

## Soft-shelled turtles (Trionychidae) from the Cenomanian of Uzbekistan



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### ABSTRACT

Localities from the Cenomanian of Uzbekistan are the oldest in Middle Asia and Kazakhstan to preserve two broadly sympatric species of trionychid turtle. Material described here comes from multiple Cenomanian formations from the Itemir locality, and from multiple localities in the Cenomanian Khodzhakul Formation. The first taxon from the locality, “*Trionyx*” cf. *kyrgyzensis*, has multiple morphological similarities with the older, Early Cretaceous “*Trionyx*” *kyrgyzensis*. In contrast, the second taxon, “*Trionyx*” *dissolutus*, has multiple similarities with “*Trionyx*” *kansaiensis*, one of two species of trionychid found in younger Late Cretaceous localities. “*Trionyx*” *dissolutus* bears some superficial resemblance to other trionychid taxa within the clade Plastomenidae because of its highly ossified plastron with a hyoplastral lappet and an epiplastral notch. However, Plastomenidae is diagnosed primarily through characters that are absent or cannot be observed in the available material of “*T.*” *dissolutus*, and other shared features are plesiomorphic. In addition, “*T.*” *dissolutus* shares other synapomorphies with Trionychinae. A heavily ossified plastron may be more homoplastic within Trionychidae than has been previously recognized. Finally, we provide an improved understanding of the subtle similarities and differences between several closely related Cretaceous turtle assemblages of Middle Asia and Kazakhstan.

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### 1. Introduction

Trionychidae Gray 1825, or soft-shelled turtles, are a group of aquatic cryptodires (Meylan, 1987). The phylogeny and taxonomy of extinct species within this group are still not well understood (Meylan, 1987; Gardner et al., 1995; Karl, 1998; Joyce and Lyson, 2011). The lack of understanding is especially problematic for Cretaceous trionychids, which are important for understanding the early diversification and evolution of the family (Danilov and Vitek, 2012) provided a review of Cretaceous trionychids of Asia).

This paper continues a series of publications on Cretaceous trionychids of Asia (Danilov and Vitek, 2009; Vitek and Danilov, 2010, 2012, 2013; Danilov and Vitek, 2012, 2013) and is devoted to trionychids from the early Late Cretaceous (Cenomanian) of Uzbekistan, situated in the region called Middle Asia and Kazakhstan (Fig. 1; see Vitek and Danilov [2010] for more details about the geography of Middle Asia and Kazakhstan). The material described in this paper comes from localities in the early Cenomanian Khodzhakul Formation of the southwestern Kizylkum Desert area,

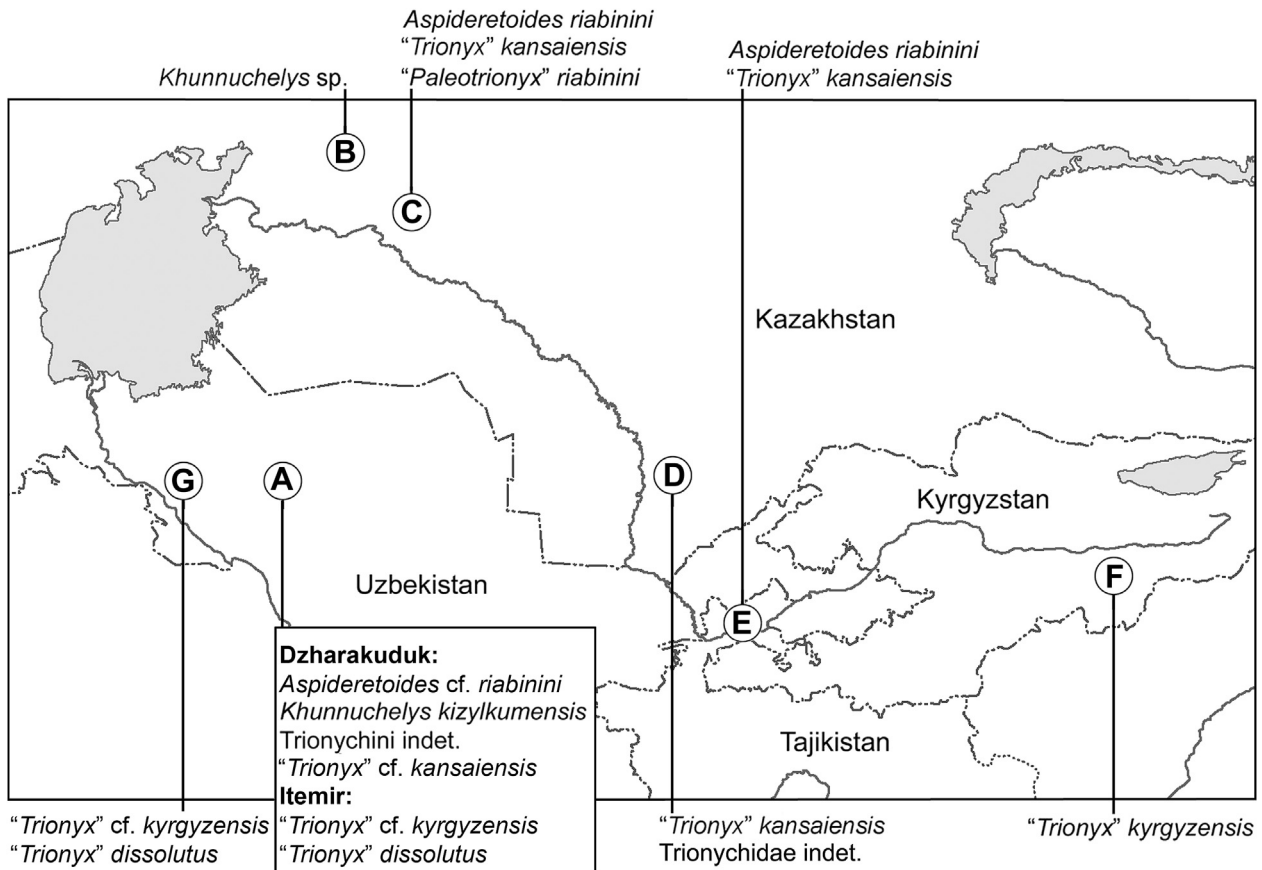
Karakalpakistan, and from the Cenomanian of the Itemir locality in the central Kizylkum Desert, Navoi Viloyat (district) (Fig. 1). The localities of the Khodzhakul Formation include Chelypyk (SCH-1 and SCH-“B” sites), Khodzhakul I (SKH-20 site), Khodzhakulsai (SKH-4, SKH-5, and SKH-25 sites), and Sheikhdzheili (SSHD-8 and SSHD-8a sites) (see Averianov and Archibald [2005] for more details about the localities of the Khodzhakul Formation). In addition, one more locality known as Khodzhakul II (SKH-26 site) contains Cenomanian remains from the Khodzhakul Formation which were redeposited in Late Paleocene sands (Nessov, 1997). The described material from Itemir comes from several Cenomanian members (formations) of the following sites: CDZH-3, CDZH-5b, CDZH-10, CDZH-12 and IT-1 (see Nessov (1997) and Averianov and Sues (2007) for more details about the Itemir locality).

Trionychid material from the Khodzhakul Formation was mentioned in the literature (Nessov, 1977a, 1985, 1986; Kordikova, 1992, 1994; Nessov, 1997), but was never described. The trionychid material from the Itemir locality was mentioned and partially illustrated (Nessov, 1984, 1985; Kordikova, 1992, 1994; Nessov, 1997; Danilov and Vitek, 2009, 2012).

The trionychid material described in this paper consists of numerous shell fragments. It is assigned to two shell-based taxa, “*Trionyx*” cf. *kyrgyzensis* Nessov, 1995 and “*Trionyx*” *dissolutus* sp.

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**Fig. 1.** Map showing main localities of Cretaceous trionychids in Middle Asia and Kazakhstan. A – Dzharakuduk; B – Baybishe; C – Shakh Shakh; D – Kyrkkuduk I; E – Kansai; F – Kылodzhun; G – localities of the Khodzhakul Formation (see Vitek and Danilov (2010, 2012, 2013) and Danilov and Vitek (2013) for data on localities other than localities of the Khodzhakul Formation and Itemir).

nov. Material that cannot be confidently attributed to these two taxa is considered Trionychidae indet.

The material for this study was collected by L.A. Nessov between 1977 and 1994 and by the international Uzbek/Russian/British/American/Canadian Joint Paleontological Expeditions (URBAC) led by J.D. Archibald between 1997 and 2006.

Anatomical terminology follows Meylan (1987), Gardner and Russell (1994), and Karl (1999).

**Institutional Abbreviations** – ZIN PH, Paleoherpological collection, Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia.

## 2. Systematic paleontology

Testudines Batsch, 1788

Cryptodira Cope, 1868

Trionychidae Gray, 1825

Trionychinae Gray, 1825

Trionychinae incertae sedis

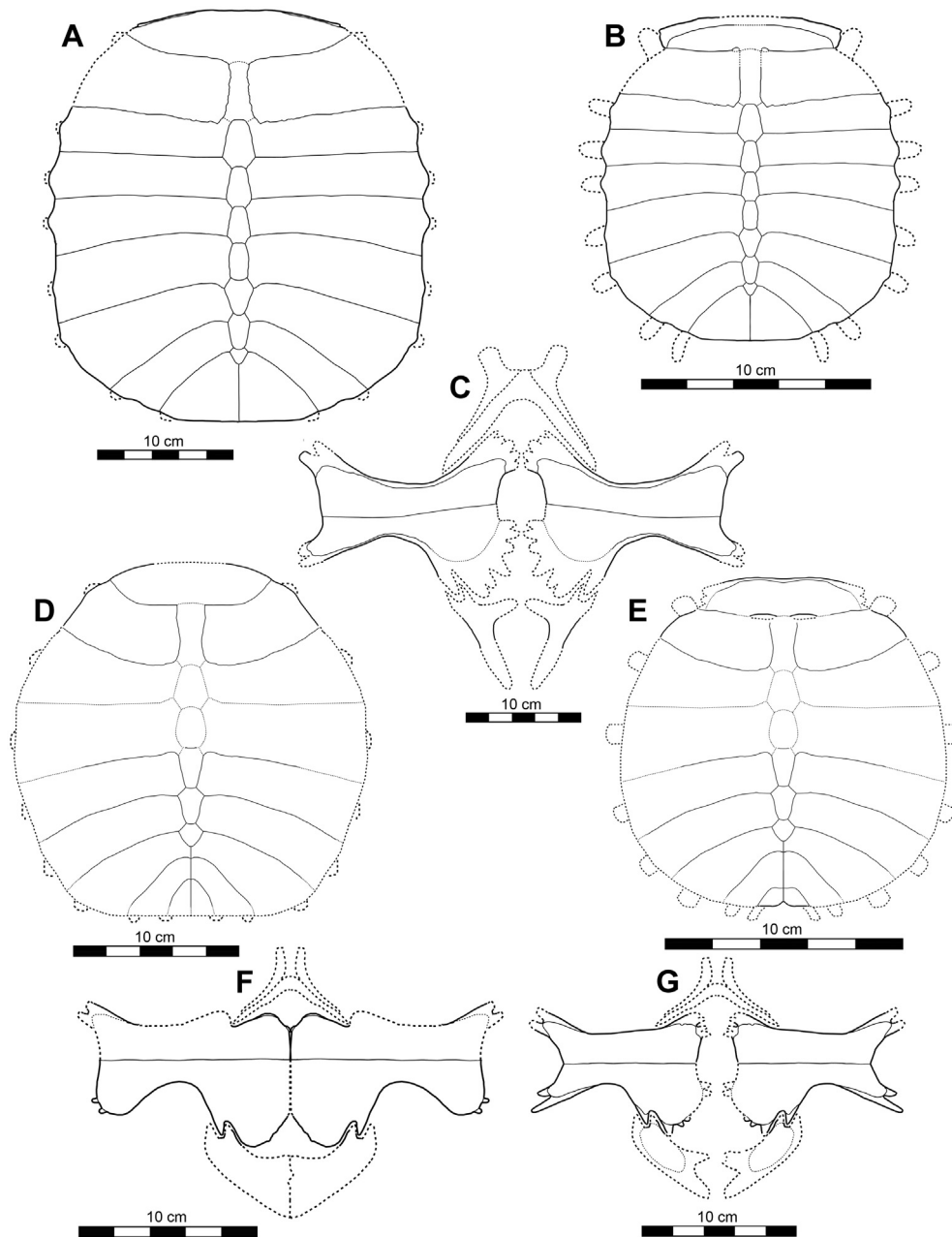
"Trionyx" cf. *kyrgyzensis* Nessov, 1995

**Referred material.** Khodzhakul Formation: ZIN PH 1/122 (SSHD-8a), ZIN PH 2/122 (SKH-4), ZIN PH 3/122 (SKH-26), ZIN PH 27/122 (SSHD-8a), ZIN PH 30/122 (SKH-20), partial nuchal; ZIN PH 15/122 (SSHD-8), hexagonal neural; ZIN PH 69/122 (SSHD-8), tetragonal neural; ZIN PH 14/122 (SKH-20), pentagonal neural; ZIN PH 6/122 (SSHD-8), partial costal 1; ZIN PH 7/122 (SSHD-8a), partial costal 2?; ZIN PH 37/122 (SSHD-8a), partial costal 5; ZIN PH 9/122 (SSHD-

8a), partial costal 7?; ZIN PH 5/122 (SSHD-8), partial costal 8; ZIN PH 11/122 (SKH-4), partial costal 8?; ZIN PH 10/122 (SSHD-8a), partial costal; ZIN PH 16/122 (SKH-25), ZIN PH 17/122 (SKH-25), ZIN PH 23/122 (SKH-25), ZIN PH 24/122 (SKH-25), partial hyoplastra; ZIN PH 18/122 (SSHD-8a), ZIN PH 20/122 (SKH-25), ZIN PH 21/122 (SKH-25), ZIN PH 22/122 (SKH-25), partial hypoplastra; ZIN PH 58/122 (SKH-25), ZIN PH 59/122 (SCH-1), partial xiphoplastra; Itemir locality: ZIN PH 56/86 (CDZH-5b), partial nuchal; ZIN PH 57/86 (IT-1), costal 8; ZIN PH 54/86 (CDZH-12), ZIN PH 55/86 (CDZH-12), external impressions of partial costals 7 and 8.

**Locality, Horizon, and Age.** Chelpyk, Khodzhakul I and II, Khodzhakulsai, and Sheikhdzheili localities, southwestern Kizylkum Desert area, Karakalpakistan, Uzbekistan; Khodzhakul Formation, early Cenomanian. Itemir locality, Central Kizylkum Desert, Navoi Viloyat (district), Uzbekistan; Cenomanian.

**Description of material from the Khodzhakul Formation.** *Shell.* A reconstruction (Fig. 2A), based on the largest nuchal fragment (ZIN PH 2/122; Fig. 3A), is approximately 30 cm long. A smaller partial nuchal (ZIN PH 3/122; Fig. 3B) with a callosity restricted to the posteromedial part of the bone comes from an individual, likely a juvenile, only about 15 cm long (Fig. 2B). Carapace shape was probably oval, but without complete costals 2–7 it is impossible to say for certain. It is possible that the carapace was more circular. The anterior and posterior margins are both broadly convex, following the terminology of Gardner and Russell (1994). The lateral margin is weakly scalloped. It is unclear whether or not this species was sexually dimorphic. Sculpturing



**Fig. 2.** Reconstructions of shells of trionychids from the Khodzshakul Formation and Itemir. A, adult carapace; B, juvenile carapace; C, plastron of *Trionyx* cf. *kyrgyzensis*. D, adult carapace; E, juvenile carapace; F, adult plastron; G, juvenile plastron of *Trionyx* *dissolutus* sp. nov.

is a pattern of wide, irregularly shaped pits. In smaller specimens, the ridges surrounding the pits are thinner and more pronounced, similar to the sculpturing seen in *T.* *kyrgyzensis* (Nessov, 1995). In general, this sculpturing is more similar to that of *Aspideretoides riabinini* (Kuznetsov and Chkhikvadze, 1987), than to that of *Trionyx kansaiensis* (Vitek and Danilov, 2010) (see Vitek and Danilov, 2010; Danilov et al., in press).

**Nuchal.** Available nuchal fragments do not preserve the medial part of the nuchal. Therefore, it is unknown where the first thoracic vertebra contacted the nuchal. The costiform processes are united, in contrast to the divided processes of cyclanorbines. A rough estimate based on two different nuchals (ZIN PH 1/122 and ZIN PH 3/122) is that the nuchals were 4.5–5 times wider than long, similar to all Asian Cretaceous trionychids with

preserved nuchals (Danilov and Vitek, 2012), but contrary to the hypothesized ancestral state for trionychids (Meylan, 1987). The extent of the sculptured callosity across the plate varies with size. Smaller nuchals (ZIN PH 3/122, ZIN PH 27/122; Fig. 3C) have a smaller callosified area than larger nuchals (ZIN PH 1/122; Fig. 3D), which in turn have a smaller callosified area than the largest nuchals (ZIN PH 2/122). In general, the nuchals are well-sutured to the first costals (ZIN PH 1/122) with a relatively straight suture between the two plates. A few millimeters of the posterior margin may lie inside the first costals. Only one small, presumably juvenile specimen (ZIN PH 30/122; Fig. 3E) has postnuchal fontanelles.

**Neurals.** No preneurals or neurals 1 could be assigned to this species. The medial margin of costal 1 (ZIN PH 6/122; Fig. 3F) does





**Fig. 3.** *Trionyx* cf. *kyrgyzensis* specimens from the Khodzhakul Formation. A, ZIN PH 2/122, partial nuchal in external view; B, ZIN PH 3/122, partial nuchal in external view; C, ZIN PH 27/122, partial nuchal in external view; D, ZIN PH 1/122, partial nuchal in external view; E, ZIN PH 30/122, partial nuchal in external view; F, ZIN PH 6/122, partial costal 1 in external view; G, ZIN PH 37/122, partial costal 5 in external view; H, ZIN PH 5/122, partial costal 8 in external view; I, ZIN PH 11/122, partial costal 8? in external view; J, ZIN PH 15/122, hexagonal neural in external view; K, ZIN PH 69/122, tetragonal neural in external view; L, ZIN PH 14/122, pentagonal neural in external view; M, ZIN PH 10/122, partial costal in visceral view; N, ZIN PH 7/122, partial costal 2? in external view; O, ZIN PH 9/122, partial costal 7? in external view; P, ZIN PH 18/122, partial hypoplastron in external view; Q, ZIN PH 20/122, partial hypoplastron in external view; R, ZIN PH 16/122, partial hypoplastron in external view; S, ZIN PH 17/122, partial hypoplastron in external view; T, ZIN PH 23/122, partial hypoplastron in external view; U, ZIN PH 24/122, partial hypoplastron in external view; V, ZIN PH 22/122, partial hypoplastron in external view; W, ZIN PH 21/122, partial hypoplastron in external view; X, ZIN PH 59/122, partial xiphiplastron in external view; Y, ZIN PH 58/122, partial xiphiplastron in external view.

not indicate the presence of a preneural, but this does not necessarily mean that a preneural was absent. A mostly complete costal 5 (ZIN PH 37/122; Fig. 3G) indicates that neural 5 was tetragonal. The anteriomedial margin of costal 8 (ZIN PH 5/122, ZIN PH 11/122; Fig. 3H, I) indicates that the final neural was positioned between costals 7 and 8. Therefore, it is most likely that this species had eight neurals. Neurals 1–4 were hexagonal short-sided posteriorly

(ZIN PH 15/122; Fig. 3J), neural 5 was tetragonal (ZIN PH 69/122; Fig. 3K), neurals 6 and 7 were hexagonal short-sided anteriorly, and neural 8 was reduced and pentagonal (ZIN PH 14/122; Fig. 3L).

**Costals.** Eight costals are present, with costal 8 triangular, unreduced, and approximately as long as it is wide (ZIN PH 5/122). Costals 8 meet partially at the midline. Costals 7 and 8 make up the posterior margin of the carapace. There is no depression on costal 8

for contact with the ilium. Most sutures between costals are straight, with no over- or underlap. The exception is a posterior fragment of what is probably costal 6 (ZIN PH 10/122; Fig. 3M). The anterior margin of costal 7 grew past the suture and underlapped this costal. All of the costal rib ends are broken off at the costal margin (ZIN PH 7/122, ZIN PH 9/122; Fig. 3N, O), making it impossible to tell how long the free rib ends were.

**Plastron.** No epiplastra or entoplastra could be identified among the material from the Khodzhakul Formation. The hyo- and hypoplastra are covered in a callosity, but the callosity is either weakly sculptured (e.g. ZIN PH 18/122, Fig. 3P) or lacks sculpturing (e.g. ZIN PH 20/122; Fig. 3Q). The xiphiplastra lack callosities entirely.

**Hyoplastra and hypoplastra.** The hyoplastra and hypoplastra are not fused together. There is no extensive midline contact between the hyoplastra and hypoplastra. The length of the plastral bridge is approximately one-quarter the width of the hypoplastron (Fig. 2C).

The medial lobe of the hyoplastron consists of several small processes that are left exposed and not entirely covered by a callosity (ZIN PH 16/122, ZIN PH 17/122; Fig. 3R, S). The two lateral hyoplastral processes are similarly left exposed (ZIN PH 23/122, ZIN PH 24/122; Fig. 3T, U). While both lobes extend anteriorly past the bridge, neither is significantly longer than the other.

The medial lobe of the hypoplastron is not entirely preserved, but a fragment (ZIN PH 22/122; Fig. 3V) indicates that the medial hypoplastral processes were numerous and undivided (clustered). The lateral lobe of the hypoplastron (ZIN PH 21/122; Fig. 3W) extends laterally past the suture between the hyoplastron and hypoplastron.

**Xiphiplastra.** Two central fragments of xiphiplastra are preserved (ZIN PH 58/122, ZIN PH 59/122; Fig. 3X, Y). Both indicate a long, thin posterior process.

**Description of material from Itemir.** Sculpturing of the carapace material from Itemir matches the sculpturing of the material from the Khodzhakul Formation. A partial nuchal (ZIN PH 56/86; Fig. 4A) is entirely covered by a callosity except for anterior-most edge, which is exposed, and the posterior margin, which lay inside the first costal. The costal 8 (ZIN PH 57/86; Fig. 4B) is triangular, with a space at the anteromedial margin for neural 8. Two impressions of costals 7 and 8 (ZIN PH 54/86, ZIN PH 55/86; Fig. 4C, D) show similar features.

Trionychinae incertae sedis

“*Trionyx*” *dissolutus* sp. nov.

Trionychidae indet.: Nesson, 1984:figs. 6, 7, 9; 1997:137, pl. 34, fig. 17; pl. 35, fig. 7; Kordikova, 1994:344.

*Trionyx* sp.: Nesson, 1985:216.

*Trionyx* s. lato: Kordikova, 1992:133.

Trionychinae indet.: Nesson, 1997:137.

Trionychini indet.: Danilov and Vitek, 2009:55.

Trionychini indet. 1: Danilov and Vitek, 2012:425.

**Etymology.** The species name *dissolutus* (Latin) means dissolved, and is used for the shell material that dissolved away and left impressions at the Itemir locality.

**Holotype.** ZIN PH 51/86 (formerly CCMGE 7/11659; CDZH-12), external and visceral impressions of posterior part of carapace of one individual.

**Referred material.** Itemir locality: ZIN PH 58/86 (CDZH-10), partial nuchal; ZIN PH 50/86 (CDZH-3), partial hyoplastron; ZIN PH 52/86 (CDZH-12), external impression of partial hyoplastron and hypoplastron; ZIN PH 59/86 (CDZH-10), partial xiphiplastron. Khodzhakul Formation: ZIN PH 32/122 (SSHD-8a), partial nuchal and costal 1; ZIN PH 25/122 (SKH-20), ZIN PH 29/122 (SSHD-8a), partial nuchals; ZIN PH 33/122 (SKH-25), ZIN PH 34/122 (SSHD-8), partial costals 1; ZIN PH 39/122 (SSHD-8a), partial costal 6; ZIN PH 42/122 (SSHD-8), 43/122 (SSHD-8a), costal 8; ZIN PH 44/122 (?), hexagonal neural; ZIN PH 46/122 (SKH-5), ZIN PH 50/122 (SSHD-8a), ZIN PH 54/122 (?), partial hyoplastra; ZIN PH 47/122 (SKH-5), ZIN PH 48/122 (SKH-26), ZIN PH 49/122 (SSHD-8a), ZIN PH 51/122 (SKH-25), ZIN PH 52/122 (SKH-25), ZIN PH 53/122 (SSHD-8), ZIN PH 57/122 (SKH-20), partial hypoplastra; ZIN PH 55/122 (SSHD-8a), partial xiphiplastron.

**Locality, Horizon, and Age.** Itemir locality, Central Kizylkum Desert, Navoi Viloyat (district), Uzbekistan; Cenomanian. Khodzhakul I and II, Khodzhakulsai, and Sheikhdzheili localities, southwestern Kizylkum Desert area, Karakalpakistan, Uzbekistan; Khodzhakul Formation, early Cenomanian.

**Diagnosis.** A trionyhid with a shell length about 24 cm, which can be differentiated from all other Cretaceous trionychids with known shells by the presence of six neurals and neural reversal anterior to neural 4. In addition, it can be differentiated from all Cretaceous trionychids, except for members of the clade *Plastomenidae* Hay, 1902, by the presence of an epiplastral notch on the hyoplastron. In addition it can be differentiated from all Cretaceous trionychids, except for *Hutchemys* spp., by extensive medial contact between the hyo- and hypoplastra. In addition, it can be differentiated from *Axestemys* spp. by its smaller size and two lateral hyoplastral processes; from *Gilmoremys lancensis* (Gilmore, 1928) by its smaller size and small costals 8; from “*Trionyx*” *kansaiensis* by its smaller

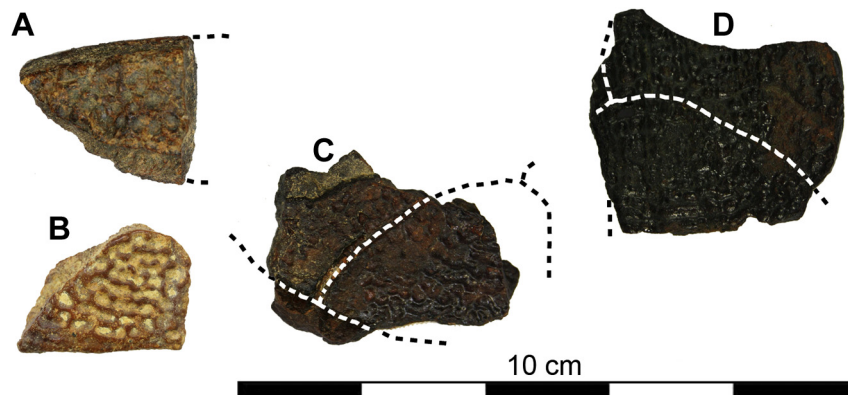


Fig. 4. “*Trionyx*” cf. *kyrgyzensis* specimens from Itemir. A, ZIN PH 56/86, partial nuchal in external view; B, ZIN PH 57/86, costal 8 in external view; C, ZIN PH 54/86, external impression of partial costals 7 and 8; D, ZIN PH 55/86, external impression of partial costals 7 and 8.



size, weak or absent nuchal emargination, small costals 8 and divided medial hypoplastral processes; from “*Trionyx*” *gobiensis* Danilov et al., in press and “*T.*” *kyrgyzensis* by its small costals 8, and divided medial hypoplastral processes. See Table 1 for further differences between “*Trionyx*” *dissolutus* and other Cretaceous trionychids.

**Description of the holotype.** Impressions of a posterior half of a carapace (ZIN PH 51/86; Fig. 5) preserve costals 4–8 and neurals 4–6. Sculpturing of the specimen is unclear. Both costals 7 and 8 are relatively small compared to the other costals. Neurals 4 and 5 are both hexagonal and short-sided anteriorly. Neural 6 is reduced, pentagonal, and lies between the pairs of costals 5 and 6. This arrangement indicates that neural reversal occurred prior to neural 4. A reconstruction of the rest of the carapace, based on other material from both Itemir and the Khodzhaikul Formation, is approximately 24 cm long (Fig. 2D; see more about reconstruction below).

**Description of other material from Itemir.** Sculpturing is identical to the type seen in the material from the Khodzhaikul Formation (see below). A partial nuchal (ZIN PH 58/86; Fig. 6A, B) preserves a depression for the contact with the first thoracic vertebra at either the center or anterior of the nuchal. The nuchal emargination is weak.

A partial medial hyoplastron (ZIN PH 50/86; Fig. 6C, D) shows the beginnings of a hyoplastral shoulder or an anterior flap and epiplastral notch like the kind seen in Plastomenidae (Joyce et al., 2009; Hutchison, 2009; Joyce and Lyson, 2011). The medial processes are still uncovered by the callosity in this specimen. The callosity extends medially past the processes, but there is no suture at the medial margin to indicate that the hyoplastra were sutured at the midline. A partial impression of the hyo- and hypoplastral bridge (ZIN PH 52/86; Fig. 6E) shows that the angle between the medial and lateral lobes is wide. A fragment of a xiphiplastron (ZIN PH 59/86; Fig. 6F, G) is preserved with a callosity and sculpturing identical to other elements from this species.

**Description of material from the Khodzhaikul Formation. Shell.** A reconstruction (Fig. 2D) with a size estimate based on an articulated partial nuchal and costal 1 (ZIN PH 32/122; Fig. 7A, B) is approximately 17 cm long. A more tentative estimate, based on an

isolated hexagonal neural (ZIN PH 44/122; Fig. 7C), is about 22 cm long. Given evidence from Itemir (discussed above), this species may have been even larger, about 24 cm long. A reconstruction of a more juvenile specimen, scaled based on a partial nuchal (ZIN PH 25/122; Fig. 7D) with a large uncallosified anteromedial margin is approximately 13 cm long (Fig. 2E). Whether or not this species was sexually dimorphic is unclear. A lack of complete costals 1–7 makes estimation of the carapace shape impossible. The shape given in the reconstruction is tentative. Sculpturing is composed of rounded ridges more closely spaced than those in “*Trionyx*” cf. *kyrgyzensis* and more often forms a pattern of furrows rather than pits. This pattern gives an overall impression of much finer sculpturing than that seen in “*T.*” cf. *kyrgyzensis*. In general, this pattern is similar to those of “*Trionyx*” *kansaiensis* (see Vitek and Danilov, 2010).

**Nuchal.** Reconstruction based on two different nuchals (ZIN PH 32/122, ZIN PH 29/122) show that the nuchal is approximately four times wider than long, similar to all Cretaceous Asian trionychids with a preserved nuchal (Danilov and Vitek, 2012). The nuchal emargination is weak. The costiform processes (sensu Meylan, 1987) are united (ZIN PH 29/122). The extent of sculpturing on the plate varies widely and correlates with size. Smaller trionychids (ZIN PH 25/122, ZIN PH 29/122; Fig. 7D–F) are not fully covered in a callosity, whereas larger specimens (ZIN PH 32/122) are entirely covered. A few millimeters of the posterior edge of the nuchal underlie the anterior edge of costal 1 (ZIN PH 33/122; Fig. 7G). Postnuchal fontanelles are present in smaller specimens (ZIN PH 25/122; Fig. 7D).

**Neurals.** The medial margin of costal 1 (ZIN PH 34/122; Fig. 7H) does not indicate the presence of a preneural, but neither does it definitely mean that a preneural was absent. No preneurals or neurals 1 were found that could give an indication whether or not a preneural was present. A hexagonal neural (ZIN PH 44/122; Fig. 7C) belongs to this species but which neural it is in the series and how many neurals there were in total is unknown.

**Costals.** An incomplete costal 6 (ZIN PH 39/122; Fig. 7K) is relatively large. Its lateral margin indicates that it made up part of the posterior margin of the carapace. This arrangement indicates that costals 7 and 8 were probably small relative to the other costals. Two costals 8 are preserved. The first one (ZIN PH 43/122; Fig. 7I) is reduced and eye-shaped. Another costal 8 (ZIN

**Table 1**

Comparison of shell characters of some species of Cretaceous trionychids. For data on species other than “*Trionyx*” *dissolutus* see Danilov et al. (in press).

Characters	“ <i>Aspideretes</i> ” <i>maortuensis</i>	<i>Aspideretoides</i> <i>riabinini</i>	<i>Gilmoremys</i> <i>lancensis</i>	<i>Gobiapalone</i> <i>breviplastra</i>	<i>Gobiapalone</i> <i>orlovi</i>	“ <i>Trionyx</i> ” <i>dissolutus</i>	“ <i>Trionyx</i> ” <i>gobiensis</i>	“ <i>Trionyx</i> ” <i>kansaiensis</i>	“ <i>Trionyx</i> ” <i>kyrgyzensis</i>	“ <i>Trionyx</i> ” <i>shiluutulensis</i>
Maximum carapace length, mm	300*	500*	340	260*	335	240*	130*	750*	150*	225
Nuchal emargination	?	Weak	Absent	Weak or absent	Weak or absent	Weak	Weak or absent	Strong	Absent	Weak
Preneural	?	Present	Present	Absent	Absent	?	Absent	Absent	?	Present
Number of neurals	8	7	7	7 or 8 or 9	7 or 8	6	7 or 8	7 or 8	8	8
Neural reversal	5	5 or 6	6	5	5	Prior to 4	5	5	5	6
Costals 8	Small	Small	Large	Small or absent	Small	Small	Large	Large	Large	Small
Epiplastral notch on hyoplastron	Absent	Absent	Present	Absent	Absent	Present	?	Absent	Absent	?
Medial processes of hyoplastron	Present	Present	Absent	Present	Present	Absent	?	Present	Present	?
Lateral hyoplastron lobe in relation to medial hyoplastron lobe	?	Shorter	Almost equal	Shorter	Shorter	?	?	Longer	Longer	?
Ratio of minimal bridge length to maximal hypoplastron length	?	About 50%	About 100%	About 50%	About 50%	?	?	50–60%	About 50%	?
Extensive medial contact of hyo- and hypoplastra	No	No	No	No	No	Yes	?	No	No	?
Medial hypoplastral processes	Clustered	Divided	?	Divided	Divided	Divided	?	Clustered	Clustered	?
Number of sculptured plastral callosities	At least 2	At least 4	At least 4	5	5	At least 4	?	At least 2	Absent	?

\* Estimation

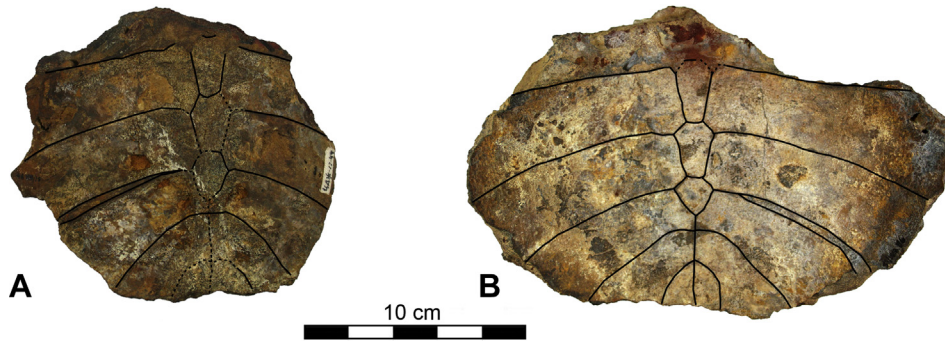


Fig. 5. “*Trionyx*” *dissolutus* sp. nov. holotype specimen from Itemir (ZIN PH 51/86). A, visceral impression of posterior part of carapace; B, external impression of the same.

PH 42/122; Fig. 7J) is similarly reduced, but longer antero-posteriorly and more triangular. The full costal was probably at least as long as it was wide, if not longer. There is no depression for contact with the ilium. The callosity on one lateral costal 1 fragment (ZIN PH 33/122) and on the fragment of costal 6 (ZIN PH 39/122) has grown to cover the entire rib. Otherwise, ribs are

broken off at the edge of costals, and the length of the free ends of the ribs are unknown.

*Plastron*. No epiplastra or entoplastra among the material from the Khodzhaikul Formation could be assigned to this species. The hyoplastra, hypoplastra and xiphiplastra are covered in callosities with a sculpture pattern similar to the pattern on the carapace.

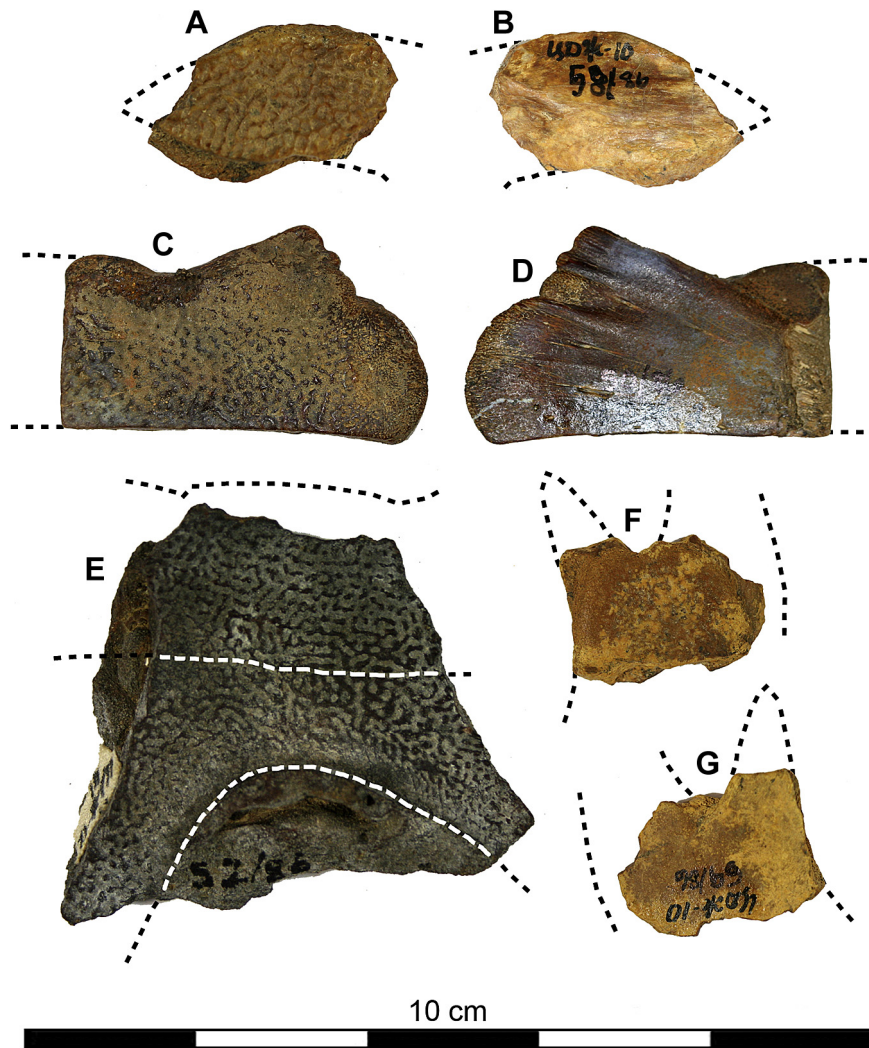
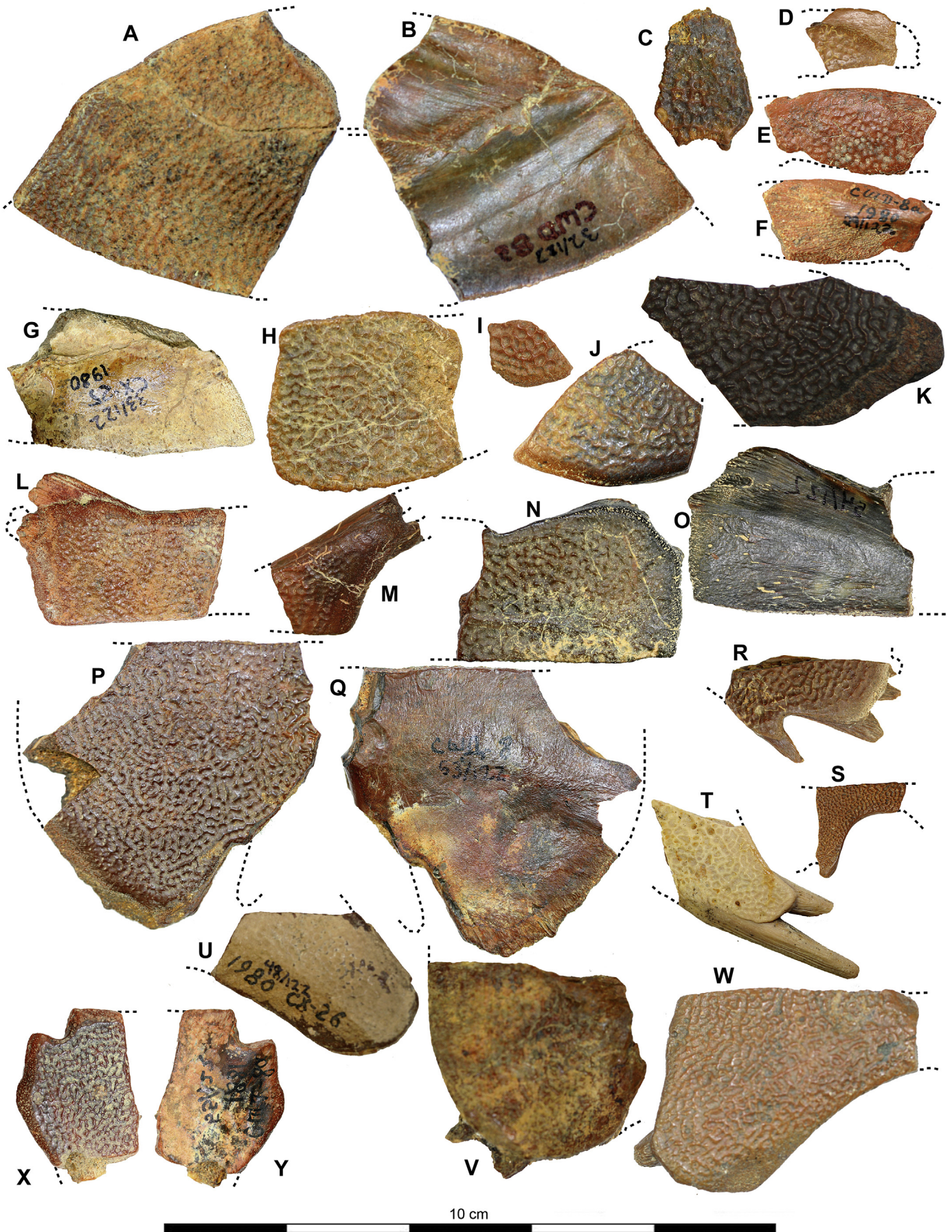
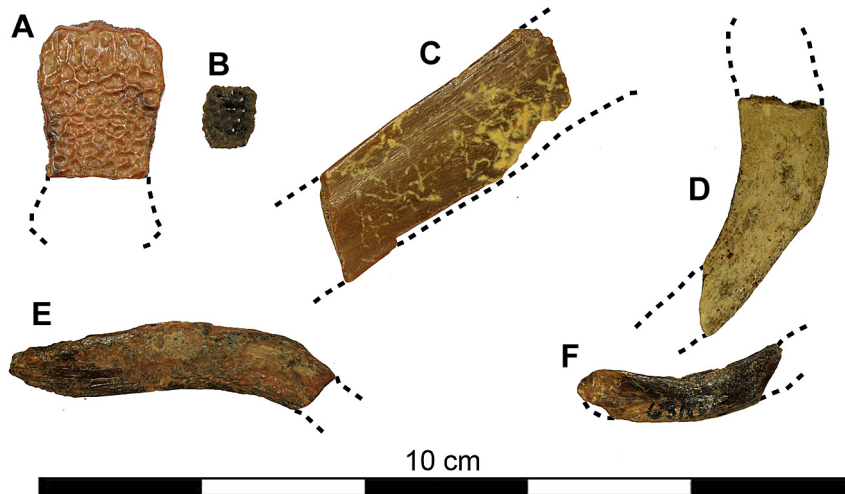


Fig. 6. “*Trionyx*” *dissolutus* sp. nov. specimens from Itemir. A, B, ZIN PH 58/86, partial nuchal in external (A) and visceral (B) views; C, D, ZIN PH 50/86, partial hyoplastron in external (C) and visceral (D) views; E, ZIN PH 52/86, external impression of partial hyoplastron and hypoplastron; F, G, ZIN PH 59/86, partial xiphiplastron in external (F) and visceral (G) views.









**Fig. 8.** Trionychidae indet. specimens from the Khodzhaikul Formation. A, ZIN PH 68/122, partial neural 1 in external view; B, ZIN PH 66/122, tetragonal neural in external view; C–F, partial entoplastra or epiplastra? in external or visceral views: C, ZIN PH 60/122; D, ZIN PH 61/122; E, ZIN PH 62/122; F, ZIN PH 63/122.

*Hyoplastra and hypoplastra.* The hyoplastra and hypoplastra are not fused together. The plastral bridge is approximately one-third the width of the hypoplastron (Fig. 2F, G).

A smaller medial hyoplastron fragment (ZIN PH 46/122; Fig. 7L) has multiple small processes. They are broken and an exact count is impossible. The callosity does not entirely cover these processes, and instead forms a relatively straight anterior margin, and therefore a hyoplastral lappet. In another, larger medial hyoplastron fragment (ZIN PH 54/122; Fig. 7N, O), the callosity has covered all but 1–2 mm of the medial processes. The callosity's medial margin indicates that it contacted the other hyoplastron at the midline. In addition, the fragment shows the beginning of a shoulder, or an anterior flap and epiplastral notch like the kind seen in *Plastomenidae*. The lateral hyoplastral processes (ZIN PH 50/122; Fig. 7M) are angled and extend laterally past the hyo- hypoplastral suture.

The medial hypoplastral processes are divided into anteromedial and posteromedial groups (ZIN PH 53/122; Fig. 7P, Q). Smaller specimens (ZIN PH 52/122; Fig. 7R), are less extensively callosified and the processes are still exposed. Larger specimens (ZIN PH 53/122) have processes entirely covered by a callosity. The hypoplastral bridge (ZIN PH 57/122; Fig. 7S) has a relatively broad curve that is more similar to the hypoplastral bridge of most trionychines than to that of Paleogene *plastomenids* or other well-ossified trionychids. The two lateral hypoplastral processes are left exposed on some specimens (ZIN PH 51/122; Fig. 7T), but in others are covered by large, rounded callosities, that extend to form a nearly perpendicular margin with the hyo-hyoplastral suture in some specimens (ZIN PH 48/122, ZIN PH 47/122, ZIN PH 49/122, Fig. 7U–W).

*Xiphiplastron.* ZIN PH 55/122 (Fig. 7X, Y) probably represents the anterolateral part of the xiphiplastron. The preserved part is completely covered by a callosity.

#### Trionychidae indet.

*Referred material.* ZIN PH 68/122 (SSHD-8), partial neural 1; ZIN PH 66/122 (?), tetragonal neural; ZIN PH 60/122 (SCH-“V”), ZIN PH 61/

122 (SKH-25), ZIN PH 62/122 (?), ZIN PH 63/122 (?), partial entoplastra or epiplastra?.

*Locality, Horizon, and Age (referred material).* Chelpyk and Sheikhdzheili localities, southwestern Kizylkum Desert area, Karakalpakstan, Uzbekistan; Khodzhaikul Formation, early Cenomanian.

*Description.* One anterior neural 1 fragment (ZIN PH 68/122; Fig. 8A) and a small tetragonal neural (ZIN PH 66/122; Fig. 8B), have sculpturing that could conceivably belong to either species present in the Khodzhaikul Formation.

Among the collected material there are several long, thin, uncallosified specimens (ZIN PH 60/122, ZIN PH 61/122, ZIN PH 62/122, ZIN PH 63/122; Fig. 8C–F) that do not resemble free ends of ribs. They are interpreted as entoplastron or epiplastron fragments. One fragment (ZIN PH 60/122) is wide and flattened, similar to the entoplastron of *Trionyx kyrgyzensis*, and another (ZIN PH 61/122) most resembles the medial epiplastron of *T. kyrgyzensis*.

### 3. Discussion

The examined shell material of trionychids from Itemir and the Khodzhaikul Formation is assigned to *Trionyx* cf. *kyrgyzensis*, *T. dissolutus* sp. nov. and Trionychidae indet. The material referred to Trionychidae indet. may belong to one of the two described trionychid taxa.

*Trionyx* cf. *kyrgyzensis* is assigned to Trionychinae based on the combination of the following characters: the nuchal is at least three times wider than long, the neural series contains at least one reversal in neural orientation (synapomorphies of Trionychinae sensu Meylan, 1987), and eight neurals are present (as compared to *Plastomenidae* which have seven neurals; Joyce and Lyson, 2011). *Trionyx* cf. *kyrgyzensis* is very similar to *T. kyrgyzensis* in the general morphology of the shell elements and sculpture pattern, but differs from it in size and greater degree of ossification in the

**Fig. 7.** *Trionyx dissolutus* sp. nov. specimens from the Khodzhaikul Formation. A, B, ZIN PH 32/122, partial nuchal and costal 1 in external (A) and visceral (B) views; C, ZIN PH 44/122, hexagonal neural in external view; D, ZIN PH 25/122, partial nuchal in external view; E, F, ZIN PH 29/122, partial nuchal in external (E) and visceral (F) views; G, ZIN PH 33/122, partial costal 1 in visceral view; H, ZIN PH 34/122, partial costal 1 in external view; I, ZIN PH 43/122, costal 8 in external view; J, ZIN PH 42/122, costal 8 in external view; K, ZIN PH 39/122, partial costal 6 in external view; L, ZIN PH 46/122, partial hyoplastron in external view; M, ZIN PH 50/122, partial hyoplastron in external view; N, O, ZIN PH 54/122, partial hyoplastron in external (N) and visceral (O) views; P, Q, ZIN PH 53/122, partial hypoplastron in external (P) and visceral (Q) views; R, ZIN PH 52/122, partial hypoplastron in external view; S, ZIN PH 57/122, partial hypoplastron in external view; T, ZIN PH 51/122, partial hypoplastron in external view; U, ZIN PH 48/122, partial hypoplastron in external view; V, ZIN PH 47/122, partial hypoplastron in external view; W, ZIN PH 49/122, partial hypoplastron in external view; X, Y, ZIN PH 55/122, partial xiphiplastron in external (X) and visceral (Y) views.

shell. It is unclear if these differences are ontogenetic or specific. [Nessov \(1995\)](#) considered “*T.* *kyrgyzensis*” material to be from adult specimens, based on the fact that other fossil turtle material in the locality came from adult specimens. [Nessov’s \(1995\)](#) reconstruction of “*T.* *kyrgyzensis*” did not show postnuchal fontanelles, but an examination of the holotype material shows that the posteromedial margin of the nuchal, the medial margin of costal 1, neural 1, and a possible preneural are not preserved, so whether or not “*T.*” *kyrgyzensis* had postnuchal fontanelles is unclear. [Nessov \(1995\)](#) tentatively reconstructed “*T.*” *kyrgyzensis* with a preneural, but as is the case with postnuchal fontanelles, there is no clear evidence for this decision. Long free rib ends of “*T.*” *kyrgyzensis* may represent an ontogenetic character. To clarify these questions, new material of “*T.*” *kyrgyzensis* is needed.

“*Trionyx*” *dissolutus* demonstrates characters of both Trionychinae and Plastomenidae. The trionychine characters of “*T.*” *dissolutus* include a nuchal that is at least three times wider than long, and a neural series that contains at least one reversal in neural orientation. Moreover, previously, the holotype specimen of “*T.*” *dissolutus* was assigned to Trionychini [Gray, 1825](#) as Trionychini indet. 1 based on the presence of seven or fewer neurals ([Danilov and Vitek, 2012](#)). It is important to note that although [Meylan’s \(1987\)](#) cladistic analysis recovered a monophyletic Trionychini, subsequent phylogenetic analyses have not ([Engstrom et al., 2004](#); [Joyce and Lyson, 2010](#)).

The extensive callosities, especially the anterior hyoplastral flap, seen in “*Trionyx*” *dissolutus* are reminiscent of the plastron of Plastomenidae, an extinct clade of trionychids from the Cretaceous – Paleogene of North America ([Hutchison, 2009](#); [Joyce et al., 2009](#); [Joyce and Lyson, 2010, 2011](#)). Characters diagnosing Plastomenidae and uniting them with Cyclanorbinae [Hummel, 1929](#) have recently been revised ([Joyce et al., 2009](#); [Joyce and Lyson 2010, 2011](#)). Among the symplesiomorphies between plastomenids and cyclanorbines are the fusion of the hyo- and hypoplastron, the absence of postnuchal fontanelles, and the presence of a depression for contact with the ilia on costals 8. None of these characters are present in “*T.*” *dissolutus*. Other characters, such as the presence of a preneural and seven callosities on the plastron, are unknown for “*T.*” *dissolutus*.

Three of the four characters that unite Plastomenidae and Cyclanorbinae are skull characters, which are not currently useful for “*Trionyx*” *dissolutus*. The fourth, the hypo-xiphiplastral contact with the hypoplastron lateral to the xiphiplastron, is not present in “*T.*” *dissolutus*.

Of the six synapomorphies that unite Plastomenidae, only three are shell characters: the nuchal is at least four times wider than long, seven neurals in addition to the preneural and xiphiplastra contact one another along their entire length ([Joyce and Lyson, 2011](#)). Of these characters, “*T.*” *dissolutus* demonstrates only similar proportions of the nuchal, which alone is not diagnostic because it is also present in members of Trionychinae. In contrast to Plastomenidae, “*T.*” *dissolutus* has only six neurals. [Hutchison’s \(2009\)](#) diagnosis of Plastomeninae includes two characters: the posterolateral arm of the epiplastron reduced or absent, and hypo-xiphiplastra that lack fontanelles and have patent sutures in adults. These characters are either unknown or not present in “*T.*” *dissolutus*.

The combination of characters seen in “*Trionyx*” *dissolutus* indicates that it is not a plastomenid, despite having some superficial resemblance. For this reason and because “*T.*” *dissolutus* shares trionychine synapomorphies we place it in Trionychinae incertae sedis. “*Trionyx*” *dissolutus* demonstrates that a heavily ossified plastron may be more homoplastic within Trionychidae than has been previously recognized.

The conclusion that “*Trionyx*” *dissolutus* is not a plastomenid is in agreement with our previous statement that, at present, no

diagnosable specimens of Plastomenidae are known from the Cretaceous of Asia ([Danilov and Vitek, 2012](#)). On the other hand, new data on Cretaceous trionychids of Asia suggest that most supra-generic clades of modern trionychids (including the cyclanorbine-plastomenid clade) had already evolved in Asia by the Late Cretaceous and should be present in the fossil record ([Danilov et al., in press](#)).

Thus, our study demonstrates the presence of two shell-based trionychid taxa in Itemir and in localities of the Khodzhaikul Formation. Previously, one or two trionychid taxa were reported from these localities (see [Nessov, 1997](#)): *Palaeotrionyx* sp. and Trionychinae indet. (Chelpyk, Khodzhakulsai, Sheikhdzheili); Trionychidae indet. (Khodzhaikul I and II); Trionychidae indet. or Trionychinae indet. (Itemir). Our determinations are different: “*Trionyx*” cf. *kyrgyzensis* and “*T.*” *dissolutus*. “*Trionyx*” cf. *kyrgyzensis* is larger than “*T.*” *kyrgyzensis*, the only trionychid taxon from the older (early-middle Albian) Alamyshek Formation of Kyrgyzstan). Both “*T.*” cf. *kyrgyzensis* and “*T.*” *dissolutus* are smaller than trionychids (*Aspideretoides* cf. *riabinini* and “*Trionyx*” cf. *kansaiensis*) from younger (late Turonian) Bissekty Formation of Dzharakuduk (Uzbekistan), which are in turn smaller than trionychids (*A. riabinini* and “*T.*” *kansaiensis*) from the early Santonian Yalovach Formation of Kansai (Tadzhikistan) and Santonian – early Campanian Bostobe Formation of Shakh Shakh (Kazakhstan) ([Vitek and Danilov, 2010](#); [Danilov and Vitek, 2013](#)). It is interesting that patterns of the shell sculpturing of “*T.*” cf. *kyrgyzensis* and “*T.*” *dissolutus* are similar to those of *A. riabinini* and “*T.*” *kansaiensis* respectively. In addition, “*T.*” *dissolutus* is similar to “*T.*” cf. *kansaiensis* and Trionychidae indet. specimens from Dzharakuduk in degree of ossification and configuration of plastral bones. These similarities may indicate close relationships between “*T.*” *dissolutus* and “*T.*” cf. *kansaiensis*.

Our results improve our understanding of the taxa of Trionychidae within assemblages of the Khodzhaikul Formation and Itemir as well as similarities and differences between Cretaceous turtle assemblages of Middle Asia and Kazakhstan in general. In addition to the same trionychid species, turtle assemblages of the Khodzhaikul Formation and Itemir share the presence of the same families, genera and species, which are *Adocus* [Cope, 1868](#) (Adocidae [Cope, 1870](#)), “*Ferganemys*” *itemirensis* [Nessov, 1981](#) (Adocidae), *Kizylkumemys schultzi* [Nessov, 1976](#) (Carettochelyidae [Boulenger, 1887](#)), and *Anatolemys oxensis* [Nessov et Khosatzky in Nessov, 1977a](#) (Macrobaenidae [Sukhanov, 1964](#)). The differences between these turtle assemblages are the following ([Table 2](#)): 1) potentially different species of *Adocus* (*Adocus* sp. in Itemir and *Adocus kizylkumensis* in the Khodzhaikul Formation ([Syromyatnikova and Danilov, 2009](#)); 2) the presence of *Khodzhaikulemys occidentalis* ([Nessov in Nessov and Krasovskaya, 1984](#)) (Lindholmemydidae [Chkhikvadze in Shuvalov and Chkhikvadze, 1975](#)) in the Khodzhaikul Formation ([Nessov and Krasovskaya, 1984](#); [Danilov, 1999](#)); 3) the presence of a second macrobaenid in the Khodzhaikul Formation (Macrobaenidae indet.; = *Kirgizemys* sp.; = *Kirgizemys*(?) sp.; = cf. *Kirgizemys* sp.; [Nessov, 1997](#)); 4) the presence of Nanshiungchelyidae indet. in the Khodzhaikul Formation ([Danilov and Syromyatnikova, 2008](#)); 5) the presence of a problematic shell-based taxon *Parathalassemys cava* [Nessov in Nessov and Krasovskaya, 1984](#) in Itemir ([Nessov and Krasovskaya, 1984](#)); 6) the presence of a problematic shell-based taxon *Tienfucheloides undatus* [Nessov, 1978](#) in the Khodzhaikul Formation ([Nessov, 1978](#)); 7) the presence of a problematic skull-based taxon *Oxemys gutta* [Nessov, 1977b](#) in the Khodzhaikul Formation ([Nessov, 1977b](#)). Most probably, these differences are explained by a lack of knowledge concerning the turtle assemblages of the Khodzhaikul Formation and Itemir and the fragmentary nature of the material. Both of these Cenomanian turtle assemblages have similarities with the



**Table 2**

Turtle assemblages from some Cretaceous localities of Middle Asia and Kazakhstan (see Fig. 1 for map). Data about the composition of assemblages are taken from the following publications: Nessov (1997); Vitek and Danilov (2010); Danilov et al. (2011); Danilov and Vitek (2012); Vitek and Danilov (2012). See text for other details.

Baybishe and Shakh Shakh (Bostobe Fm., Santonian – early Campanian)	Dzharakuduk (Bissekty Fm., late Turonian)	Itemir (Cenomanian)	Kansai (Yalovach Fm., early Santonian)	Localities of the Khodzshakul Fm. (early Cenomanian)	Kylodzhun (Alamyshik Fm., early-middle Albian)	Kyrkkuduk I (Syuk Syuk Fm. & ?Darbaza Fm., Santonian – ? middle Campanian)
Adocidae						
<i>Adocus bostobensis</i>	<i>Adocus aksary</i>	<i>Adocus</i> sp.	<i>Adocus foveatus</i>	<i>Adocus kizylkumensis</i>		–
<i>Shachemys baibolatica</i>	<i>Shachemys ancestralis</i>	“ <i>Ferganemys</i> ” <i>itemirensis</i>	<i>Shachemys baibolatica</i>	“ <i>Ferganemys</i> ” <i>itemirensis</i>	<i>Ferganemys verzilini</i>	<i>Shachemys</i> sp.
Carettochelyidae						
–	–	<i>Kizylkumemys schultzi</i>	–	<i>Kizylkumemys schultzi</i>	–	–
Lindholmemydidae						
<i>Lindholmemys</i> sp. cf. <i>L. gravis</i>	<i>Lindholmemys elegans</i>	–	<i>Lindholmemys gravis</i>	<i>Khodzshakulemys occidentalis</i>		<i>Lindholmemys</i> sp.
Macrobaenidae						
<i>Anatolemys maximus</i>	<i>Anatolemys</i> sp. cf. <i>maximus</i>	<i>Anatolemys oxensis</i>	<i>Anatolemys maximus</i>	<i>Anatolemys oxensis</i>	<i>Kirgizemys exaratus</i>	–
–	Macrobaenidae indet.	–	–	Macrobaenidae indet.	–	–
Nanhsiungchelyidae						
–	–	–	–	Nanhsiungchelyidae indet.	–	–
Trionychidae (shell-based taxa)						
<i>Aspideretoides riabinini</i>	<i>Aspideretoides</i> cf. <i>riabinini</i>	“ <i>Trionyx</i> ” cf. <i>kyrgyzensis</i>	<i>Aspideretoides riabinini</i>	“ <i>Trionyx</i> ” cf. <i>kyrgyzensis</i>	“ <i>Trionyx</i> ” <i>kyrgyzensis</i>	–
“ <i>Trionyx</i> ” <i>kansaiensis</i>	“ <i>Trionyx</i> ” cf. <i>kansaiensis</i>	“ <i>Trionyx</i> ” <i>dissolutus</i>	“ <i>Trionyx</i> ” <i>kansaiensis</i>	“ <i>Trionyx</i> ” <i>dissolutus</i>	–	“ <i>Trionyx</i> ” <i>kansaiensis</i>
“ <i>Paleotrionyx</i> ” <i>riabinini</i>	–	–	–	–	–	–
–	Trionychidae indet.	–	–	–	–	Trionychidae indet.
Trionychidae (skull-based taxa)						
<i>Khunnuchelys</i> sp. 1	<i>Khunnuchelys kizylkumensis</i>	–	–	–	–	–
–	Trionychini indet.	–	–	–	–	–
–	–	–	Trionychidae indet. 4	–	–	–
Testudines incertae sedis						
–	–	–	–	<i>Oxemys gutta</i>	–	–
–	–	<i>Parathalassemys cava</i>	–	–	–	–
–	–	–	–	<i>Tienfucheloides undatus</i>	–	–
–	–	Testudines indet.	–	Testudines indet.	–	–

older (early-middle Albian) turtle assemblage of Kylodzhun (see above) in the presence of *Ferganemys* Nessov and Khosatzky, 1977 (Adocidae), Macrobaenidae and “*Trionyx*” (Trionychidae). The differences between these assemblages are different genera and species within mentioned families and genera (see Table 2). On the other hand, the Cenomanian turtle assemblages have similarities with the younger (late Turonian) turtle assemblage of Dzharakuduk in the presence of *Adocus* (Adocidae), the second adocid (“*Ferganemys*” *itemirensis* in the Khodzshakul Formation and Itemir and *Shachemys ancestralis* Nessov in Nessov and Krasovskaya, 1984 in Dzharakuduk which are closely related; Syromyatnikova, 2011), Lindholmemydidae, *Anatolemys* (Macrobaenidae), the second macrobaenid (Macrobaenidae indet.) and “*Trionyx*” (Trionychidae). The differences between these assemblages are different genera and species within mentioned families and genera, the absence of Carettochelyidae, Nanhsiungchelyidae and the above-mentioned problematic taxa in Dzharakuduk, and the presence of *Aspideretoides* cf. *riabinini* in Dzharakuduk. These differences reflect a large change in the turtle assemblages composition, which took place in Middle Asia in the early Turonian, when small, thin-shelled turtles were replaced with large and thick-shelled ones (Nessov, 1985, 1997). These changes are thought to have been caused by a large early Turonian transgression as well as by the appearance of a large turtle-eating crocodile (*Shamosuchus*) and large predatory fishes (Ichthyodectidae) (Nessov, 1985).

The similarities between the turtle assemblages of the Khodzshakul Formation and Itemir, on the one hand, and between these Cenomanian assemblages and turtle assemblage of Dzharakuduk,

on the other hand, are not surprising in view of their geographic proximity and similar ages and are in close agreement with data on other vertebrates (Averianov and Sues, 2012).

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