A New Soft-Shelled Trionychid Turtle of the Genus Khunnuchelys from the Upper Cretaceous Bostobe Formation of Kazakhstan

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A new soft-shelled trionychid turtle of the genus *Khunnuchelys* from the Upper Cretaceous Bostobe Formation of Kazakhstan

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Previously unpublished trionychid turtle material from the Upper Cretaceous (Santonian–lower Campanian) Bostobe Formation from the Baybishe and Baykhozha localities in Kazakhstan is described. The material represents a new species of *Khunnuchelys*, a large, skull-based clade of Cretaceous Asian trionychids. Concordant with other partial skulls and fragmentary specimens described previously, *Khunnuchelys lophorhothon* sp. nov. has the unusual features of a beak-like maxilla and a vaulted, expanded triturating surface. In addition, the specimens reveal novel features including a constricted skull roof. Although estimates of the length of the carapace differ depending on estimation method, the skull belonged to a turtle of comparable size to the shell-based species "*Trionyx*" *kansaiensis* from the same formation. It is likely that *K. lophorhothon* and "*T.*" *kansaiensis* are synonymous, but this can be proved only by a find of associated skull and shell material.

Key words: Testudines, Trionychidae, Trionychia, *Khunnuchelys lophorhothon,* Cretaceous, Kazakhstan.

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Introduction

The family Trionychidae Gray, 1825, or soft-shelled turtles, is a group of mostly highly 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 because the earliest records of trionychids and their diversification come from that time period (see Danilov and Vitek 2012 for 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). It is the first description of two skulls from the Bostobe Formation of Kazakhstan that we assign to *Khunnuchelys* Brinkman, Nessov, and Peng, 1993 (Fig. 1; see Vitek and Danilov 2010 for more details about the geography of Middle Asia and Kazakhstan). Anatomical terminology follows Gaffney (1979).

Khunnuchelys currently contains the only skull-based species of Cretaceous trionychids from Asia (Brinkman et al. 1993), and consists of two species: *K. erinhotensis* Brinkman, Nessov, and Peng, 1993 (type species) and *K. kizylkumensis* Brinkman, Nessov, and Peng, 1993. The former was named on the basis of an incomplete skull from Erinhot (Inner Mongolia, China, Iren Dabasu Formation, Santonian; Brinkman et al. 1993; Averianov and Sues 2012). The latter was based on two braincases and a maxilla from Dzharakuduk (Central Kizylkum Desert, Uzbekistan, Bissekty Formation, late Turonian; Brinkman et al. 1993). Additional fragmentary material of *K. kizylkumensis* was recently described from Dzharakuduk (Vitek and Danilov 2013).

The present specimens have already been noted (*Khunnuchelys* 1 and 2 of Danilov and Vitek 2012). The first spec-

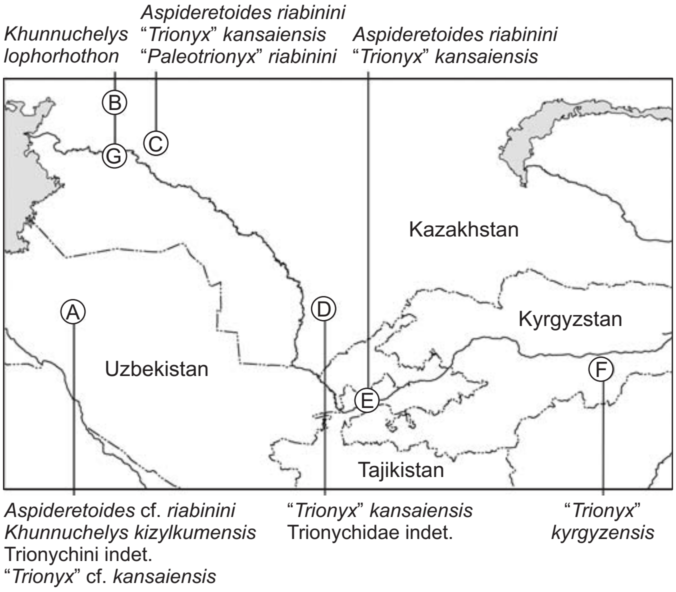


Fig. 1. Map showing main localities of Cretaceous trionychids in Middle Asia and Kazakhstan. A, Dzharakuduk; B, Baybishe; C, Shakh-Shakh; D, Kyrkkuduk I; E, Kansai; F, Kylodzhun; G, Baykhozha. See Vitek and Danilov (2010, 2012, 2013) and Danilov and Vitek (2013) for data on localities other than Baykhozha.

imen (*Khunnuchelys* sp. 1 of Danilov and Vitek 2012; ZIN PH 5/55) is an incomplete skull from Baybishe. Originally it was considered a skull roof of a hadrosaur and identified as cf. *Lophorhothon* by Nessov (1995). Later, this skull was attributed to *Khunnuchelys* (Glinskiy 2008; Glinskiy and Danilov 2008), but has never been described in detail or figured.

The second specimen (*Khunnuchelys* sp. 2 of Danilov and Vitek 2012; ZIN PH 1/146) is also an incomplete skull, but comes from Baykhozha locality. This specimen was found by the Russian geologist Mikhail E. Voskoboynikov in 1948 and studied by Lev I. Khosatzky. Although it has been mentioned in print (Khosatzky 1957; Rozhdestvensky and Khosatzky 1967; Kordikova 1994; Nessov 1997) it has never been described. This specimen is currently on loan to Elena G. Kordikova, who was unable to be contacted for return of the specimen. Therefore, the description of this skull was written based on the personal observations of one of the authors (AOA), and further observations based on old photographs of the skull.

Institutional abbreviations.—ZIN PH, Paleoherpetological collection, Zoological Institute of the Russian Academy of Science, St. Petersburg, Russia.

Systematic palaeontology

Testudines Batsch, 1788

Cryptodira Cope, 1868

Trionychidae Gray, 1825

Trionychinae Gray, 1825

Genus *Khunnuchelys* Brinkman, Nessov, and Peng, 1993

Type species: *Khunnuchelys erinhotensis* Brinkman, Nessov, and Peng, 1993, Northeast of Erinhot, Inner Mongolia, People's Republic of China, Iren Dabasu Formation, Upper Cretaceous.

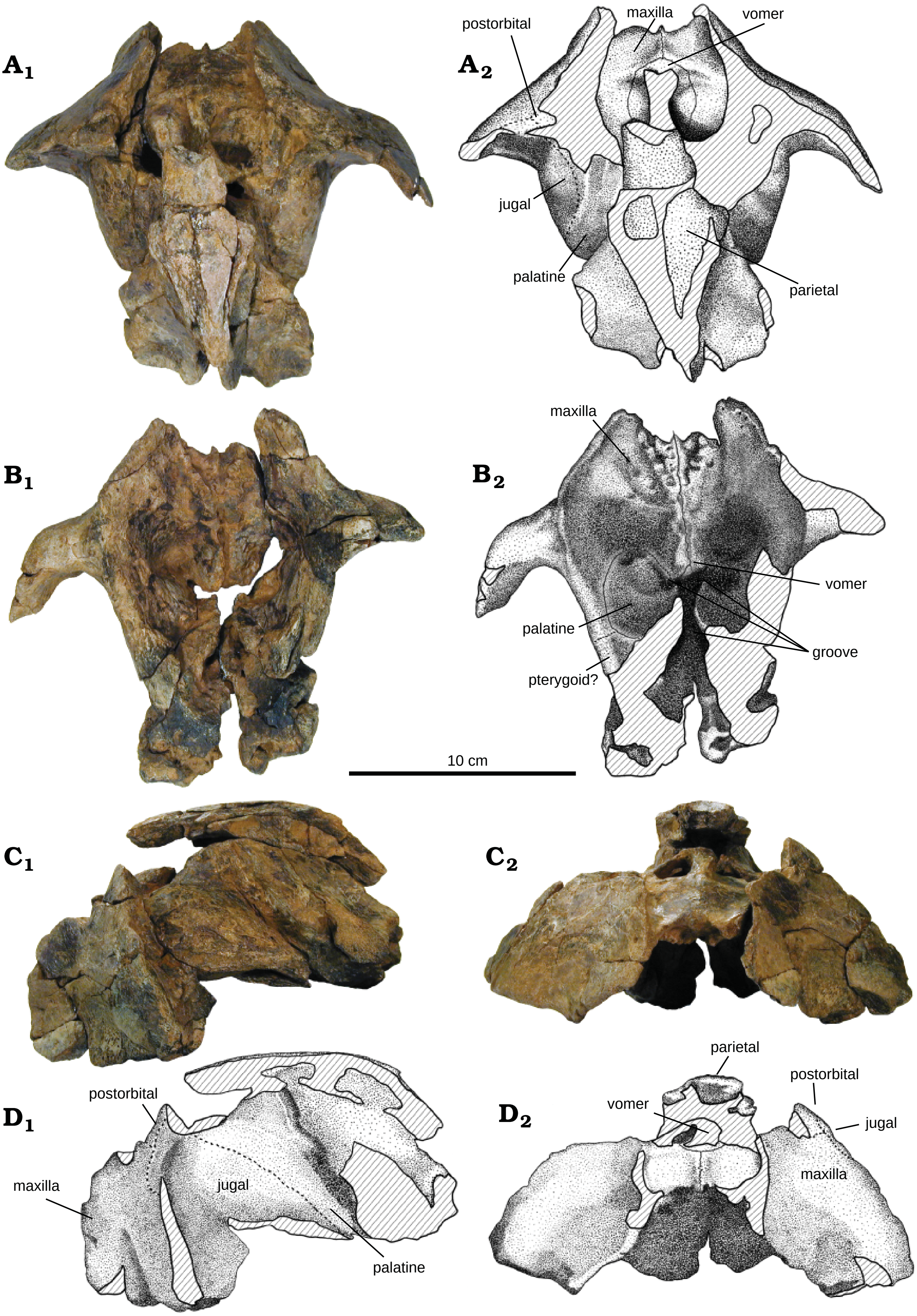
Emended diagnosis.—A trionychid in which the orbits face strongly forwards; the suborbital region of the maxilla is deep; the palate is vaulted; the triturating surfaces of the maxilla and dentary are beak-like; the triturating surfaces of the maxillae meet at the midline, forming a mid-ventral ridge; the internal nares are located far posteriorly and are roofed by the palatines and maxillae; the anterolateral corner of the palatine and posterolateral corner of the maxilla are greatly enlarged to form about half of the triturating surface; the maxilla and jugal are swollen to form a broadly convex surface in dorsal view; the postorbital contacts the maxilla, excluding the jugal from the margin of the orbit; the roof of the skull is constricted to expose the palatine in dorsal view; the descending process of the parietal does not participate in the processus trochlearis oticum; a posteriorly facing occipital surface is bordered dorsally by a rounded ridge formed by the opisthotic and supraoccipital; a concave surface is present on the occiput above the fenestra postotica and lateral to the foramen magnum; the occipital surface of the exoccipital faces posteriorly; nervi hypoglossi exit via a single foramen in the exoccipital. Similar to *Conchochelys* in the presence of a deeply excavated palate, extensively developed secondary palate with broad contact of the maxillae at the midline, grooves extending backwards from the internal choanal openings, and short basioccipital region. Similar to *Dogania* in that the prefrontal makes a small contribution to the orbit margin between the frontal and maxilla. Emended from Brinkman et al. (1993) and Vitek and Danilov (2013).

Geographic and stratigraphic range.—Asia (China, Kazakhstan, and Uzbekistan), Upper Cretaceous (Iren Dabasu Formation, Santonian; Bissekty Formation, upper Turonian; Bostobe Formation, Santonian–lower Campanian).

Khunnuchelys lophorhothon sp. nov.

1957 Trionychid; Khosatzky 1957: 18.
1967 Trionychid; Rozhdestvensky and Khosatzky 1967: 87.
1994 Trionychidae indet.; Kordikova 1994: 345.
1995 cf. *Lophorhothon*; Nessov 1995: 107.
1997 *Khunnuchelys* sp.; Nessov 1997: 110.
2008 *Khunnuchelys* sp.; Glinskiy and Danilov 2008: 19.
2008 *Khunnuchelys riabinini* (Kuznetsov and Chkhikvadze, 1987); Glinskiy 2008: 23.
2009 *Khunnuchelys* sp.; Danilov and Vitek 2009: 53.
2010 *Khunnuchelys* sp.; Vitek and Danilov 2010: 390.
2012 *Khunnuchelys* sp. 1; Danilov and Vitek 2012: 9.
2012 *Khunnuchelys* sp. 2; Danilov and Vitek 2012: 9.

Fig. 2. Holotype of the trionychid turtle *Khunnuchelys lophorhothon* sp. nov. from Baybishe, northeastern Aral Sea region, Kazakhstan, Bostobe Formation, Santonian–lower Campanian, Upper Cretaceous; ZIN PH 5/55, a partial skull; in dorsal (**A**), ventral (**B**), lateral (**C**), and anterior (**D**) views. Photographs (A_1–D_1), explanatory drawings (A_2–D_2). →


A1
A2
postorbital
maxilla
vomer
jugal
palatine
parietal
B1
B2
maxilla
vomer
palatine
groove
pterygoid?
10 cm
C1
C2
D1
postorbital
maxilla
jugal
palatine
D2
parietal
postorbital
vomer
jugal
maxilla

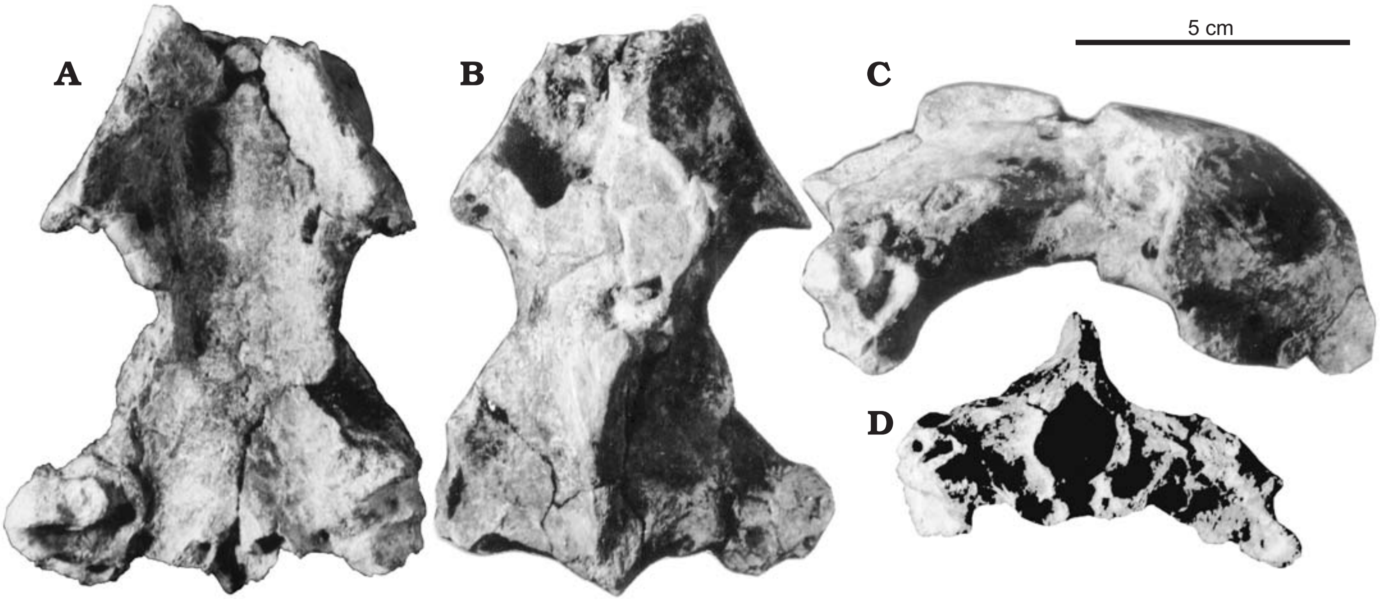


Fig. 3. The trionychid turtle *Khunnuchelys lophorhothon* sp. nov. from Baykhozha, northeastern Aral Sea region, Kazakhstan, Bostobe Formation, Santonian–lower Campanian, Upper Cretaceous; ZIN PH 1/146, a partial skull; in ventral (**A**), dorsal (**B**), lateral (**C**), and posterior (**D**) views.

Etymology: Named after *Lophorhothon*, the hadrosaur, to which the holotype of this species was originally attributed (see Introduction).

Holotype: ZIN PH 5/55, a partial skull from Baybishe.

Type locality: Baybishe and Baykhozha, northeastern Aral Sea region, Kazakhstan.

Type horizon: Bostobe Formation, Santonian–lower Campanian (see Nessov 1997).

Material.—ZIN PH 1/146, a partial skull from Baykhozha.

Diagnosis.—A species of *Khunnuchelys* which can be differentiated from other species of this genus in that the palatines not only form the lateral walls of the grooves that open posteriorly from the apertura narium interna, but also form part of the floor of these grooves, leaving the grooves less ventrally exposed. In addition, it can be differentiated from *K. erinhotensis* in that the upper margin of the external nares is located dorsal to the ventral orbit margins, and in that the foramen jugularis posterius is confluent with the fenestra postotica.

Description.—The holotype (ZIN PH 5/55; Fig. 2), consists of mostly complete maxillae, palatines, and the vomer, as well as much of the parietal and part of the jugal. The parietals and palatines are broken anterodorsal to where the ventral margin of the skull and the foramen nervi trigemini would be. Sutures are mostly obliterated, either from damage to the skull or co-ossification of the bones. Therefore, many of the sutures are shown in illustrations by dotted lines, indicating uncertainty. This skull fragment is approximately 16 cm long. Based on the proportions of the fragment, the condylobasal length was probably 20–24 cm, and the complete skull (including the supraoccipital crest) was probably 30–40 cm long at the midline.

The second skull (ZIN PH 1/146; Fig. 3) is smaller and only partly preserved. It is missing parts of the maxillae and prefrontals, the jugals, the basioccipitals, the supraoccipital crest, and the left quadrate. Preservation of this skull is poor and sutures between bones are not visible. The length of the preserved partial skull is approximately 9 cm. Calculations suggest an estimated condylobasal length of 11 cm and an estimated total skull length of about 17 cm. The skull is unique among specimens of *Khunnuchelys* in that the ventral margin of the skull is generally well preserved. It indicates that the skull is arched antero-posteriorly.

In ZIN PH 5/55 (Fig. 2), the preserved maxillae do not extend anteriorly as far as the margins of the external nares. In dorsal view (Fig. 2A), they articulate with the jugals posterolaterally and the postorbitals posteromedially near where the margin of the orbits would be. The relative snout length is unclear, but the cheek region of the maxillae is short, deep, and broadly flared. The palate is vaulted and expanded both anteriorly and posteriorly (Fig. 2B), causing the maxillae to bulge posterolaterally (Fig. 2C). The palate is similarly vaulted in ZIN PH 1/146. In that specimen, the ventral margin of the right maxilla is preserved, indicating a single, flattened beak with no separate triturating surface of any kind (Fig. 3A). The lack of a separate triturating surface is only known in other species of *Khunnuchelys* and in *Conchochelys admiribalis* Hay, 1905. The more complete facial portion of ZIN PH 1/146 is short (Fig. 3B). Although the dorsal margin of the external nares in ZIN PH 1/146 is broken, the segment of the margin that is still complete extends dorsal to the ventral orbit margins (Fig. 3C).

Parts of the maxillae and prefrontals are broken off in ZIN PH 5/55, exposing the nares and the palate dorsally, including the midline narial ridge formed by the vomer (Fig. 2A). The nares are floored by both the maxillae and vomer. Laterally, they are walled by the maxillae. Anteriorly, the vomer has a dorsal fork that would most likely have contacted the prefrontals in the roof of the nares. Along the posterior midline of the nares, the vomer forms a dorsal midline ridge that arches posterolaterally to enclose the narial canals and contact the maxillae. In ventral view, the vomer is exposed posterior to the maxillae on the midline but does not articulate with the palatines. This lack of contact was potentially present in the complete skull but this area of the skull is not well preserved. Part of the external nares is preserved in ZIN PH 1/146, but the dorsal margin is broken and potential emargination cannot be discerned.

In ZIN PH 5/55, the maxillae meet at the midline in ventral view, forming a median ridge similar to that described in *K. erinhotensis*. The preserved margins of the apertura narium interna are formed by the maxillae and palatines in ZIN PH 5/55. Like other species of *Khunnuchelys*, the palate has two grooves that open posteriorly from the apertura narium interna. The grooves meet at the midline and continue as a single groove posteriorly. The palatines not only form the lateral walls of these grooves, but also form part of the floor for the grooves, leaving the grooves less ventrally exposed than is apparent in other species of *Khunnuchelys*. Anteriorly, this secondary floor of the palatine may have contacted the maxillae, fully closing the grooves at certain points. In the smaller specimen, ZIN PH 1/146, no internal midline ridge or grooves can be identified from photographs. However, observations by AOA indicate that part of the palatal surface is covered in matrix. In lateral view, the palatines do not contribute to the wall of the braincase, instead contributing to the posterolateral bulge of the palate in ZIN PH 5/55.This contribution is the same as the jugal process described by Brinkman et al. (1993).

The jugal and postorbital are both preserved as fragments sutured to the left maxilla (ZIN PH 5/55). Although the orbit margins are not preserved, it is clear that the jugal contacts the postorbital medially and the jugal and postorbital contact the maxilla anteroventrally. This arrangement indicates that the postorbital prevented the jugal from contributing to the orbit margin. The jugal makes up about half of the posterolateral bulge of the palate (Fig. 2A).

In dorsal view, the skull roof is constricted anteriorly, leaving the dorsolateral surface of the palate exposed (Figs. 2A, 3B). Within the lower temporal fossa, the anterior margin of bone formed by the prootic and parietal is bent at an angle similar to other specimens of *Khunnuchelys* (Brinkman et al. 1993). In lateral view (ZIN PH 1/146; Fig. 3C), bone completely surrounds the incisura columella auris, and a thin ridge of bone protrudes from the structure within the cavum tympani.

In posterior view, a dorsal rounded ridge is present and separates the dorsal and posterior surface of the skull (ZIN PH 1/146; Fig. 3D). Below this ridge, lateral to the foramen magnum, is a concave surface. Both features are considered diagnostic for *Khunnuchelys*. Each exoccipital has a single foramen nervum hypoglossum. The foramen jugularis posterius is confluent with the fenestra postotica, as in *Khunnuchelys kizylkumensis* but unlike *K. erinhotensis*.

Discussion and conclusions

The type skull (ZIN PH 5/55) is attributed to *Khunnuchelys* based on a deep suborbital region of the maxilla, the presence of a vaulted palate, triturating surfaces of the maxillae that meet along the midline, posteriorly positioned internal nares, palatines and maxillae that form much of the triturating surface, maxillae and jugals that form broadly convex surfaces in dorsal view; postorbitals that contact the maxillae and exclude the jugal from the orbital margin, and a descending flange of the parietal that does not participate in the formation of the processus trochlearis oticum. The referred skull (ZIN PH 1/146) is attributed to *Khunnuchelys* based on the presence of beak-like maxillae and a vaulted palate, and a descending process of the parietal that does not participate in the formation of the processus trochlearis oticum. The lack of parietal participation in the processus trochlearis oticum is an ancestral feature in comparison to all extant trionychids, in which the parietal always contributes to the processus trochlearis oticum to some degree (Meylan 1987).

Both these specimens are referred to the same new species because of their similarities in palate morphology, constriction of the skull roof, and their similar age (formation) and provenance. In addition, specimen ZIN PH 5/55 has the autapomorphic feature of palatines that partially floor the internal grooves of the aperture narium interna. That feature is covered by matrix in ZIN PH 1/146.

The skull ZIN PH 5/55 is large for a trionychid and comparable in size to the other known specimens of *Khunnuchelys*. The comparable region of *K. erinhotensis* is 11 cm long with an estimated condylobasal length of 16–18 cm and complete skull length of 18–25 cm. The reconstructed condylobasal skull length and complete skull length of *K. kizylkumensis* based on specimen figures (Brinkman et al. 1993) is 18–22 cm and 20–30 cm, respectively. In contrast, ZIN PH 5/55 is 16 cm long, with a total estimated condylobasal length of 20–24 cm. Additionally, we recently described new material of *K. kizylkumensis* that includes skull fragments comparable in size with ZIN PH 5/55 (Vitek and Danilov 2013).

Because most size measurements are published as bony carapace lengths and not skull lengths, it is difficult to compare the size of any species of *Khunnuchelys* and extant trionychids. One exception is Dalrymple's (1977) allometric analysis of *Apalone ferox* (Schneider, 1783). Based on analysis of 58 specimens, he arrived at a condylobasal–carapace length relationship of

$$y = 0.181x^{1.225},$$

where y is the condylobasal skull length and x is carapace length (note that variables are given as such in the description of materials and methods [Dalrymple 1977: 259], but variables are reported as opposite in the description of the results [Dalrymple 1977: 280]). Based on that equation, a trionychid with a condylobasal skull length of 24 cm should have a carapace bony disc length of 54 cm.

Only a few published descriptions of fossil trionychids include measurements of the skull and carapace of a single individual. These include "*Aspideretes*" *singularis* Hay, 1908, with a condylobasal skull length of 10.2 cm and a carapace length of 35 cm (Hay 1908), "*Amyda*" *mira* Hay, 1908 with a condylobasal skull length of 7.2 cm and a carapace length of 26.3 cm, and *Oliveremys uintaensis* Leidy, 1872, a complete skull length of 13.1 cm and a carapace length of 41 cm (Vitek 2011). None of those measurements fit with the equation calculated by Dalrymple (1977), and cast doubt on the usefulness of the equation for estimating skull or shell length of extinct trionychids. Rough estimates for carapace length based on the measurements of these few extinct species of trionychids are anywhere from 68 to 125 cm. Although the latter estimate has a wide range, we think that the larger estimated size better reflects the size of the bony disc of *K. lophorhothon* than the estimate from Dalrymple's (1977) equation.

Shell fragments from the Kansai and Shakh-Shakh localities of the Bostobe Formation come from a trionychid with an adult carapace length of at least 75 cm (Vitek and Danilov 2010). The shell material was referred to "*Trionyx*" *kansaiensis* Vitek and Danilov, 2010, and although both skull and shell material from gigantic trionychids have been described from the Bostobe Formation, none of the shell and skull material has been found associated. Therefore, although we think it is highly likely that *K. lophorhothon* and "*T.*" *kansaiensis* are the same taxon based on their corresponding size and the lack of evidence for other gigantic trionychids in these localities, we do not have direct evidence for synonymy (see also Vitek and Danilov 2010; Danilov and Vitek 2012).

Within the Bostobe Formation, there are two shell morphotypes in addition to those mentioned above. These additional morphotypes are identified as *Aspideretoides riabinini* Kuznetsov and Chkhikvadze, 1987 and "*Paleotrionyx*" *riabinini* Kuznetsov and Chkhikvadze, 1987 (see Vitek and Danilov 2010). However, no skull material other than that of *K. lophorhothon* is known for trionychids from this formation. Additional collecting from the Bostobe Formation is required to identify skulls for these carapaces.

The description of *K. lophorhothon* reveals parts of the skull, such as the almost complete ventral margin, which were not preserved in other specimens of *Khunnuchelys*. The new material reveals new characters that appear to be apomorphic for the clade *Khunnuchelys* although they may alternatively be autapomorphic for *K. lophorhothon*. Provisionally, we have interpreted them as apomorphic for *Khunnuchelys* and emended the diagnosis of the clade accordingly. These characters are constriction of the skull roof that reveals the dorsal surface of the palate and the triturating surface of the maxillae confluent with the rest of the arched palate.

A close relationship between *Khunnuchelys* and the North American *Conchochelys admiribalis* Hay, 1905 was previously hypothesized (Brinkman et al. 1993). They are broadly similar in the presence of a vaulted palate and broad contact between the maxillae at the midline, but differ in the posterior expansion of the triturating surface and the midventral ridge on the secondary palate. Because of the poor preservation of the only known specimen of *Conchochelys admiribalis*, it is unclear if that taxon has a similarly restricted skull roof and parietal that does not contribute to the processus trochlearis oticum. Based on what we can observe about the specimen, those characters are likely present, but most sutures are obliterated and the addition of plaster to the specimen makes comparison between the dorsal and ventral extents of the skull difficult. We agree with previous conclusions, both that *Khunnuchelys* and *Conchochelys* are probably closely related and that better preserved material, including postcranial elements, is necessary to understand those relationships.

Both *Khunnuchelys* and *Conchochelys* have been hypothesized to be molluscivorous (Hay 1905; Brinkman et al. 1993). The lower jaws of the latter remain unknown, but dentary fragments of *Khunnuchelys kizylkumensis* were recently described (Vitek and Danilov 2013). Both the upper and lower jaws of this taxon were beak-like, supporting the hypothesis that those turtles were crushing hard shells, either of molluscs or of other, smaller turtles. The triturating surfaces of *Khunnuchelys* and *Conchochelys* are different from all other known trionychids, including extant taxa. Therefore, inferring the dietary ecology of those taxa, especially with no knowledge of the morphology of the keratinous sheaths on the jaws, remains speculative.

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