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TURTLES OF THE GENUS *FERGANEMYS* NESSOV ET KHOSATZKY, 1977 (ADOCIDAE): SHELL MORPHOLOGY AND PHYLOGENETIC POSITION

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ABSTRACT

This paper describes the morphology and variation of the shell in turtles of the genus *Ferganemys* Nessov et Khosatzky, 1977 (Adocidae). *Ferganemys itemirensis* Nessov, 1981 is described in detail for the first time based on previously published and new material (more than 400 isolated shell plates) from the Upper Cretaceous (Cenomanian) of Uzbekistan. New diagnoses and shell reconstructions for two species of *Ferganemys* are given. Inclusion of new observations of *Ferganemys* into a phylogenetic analysis of Adocusia (the clade uniting Adocidae and Nanhsiungchelyidae) does not support the monophyly of this genus, but rather suggests that *Ferganemys* species form a polytomy with the *Shachemys* clade.

Key words: Adocidae, Cretaceous, *Ferganemys*, Testudines, Uzbekistan

ЧЕРЕПАХИ РОДА *FERGANEMYS* NESSOV ET KHOSATZKY, 1977 (ADOCIDAE): МОРФОЛОГИЯ ПАНЦИРЯ И ФИЛОГЕНЕТИЧЕСКОЕ ПОЛОЖЕНИЕ

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РЕЗЮМЕ

В работе описывается морфология и изменчивость панциря черепах рода *Ferganemys* Nessov et Khosatzky, 1977 (Adocidae). Ранее установленный таксон *Ferganemys itemirensis* Nessov, 1981 впервые описывается подробно на основе ранее опубликованных и новых материалов (более 400 изолированных пластинок панциря) из позднего мела (сеноман) Узбекистана. Приводятся новые диагнозы и реконструкции панцирей ферганемисов. Включение новых данных по *Ferganemys* в филогенетический анализ Adocusia (клады объединяющей Adocidae и Nanhsiungchelyidae) не поддерживает монофилию рода, а скорее предполагает, что виды ферганемиса образуют политомию с кладой *Shachemys*.

Ключевые слова: Adocidae, мел, *Ferganemys*, Testudines, Узбекистан

INTRODUCTION

The genus *Ferganemys* Nessov et Khosatzky, 1977 was established for *Ferganemys verzilini* Nessov et Khosatzky, 1977, a small species (up to 20 cm in the shell length) of freshwater turtles, based on fragmentary shell and skull material from the Lower Cretaceous (Albian) of Kyrgyzstan (Fig. 1; Kylodzhun locality; Nessov 1977; Nessov and Khosatzky 1977).

Confident attribution of *Ferganemys verzilini* to the family Adocidae Cope, 1870, subfamily Shachemydinae Khosatzky in Nessov et Khosatzky, 1977, is supported by a number of characters, including sculpturing of the shell surface with relatively small and regular pits, weak rib heads and costal rib thickenings, and low marginals that are restricted to the peripherals (Nessov 1977; Nessov and Khosatzky 1977; Danilov et al. 2007; Danilov and Syromyat-

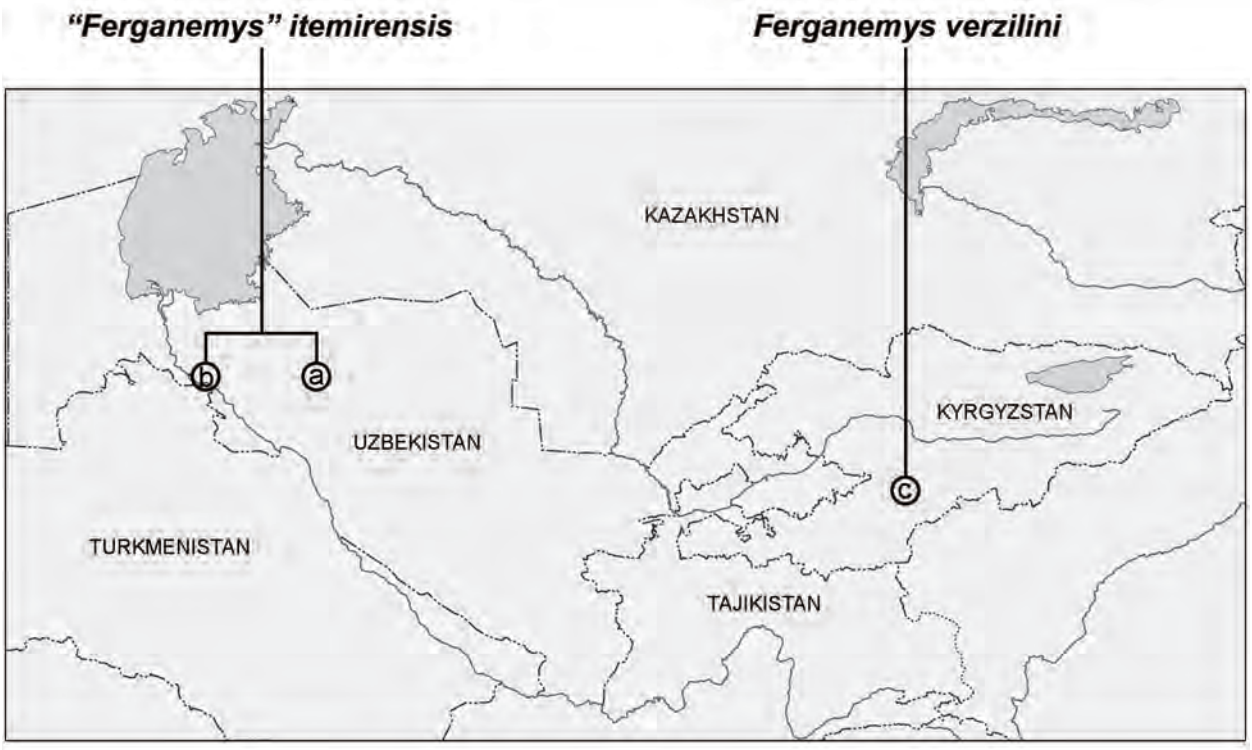


Fig. 1. Map showing the geographic distribution of "*Ferganemys*" Nessov et Khosatzky 1977 in the Cretaceous of Asia (confirmed data only): a – Itemir, Central Kyzylkum, Uzbekistan; Kulbikin Member, Cenomanian, Upper Cretaceous; b – Chelpyk, Khodzhakulsay and Sheikhdzheili, Sultanuvais Range, Uzbekistan; upper part of the Khodzhakul Formation, early Cenomanian, Upper Cretaceous; c – Kylodzhun (=Klaudzin) locality; south-eastern Fergana Depression, Kyrgyzstan; upper part of the Alamyshik Formation, lower-middle Albian, Lower Cretaceous.

nikova 2009a, 2009b). The placement of *Ferganemys* within the subfamily Adocinae Cope, 1870 suggested by Nessov and Krasovskaya (1984) is not supported by modern phylogenetic studies (Lapparent de Broin 2004; Danilov and Syromyatnikova 2009a, 2009b). *Ferganemys* differs from the closely related genus *Shachemys* Kuznetsov, 1976 (Cretaceous of Asia) mainly by the presence of primitive characters, such as the presence of seven neurals and two suprapygals, absence of an epi-entohyoplastral hinge (in adults), and sculpturing of the shell (Danilov et al. 2007; see below). The second species of *Ferganemys*, *Ferganemys itemirensis* Nessov, 1981, is based on two imprints of shell fragments from the Upper Cretaceous (Cenomanian) of Uzbekistan (Fig. 1; Itemir locality; Nessov 1981). Additional fragmentary shell specimens from other localities in Uzbekistan (Khodzhakul[1], Khodzhakulsay and Sheikhdzheili) were later referred to *F. itemirensis* (Nessov and Krasovskaya 1984). A reconstruction of the shell of *F. itemirensis* and some additional details of its shell morphology were provided by Nessov (1986: 18, 19, fig. 8). According to published data, *F. itemirensis* differs from *F. verzilini* by larger shell size (up to 40 cm), thickened elements of the shell, and other characters (see below). However, the abundant material that was the basis for the published shell reconstruction of *F. itemirensis* has never been described. New material of this species was collected during the last few years (see Material and methods) demanding a comprehensive review of this taxon. As shown by Syromyatnikova and Danilov (2009), at least a part of the material assigned to *F. itemirensis* actually belongs to the genus *Adocus* Cope, 1868.

[1] Khodzhakul locality (lower part of the Khodzhakul Formation, early Cenomanian) was indicated by mistake and has no any remains of *Ferganemys*. Other member of Adocidae, *Adocus kizylkumensis* Nessov, 1981, was described from this locality (Nessov 1981).

The aim of this paper is to provide detailed descriptions of the shell morphology of *F. itemirensis* based on the study of published and new specimens. New observations allow clarifying the diagnostic characteristics of *Ferganemys* species and studying their phylogenetic position. Syromyatnikova (2009) published some preliminary results of this study. As this study does not support the monophyly of *Ferganemys* (see below), I hereinafter refer to *F. itemirensis* as "*Ferganemys*" *itemirensis*.

Institutional abbreviations. CCMGE, Chernyshev's Central Museum of Geological Exploration, Saint Petersburg, Russia; ZIN PH (=ZIN PHT), Paleoherpetological collection, Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia.

MATERIAL AND METHODS

This study is based on abundant material (more than 400 isolated shell fragments) on "*F.*" *itemirensis* from the following localities: Itemir, Central Kyzylkum, Uzbekistan; Kulbike Member, Cenomanian, Upper Cretaceous (collections ZIN PH 86 and ZIN PHT K77); Chelpyk, Khodzhakulsay and Sheikhdzheili, Sultanuvais Range, Uzbekistan; upper part of the Khodzhakul Formation, lower Cenomanian, Upper Cretaceous (collections CCMGE 12086, 12458; ZIN PH 87 and ZIN PHT S74 and S75). All these materials were collected by expeditions of Lev Nessov and his students from Leningrad (St. Petersburg) State University (up to 1994) and by the international paleontological URBAC expeditions (1997–2008). For detailed list of materials on "*F.*" *itemirensis* see Systematics.

For comparison we used material on *F. verzilini* (collection ZIN PH T/F67) including about 3000 shell fragments from Kylodzhun (=Klaudzin) locality, south-eastern Fergana Depression, Kyrgyzstan; upper part of the Alamyshik Formation, lower-middle Albian, Lower Cretaceous (see Nessov and Khosatzky 1977). Besides that, some data on the shell morphology of the genera *Adocus* and *Shachemys* were also used (see Danilov et al. 2007; Syromyatnikova and Danilov 2009).

Anatomical terms of the shell follow Zangerl (1969) and Hutchison and Bramble (1981).

The phylogenetic position of the species of *Ferganemys* was analyzed using computer assisted cladistic analysis. The list of characters and the data matrix are based on the analysis of Danilov and Syromyatnikova (2009a, 2009b), but the following changes were undertaken: character 42 (cervical scale) for "*F.*" *itemirensis* is changed from "0" (present) to "0/1" (present or absent); character 67 (number of inframarginal scales) for *F. verzilini* is changed from "0" (four or three pairs) to "1" (two pairs); character 68 (additional pair of inframarginal scales on the hyoplastron) is removed (see Discussion). We add to the analysis two additional characters: 68 (neural 1): "0" (widened posteriorly), "1" (constricted posteriorly); 75 (medial part of hypoplastron): "0" (not thickened), "1" (thickened). See Appendix 1 for the distribution of character states among taxa sampled.

The final data matrix includes 75 osteological characters for 23 taxa. The data matrix was assembled using NDE 0.5.0 (Page 2001) and analyzed with PAUP 4.0b 10 (Swofford 2002). 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 Shachemydinae Khosatzky in Nessov et Khosatzky, 1977

Genus *Ferganemys* Nessov et Khosatzky, 1977

Remarks. In addition to the specimens described below, remains of *Ferganemys* sp. (without any descriptions and illustrations) were reported from the following localities: Ayazkala, southern Ayazkala Upland, south-western Kyzylkum; upper part of the Khodzhakul Formation, early Cenomanian, Upper Cretaceous (Nessov 1997: 140); Karatepa, Sultanuvais Range, Uzbekistan; upper part of the Khodzhakul Formation, early Cenomanian; Khodzhakul (=Khodzhakul II), Sultanuvais Range, south-western Kyzylkum, Uzbekistan; phosphate sand, late Paleocene, Paleogene (probably, Cretaceous) (as *Ferganemys* sp. cf. *F. itemirensis*; Nessov 1997, p. 155).

Ferganemys verzilini Nessov et Khosatzky, 1977
(Fig. 2A)

Ferganemys verzilini Nessov and Khosatzky, 1977: 249, figs. 1–3, pl., figs. 1–24; Nessov 1977: 78, figs. 1, 2, XII, XIII (figs. 1, 2); Nessov and Yulinen 1977: 54; Nessov 1986: fig. 7; Nessov 1987: fig. 5, pl. I, fig. 15, pl. II, fig.

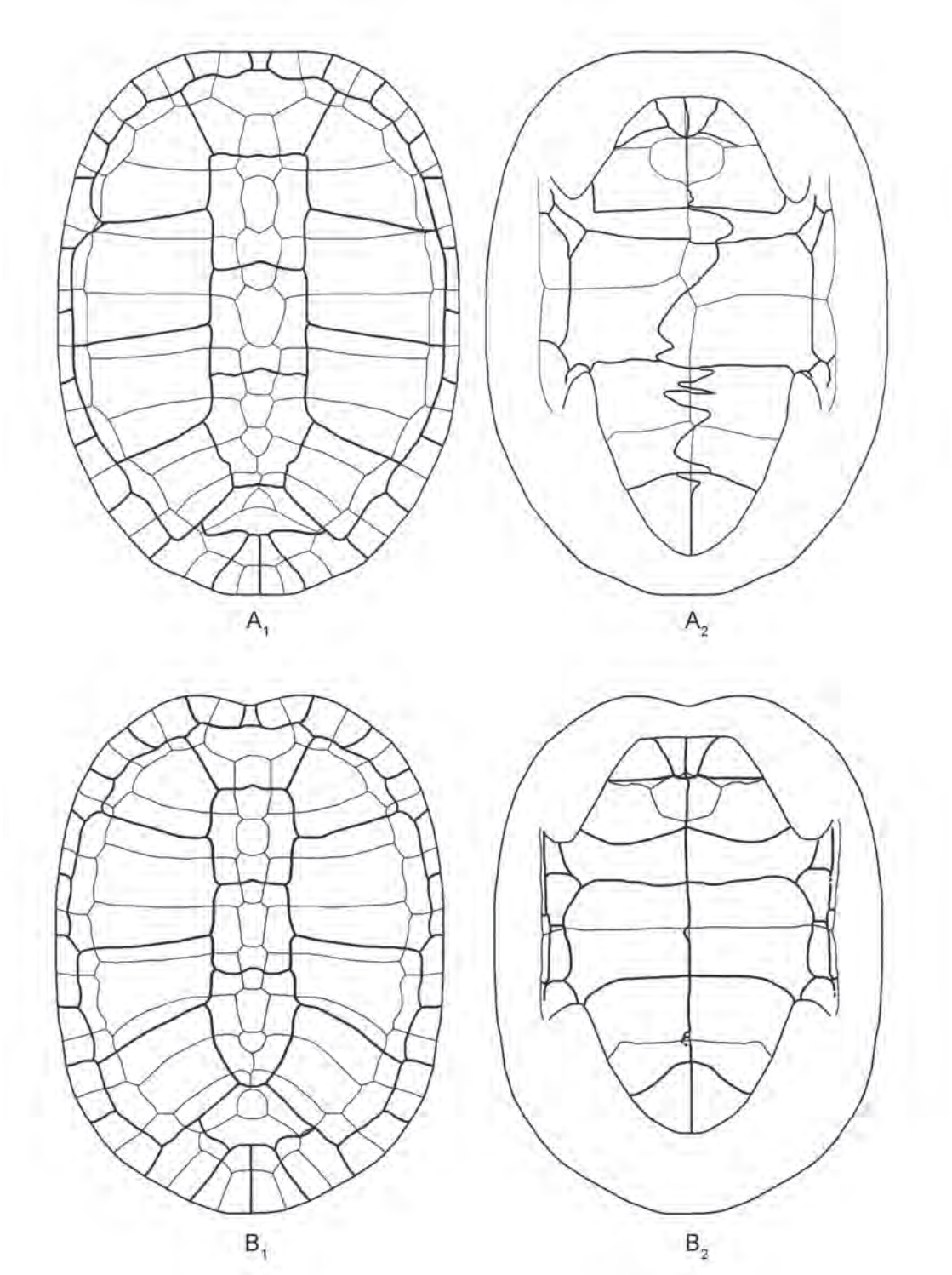


Fig. 2. *Ferganemys*, new reconstructions of the shell: A – *Ferganemys verzilini* Nessov et Khosatzky, 1977: A_1 – dorsal view; A_2 – ventral view; B – "*Ferganemys*" *itemirensis* Nessov, 1981: B_1 – dorsal view; B_2 – ventral view. The outlines of the carapace and plastron are shown approximately. Without scale. Variation of scalation is shown in the left and right parts of the shell.

7; Nessov 1997: 117, pl. 35, figs. 8, 9; pl. 36–38; Danilov and Syromyatnikova 2009a: 69, 71, 82; 2009b: 44, 50; Syromyatnikova 2009: 39.

Holotype. ZIN PH T/F67-7, partial plastron (Nessov and Khosatzky 1977, pl., fig. 1); Kylodzhun (=Klaudzin) locality, south-eastern Fergana Depression, Kyrgyzstan; upper part of the Alamyshik Formation, lower-middle Albian, Lower Cretaceous.

Material. About 3000 shell fragments from the type locality.

Differential diagnosis. A species of *Ferganemys* that can be differentiated from "*F.*" *itemirensis* and *Shachemys* spp. by smaller size of the shell (except *Shachemys laosiana* Lapparent de Broin, 2004), absence of nuchal emargination (except *Sh. laosiana*), wide anterior border of the nuchal, upturned free edges of nuchal and anterior peripherals, presence of bulges at places of attachment of plastral buttresses on the peripherals 2 and 8, long and posteriorly narrow posterior lobe of the plastron, presence of one or two pairs of inframarginals, strongly sinuous midline sulcus, weakly thickened medial border of hypoplastra. It can also be differentiated from "*F.*" *itemirensis* by the presence of posteriorly widened hexagonal neural 1, wider neurals, thinner neurals and posterior peripherals, and a wide and short (nearly square) cervical. For additional differences, see Table 1.

Distribution. Type locality.

"*Ferganemys*" *itemirensis* Nessov, 1981
(Figs. 2B; 3–5)

Ferganemys itemirensis Nessov, 1981: 70, figs. III, 6, 7; Nessov and Krasovskaya 1984: 23, pl. 3, figs. 21–28, pl. 4, fig. 14; Nessov 1986: fig. 8; Nessov 1997: 138, 139, pl. 34, figs. 5, 6, 10–15, 18, pl. 35, figs. 1, 2; Danilov and Syromyatnikova 2009a: 69, 71, 82; Syromyatnikova 2009: 39; Danilov and Syromyatnikova 2009b: 44, 50.
Ferganemys, Nessov 1981: 71, pl. III, figs. 8–10.
Ferganemys verzilini (Chelpyk), Nessov 1997: 140.
Ferganemys sp., Nessov 1997: pl. 34, figs. 7–9.
Adocidae indet., Nessov 1997: pl. 33, fig. 6.

Holotype. ZIN PHT K77-1, imprint of the posterior part of carapace (Fig. 4I; Nessov 1981: fig. III 7); Itemir locality, Central Kyzylkum, Uzbekistan; Kulbike Member, Cenomanian, Upper Cretaceous.

Paratype. ZIN PHT K77-2, imprint of the interior (dorsal) surface of hyo-, epi- and entoplastron, as well as a neural from the type locality (Fig. 4J; Nessov 1981: fig. III 6).

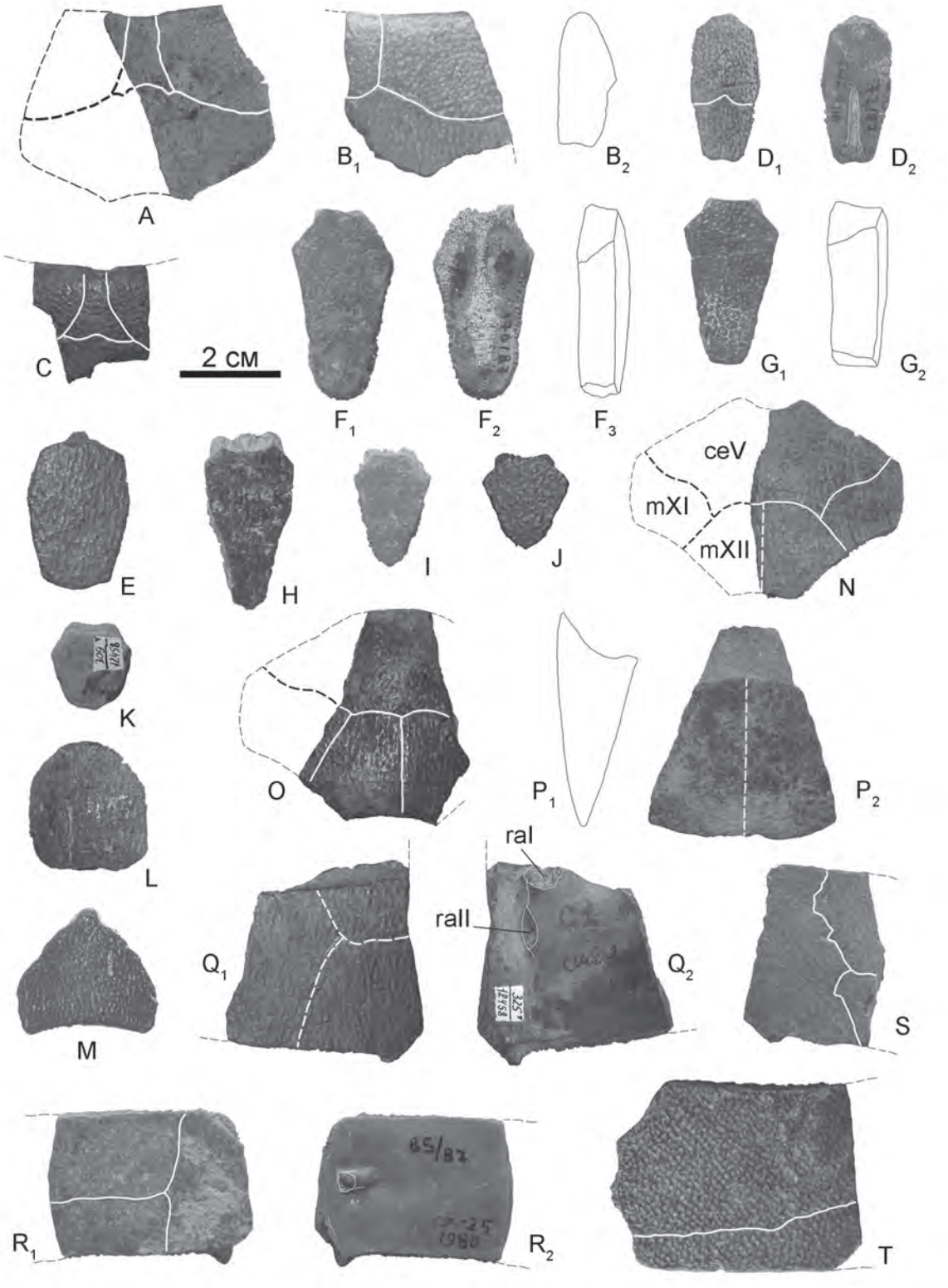
Material. Chelpyk, Khodzhakulsay and Sheikhdzheili localities, Sultanuvais Range, Uzbekistan; upper part of the Khodzhakul Formation, lower Cenomanian, Upper Cretaceous: **nuchals**: CCMGE 21/12086, 304–308/12458, 436/12458; ZIN PH 50–56/87, 190–194/87, 249/87, 250/87; ZIN PHT S75-22, S75-27; **neurals 1**: ZIN PH 72/87, 73/87; **neural 2**: CCMGE 311/12458; **neurals**: CCMGE 310/12458, 312–314/12458, 316–321/12458, 438/12458, 448–452/12458; ZIN PH 57–71/87, 176–188/87, 251–255/87; ZIN PHT S75-24, S75-25, S74-1; **neurals 7**: CCMGE 309/12458, 315/12458; ZIN PH 189/87; **suprapygals 1**: CCMGE 437/12458; ZIN PH 74/87, 75/87; **suprapygals 2**: CCMGE 351–354/12458, 446/12458; ZIN PH 244/87; ZIN PHT S75-26; **pygals**: CCMGE 390/12458; ZIN PH 170/87, 171/87; **costals**: CCMGE 324/12458, 325/12458, 443/12458; ZIN PH 76/87, 77/87; **costals 7**: CCMGE 343/12458; ZIN PH 93/87; **costals 8**: CCMGE 323/12458, 344/12458, 345/12458, 439/12458; ZIN PH 90–92/87, 173/87; **costals 7+8**: CCMGE 440/12458; **peripherals 1**: CCMGE 355–365/12458, 376/12458; ZIN PH 94–101/87, 110/87, 135–138/87, 149/87; ZIN PHT S75–20; **peripherals 2**: CCMGE 27/12086, 367/12458, 385/12458; ZIN PH 102–109/87, 141–146/87; **peripherals 3**: CCMGE 366/12458, 369/12458; ZIN PH 111–113/87; **bridge peripherals**: CCMGE 368/12458, 370/12458, 374/12458, 444/12458; ZIN PH 114/87, 115/87, 118–134/87, 139/87, 140/87, 148/87, 235–243/87; **peripheral 7**: ZIN PH 150/87; **peripherals 8**: CCMGE 371–373/12458; ZIN PH 151–154/87; **peripheral 9**: ZIN PH 155–157/87; **peripherals 10**: CCMGE 380/12458, 391/12458, 392/12458; ZIN PH 160/87, 161/87; **peripherals 11**: CCMGE 379/12458, 383/12458, 384/12458, 386/12458; ZIN PH 162–169/87; **epiplastra**: CCMGE 22–26/12086, 28a/12086, 395–397/12458, 399–406/12458; ZIN PH 195–204/87, 233/87, 234/87; **entoplastra**: CCMGE 394/12458, 398/12458, 442/12458; ZIN PH 205–209/87; **hyoplastra**: CCMGE 407/12458, 408/12458, 414/12458, 417/12458, 418/12458, 424/12458; ZIN PH 210–213/87, 232/87; **hypoplastra**: CCMGE 413/12458, 415/12458, 420/12458, 421/12458, 429–435/12458, 442/12458; ZIN PH 214–222/87, 227–229/87; **bridge parts of plastron**: CCMGE 410–412/12458, 416/12458, 419/12458, 422/12458, 423/12458, 425–427/12458; **xiphiplastra**: CCMGE 441/12458, 445/12458, 447/12458; ZIN PH 223–226/87.

Table 1. Comparison of shell characters of some representatives of Adocidae.

Characters	*Adocus*	*F. verzilini*	*"F." itemirensis*	*Shachemys*
Number of neurals	6	6 or 7	7	Absent or only first
Number of suprapygals	2	2	2	1
1 and 2 thoracic ribs	Lie close to each other	Lie close to each other	Lie close to each other	Separated by a gap
Free edge of anterior peripherals	Acute or rounded, with upturned edge	Rounded, with upturned edge	Rounded without upturned edge	Rounded, without upturned edge
Cervical scale	Present	Present	Absent or present	Absent
Vertebral 1 overlapping peripherals 2	Absent	Absent	Absent	Present
Marginals strongly overlapping costals	Present (4–11 pairs)	Absent (except 11 pairs)	Absent (except 11 pairs)	Absent (except 11 pairs)
Epi-entohyoplastral hinge	Absent	Absent or present	Absent or present	Present
Entoplastron wedges between epiplastra	Present	Absent	Absent	Absent
Gulars overlapping entoplastron	Present	Absent or present	Absent or present	Absent
Pectorals overlap entoplastron	Absent or present	Absent	Absent	Absent or present
Midline sulcus of the plastron	Sinuous	Sinuous	Straight	Straight or sinuous
Number and shape of the inframarginals	Three or four pairs, narrow	One or two pairs, narrow	Four pairs, narrow	Four pairs, wide
Sculpturing of the shell surface	Pitted	Pitted	Pitted	Dotted

Itemir locality, Central Kyzylkum, Uzbekistan; Kulbike Member, Cenomanian, Upper Cretaceous: **nuchal**: ZIN PH 20/86; **neural**: ZIN PH 21/86; **peripherals 1**: ZIN PH 22/86, 23/86, 26/86; **peripherals 2**: ZIN PH 29/86, 30/86; **bridge peripheral**: ZIN PH 25/86; **peripherals 8**: ZIN PH 27/86, 28/86; **peripheral 9**: ZIN PH 31/86; **peripheral 10**: ZIN PH 32/86; **imprint of posterior part of carapace**: ZIN PHT K77-1 (holotype); **hyoplastron**: ZIN PH 34/86; **hypoplastra**: ZIN PH 35/86, 36/86; **imprint of interior surface of hyo-, epi- and entoplastron and neural:** ZIN PHT K77-2 (paratype).

Differential diagnosis. "*Ferganemys*" *itemirensis* differs from *F. verzilini* and *Shachemys* spp. by the presence of thickened neurals and posterior peripherals and more thickened medial border of the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hypoplastra. It can also be differentiated from *F. verzilini* by larger size of the shell, presence of a nuchal emargination, narrow anterior border of the nuchal, rounded free edges of the nuchal and anterior peripherals, presence of a posteriorly constricted neural 1, narrower neurals, absence of bulges at places of attachment of the plastral buttresses on the peripherals 2 and 8, trapezoid-shaped cervical, short and wide posterior lobe of the plastron, presence of four pairs of inframarginal scales, straight midline sulcus. For additional differences, see Table 1.

Description. The shell length is estimated at 40 cm (based on ZIN PH 136/87). The shape of the carapace can be reconstructed only approximately (Fig. $2B_1$). The anterior part of carapace bears a small nuchal emargination, which is restricted to the nuchal.

The nuchal (Fig. 3A–C) is hexagonal. The anterior border of the nuchal is slightly concave and rounded or angled in the cross-section. The lateral borders of the nuchal are nearly straight. The posterior border is concave and contacts neural 1. The described morphology is similar to that of *Shachemys* spp. (except *Sh. laosiana* with a straight anterior border of nuchal). In *F. verzilini* the nuchal has a straight and wide anterior border.

The neurals are represented by seven elements (Fig. 3D–K). There are complete neurals 1, 2 and 7, whereas the number and shape of the other elements are determined approximately based on surrounding plates. All neurals, except neural 1, are relatively narrow (ratio of the neural width to its length is about 1/2) and thick (Fig. 3F, G). Neural 1 is long and tetragonal with slightly convex lateral borders. The anterior border of neural 1 is slightly wider than the posterior one. A similarly long and narrow neural 1 is known in *Shachemys* spp. In *F. verzilini*, neural 1 is a posteriorly widened hexagonal element as in all other adocids. Neural 2 (Fig. 3E) is about the same shape, but shorter. Its borders are convex, the posterior border is slightly narrower than the anterior one. Neurals 3–7 are hexagonal with short anterolateral borders. Neural 7 (Fig. 3J, K) is short and pentagonal with rounded or acute posterior border. In *F. verzilini*, the neurals are represented by six or seven relatively wide elements. There are two suprapygals. Suprapygal 1 (Fig. 3L, M) is small, varies in shape from almost rectangular, with straight posterior and convex anterior borders (Fig. 3L), to triangular with concave posterior border (Fig. 3M). Suprapygal 2 is represented by fragmentary remains (Fig. 3N, O). It seems to be octagonal and have a straight or concave anterior border that contacted with suprapygal 1, a straight anterolateral borders that contacted costals 8, convex lateral borders that contacted peripherals 10, and concave posterolateral and posterior borders that contacted peripherals 11 and the pygal respectively. The thickness of suprapygal 2 increases posteriorly. The pygal (Fig. 3P) is trapezoid-shaped (ratio of the anterior pygal width to its posterior width is about 1/2) with straight lateral borders. The pygal is thickened along its anterior border; its posterior (free) edge is angled in the cross-section.

The costals are represented by fragmentary remains (Figs. 3Q–T; 4A, B), complete plates are absent. There are fragments of costals 1, 3, 7 and 8, as well as the lateral and medial parts of indeterminate costals. Rib heads and rib thickenings of costals are weak, a synapomorphy of Adocidae. On the internal surface of costal 1 (Fig. $3Q_2$), scars of thoracic ribs 1 and 2 lie close to each other (in contrast to *Shachemys* where

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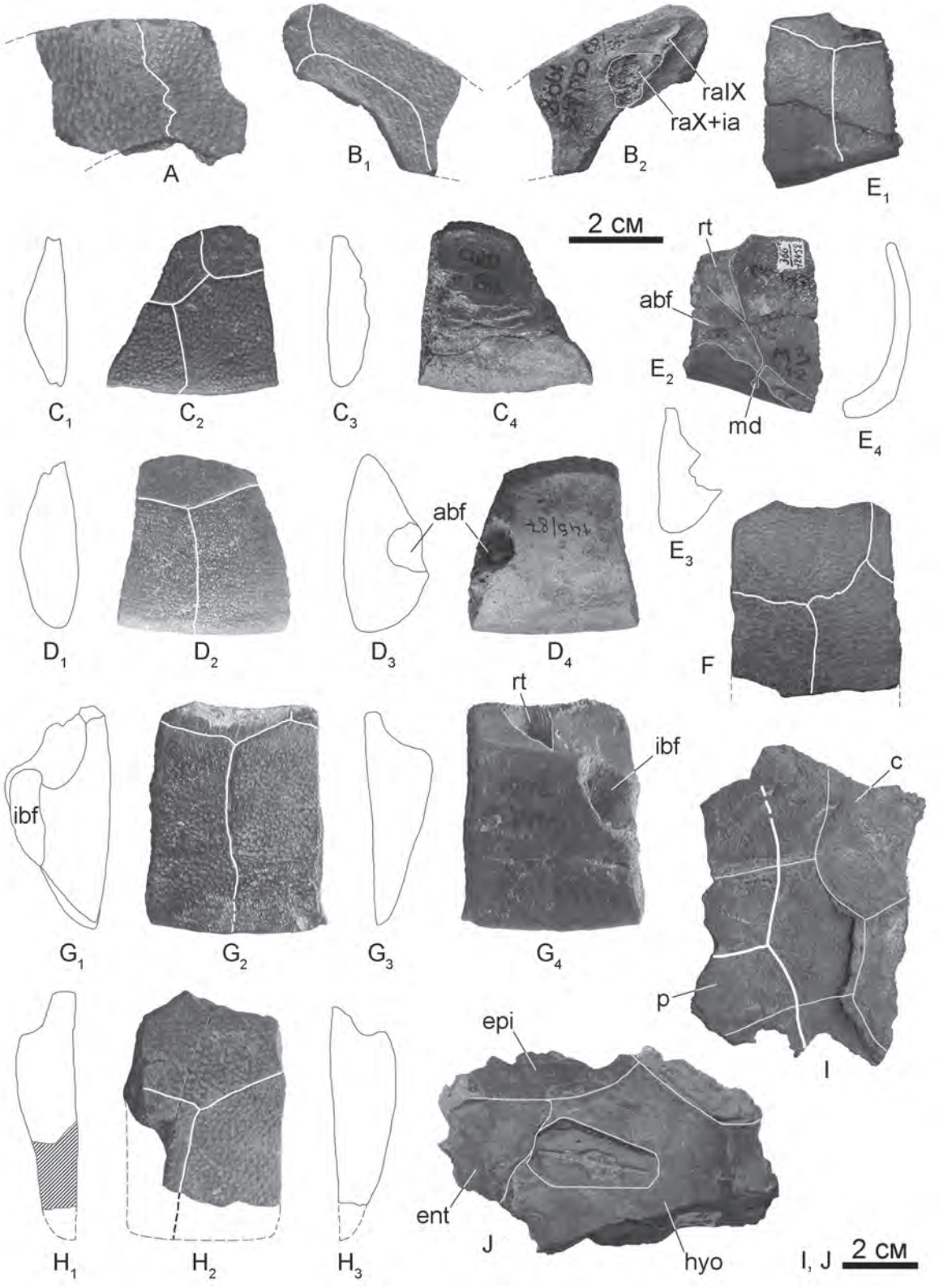
Fig. 3. "*Ferganemys*" *itemirensis* Nessov, 1981, shell fragments: A, C–T – Chelpyk, Khodzhakulsay and Sheikhdzheili, Sultanuvais Range, Uzbekistan; upper part of the Khodzhakul Formation, early Cenomanian, Upper Cretaceous; B – Itemir, Central Kyzylkum, Uzbekistan; Kulbikin Member, Cenomanian, Upper Cretaceous: A – CCMGE 21/12086, fragment of nuchal in dorsal view; B – ZIN PH 20/86, fragment of nuchal: B_1 – dorsal view, B_2 – lateral view; C – CCMGE 308/12458, fragment of nuchal in dorsal view; D – ZIN PH 72/87, neural 1: D_1 – dorsal view; D_2 – ventral view; E – CCMGE 311/12458, neural 2 in dorsal view; F – ZIN PH 176/87, neural: F_1 – dorsal view; F_2 – ventral view; F_3 – lateral view; G – ZIN PH 57/87, neural: G_1 – dorsal view; G_2 – lateral view; H – ZIN PH 117/87, neural in dorsal view; I – ZIN PH 185/87, neural in dorsal view; J – CCMGE ?488–452/12458, neural 7 in dorsal view; K – CCMGE 309/12458, neural 7 in dorsal view; L – CCMGE 437/12458, suprapygal 1 in dorsal view; M – ZIN PH 74/87, suprapygal 1 in dorsal view; N – CCMGE 351/12458, fragment of suprapygal 2 in dorsal view; O – CCMGE 353/12458, fragment of suprapygal 2 in dorsal view; P – CCMGE 390/12458, pygal: P_2 – lateral view, P_1 – dorsal view; Q – CCMGE 325/12458, fragment of left costal 1 Q_1 – dorsal view, Q_2 – ventral view; R – ZIN PH 85/87, fragment of left costal 4: R_1 – dorsal view, R_2 – ventral view; S – ZIN PH 83/87, medial part of right costal ?4 in dorsal view; T – ZIN PH 174/87, lateral part of costal in dorsal view.
Abbreviations: abf – axillary buttress fossa; c – costale; ce – central; egu – extragular; ent – entoplastron; epi – epiplastron; gu – gular; hu – humeral; hyo – hyoplastron; ia – ilial attachment; ibf – inguinal buttress fossa; im – inframarginal; m – marginal; md – musk duct; p – peripheral; pa – pelvis attachment; pe – pectoral; ra – ribhead attachment; rf – rib fossa. Arabic numerals designate element numbers. Breakages are hatched.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hyo
I, J 2 см
H1
H2
H3

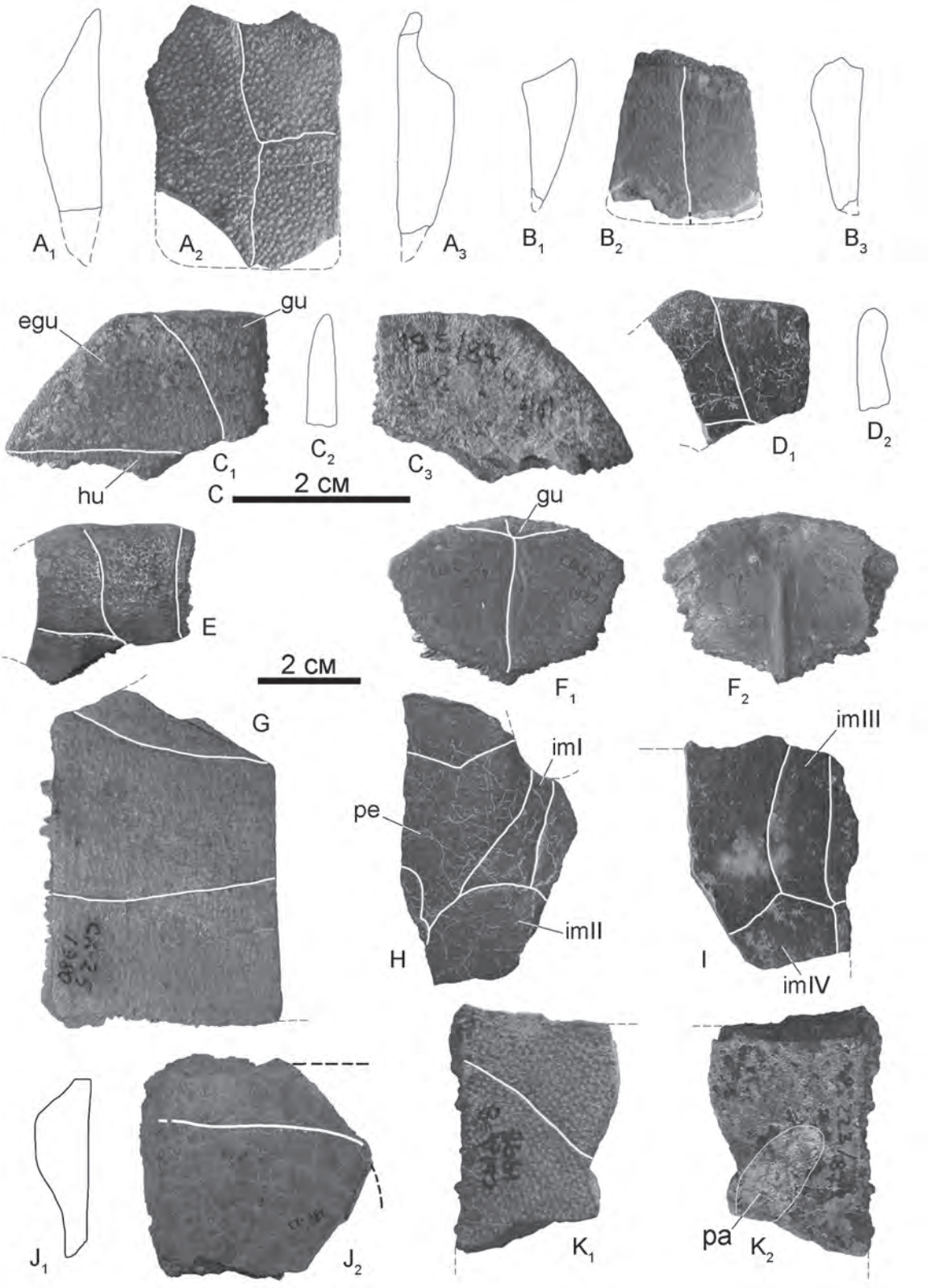
they are separated by a gap). Costal 7 (Fig. 4A) has a rounded notch in the anterior part of its medial border for contact with neural 7. Costals 8 (Fig. 4B) contact each other at the midline; they have a rounded notch in their posterior half for contact with suprapygal 1.

The peripherals (Figs. 4C–J; 5A, B) are represented by relatively complete fragments, however the bridge peripherals are very fragmentary. The free edges of the anterior peripherals (1–3) are thickened and rounded in the cross-section (Fig. 4C–E), whereas the free edges of the posterior ones (8–11) are thin and angled in the cross-section (Figs. 4G, H; 5A, B). The observed morphology is similar to that of *Shachemys* spp., whereas in *F. verzilini* the free edges of nuchal and anterior peripherals are upturned in cross-section. Internally, peripherals 3–10 bear triangular-shaped grooves for the ribs of the corresponding costals (Fig. $4E_2$, G_4). Peripheral 1 (Fig. 4C) is trapezoid-shaped, its medial length is about twice as short as the length of the free edge. The thickness of peripheral 1 is constant throughout its length. Peripheral 2 (Fig. 4D) is much thickened along the posterior border. Internally peripheral 2 lacks the bulge that is known in *F. verzilini* and members of *Adocus* (see Syromyatnikova and Danilov 2009). This bulge is absent also in species of *Shachemys*. The fossa for the axillary buttress is deep with rounded anterior (Fig. $4D_4$) and elongated posterior portion (Fig. $4E_2$). The groove for the musk duct is located in peripheral 3, where it crosses the plastron-carapace suture (Fig. $4E_2$). Peripheral 8 (Fig. 4G) is much thickened in the middle part of its length. Similar to peripheral 2, peripheral 8 has no bulge internally. These bulges are also absent in *Shachemys* spp. but present in *F. verzilini* and members of *Adocus*. The shape of the fossa for the inguinal buttress is not clear, but its posterior part is deep and rounded occupying anterior part of peripheral 8 (Fig. $4G_4$). Peripheral 9 (Fig. 4H) is nearly equal in its thickness. Peripheral 10 (Fig. 5A) has a straight and short posteromedial border contacting with suprapygal 2. The thickness of peripheral 10 is slightly decreased posteriorly. Peripheral 11 (Fig. 5B) is trapezoid-shaped, seems to be narrower than peripheral 10. The medial border of peripheral 11 is strongly thickened posteriorly, its sutural surface is slightly oblique for contact with suprapygal 2.

The cervical scale (Fig. 3A, C) is usually present and represented by a wide trapezoid-shaped element, narrowed in the middle part and widened posteriorly. In some specimens cervical is absent (Fig. 3B). The cervical in *F. verzilini* is wide and short (nearly square), whereas in *Shachemys* spp. it is absent. The shape of the vertebrals is not clear and allow for only an approximate reconstruction (Fig. $2B_1$). Vertebral 1 is trapezoid-shaped, widened anteriorly, overlaps peripherals 1 and in contact with marginals 2. Vertebrals 2–4 seem to be narrow and longer than wide. Vertebral 5 is hexagonal, widens posteriorly, covers most of the costals 8 width and about half of suprapygal 2. The exact shape of pleurals is unclear. They seem to be generally wide, covering the medial thirds of the peripherals (Figs. $4C_2$, D_2, E_1, F, G_2, H_2; $5A_2$). All marginals are restricted to the peripherals, except marginals 11 and 12, which overlap costals 8 and suprapygal 2 (Fig. 3N). Similar marginals are known in *F. verzilini* and *Shachemys* spp. except marginals 5 which can overlap onto the costal 2 as a variation.

The plastron is represented by several complete and fragmentary epiplastra, entoplastra, and hyo-, hypo- and xiphiplastra. The precise shape and proportions of the plastral lobes are unclear (Fig. $2B_2$). The anterior lobe of the plastron seems to be truncated anteriorly. The posterior lobe is relatively wide at its base. In *F. verzilini* the posterior lobe is longer and posteriorly narrow. The epiplastron (Fig. 5C–E) has a relatively wide and straight anterior border, which

Fig. 4. "*Ferganemys*" *itemirensis* Nessov, 1981, shell fragments: A–G – Chelpyk, Khodzhakulsay and Sheikhdzheili, Sultanuvais Range, Uzbekistan; upper part of the Khodzhakul Formation, early Cenomanian, Upper Cretaceous; H–J – Itemir, Central Kyzylkum, Uzbekistan; Kulbikin Member, Cenomanian, Upper Cretaceous: A – CCMGE 343/12458, fragment of left VII costal in dorsal view; B – ZIN PH 90/87, fragment of right costal 8: B_1 – dorsal view, B_2 – ventral view; C – ZIN PH 137/87 left peripheral 1: C_1 – cross section at anterior border, C_2 – dorsal view, C_3 – cross section at posterior border, C_4 – ventral view; D – ZIN PH 145/87, left peripheral 2: D_1 – cross section at posterior border, D_2 – dorsal view, D_3 – cross section at anterior border, D_4 – ventral view; E – CCMGE 366/12458, right peripheral 3: E_1 – dorsal view, E_2 – ventral view, E_3 – cross section at anterior border, E_4 – cross section at posterior border; F – CCMGE 374/12458, fragment of bridge peripheral in dorsal view; G – ZIN PH 151/87, left peripheral 8: G_1 – cross section at anterior border, G_2 – dorsal view, G_3 – cross section at posterior border, G_4 – ventral view; H – ZIN PH 31/86, left peripheral 9: H_1 – cross section at anterior border, H_2 – dorsal view, H_3 – cross section at posterior border; I – ZIN PHT K77-1 (holotype), mould of posterior part of carapace in dorsal view; J – ZIN PHT K77-2 (paratype), mould of dorsal surface of hyo-, epi- and entoplastron, as well as neural in dorsal view. See Fig. 3 for abbreviations and designations.


A1
A2
A3
B1
B2
B3
egu
gu
hu
C1
C2
C3
C
2 см
D1
D2
E
2 см
gu
F1
F2
G
imI
pe
imII
H
imIII
I
imIV
J1
J2
K1
pa
K2

is longer than the length of the epiplastral symphysis. The anterior border of the epiplastra has a small process laterally (Fig. $5D_1$) resulted in the concave anterior border of the epiplastron. The posterior border of the epiplastron is concave medially for contact with the entoplastron and slightly curved laterally for contact with the hyoplastron. The internal surface of the epiplastron is concave. The entoplastron (Fig. 5F) is a large, hexagonal element with a length about 2/3 of its width; its anterior border is convex and wedges between the epiplastra. The lateral and posterior borders are nearly straight. The dorsal surface of the entoplastron bears a Y-shaped system of ridges. The hyo-, hypo- and xiphiplastra are represented by highly fragmentary specimens (Fig. 5J–K). The hyoplastron has slightly curved anterior borders. The hypoplastron is much thickened medially (Fig. $5J_1$). The xiphiplastron (Fig. 5K) bears an elongated oval-shaped fossa for pelvic attachment.

The plastral scalation can be reconstructed only partially (Fig. $2B_2$). The gulars become narrower posteriorly (Fig. $5C_1$, D_1, E) and cover about 1/3 of the external surface of the epiplastra and slightly overlap the entoplastron (Fig. $5F_1$). The extragulars are relatively large covering about 2/3 of the external surface of the epiplastra (Fig. $5C_1$), with straight or slightly curved posterior borders, which do not reach the posterior borders of the epiplastra. The exact shape of the pectoral is unclear, but, as reconstructed, it seems to be about the same length in medial and lateral parts with a small waist in the lateral third of their length. The pectorals do not overlap the entoplastron (Fig. $2B_2$) and contact with inframarginals 1 and 2 laterally (Fig. 5H). The abdominal-femoral sulcus is slightly convex; the femoral-anal sulcus is slightly S-shaped. The inframarginals are represented by a complete row of four scales. The available specimens (Fig. 5H, I) indicate that the inframarginals were restricted to the plastron. Inframarginal 1 (Fig. 5H) is trapezoid and widened posteriorly. Inframarginal 2 has a similar shape, but widens anteriorly, longer and wider than the anterior one. Inframarginal 3 (Fig. 5I) is tetragonal and relatively narrow. Inframarginal 4 widens posteriorly and is shorter than the other inframarginals. Four inframarginals are also known in *Shachemys* spp., whereas *F. verzilini* has one or two pairs of inframarginals.

The midline sulcus is straight as in members of *Shachemys*. *F. verzilini* demonstrates a sinuous midline sulcus. The skin-scale sulcus lies very close to the free edges of the carapace and plastron.

Remarks. The nuchal (ZIN PHT S75-27) previously referred to Adocidae from Khodzhakulsay (Nessov 1981: 71) is here assigned to "*F.*" *itemirensis*.

Distribution. Type locality; Chelpyk, Khodzhakulsay and Sheikhdzheili localities, Sultanuvais Range, Uzbekistan; upper part of the Khodzhakul Formation, lower Cenomanian, Upper Cretaceous.

DISCUSSION

The morphology of *Ferganemys*. Our study of *Ferganemys* reveals previously unknown and misunderstood characters as well as emends the characteristics of the species of *Ferganemys*. Among the most important characters of *F. verzilini* are the presence of peculiar bulges at the place of attachment of the plastral buttresses on peripherals 2 and 8 which are absent in "*F.*" *itemirensis*. A similar morphology of peripherals 2 and 8 is present in some species of *Adocus* (Syromyatnikova and Danilov 2009). Our observation of material of *F. verzilini* does not confirm the presence of four pairs of inframarginals on the plastron, as it was previously figured (Nessov 1986: 18, fig. 7). This species has only one anterior pair of inframarginals and sometimes retains a posterior pair of inframarginals (Fig. $2A_2$). At the same time, the anterior pair of inframarginals is displaced posteriorly and has no contact with the axillary notch.

Fig. 5. "*Ferganemys*" *itemirensis* Nessov, 1981, shell fragments, Chelpyk, Khodzhakulsay and Sheikhdzheili, Sultanuvais Range, Uzbekistan; upper part of the Khodzhakul Formation, early Cenomanian, Upper Cretaceous: A – ZIN PH 161/87, right peripheral 10: A_1 – cross section at posterior border, A_2 – dorsal view, A_3 – cross section at anterior border; B – ZIN PH 164/87, right peripheral 11: B_1 – cross section at anterior border, B_2 – dorsal view, B_3 – cross section at posterior border; C – ZIN PH 195/87, right epiplastron: C_1 – ventral view, C_2 – cross section at medial border (symphysis), C_3 – dorsal view; D – ZIN PH 196/87, right epiplastron: D_1 – ventral view, D_2 – cross section at medial border (symphysis); E – CCMGE 402/12458, right epiplastron in ventral view; F – ZIN PH 205/87, entoplastron: F_1 – ventral view, F_2 – dorsal view; G – CCMGE № 408/12458, fragment of left hyoplastron in ventral view; H – CCMGE 418/12458, fragment of left hyoplastron in ventral view; I – ZIN PH 220/87, lateral part of left hypoplastron, in ventral view; J – CCMGE 432/12458, fragment of left hypoplastron: J_1 – ventral view, J_2 – cross section at medial border (symphysis); K – CCMGE 223/12458, fragment of left xiphiplastron: K_1 – ventral view, K_2 – dorsal view. See Figure 3 for abbreviations and designations.

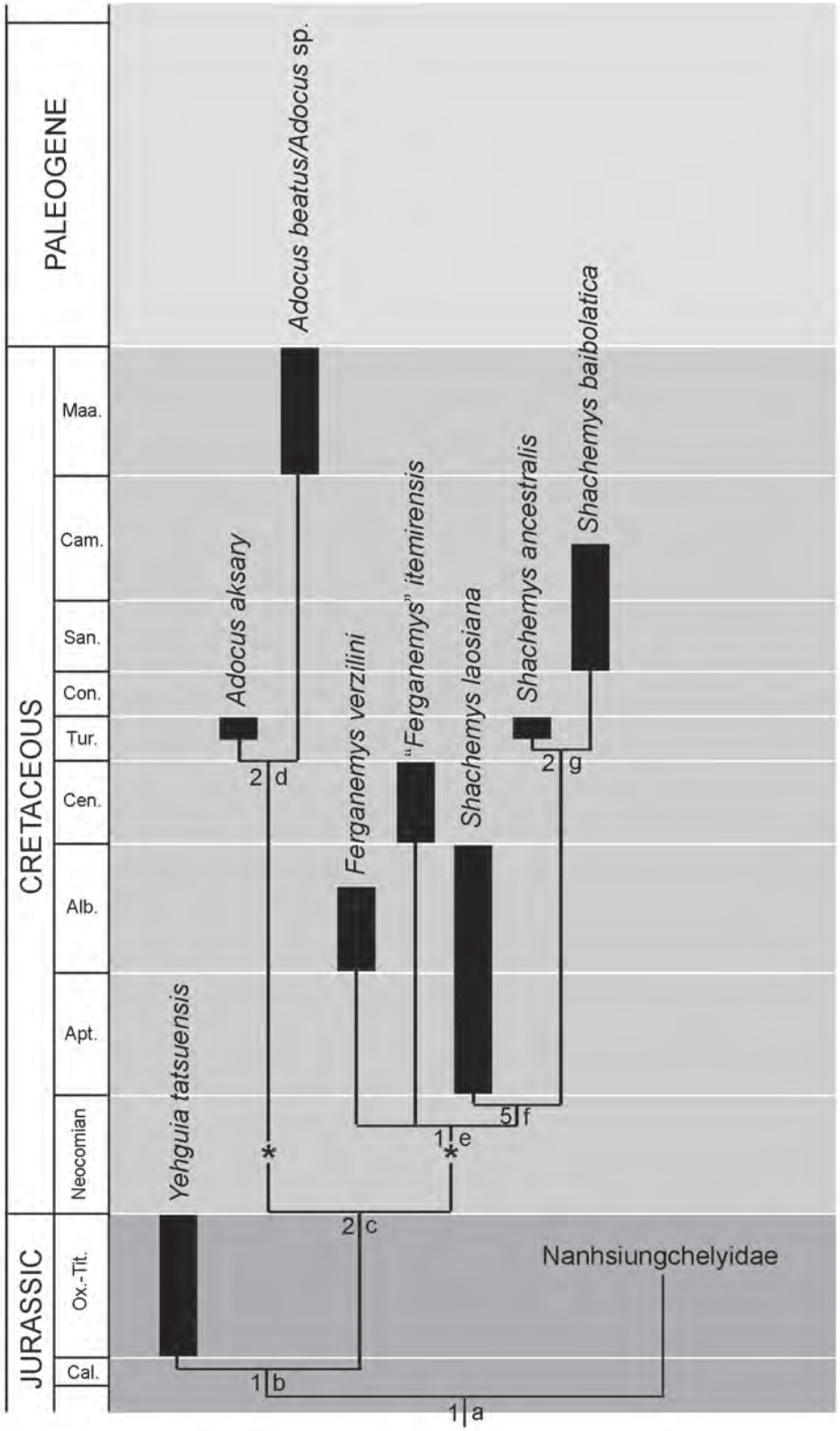


Fig. 6. Phylogeny of Adocusia showing the hypothesized position "*Ferganemys*" *itemirensis* and *F. verzilini*. Outgroups and nanhsiungchelyid taxa are not shown. Black boxes indicate ranges of adocid taxa (Sukhanov 2000; Danilov and Parham 2006). Letters designate nodes with the following unambiguous synapomorphies: a) Adocusia: neural formula 6>4<6<6<6, plastron-carapace connection sutural; b) Adocidae: shape of pygal longer than wide, sculpturing of the shell surface with relatively small and regular pits or dots, shell scale sulci shallow and narrow; c) rib heads weak, rib thickenings absent; d) *Adocus*: medial contact of palatines absent, marginals overlap costals in the middle and posterior parts of the carapace; e) Shachemydinae: entoplasron shortened and truncated anteriorly, extragular/humeral sulcus close or coincides with the epi-entohyoplatsral suture; f) *Shachemys*: only 1st or no neural present, present one suprapygal, costal attachment of the first thoracic rib is distant from the second, cervical absent, anterior border of vertebral 1 contacts peripherals 2, sculpturing of the shell surface with dots; g) nuchal emargination formed by the nuchal and peripheral 1, sulcus between pleural 3 and marginals 7–9 situated near suture of peripherals and costals. Asterisk «*» designate the most early records of members of the clades. Numbers are Bremer indices.

Abbreviations: Alb. – Albian; Apt. – Aptian; Cal. – Callovian; Cam. – Campanian; Cen. – Cenomanian; Con. – Coniacian; Maa. – Maastrichtian; Ox. – Oxfordian; San. – Santonian; Tit. – Tithonian; Tur. – Turonian.

Another important character of *F. verzilini* is a weak overlapping of marginal 5 onto costal 2 as a variation (Fig. $2A_1$; Nessov and Khosatzky 1977). A similar overlap was mentioned only for *Shachemys laosiana* (Lapparent de Broin 2004) and could be a primitive for Shachemydinae.

Our observation of materials of "*F.*" *itemirensis* reveals and/or confirms some details of its shell morphology that include the presence of a posteriorly constricted tetragonal neural 1, four pairs of inframarginals (Fig. $2B_2$), and a strong thickenings of the medial border of the hypoplastra. The presence of a complete row of inframarginals were mentioned previously (Nessov 1986, fig. 7), however, their position differs from the published one. The thickenings of the medial border of the hypoplastra in "*F.*" *itemirensis* are relatively well developed, whereas in *F. verzilini* they are weak, but more developed than in other adocids. "*F.*" *itemirensis* show some variable characters in shape of suprapygal 1 and the cervical scale (see Description). Besides that, the shape of vertebral 5, gulars, extragulars and pectorals are variable in both species (Fig. 2).

Our observation of all available materials does not confirm the following differences between species of *Ferganemys* mentioned by Nessov and Krasovskaya (1984): length of posterior marginals; ingrowths of ilium in narrow fossa of costal 8; shape of the posterior border of the plastron; curve of the femoral-anal sulcus and shape of the posterior borders of epiplastra. On the other hand, new differences are revealed in shape of the nuchal and neural 1; width of the neurals; shape of free edge of the nuchal and anterior peripherals; morphology of peripherals 2 and 8 in place of attachment of plastral buttresses; thickness of neurals and posterior peripherals; shape of cervical; thickenings of medial border of hypoplastron; length of the posterior lobe of the plastron; number of inframarginals and shape of the midline sulcus of plastron. In addition, "*F.*" *itemirensis* is similar to species of *Shachemys* in the following characters: constricted posteriorly neural 1; absence of the bulge in place of attachment of plastral buttresses on peripherals 2 and 8 and reduction of cervical. All of these new observations allow us to present new shell reconstructions of "*Ferganemys*" species (Fig. 2).

The phylogenetic position of *"Ferganemys" itemirensis*. Inclusion of new data on these species in the phylogenetic analysis of Adocusia (see Danilov and Syromyatnikova 2009a, 2009b) does not support a monophyletic clade of the genus *Ferganemys*. The result of our phylogenetic analysis consists of 38 trees with 128 steps, the consistency index is 0.65, and the retention index is 0.81. The resulting strict consensus tree is given in Fig. 6. This tree demonstrates that species of *Ferganemys* are placed in a polytomy with the *Shachemys* clade. The topology of the other clades is the same as in the latest analysis of this group (see Danilov and Syromyatnikova 2009a, 2009b). Distribution of synapomorphies is given in caption to Fig. 6. In the previous analysis (Danilov and Syromyatnikova 2009a, 2009b), *Ferganemys* was monophyletic. Thus, the systematic position of "*F.*" *itemirensis* within the Shachemydinae is unclear. Possibly, "*F.*" *itemirensis* could likely belong to the *Ferganemys* or to a separate genus as sister to *Shachemys*. Further resolving the phylogenetic position of "*F.*" *itemirensis* will require detailed study of Shachemydinae taxa and additional materials of skull and non-shell postcrania.

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Appendix 1. Details about characters added to matrix of Danilov and Syromyatnikova (2009a, b).

Character 68. Neural 1: "0" (widened posteriorly), "1" (constricted posteriorly); **Codings**: *Xinjiangchelys levensis*, 1; *X. tianshanensis*, 1; *Carettochelys insculpta*, 1; *Apalone ferox*, 1; *Yehguia tatsuensis*, ?; *Adocus aksary*, 0; *A. beatus/Adocus* sp., 0; "*Ferganemys*" *itemirensis*, 1; *F. verzilini*, 0; *Shachemys ancestralis*, 1; *Sh. baibolatica*, 1; *Sh. laosiana*, 1; *Kharakhutulia kalandadzei*, 0; *Zangerlia testudinimorpha*, 0; *Z. neimongolensis*, ?; *Z. ukhaachelys*, ?; *Hanbogdemys orientalis*, 0; *Anomalochelys angulata*, 0; *Nanhsiungchelys wuchingensis*, 0; *Basilemys variolosa*, 0; *B. nobilis*, 0; *B. sinuosa*, 0; *B. praeclara*, 0.

Character 75. Medial part of hypoplastron: "0" (not thickened), "1" (thickened). **Codings:** *Xinjiangchelys levensis*, 0; *X. tianshanensis*, 0; *Carettochelys insculpta*, 0; *Apalone ferox*, 0; *Yehguia tatsuensis*, ?; *Adocus aksary*, 0; *A. beatus/Adocus* sp., 0; "*Ferganemys*" *itemirensis*, 1; *F. verzilini*, 1; *Shachemys ancestralis*, 0; *Sh. baibolatica*, 0; *Sh. laosiana*, 0; *Kharakhutulia kalandadzei*, 0; *Zangerlia testudinimorpha*, ?; *Z. neimongolensis*, ?; *Z. ukhaachelys*, ?; *Hanbogdemys orientalis*, ?; *Anomalochelys angulata*, ?; *Nanhsiungchelys wuchingensis*, ?; *Basilemys variolosa*, ?; *B. nobilis*, ?; *B. sinuosa*, ?; *B. praeclara*, ?.