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Source: *Acta Palaeontologica Polonica*, 53(4) : 601-614

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: <https://doi.org/10.4202/app.2008.0405>

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The description and phylogenetic position of a new nanhsiungchelyid turtle from the Late Cretaceous of Mongolia

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Sukhanov, V.B., Danilov, I.G., and Syromyatnikova, E.V. 2008. The description and phylogenetic position of a new nanhsiungchelyid turtle from the Late Cretaceous of Mongolia. *Acta Palaeontologica Polonica* 53 (4): 601–614.

This paper describes a new nanhsiungchelyid turtle, *Kharakhutulia kalandadzei* gen. et sp. nov., based on two partial shells and additional shell fragments from the lower part of the Bainshire Formation (Upper Cretaceous, Cenomanian–lower Turonian) of the Khara Khutul locality of Eastern Mongolia. Our phylogenetic analysis places *Kharakhutulia kalandadzei* as the most basal member of the Nanhsiungchelyidae and suggests new relationships within this group. Previously reported nanhsiungchelyid specimens from the Khara Khutul are reassigned to Nanhsiungchelyidae indet. and *Hanbogdemys* sp. indet. Thus the Khara Khutul includes at least two valid taxa of nanhsiungchelyids. Our analysis of the nanhsiungchelyid record in Asia shows that other localities have only a single representative of this clade, making Khara Khutul a unique site. The basal phylogenetic position of *Kharakhutulia kalandadzei* emphasizes the importance of the study of this and other Cenomanian–Turonian localities of Asia to better understand the basal diversification of the Nanhsiungchelyidae.

Key words: *Kharakhutulia*, Nanhsiungchelyidae, Cryptodira, Testudines, Upper Cretaceous, Mongolia.

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Introduction

Nanhsiungchelyidae Yeh, 1966 is a group of cryptodiran turtles, known only from the Cretaceous of Asia and North America and peculiar by a combination of aquatic and terrestrial features (Sukhanov 2000; Hutchison 2000; Hirayama et al. 2001; Joyce and Norell 2005). According to recent phylogenetic studies (Meylan and Gaffney 1989; Brinkman and Nicholls 1993; Brinkman 1998; Danilov and Parham 2006; Joyce 2007), the Nanhsiungchelyidae are considered to be closely related to the Adocidae Cope, 1870. Relationships within the Nanhsiungchelyidae were explored in a series of recent publications (Brinkman and Nicholls 1993; Brinkman and Peng 1996; Hirayama et al. 2001; Joyce and Norell 2005) which agree in considering this group monophyletic and in distinguishing two clades within it. The first clade unites all species of the North American genus *Basilemys* Hay, 1902, whereas the second one consists of the Asian taxa *Hanbogdemys orientalis* (Sukhanov and Narmandakh, 1975) and *Nanhsiungchelys wuchingensis* Yeh, 1966, and, when included in the analysis, also *Anomalochelys angulata* Hirayama, Sakurai, Chitoku, Kawakami, and Kito, 2001. How-

ever, all analyses differ in the position of the remaining Asian taxa and in the interpretation of which clade should be considered the most basal relative to *Basilemys*. Our paper describes a new nanhsiungchelyid *Kharakhutulia kalandadzei*, gen. et sp. nov., from the lower part of the Bainshire Formation (Late Cretaceous, Cenomanian–lower Turonian) of the Khara Khutul locality of Eastern Mongolia. Our phylogenetic analysis places this taxon as the most basal member of the Nanhsiungchelyidae and suggests new relationships within this group (Fig. 1). In addition, the new turtle from the Khara Khutul allows a review of previous records of the Nanhsiungchelyidae from this locality. We also review previously published records of nanhsiungchelyids in Asia thus setting the stage for future work.

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

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; IGM, Institute of Geology, Ulaanbaatar, Mongolia; IP, Institute of Paleobiology, Georgian Academy of Sciences, Tbilisi, Georgia; PIN, Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; YPM, Yale Peabody Museum, New Haven, USA.

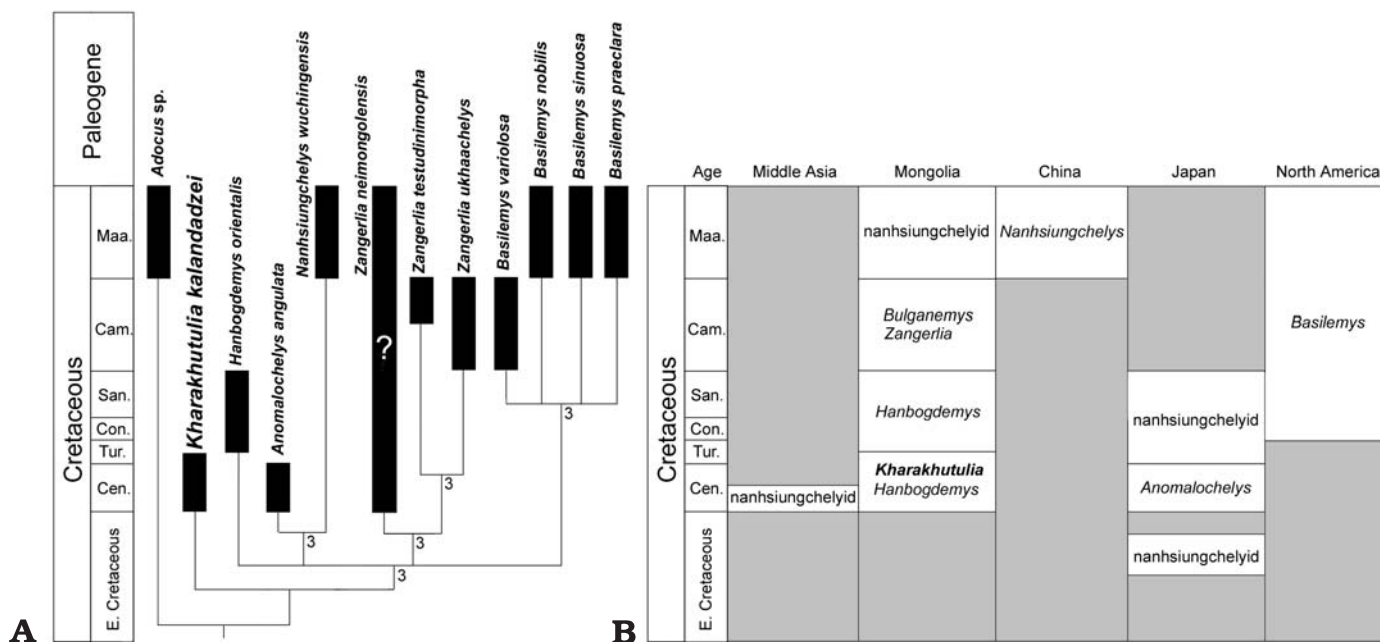


Fig. 1. Phylogeny and distribution of Nanhsiungchelyidae. **A.** Phylogeny of Nanhsiungchelyidae showing the hypothesized position of *Kharakhutulia kalandadzei*. This is a strict consensus of 18 phylogenetic trees resulting from this study (see Discussion for description of the tree). Numbers designate Bremer support indices. Black boxes indicate ranges of nanhsiungchelyid taxa and *Adocus* sp. **B.** Temporal and geographic distribution of Nanhsiungchelyidae. Data on *Zangerlia neimongolensis* are not included due to uncertainty of its age. Gaps in record are filled with grey. See Fig. 8 and Appendix 3 for details of Asian records. Temporal distribution of nanhsiungchelyids in North America is given according to Hutchison (2000). Abbreviations: Cam, Campanian; Cen., Cenomanian; Co., Coniacian; E., Early; Maa., Maastrichtian; San., Santonian; Tur., Turonian.

Materials and methods

In addition to the four specimens described below, our study relies on published data and personal observations (when noted) on the following taxa of adocids and nanhsiungchelyids for comparative purposes: *Adocus beatus* (Leidy, 1865) (Hay 1908; IGD personal observations of YPM 782, holotype of *A. punctatus* Marsh, 1890); *Adocus* sp. (Meylan and Gaffney 1989); *Anomalochelys angulata* Hirayama, Sakurai, Chitoku, Kawakami, and Kito, 2001 (Hirayama et al. 2001); *Basilemys variolosa* (Cope, 1876) (Langston 1956; IGD personal observations of AMNH 1465); *Basilemys nobilis* Hay, 1911 (Langston 1956); *Basilemys sinuosa* Riggs, 1906 (Riggs 1906); *Basilemys praeclara* Hay, 1911 (Brinkman and Nicholls 1993); *Hanbogdemys orientalis* (Sukhanov and Narmandakh, 1975) (Sukhanov and Narmandakh 1975, 1977); *Nanhsiungchelys wuchingensis* Yeh, 1966 (Yeh 1966; Hirayama et al. 2001); *Zangerlia neimongolensis* Brinkman and Peng, 1996 (Brinkman and Peng 1996); *Zangerlia testudinimorpha* Młynarski, 1972 (Młynarski 1972); *Zangerlia ukhaachelys* Joyce and Norell, 2005 (Joyce and Norell 2005; IGD personal observations of IGM 90/1, holotype of *Z. ukhaachelys*).

The phylogenetic analysis of the Nanhsiungchelyidae by Joyce and Norell (2005) was the basis of our analysis. The character matrix of Joyce and Norell (2005) was changed in the following ways: character 18 for *Anomalochelys angulata* and *Nanhsiungchelys wuchingensis* is changed from “1”

to “2” and from “2” to “1” respectively, according to the literature (Hirayama et al. 2001; Yeh 1966); character 20 (costiform processes of nuchal) is slightly reformulated so that state (0) is changed from “absent” to “absent or small”; scoring of characters 36 (humero-pectoral sulcus) and 39 (participation of pectoral to rim of axillary notch) for *Zangerlia testudinimorpha* is changed from “0” to “?” and from “a” to “?” respectively, as the condition of both characters are not sufficiently evident to us from the published figures (Młynarski 1972: fig. 1, pl. 28); character 40 (Geographical distribution) was removed. We add to the analysis two additional characters: 40 (sculpturing of the shell) and 41 (overlapping of scales on the dorsal surface of the plastron). Hirayama et al. (2001) united these two characters in their character 16. Joyce and Norell (2005) did not use this character(s) because they found it difficult to objectively compare or homologize the sculpturing in different Nanhsiungchelyidae. In fact, sculpturing of the Nanhsiungchelyidae can be distinguished from those of the Adocidae in consisting of relatively bigger irregular pits and grooves, whereas in the Adocidae the pits and grooves are smaller and arranged more regularly. We consider the sculpturing as important for distinguishing these groups and return this character to the analysis. Overlapping of scales onto the dorsal surface of plastral lobes also diagnoses nanhsiungchelyids from adocids. See Appendix 1 for distribution of character states of these new characters. The mentioned changes do not make serious influence to the results of the analysis: the consensus tree ap-

pears to be the same as in three of four analyses of Joyce and Norell (2005). See Appendix 2 for characters coded for *Kharakhutulia kalandadzei*. The data matrix was assembled using NDE 0.5.0 (Page 2001) and analyzed using PAUP 4.0b10 (Swofford 2002). A single phylogenetic analysis was performed with all characters reversible and of equal weight. The multistate characters were unordered. Bremer supports were calculated using Autodecay 4.0.1 (Eriksson 1998). Measurements of the specimens are given in Table 1.

Systematic paleontology

Testudines Batsch, 1788

Cryptodira Cope, 1868

Nanhsiungchelyidae Yeh, 1966

Genus *Kharakhutulia* nov.

Etymology: After the fossil locality Khara Khutul.

Type species: *Kharakhutulia kalandadzei* gen. et sp. nov., by monotypy.

Diagnosis.—As for the type species.

Kharakhutulia kalandadzei gen. et sp. nov.

Figs. 2–6.

Etymology: In honour of Dr. Nikolai N. Kalandadze, who collected the specimens.

Type material: Holotype: PIN 5268-1 (Figs. 2–4), a partial shell missing its right and posterior periphery. Paratypes: PIN 5268-2 (Figs. 5, 6), a partial shell including left lateral fragment of the carapace and left half of the plastron; PIN 5268-3 (Fig. 5), fragment of a carapace, including pygal and sutured fragments of peripherals 11; PIN 5268-4 (Fig. 5), left bridge peripheral. PIN 5268-3 and PIN 5268-4 may belong to the same individual as PIN 5268-1 or PIN 5268-2. There are a number of other shell fragments belonging either to PIN 5268-1 or/and PIN 5268-2.

Type locality: Khara Khutul (= Khara Khutul Ula; = Khar Hötöl Uul), 90 km SW from the town of Sainshand, Dornogov Aimag (Eastern Gobi), Mongolia. All materials were collected in 1976 in course of Soviet-Mongolian Paleontological Expedition by Dr. Nikolai N. Kalandadze.

Type horizon: Lower part of the Bainshire Formation, Upper Cretaceous (Cenomanian–lower Turonian) (Kalandadze and Kurzanov 1974; Shuvalov and Chkhikvadze 1975; Shuvalov 2000; Suzuki and Narmandakh 2004).

Included species.—Type and only species.

Diagnosis.—A nanhsiungchelyid which can be differentiated from all other members of the family by relatively small size (except *Zangerlia testudinimorpha* and *Z. ukhaachelys*), shallow nuchal notch formed by small and trapezoid nuchal and peripherals 1 (except species of *Basilemys*), narrow neurals (except *Basilemys nobilis* and *B. variolosa*), contact of costals 7 at midline posterior to neural 7 (except *B. nobilis*), vertebral 1 widened anteriorly, in contact with marginals 2 (except *B. nobilis* and *B. variolosa*), presence of gular and anal notches, anterior plastral lobe covered by carapace in dorsal view and gulars weakly extend onto shallow anterior plastral lip. Besides that it can be differentiated from species of *Basilemys* by vertebral and pleural scales do not strongly overlap onto peripherals and four pairs of inframarginals present which fully

separate marginals from plastral scales; from *Hanbogdemys orientalis* by costiform processes of nuchal very small; and from species of *Zangerlia* by posterior peripherals flared, not shortened.

Distribution.—Lower part of the Bainshire Formation, Cenomanian–lower Turonian, Khara Khutul, Mongolia.

Description and comparison

Shell.—The length of the shell of PIN 5268-1 is estimated at about 25 cm and its width, at about 19 cm. The shell of PIN 5268-2 is estimated to be 23 cm, whereas its width is hard to estimate. The plastron is estimated to approximate 78% of the carapace length and does not reach the carapace rim either anteriorly or posteriorly. The absence of fontanelles and the presence of well-formed sutures in both shells may indicate that they belong to adult individuals. Its relatively small size distinguishes *Kharakhutulia kalandadzei* from most members of the Nanhsiungchelyidae (except *Zangerlia testudinimorpha* and *Z. ukhaachelys*) which are large, reaching from 50 cm to 90 cm in the shell length (Hirayama et al. 2001). The general outline of the shell can be reconstructed based on PIN 5268-1 as oval-shaped, slightly widened posteriorly, with a nuchal notch anteriorly. The nuchal notch is formed by the nuchal and peripherals 1, shallow, and similar to those in species of *Basilemys*. The carapace is not domed and similar in this respect to *Hanbogdemys orientalis*. The surface of the shell is covered with a characteristic nanhsiungchelyid type of sculpture, consisting of irregular grooves and pits (pock-marks). Scale sulci are deep and very distinct.

Carapace.—The nuchal is small (in comparison with *Anomalochelys angulata* and *Nanhsiungchelys wuchingensis*) and hexagonal. It is relatively short (ratio of the nuchal length to its maximal width is 0.43), like in most other nanhsiungchelyids (the same ratio is less than 0.50), except species of *Basilemys* (the same ratio is more than 0.50), and strongly narrowed anteriorly (ratio of the nuchal anterior width to maximal width—0.55, which is less than in the other nanhsiungchelyids and close to *Hanbogdemys orientalis*, in which the same ratio is 0.59). Internally, it bears very small costiform processes, which slightly enters peripherals 1. Among Nanhsiungchelyidae well-developed costiform processes are known only in *H. orientalis*, where they reach peripherals 2, whereas the other members of the family either have no costiform processes or their condition is unclear (Joyce and Norell 2005).

The neurals are represented by at least seven elements. The neural series is narrow in relation to the carapace width (ratio of neural 4 width to the estimated carapace width—0.07). Neural 1, the largest neural, is hexagonal and short-sided posteriorly. Neural 2 is rectangular. Neurals 3–6 are hexagonal and short-sided anteriorly (shape of neural 3 is mainly reconstructed from the surrounding elements). Neural 7 is pentagonal and short-sided anteriorly. The shape of neural 7 indicates that neural 8 was either separated from

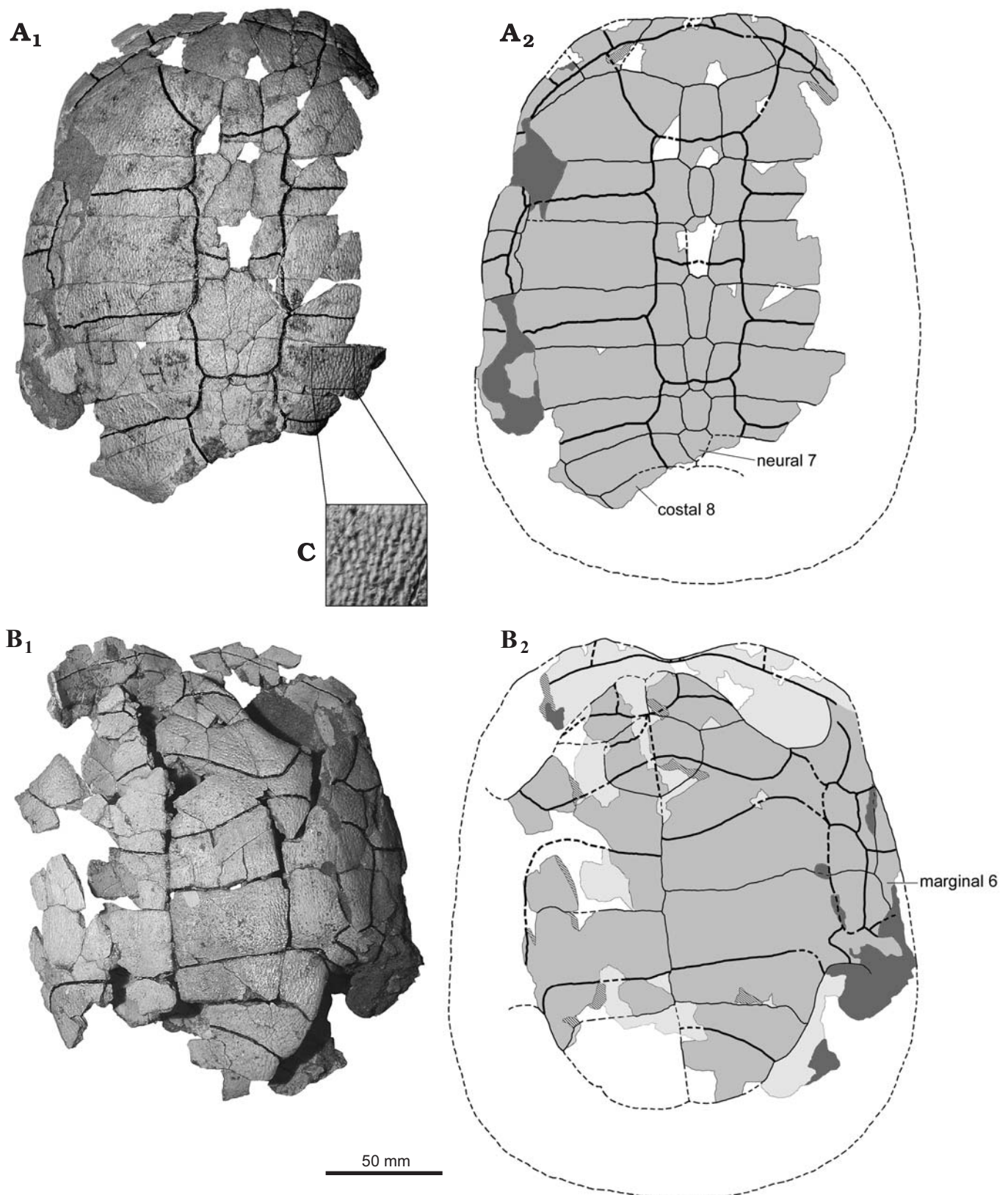


Fig. 2. Nanhsiungchelyid turtle *Kharakhutulia kalandadzei* gen. et sp. nov., PIN 5268-1 (holotype), Khara Khutul locality, 90 km SW from Sainshand Town, Dornogov Aimag, Mongolia; lower part of the Bainshire Formation, Cenomanian–lower Turonian. **A.** Shell in dorsal view, photograph (A₁) and explanatory drawing of the same (A₂). **B.** Shell in ventral view, photograph (B₁) and explanatory drawing of the same (B₂). **C.** Magnified area of the carapace surface with the sculpturing. Bones are filled with grey (foreground) and light-grey (background). Matrix is filled with dark-grey. Breakages are hatched.

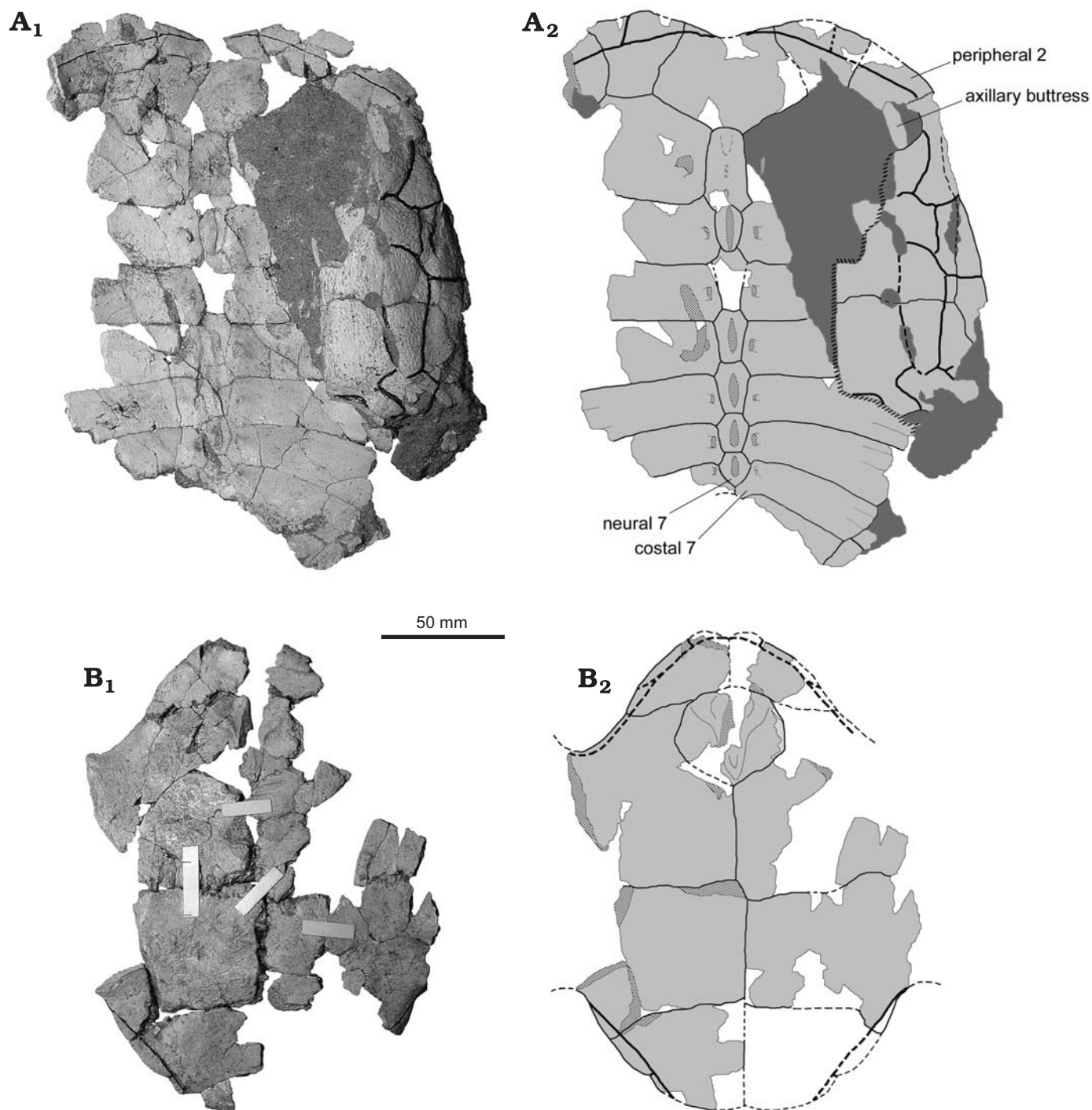


Fig. 3. Nanhsiungchelyid turtle *Kharakhutulia kalandadzei* gen. et sp. nov., PIN 5268-1 (holotype), Khara Khutul locality, 90 km SW from Sainshand Town, Dornogov Aimag, Mongolia; lower part of the Bainshire Formation, Cenomanian–lower Turonian. **A.** Shell in ventral view, plastron removed, photograph (A₁) and explanatory drawing of the same (A₂). **B.** Plastron in dorsal view, photograph (B₁) and explanatory drawing of the same (B₂). Bones are filled with grey. Matrix is filled with dark-grey. Breakages are hatched.

neural 7 by a medial contact of costals 7 and/or 8, or absent. Internally the neurals bears either scars (neural 1) or remnants (neurals 2, 4–7) of trunk vertebrae. Most other Nanhsiungchelyidae usually have eight neurals and the same neural formula (6>4<6<6<6<6<6). Seven neurals are known in *Basilemys nobilis* (Wiman 1933: pl. 4: 1). This spe-

cies, as well as *B. variolosa* (Langston 1956: fig. 2), are also similar to the new taxon in the narrowness of the neurals, whereas the other Nanhsiungchelyidae seem to have a wider neural series. The same neural formula is also characteristic of Adocidae. The number of neurals in Adocidae is variable from six in most members of the group to seven in some rep-

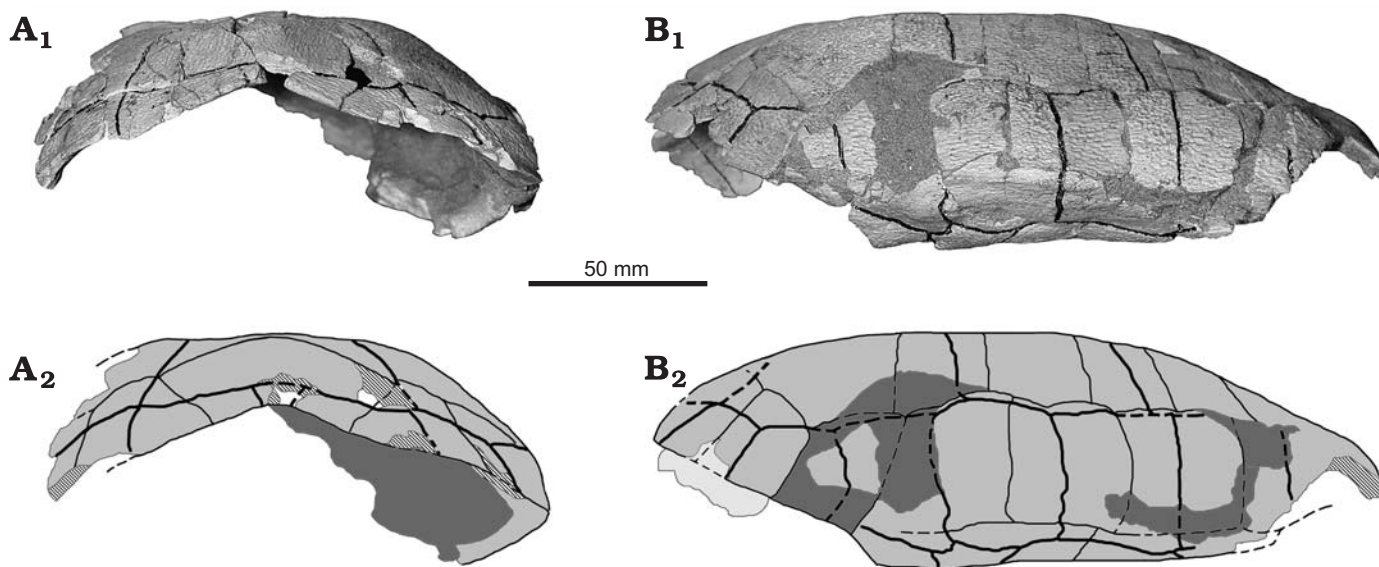


Fig. 4. Nanhsiungchelyid turtle *Kharakhutulia kalandadzei* gen. et sp. nov., PIN 5268-1 (holotype), Khara Khutul locality, 90 km SW from Sainshand Town, Dornogov Aimag, Mongolia; lower part of the Bainshire Formation, Cenomanian–lower Turonian. **A.** Shell in anterior view, plastron removed, photograph (A₁) and explanatory drawing of the same (A₂). **B.** Shell in left lateral view, plastron removed, photograph (B₁) and explanatory drawing of the same (B₂). Bones are filled with grey (foreground) and light-grey (background). Matrix is filled with dark-grey. Breakages are hatched.

representatives. The width of the neurals in Adocidae is variable, being relatively narrow in *Adocus* sp. (Meylan, Gaffney 1989: fig. 11) and wider in *Adocus beatus* (Hay 1908: fig. 296). Suprapygal elements are missing. The pygal (PIN 5268-3) is a rectangular element, wider than long, with straight anterior and posterior, and convex lateral borders. Its morphology generally corresponds to those of the other Nanhsiungchelyidae, except that in some members of the family the pygal looks trapezoid-shaped, widened posteriorly. In the Adocidae, the pygal is usually an elongated trapezoid-shaped element widened posteriorly.

The costals are best visible in PIN 5268-1: medial parts of costals 6–7 on the right side and complete costals 1–7 and anterolateral part of costal 8 on the right side. Costals 2 and 4 seem to have parallel anterior and posterior borders, whereas costals 3, 5–7 are wider laterally than medially. No costal-peripheral fontanelles are visible. Internally costals demonstrate well developed ribheads and weak rib thickenings. The shape of the first thoracic rib cannot be established. The free rib ends of the costals enter triangular-shaped grooves on the internal surface of the corresponding peripherals. The described morphology of the costals generally corresponds to those of the other Nanhsiungchelyidae. On the contrary, Adocidae are characterized by weak ribheads and, as a rule, absence of any rib thickenings.

The peripherals are best preserved on the left side of PIN 5268-1, where they are represented by 1–7 elements. Their morphology has no peculiarities except that free edge of peripheral 1 is rounded and not angled like in some Nanhsiungchelyidae with a deep nuchal notch. The free edge of the anterior and bridge peripherals is slightly upturned as is common in some Adocidae and basal eucryptodirans. The fossa for the axillary buttress on peripheral 2 is visible on PIN

5268-2. The plastral plates of bridge peripherals seem to be relatively narrow. Peripherals 11, partially visible on PIN 5268-3, are not shortened and slightly flared.

The following scales of the carapace are observable: the cervical, vertebrals 1–4, pleurals 1–4 and marginals 1–7. The cervical of PIN 5268-1 is reconstructed as wide trapezoid-shaped in dorsal view, whereas its anterior and ventral shape is not clear. In PIN 5268-2, the cervical is smaller and rectangular in dorsal view, but trapezoid-shaped widened ventrally in anterior view, and almost not represented in ventral view, on the internal surface of the nuchal. The shape of the cervical in the other Nanhsiungchelyidae could not be clearly established from the published figures, being in most cases rectangular or trapezoid-shaped in dorsal view. Vertebral 1 is much widened anteriorly, contacting marginals 2 and having rounded lateral borders. Vertebrals 2–4 are longer than wide, much narrower than vertebral 1 (width of vertebral 3 makes up about 23% of the carapace width), either almost rectangular (vertebrals 2 and 3) or hexagonal (vertebral 4). Most other Nanhsiungchelyidae with known vertebral pattern have vertebral 1 narrower anteriorly, sometimes lyre-shaped, contacting only medial part of marginals 1. An anteriorly widened vertebral 1 is known as a variation in *Basilemys nobilis* (Gilmore 1935: fig. 13) and *B. sinuosa* (Riggs 1906: pl. 76). *Hanbogdemys orientalis* and species of *Basilemys* further differ from the new taxon in having narrower vertebrals 2–4. For instance, the width of vertebral 3 makes up about 17% of the carapace width in *H. orientalis*. The posterior borders of the pleurals are a little oblique and situated closer to the posterior borders of the corresponding costals. Laterally pleurals 1 and 2 clearly overlaps the corresponding peripherals, but not as strong as in species of *Basilemys*. The pleural-marginal sulcus gradually approaches the costal-peripheral suture from marginals 1 to 3

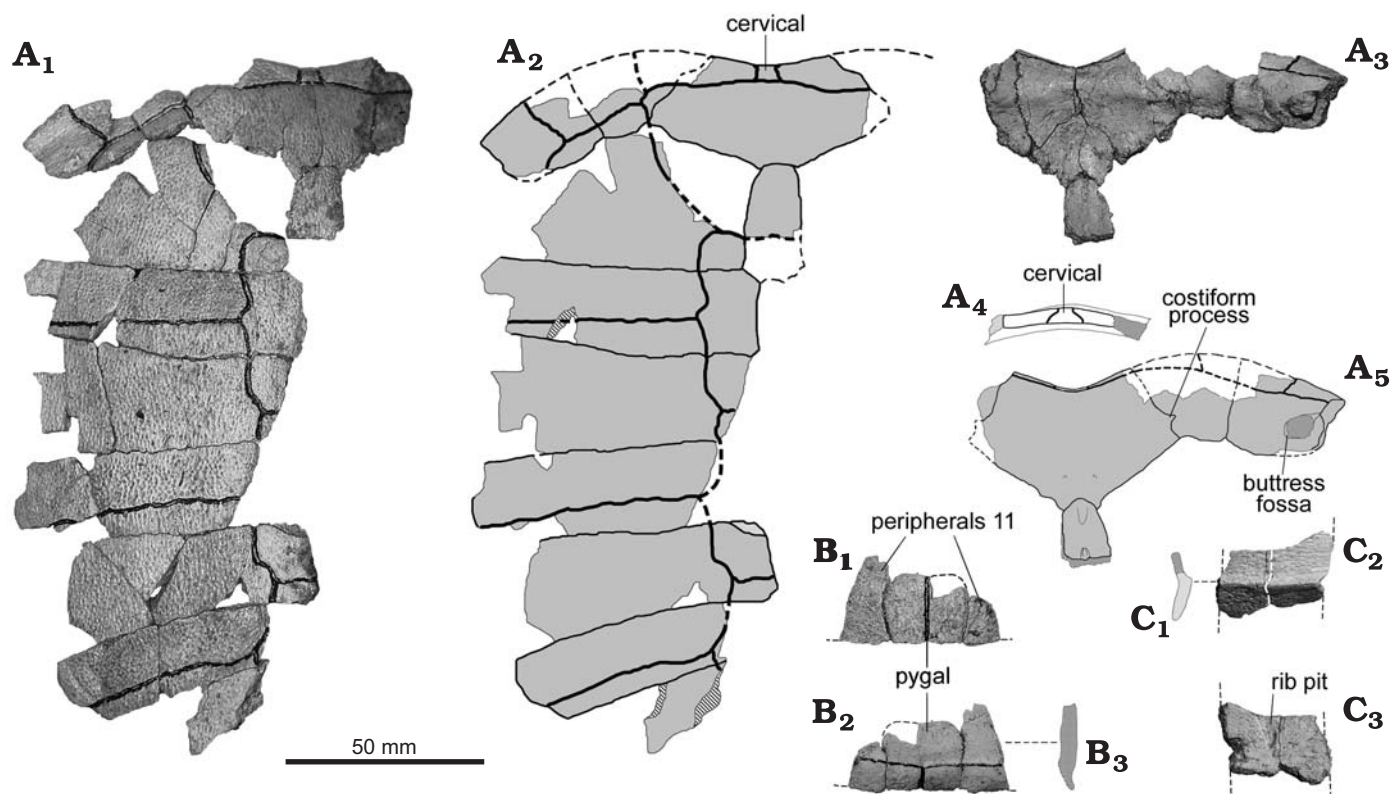


Fig. 5. Nanhsiungchelyid turtle *Kharakhutulia kalandadzei* gen. et sp. nov., Khara Khutul locality, 90 km SW from Sainshand Town, Dornogov Aimag, Mongolia; lower part of the Bainshire Formation, Cenomanian–lower Turonian. **A.** PIN 5268-2. Part of the carapace in dorsal view, photograph (A₁) and explanatory drawing of the same (A₂). Nuchal with neural 1 and peripherals 1 and 2 in ventral view, photograph (A₃) and explanatory drawing of the same (A₅); A₄, nuchal in anterior view, drawing. **B.** PIN 5268-3. Pygal and fragments of peripherals 11 in dorsal (B₁) and ventral (B₂) views, photographs; B₃, cross-section of peripheral 11, drawing. **C.** PIN 5268-4, bridge peripheral in anterior (C₁), external (C₂), and internal (C₃) views, drawing (C₁), and photographs (C₂, C₃). Bones are filled with grey. Breakages are hatched.

and lies on peripherals close to the costal-peripheral suture further posteriorly. Marginals 4–6 clearly extend on to the bridge of the plastron. The ventromedial edge of marginal 6 is expanded, like in some members of Nanhsiungchelyidae. On the internal surface of the carapace, the skin-scale sulcus lies very close to the anterior rim of the carapace medially and more distant from it laterally.

Plastron.—Although the plastra of PIN 5268-1 and PIN 5268-2 are not complete (both missing most of their right lateral parts), all important details of their morphology can be observed. Both plastra have no fontanelles, unlike those described for the similarly sized *Zangerlia testudinimorpha* and *Z. ukhaachelys*. The ventral surface of the plastra is flat without concavities, known in males of many turtle species (Ernst and Barbour 1989). The plastron was suturally attached to the carapace. The anterior buttress contact with peripheral 2 is well visible in PIN 5268-1 (Fig. 2A), whereas the contact of the posterior buttress with peripheral 8, known in all adocids, other nanhsiungchelyids and basal eucryptodirans, is not observable. The minimal length of the bridge is about 50% of the plastron length. The lobes of the plastron are wider than long (ratios of their midline length to width at the base are 0.38 for both lobes in PIN 5268-2). The length of each lobe makes up about 25% of the plastron length. The an-

terior lobe narrows distally stronger than the posterior one, but is not pointed and does not reach the anterior carapace rim. In most other nanhsiungchelyids, where known, the anterior lobe reaches farther anteriorly than the carapace rim (Joyce and Norell 2005) and is pointed in *Hanbogdemys orientalis* and most *Basilemys*. There is a small gular notch, well visible in PIN 5268-2, whereas in PIN 5268-1 this region is damaged. A wide and shallow anal notch is present in PIN 5268-2, whereas in PIN 5268-1 it is either absent or very small. These differences in the size of the anal notch may be sex dependent. If this is correct, then males have bigger anal notch, as in many modern turtles (Ernst and Barbour 1989). Both lobes are thickened along the free edge, like in the other Nanhsiungchelyidae. However, the anterior plastral lip is relatively shallow and without a broad dorsal extension of the gulars. In other Nanhsiungchelyidae, both gular and anal notches are absent, and the anterior plastral lip is much thickened with a broad dorsal extension of the gulars.

The epiplastra have no peculiarities except those connected with features of the anterior lobe mentioned above. The entoplastron is a large hexagonal-shaped element that has contact with surrounding elements typical for most nanhsiungchelyids. Its dorsal surface bears a well-developed V-shaped system of ridges. The hyoplastron and hypoplastron make

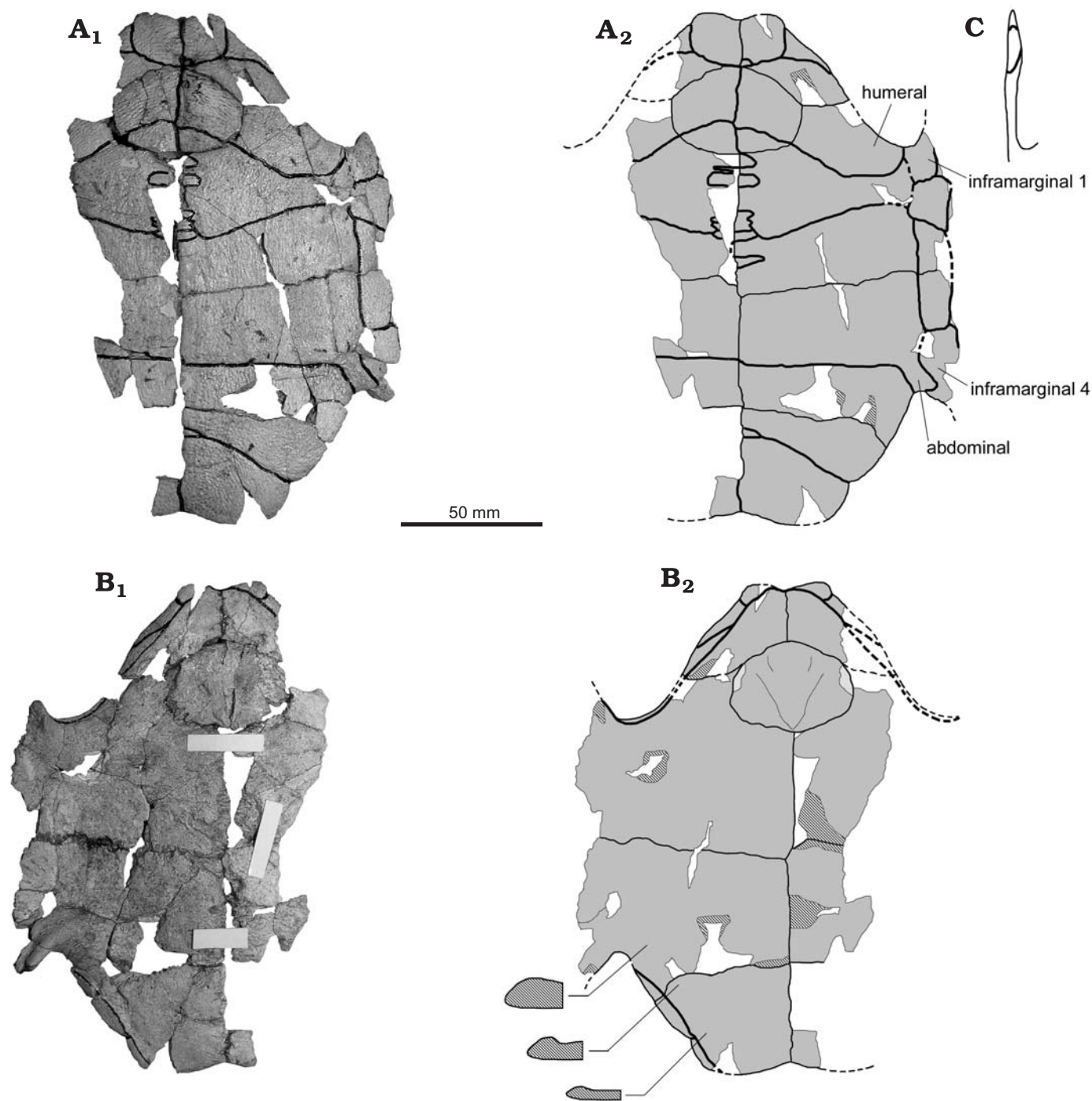


Fig. 6. Nanhsiungchelyid turtle *Kharakhutulia kalandadzei*, gen. et sp. nov., PIN 5268-2, Khara Khutul locality, 90 km SW from Sainshand Town, Dornogov Aimag, Mongolia; lower part of the Bainshire Formation, Cenomanian–lower Turonian. **A.** Plastron in dorsal view, photograph (A₁) and explanatory drawing of the same (A₂). **B.** Plastron in ventral view, photograph (B₁) and explanatory drawing of the same (B₂), showing cross-sections of the posterior lobe. **C.** Anterior lobe in left lateral view, drawing. Bones are filled with grey. Breakages are hatched.

equal contributions to the bridge length. The length of the xiphiplastron is about 80% of the posterior lobe length along the midline. The free edge of the hypo-xiphiplastral suture is more distant from the base of the posterior lobe than at the midline. The xiphiplastron is clearly notched at the femoral-anal sulcus.

The plastral scales are represented by a complete set including the gulars, extragulars, humerals, pectorals, abdominals, femorals, anals and four pairs of inframarginals. The condition of the gulars, separated or fused, is unclear. The gulars touch the entoplastron, but do not overlap it. This condition is somewhat similar to *Hanbogdemys orientalis*, a

Table 1. Measurements (in mm) of the shells of *Kharakhutulia kalandadzei* gen et sp. nov. “?”, element unmeasurable; “!”, element not preserved; “R” and “L” designate right and left measurements.

Characters	Holotype	PIN 5268-2	PIN 5268-3
Nuchal (length/width)	35.7/59.0	30.2/?	!
Neurals (length/width)			
Neural 1	33.3/16.6	?	!
Neural 2	18.4/9.5	!	!
Neural 4	21.8/10.6	!	!
Neural 5	19.6/11.0	!	!
Neural 6	15.3/11.6	!	!
Neural 7	12.0/13.0	!	!
Pygal (length/width)	!	!	16.5/20.8
Costals (length/length medial/length lateral)			
Costal 1	?/27.8/?	?	!
Costal 2	66.8/16.8/?	?/15.9/?	!
Costal 3	?/17.6/27.0	?	!
Costal 4	?/18.9/22.5	?	!
Costal 5	?/16.3/?	?	!
Costal 6	59.0/12.3/21.0	?	!
Costal 7	51.2/11.4/18.4	?	!
Peripherals (length along free edge/width of dorsal plate at the middle)			
Peripheral 1	35.3/29.8	?	!
Peripheral 2	30.6/25.9	?/22.4	!
Peripheral 5	27.7/31.6	!	!
Cervical (length/width)	?	5.5/8.7	!
Vertebrales (length/width)			
Vertebral 1	51.3/68.0	?	!
Vertebral 2	46.3/38.3	?	!
Vertebral 3	42.4/37.6	?	!
Vertebral 4	?/36.5	?	!
Pleurals (width/length medial/length lateral)			
Pleural 1	?/21.0/?	?	!
Pleural 2	?/44.5/47.7	?/39.6/?	!
Pleural 3	?/41.2/?	?/35.1/?	!
Marginals (height/length along free edge)			
Marginal 2	18.6/31.7	?	!
Marginal 3	19.0/32.5	?	!
Marginal 5	29.4/?	!	!
Marginal 6	28.4/27.6	!	!
Marginal 7	?/26.5	!	!
Plastron (length maximal/along the midline)	?	169.1/165.0	!
Bridges (length minimal)	87.4	L81.8	!
Anterior lobe (length/width at the base)	?/115.0	44.8/112.0	!
Posterior lobe (length/width at the base)	?/134.2	47.6/122.6	!
Epiplastron (length medial)	?	17.4	!
Entoplastron (length/width)	34.6/43.5	30.8/43.3	!
Hyoplastron (length medial)	R46.6; L44.5	L45.2	!
Hypoplastron (length medial)	R40.5; L45.3	R43.6; L36.3	!
Xiphiplastron (length medial)	?	L34.7	!
Gulars (length medial)	?	R16.4	!
Extragulars (length medial)	?	R10.7; L11.3	!
Humeral (length medial)	?	R19.5	!
Pectorals (length medial)	R35.5; L39.1	L34.4	!
Abdominals (length medial)	R49.5; L53.4	L44.5	!
Femorals (length medial)	?	23.8	!
Anal (length medial)	?	25.2	!
Inframarginals (length at contact with plastral scales/length at contact with marginals/width at contact with anterior scale/maximal width)			
Inframarginal 1	?/21.3/?/22.5	12.5/?/17.2	!
Inframarginal 2	?/16.3/?/?	12.0/?/11.4/19.5	!
Inframarginal 3	40.5/37.5/17.0	37.5/?/13.8/?	!
Inframarginal 4	14.6/?/?/?	19.8/?/8.7/15.8	!

taxon that differs, however, by having a small overlapping of the gulars onto the entoplastron. The extragulars are small triangular scales separated by a wide contact of the gulars and humerals, most similar to the condition in *Hanbogdemys orientalis*. The pectoral is strongly increased in length medially, and the humeral-pectoral sulcus clearly intersects the entoplastron, like in all Nanhsiungchelyidae known in this respect. Laterally the pectoral contacts inframarginals 1 and 2, and does not contribute to the anterior plastral rim like in all other Nanhsiungchelyidae. On the contrary, Adocidae and basal eucryptodirans usually have a wide contribution of the pectorals to the anterior plastral rim. The abdominal has a small posterolateral process that contributes to the rim of the inguinal notch and hinders contact between the femoral and the posterior inframarginal. The same morphology is observed in some species of *Basilemys* and *Zangerlia ukhaachelys*, whereas in the other Nanhsiungchelyidae the abdominal is separated from the inguinal notch. In the Adocidae this character is also variable. The inframarginals are represented by a complete row of four scales and well visible on both PIN 5268-1 and PIN 5268-2. They are restricted to the plastron and little distant from the plastron-carapace suture. Inframarginal 1 embraces the axillary notch anteriorly, contacts inframarginal 2 posteriorly, having a short contact with the humeral and a longer contact with the pectoral medially. Its lateral contacts, besides marginal 4 are not clear. The shape of inframarginal 1 in PIN 5268-1 differs from those in PIN 5268-2 in being relatively bigger, much wider anteriorly and having a shorter contact with inframarginal 2. Inframarginal 2 is irregularly pentagonal-shaped, contacting inframarginal 1 anteriorly, inframarginal 3 posteriorly, pectoral and slightly abdominal medially, and marginals 4 and 5 laterally. Inframarginal 3 is an elongate tetragonal element, about three times longer than wide, spans the hyo-/hypoplastral suture. It is about twice longer than the other inframarginals and contacts inframarginal 2 anteriorly, inframarginal 4 posteriorly, the abdominal medially and marginals 5 and 6 laterally. Inframarginal 4 contacts inframarginal 3 anteriorly, contributes to the rim of the inguinal notch posteriorly and has an S-shaped medial contact with the abdominal. Its lateral contacts are not clear beyond the short contact with marginal 6 and a longer one with marginal 7. This element in PIN 5268-1 is clearly shorter than in PIN 5268-2. In general, the described inframarginal pattern is most similar to *H. orientalis* in the presence of a complete row of the inframarginals and in that inframarginal 3 is the longest. However, the inframarginals of the new taxon differs from those of *H. orientalis* in being wider, less distant from the plastron-carapace suture, inframarginal 3 less elongated, and in the absence of the inframarginal 4-femoral contact. The midline sulcus is strongly sinuous within pectorals and anterior part of abdominals in PIN 5268-2, and straight in PIN 5268-1. The similarly sinuous midline sulcus is found in *Basilemys* and also common in Adocidae. In addition to the gulars, the other plastral scales (extragulars, humerals, femorals and anals) considerably overlap onto the dorsal surface of the

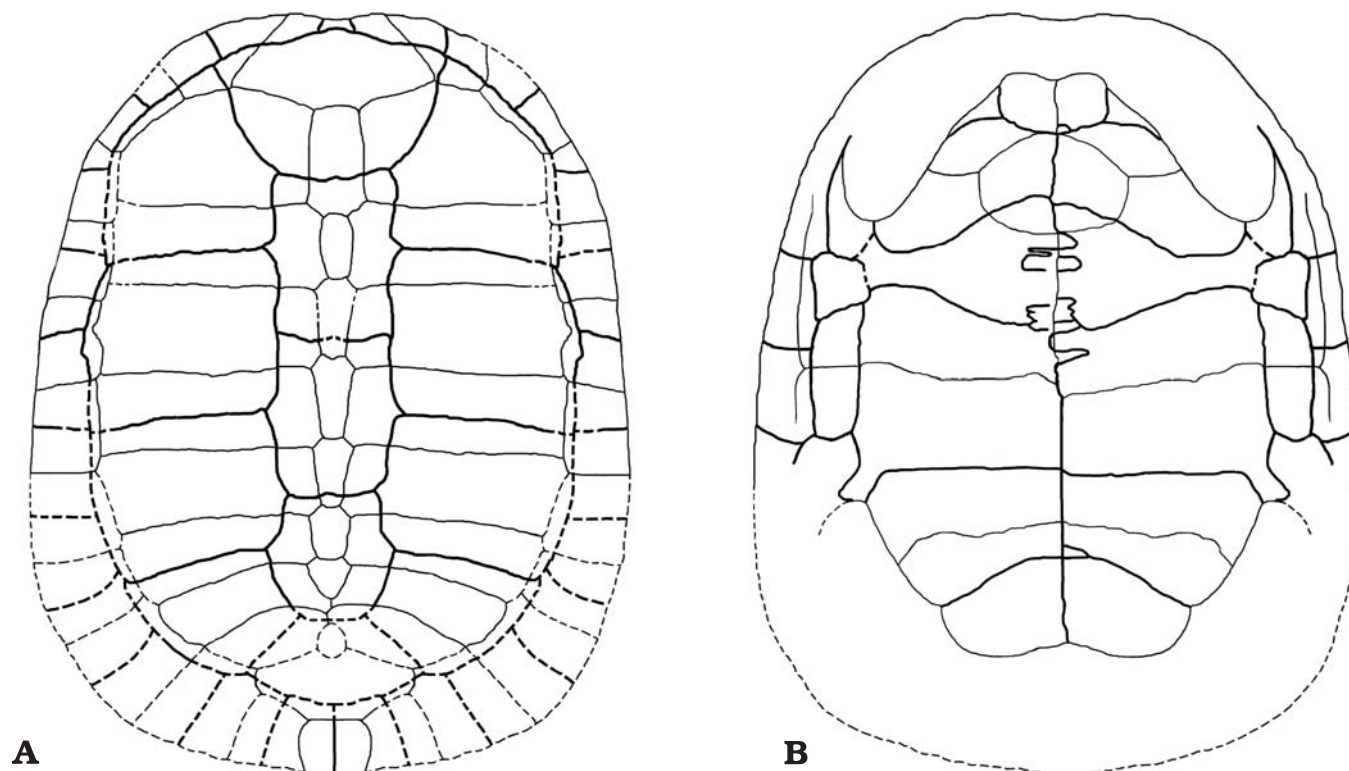


Fig. 7. Reconstruction of the shell of *Kharakhutulia kalandadzei*, gen. et sp. nov., in dorsal (A) and ventral (B) views.

plastron, similar to the condition in most other Nanhsiungchelyidae. The examined specimens demonstrate some anomalies of the plastral scalation. PIN 5268-1 has an additional sulcus on the entoplastron, indicating of a big abnormal scale within the right humeral. PIN 5268-2 has a small additional scale in the posterior part of the gulars. A reconstruction of the shell of *Kharakhutulia kalandadzei* is presented in Fig. 7.

Discussion

The morphology and phylogenetic position of *Kharakhutulia kalandadzei*.—We assign *Kharakhutulia kalandadzei* to the Nanhsiungchelyidae based on the combination of the following characters (reliable nanhsiungchelyid synapomorphies are marked with an asterisk): a shell with sutural plastron-carapace connection and plastral buttresses contacting only peripherals; neural formula $6 > 4 < 6 < 6 < 6 < 5$?, sculpturing of the shell with relatively big and irregular grooves and pits*, deep scale sulci, ribheads and rib thickenings of costals normally developed, pygal wider than long, pleural-marginal sulcus situated on peripherals, relatively long bridges and shortened plastral lobes, absence of a pectoral contribution to the axillary rim*, expansion of the ventromedial edge of marginal 6*, and overlapping of scales on the dorsal surface of plastral lobes*. The characters given in the diagnosis (see “Systematic paleontology”) clearly differentiate the described turtle as a new genus and species of the Nanhsiungchelyidae.

The result of our phylogenetic analysis consists of 18 trees with 52 steps, consistency index is 0.85, and retention index is 0.77. The resulting strict consensus tree is given in Fig. 1. According to our phylogenetic analysis, *Kharakhutulia kalandadzei* is the most basal among the Nanhsiungchelyidae, the sister to a clade that includes all other taxa. The other nanhsiungchelyids are grouped into four clades forming a polytomy: *Hanbogdemys orientalis*, *Anomalochelys unguolata* + *Nanhsiungchelys wuchingensis*, *Zangerlia*, and *Basilemys*. This result is in agreement with one of four analyses of Joyce and Norell (2005: fig. 6, characters ordered, excluding geography) in that both analyses show the polytomy of the mentioned clades, but differs from it in that species of *Basilemys* form a polytomy. Most importantly, our analysis does not support a monophyletic clade of Asian nanhsiungchelyids retrieved by other three analyses of Joyce and Norell (2005). Another important result of our analysis is that it positively demonstrates that Asian nanhsiungchelyids gave rise to North American ones, an idea suggested by a number of previous studies (Brinkman and Nicholls 1993; Brinkman and Peng 1996; Hutchison 2000; Hirayama et al. 2001).

In its overall morphology *Kharakhutulia* looks transitional between Adocidae and more advanced members of the Nanhsiungchelyidae. Its primitive characters include an incomplete or interrupted neural series, an anteriorly wide vertebral 1, a short anterior plastral lobe, a full set of four inframarginals, and a shallow epiplastral lip.

The presence of a costiform processes of the nuchal is sometimes listed for the diagnosis of the Nanhsiungchely-

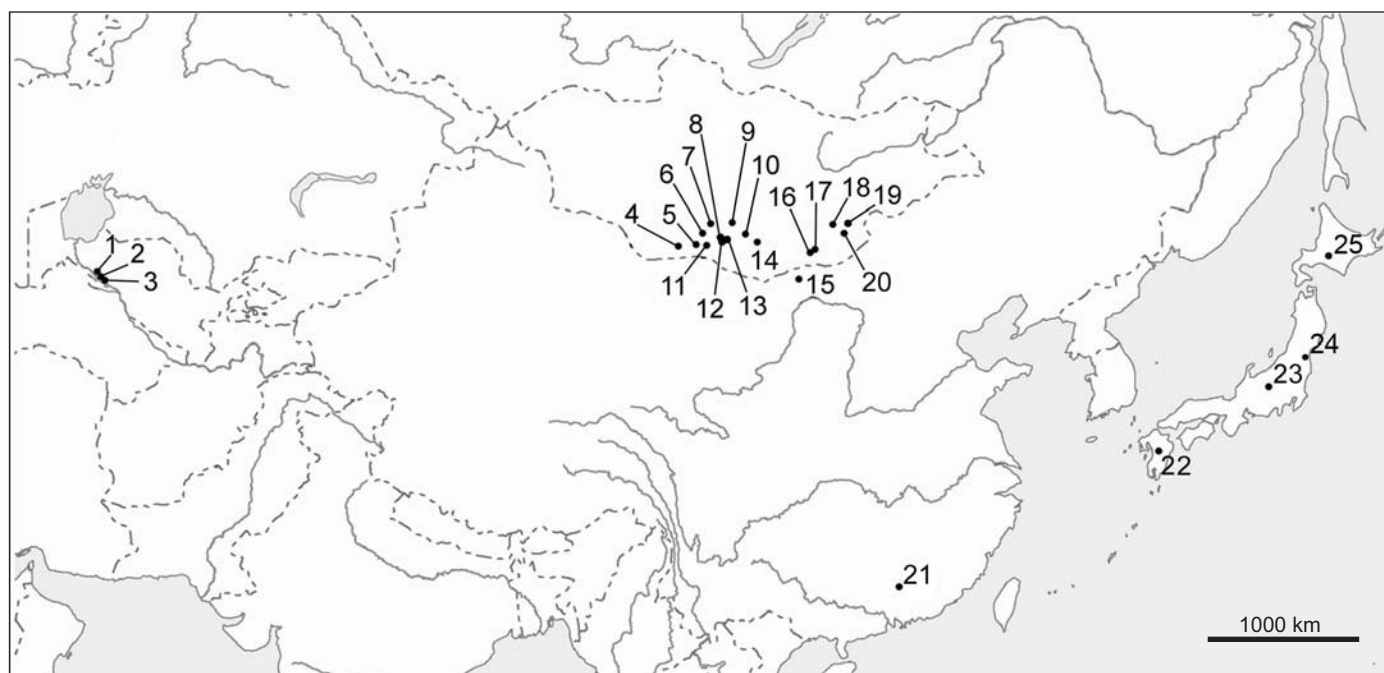


Fig. 8. Map showing all known occurrences of the nanhsiungchelyid turtles in Asia (see Appendix 3 for corresponding taxa and references). 1–3. Chelpyk (1), Khodzhaikul I (2), and Khodzhaikulsai+Sheikhdzheili II (3), Sultanuvais Ridge, Uzbekistan, Khodzhaikul Formation, lower Cenomanian. 4. Khermeen Tsav II, Gov-Altai Aimag, Mongolia, Nemegt Formation, Maastrichtian. 5. Nemegt+Khulsan, Gov-Altai Aimag, Mongolia, Barungoyot and Nemegt Formations, upper Campanian–Maastrichtian. 6. Shiregin Gashun, Gov-Altai Aimag, Mongolia, upper part of the Bainshire Formation, upper Turonian–Santonian. 7. Khuren Tsav, Gov-Altai Aimag, Mongolia, Nemegt Formation, Maastrichtian. 8. Zamyin Chond (= Dzamin Chond), Umnegov Aimag, Mongolia, lower part of the Barungoyot Formation, upper Campanian. 9, 10. Abdrant Nuru (9) and Bain Dzak (10), Umnegov Aimag, Mongolia, Djadokhta Formation, Campanian. 11. Ukhaa Tolgod, Gov-Altai Aimag, Mongolia, Djadokhta Formation, Campanian. 12. Yagaan Khovil, Umnegov Aimag, Mongolia, lower part of the Barungoyot Formation, upper Campanian. 13. Udyn Sayr, Umnegov Aimag, Mongolia, Djadokhta Formation, Campanian. 14. Boro Khamarin, Bulgan Somon, Umnegov Aimag, Mongolia, Barungoyot Formation, upper Campanian. 15. Nuchidaba, Bayan Mandahu, Inner Mongolia, China, Upper Cretaceous redbeds. 16. Baishin Tsav, Dornogov Aimag, Mongolia, upper part of the Bainshire Formation, upper Turonian–Santonian. 17. Amtgai, Dornogov Aimag, Mongolia, upper part of the Bainshire Formation, upper Turonian–Santonian. 18. Khara Khutul, Dornogov Aimag, Mongolia; lower part of the Bainshire Formation, Cenomanian–lower Turonian. 19, 20. Khongil Tsav (19) and Bain Shire (20), Dornogov Aimag, Mongolia, Bainshire Formation, Cenomanian–Santonian. 21. Nanxiong, Guangdong, China, Nanxiong Formation, Maastrichtian. 22. Amagimi Dam of Mifune, Kumamoto Prefecture, Kyushu, Japan, Mifune Group, Coniacian–Santonian. 23. Katsuyama, Fukui Prefecture, Japan, Kitadani Formation, Barremian or Aptian. 24. Sakurazawa in Oriki, Hironomura, Fukushima Prefecture, Japan, lower Futaba Formation, Coniacian–Santonian. 25. Hobetsu-cho, Central Hokkaido, Japan, Yezo Supergroup, Cenomanian.

idae (Sukhanov 2000). Our study, as well as studies of other authors (Hirayama et al. 2001), shows that the costiform processes of the nuchal are absent, very small, or their condition is unknown in most members of the Nanhsiungchelyidae. In this group, the well-developed costiform processes are present only in *Hanbogdemys orientalis* and *Hanbogdemys* sp. from the Khara Khutul (see below) and should be considered homoplastically derived relative to other turtles with costiform processes (Joyce 2007).

Nanhsiungchelyids of the Khara Khutul.—Seven turtle taxa have been reported from the Khara Khutul prior to this study: Adocidae indet., *Charitonyx tajanikolaevae* Chkhikvadze, 1980 (Nanhsiungchelyidae, see below), *Hanbogdemys orientalis* (Nanhsiungchelyidae), *Hoplochelys* sp. (= *Kirgizemys* sp.; Macrobaenidae), *Kizylkumemys schultzi mirabilis* Nessov, 1981 (Carettochelyidae), *?Zangerlia* sp. (Nanhsiungchelyidae), and Trionychidae indet. (Shuvalov and Chkhikvadze 1975; Nessov and Khosatzky 1978; Chkhikvadze 1980;

Čkhikvadze 1987; Nessov 1981, 1987; Khosatzky 1999; Suzuki and Narmandakh 2004). Below we consider previous records of the Khara Khutul nanhsiungchelyids in more detail.

?Zangerlia sp. was mentioned in the list of turtles of the Khara Khutul by Shuvalov and Chkhikvadze (1975) without any figure, museum number, description and argumentation, which would underline such an assignment. By this reason, until more information is available, this record should be tentatively considered as Nanhsiungchelyidae indet.

Charitonyx tajanikolaevae was established based on fragmentary shell and postcranial remains (IP 11-2-2) from the Khara Khutul locality and placed into a separate subfamily Charitonychinae Chkhikvadze, 1980 of the family Sinaspideretidae Čkhikvadze, 1987¹, considered transitional between the Adocidae (including Nanhsiungchelyidae) and the Triony-

¹ The name Sinaspideretidae Chkhikvadze, 1970 is not available as was published without diagnosis (ICZN 1999: art. 13.1.1.). The available name is Sinaspideretidae Čkhikvadze, 1987.

chidae Gray, 1825 (Chkhikvadze 1980). No illustrations of this species appeared until 1987, when a few shell fragments were figured (Chkhikvadze 1987: pl. 4). Later, the type genus of the Sinaspideretidae—*Sinaspideretes* Young and Chow, 1953—was suggested to belong to the Carettochelyidae Boulenger, 1887 (Meylan and Gaffney 1992). Thus, the name Sinaspideretidae is a probable junior synonym of the Carettochelyidae. *Charitonyx tajanikolaevae* is characterized by a set of characters (sculptured shell surface, deep scale sulci, presence of peripherals), which clearly indicate that it belongs to the Nanhsiungchelyidae. The fragmentary material of this species does not allow comprehensive comparison with the other Nanhsiungchelyidae. Most characters of *Ch. tajanikolaevae*, like the narrow vertebrals, pleural-marginal sulcus lying close to the costal-peripheral suture, the posterior infra-marginal smaller than the penultimate one, and absence of the femoral-inframarginal contact (Chkhikvadze 1980), are characteristic of many Asiatic Nanhsiungchelyidae. Two more characters of *Ch. tajanikolaevae*, the small size (20–25 cm) and the pentagonal-shaped neural (Chkhikvadze 1980), are reminiscent of *Kharakhutulia kalandadzei*. However, other characters of *Ch. tajanikolaevae*, like the presence of costal-peripheral fontanelles and the scalation of the inguinal region (Chkhikvadze 1987: pl. 4, middle figure in the right column) differentiate it from the new taxon and the other Nanhsiungchelyidae. Furthermore, it appears that part of the materials of *Ch. tajanikolaevae*, such as “part of the humeral bone and ilial bone of the trionychid type” (Chkhikvadze 1980: 502), may belong to the Trionychidae, because Nanhsiungchelyidae have a very distinct morphology of these elements. In summary, it is clear that *Ch. tajanikolaevae* is represented by very fragmentary materials, it is poorly described and figured, it cannot be properly diagnosed below the family level, and it might be a chimera of a nanhsiungchelyid and a trionychid. For these reasons we consider *Ch. tajanikolaevae* as a nomen dubium and ignore it from further considerations.

Hanbogdemys orientalis (as *Basilemys orientalis*) was reported by Nesson (1987: pl. 1: 13a, b), from the Khara Khutul locality based on a single nuchal. This specimen demonstrates an autapomorphy of *Hanbogdemys orientalis*, the presence of a well-developed costiform processes, but differs from the type species in the wider vertebral 1. This difference as well as the older age of the Khara Khutul specimen (the type specimen of *H. orientalis* comes from the upper part of the Bainshire Formation [upper Turonian–Santonian] of the Baishin Tsav locality, Dornogov, Mongolia; Sukhanov and Narmandakh 1975, 1977; Sukhanov 2000; Sukhanov and Narmandakh 2006) suggest that it may be a distinct species from *H. orientalis*, although more materials from this locality are needed to demonstrate this. Until this is done we consider this record as *Hanbogdemys* species indeterminate.

Our review of the previous records of the Khara Khutul nanhsiungchelyids shows there are two valid taxa there, *Hanbogdemys* sp. indet. and *Kharakhutulia kalandadzei*. Our analysis of the nanhsiungchelyid record in Asia (Fig. 8)

shows that other localities have only a single representative of this clade, making Khara Khutul a unique site. The basal phylogenetic position of *Kharakhutulia* emphasizes the importance of studying of this and other Cenomanian–Turonian localities of Asia for better understanding of the basal diversification of the Nanhsiungchelyidae.

Acknowledgments

The authors thank Andrei V. Bochkov (Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia) for help with the phylogenetic analysis. James F. Parham (California Academy of Sciences, San Francisco, USA) gave some important comments. IGD thanks Mark A. Norell and Carl Mehling (both AMNH) for access to the turtle collection of AMNH and to the holotype of *Zangerlia ukhaachelys*; Walter G. Joyce (YPM) for access to the turtle collections of YPM and hospitality. Walter G. Joyce and Julien Claude (Institut des sciences de l'évolution, Montpellier, France) are thanked for reviewing the manuscript and useful comments. This study was done under financial support of a grant of the President of the Russian Federation to the Leading Scientific Schools (NSH-119.2008.4) and grant of the Russian Foundation for Basic Research (08-05-00557-a).

References

- Batsch, G.C. 1788. *Versuch einer Anleitung, zur Kenntniß und Geschichte der Thiere und Mineralien*. 528 pp. Akademische Buchhandlung, Jena.
- Boulenger, G.A. 1887. On a new family of pleurodiran turtles. *Annals and Magazine of Natural History* 19: 170–172.
- Brinkman, D.B. 1998. The skull and neck of the Cretaceous turtle *Basilemys* (Trionychoidea, Nanhsiungchelyidae), and the interrelationships of the genus. *Paludicola* 1: 150–157.
- Brinkman, D. and Nicholls, E. 1993. New specimen of *Basilemys praeclara* Hay and its bearing on the relationship of the Nanhsiungchelyidae (Reptilia: Testudines). *Journal of Paleontology* 67: 1027–1031.
- Brinkman, D. and Peng, J.-H. 1996. A new species of *Zangerlia* (Testudines: Nanhsiungchelyidae) from the Upper Cretaceous redbeds and Bayan Mandahu, Inner Mongolia, and the relationships of the genus. *Canadian Journal of Earth Sciences* 33: 526–540.
- Cope, E.D. 1868. On the origin of genera. *Proceedings of the Academy of Natural Sciences of Philadelphia* 1868: 242–300.
- Cope, E.D. 1870. On the Adocidae. *Proceedings of the American Philosophical Society* 11: 547–553.
- Chkhikvadze, V.M. [Čhikvadze, V.M.] 1970. Classification of the subclass Testudinata [in Russian]. 16-aâ Naučnaâ Sessia Instituta Paleobiologii Akademii Nauk Gruzinskoi SSR: 7–8.
- Chkhikvadze, V.M. [Čhikvadze, V.M.] 1980. On the question of the origin of the soft-shelled turtles [in Russian]. *Bulletin of the Academy of Sciences of the Georgian SSR* 100 (2): 501–503.
- Čhkhikvadze, V.M. 1987. Sur la classification et le caractères de certaines tortues fossiles d'Asie rares et peu étudiées. *Studia Palaeocheloniologica* 2: 55–86.
- Danilov, I.G. and Parham, J.F. 2006. A redescription of “*Plesiochelys tatsuensis*” from the Late Jurassic of China, with comments on the antiquity of the crown clade Cryptodira. *Journal of Vertebrate Paleontology* 26: 573–580.
- Eriksson T. 1998. *AutoDecay*. 4.0.1. (Program distributed by author). Department of Botany, Stockholm University, Stockholm.
- Ernst, C.H. and Barbour, R.W. 1989. *Turtles of the World*. 313 pp. Smithsonian Institution Press, Washington, D.C.

- Gray, J.E. 1825. A Synopsis of the genera of reptiles and amphibia, with a description of some new species. *Annals of Philosophy* 10: 193–217.
- Hay, O.P. 1902. Bibliography and catalogue of fossil Vertebrata of North America. *Bulletin of the United States Geological Survey* 179: 1–868.
- Hay, O.P. 1908. *The Fossil Turtles of North America*. 568 pp. Carnegie Institution of Washington, Washington, D.C.
- Hirayama, R. 1998. Fossil turtles from the Mifune Group (Late Cretaceous) of Kumamoto Prefecture, Western Japan [in Japanese]. *Report of the Research on the Distribution of Important Fossils in Kumamoto Prefecture. Dinosaurs from the Mifune Group, Kumamoto Prefecture, Japan*, 85–99. Mifune Town Education Board, Mifune.
- Hirayama, R. 2002. Preliminary report of the fossil turtles from the Kitadani Formation (Early Cretaceous) of the Tetori Group of Katsuyama, Fukui Prefecture, Central Japan [in Japanese]. *Memoir of the Fukui Prefectural Dinosaur Museum* 1: 29–40.
- Hirayama, R., Sakurai, K., Chitoku, T., Kawakami, G., and Kito, N. 2001. *Anomalochelys angulata*, an unusual land turtle of family Nanshiungchelyidae (Superfamily Trionychoidea; Order Testudines) from the Upper Cretaceous of Hokkaido, North Japan. *Russian Journal of Herpetology* 8: 127–138.
- Hutchison, J.H. 2000. Diversity of Cretaceous turtle faunas of Eastern Asia and their contribution to the turtle faunas of North America. *Paleontological Society of Korea Special Publication* 4: 27–38.
- Hutchison, J.H. and Bramble, D.M. 1981. Homology of the plastral scales of the Kinosternidae and related turtles. *Herpetologica* 37: 73–85.
- ICZN 1999. *International Code of Zoological Nomenclature* (4th edition). xxxix + 306 pp. International Trust for Zoological Nomenclature, The Natural History Museum, London.
- Joyce, W.G. 2007. Phylogenetic relationships of Mesozoic turtles. *Bulletin of the Peabody Museum of Natural History* 48 (1): 3–102.
- Joyce, W.G. and Norell, M.A. 2005. *Zangerlia ukhaachelys*, new species, a nanshiungchelyid turtle from the Late Cretaceous of Ukhaa Tolgod, Mongolia. *American Museum Novitates* 3481: 1–19.
- Kalandadze, N.N. and Kurzanov, S.M. 1974. The Lower Cretaceous localities of terrestrial vertebrates in Mongolia [in Russian]. *Trudy Sovmestnoj Sovetsko-Mongol'skoj Paleontologičeskoj Ekspedicii* 1: 288–295.
- Khosatzky, L.I. [Hozackij, L.I.] 1999. Trionychid turtles of the Cretaceous of Mongolia [in Russian]. *Voprosy paleontologii* 11: 141–149.
- Langston, W. 1956. The shell of *Basilemys variolosa* (Cope). *Bulletin of the National Museum of Canada* 142: 155–165.
- Leidy, J. 1865. Memoir on the extinct reptiles of the Cretaceous formations of the United States. *Smithsonian Contributions to Knowledge* 14: 1–135.
- Lucas, S.G. 2001. *Chinese Fossil Vertebrates*. 375 pp. Columbia University Press, New York.
- Meylan, P.A. and Gaffney, E.S. 1989. The skeletal morphology of the Cretaceous cryptodiran turtle, *Adocus*, and the relationships of the Trionychoidea. *American Museum Novitates* 2941: 1–60.
- Meylan, P.A. and Gaffney, E.S. 1992. *Sinaspideretes* is not the oldest trionychid turtle. *Journal of Vertebrate Paleontology* 12: 257–259.
- Młynarski, M. 1972. *Zangerlia testudinimorpha* n. gen., n. sp., a primitive land tortoise from the Upper Cretaceous of Mongolia. *Palaeontologia Polonica* 27: 85–92.
- Młynarski, M. and Narmandakh, P. 1972. New turtle remains from the Upper Cretaceous of the Gobi Desert, Mongolia. *Palaeontologia Polonica* 27: 95–102.
- Nessov, L.A. [Nesov, L.A.] 1981. On the turtle of the family Dermatemydidae from the Cretaceous of Amur River Basin and some other rare findings of remains of ancient turtles of Asia [in Russian]. In: L.J. Borkin (ed.), *Herpetological Investigations in Siberia and the Far East*, 69–73. Zoological Institute, Academy of Sciences of the USSR, Leningrad.
- Nessov, L.A. [Nesov, L.A.] 1987. On some Mesozoic turtles of the Soviet Union, Mongolia and China, with comments on systematics. *Studia Palaeocheloniologica* 2: 87–102.
- Nessov, L.A. [Nesov, L.A.] 1997. *Cretaceous nonmarine vertebrates of Northern Eurasia* [in Russian]. 218 pp. St. Petersburg State University, Institute of Earth's Crust, St. Petersburg.
- Nessov L.A. [Nesov, L.A.] and Khosatzky L.I. [Hozackij, L.I.] 1978. A turtle from the Early Cretaceous of Kirghizia [in Russian]. *Ežegodnik Vsesoūznogo Paleontologičeskogo Obščestva* 21: 267–279.
- Nessov, L.A. [Nesov, L.A.] and Krasovskaya, T.B. [Krasovskaâ, T.B.] 1984. Changes in the composition of turtles assemblages of Late Cretaceous of Middle Asia [in Russian]. *Vestnik Leningradskogo Gosudarstvennogo Universiteta* 3: 15–25.
- Page, R.D.M. 2001. *WinClada version 1.00.08*. <http://www.cladistics.com>.
- Riggs, E.S. 1906. The carapace and plastron of *Basilemys sinuosus*, a new fossil tortoise from the Laramie Beds of Montana. *Field Columbian Museum, Geological Series* 2: 249–256.
- Shuvalov, V.F. 2000. The Cretaceous stratigraphy and paleobiogeography of Mongolia. In: M.J. Benton, M.A. Shishkin, D.M. Unwin, and E.N. Kurochkin (eds.), *The Age of Dinosaurs in Russia and Mongolia*, 256–278. Cambridge University Press, Cambridge.
- Shuvalov, V.F. [Šuvalov, V.F.] and Chkhikvadze, V.M. [Čhikvadze, V.M.] 1975. New data on Late Cretaceous turtles of South Mongolia [in Russian]. *Trudy Sovmestnoj Sovetsko-Mongol'skoj Paleontologičeskoj Ekspedicii* 2: 214–229.
- Sukhanov, V.B. 2000. Mesozoic turtles of Middle and Central Asia. In: M.J. Benton, M.A. Shishkin, D.M. Unwin, and E.N. Kurochkin (eds.), *The Age of Dinosaurs in Russia and Mongolia*, 309–367. Cambridge University Press, Cambridge.
- Sukhanov, V.B. [Suhanov, V.B.] and Narmandakh P. [Narmandah, P.] 1975. Turtles of the *Basilemys* group (Chelonia, Dermatemydidae) in Asia [in Russian]. *Trudy Sovmestnoj Sovetsko-Mongol'skoj Paleontologičeskoj Ekspedicii* 2: 94–101.
- Sukhanov, V.B. [Suhanov, V.B.] and Narmandakh P. [Narmandah, P.] 1977. The shell and limbs of *Basilemys orientalis* (Chelonia, Dermatemydidae): a contribution to the morphology and evolution of the genus [in Russian]. *Trudy Sovmestnoj Sovetsko-Mongol'skoj Paleontologičeskoj Ekspedicii* 4: 57–79.
- Sukhanov, V.B. and Narmandakh, P. 2006. New taxa of Mesozoic turtles from Mongolia. In: I.G. Danilov and J.F. Parham (eds.), *Fossil Turtle Research, Vol. 1*, 119–127. Zoological Institute of the Russian Academy of Sciences, St. Petersburg (Russian Journal of Herpetology, 13, Supplement).
- Suzuki, Sh. and Narmandakh, P. 2004. Change of the Cretaceous turtle faunas in Mongolia. *Hayashibara Museum of Natural Sciences Research Bulletin* 2: 7–14.
- Swofford, P.L. 2002. *PAUP, Version 4.0b10*. Sunderland, MA: Sinauer Associates.
- Tokunaga, S. and Shimizu, S. 1926. The Cretaceous Formation of Futaba in Iwaki and Its Fossils. *Journal of the Faculty of Science, University of Tokyo (Section 2)* 1 (6): 181–212.
- Yeh, H.-K. 1966. A new Cretaceous turtle of Nanshiung, Northern Kwangtung. *Vertebrata Palasiatica* 10: 191–200.
- Zangerl, R. 1969. The turtle shell. In: C. Gans, A. d'Bellairs, and T.S. Parsons (eds.), *Biology of Reptilia, Vol. 1, Morphology A*, 311–339. Academic Press, New York.

Appendix 1

Details about new characters added to matrix of Joyce and Norell (2005). 40. Sculpturing of the shell surface with relatively big and irregular pits and grooves: (0) absent; (1) present. 41. Overlapping of scales on the dorsal surface of plastral lobes: (0) absent; (1) present. Codings: *Adocus* sp., 40(0), 41(0); *Zangerlia testudinimorpha*, 40(1), 41(?); *Zangerlia nei-*

mongolensis, 40(1), 41(?); *Zangerlia ukhaachelys*, 40(1), 41(1); *Basilemys variolosa*, 40(1), 41(1); *Basilemys nobilis*, 40(1), 41(1); *Basilemys sinuosa*, 40(1), 41(1); *Basilemys praeclara*, 40(1), 41(1); *Hanbogdemys orientalis*, 40(1), 41(1); *Anomalochelys angulata* 40(1), 41(1); *Nanhsiungchelys wuchingensis*, 40(1), 41(1); *Kharakhutulia kalandadzei*, 40(1), 41(1).

Appendix 2

Characters coded for *Kharakhutulia kalandadzei* and added to the matrix of Joyce and Norell (2005):

????????? ????0?000 ?10???1?0 0?00010111 1.

Appendix 3

Taxa and references for known occurrences of nanhsiungchelyid turtles in Asia (see Fig. 8 for map of occurrences, locality, formation and age data).

- 1–3. Chelypyk (1), Khodzhakul I (2) and Khodzhakulsai + Sheikh-dzheili II (3): *Nanhsiungchelyidae* indet. (as *Basilemys* sp. and/or *Nanhsiungchelyidae* indet.; Nessov 1981; Nessov and Krasovskaya 1984; Nessov 1997).
4. Khermeen Tsav II: *Nanhsiungchelyidae* indet. (Suzuki and Narmandakh 2004).
5. Nemegt and Khulsan: *Zangerlia testudinimorpha* (Mlynarski 1972) and *Nanhsiungchelyidae* indet. (as ?*Zangerlia* sp.; Mlynarski and Narmandakh 1972).
6. Shiregin Gashun: *Nanhsiungchelyidae* indet. (as ?*Zangerlia* sp.; Shuvalov and Chkhikvadze 1975).
7. Khuren Tsav: *Nanhsiungchelyidae* indet. (as ?*Zangerlia* sp.; Shuvalov and Chkhikvadze 1975).
8. Zamyn Chond (= Dzamin Chond): *Zangerlia dzamynchondi* Sukhanov and Narmandakh, 2006 (Sukhanov 2000; Sukhanov and Narmandakh 2006) and *Nanhsiungchelyidae* indet. (Suzuki and Narmandakh 2004).
- 9, 10. Abdrant Nuru (9) and Bain Dzak (10): *Nanhsiungchelyidae* indet. (Suzuki and Narmandakh 2004).
11. Ukhaa Tolgod: *Zangerlia ukhaachelys* (Joyce and Norell 2005).
12. Yagaan Khovil: *Bulganemys jaganchobili* Sukhanov and Narmandakh, 2006 (Sukhanov 2000; Sukhanov and Narmandakh 2006) and *Nanhsiungchelyidae* indet. (Suzuki and Narmandakh 2004).
13. Udyn Sayr: *Nanhsiungchelyidae* indet. (Suzuki and Narmandakh 2004).
14. Boro Khamarin: *Nanhsiungchelyidae* indet. (as *Basilemys* sp.; Sukhanov and Narmandakh 1975).
15. Nuchidaba: *Zangerlia neimongolensis* (Brinkman and Peng 1996).
16. Baishin Tsav: *Hanbogdemys orientalis* (Sukhanov and Narmandakh 1975, 1977, 2006; Sukhanov 2000) and *Nanhsiungchelyidae* indet. (Suzuki and Narmandakh 2004).
17. Amtgai: *Nanhsiungchelyidae* indet. (Suzuki and Narmandakh 2004).
18. Khara Khutul: *Hanbogdemys* sp. (as *Hanbogdemys orientalis*; Nessov 1987), *Kharakhutulia kalandadzei* (this study), *Nanhsiungchelyidae* indet. (as ?*Zangerlia* sp., Shuvalov and Chkhikvadze 1975; as *Charitonyx tajanikolaevae*, Chkhikvadze 1980; Čkhikvadze 1987).
- 19, 20. Khongil Tsav (19) and Bain Shire (20): *Nanhsiungchelyidae* indet. (Suzuki and Narmandakh 2004).
21. Nanxiong: *Nanhsiungchelys wuchingensis* (Yeh 1966; Lucas 2001).
22. Amagimi Dam of Mifune: *Nanhsiungchelyidae* indet. (as *Basilemys* sp., Hirayama 1998; personal communication of Ren Hirayama to IGD, 2007).
23. Katsuyama: *Nanhsiungchelyidae* indet. (as *Basilemys* sp.; Hirayama 2002).
24. Sakurazawa in Oriki: *Nanhsiungchelyidae* indet. (as *Basilemys* sp.; Tokunaga and Shimizu 1926).
25. Hobetsu-cho: *Anomalochelys angulata* (Hirayama et al. 2001).