplastral suture. In most other *Adocus*, the gulars overlap the entoplastron. The extragulars are relatively large, covering about 1/3 of the external surface of the epiplastra, with the medial borders being distinctly shorter than the length of the epiplastral symphysis. The lateral borders of the extragulars reach the level of the anterior border of the entoplastron (on the left side) or even behind it (on the right side) posteriorly. The extragulars of *A. beatus* and *A. bossi* are of similar shape, whereas in *A. amtgai* the lateral borders of the extragulars extend further posteriorly. The pectorals are relatively short along the midline (their medial length is about 12% of the plastron length), overlapping the entoplastron, becoming even shorter (forming a waist) in the lateral portion. The pectorals contribute to the rim of the axillary notch, as in other adocids. The pectorals of other species of *Adocus* are variable in either overlapping (*A. annexus* and *A. beatus*) or not overlapping the entoplastron (*A. agilis*, *A. bossi*, *A. kirtlandius*, *A. substrictus* and "*A.*" *orientalis*). The abdominals are shorter than the femorals (the ratio of the length of abdominals to the length of the femorals is about 0.9) and contribute to the rim of the inguinal notches. Among the members of *Adocus*, the closest femoral/abdominal ratio known occurs in *A. beatus* (1.1), whereas in other species it is greater, i.e. the abdominals are distinctly longer than the femorals (see Table 1). The femoral-anal sulcus is directed posterolaterally from the midline and slightly S-shaped. The midline sulcus is not observable and probably coincides with the midline suture. The inframarginals are represented by four pairs of relatively wide elements, which extend slightly onto peripherals (except inframarginals 1 and 2 of the left side). Inframarginal 1 is small, wider than long, and contributes to the axillary rim. Inframarginals 2–4 are larger than inframarginal 1 and about the same size as each other. Inframarginal 2 contacts the pectoral and abdominal medially and marginal 4 laterally (visible on the left side). Inframarginals 3 and 4 contact the abdominal

Table 1. Comparison of some Late Cretaceous species of *Adocus* in shell characters (after Syromyatnikova and Danilov (2009) with modifications).

Characters	*A. aksary*	*A. amtgai*	*A. beatus*	*A. bossi*	*A. kirtlandius*	*A. planus*	*Adocus* sp. 1	*Adocus* sp. 2
Length of the shell	400 mm*	400 mm	500 mm	700 mm*	500 mm*	300 mm*	?	500 mm
Nuchal emargination	Weak	Weak	Weak or absent	Absent	?	?	Weak or absent	?
Number of neurals	6	?	6 or 7	6	6	?	?	?
Neural 6	Shortened	?	Not shortened	Shortened	Shortened	?	Not shortened	?
Number of suprapygals	2	2	2	1	2	2	?	?
Cervical	Lens- or trapezoid-shaped, expanded anteriorly or posteriorly	Trapezoid-shaped, expanded anteriorly	Trapezoid-shaped, expanded anteriorly	Trapezoid-shaped, expanded posteriorly	?	?	?	?
Vertebral 5	Narrow	?	Relatively wide	Narrow	Relatively wide	?	?	?
Pleurals 2–4	?	Narrow (width makes up 30% of length)	Wide (width makes up 60% of length)	Wide (width makes up 60% of length)	Wide (width makes up 60% of length)	?	Wide (width makes up 60% of length)	?
Marginals overlapping onto costals	Beginning with marginal 3 or 4	Beginning with marginal 4	Beginning with marginal 5	Beginning with marginal 5	Beginning with marginal 5	?	Beginning with marginal 5	?
Width of anterior border of epiplastron	Less than length of epiplastral symphysis	More than length of epiplastral symphysis	More than length of epiplastral symphysis	More than length of epiplastral symphysis	?	?	More than length of epiplastral symphysis	More than length of epiplastral symphysis
Dorsal surface of epiplastron	Concave	?	?	?	?	?	?	?
Ratio of length of posterior lobe to plastron length	?	37%	38%	32%	?	34%	28%	35%

Table 1. *Continued.*

Characters	*A. aksary*	*A. amtgai*	*A. beatus*	*A. bossi*	*A. kirtlandius*	*A. planus*	*Adocus* sp. 1	*Adocus* sp. 2
Ratio of length of bridge to plastron length	?	38%	40%	41and 46%	?	35%*	49%	40%
Ratio of length of xiphiplastron to length of posterior lobe	?	75%	73%	79%	72%	76%	67%	72%
Width of anterior border of gulars	Less than length of epiplastral symphysis	More than length of epiplastral symphysis	More than length of epiplastral symphysis	Variable	Equal to length of epiplastral symphysis	?	More than length of epiplastral symphysis	Less than length of epiplastral symphysis
Extension of gulars onto entoplastron	Present or absent	Present	Present or absent	Present	?	Absent	Present	Present
Ratio of length of extragular medial border to length of epiplastral symphysis	0.9	0.6	0.6	0.7	0.5	?	0.9	0.6
Pectorals extension onto the entoplastron	Present or absent	Present	Present	Absent	Absent	Present	Absent	Absent
Ratio of length of abdominals to length of femorals	?	1.6	1.1	2.9 and 1.5	1.3	0.9	2.1	1.4
Number of inframarginals	?	3 or 4 pairs	4 pairs	3 pairs	4 pairs	4 pairs	4 pairs	?
Inframarginals	?	Relatively wide	Relatively narrow	Relatively narrow	Relatively wide	Relatively wide	Relatively narrow	?
Inframarginal 1	?	Longer than wide	Wider than long	Longer than wide	Longer than wide	Wider than long	Longer than wide	Longer than wide
Inframarginal 3	?	Shortened	Elongated	Elongated	Elongated	Shortened	Shortened	?

Note: * – denotes estimated measurements.

Table 2. Measurements (in mm) of the plastron of *Adocus planus*; "–", element unmeasurable; "d" and "s" designate right and left measurements, respectively.

Plastron (length/width)	~204/158
Thickness of plastron (along midline near the hypo-xiphiplastral suture)	~5.5
Bridge (length)	70d, 70s
Anterior lobe (length/width at the base)	–/112
Posterior lobe (length/width at the base)	75/99
Entoplastron (length/width/thickness posteriorly)	38/52/~5
Hyoplastron (length medial)	155d, 37s
Hypoplastron (length medial)	52d, 56s
Xiphiplastron (length medial)	59d, 54s
Humerals (length medial)	28
Pectorals (length medial)	~26
Abdominals (length medial)	42d, 46s
Femorals (length medial)	48d, 43s
Anals (length medial)	38d, 40s

medially and marginal (7?) laterally. Inframarginal 3 spans the hyo-hypoplastral suture, but is not as strongly elongated as in most other *Adocus* (except *A. amtgai* and *"A." kazachstanica*). Inframarginal 4 is elongated posterolaterally and contributes largely to the inguinal rim. Overlapping of plastral scutes on to the dorsal surface of the plastral lobes (visible on the epiplastra and the posterior lobe; Fig. 1E, F) is weak or absent, as in other adocids.

For measurements of the plastral elements, see Table 2.

DISCUSSION

The reexamination of the holotype of *Adocus planus* allows us to present new images of this specimen (Fig. 1). Our observations and reconstruction differ from those previously published (e.g. Sukhanov 2000, fig. 17.21) in the following details; the precise shape of suprapygal 1 is unclear, the cervical scute is not observable as well as the position of the skin-scute sulcus on the posterior edge of the carapace, the epiplastra, gulars and extragulars were longer anteriorly, although the precise outline of the anterior border of the anterior plastral lobe remains unclear, the entoplastron is wider than long and more strongly overlapped by the pectorals, the axillary notches are shorter and the inguinal ones are longer. In addition, we report new details of the morphology of the costals and dorsal surface of the plastron (see Description).

The following characters support assignment of *Adocus planus* to the Adocidae: (1) adocid-type sculpturing, (2) narrow and shallow scute sulci, (3) weak ribheads, (4) weak rib thickenings of the costals, (5) relatively short plastral bridges (less than 50% of plastron length), (6) relatively long posterior plastral lobe (more than 30% of plastron length), (7) presence of the pectoral contribution to the axillary rim, and (8) absence of the overlapping of scutes on to the dorsal surface of plastral lobes. All these characters differentiate the Adocidae from the Nanhsiungchelyidae (see Danilov and Syromyatnikova 2008). Characters 1 and 2 represent adocid synapomorphies, whereas characters 3 and 4 unite all adocids except *Yehguia tatsuensis* (Danilov and Syromyatnikova 2009a, b). Although the main synapomorphy of *Adocus* (overlapping of the marginals onto the costals in the middle and posterior portions of the shell) is not observable in *A. planus*, this species is referred to *Adocus* based on similarity in several other characters, including; vertebral 5 narrower than more anterior vertebrals, strong posterior

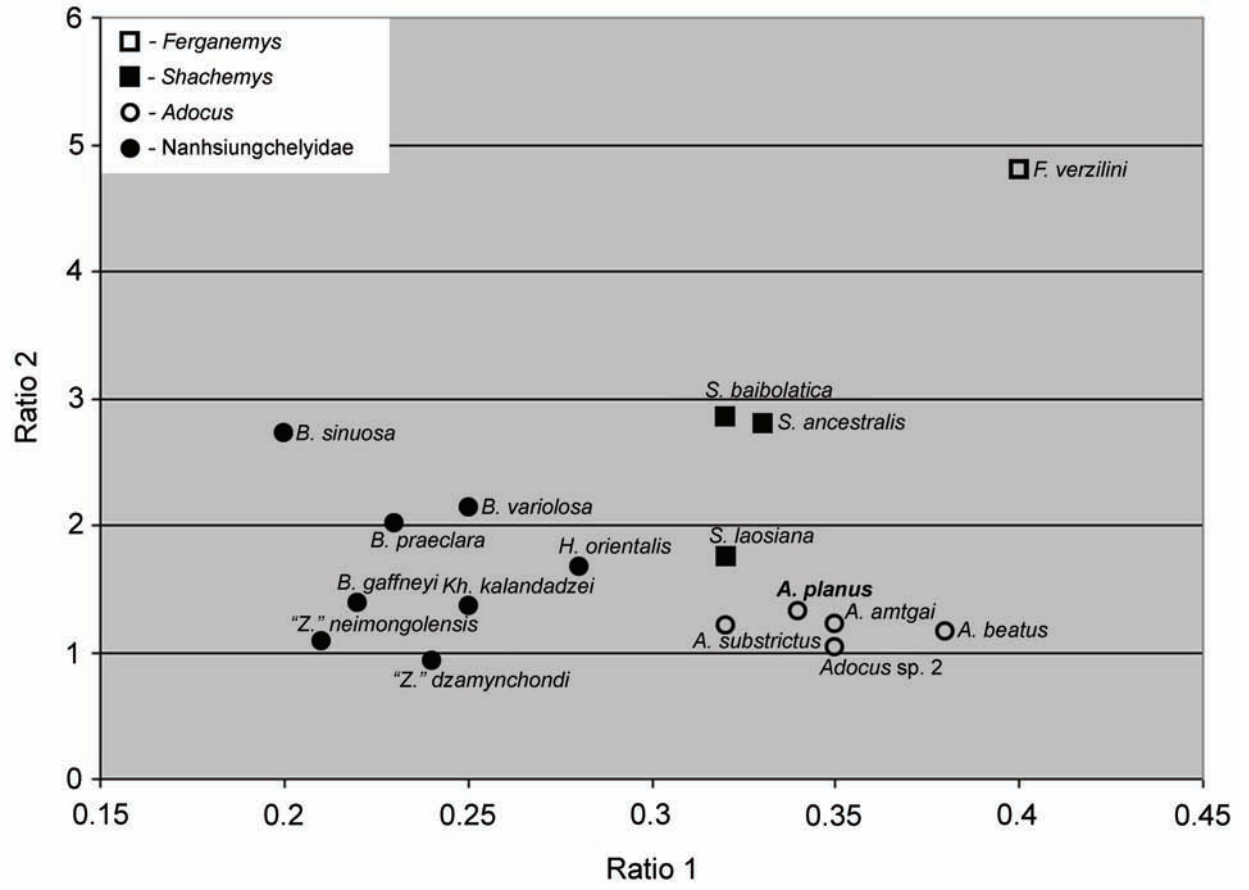

Fig. 2. Correlation between the ratio 1 (length of the posterior lobe/plastron length) and ratio 2 (length of the posterior lobe/distance between the posterior end of the plastron and the posterior rim of the carapace) in some Adocusia. The values of the ratios are the following (ratio 1/ratio 2): *Adocus amtgai* – 0.35/1.22; *A. beatus* – 0.38/1.16; *A. planus* – 0.34/1.33; *Adocus* sp. 2 – 0.35/1.04; *A. substrictus* – 0.32/1.20; *Ferganemys verzilini* – 0.40/4.8; *Shachemys ancestralis* – 0.33/2.80; *S. baibolatica* – 0.32/2.86; *S. laosiana* – 0.32/1.76; *Basilemys gaffneyi* – 0.22/1.39; *B. praeclara* – 0.23/2.02; *B. sinuosa* – 0.2/2.71; *B. variolosa* – 0.25/2.14; *Hanbogdemys orientalis* – 0.28/1.67; *Kharakhutulia kalandadzei* – 0.25/1.36; "*Zangerlia*" *dzamynchondi* – 0.24/0.93; "*Z.*" *neimongolensis* – 0.21/1.08.

extension of the epiplastron, and a relatively long distance between the posterior end of the plastron and the posterior rim of the carapace. The two former characters were discussed above (see Material and methods). The relatively long distance between the posterior end of the plastron and the posterior rim of the carapace is characteristic of *Adocus*, in which the ratio of the length of the posterior plastral lobe to this distance is 1.04–1.33 (Fig. 2). In the species of *Shachemys* and *Ferganemys verzilini* this distance is smaller and the same ratio is 1.76–2.86 and 4.80 respectively. In the Nanhsiungchelyidae, the same ratio varies from 0.93 to 2.71, but, as was mentioned above, this group is clearly differentiated from the Adocidae by the relatively shorter posterior lobe. *Adocus planus* is grouped together with other species of *Adocus* on the basis of the suggested ratio.

The genus *Shineusemys* was distinguished from other adocids by relatively shorter abdominals with their medial length less than that of the femorals (Sukhanov 2000). In addition, *Shineusemys* was distinguished from *Adocoides* (here *Adocus amtgai*) in relative length of the plastral bridges and size of the epiplastra (Sukhanov 2000). The abdominals of *A. planus* are shorter than the femorals along the midline (the abdominal/femoral ratio is 0.9). In other species of *Adocus*, the abdominals are longer than the femorals and the abdominal/femoral ratio varies from 1.1 to 2.9 (Table 1). The same ratio is 1.2 in *Ferganemys verzilini* and 1.00–1.35 in species of *Shachemys*. The

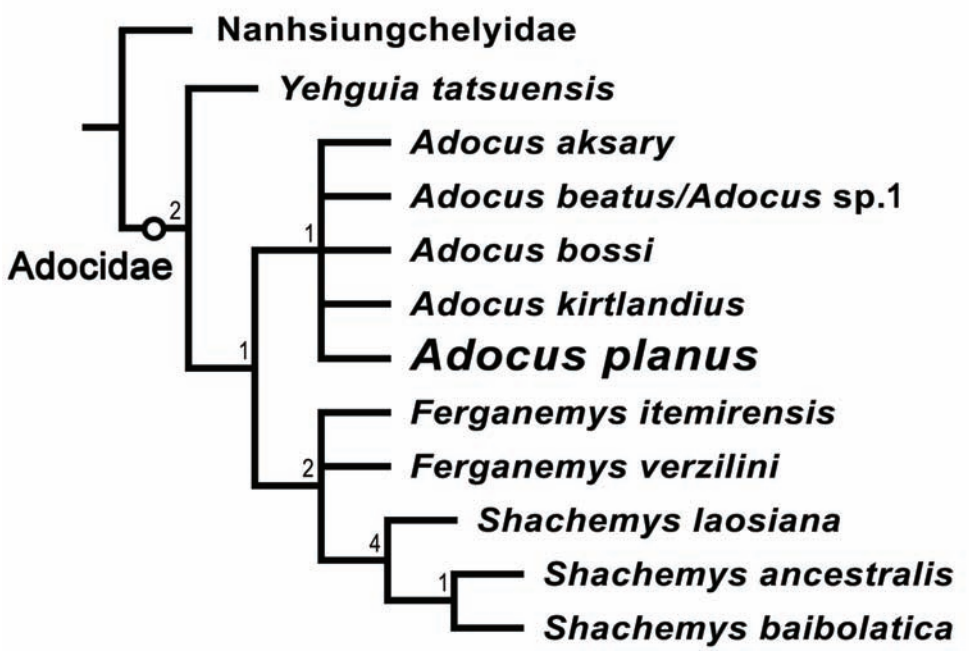

Fig. 3. A strict consensus of 94 phylogenetic trees showing hypothesized position of *Adocus planus* (see Discussion for description of the tree). Outgroups and nanhsiungchelyid taxa are not shown. Numbers designate Bremer support indices.

length of the plastral bridge in *A. planus* is about 35% of the plastron length. In other species of *Adocus*, this value varies from 38% to 49%, being the smallest in *A. amtgai* (see Table 1). In other adocids, this value is 38% in *Ferganemys verzilini* and 40–46% in species of *Shachemys*. The size of the epiplastra is unclear in *A. planus* since its anterior portion is missing and, therefore, this character cannot be used for comparison. Thus, all the characters previously used for distinguishing *Shineusemys* from other adocids are either variable in adocids or unknown. For this reason, we do not consider *Shineusemys* to be a separate genus of adocids and place it in the synonymy with *Adocus*.

Within *Adocus*, *A. planus* is most similar to *A. amtgai* in the length of the plastral bridge, length of the xiphiplastron, relatively wide inframarginals, and shortened inframarginals 3 (for comparison with other species of *Adocus* see Table 1). Both *A. amtgai* and *A. planus* come from the same Bainshire Formation of Mongolia, but are from different stratigraphic levels: *A. planus* is from the lower part (Cenomanian – early Turonian) and *A. amtgai* is from the upper part (late Turonian – Santonian). Thus, the morphological similarity and close provenance of *A. amtgai* and *A. planus* probably indicate close evolutionary relationships of these species. These relationships should be reviewed further after a more detailed study of *Adocus amtgai* (Syromyatnikova et al. in prep.) and reexamination of the additional material of *Adocus planus*.

The result of our phylogenetic analysis consists of 94 trees with 147 steps, a consistency index of 0.57 and a retention index of 0.76. The resulting strict consensus tree is given in Fig. 3. This tree demonstrates that *A. planus* is placed in the *Adocus* clade, thus confirming the assignment of this species to the genus *Adocus*. Within the *Adocus* clade all species (both from Asia and North America) form an unresolved polytomy. The *Adocus* clade is supported by the following synapomorphies: 49(1), marginals overlapping onto costals at the middle and posterior part of carapace; 76(1), vertebral 5 narrower than more anterior vertebrals; 77(1), strong posterior extension of the epiplastra. The topology of the rest part of the tree agrees with previous analyses (Danilov and Syromyatnikova 2009a, b; Syromyatnikova 2011). Further resolution of the phylogenetic position of *A. planus* will require additional material and detailed study of other species of *Adocus* from the Late Cretaceous of Asia and North America.

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Appendix 1. Details about characters and taxa added to the character/taxon matrix of Danilov and Syromyatnikova (2009a, b) with additions from Syromyatnikova (2011).

Character 76. Vertebral 5: (0) as wide as or wider than more anterior vertebrals; (1) narrower than more anterior vertebrals. **Codings**: *Xinjiangchelys levensis*, ?; *X. tianshanensis*, 0; *Carettochelys insculpta*, –; *Apalone ferox*, –; *Yehguia tatsuensis*, ?; *Adocus aksary*, 1; *A. beatus/Adocus* sp. 1; *A. bossi*, 1; *A. kirtlandius,* 1; *A. planus,* 1; "*Ferganemys*" *itemirensis*, 0; *F. verzilini*, 0; *Shachemys ancestralis*, 0; *S. baibolatica*, 0; *S. laosiana*, 0; *Kharakhutulia kalandadzei*, ?; *Zangerlia testudinimorpha*, 0; *Z. neimongolensis*, 0; *Z. ukhaachelys*, ?; *Hanbogdemys orientalis*, 0; *Anomalochelys angulata*, ?; *Nanhsiungchelys wuchingensis*, ?; *Basilemys variolosa*, 0; *B. gaffneyi*, 0; *B. sinuosa*, 0; *B. praeclara*, ?.

Character 77. Posterior extension of the epiplastra: (0) weak, epiplastra extend posteriorly for 1/3 or less of the entoplastron length; (1) strong, epiplastra extend posteriorly for more than 1/3 of the entoplastron length. **Codings**: *Xinjiangchelys levensis*, 0; *X. tianshanensis*, 0; *Carettochelys insculpta*, –; *Apalone ferox*, –; *Yehguia tatsuensis*, 0; *Adocus aksary*, 1; *A. beatus/Adocus* sp. 1; *A. bossi*, 1; *A. kirtlandius,* 1; "*Ferganemys*" *itemirensis*, 0; *F. verzilini*, 0; *Shachemys ancestralis*, 0; *S. baibolatica*, 0; *S. laosiana*, 0; *Kharakhutulia kalandadzei*, 1; *Zangerlia testudinimorpha*, ?; *Z. neimongolensis*, 1; *Z. ukhaachelys*, ?; *Hanbogdemys orientalis*, 1; *Anomalochelys angulata*, ?; *Nanhsiungchelys wuchingensis*, 1; *Basilemys variolosa*, 1; *B. gaffneyi*, 1; *B. sinuosa*, 1; *B. praeclara*, 1.

Appendix 2. Characters coded for *Adocus planus*, *A. bossi*, and *A. kirtlandius* and added to the character/taxon matrix of Danilov and Syromyatnikova (2009a, b) with additions from Syromyatnikova (2011).

Adocus planus: ?????????? ?????????? ??????00?0 ???010011? 0??????0?? ?100001020 0000100?00 1001??1

Adocus bossi: ?????????? ?????????? ??????0?00 ?101000??? 0000000010 010000100? 001000001? 1001?11

Adocus kirtlandius: ?????????? ?????????? ??????0??? ?100000??? 0?00000010 01000010?? ???001001? 1001?11