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NEW MATERIAL AND A REVISION OF TURTLES OF THE GENUS *ADOCUS* (ADOCIDAE) FROM THE LATE CRETACEOUS OF MIDDLE ASIA AND KAZAKHSTAN

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ABSTRACT

This paper reviews shell material of the turtle genus *Adocus* (Adocidae) from the Late Cretaceous of Middle Asia and Kazakhstan. Three previously recognized species of *Adocus* from this area are described in detail based on published and new material. The previously recognized species are *A. aksary* (Dzharakuduk, Uzbekistan; late Turonian), *A. foveatus* (Kansai, Tajikistan; early Santonian), and *A. kizylkumensis* (Khodzhakul, Khodzhakulsay and Sheikhdzheili, Uzbekistan; early Cenomanian). Material of additional forms of *Adocus* are described, two of these are named as new species: *Adocus dzhurtasensis*, sp. nov. (Dzhurtas, Kazakhstan; Santonian – early Campanian), *Adocus bostobensis*, sp. nov. (Akkurgan, Baybishe, Buroinak, and Shakh-Shakh, Kazakhstan; Santonian – early Campanian), and *Adocus* sp. indet. (Itemir, Uzbekistan; Cenomanian).

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

РЕЗЮМЕ

В работе ревизуются панцирные материалы по черепахам рода *Adocus* (Adocidae) из позднего мела Средней Азии и Казахстана. На основе опубликованных и новых материалов детально описываются три вида адокусов, известных ранее из этого региона: *A. aksary* (Джаракудук, Узбекистан; поздний турон), *A. foveatus* (Кансай, Таджикистан; ранний сантон) и *A. kizylkumensis* (Ходжакуль, Ходжакульсай и Шейхджейли, Узбекистан; ранний сеноман). Кроме того, описывается материал по дополнительным формам адокусов, две из которых устанавливаются в качестве новых видов: *Adocus dzhurtasensis*, sp. nov. (Джуртас, Казахстан; сантон – ранний кампан), *Adocus bostobensis*, sp. nov. (Аккурган, Байбише, Буройнак и Шах-Шах, Казахстан; сантон – ранний кампан) и *Adocus* sp. indet. (Итемир, Узбекистан; сеноман).

INTRODUCTION

The genus *Adocus* Cope, 1868 unites about 20 species of medium to large freshwater turtles known from the Cretaceous and Paleogene of Asia and North America (Hutchison 2000; Sukhanov 2000). *Adocus* is the generotypus of the extinct cryptodiran family Adocidae Cope, 1870, presently considered a member of the stem-trionychian clade Adocusia (Fig. 1; Danilov and Parham 2006, 2008). Adocidae are divided into two subfamilies: Adocinae Cope, 1870, with a single genus *Adocus* (see below), and Shachemydinae Khosatzky, 1977, uniting several genera from the Cretaceous of Asia (Nessov 1977; Nessov and Khosatzky 1977a; Lapparent de Broin 2004). *Adocus* is diagnosed mainly by the overlapping of marginal scales onto the costals in the middle and posterior parts of the shell, whereas other adocids and most other turtles have marginals that are restricted to the peripherals. Besides that, *Adocus* is characterized by sculpturing of the shell surface with relatively small and regular pits, which usually help to determinate presence of *Adocus* in assemblages even by small shell fragments. It is worth noting that similar, but diagnostically different, sculpturing is known in other

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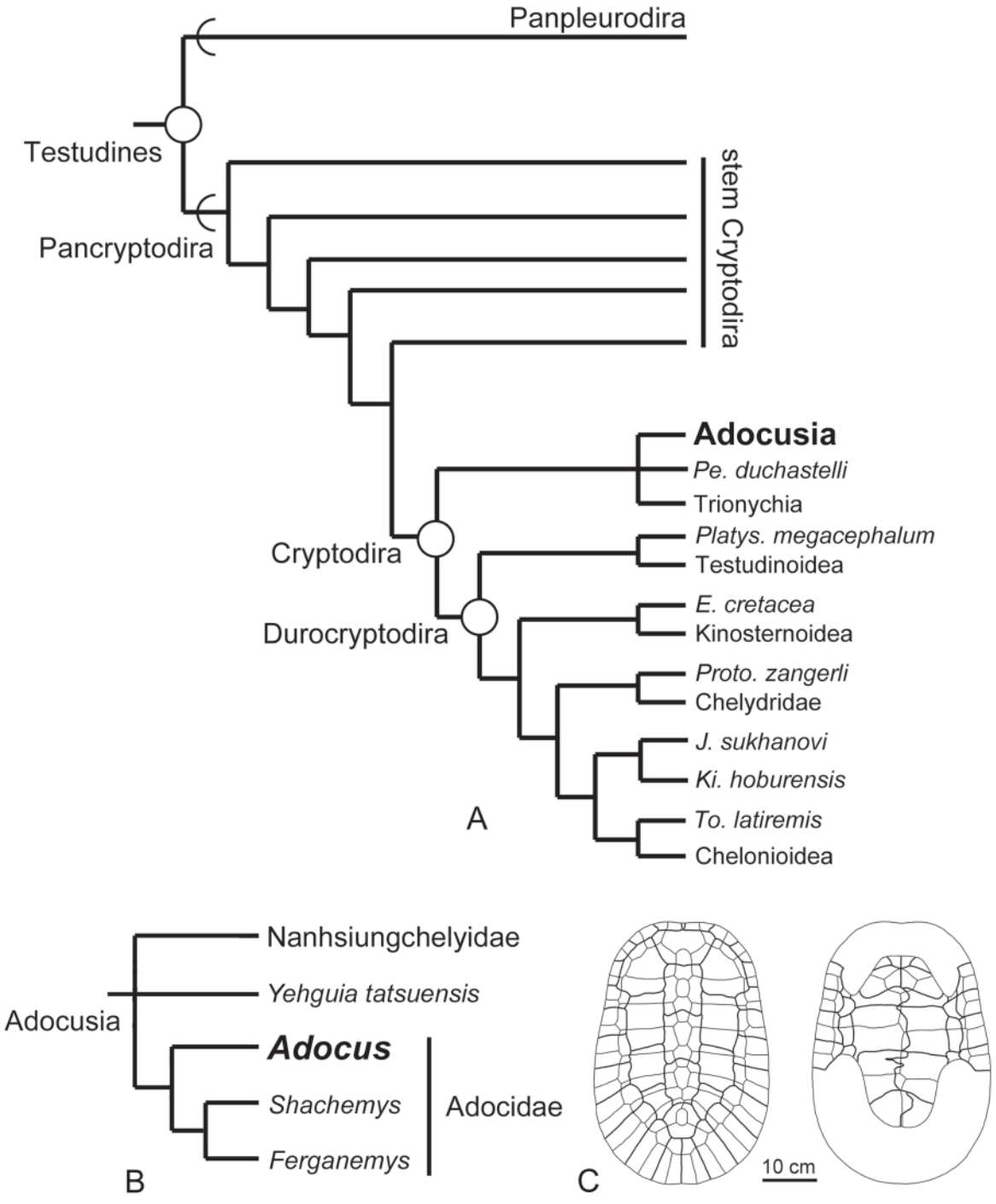

Fig. 1. Illustration of the phylogenetic position and general morphology of the genus *Adocus*: A – phylogenetic position of the clade Adocusia (after Danilov and Parham 2008, with changes); B – a hypothesis of relationships of Adocusia, showing position of Adocidae and *Adocus* (after Danilov and Parham 2006, with changes). C – shell of *Adocus beatus* (=*A. punctatus*) in dorsal (left) and ventral (right) views (after Hay 1908, with changes). Abbreviations: *E.*, *Emarginachelys*; *J.*, *Judithemys*; *Ki.*, *Kirgizemys*; *Pe.*, *Peltochelys*; *Platys.*, *Platysternon*; *Proto.*, *Protochelydra*; *To.*, *Toxochelys*. Circles and open semi-circles designate node based and stem based taxa respectively.

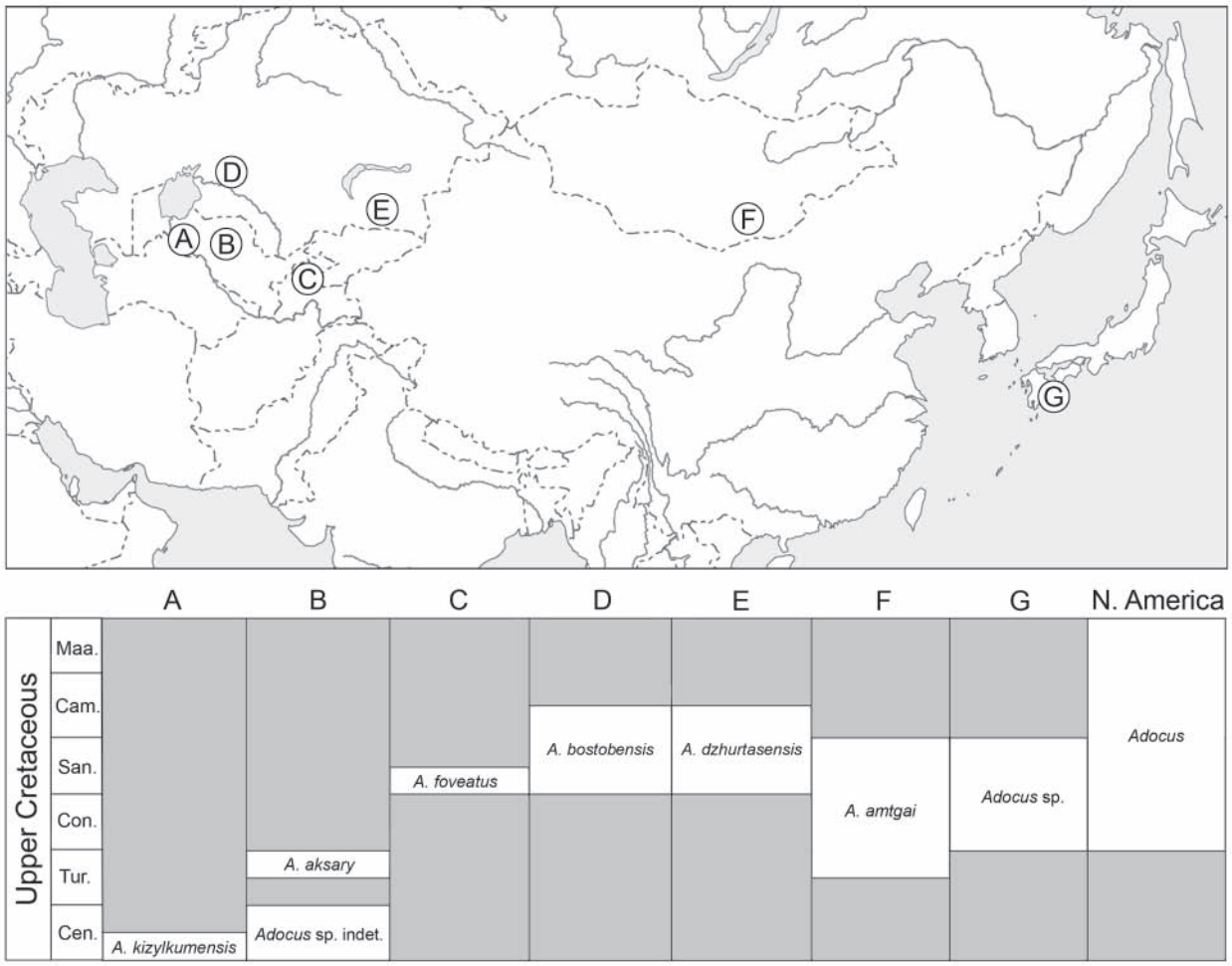

Fig. 2. Map showing geographic and temporal distribution of *Adocus* in the Late Cretaceous of Asia (confirmed data only) and North America: A – Sheikhdzheili and Khodzhakulsay, Sultanuvais Range, Uzbekistan; Khodzhakul Formation, early Cenomanian (Nessov 1981, 1997; our data). B – Itemir and Dzharakuduk, Central Kyzylkum, Uzbekistan; Cenomanian and late Turonian respectively (Nessov and Krasovskaya 1984; our data). C – Kansai, Fergana Depression, Tajikistan; Yalovach Formation, early Santonian (Khosatzky and Nessov 1977; our data). D – Akkurgan, Baybishe, Buroynak and Shakh-Shakh localities, northeastern Aral Sea area, Kazakhstan; Bostobe Formation, Santonian – early Campanian (Nessov 1997; our data). E – Dzhurtas, Dzhungar Alatau Ridge, Kazakhstan; Santonian – early Campanian (Nessov 1995; our data). F – Amtgai, Dornogov Aimag, Mongolia; upper part of the Bainshire Formation, late Turonian – Santonian (Narmandakh 1985; Sukhanov, 2000); G – Amagimi Dam of Mifune, Kumamoto Prefecture, Kyushu, Japan; Mifune Group, Coniacian – Santonian (Hirayama 1998; pers. comm. to IGD, 2007). Temporal distribution of *Adocus* in the Late Cretaceous of North America is given according to Hutchison (2000).

adocids, members of the family Nanhsiungchelyidae Yeh, 1966 and some related turtles (see Danilov and Parham 2006; Danilov et al. 2007; Danilov and Syromyatnikova 2008).

Turtles of the genus *Adocus* first appeared in Asia in the Early Cretaceous (Barremian or Aptian; Hirayama 2002), were widely distributed there in the Late Cretaceous (up to the Santonian – early Campanian), then disappeared until the Late Paleocene – Early Oligocene interval (Nessov 1997; Chkhikvadze 1990). In North America, *Adocus* appears in the Turonian or Coniacian and is known continuously to the end of the Paleocene (Hutchison 2000). Three of the four named species of *Adocus*, known in the Late Cretaceous of Asia (Fig. 2), have been described from the area that Soviet/Russian geographers have traditionally called Middle Asia and Kazakhstan and generally

corresponds to Central Asia in the American tradition. These species are: *Adocus aksary* Nessov in Nessov et Krasovskaya, 1984 (Dzharakuduk, Uzbekistan; late Turonian); *A. foveatus* Nessov et Khosatzky in Khosatzky et Nessov, 1977 (Kansai, Tajikistan; early Santonian); and *A. kizylkumensis* Nessov, 1981 (Khodzhakul, Uzbekistan; early Cenomanian). All of the above mentioned *Adocus* species from the Late Cretaceous of Middle Asia were based on few and fragmentary specimens which has hindered comparisons with other species of the genus. Besides that, numerous records of *Adocus* sp. have been reported from other Upper Cretaceous localities of Middle Asia and Kazakhstan (Nessov 1997). Most of these latter specimens remain undescribed.

Meylan and Gaffney (1989) stated that the alpha taxonomy of the genus *Adocus* is in need of revision, but over the past 20 years little progress has been made. Recently, one of the Asian species of this genus, *Adocus amtgai* Narmandakh, 1985 from the Late Cretaceous of Mongolia (Narmandakh 1985), was established as a new genus *Adocoides* Sukhanov et Narmandakh, 2006 (Sukhanov 2000; Sukhanov and Narmandakh 2006). In our opinion, this genus is based on highly variable characters within *Adocus* and so its separation into a new genus may be premature (see Discussion). Besides that, the establishment of *Adocoides* necessarily raises questions about the monophyly and generic attribution of other Asian *Adocus* that cannot be solved now due to the quality of the available specimens. For these reasons, until more information available, we retain *Adocus amtgai* and all other Asian forms within the genus *Adocus* pending further study.

The aim of this paper is to provide new data on *Adocus* from the Late Cretaceous of Middle Asia and Kazakhstan derived from our study of both published and new specimens from several localities of the region. Detailed information about this material is given in the Systematics section (see below). Two new species from Kazakhstan are described.

Anatomical terms of the shell follow Zangerl (1969) and Hutchison and Bramble (1981). Previously, characters of the shell sculpturing were used for distinguishing of *Adocus* species by some authors (Khosatzky and Nessov 1977; Nessov 1981; Nessov and Krasovskaya 1984). Our preliminary observation of these characters shows that they are not clearly defined and rather variable. For this reason, until special study of sculpturing variation in *Adocus*, the sculpturing is omitted from further consideration.

MATERIAL

In addition to the material described in the Systematics section, our study relies on published data on the following taxa of adocids for comparative purposes: best known Late Cretaceous members of *Adocus*: *Adocus amtgai* (Narmandakh 1985; Sukhanov 2000; Sukhanov and Narmandakh 2006); *A. beatus* (Leidy, 1864) [=*A. lacer* Hay, 1908; =*A. punctatus* Marsh, 1890] (Hay 1908; White 1972); *A. bossi* Gilmore, 1919 (Gilmore 1919); *A. kirtlandius* Gilmore, 1919 (Gilmore 1919) and *Adocus* sp. from the Late Cretaceous of USA (Meylan and Gaffney 1989); other adocids: species of the genus *Ferganemys* Nessov et Khosatzky, 1977: *F. itemirensis* Nessov, 1981 (Nessov 1981; Nessov and Krasovskaya 1984) and *Ferganemys verzilini* Nessov et Khosatzky, 1977 (Nessov and Khosatzky 1977b); species of the genus *Shachemys* Kuznetsov, 1976: *S. ancestralis* Nessov in Nessov et Krasovskaya, 1984 and *S. baibolatica* Kuznetsov, 1976 (for review see Danilov et al. 2007).

Institutional abbreviations. CCMGE – Chernyshev's Central Museum of Geological Exploration, St. Petersburg, Russia; IZK – Institute of Zoology of the Academy of Sciences of Kazakhstan, Almaty, Kazakhstan; PIN – Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; ZIN PH (=ZIN PHT) – Paleoherpetological collection, Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia.

SYSTEMATICS

Family Adocidae Cope, 1870

Subfamily Adocinae Cope, 1870

Genus *Adocus* Cope, 1868

Adocus aksary Nessov in Nessov et Krasovskaya, 1984

(Figs. 3; 4; 5A–L; 6A–M)

Adocus aksary: Nessov and Krasovskaya 1984, p. 23, pl. 4, figs. 1–4; Nessov 1985, p. 218; Nessov 1997, p. 145; Syromyatnikova and Danilov 2007, p. 49.

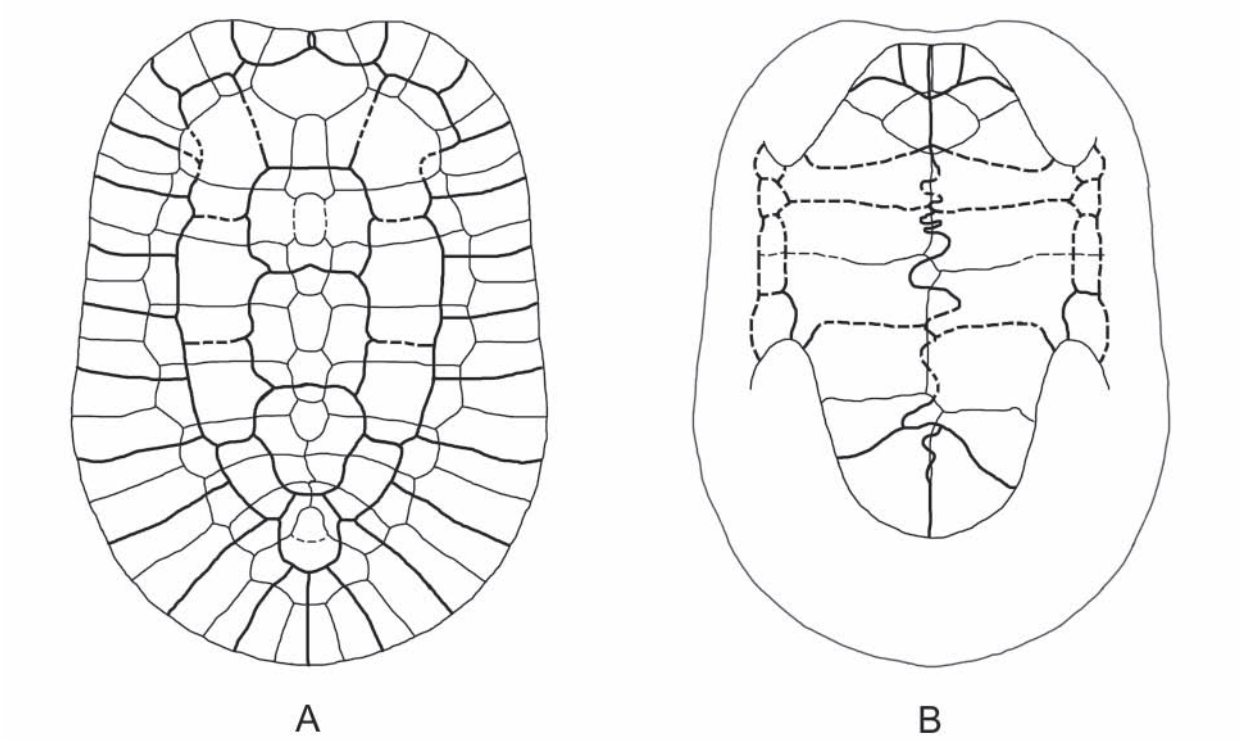

Fig. 3. *Adocus aksary*, reconstruction of the shell, Dzharakuduk, Central Kyzylkum, Uzbekistan; Bissekty Formation, late Turonian: A – dorsal view; B – ventral view. The outlines of the carapace and plastron are shown approximately. Without scale.

Lindholmemys elegans (part.): Nessov 1986, fig. 11.

Ferganemys sp.: Nessov 1997, p. 145, pl. 34, fig. 16.

"Adocus" aksari (sic.): Sukhanov 2000, p. 333.

"Adocus" aksary: Danilov and Parham 2005, p. 789.

Adocidae gen. et sp. indet.: Danilov and Parham 2005, p. 790, figs. 1–3.

Holotype. CCMGE 10/12086, left peripheral 3 (in the original description the holotype was mistakenly determined as peripheral 4); Dzharakuduk (=Dzhirakuduk II; Nessov 1997, p. 144) locality, Central Kyzylkum, Uzbekistan; Bissekty Formation, late Turonian.

Fig. 4. *Adocus aksary*, shell fragments, Dzharakuduk, Central Kyzylkum, Uzbekistan; Bissekty Formation, late Turonian: A – ZIN PH 1/84, nuchal in dorsal view; B – ZIN PH 2/84, fragment of nuchal: B_1 – dorsal view; B_2 – anterior view; C – ZIN PH 5/84, fragment of nuchal in dorsal view; D – ZIN PH 33/84, fragment of nuchal in dorsal view; E – ZIN PH 165/84, neural 1 in dorsal view; F – ZIN PH 24/84, neural 1: F_1 – dorsal view; F_2 – ventral view; G – ZIN PH 7/84, neural 3: G_1 – dorsal view; G_2 – ventral view; H–J, undetermined neurals in dorsal view: H – ZIN PH 18/84; I – ZIN PH 11/84; J – ZIN PH 9/84; K – ZIN PH 12/84, neural 4 in dorsal view; L – ZIN PH 26/84, fragment of suprapygal 2 in dorsal view; M – ZIN PH 28/84, fragment of pygal in dorsal view; N – ZIN PH 163/84, lateral fragment of costal 1 in dorsal view; O – ZIN PH 164/84, fragment of left costal 1: O_1 – dorsal view; O_2 – ventral view; P – ZIN PH 154/84, medial fragment of right costal 3 in dorsal view; Q – ZIN PH 146/84, left costal 4: Q_1 – dorsal view; Q_2 – ventral view; R – ZIN PH 144/84, lateral fragment of left costal 4 in dorsal view; S – ZIN PH 157/84, lateral fragment of costal 3 or 5 in dorsal view; T – ZIN PH 150/84, shell fragment in dorsal view; U – ZIN PH 143/84, medial fragment of left costal 6 in dorsal view; V – ZIN PH 148/84, medial fragment of left costal 7 in dorsal view; W – ZIN PH 147/84, fragment of left costal 6 in dorsal view; X – ZIN PH 120/84, left costal 8: X_1 – dorsal view; X_2 – ventral view; Y – ZIN PH 34/84, left peripheral 1: Y_1 – anterior view; Y_2 – dorsal view; Y_3 – posterior view. A–X and Y_2 – photographs. Y_1 and Y_3 – drawings. Abbreviations: abd – abdominal; abf – axillary buttress fossa; c – costal; ce – cervical; egu – extragular; ent – entoplastron; epi – epiplastron; fr – free rib; gu – gular; hyo – hypoplastron; hypo – hypoplastron; hu – humeral, ia – ilial attachment; ibf – inguinal buttress fossa; im – inframarginal; m – marginal; md – musk duct; n – neural; nu – nuchal; p – peripheral; pa – pelvis attachment, pe – pectoral; ra – ribhead attachment; sp – suprapygal; v – vertebral; xi – xiphiplastron. Arabic numerals designate element numbers. In drawings: sutures are filled with grey; breakages are hatched.

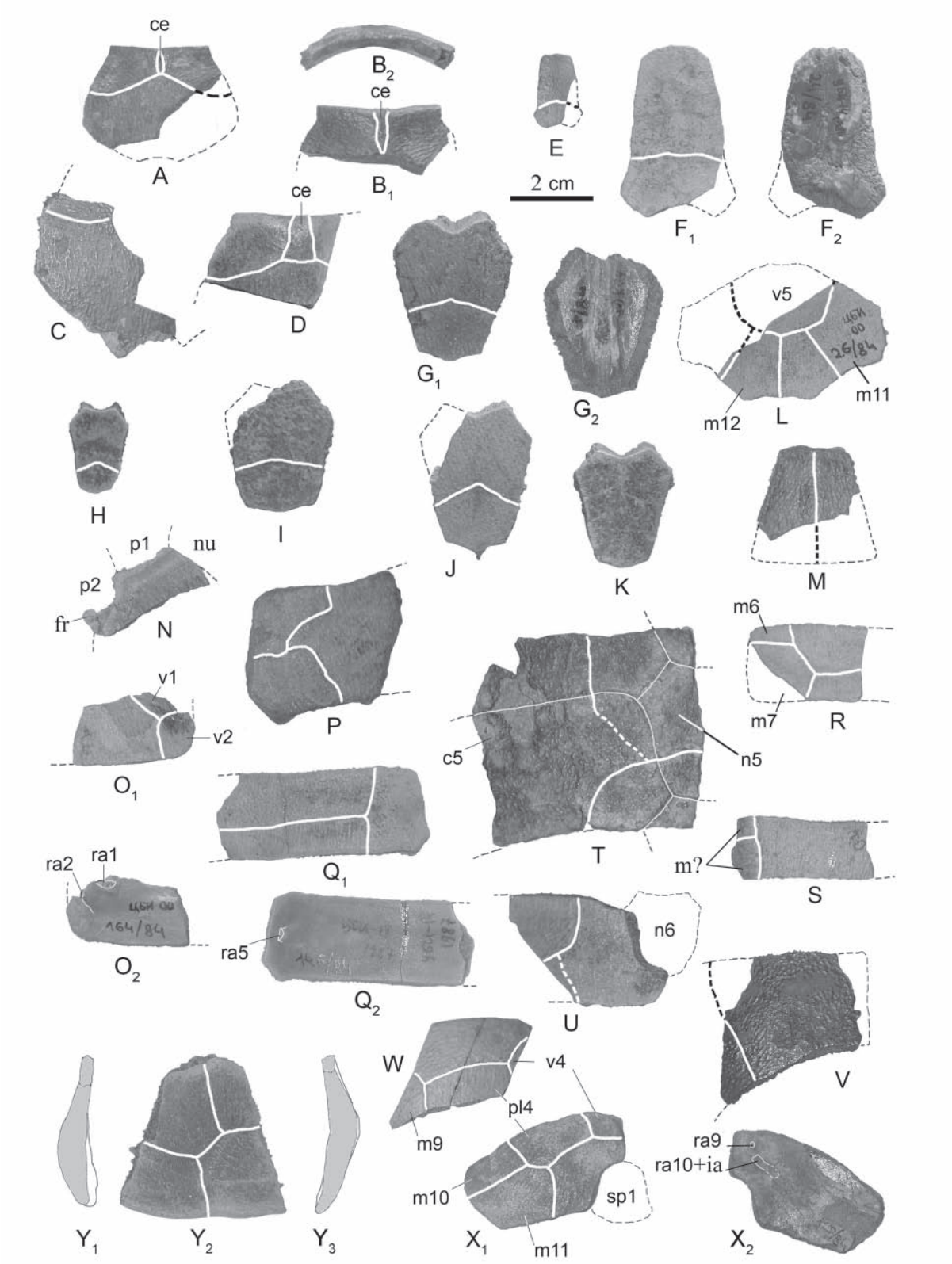
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Table 1. Comparison of shell characters of some Late Cretaceous species of *Adocus* (see text for references).

Characters	*A. amtgai*	*A. aksary*	*A. beatus*	*A. bossi*
Length of the shell	40 cm	40 cm	50 cm	70 cm
Nuchal emargination	Weak	Weak	Weak or absent	Absent
Number of neurals	?	6	6 or 7	6
Neural 6	?	Shortened	Not shortened	Shortened
Number of suprapygals	?	2	2	1
Width of anterior border of epiplastron	More than length of epiplastral symphysis	Less than length of epiplastral symphysis	More than length of epiplastral symphysis	More than length of epiplastral symphysis
Cervical	Trapezoid-shaped, expanded anteriorly	Lens- or trapezoid-shaped, expanded anteriorly or posteriorly	Trapezoid-shaped, expanded anteriorly	Trapezoid-shaped, expanded posteriorly
Vertebral 5	?	Narrow	Relatively wide	Narrow
Pleurals 2–4	Narrow (width makes up 30% of length)	?	Wide (width makes up 60% of length)	Wide (width makes up 60% of length)
Marginals overlapping onto the costals	Beginning with marginal 4	Beginning with marginal 3 or 4	Beginning with marginal 5	Beginning with marginal 5
Width of anterior border of gulars	More than length of epiplastral symphysis	Less than length of epiplastral symphysis	More than length of epiplastral symphysis	Variable
Extension of gulars onto the entoplastron	Present	Present or absent	Present or absent	Present
Ratio of length of extragular medial border to length of epiplastral symphysis	0.6	0.9	0.6	0.7
Pectorals extension onto the entoplastron	Present	Present or absent	Present	Absent
Number of inframarginals	3 pairs	?	4 pairs	3 pairs

Table 1 (extended)

A. bostobensis	*A. dzhurtasensis*	*A. foveatus*	*A. kirtlandius*	*A. kizylkumensis*
100 cm	65 cm	50 cm	50 cm	40 cm
Weak	Strong	?	?	Weak or absent
?	?	?	6	?
?	?	?	Shortened	?
?	?	2	2	?
?	?	More than length of epiplastral symphysis	?	?
Narrow, slightly expanded posteriorly	Reduced	?	?	Trapezoid-shaped, expanded posteriorly
?	?	?	Relatively wide	?
?	?	?	Wide (width makes up 60% of length)	?
?	?	Beginning with marginal 5	Beginning with marginal 5	Beginning with marginal 5
?	?	Equal to length of epiplastral symphysis	?	?
?	?	Present	?	?
?	?	0.5	?	?
?	?	Absent	Absent	?
?	?	?	4 pairs	?

Material (shell only). ZIN PH 1–2/84, 4–6/84, nuchals; ZIN PH 24/84, 165/84, neurals 1; ZIN PH 7/84, neural 3; ZIN PH 12/84, 19/84, neurals 4; ZIN PH 13/84, neural 5; ZIN PH 26/84, 27/84, 132/84, suprapygals 2; ZIN PH 28–32/84, pygals; ZIN PH 3/84, 163/84, 164/84, costals 1; ZIN PH 154/84, costal 3; ZIN PH 144/84, 146/84, costals 4; ZIN PH 185/84, costal 5; ZIN PH 150/84, costals 5+6+neural 5; ZIN PH 143/84, 147/84, costals 6; ZIN PH 148/84, costal 7; ZIN PH 120–122/84, costals 8; ZIN PH 157/84, undeterminate costal; ZIN PH 34–40/84, 57/84 peripherals 1; CCMGE 30/12086, ZIN PH 21/84, 42–56/84, 58/84, 59/84, peripherals 2; ZIN PH 25/84, 61–68/84, 72/84, 75/84, 166/84, 167/84, 187/84, peripherals 3; ZIN PH 170/84, peripheral 6; ZIN PH 60/84, 74/84, 76–78/84, 168/84, 188/84, peripherals 7; ZIN PH 79–91/84, 172/84, 173/84, peripherals 8; ZIN PH 171/84, peripherals 7+8; CCMGE 29/12086, ZIN PH 92–95/84, 98/84, 174/84, peripherals 9; ZIN PH 96/84, 97/84, 105/84, 175/84, 176/84, 177/84, peripherals 10; ZIN PH 111–118/84, 195/84, peripherals 11; ZIN PH 69–71/84, 73/84, 169/84, 189–191/84, bridge peripherals; CCMGE 31/12086, ZIN PH 123–125/84, epiplastra; ZIN PH 126–129/84, entoplastra; ZIN PH 181/84, hyoplastron+hypoplastron; ZIN PH 119/84, 131/84, hyoplastra; ZIN PH 135–139/84, xiphiplastra; the specimens were collected in the type locality in different years by L.A. Nessov and URBAC expeditions.

Differential diagnosis. A species of *Adocus* that can be differentiated from other species of the genus by its smaller shell size (except *A. amtgai* and *A. kizylkumensis*), narrowed vertebral 5 (except *A. bossi*), overlapping of marginals onto the costals beginning with marginal 3 or 4 (except *A. amtgai*), narrower anterior border of the epiplastron, narrowed gulars (except *A. bossi*), and longer medial border of the extragular. It can also be differentiated from *A. beatus* by a shorter neural 6 and from *A. bossi* by the presence of nuchal emargination and two suprapygals. For more detailed comparison see Table 1.

Description. The length of the shell is estimated at about 40 cm (based on CCMGE 29/12086). The shape of carapace can be reconstructed only approximately (Fig. 3), the width of the anterior part of the carapace is not clear. The nuchal emargination is not strong, restricted to the nuchal and anterior parts of peripherals 1. In other *Adocus*, the anterior part of carapace can be narrowed (*Adocus beatus*) or widened (*A. bossi*), and the nuchal emargination is either present (*A. amtgai*, *A. beatus*) or absent (*A. beatus*, *A. bossi*).

The nuchal (Fig. 4A–D) is hexagonal, although its exact proportions are not clear. The anterior border of the nuchal is wide (ratio of the nuchal anterior width to its maximum width is 0.7 in ZIN PH 1/84), slightly concaved, rounded or angled in the cross-section, and upturned in lateral parts. The anterolateral borders of the nuchal are S-shaped (concave anteriorly and convex posteriorly) and longer than the posterolateral borders which are slightly convex. The posterior border is concave and contacts with neural 1. In most other *Adocus*, proportions of the nuchal are similar to that in *A. aksary*. The notch of the anterior border is present or absent (see above) and the ratio of the nuchal's anterior width to its maximum width varies from 0.7 (*Adocus beatus, A. bossi*) to 1.0 (*A. amtgai*).

There are six neurals. Neurals 1, 3, 4 and 5 are represented by specimens (Fig. 4E–K), whereas the shapes of the others are reconstructed based on surrounding plates. The neural formula is typical for *Adocus*: neural 1 is hexagonal short-sided posteriorly, neural 2 is tetragonal, neurals 3–5 are hexagonal and short-sided anteriorly, and neural 6 is pentagonal and short-sided anteriorly. All neurals are relatively wide and thin. Internally, neural 1 (Fig. 4F) bears a scar from the first trunk vertebrae. Neural 6 is shortened. Most other *Adocus* have eight neurals and a shortened neural 6 (except *A. beatus*).

There are two suprapygals. Suprapygal 1 is not represented by specimens and so is reconstructed based on surrounding elements as a small and bell-shaped plate. Suprapygal 2 (Fig. 4L) is wider than suprapygal 1 and heptagonal- or octagonal-shaped. It contacts costals 8 by straight anterolateral borders, peripherals 10 by concave lateral borders, peripherals 11 by slightly convex posterolateral borders, and the pygal by concave posterior border. Similar suprapygals are known in other *Adocus*, except *A. bossi,* which has no suprapygal 1.

The pygal (Fig. 4M) is longer than wide (ratio of the pygal length to its posterior width is 0.9 in ZIN PH 31/84), trapezoid-shaped (ratio of the anterior pygal width to its posterior width is about 0.65), and has straight lateral borders. The free edge of the pygal is slightly upturned. The described morphology is similar to that in other members of *Adocus*.

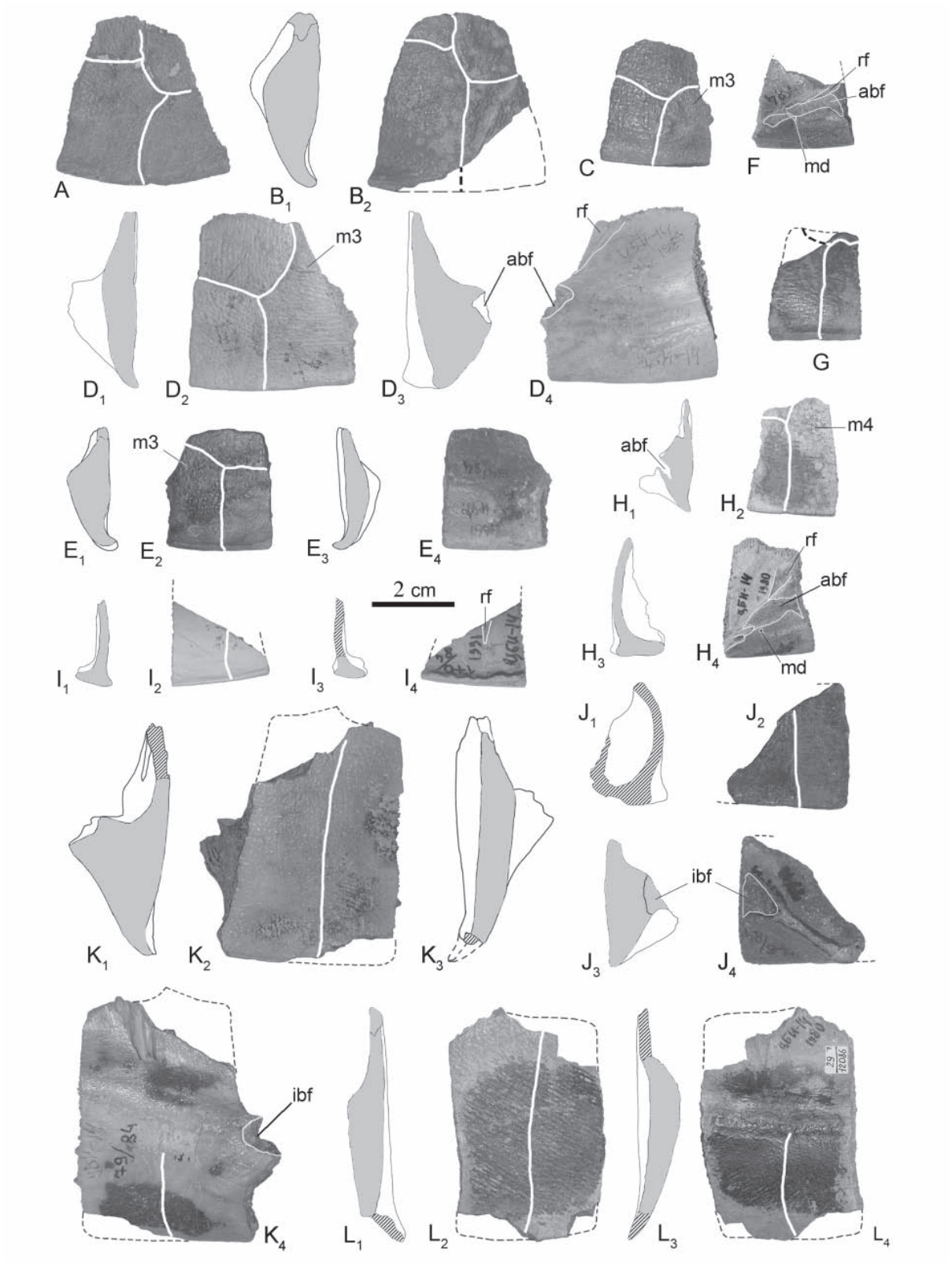
The costals are represented by the medial parts of costals 1, 3–7, and complete costal 8 (Fig. 4N–X). Besides that, there are a number of lateral fragments

of indeterminate costals. Ribheads and rib thickenings of costals are weak as in all other adocids. On the internal surface of costal 1, scars of thoracic ribs 1 and 2 lie close to each other. Posterior costals contacted at midline. Costals 6 contact each other along the posterior thirds of their medial length, costals 7 through all their medial length, and costals 8 along the anterior half of their medial length. Costal 8 has a rounded notch in its posterior half for contact with suprapygal 1. Other *Adocus* demonstrate patterns of the posterior costals different from the described above: *Adocus kirtlandius* has a shorter contact of costals 8, whereas *A. bossi* has longer contacts of costals 8, and *A. beatus* has no contact of costals 6.

The peripheral series (Figs. 4Y; 5A–L; 6A, B) is represented by complete or almost complete peripherals 1–3 and 8–11, but only lateral parts of peripherals 4–7. The free edges of the anterior peripherals are upturned and may be rounded or angled in the cross-section. The bridge peripherals are L-shaped with upturned free edges. The dorsal (carapacial) plates of the bridge peripherals are about twice as wide as the ventral (plastral) ones. The posterior peripherals are wider than the anterior ones. The shape of anterior and posterior sections of the same peripherals varies considerably by thickness and degree of development of the upturned free edges. Internally, peripherals 2–10 bear triangular-shaped grooves for free ribs of the corresponding costals. The anterior and posterior sutural surfaces of peripherals 2, 8, and adjacent peripherals are slightly oblique, which suggests some overlapping of these peripherals. Peripheral 2 overlaps peripheral 1 and peripheral 8 overlaps peripheral 9. Peripheral 1 looks trapezoid-shaped (Figs. 4Y; 5A, B), its medial length is about twice as short as the length of the free edge. The thickness of peripheral 1 is constant through its length. There is no notch for a costiform-like process on the internal surface of peripheral 1 as is known in *Adocus beatus* (Hay 1908, fig. 300). Peripheral 2 (Fig. 5C–E) is thickened along the posterior border, where internally it forms a posteriorly directed bulge that slightly overlaps peripheral 3. The fossa for the axillary buttress is deep and elongated anteroposteriorly, occupying the bulge of peripheral 2 and anterior portion of peripheral 3 (Fig. 5H). The groove for the musk duct is located in peripheral 3, where it crosses the plastron-carapace suture (Fig. 5F). Musk ducts have not been reported in other *Adocus*, but are known in *Ferganemys* and *Shachemys* (Danilov et al. 2007). Peripheral 4 (Fig. 5I) has an upturned free edge and loose connection with the plastron. Peripheral 7 (Fig. 5J) has no musk duct groove. The anterior border of peripheral 8 (Fig. 5K) is thickened. Similar to peripheral 2, peripheral 8 forms an anteriorly directed bulge that overlaps peripheral 7. The fossa for the inguinal buttress is oval-shaped, occupying posterior third of peripheral 7 and the end of the bulge of peripheral 8. Peripheral 9 (Fig. 5L) and posterior ones are almost equal in their thickness. The posteromedial border of peripheral 10 (Fig. 6A) contacts suprapygal 2. Peripheral 11 (Fig. 6B) is narrower than peripheral 10 and slightly thickened posteriorly on the border with the pygal.

The size and shape of the carapacial scales are not always clear (Fig. 3). The cervical scale (Fig. 4A, B, D) is strongly variable from narrow lens-shaped to trapezoid, expanded anteriorly (as in *Adocus amtgai* and *A. beatus*) or posteriorly (as in *A. bossi*). The vertebrals get narrower posteriorly. Vertebral 1 is trapezoid-shaped, widened anteriorly and in contact with marginals 2. Vertebral 2 seems to be shorter than vertebral 3. The shapes of vertebrals 2 and 3 are variable depending on the width of the intervertebral sulci. Vertebral 4 is narrowed posteriorly, like in most other members of *Adocus*. Vertebral 5 is small and oval-shaped. In other *Adocus*, vertebral 5 varies from hexagonal (*Adocus beatus*) to narrow oval (*A. amtgai*, *A. bossi*). The exact shape of pleurals is unclear. They seem to get smaller from anterior to posterior ones. Pleural 1 may extend onto peripherals 1, 2, and sometimes 3 as in *Adocus amtgai*, whereas in other species pleural 1 extends onto peripherals 1–4. Marginals 1 and 2 are restricted to peripherals and cover from 1/2 to 2/3 of their external surface (Figs. 4Y; 5A–E). Marginal 3 may be restricted to the peripherals or overlap onto the costals like all more posterior marginals (Figs. 4R, S; 5D, G, H). In other species of *Adocus*, except *A. amtgai*, the overlapping of marginals onto the costals begins with marginal 5. The skin-scale sulcus lies very close to the free edge of the nuchal and anterior part of peripheral 1 and in the middle part of more posterior peripherals.

The plastron is represented by an almost complete epiplastron and entoplastron, as well as by isolated fragments of these and another plastral plates. The precise shape and proportions of the plastral lobes are not clear and allow for only an approximate reconstruction (Fig. 3). According to the available specimens, the anterior lobe of the plastron was shorter


A
B1
B2
C
m3
F
rf
abf
md
D1
D2
m3
D3
abf
D4
rf
G
E1
E2
m3
E3
E4
H1
abf
H2
m4
2 cm
I1
I2
I3
I4
rf
H3
H4
rf
abf
md
J1
J2
K1
K2
K3
J3
ibf
J4
K4
ibf
L1
L2
L3
L4

than the posterior one and truncated anteriorly. The gular and anal notches are absent as in other *Adocus*.

The epiplastron (Fig. 6C–E) has a relatively narrow anterior border, which is less than the length of the epiplastral symphysis. In other *Adocus*, the anterior border of the epiplastron is relatively wider, being wider than the length of the epiplastral symphysis.

The entoplastron (Fig. 6F–H) is a large hexagonal or tetragonal element, with more or less developed lateral borders. Its dorsal surface bears a Y-shaped system of ridges continued posteriorly by a wedge-shaped process. The similar hexagonal-shaped entoplastron is observed in other species of *Adocus*.

The hyoplastra and hypoplastra are represented by very fragmentary remains (Fig. 6I, J), but allow the shape of the inguinal notch and some characters of the plastral scalation to be determined (see below).

The xiphiplastron (Fig. 6K–M) is longer than wide, narrowed posteriorly, with a rounded free edge. Internally, it bears an oval-shaped fossa where the pelvis was ligamentously attached.

The plastral scalation can be reconstructed only partially (Fig. 3). The gulars (Fig. 6C–E) are relatively narrow (their anterior width is less than the length of the epiplastral symphysis). They may or may not overlap the entoplastron. In other *Adocus* species these characters of the gulars are also variable. The extragulars (Fig. 6D) are relatively large covering about 1/3 of the external surface of the epiplastra, with long medial borders that comprise about 0.9 of the epiplastral symphysis length. In other *Adocus*, the extragulars are about the same size but with shorter medial borders that comprise about 0.7 of the epiplastral symphysis length. The shape of the pectorals is unclear. The humeral-pectoral sulcus may or may not intersect the entoplastron. The variation in this character is also known in other *Adocus* species. The abdominal contributes to the rim of the inguinal notch. The femoral-anal sulcus is either straight or slightly S-shaped. Inframarginals are represented only by medial parts of elements 3 and 4 (Fig. 6I). Inframarginal 4 is much wider than inframarginal 3. The midline sulcus between the pectorals to the anals is strongly sinuous (Fig. 6J, K) as in most members of *Adocus*. The skin-scale sulcus lies along free edge of the plastral lobes.

Remarks. The isolated turtle skull from the Dzharakuduk locality, primarily attributed to *Lindholmemys elegans* Riabinin, 1935 (Nessov 1986, fig. 11), and later referred to Adocidae gen. et sp. indet. (Danilov and Parham 2005), can now be assigned with confidence to *Adocus aksary*. This new assignment is based on the close similarity of this skull with those of *Adocus* from the Late Cretaceous of USA (Meylan and Gaffney 1989) as well as the significant differences between the skulls of *Adocus* and *Shachemys* (Lapparent de Broin 2004). The latter genus includes *Shachemys ancestralis*, the second adocid in the Dzharakuduk assemblage (Danilov et al. 2007).

The fragmentary material from the type locality, previously referred to *Ferganemys* sp. (Nessov 1997, p. 145), should be assigned to *Adocus aksary*. For instance, the figured peripheral 2 (Fig. 5C; Nessov 1997, pl. 34, fig. 16) demonstrates the characteristic upturned free edge and another features of *Adocus*.

Distribution. Bissekty Formation, late Turonian; Dzharakuduk locality, Central Kizylkum, Uzbekistan.

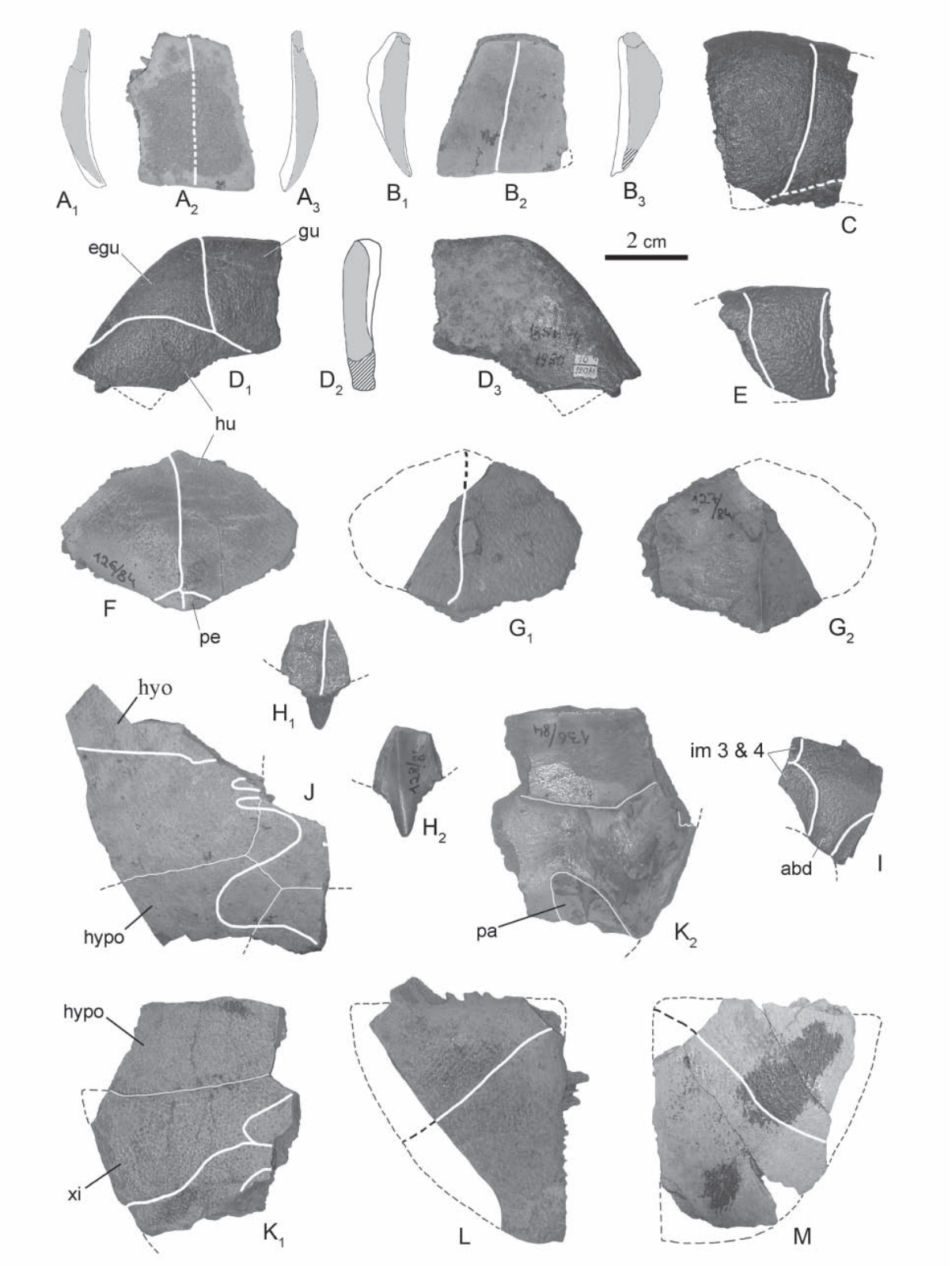
Adocus foveatus Nessov et Khosatzky in Khosatzky et Nessov, 1977

(Fig. 7A–E)

Adocus foveatus: Khosatzky and Nessov 1977, p. 116, fig. 1; Narmandakh 1985, p. 86; Nessov 1981, p. 70; Nessov 1985, p. 220; Nessov 1987, pl. I, fig. 12; Nessov 1997, p. 131, pl. 33, figs. 8, 9; pl. 34, figs. 1–3; Syromyatnikova and Danilov 2007, p. 49.

"*Adocus*" *foveatus*: Sukhanov 2000, p. 333.

Fig. 5. *Adocus aksary*, shell fragments, Dzharakuduk, Central Kyzylkum, Uzbekistan; Bissekty Formation, late Turonian: A – ZIN PH 36/84, right peripheral 1 in dorsal view; B – ZIN PH 35/84, right peripheral 1: B_1 – posterior view, B_2 – dorsal view; C – ZIN PH 43/84, left peripheral 2 in dorsal view; D – CCMGE 30/12086, left peripheral 2: D_1 – anterior view; D_2 – dorsal view; D_3 – posterior view; D_4 – ventral view; E – ZIN PH 54/84, right peripheral 2: E_1 – posterior view; E_2 – dorsal view; E_3 – anterior view; E_4 – ventral view; F – ZIN PH 64/84, fragment of left peripheral 3 in ventral view; G – ZIN PH 67/84, right peripheral 3 in dorsal view; H – CCMGE 10/12086 (holotype), left peripheral 3: H_1 – anterior view; H_2 – dorsal view; H_3 – posterior view; H_4 – ventral view; I – ZIN PH 170/84, fragment of right peripheral 4: I_1 – posterior view: I_2 – dorsal view; I_3 – anterior view; I_4 – ventral view; J – ZIN PH 76/84, right peripheral 7: J_1 – anterior view; J_2 – dorsal view; J_3 – posterior view; J_4 – ventral view; K – ZIN PH 79/84, left peripheral 8: K_1 – anterior view; K_2 – dorsal view; K_3 – posterior view; K_4 – ventral view; L – CCMGE 29/12086, left peripheral 9: L_1 – anterior view; L_2 – dorsal view; L_3 –posterior view; L_4 – ventral view. A, B_2, C, D_2, D_4, E_2, E_4, F, G, H_2, H_4, I_2, I_4, J_2, J_4, K_2, K_4, L_2, L_4 – photographs. B_1, D_1, D_3, E_1, E_3, H_1, H_3, I_1, I_3, J_1, J_3, K_1, K_3, L_1, L_3, – drawings. See Figure 3 for abbreviations and designations.


A1
A2
A3
B1
B2
B3
C
2 cm
egu
gu
D1
D2
D3
E
hu
F
pe
G1
G2
H1
hyo
J
H2
im 3 & 4
abd
I
hypo
pa
K2
hypo
xi
K1
L
M

Holotype. ZIN PHT F64-11, left peripheral 4 (Fig. 7C; Khosatzky and Nessov 1977, fig. 1); Kansai locality, Fergana Depression, Tajikistan; Yalovach Formation, early Santonian.

Material. ZIN PH 590/64, costal 5; ZIN PH 591/64, costals 7+8; ZIN PH 593/64, undetermined costal fragment; ZIN PH 592/64, epiplastron; ZIN PH 594/64, entoplastron; ZIN PH 582–588/84, undetermined shell fragments; the specimens were collected by expeditions of PIN in 1960s in the type locality.

Differential diagnosis. A species of *Adocus* that can be differentiated from *A. aksary* by larger size of the shell, wider anterior border of the epiplastron, overlapping of marginals onto the costals beginning with marginal 5, wider gular and shorter medial border of the extragular. For more detailed comparison with other species see Comparison sections below and Table 1.

Description. The length of the shell is estimated at about 50 cm (based on ZIN PH 590/64). Costal 8 is notched posteriorly for contact with suprapygal 1 (Fig. 7B). The free edge of peripheral 4 is strongly upturned anteriorly (Fig. 7C). The epiplastron (Fig. 7D) has a wide and straight anterior border, which is more than the length of epiplastral symphysis. The entoplastron is wide and hexagonal (Fig. 7E), with well developed lateral borders. The marginals overlap onto the costals beginning with marginal 5. The gular is relatively wide (its anterior width is about equal to the length of the epiplastral symphysis) and overlaps the entoplastron. The extragular is relatively small, with a short medial border (about 0.5 of length of epiplastral symphysis). The humeral-pectoral sulcus does not cross the entoplastron.

Remarks. We were not able to examine the material from other localities of the Yalovach Formation (Zamuratsho and Kizylpilyal I, Fergana Depression, Tajikistan; Nessov 1997, pp. 131, 132) reported as *Adocus* sp. cf. *A. foveatus*. Specimens from the Kazakhstan localities Akkurgan, Baybishe I, Buroynak I and II, and Shakh-Shakh, reported as *Adocus foveatus* or *Adocus* sp. cf. *A. foveatus* (Nessov 1997) are considered herein as *Adocus bostobensis*, sp. nov. (see below).

Distribution. Yalovach Formation, early Santonian; Kansai locality, Fergana Depression, Tajikistan.

Adocus kizylkumensis Nessov, 1981
(Fig. 7F–N)

Adocus kizylkumensis: Nessov 1981, p. 70, pl. III, figs. 4, 5; Nessov 1985, p. 216; Narmandakh 1985, p. 86; Nessov 1997, p. 135, pl. 33, figs. 7, 11; Syromyatnikova and Danilov 2007, p. 49.

"*Adocus*" *kizylkumensis*: Sukhanov 2000, p. 333.

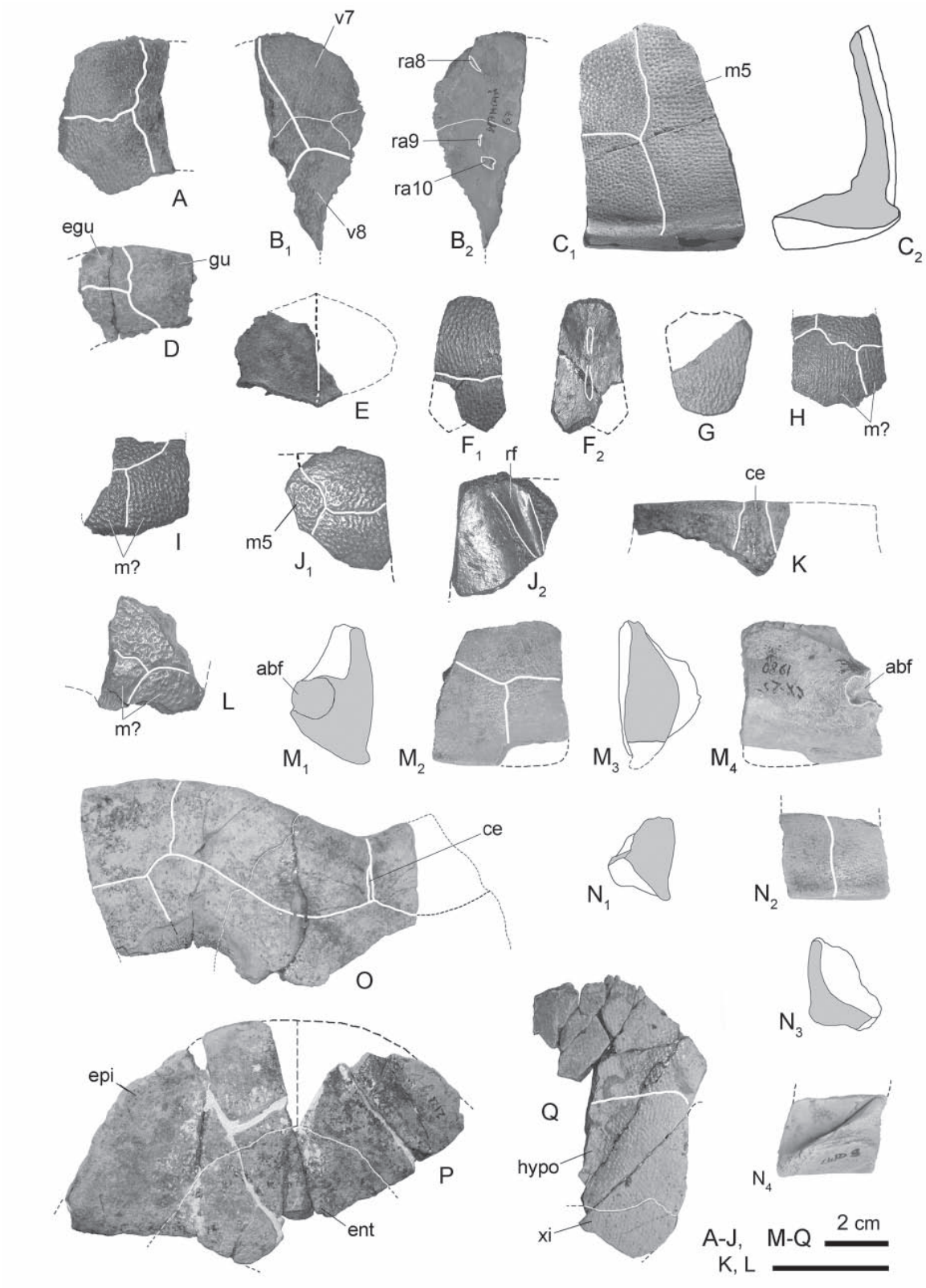
Adocus from the Cenomanian of Sheikhdzheili: Nessov 1981, p. 70.

Adocus (?) sp. (Sheikhdzheili II and Khodzhakulsay): Nessov 1997, pp. 138, 139.

Holotype. ZIN PHT S75-15, lateral part of undetermined costal (Fig. 7I; Nessov 1981, pl. III, fig. 5); Khodzhakul locality (=Khodzhakul I; Nessov 1997, p. 134), Sultanuvais Range, Uzbekistan; lower part of the Khodzhakul Formation, early Cenomanian.

Material. ZIN PH 13/87, neural 1; ZIN PH 8/87, neural 4(?); ZIN PH S78-1, costal 6; ZIN PH 12/87, peripheral 4; ZIN PH 9/87, bridge peripheral; type locality. ZIN PH 20/87, fragment of nuchal; ZIN PH 21/87, undetermined costal fragment; ZIN PH 3/87 and 4/87, peripherals 2; ZIN PH 1/87, peripheral 3; ZIN PH 2/87, peripheral 7; ZIN PH 5/87, undetermined peripheral fragment; ZIN PH 6/87 and 7/87, bridge peripherals; Sheikhdzheili (=Sheikhdzheili II; Nessov 1997, p. 138) and Khodzhakulsay localities, Sultanuvais Range, Uzbekistan; upper part of the Khodzhakul Formation, early Cenomanian.

Fig. 6. *Adocus aksary*, shell fragments, Dzharakuduk, Central Kyzylkum, Uzbekistan; Bissekty Formation, late Turonian: A – ZIN PH 96/84, right peripheral 10: A_1 – posterior view; A_2 – dorsal view; A_3 – anterior view; B – ZIN PH 113/84, left peripheral 11: B_1 – anterior view; B_2 – dorsal view; B_3 – posterior view; C – ZIN PH 124/84, medial part of left epiplastron in ventral view; D – CCMGE 31/12086, right epiplastron: D_1 – ventral view; D_2 – medial view; D_3 – dorsal view; E – ZIN PH 123/84, medial part of right epiplastron in ventral view; F – ZIN PH 126/84, entoplastron, in ventral view; G – ZIN PH 127/84, entoplastron: G_1 – ventral view; G_2 – dorsal view; H – ZIN PH 128/84, posterior part of entoplastron: H_1 – ventral view; H_2 – dorsal view; I – ZIN PH 131/84, fragment of right hypoplastron in ventral view; J – ZIN PH 181/84, fragment of hyoplastron+hypoplastron in ventral view; K – ZIN PH 136/84, fragment of hyoplastron+xiphiplastron: K_1 – ventral view; K_2 – dorsal view; L – ZIN PH 138/84, right xiphiplastron in ventral view; M – ZIN PH 137/84, right xiphiplastron in ventral view. A_2, B_2, C, D_1, D_3, E–M – photographs. A_1, A_3, B_1, B_3, D_2 – drawings. See Figure 3 for abbreviations and designations.


A
v7
v8
B1
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m5
C1
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J1
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abf
M1
M2
M3
abf
M4
ce
O
N1
N2
N3
epi
P
ent
Q
hypo
xi
N4
A-J, M-Q
K, L
2 cm

Differential diagnosis. A species of *Adocus* that can be differentiated from other species of the genus by smaller shell size (except *A. amtgai* and *A. kizylkumensis*). Besides that, it can be differentiated from *A. aksary* and *A. amtgai* by the straight anterior border of the nuchal and overlapping of marginals onto the costals beginning with marginal 5; from *A. amtgai* and *A. beatus* – by shape of the cervical scale. For more detailed comparison see Table 1.

Description. The length of the shell is estimated at about 40 cm (based on ZIN PH 4/87). The nuchal (Fig. 7K) has a straight anterior border, that suggests weak or absent nuchal emargination. The free edge of the nuchal is slightly upturned laterally. The neurals (Fig. 7F, G) are relatively wide and thin. The costals (Fig. 7H, I, L) have no specific peculiarities. The free edge of the anterior peripherals is upturned with a rounded cross-section (Fig. 7M). The morphology of peripherals 2 and 3 generally corresponds to those of *Adocus aksary* (see above), except that musk duct foramen in peripheral 3 is absent. The cervical (Fig. 7K) is trapezoid-shaped, and widened posteriorly. The marginals overlap onto the costals beginning with marginal 5 (Fig. 7J). The degree of this overlapping is variable (Fig. 7H, I, L).

Remarks. *Adocus* from the upper part of the Khodzhakul Formation (Sheikhdzheili II and Khodzhakulsay localities) was considered as *Adocus* (?) sp. (Nessov 1997) due to an assumed difference in age of the lower (late Albian) and upper (early Cenomanian) parts of the Khodzhakul Formation. More recently the whole Khodzhakul Formation is considered to be early Cenomanian in age (Averianov and Archibald 2005). The available specimens do not allow us to differentiate *Adocus* from different parts of the Khodzhakul Formation. For this reason, we refer all *Adocus* from there to *Adocus kizylkumensis*.

Distribution. Khodzhakul Formation, early Cenomanian; localities of the Sultanuvais Range, Uzbekistan.

Adocus dzhurtasensis, sp. nov.
(Fig. 7O–Q)

Adocus sp.: Nessov 1995, p. 136, fig. 2; Nessov 1997, p. 113; Syromyatnikova and Danilov 2007, p. 49.

Holotype. ZIN PHT K27-1, nuchal+left peripheral 1; Dzhurtas locality, Dzhungar Alatau Ridge, south-eastern Kazakhstan; Santonian – early Campanian (Nessov 1995).

Material. ZIN PH 3/92, epiplastron; ZIN PH 1/92, fragment of the anterior lobe, including epiplastra and entoplastron; ZIN PH 4/92, hypoplastron; ZIN PH 5/92, xiphiplastron. The new material was collected by E.I. Belyaeva and M.G. Prokhorov in 1927 in the type locality.

Etymology. The species name is after Dzhurtas locality.

Differential diagnosis. A species of *Adocus* that can be differentiated from other members of *Adocus* by strong nuchal emargination, narrow anterior border of the nuchal, and reduced cervical scale. Besides that, it can be differentiated from all Asiatic *Adocus* by enlarged and thickened elements of the shell, and from *A. foveatus* by more rounded anterior plastral lobe.

Description. The length of the shell is estimated at about 65 cm (based on ZIN PHT K27-1). The anterior border of the carapace has a strong nuchal emargination formed by the nuchal and peripherals 1. The nuchal is deeply emarginated and narrow anteriorly (Fig. 7O). The free edge of the nuchal is not upturned, whereas the free edge of peripheral 1 is

Fig. 7. A–E – *Adocus foveatus*, shell fragments, Kansai, Fergana Depression, Tajikistan; Yalovach Formation, early Santonian: A – ZIN PH 590/64, medial part of right costal 5 in dorsal view; B – ZIN PH 591/64, medial parts of left costals 7+8: B_1 – dorsal view; B_2 – ventral view; C – ZIN PHT F64-11 (holotype), left peripheral 4: C_1 – dorsal view; C_2 – anterior view; D – ZIN PH 592/64, medial part of right epiplastron in ventral view; E – ZIN PH 594/64, entoplastron in ventral view; F–N – *Adocus kizylkumensis*, shell fragments, Khodzhakul, Khodzhakulsay and Sheikhdzheili localities, Sultanuvais Range, Uzbekistan; Khodzhakul Formation, early Cenomanian: F – ZIN PH 13/87, neural 1: F_1 – dorsal view; F_2 – ventral view; G – ZIN PH 8/87, neural 4 in dorsal view; H – ZIN PHT S78-1, lateral part of left costal 6 in dorsal view; I – ZIN PHT S75-15 (holotype), lateral part of undetermined costal in dorsal view; J – ZIN PH 12/87, fragment of right peripheral 4: J_1 – dorsal view; J_2 – ventral view; K – ZIN PH 20/87, fragment of nuchal in dorsal view; L – ZIN PH 21/87, lateral fragment of costal in dorsal view; M – ZIN PH 4/87, peripheral 2: M_1 – posterior view; M_2 – dorsal view; M_3 –anterior view; M_4 – ventral view; N – ZIN PH 1/87, peripheral 3: N_1 – anterior view; N_2 – dorsal view; N_3 – posterior view; N_4 – ventral view; O–Q – *Adocus dzhurtasensis*, sp. nov., shell fragments, Dzhurtas, Dzhungar Alatau Ridge; Kazakhstan, Santonian – early Campanian: O – ZIN PHT S 27-1 (holotype), fragment of nuchal + left peripheral 1 in dorsal view; P – ZIN PH 1/92, fragment of anterior lobe in ventral view; Q – ZIN PH 4/92, fragment of left hypoplastron in ventral view. A–C_1, D–L, M_2, M_4, N_2, N_4–Q – photographs. C_2, M_1, M_3, N_1, N_3 – drawings. See Figure 3 for abbreviations and designations.

slightly upturned. The anterior lobe of the plastron is rounded (Fig. 7P). The epiplastra are strongly thickened anteriorly. The entoplastron seems to be a wide tetragonal. The free edge of the hypoplastron is long and almost parallel to the plastron midline (Fig. 7Q). The cervical scale is strongly reduced.

Distribution. Santonian – early Campanian; Dzhurtas locality, Dzhungar Alatau Ridge, Kazakhstan.

Adocus bostobensis, sp. nov.
(Fig. 8A–N)

Basilemys sp.: Kuznetsov 1977, p. 124; Kuznetsov and Chkhikvadze 1987, p. 33.

Adocus foveatus (part.): Nessov 1985, p. 220.

Adocus foveatus (Buroynak, Baybishe and other localities of northeastern Aral Sea area): Nessov 1995, p. 136.

Adocus foveatus (Akkurgan, Baybishe I, Shakh-Shakh): Nessov 1997, pp. 109, 111.

Adocus sp. cf. *Adocus foveatus* (Buroynak I): Nessov 1997, p. 111.

Adocus sp. (Buroynak II): Nessov 1997, p. 111;

Adocus sp. (Akkurgan, Baybishe, Boroynak, Shakh-Shakh): Syromyatnikova and Danilov 2007, p. 49.

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

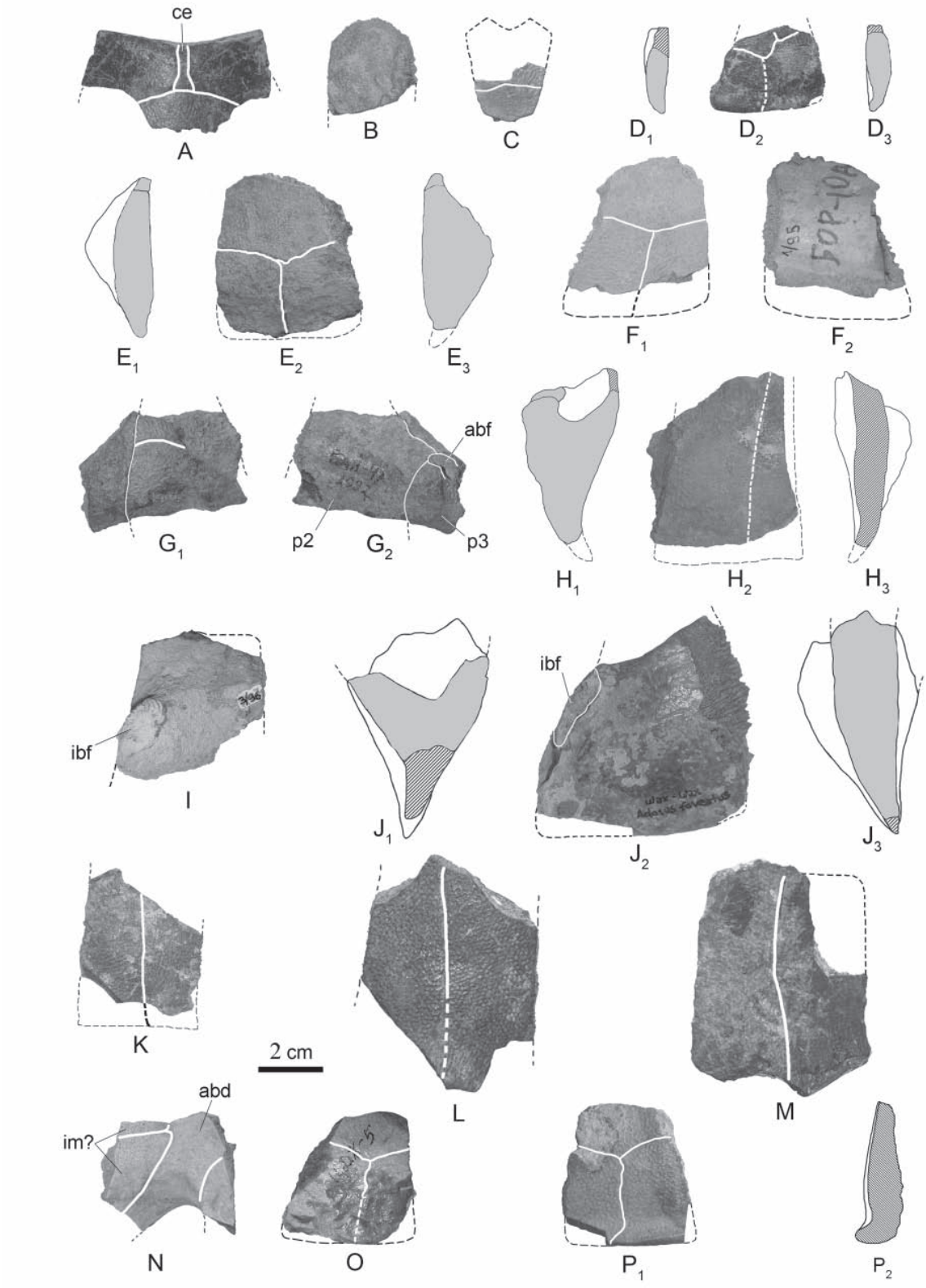
Material. ZIN PH 14/94, neural 1; ZIN PH 4/94, undetermined costal fragment; ZIN PH 2/94, peripherals 2+3; ZIN PH 3/94, peripheral 8; ZIN PH 11/94, bridge peripheral; ZIN PH 5/94, hypoplastron; ZIN PH 6/94, hypoplastron+xiphiplastron; ZIN PH 7-13/94, undetermined shell fragments; type locality. ZIN PH 1/96, peripheral 1; ZIN PH 2/96, 3/96, peripherals 8; ZIN PH 4/96, undetermined shell fragment; Akkurgan locality. ZIN PH 6/95, neural; ZIN PH 1/95, peripheral 2; ZIN PH 7/95, peripheral 9; ZIN PH 2/95, 3/95, undetermined fragments of peripherals; ZIN PH 4/95, 5/95, 8/95, 9/95, undetermined shell fragments; Buroynak locality (=Buroynak I and II; Nessov 1997, pp. 110, 111). ZIN PH 95/10, peripheral 1; ZIN PH 96/10, peripheral 2; ZIN PH 103/10, 104/10, peripherals 8; IZK 3970 and 3971, posterior peripherals; Shakh-Shakh locality. All localities are from the northeastern Aral Sea area, Kazakhstan; Bostobe Formation, Santonian–early Campanian.

Etymology. The species name is after Bostobe Formation.

Differential diagnosis. A species of *Adocus* that can be differentiated from other members of *Adocus* by larger shell size. Besides that, it can be differentiated from other *Adocus* of the studied area by shape of the cervical and from *A. bossi* by the presence of the nuchal emargination. Additional differences from *Adocus dzhurtasensis* are given above.

Description. The length of the shell is estimated at 100 cm (based on ZIN PH 103/10). The nuchal (Fig. 8A) is weakly emarginated anteriorly. The free edge of the nuchal is slightly upturned laterally. The neurals are relatively wide and thin (Fig. 8B, C). The peripherals show no differences from those of *Adocus askary* (Fig. 8D–M) except that the grooves for the musk ducts are absent in the available specimens. Peripheral 8 is from a large individual (Fig. 8J; ZIN PH 103/10) and has an oblique posterior sutural surface that suggests a strong overlapping of peripheral 8 with peripheral 9. The cervical is narrow and slightly widened in its posterior third (Fig. 8A). The hypoplastron fragment (Fig. 8N) shows parts of the abdominal, femoral, and two posterior inframarginals. The most posterior inframarginal (?4) is separated from the femoral by the abdominal.

Fig. 8. A–N – *Adocus bostobensis*, sp. nov., shell fragments, Akkurgan, Baybishe, Buroynak and Shakh-Shakh localities, northeastern Aral Sea area, Kazakhstan; Bostobe Formation, Santonian – early Campanian: A – ZIN PH 1/94 (holotype), fragment of nuchal in dorsal view; B – ZIN PH 14/94, fragment of neural 1 in dorsal view; C – ZIN PH 6/95, fragment of neural (?)5 in dorsal view; D – ZIN PH 95/10, fragment of left peripheral 1: D_1 – anterior view; D_2 – dorsal view; D_3 – posterior view; E – ZIN PH 96/10, left peripheral 2: E_1 – anterior view; E_2 – dorsal view; E_3 – posterior view; F – ZIN PH 1/95, fragment of right peripheral 2: F_1 – dorsal view; F_2 – ventral view; G – ZIN PH 2/94, fragments of right peripherals 2+3: G_1 – dorsal view; G_2 – ventral view; H – ZIN PH 2/96, left peripheral 8: H_1 – anterior view; H_2 – dorsal view; H_3 – posterior view; I – ZIN PH 3/96, fragment of right peripheral 8 in ventral view; J – ZIN PH 103/10, left peripheral 8: J_1 – anterior view; J_2 – ventral view; J_3 – posterior view; K – ZIN PH 3/94, fragment of right peripheral 8 in dorsal view; L – IZK 3970, posterior peripheral in dorsal view; M – IZK 3971, posterior peripheral in dorsal view; N – ZIN PH 5/94, fragment of right hypoplaston in ventral view; O–P – *Adocus* sp. indet., shell fragments, Itemir, Central Kyzylkum, Uzbekistan; Bortesken Member, Cenomanian: O – ZIN PH 1/86, right peripheral 2 in dorsal view; P – ZIN PH 2/86, left peripheral 2: P_1 – dorsal view; P_2 – posterior view. A–C, D_2, E_2, F–G, H_2, I, J_2, K–O, P_1 – photographs. D_1, D_3, E_1, E_3, H_1, H_3, J_1, J_3, P_2 – drawings. See Figure 3 for abbreviations and designations.


ce
A
B
C
D1
D2
D3
E1
E2
E3
F1
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G1
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H1
H2
H3
ibf
I
J1
ibf
J2
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2 cm
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O
P1
P2

Remarks. The posterior peripherals (IZK 3970 and 3971) with a characteristic sculpturing from the Shakh-Shakh locality, long considered as a nanhsiungchelyid (*Basilemys* sp.; Kuznetsov 1977; Kuznetsov and Chkhikvadze 1987), were assigned to *Adocus foveatus* by Nessov (1997, p. 109) based on photographs. Our observation of these specimens (Fig. 8L, M) confirms their assignment to *Adocus*. Material from this and other localities of the Bostobe Formation (Akkurgan, Baybishe I, Buroynak I and II) were considered as *A. foveatus*, *Adocus* sp. cf. *A. foveatus*, or *Adocus* sp. (see Nessov 1997) without any evidence. Here we consider all these specimens as *Adocus bostobensis* sp. nov.

Distribution. Bostobe Formation, Santonian – early Campanian; localities of the northeastern Aral Sea area, Kazakhstan.

***Adocus* sp. indet.**
(Fig. 8O, P)

Material. ZIN PH 1/86, peripheral 2; CDZH-5 local site; ZIN PH 2/86, peripheral 2; CDZH-3 local site; Itemir locality, Central Kyzylkum, Uzbekistan; Bortesken (CDZH-5) and Dzharakuduk (CDZH-3) members, Cenomanian (Nessov 1997).

Description. The shell length is estimated at 30 cm (based on ZIN PH 1/86). The peripherals have a typical *Adocus* morphology: the free edge is upturned and the surface of the plates is covered with a characteristic sculpturing.

Remarks. The described specimens present the first reliable remains of *Adocus* from Itemir locality. Previously, only *Ferganemys itemirensis* Nessov, 1981 (Nessov 1981), Adocidae: cf. *Ferganemys* or cf. *Adocus* and Adocidae indet. (Nessov 1997, pp. 136, 137) have been mentioned from Itemir. The finding of *Adocus* sp. indet. in Itemir represents a new link between turtle assemblage of Itemir and those of the Khodzhakul Formation (Nessov 1997). *Adocus* sp. indet. from Itemir is similar to *A. kizylkumensis* from the Khodzhakul Formation in its small size.

DISCUSSION

Our study allows us to emend the diagnoses of the previously known *Adocus* species from the Late Cretaceous of Middle Asia and Kazakhstan and describe new material of *Adocus* from this region. Our study makes *Adocus aksary* one of the best known Asiatic members of the genus, being represented by the skull and most parts of the shell. Other species of *Adocus* from the region of the study (*Adocus bostobensis*, *A. dzhurtasensis*, *A. foveatus*, and *A. kizylkumensis*) are known only by some details of shell morphology. On the whole, our data demonstrate a greater diversity of the Santonian–Campanian *Adocus* of Middle Asia and Kazakhstan than previously known.

New specimens allow us to present the shell reconstruction of *Adocus aksary*. Among new characters of this species, the most interesting is the extension of the marginals onto the costals beginning with marginals 3 or 4, but not with marginal 5 as previously reported by Nessov and Krasovskaya (1984). In this character, *A. aksary* is similar to *A. amtgai*. However, here we refrain from uniting of these two species within the proposed genus *Adocoides* until further study of the available undescribed material on *A. amtgai* (Danilov et al. in preparation).

New specimens of *Adocus aksary* give us some idea about variation of the shell characters in this species. This include, besides mentioned variation in the marginal extension onto the costals, shape of the cervical and vertebrals, and position of the gular-humeral and humeral-pectoral sulci in relation to the entoplastron. Similar variation is known in other *Adocus* species (see Table 1).

Our study also presents new observations on *Adocus* morphology in general. These include details of morphology of peripherals 2 and 8, which have peculiar bulges in place of attachment of plastral buttresses in all *Adocus* studied by us. Among other examined adocids, similar bulges are present only in *Ferganemys verzilini*, whereas in *F. itemirensis* and species of *Shachemys* bulges are absent. Another important character, although noted only in *Adocus aksary*, is the presence of one pair of the musk ducts at peripheral 3/hyoplastron border. The presence of the musk ducts (two pairs) has been recently reported in species of *Ferganemys* and *Shachemys* (Danilov et al. 2007) and is reported here for *Adocus* for the first time.

Besides the specimens described above, remains of *Adocus* from the Late Cretaceous of Middle Asia and Kazakhstan have been reported from the following localities: Baytuma, Kazakhstan, Sasykol Formation, Late Cretaceous (*Adocus* sp.; Nessov 1997, p. 115); Dzharakuduk (=Dzhirakuduk II), Central Kyzylkum, Uzbekistan; lower part of the Aytym For-

mation, Santonian (cf. *Adocus* sp.; ibid., p. 152); Kan, northern Fergana, Kyrgyzstan; Sharikhan Formation, Cenomanian (*Adocus* sp. or large-sized *Ferganemys* sp; ibid., p. 118); Karakul, Uzbekistan, Sultanbobo Formation, late Aptian (cf. *Adocus* sp.; ibid., p. 133); Kizylpilyal II, north-western Fergana, Tajikistan, lower part of Palvantash Formation, late Santonian – ?early Campanian (*Adocus foveatus*; ibid., p. 132); Syuk-Syuk, Circum-Tashkent Chul, Kazakhstan; Syuk-Syuk Formation, Santonian (*Adocus*? sp.; ibid., p. 108); Shatyrtyube I, Central Kyzylkum, Uzbekistan; Santonian sands and gravelites (*Adocus* sp., ibid., p. 154). Our examination of turtle specimens from the Syuk-Syuk and Shatyrtyube I localities in ZIN PH collections, used by Nessov in his study, does not reveal any remains of *Adocus*. Thus, the presence of *Adocus* in these and other mentioned localities needs confirmation.

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