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NEW MATERIAL AND PHYLOGENETIC POSITION OF *ADOCUS BOSTOBENSIS*, A POORLY KNOWN ADOCID TURTLE FROM THE LATE CRETACEOUS OF KAZAKHSTAN

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ABSTRACT

This paper presents a description of a new material of *Adocus bostobensis*, a poorly known adocid turtle from the Late Cretaceous of Kazakhstan. The new material of *A. bostobensis* comes from the Bostobe Formation (Santonian – early Campanian) of Shakh-Shakh II locality (northeastern Aral Sea area, Kazakhstan) and includes about 30 shell fragments and several elements of non-shell postcrania, potentially, from a single individual. This material allows us to reveal some previously unknown characters of *Adocus bostobensis*, improve its diagnosis and include this species in a phylogenetic analysis of Adocusia (Adocidae + Nanhsiungchelyidae) for the first time. The phylogenetic analysis places *A. bostobensis* in a clade with *A. aksary* and *A. amtgai* (both from the Late Cretaceous of Asia). Finally, our study demonstrates presence of at least two different lineages of *Adocus* (*A. bostobensis* and *A. foveatus*) in the Santonian of Western Asia.

Key words: Adocidae, *Adocus*, Asia, Late Cretaceous, Kazakhstan, turtles

НОВЫЙ МАТЕРИАЛ И ФИЛОГЕНЕТИЧЕСКОЕ ПОЛОЖЕНИЕ *ADOCUS BOSTOBENSIS*, ПЛОХО ИЗВЕСТНОЙ АДОЦИДНОЙ ЧЕРЕПАХИ ИЗ ПОЗДНЕГО МЕЛА КАЗАХСТАНА

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РЕЗЮМЕ

Эта статья представляет описание нового материала по *Adocus bostobensis*, плохо известной адоцидной черепахи из позднего мела Казахстана. Новый материал происходит из бостобинской свиты (сантон – ранний кампан) местонахождения Шах-Шах II (Северо-Восточное Приаралье, Казахстан) и включает около 30 фрагментов панциря и некоторые кости непанцирного посткрания, предположительно, от одного индивида. Этот материал позволяет нам выявить ранее неизвестные признаки *A. bostobensis*, улучшить его диагноз и впервые включить этот вид в филогенетический анализ Adocusia (Adocidae + Nanhsiungchelyidae). Филогенетический анализ помещает *A. bostobensis* в одну кладу с *A. aksary* и *A. amtgai* (оба из позднего мела Азии). Наконец, наше исследование демонстрирует присутствие не менее двух линий рода *Adocus* (*A. bostobensis* и *A. foveatus*) в сантоне Западной Азии.

Ключевые слова: Adocidae, *Adocus*, Азия, поздний мел, Казахстан, черепахи

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INTRODUCTION

Adocus bostobensis Syromyatnikova et Danilov, 2009 is a poorly known Asiatic representative of the genus *Adocus* Cope, 1868 (Adocidae Cope, 1870). This species was described based on a few isolated shell plates from several localities (Akkurgan, Baybishe I, Buroynak I and II and Shakh-Shakh) of the Bostobe Formation (Santonian – early Campanian) of northeastern Aral Sea area, Kazakhstan (see Syromyatnikova and Danilov 2009).

Recently, new material of *A. bostobensis* was collected from Shakh-Shakh II locality, northeastern Aral Sea area, Kazakhstan. This material includes about 30 shell fragments (mostly carapace), an ilium fragment and a complete ischium, which, probably, belong to a single individual. In this paper we provide a detailed description of this new material, improve the diagnosis of *A. bostobensis* and include this species in a phylogenetic analysis.

Institutional abbreviations. YPM – Yale Peabody Museum, New Haven, USA; ZIN PH – Paleoherpeto-logical collection, Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia.

MATERIAL AND METHODS

In addition to the material described below, our study relies on published data and personal observations on the following species of *Adocus*: *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. 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. dzhurtasensis* Syromyatnikova et Danilov 2009 from the Late Cretaceous of Kazakhstan (Nessov 1995; Syromyatnikova and Danilov 2009); *A. foveatus* Nessov et Khosatzky in Khosatzky et Nessov, 1977 from the Late Cretaceous of Tajikistan (Khosatzky and Nessov 1977; Syromyatnikova and Danilov 2009); *A. hesperius* Gilmore, 1919 from the Paleocene of USA (Gilmore 1919); *A. kizylkumensis* Nessov, 1981 from

the Late Cretaceous of Uzbekistan (Nessov 1981; Syromyatnikova and Danilov 2009); *A. planus* (Sukhanov et Narmandakh, 2006) from the Late Cretaceous of Mongolia (Sukhanov 2000; Syromyatnikova et al., 2012); and *A. substrictus* Hay, 1908 from the Paleocene of USA (Hay 1908).

In order to determine the phylogenetic position of *Adocus bostobensis* we performed a phylogenetic analysis of Adocusia Danilov et Parham, 2006 (Adocidae + Nanhsiungchelyidae Yeh, 1966, using the character/taxon matrix of Danilov and Syromyatnikova (2009a, b) with additions from Syromyatnikova (2011), and Syromyatnikova et al. (2012) (see Appendix 1 for characters coded for *A. bostobensis*). The final data matrix includes 78 osteological characters for 27 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

Family Adocidae Cope, 1870

Subfamily Adocinae Cope, 1870

Genus *Adocus* Cope, 1868

Adocus bostobensis

Syromyatnikova et Danilov, 2009

(Fig. 1)

See Syromyatnikova and Danilov (2009) for synonymies and references.

Holotype. ZIN PH 1/94, nuchal fragment; Baybishe locality (= Baybishe I; Nessov 1997, p. 111), northeastern Aral Sea area, Kazakhstan; Bostobe Formation, Santonian – early Campanian.

Previously referred material. See Syromyatnikova and Danilov (2009).

Newly referred material. ZIN PH 105/10, even neural; ZIN PH 106/10 and 107/10, distal parts of even costals; ZIN PH 108/10, fragment of left costal 8; ZIN PH 109/10, left peripheral 1; ZIN PH 110/10, right peripheral 3; ZIN PH 111/10, left peripheral 4; ZIN PH 112/10, fragment of right peripheral 8; ZIN PH 113/10, fragment of right peripheral 11; ZIN PH 114/10, fragment of left hyoplastron; ZIN PH 115/10, fragment of right ilium; ZIN PH 116/10,

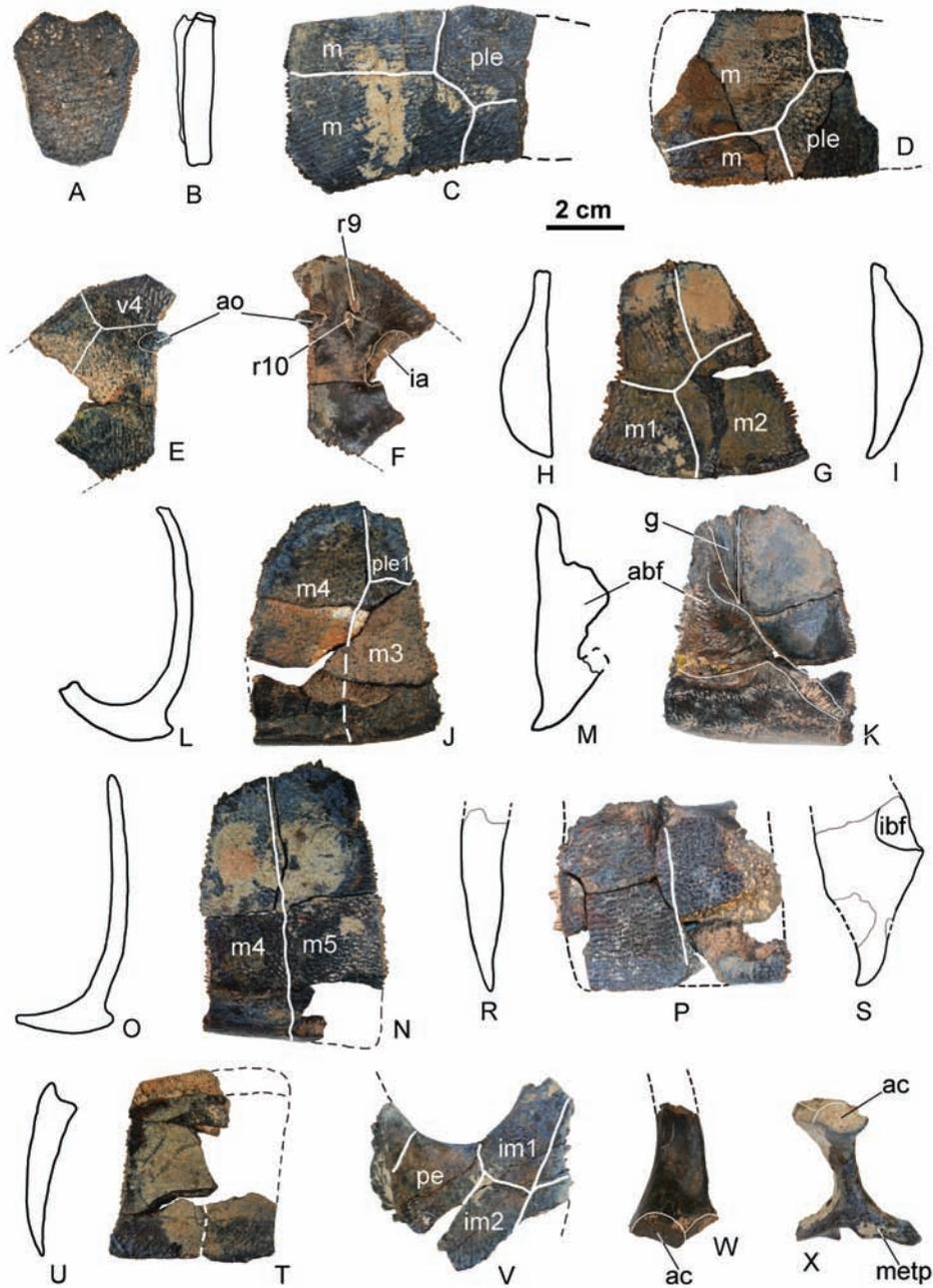


Fig. 1. *Adocus bostobensis*, shell fragments, Shakh-Shakh II locality, northeastern Aral Sea area, Kazakhstan; Bostobe Formation, Santonian – early Campanian: A, B – ZIN PH 105/10, even neural in dorsal (A) and lateral (B) views; C – ZIN PH 106/10, distal part of even costal in dorsal view; D – ZIN PH 107/10, distal part of even costal in dorsal view; E, F – ZIN PH 108/10, fragment of costal 8 in dorsal (E) and ventral (F) views; G–I – ZIN PH 109/10, peripheral 1 in dorsal (G), anterior (H) and posterior (I) views; J–M – ZIN PH 110/10, peripheral 3 in dorsal (J), ventral (K), posterior (L) and anterior (M) views; N, O – ZIN PH 111/10, peripheral 4 in dorsal (N), anterior (O) views; P–S – ZIN PH 112/10, fragment of peripheral 8 in dorsal (P), posterior (R) and anterior (S) views; T, U – ZIN PH 113/10, fragment of peripheral 11 in dorsal (T) and posterior (U) views; V – ZIN PH 114/10, fragment of hyoplastron in ventral view; W – ZIN PH 115/10, right ilium in lateral view; X – ZIN PH 116/10, left ischium in lateral view. A, C, D–G, J, K, N, P, T, V–X – photographs. B, H, I, L, M, O, R, S, U – drawings. **Abbreviations:** abf – axillary buttress fossa; ac – acetabulum; ao – additional ossification; c – costal; g – groove for free rib; ibf – inguinal buttress fossa; im – inframarginal; m – marginal; metp – metischial process; p – peripheral; pe – pectoral; ple – pleural; r – ribhead; v – vertebral. Arabic numerals designate element numbers; tentative sutures are shown with dashed lines.

left ischium; Shakh-Shakh II locality, northeastern Aral Sea area, Kazakhstan; Bostobe Formation, Santonian–early Campanian. All specimens are believed to belong to a single individual, as they were all collected all together on a small spot and complement each other.

Differential diagnosis (emended). A species of *Adocus* that can be differentiated from other members of *Adocus* by larger shell size (estimated at 100 cm). In addition, it can be differentiated from other Asiatic species of the genus by shape of the cervical (narrow and slightly widened in its posterior third) and absence of suprapygal 1; from *A. aksary*, *A. kizylkumensis* and *A. foveatus* by wider marginals and narrower pleurals; from *A. dzhurtasensis* by thinner elements of the shell; from *A. planus* by larger inframarginal 1, narrower inframarginal 2, and inframarginals 1 and 2 distant from the plastron-carapace suture; from *A. foveatus* and North American species of the genus by overlapping of marginals onto costals beginning with marginal 4; from *A. bossi* and *A. kizylkumensis* by presence of the nuchal emargination.

Description of the new material. All new specimens are believed to belong to a single individual with the length of the shell estimated at about 70 cm. The shell plates are covered with a characteristic adocid sculpturing with relatively small and regular pits; shell sulci are narrow and shallow (characters of adocids; Danilov and Syromyatnikova 2008, 2009a, b; Danilov et al. 2011).

The neurals are represented by one even element (ZIN PH 105/10; Fig. 1A, B), which is hexagonal short-sided anteriorly, relatively wide (ratio of the neural width to its length is 0.8) and thin, similar in proportions with neurals of such species as *A. aksary*, *A. amtgai*, *A. beatus* and *A. kizylkumensis*. Wide and thin neurals of *Adocus bostobensis* have also been previously described earlier (ZIN PH 14/94 and 6/95; Syromyatnikova and Danilov 2009).

The costals are represented by several fragments, including two distal parts of even costals (ZIN PH 106/10 and 107/10; Fig. 1C, D) and the medial part of the left costal 8 (ZIN PH 108/10; Fig. 1E, F). The rib thickenings of the costals are weak (adocid synapomorphy; see Danilov and Syromyatnikova 2009a, b). The fragment of costal 8 has a straight medial border and a short contact with the right costal 7 anteromedially. Internally, it bears ribheads 9 and 10 and a wide, thickened attachment for the ilium. At the medial border of costal 8, there is an additional

ossification represented by a small oval element. The straight medial border of costal 8 suggests the absence of suprapygal 1.

The peripherals are represented by a complete peripheral 1, complete right and partial left peripherals 3 and 4, partial peripheral 8, and peripheral 11. Peripheral 1 (ZIN PH 109/10; Fig. 1G–I) is trapezoid in dorsal view, its medial length is about twice as short as the length of the free edge. The free edge of peripheral 1 is angled in the cross-section and slightly upturned posteriorly as in most other species of *Adocus*. There is no notch for a costiform-like process on the internal surface of peripheral 1 as is known in *A. beatus* (Hay 1908, fig. 300). In general, the morphology of ZIN PH 109/10 corresponds to the previously described peripheral 1 (ZIN PH 1/96; Syromyatnikova and Danilov 2009). Peripheral 3 (Fig. 1J–M) is almost rectangular. Its free edge is angled in the cross-section, and clearly upturned. Internally, peripheral 3 bears a triangular-shaped groove for the free rib of costal 1. The fossa for the axillary buttress is deep and rounded, occupying the anterior half of peripheral 3. The presence of musk ducts known in some *Adocus* spp. is unclear. Peripheral 4 (Fig. 1N–O) is rectangular, L-shaped in cross-section, and with an upturned free edge. The dorsal (carapacial) plates of peripherals 3 and 4 are more than twice as wide as the ventral (plastral) ones. Peripheral 8 (Fig. 1P–S) has an angled and slightly upturned free edge. Peripheral 8 has an oblique posterior sutural surface that suggests a strong overlapping of peripheral 8 with peripheral 9. The similar morphology of peripheral 8 has been reported for this species earlier (Syromyatnikova and Danilov 2009). The fossa for the inguinal buttress is oval-shaped, occupying the bulge of peripheral 8. Peripheral 11 (Fig. 1T, U) is narrower than bridge peripherals 3 and 4 and thickened medially. Its free edge is angled in cross-section.

The hyoplastron fragment (Fig. 1V) does not show any specific differences in morphology from those of other *Adocus* spp. However, it allows for determination of the some characters of the plastral scalation (see below).

Marginals 1 and 2 are relatively narrow (Fig. 1G), occupying approximately the lateral half of peripheral 1, whereas marginal 3 (Fig. 1J) is wider, occupying about the lateral two thirds of peripheral 3. More posterior marginals strongly overlap onto costals, probably, for more than one-third of their lateral width. The similar degree of overlapping of the

marginals onto costals is known in *A. amtgai*, which has significantly wide marginals 4–12 and very narrow pleurals 2–4.

As visible on the hyoplastron fragment, the pectoral contacts inframarginal 1 and 2 laterally and widely contributes to the rim of the axillary notch (Fig. 1V). Inframarginals 1 and 2 are relatively narrow and distant from the plastron-carapace suture.

The ilium fragment (Fig. 1W) is represented by its proximal (acetabular) portion. The ischium (Fig. 1X) is completely preserved. The metischial process is long and similar in morphology to those of *Adocus amtgai* and *Adocus* sp. from the Late Cretaceous of USA (Meylan and Gaffney 1989).

DISCUSSION

The material described in this paper is assigned to Adocidae based on adocid sculpturing with relatively small and regular grooves and pits, shallow and narrow scute sulci, weak ribheads and rib thickenings of the costals and presence of the pectoral contribution to the axillary rim (Danilov and Syromyatnikova 2008, 2009a, b; Danilov et al. 2011). This material is assigned to *Adocus* based on the marginals overlapping onto the costals in the middle and posterior parts of the carapace (Danilov and Syromyatnikova 2009a, b; Syromyatnikova and Danilov 2009). This material is assigned to *Adocus bostobensis* based on similar morphology of the comparable shell plates and because the new material comes from the same Bostobe Formation of northeastern Aral Sea area of Kazakhstan as the type material of this species (Syromyatnikova and Danilov 2009).

Study of the new material allows us to reveal some previously unknown characters of *Adocus bostobensis* and improve its diagnosis (see Systematics section). Among newly revealed characters of *A. bostobensis* are the absence of suprapygal 1, overlapping of the marginals onto costals beginning with marginal 4, and relatively wide marginals and narrow pleurals, relatively narrow inframarginals 1 and 2 that are distant from the plastron-carapace suture. The absence of suprapygal 1 is known in some North American species (*A. bossi*, *A. hesperius* and *A. substrictus*), whereas other Asiatic species either have suprapygal 1 (*A. aksary*, *A. amtgai*, *A. foveatus* and *A. planus*) or are unknown for this character (*A. dzhurtasensis* and *A. kizylkumensis*). The overlapping of the marginals onto the costals beginning with marginal 3

or 4 is known in some Asiatic species of *Adocus* (*A. aksary* and *A. amtgai*), whereas other Asiatic species are characterized by the overlapping of the marginals onto the costals beginning with marginal 5 (*A. foveatus* and *A. kizylkumensis*) or are unknown for this character (*A. dzhurtasensis* and *A. planus*). In all North American *Adocus* in which this character is observable, the marginals overlap onto the costals beginning with marginal 5. The relatively wide marginals and narrow pleurals are known in *A. amtgai*, whereas all other *Adocus* spp. in which this character is observable have relatively narrow marginals and wide pleurals (Syromyatnikova and Danilov 2009). The relatively narrow inframarginals 1 and 2 that are distant from the plastron-carapace suture are known in many species of *Adocus* in Asia and North America.

The result of our phylogenetic analysis consists of 81 trees with 150 steps (CI = 0.57, RI = 0.77). The resulting strict consensus tree is given in Fig. 2. This tree demonstrates that *Adocus bostobensis* belongs to the Asiatic clade that includes *A. aksary* and *A. amtgai*. This clade is supported by one synapomorphy, overlapping of the marginals onto the costals beginning with marginals 3 or 4. Within this clade, *A. bostobensis* is grouped with *A. amtgai* based on the presence of the nuchal emargination formed by

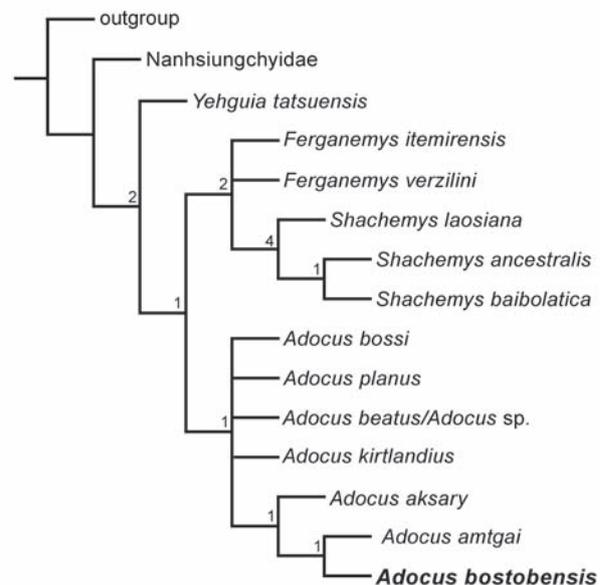


Fig. 2. A strict consensus of 81 phylogenetic trees showing hypothesized position of *Adocus bostobensis* (see Discussion for description of the tree). Outgroups and nanhsiungchelyid taxa are not shown. Numbers designate Bremer support indices.

the nuchal and peripheral 1. Other species of *Adocus* included in the analysis form a polytomy at the base of the *Adocus* clade. The topology of the rest part of the tree agrees with previous analyses (Danilov and Syromyatnikova 2009a, b; Syromyatnikova 2011; Syromyatnikova et al. 2012).

Thus, the result of our phylogenetic analysis supports the recognition of the clade of Asiatic *Adocus* revealed also by a study of Danilov et al. (in press). In our present study, this clade consists of *A. aksary*, *A. amtgai*, and *A. bostobensis*.

To conclude, our study confirms the specific status of *A. bostobensis* as was suggested previously based on small and fragmentary material (Syromyatnikova and Danilov 2009), and demonstrates the presence of at least two different lineages of *Adocus* in the Santonian of Western Asia. The first lineage, characterized by the overlapping of the marginals onto the costals beginning with marginal 3 or 4, is represented by *A. bostobensis* (Santonian – early Campanian of Kazakhstan), whereas the second lineage, characterized by the overlapping of the marginals onto the costals beginning with marginal 5, is represented by *A. foveatus* (early Santonian of Tajikistan). *Adocus dzhurtasensis* (Santonian – early Campanian of Kazakhstan) may belong to one of these lineages, or represent a third lineage of Santonian *Adocus* of Western Asia. New findings of more complete and numerous material of Cretaceous *Adocus* of Asia and North America are needed to further improve our knowledge about diversity, distribution and relationships of this genus.

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Appendix 1. Characters coded for *Adocus bostobensis* and added to the character/taxon matrix of Danilov and Syromyatnikova (2009a, b) with additions from Syromyatnikova (2011), Syromyatnikova et al. (2012): ?????????? ?????????? ??????????10
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