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New exceptionally well-preserved specimens of “*Zangerlia*” *neimongolensis* from Bayan Mandahu, Inner Mongolia, and their taxonomic significance

Nouveaux spécimens exceptionnellement bien conservés de « Zangerlia » neimongolensis de Bayan Mandahu, Mongolie intérieure, et leur signification taxonomique

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ABSTRACT

Two exceptionally well-preserved specimens of “*Zangerlia*” *neimongolensis* provide additional information on the structure of the skull, shell and limbs of this taxon. These specimens show that the carapace is more similar to that of *Hanbogdemys* than was previously recognized. A PAUP analysis results in a single most parsimonious cladogram in which the type species of *Zangerlia*, *Zangerlia testudinimorpha* is separated from other species that have been included in that genus while “*Z.*” *neimongolensis*, “*Zangerlia*” *ukaachelys* and “*Zangerlia*” *dzamynchondi* and *Jiangxichelys* are grouped together. Both specimens are exceptional in being preserved in a life-like position: one is preserved with the skull in a retracted position; the other with the head and left forelimb both protracted and in a raised position. These positions suggest that they were entombed while still alive. Thus these specimens provide additional examples of rapid burial of vertebrates in the Bayan Mandahu locality, most likely from either by sand storms that dumped massive amounts of sand over a short period of time or by collapse of individuals in burrows.

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RÉSUMÉ

Deux spécimens de « *Zangerlia* » *neimongolensis* exceptionnellement bien conservés fournissent de nouveaux renseignements sur la structure du crâne, de la carapace et des membres de ce taxon. Ces spécimens montrent que la carapace est plus semblable à celle de *Hanbogdemys* qu'on ne l'avait reconnu auparavant. Une analyse PAUP résulte en un unique

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Tortue
Mongolie intérieure

cladogramme, le plus parcimonieux, dans lequel l'espèce type de *Zangerlia*, *Zangerlia testudinimorpha*, est séparée des autres espèces qui ont été incluses dans ce genre, tandis que «*Z.*» *neimongolensis*, «*Zangerlia*» *ukaachelys* et «*Zangerlia*» *zdamynchondi* et *Jiangxichelys* sont groupées ensemble. Les deux spécimens sont exceptionnels dans le sens où ils sont conservés comme s'ils étaient vivants : l'un avec le crâne en position rétractée et l'autre avec la tête et le membre antérieur gauche tous deux étirés, en position soulevée. Ces positions suggèrent que les deux spécimens ont été ensevelis quand ils étaient encore en vie. En conséquence, ces deux spécimens constituent des exemples supplémentaires d'enfouissement brutal de vertébrés dans la localité de Bayan Mandahu, le plus probablement, soit à la suite de tempêtes de sable qui en ont déversé des quantités massives sur une courte période de temps, soit par dégradation d'individus dans des terriers.

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1. Introduction

Turtles are an important part of the Cretaceous record of vertebrates in both Asia and North America, with specimens being frequently abundant and well-preserved (Hutchison, 2000; Sukhanov, 2000). As well as providing data on the diversification and interrelationships of turtles, they provide data that helps define the pattern of interchange between Asia and North America during the Cretaceous. One group that is particularly significant to discussions of this paleobiogeographical pattern is the Nanshiungchelyidae. This group of large, terrestrial turtles likely originated in Asia, where it is represented by multiple genera, and subsequently dispersed into North America where it is represented by a single genus, *Basilemys* (Danilov and Syromyatnikova, 2008; Hutchison, 2000; Sukhanov, 2000). Vandermark et al. (2009) noted that many North American taxa with Asian origins first appear in North America during the Turonian, and this was likely a result of the extreme high temperature during this time. Since nanshiungchelyids are large, primarily terrestrial turtles, they would have been particularly sensitive to climatic controls. Thus an understanding of the interrelationships of Asian and North American members of the family would help test the hypothesis that dispersal of nanshiungchelyids into North America was episodic and climatically controlled. In this paper, the interrelationships of Asian and North American nanshiungchelyids are reevaluated on the basis of data from two new exceptionally well-preserved specimens of the nanshiungchelyid “*Zangerlia*” *neimongolensis* from the Bayan Mandahu Locality in Inner Mongolia.

The Bayan Mandahu locality has produced an assemblage of Late Cretaceous vertebrate fossils that is similar to that from the Djadokhta Formation of Mongolia (Jerzykiewicz et al., 1993). In both, the vertebrates are preserved in a desert environment containing aeolian sandstones and the assemblages are dominated by the *Protoceratops*. Also, in both of these localities preservation is sometimes exceptional, with animals occasionally preserved in life position as a result of extremely rapid burial. Perhaps the most well-known example of this is a specimen of *Protoceratops* and *Velociraptor* locked in mortal combat that was collected from the Djadokhta Formation (Kielan-Jaworowska and Barsbold, 1972). An example of

rapid burial in the Bayan Mandahu locality is provided by a specimen of an oviraptorid skeleton preserved on a nest of eggs (Dong and Currie, 1996). Both assemblages contain a member of the Nanshiungchelyidae: *Zangerlia testudinimorpha* from the Djadokhta Formation and “*Z.*” *neimongolensis* from the Bayan Mandahu locality. In placing brackets around the generic name for “*Z.*” *neimongolensis* we follow Danilov et al. (2013), who considered its generic affiliations to be uncertain. *Zangerlia testudinimorpha* is rare, with only a single specimen having been described (Danilov et al., 2013; Mlynarski, 1972), while “*Zangerlia*” *neimongolensis* is represented by multiple specimens (Brinkman and Peng, 1996). This difference in abundance is likely a reflection of environmental sensitivity of the taxon and the range in habitats sampled. In the Bayan Mandahu locality a succession of paleoenvironments extends from the margin of the basin, where alluvial fans dominated by conglomerates are present, to the center of the basin, where aeolian sandstones are preserved (Eberth, 1993). Specimens of “*Z.*” *neimongolensis* are encountered primarily in sediments deposited in a setting intermediate between the alluvial conglomerates and the dune fields. Seven individuals were collected by the Canada-China Dinosaur Project, all within this environment of deposition, with one of these including a nearly complete postcranial skeleton preserved within the posterior half of the carapace (Brinkman and Peng, 1996). While these specimens have resulted in “*Z.*” *neimongolensis* being one of the most completely known Asian nanshiungchelyids, many details of the structure of the carapace remain unknown. Extensive damaged by beetle activity (Johnston et al., 1996) and poor preservation of the surface of the shells obscured details regarding the position of sutures and sulci.

Field work in the Bayan Mandahu locality undertaken by the Inner Mongolia Museum and cooperating institutions, including the Natural History Museum of Belgium, resulted in the collection of two exceptionally well-preserved, complete skeletons of “*Z.*” *neimongolensis*. The preservation of both specimens suggests that these are the remains of individuals that were buried alive. In one of these, specimen 96NMBY-I-14, the skull and left forelimb extend forwards, with the skull raised above the plastron and the hand rotated laterally as though pushing against the sediment (Fig. 1). The surface of the skull and shell in this specimen

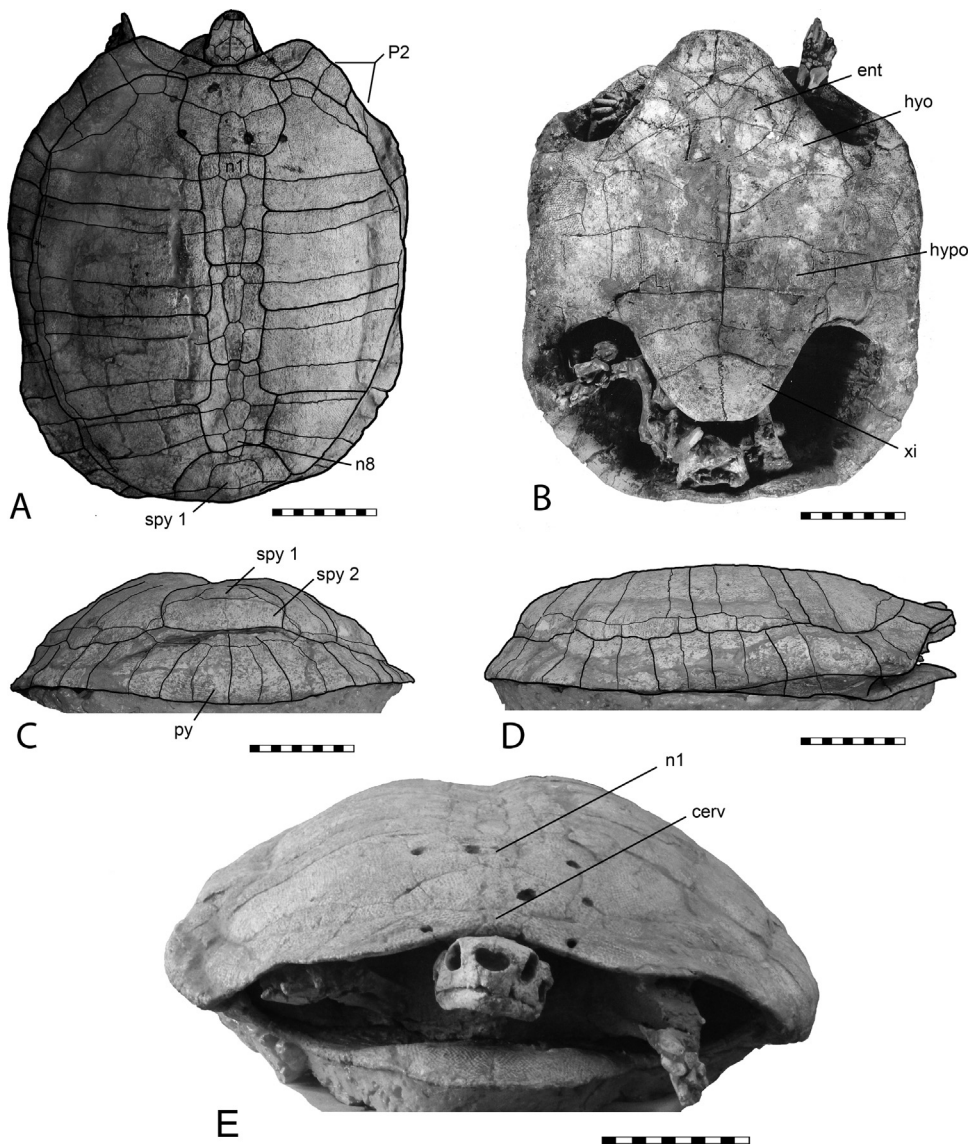


Fig. 1. “*Zangerlia*” *neimongolensis*, specimen 96NMBY-I-14 in (A) dorsal; (B) ventral; (C) posterior; (D) right lateral; and (E) anterior views. The scale bar equals 10 cm. Abbreviations: cerv: cervical scale; ent: entoplastron; hyo: hyoplastron; hypo: hypoplastron; P2: second peripheral; n1: first neural; n8: eighth neural; py: pygal; spy 1: first suprapygal; spy 2: second suprapygal; xi: xiphiplastron.

Fig. 1. «*Zangerlia*» *neimongolensis*, spécimen 96NMBY-I-14 en vues (A) dorsale; (B) ventrale; (C) postérieure; (D) latérale droite et (E) antérieure. Barre d'échelle = 10 cm. Abréviations: cerv: écaille cervicale; ent: entoplastron; hyo: hyoplastron; hypo: hypoplastron; P2: seconde périphérique; n1: première neurale; n8: huitième neurale; py: pygale; spy 1: première suprapygale; spy 2: seconde suprapygale; xi: xiphiplastron.

is well-preserved, showing details not previously visible. The second skeleton, 93NMBY-2, is preserved with the skull withdrawn into the shell (Fig. 2). Although the surface of the shell is less well-preserved, this specimen provides critical information on the morphology of the shell. Neither specimen was subjected to extensive damage from beetle activity, suggesting that they were more deeply entombed when buried than was typically the case. The purpose of this paper is to describe these specimens, evaluate the taphonomic conditions under which they are preserved, and, based on the additional anatomical information they provide, reevaluate the relationships of members of the Nanhsiungchelyidae.

Abbreviations: IMM: Inner Mongolia Museum, Hohhot, Inner Mongolia, People's Republic of China. NMBY: Nei Mongo Bowuguan, Bayan Mandahu specimens. Specimens with these acronyms are housed in the Inner Mongolia Museum, Hohhote, Inner Mongolia, People's Republic of China. IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China.

2. Systematic paleontology

Class REPTILIA
Order TESTUDINATA
Suborder CRYPTODIRA Cope, 1868

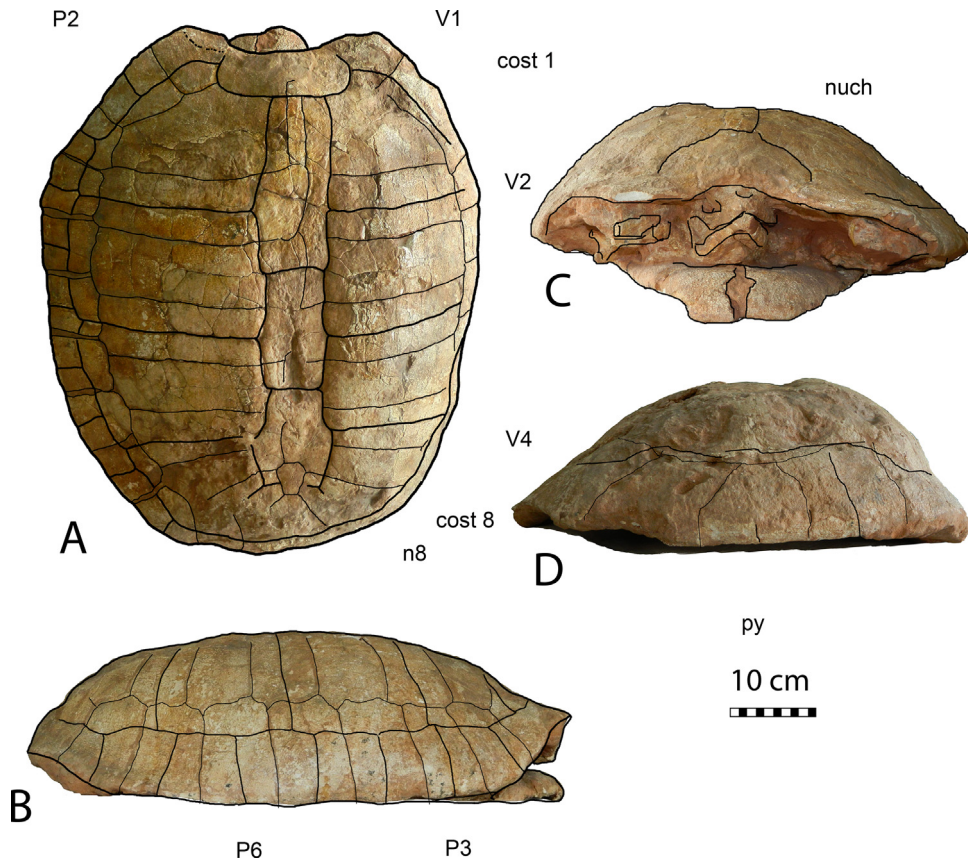


Fig. 2. (Color online.) “*Zangerlia*” *neimongolensis*, specimen 93NMBY-2 in: (A) dorsal; (B) right lateral; (C) anterior; and (D) posterior views. Abbreviations: cost 1: first costal; cost 8: eighth costal; n8: eighth neural; nuch: nuchal; P2: second peripheral; P3: third peripheral; P6: sixth peripheral; py: pygal; V1: first vertebral scale; V2: second vertebral scale; V4: fourth vertebral scale.

Fig. 2. (Couleur en ligne.) «*Zangerlia*» *neimongolensis*, spécimen 93NMBY-2 en vues dans (A) dorsale; (B) latérale droite; (C) antérieure et (D) postérieure. Abréviations: cost 1: première costale; cost 8: huitième costale; n8: huitième neurale; nuc: nuchale; P2: seconde périphérique; P3: troisième périphérique; P6: sixième périphérique; py: pygale; V1: première écaille vertébrale; V2: seconde écaille vertébrale; V4: quatrième écaille vertébrale.

Parvorder EUCRYPTODIRA Gaffney, 1975
Family NANHSIUNGCHELYIDAE Yeh, 1966
“*Zangerlia*” *neimongolensis*
Figs. 1–4

2.1. Material

Specimen 96NMBY-I-14 (IMM-Field-93NMBY-I-14): a complete skeleton with the head and left forelimb extending out of the carapace and the right forelimb withdrawn into the shell. The head is raised off the plastron, approaching the carapace, with the skull at a slight angle. The left limb is rotated so the plantar side of the hand faces dorso-laterally. Matrix around the left forelimb likely represents a natural cast of the fleshy portion of the limb. The right hand is fully retracted and near the carapace with the hand paralleling the carapace, plantar side upwards. In addition to being preserved in a life-like position, the preservation of this specimen is exceptional in that it was not heavily scavenged by beetles as was the case in all the specimens described by Brinkman and Peng (1996). Only seven small round holes near the anterior end of the carapace are likely the result of beetle

scavenging. Surface details are well-preserved, and with few exceptions sutures and sulci could be easily identified.

From Bayan-Mandahu, Wulatehouqi, Bayan Naoer Shi, Inner Mongolia, China. Discovered by Mr. Zhe-min Zhang, and collected by the Inner Mongolia Museum in 1996.

Specimen 93NMBY-2 (IMM-Field-93NMBY-2): a complete skeleton preserved with the head withdrawn into the shell. The skull is tilted upwards so the snout touches the carapace and the ventral surface is exposed in anterior view. Although surface detail is not as well-preserved, most of the features of the shell could be identified. The pattern of sutures and sulci in the taxonomically significant peripheral series was clear since these elements had separated slightly. The position of the skull indicates not only that the head could be fully withdrawn into the carapace, as would be expected given the structure of the cervical vertebrae, but that the specimen was also buried while the head was actively being held upright within the shell.

From Bayan-Mandahu, Wulatehouqi, Bayan Naoer Shi, Inner Mongolia, China. Discovered by Lian-hai Hou, Changyong Shuang, and Yu-long Dong and collected by the Inner Mongolia Museum in 1993.

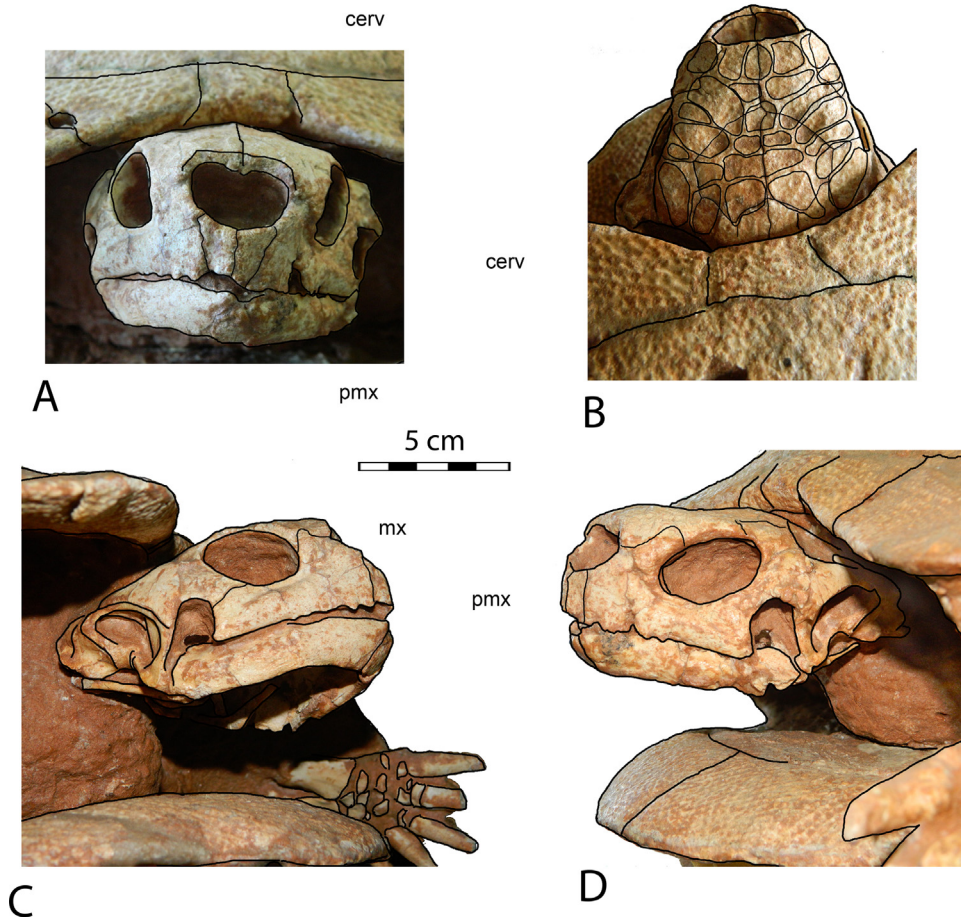


Fig. 3. (Color online.) Skull of *Zangerlia* *neimongolensis*, specimen 96NMBY-I-14 in: (A) anterior; (B) dorsal; (C) right lateral; and (D) left lateral views. Abbreviations: cerv: cervical scale; mx: maxilla; pmx: premaxilla.

Fig. 3. (Couleur en ligne.) Crâne de «*Zangerlia*» *neimongolensis*, spécimen 96NMBY-I-14 en vues (A) antérieure; (B) dorsale; (C):latérale droite et (D) latérale gauche. Abréviations : cerv : écaille cervicale ; mx : maxillaire ; pmx : prémaxillaire.

2.2. Description

The skull is partially visible in both specimens. In specimen 96NMBY-I-14 (Fig. 1) it partially extends out of the carapace and is in a raised position (Fig. 1E). Much of the lateral surface has been exposed. In specimen 93NMBY-2 (Fig. 2), the skull is withdrawn within the shell and is tilted with the snout against the carapace, so its ventral surface is visible (Fig. 2C). In general, the proportions of the skull (Fig. 3) match those of “*Z.*” *neimongolensis* as described by Brinkman and Peng (1996). The skull roof is broad so the orbits face strongly laterally. The cheek region is deeply emarginated, and the temporal emargination extends anterior to the middle of the cheek emargination. The bar between the cheek emargination and the temporal emargination is deeper than the bar between the temporal emargination and the orbit. A feature of the skull that was not apparent in specimens of “*Z.*” *neimongolensis* available to Brinkman and Peng (1996) is the large size of the external narial opening. This is wider than high, slightly smaller than the orbits, and faces slightly dorsally. The premaxilla below the external narial opening is deep, as is the maxilla

below the orbits. The ventral edge of the maxilla is weakly serrated, with the serrations larger and more distinct on the anterior end of the maxilla. The surface of the skull roof is covered by a network of scutes of moderate size. The scales are loosely arranged in a triangular area covering the central portion of the parietals and a row of medio-laterally elongate scutes on either side crossing the sutures between the parietals and the adjacent bones. As in the pattern described by Sterli and de la Fuente (2013), three mid-line scales are present. One of these covers the posterior portion of the parietal, one covers the junction between the parietal and frontal, and one covers the prefrontals. However, the arrangement of the more lateral scales does not fit easily into the pattern of scales present in meiolaniids.

Sutures of the skull roof are distinct on at least one side. The prefrontal is large and meets the postorbital above the orbit. The frontal is trapezoidal in shape with a long suture with the prefrontal, a shorter suture with the postorbital and a W-shaped suture with the parietal. The frontal-prefrontal suture is a curved suture located between the orbits. This suture was visible on the skull of IVPP 020788-7 as described by Brinkman and Peng (1996) and is in



A



B



C

Fig. 4. (Color online.) Forelimb of “*Zangerlia*” *neimongolensis*, specimen 96NMBY-I-14. A. Right forelimb in retracted position, with dorsal surface visible. B–C. Left forelimb in protracted position. (B) Dorsal surface, and (C) plantar surface. The scale bar equals 5 cm.

Fig. 4. (Couleur en ligne.) Membre antérieur de «*Zangerlia*» *neimongolensis*, spécimen 96NMBY-I-14. A. Membre antérieur droit en position rétractée, avec surface dorsale visible. B–C. Membre antérieur gauche en position étirée. (B) Surface dorsale et (C) surface plantaire. Barre d'échelle = 5 cm.

a similar position. The frontal-parietal suture, which was not preserved in IVPP 020788-7 is located posterior to the orbits.

The carapace of both specimen 96NMBY-I-14 and 93NMBY-2 agrees with that of the “Z.” *neimongolensis* specimens described by Brinkman and Peng (1996) in being slightly longer than wide and moderately domed with the peripherals facing primarily laterally (Figs. 1 and 2). A mid-dorsal depression extends from the posterior end of the first neural to the eighth neural. The posterior end of the carapace is nearly vertical with the ventral edge curving inwards. A knob at the posterior end of the neural series marks the transition from the nearly horizontal dorsal surface to the nearly vertical posterior surface of the carapace.

The surface of the carapace, best preserved in specimen 96NMBY-I-14, is evenly covered by pits that are intermediate in size between those of *Adocus* and *Basilemys*. These show no variation across the carapace.

A striking feature of the carapace is a strong nuchal emargination bordered by triangular flanges. The development of this emargination is similar to that of *Hanbogdemys orientalis*. Also, as in *Hanbogdemys*, the nuchal emargination is bordered by the nuchal and first peripheral. “Z.” *neimongolensis* was reconstructed without a nuchal emargination by Brinkman and Peng (1996) based on specimen IMM 2802, the only shell available to them that preserved the anterior end of the carapace. However, as they note, this region of the shell is poorly preserved so the apparent absence of a nuchal emargination in this specimen is most likely a result of preservation.

Sutures delineating the bones of the nuchal and neural series could be identified in specimen 96NMBY-I-14 (Fig. 1). The suprapygal series could be recognized in both specimens, at least on one side, and the pygal on 93NMBY-2 (Fig. 2). The nuchal is large and relatively short and wide. The ventral surface of the nuchal is not visible, so it is uncertain whether or not costiform processes are present. The neural series completely separates the costals in specimen 93NMBY-2, but in 96NMBY-I-14 the eighth costals contact one another at the midline posterior to the eighth neural. Neurals 1 to 6 are long and narrow. Neural 7 is shorter and relatively wider. The width of neural 8 corresponds to neural 6, but this element is much shorter. The first neural is hexagonal with short postero-lateral edges. The second one is rectangular, and the third to eighth ones are hexagonal, with short antero-lateral edges.

The first suprapygal is a subrectangular element, much narrower than the second suprapygal. The second suprapygal extends lateral to the first to contact the eighth costal.

Costal 1 is exceptionally large. The more posterior costals are of normal proportions.

The peripheral series of the specimen 96NMBY-I-14 was fully articulated, although most sutures could be identified. The peripherals of specimen 93NMBY-2 were slightly separated, so sutures were clear. The first peripheral borders the nuchal emargination and forms the antero-lateral flange. The second is rectangular. In antero-lateral view, these are slightly curved, and from the position of the limbs it appears that this curvature would have covered the retracted limb. The plastral buttress does not extend onto the second peripheral, although it may just meet the

posterior edge of this element. Peripherals 2 to 11, most clearly distinct in specimen 93NMBY-2, are tall elements, similar to those of *Adocus* in proportions.

The pygal, visible in both specimens is wider than tall.

The sulci are most completely preserved on specimen 96NMBY-I-14. The first vertebral scute is sub-hexagonal, slightly wider than long, with convex lateral edges and truncated anterior and posterior ends. The inward curvature of the anterior end of this scute results in the sulcus between the first vertebral and first pleural scute crossing the lateral edge of the nuchal. The lateral border of the first vertebral scute of specimen 93NMBY-2 is also curved, but the scute is relatively narrow.

The second to fourth vertebral scutes are very narrow and are located fully within the mid-dorsal depression, so are not visible in lateral view. The second vertebral scute is particularly long and slender in specimen 93NMBY-2. The sulcus between the pleural scutes meets the lateral edge of the vertebral scutes mid-way along their length. The fifth vertebral scute mirrors the first in being sub-hexagonal in shape. The sulcus delineating its lateral border crosses the lateral edge of the second suprapygal, so the fourth pleural scute would have extended onto that bone.

The pleural-marginal scutes are most clearly distinct on specimen 93NMBY-2. Marginals do not extend onto costals, except perhaps a minute incursion of the third or fourth marginal onto costal 2. Further posteriorly, the suture between the costals and peripherals is clearly medial to the pleural-marginal sulcus.

The sulci of the cervical and anterior marginal scutes can be seen in specimen 96NMBY-I-14. The first marginal scute is a long narrow scute that lies along the lateral edge of the nuchal emargination, covering the anterior-most corner of the flange formed by the first peripheral. The second marginal scute is exceptional in having a long narrow process extending medially to contact the antero-lateral corner of the first vertebral scute. Sulci delineating the cervical and first marginal scutes are unclear on specimen 93NMBY-2, so the position of the first marginal scute and the presence of a medial process of the second marginal scute cannot be confirmed in this individual. However, the sulci delineating the third to twelfth marginal scutes are distinct. These are rectangular in lateral view and extend two thirds of the way up the peripherals.

Information on the structure of the plastron was only available for specimen 96NMBY-I-14 (Fig. 1B). In general form, the plastron of this specimen agrees with that of the “*Z.*” *neimongolensis* specimens described by Brinkman and Peng (1996) in having a sub-triangular anterior lobe, a long bridge, and a short, wide posterior lobe. The anterior lobe of the plastron is larger than the posterior lobe, and the posterior end of the plastron is well separated from the posterior end of the carapace. Sulci generally follow the pattern described by Brinkman and Peng (1996), although the extragular scutes could not be identified. The shape of the mid-line sulcus on the posterior lobe of the plastron is not clear.

The left forelimb and both hands are visible in specimen 96NMBY-I-14 (Fig. 4). The right hand is retracted and the plantar surface is pressed against the inner surface of the carapace (Fig. 4A). The left arm is partially extended

and rotated so the plantar surface of the left hand is fully visible laterally (Fig. 4B–C). Toes are short and sub-equal in length, the length of the longest toe measured from the presumed wrist joint, which is 4 cm, is much less than the length of the forearm, which is no shorter than 6 cm long. The phalanges are short, so most of the length of the toes is a result of the presence of the long, dorso-ventrally compressed claws. The number of phalanges in each digit is uncertain because the surface of these is partially obscured by matrix.

A striking feature of the hand is the presence of dermal ossicles on the plantar surface (Fig. 4C). A large dermal ossicle is present at the base of digits 2–5, and a row of smaller ossicles is present medial to this. Ossicles were not seen on the forearm.

3. Discussion

The specimens described here are included in “*Z.*” *neimongolensis* because of similarities in the shell, particularly the moderately domed shell with a near vertical posterior end, and the morphology of the plastron. The outline of the shell of these specimens shows that a distinct nuchal emargination was present. “*Z.*” *neimongolensis* was reconstructed without a nuchal emargination by Brinkman and Peng (1996), although based on the newly available specimens this is considered to be incorrect, probably as a result of poor preservation of the most completely preserved shell available to them.

As well as allowing for a more accurate reconstruction of the shell, the new material provides additional taxonomically significant information on the position of the sulci. In particular, the pleural scutes extend well onto the peripherals. In this feature, “*Z.*” *neimongolensis* is similar to “*Zangerlia*” *dzamynchondi* and *Jiangxichelys* (Danilov et al., 2013; Tong and Mo, 2010), and different from other Asian nanshiungchelyids, in which the suture and sulci are located close together.

The preservation of the skull in place in the new specimens demonstrates that the head could be completely withdrawn into the carapace, as Brinkman and Peng (1996) assumed was the case based on the structure of the cervical vertebrae. In general the skull of the new specimen agrees with the previously described material. However, in contrast with the reconstruction presented by Brinkman and Peng (1996), the external narial opening is large and faces strongly anterodorsally. As well, scutes are present on the skull roof. The pattern of scales is similar to the pattern of homologies proposed by Sterli and de la Fuente (2013) in the presence of three mid-line scales. In other respects, it appears distinct from the pattern seen in basal turtles and homologies cannot easily be identified. The previously described specimens showed a deep cheek emargination, although the edges were not well-preserved. The new specimen more accurately preserves the shape of the emargination.

The forelimb of the new specimen provides the first fully articulated hand of “*Z.*” *neimongolensis*. As anticipated from the disarticulated elements, the toes are short, with most of their length represented by the claws. The presence of dermal ossicles in the palm of the hand is an unexpected

feature. While the presence of dermal ossicles is not unexpected since they are present in other nanhsiungchelyids, their location on the palm of the hand, with the largest ossicles at the base of the digits, has not been previously documented. Given this position, it is likely that the ossicles had a locomotor function, perhaps acting as “spurs” to help with traction in the loose substrate, rather than functioning primarily as armor.

With this revised understanding of the morphology of “Z.” *neimongolensis*, a similarity with *Hanbogdemys* is more apparent. In both taxa nuchal emargination is present (either absent or much less strongly developed in *Z. testudinimorpha*), the first marginal scute is a long narrow scute that borders the nuchal emargination, the first vertebral scute is an enlarged, sub-circular scute, the second to fourth are long narrow scutes, the fifth is a circular scute slightly smaller than the first, and the pleural scutes extend onto the peripherals. All these features are also present in *Jiangxichelys* except the shape of the fifth vertebral.

To evaluate the relationships of the Bayan Mandahu nanhsiungchelyid, a PAUP analysis was undertaken. The data matrix used by Joyce and Norell (2005) as modified by Sukhanov et al. (2008) was the basis for this. The codings used by Sukhanov et al. (2008) were modified for “Z.” *neimongolensis* based on information provided by the specimens described here. Some character codings are changed in *Nanhsiungchelys wuchingensis* and *Z. testudinimorpha* according to restudy of previously described specimens by one of us (HYT). Contrary to Danilov et al. (2013), we keep the character 16 (Steep deflection of the post part of the carapace). This character was first used by Brinkman and Peng (1996) to define the inward curving of the posterior end of the carapace.

The changes in the coding of *N. wuchingensis* based on new observation on the holotype, specimen IVPP V3106, are: character 9 is changed from 1 to 0 (basisphenoid short); character 11 is changed from? to 1 (coracoids fan-shaped); character 17 is changed from 0 to? (knob on suprapygal 1: not preserved); character 19 is changed from 1 to 0 (nuchal small trapezoidal); character 21 is changed from 1 to? (neural series: not completely preserved); character 25 is changed from 1 to? (vertebral 5/marginals X–XI: not preserved); character 37 is changed from 2 to 0 (3–4 pairs of inframarginals present); character 39 is changed from? to 1 (pectoral enter axillary notch absent).

Changes in the coding of *Z. testudinimorpha*, based on the new observation of Danilov et al. (2013), are: character 16 is changed from 1 to 0 (Steep deflection of the post part of the carapace absent based on fig. 22.5 of Danilov et al. (2013)); character 18 is changed from? to 0 (although the anterior margin of the carapace is damaged, enough is preserved to show that a cervical notch is absent); character 19 is changed from 0 to? (nuchal: not preserved); character 24 is changed from 1 to 0 (vertebral 1 contacts marginal 2); character 27 is changed from 0 to 1 (vertebral 5 reaching peripheral 10); character 36 is changed from 0 to? (entoplastron shape and position are unclear); character 38 is changed from 0 to 1 (expansion of ventromedial edge of marginal 6 present), character 39 is changed to 1 (participation of pectoral to rim of axillary notch absent) and

character 41 is changed from? to 1 (scale on dorsal surface of plastron present) according to Danilov et al. (2013).

As noted by Danilov et al. (2013), character 16 is changed in *Zangerlia ukhaachelys* from 1 to? since this part of the carapace is not preserved.

Four additional characters are added in our analysis to incorporate features that are present in “Z.” *neimongolensis* and at least one other nanhsiungchelyid. These are:

42. **First vertebral scute** (0) with straight lateral edge; (1) with convex or angled lateral edge, (2) with lateral edges converging anteriorly.
43. **Second to fourth vertebral scutes:** (0) width greater than half length; (1) width less than half length.
44. **External narial opening:** (0) small to moderate size (less than half the width of the orbit) and faces anteriorly; (1) large (more than half the width of the orbit) and faces antero-dorsally.
45. **Medial process of marginal 2:** (0) absent, (1) present.

Two additional taxa are added in our analysis: *J. ganzhouensis* Tong and Mo, 2010 and “*Zangerlia*” *dzamynchondi* Sukhanov and Narmandakh, 2006. The latter is based on the new description by Danilov et al. (2013). The updated dataset, including 14 taxa and 45 characters (see Appendix 1) is analyzed using PAUP 4.0b10 (Swofford, 2002). All characters are unordered and of equal weight. Forty-two among 45 characters have been coded in “Z.” *neimongolensis*. This represents 93% of total characters and makes this species the most completely coded nanhsiungchelyid.

The analysis resulted in a single tree of 63 steps, with CI=0.75, HI=0.25, RI=0.69 and RC=0.51. In this tree “Z.” *neimongolensis*, “Z.” *ukhaachelys*, “Z.” *dzamynchondi* and *Jiangxichelys* group together in one clade, which is sister to *Hanbogdemys* ((*Nanhsiungchelys* + *Anomalochelys*) + *Basilemys* spp.). *Kharakhutulia* is more basal and *Z. testudinimorpha* unresolved with *Adocus* and rest of nanhsiungchelyids (Fig. 5).

The cladogram resulting from our analysis shows two important points. The first is that the type species of *Zangerlia*, *Z. testudinimorpha*, is separated from other species that have been included in that genus while “Z.” *neimongolensis*, “Z.” *ukaachelys* and “Z.” *dzamynchondi* and *Jiangxichelys* are grouped together. This means that the genus *Zangerlia* as currently used is not a monophyletic unit and *Zangerlia* should include only *Z. testudinimorpha*. These results are in general agreement with those of Hirayama et al. (2001) and Danilov et al. (2013) who put all other “*Zangerlia*” but the type species in quotes. In considering the generic assignment of these species, two main options are available. One is to include them in *Jiangxichelys*, and the other is to include them in *Bulganemys*. *Bulganemys* is very similar to the specimens described here but is very poorly known. According to Danilov and Syromyatnikova (2008) and followed by Tong and Mo (2010) it is synonymous with *Hanbogdemys*. Only 13 of the 45 characters used in this analysis can be coded for *Bulganemys*, and if it is added to the PAUP analysis, all collapse except the *Basilemys* clade and the *Nanhsiungchelys* + *Anomalochelys* clade. Thus at present, there is no clear resolution to the question of

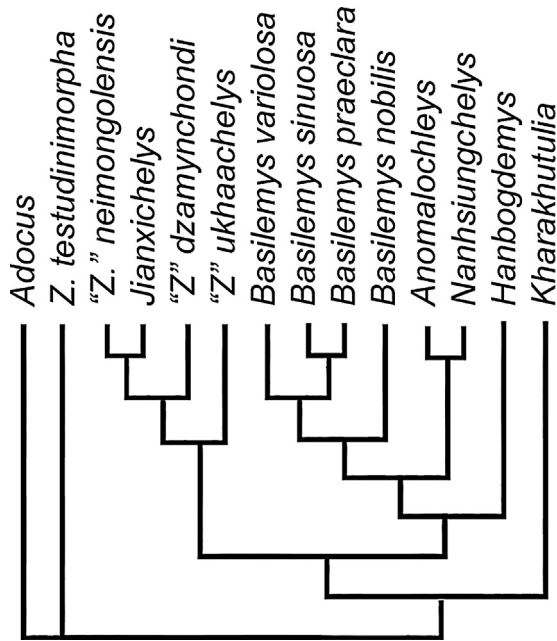


Fig. 5. Cladogram showing the single tree of 63 steps resulting from the PAUP analysis of the interrelationships of the better-known members of the Nanshiungchelyidae. See section 3 for the description of the tree.
Fig. 5. Cladogramme montrant l'arbre unique à 63 pas résultant de l'analyse PAUP des interrelations entre les membres les mieux connus des Nanshiungchelyidae. Voir la section 3 pour la description de l'arbre.

generic assignment of “*Zangerlia*” *neimongolensis*. Pending a better understanding of the anatomy of *Hanbogdemys*, *Bulganemys*, and *Z. testudinimorpha*, we follow Danilov et al. (2013) in restricting *Zangerlia* to the type species and putting all other species that have been referred to this genus in quotes.

A second important result of this analysis is that the species of *Basilemys* group together in a single clade. This result suggests that there was a single dispersal event from Asia to North America, rather than a series of dispersal events.

3.1. Taphonomic considerations

Clearly a life-like posture such as is seen in specimen 96NMBY-I-14 could only be preserved as a result of rapid burial of a living individual. The posture of this specimen with a partially protracted hand and the head both being raised off the substrate has the appearance of an individual that died in the process of digging out of the entombing sand. Such rapid burial has been documented in other instances in the Bayan Mandahu locality, a striking example being a group of juvenile ankylosaurs that were preserved together (Jerzykiewicz et al., 1993).

In addition to being preserved in a life-like pose, both specimens are exceptional compared with other vertebrate fossils from Bayan Mandahu in lacking the evidence of beetle activity, which resulted in loss of large areas of bone in many of the vertebrate fossils from that locality. The presence of only a minor amount of beetle activity is presumably a result of the specimen being buried at a sufficient

depth to prevent beetles from reaching the carcass. Thus as well as being rapidly buried, the specimens were likely buried relatively deeply.

Two hypotheses have been presented to explain the rapid and relative deep burial of some of the vertebrates from Bayan Mandahu locality in Inner Mongolia and the Djadokhta Fm. of Mongolia. One is that sand storms dumped massive amounts of sand over a short period of time, either burying them directly or resulting in dune collapse burying individuals that were in the lee of the dune. A second is that individuals were occupying tunnels that collapsed on them. Either of these hypotheses would explain the entombment of the two specimens described here.

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Appendix 1. Revised list of characters and their states and revised character matrix

List of characters:

1. **Numerous deep cranial scute sulci on dermal roofing elements:** (0) absent; (1) present (Joyce and Norell, 2005: character 1).
Comment: “*Zangerlia*” *neimongolensis* coding changed from 0 to 1 based on the presence of scutes of the skull of specimen 96NMBY-I-14.
2. **Extensive postorbital squamosal contact due to the great anterior extent of the squamosal and the great posterior extent of the postorbital:** (0) absent; (1) present (Joyce and Norell, 2005: character 2).
3. **Extent of upper temporal emargination:** (0) foramen stapedio-temporale fully exposed in dorsal view; (1) foramen stapedio-temporale concealed in dorsal view (Joyce and Norell, 2005: character 3).
4. **Extent of lower temporal emargination:** (0) moderately developed, processus pterygoideus externus barely visible in lateral view; (1) absent or shallow, processus pterygoideus externus concealed in lateral view (Joyce and Norell, 2005: character 4).
5. **Lingual ridges of maxilla:** (0) double; (1) single or absent (Joyce and Norell, 2005: character 5).
6. **Antorbital groove on the surface of the maxilla along the anteroventral rim of the orbit:** (0) absent; (1) present (Joyce and Norell, 2005: character 6).
7. **Medial contact of palatines:** (0) absent; (1) present (Joyce and Norell, 2005: character 7).
8. **Incisura columella auris:** (0) open posteriorly; (1) closed posteriorly (Joyce and Norell, 2005: character 8).

9. **Size and contacts of the basisphenoid:** (0) basisphenoid short, anteriorly only in contact with pterygoid; (1) basisphenoid elongate, anteriorly in contact with vomer or palatine (Joyce and Norell, 2005: character 9).
10. **Central morphology of the eighth cervical:** (0) opisto-coelous; (1) biconvex (Joyce and Norell, 2005: character 10).
11. **Coracoid:** (0) flat and elongate; (1) flat, fan-shaped (Joyce and Norell, 2005: character 11).
12. **Size and medial contact of thyroid fenestrae:** (0) fenestrae large and confluent; (1) fenestrae small, medial contact absent (Joyce and Norell, 2005: character 12).
13. **Thelial process of ilium:** (0) present; (1) absent (Joyce and Norell, 2005: character 13).
14. **Length of manual and pedal digits:** (0) digits elongate, typically three phalanges per digit; (1) digits shortened, less than three phalanges per digit (Joyce and Norell, 2005: character 14).
15. **Limb osteoderms:** (0) absent; (1) present (Joyce and Norell, 2005: character 15).
16. **Steep deflection of the postneural part of the carapace:** (0) absent, posterior peripherals greatly flared; (1) present, posterior peripherals shortened (Joyce and Norell, 2005: character 16).
17. **Knobby protrusion of the carapace at the position of the first suprapygal:** (0) absent; (1) present (Joyce and Norell, 2005: character 17).
18. **Nuchal notch:** (0) absent or shallow; (1) present, formed by the nuchal and peripheral I; (2) present, formed by nuchal only (Joyce and Norell, 2005: character 18).
Comment: “*Zangerlia*” *neimongolensis* coding changed from 0 to 1 based on the presence of a nuchal emargination bordered by the nuchal and first peripheral in both specimen 96NMBY-I-14 and specimen 93NMBY-2.
19. **Shape and size of nuchal:** (0) small and trapezoid; (1) large and V-shaped (Joyce and Norell, 2005: character 19).
Comment: “*Zangerlia*” *neimongolensis* coding changed from? to 0 based on the shape of the nuchal scute in specimen 96NMBY-I-14.
20. **Costiform process of nuchal:** (0) absent; (1) present (Joyce and Norell, 2005: character 20).
21. **Neurals:** (0) neurals VII and VIII reduced or lost; (1) full set of eight neurals present (Joyce and Norell, 2005: character 21).
22. **Contacts of suprapygals with peripherals:** (0) contact with peripherals X and XI; (1) contact with peripheral XI only (Joyce and Norell, 2005: character 22).
23. **Shape of pygal:** (0) longer than wide; (1) wider than long (Joyce and Norell, 2005: character 23).
24. **Anterior contacts of vertebral I:** (0) anterior side very wide, in contact with marginal II; (1) anterior side moderately wide, in contact with marginal I; (2) anterior side constricted, primarily in contact with cervical only (Joyce and Norell, 2005: character 24).
25. **Contacts of vertebral V with marginals X and XI:** (0) vertebral V only in contact with half the length of marginal XI; (1) vertebral V contacts full length of marginal XI and may even contact marginal X (Joyce and Norell, 2005: character 25).
26. **Position of vertebral V relative to suprapygals:** (0) vertebral V only partially covers suprapygals; (1) vertebral V fully, or almost fully, covers the suprapygals (Joyce and Norell, 2005: character 26).
27. **Position of vertebral V relative to peripheral X:** (0) vertebral V does not reach peripheral X; (1) vertebral V clearly covers part of peripheral X (Joyce and Norell, 2005: character 27).
28. **Sulcus between pleural I and marginals II and III:** (0) clearly situated on peripherals; (1) situated on or near suture of peripherals and costals or clearly situated on costals (Joyce and Norell, 2005: character 28).
Comment: “*Zangerlia*” *neimongolensis* coding changed from 1 to 0 based on the position of first pleural scute in specimen 93NMBY-2, where the sulcus is located primarily on the peripherals, only contacting the costal-peripheral suture at its posteriolateral margin.
29. **Sulcus between pleural III and marginals VII–IX:** (0) clearly situated on costals; (1) situated near suture of peripherals and costals; (2) clearly situated on peripherals (Joyce and Norell, 2005: character 29).
Comment: “*Zangerlia*” *neimongolensis* coding changed from 1 to 2 based on the position of the sulcus well down on the peripherals in specimen 93NMBY-2.
30. **Extent of anterior plastral lobe:** (0) anterior lobe covered by carapace in dorsal view; (1) anterior lobe protrudes farther anterior than carapace (Joyce and Norell, 2005: character 30).
31. **Extragulars:** (0) present; (1) absent (Joyce and Norell, 2005: character 31).
32. **Fusion of gulars:** (0) absent; (1) present (Joyce and Norell, 2005: character 32).
33. **Size and medial contact of extragulars:** (0) extragulars small or absent, and, if present, do not meet medially; (1) extragulars elongate, in medial contact with another, thus hindering a contact between gulars and humerals (Joyce and Norell, 2005: character 33).
34. **Broad dorsal extension of gulars onto thickened anterior plastral lip:** (0) absent; (1) present (Joyce and Norell, 2005: character 34).
35. **Position of gulars and extragulars relative to entoplastron:** (0) scutes do not overlap entoplastron; (1) scutes overlap onto entoplastron (Joyce and Norell, 2005: character 35).
36. **Humero-pectoral sulcus:** (0) does not intersect entoplastron; (1) intersects entoplastron (Joyce and Norell, 2005: character 36).
37. **Inframarginals:** (0) four or three pairs; (1) two pairs; (2) absent (Joyce and Norell, 2005: character 37).
38. **Expansion of the ventromedial edge of marginal VI:** (0) absent; (1) present (Joyce and Norell, 2005: character 38).
39. **Participation of pectoral to rim of axillary notch:** (0) present; (1) absent (Joyce and Norell, 2005: character 39).
40. **Sculpturing of the shell surface** with relatively big and irregular pits and grooves: (0) absent; (1) present (Sukhanov et al., 2008: character 40).

41. **Overlapping of scales on the dorsal surface of plastral lobes:** (0) absent; (1) present (Sukhanov et al., 2008: character 41).
42. **First vertebral scute** (0) with straight lateral edge; (1) with convex or angled lateral edge, (2) with lateral edges converging anteriorly (new character).
43. **Second to fourth vertebral scutes:** (0) width greater than half length; (1) width less than half length (new character).
44. **External narial opening:** (0) small to moderate size (less than half the width of the orbit) and faces anteriorly; (1) large (more than half the width of the orbit) and faces antero-dorsally (new character).
45. **Medial process of marginal 2:** (0) absent; (1) present (new character).

TAXON-CHARACTER MATRIX

	11	21	31
<i>Adocus</i> sp.	0000000000	0000000000	00000a0000 00000
<i>Zangerlia testudinimorpha</i>	???????????	??11110??	?????00111 100??
"Z." <i>neimongolensis</i>	100011?101	001111110?	1011000021 0011110111 ?1111
"Z." <i>ukhaachelys</i>	000011????	?????1?10?	?1?1??0111 ?1?1?00111 ?1?1?
<i>Basilemys variolosa</i>	000001?1??	1111100000	1011101021 0001111111 111?0
<i>Basilemys nobilis</i>	???????????	???110000?	0011101021 0101111111 111?0
<i>Basilemys sinuosa</i>	???????????	?????0000?	101a101021 0011111111 111?0
<i>Basilemys praeclara</i>	???????????	?????0?0?	?1?1?10102? 001111??1? 111?0
<i>Hanbogdemys orientalis</i>	???????????	1111?00101	1011000111 0101010111 111?0
<i>Anomalochelys angulata</i>	???????????	?????01110	1??2?????1? 01011??11 120?0
<i>Nanhsiungchelys wuchingensis</i>	1111??110?	1?1110?20?	???2???111 1101112?11 12010
<i>Kharakhutulia kalandadzei</i>	???????????	?????0?000	?10??1?10 0?00010111 111?0
<i>Jianxichelys ganzhouensis</i>	???????????	?????1110?	1011000021 ??????????1 211?1
"Z." <i>dzamynchondi</i>	???????????	?????0110?	?11??1?021 0?01010111 1???0

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