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Gravemys Sukhanov and Narmandakh, 1983 (Testudinoidea: Lindholmemydidae) from the Late Cretaceous of Asia: new data

IGOR DANILOV
Department of Herpetology, Zoological Institute of Russian Academy of Sciences, Universitetskaya Emb. 1, 199034, St. Petersburg, Russia. E-mail: dig@mail333.com

The study of new specimens of *Gravemys barsboldi,* a rare lindholmemydid turtle from the Late Cretaceous of Mongolia, reveals new details regarding its morphology. These include a clear overlapping of marginal 12 onto suprapygal 2, inguinal buttress reaching the two thirds of the width of costal 5 and contacting the costals 5-6 suture laterally, variably shaped inframarginals and viability (straight or sinuous) medial pectoral sulcus. *Gravemys hutchisoni*, sp. n., is based on the paratype specimen of *Mongolemys trufanensis* Yeh, 1974, from the Late Cretaceous of Turfan (Xinjiang, China). This new assignment is based on the similarity in shape of the plastral lobes, the presence of four pairs of inframarginals that strongly onlap the peripherals, and a shortened entoplastron.

INTRODUCTION

The Lindholmemydidae Čkhikvadze, 1975[1] (Shuvalov and Čkhikvadze 1975) is an extinct family of freshwater turtles known from the Cretaceous and Paleocene of Asia. Currently, it is considered a basal group of testudinoids and characterized by the presence of additional inframarginal scales (Hirayama 2000; Sukhanov 2000; Danilov 2001). Thus, study of lindholmemydids is important for understanding the early stages of testudinoid evolution. Data on morphology and distribution of lindholmemydids are scarce (Sukhanov 2000). This is especially true of the genus *Gravemys* Sukhanov and Narmandakh 1983. Until recently, the only species of this genus, *G. barsboldi* (Sukhanov and Narmandakh 1974), was known only by two specimens from the Late Cretaceous (Nemegt Formation, Maastrichtian) of Mongolia (Sukhanov and Narmandakh 1983). Due to incompleteness, some details of shell morphology and variation of characters remained poorly known.

This paper presents a description of new material of *G. barsboldi* from the Late Cretaceous localities of Mongolia that are stored in the collection of the Zoological Institute of Russian Academy of Sciences (St. Petersburg), and previously unknown characters of this species and genus. This paper also presents a description of a new species of *Gravemys*, based on the paratype specimen of *Mongolemys trufanensis* Yeh, 1974 from the Late Cretaceous of China. Localities mentioned in the text are shown in Fig. 1.

Institutional abbreviations: **PIN**—Paleontological Institute of Russian Academy of Sciences (Moscow); **IG**—Department of Paleontology and Stratigraphy, Institute of Geology, Mongolian People's Republic (Ulan-Bator); **IVPP**—Institute of Vertebrate Paleontology and Paleoanthropology of Chinese Academy of Sciences (Beijing); **ZISP PH**—Zoological Institute of Russian Academy of Sciences (St. Petersburg), Paleoherpetological Collection.

[1] The taxon Lindholmemydidae was proposed by Čkhikvadze (1970), but no diagnosis was given until publication of Shuvalov and Čkhikvadze (1975). Thus, according to ICZN, the name became available only since 1975.

SYSTEMATIC PALEONTOLOGY

ORDER TESTUDINES
SUPERFAMILY TESTUDINOIDEA Batsch 1788
FAMILY LINDHOLMEMYDIDAE Čkhikvadze 1975 (in Shuvalov and Čkhikvadze 1975)
GENUS *GRAVEMYS* Sukhanov and Narmandakh 1983
Mongolemys Sukhanov and Narmandakh 1974, 1976 (in part), Yeh, 1974 (in part), 1994 (in part), Sun et al., 1992 (in part).
Gravemys Sukhanov and Narmandakh 1983, p. 44.

Type species—*Mongolemys barsboldi* Sukhanov and Narmandakh 1974; Upper Cretaceous, Nemegt Formation; Mongolia, Southern Gobi.

Included species—Type species and *G. hutchisoni* sp. nov.

Diagnosis (emended after Sukhanov and Narmandakh, 1983)—Middle-sized turtles (up to 30 cm) with moderate shell height (no more than half of its width). Carapace is widened and truncated anteriorly. Nuchal emargination is large. Bridges are relatively long (60–72.5% of the plastron width and 45% of its length). Contribution of the hyoplastron to the bridge length is greater than that of the hypoplastron. Axillary buttress reaches about mid-width of the first costal. Inguinal buttress reaches about 2/3 width the fifth costal. Both plastral lobes are wedge-shaped (subtriangular); the anterior one is wider at its base and almost one-half the length of the posterior one. An Anal notch is present. Shell bones are thick. The first costal contacting peripherals 1–4. Connection between the costals and peripherals in the bridge area is weak. The ribs ends insert into peripherals but are exposed viscerally. Cervical scale relatively large, its length equals width and occupies a third or more of nuchal length. The width of vertebrals 2–4 is considerably less than their length. Posterior marginals high, but not onlapping costals (except costal 11). The 12th marginals just onlap the second

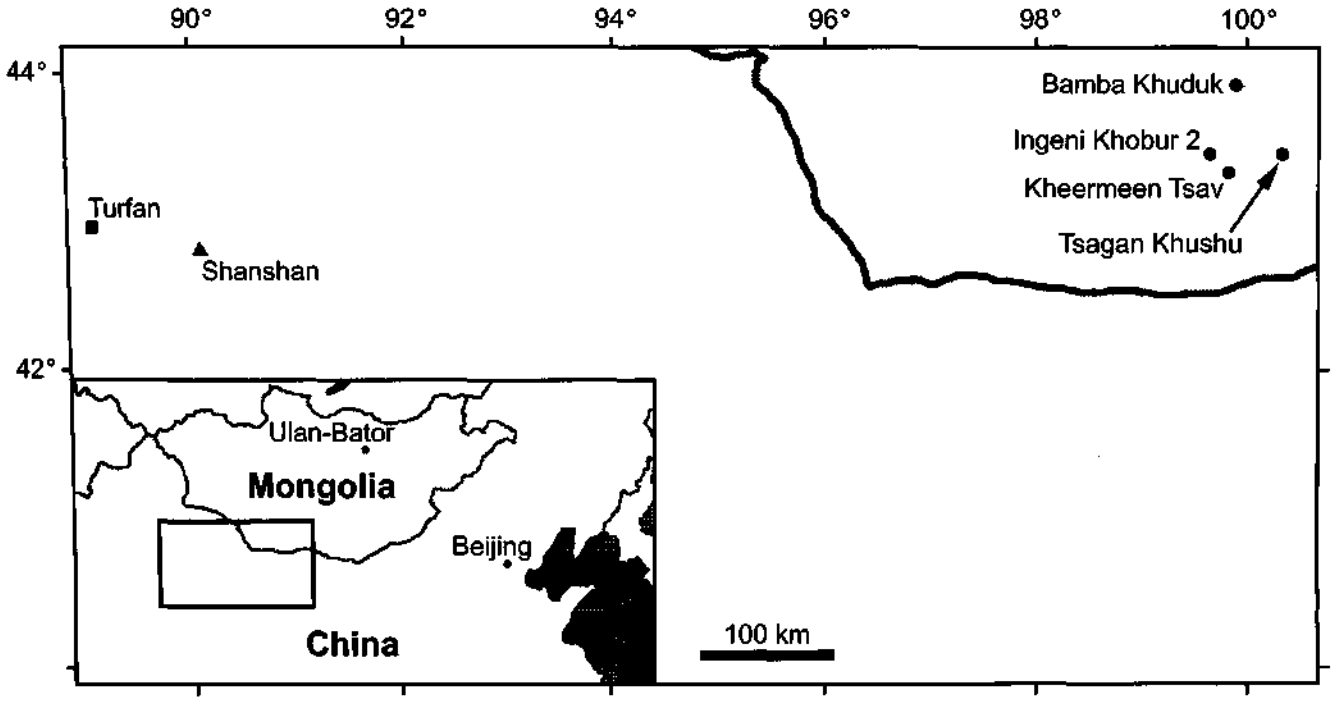

Fig. 1. Map that shows localities mentioned in the text. Circles designate findings of *Gravemys barsboldi*, square – *Gravemys hutchisoni* sp. nov, triangle – "*Mongolemys*" *trufanensis*.

suprapygal. The skin-scale sulcus is located on the internal surface of the carapace far from the free edge occupying 50–60% of the peripheral and 20% of the nuchal height. The entoplastron is large, hexagonal, and wider than long. The gular scales extensively overlap the entoplastron. There is a complete row of four inframarginals, which are shifted laterally and encroach considerably on to the peripherals. Medially they do not reach line connecting centers of axillary and inguinal notches. The shell is covered with a sculpture consisting of tubercles, gathered in rows, or ridges.

Distribution—Late Cretaceous, Central Asia.

Gravemys barsboldi (Sukhanov and Narmandakh 1974)
Figures 2–4.

Mongolemys barsboldi Sukhanov and Narmandakh 1974, p. 145, Sukhanov and Narmandakh 1976, p. 123, fig. 6.
Gravemys barsboldi Sukhanov and Narmandakh 1983, p. 47, Pls. I–VIII, figs. 1–5.

Holotype—IG (without number); almost complete shell; Mongolia, Southern Gobi, Khermeen Tsav locality; Upper Cretaceous (Maastrichtian), Nemegt Formation. Sukhanov and Narmandakh (1983) noted that the holotype was found in Khermeen Tsav in 1972 by R. Barsbold in the layers transitional from Barun Goyot to Nemegt Formations. For this reason they indicated its provenance as "(?) upper part of Barun Goyot Formation." All other specimens of this species are from the Nemegt Formation. By this reason, I think that the Barsbold specimen is probably Nemegtian in age as well.

Previously referred material—PIN 4064-1, almost complete shell (without posterior portion of the carapace back from fifth neural, left fifth costals and eighth peripherals) from the Bamba-Khuduk (Sukhanov and Narmandakh, 1983, Pls. IV–VII, VIII, figs. 1, 5).

Newly referred material—ZISP PH 1/21, fragmentary shell from the Ingeni Khobur 2 (collected by R. Barsbold, 1968); ZISP PH 1/24, fragment of plastron, including parts of right and left hyoplastra, from the Tsagan Khushu (collected by N. N. Verzilin, 1978); all from Upper Cretaceous, Nemegt Formation.

Diagnosis—Epiplastron is large (maximum length approximately equals width). Entoplastron is shifted posteriorly, close to the posterior edge of the anterior plastral lobe. Bridge length is 60–70% of of the plastron width. Anal notch is well developed. Humeral-pectoral sulcus lies posterior to a line connecting centers of axillary notches. Pectoral scale narrows medially. Inframarginals are almost rectangular.

Distribution—Upper Cretaceous, Nemegt Formation; Southern Gobi, Mongolia.

Description—ZISP PH 1/21 (Fig. 2) is represented by an incomplete carapace (the left costals, left peripherals 1–3 and 11, right peripherals 7–11, neurals 2–4, both suprapygals and pygal) and fragments of plastron. The estimated length of the carapace is about 28 cm (i.e., almost the same as in two described specimens (Sukhanov and Narmandakh 1983)). Judging from the preserved portion of the carapace, its shape is typical for the species. The neurals 2–4 are hexagonal and short sided anteriorly (as in the holotype), with lengths exceeding their width. The first suprapygal, as in

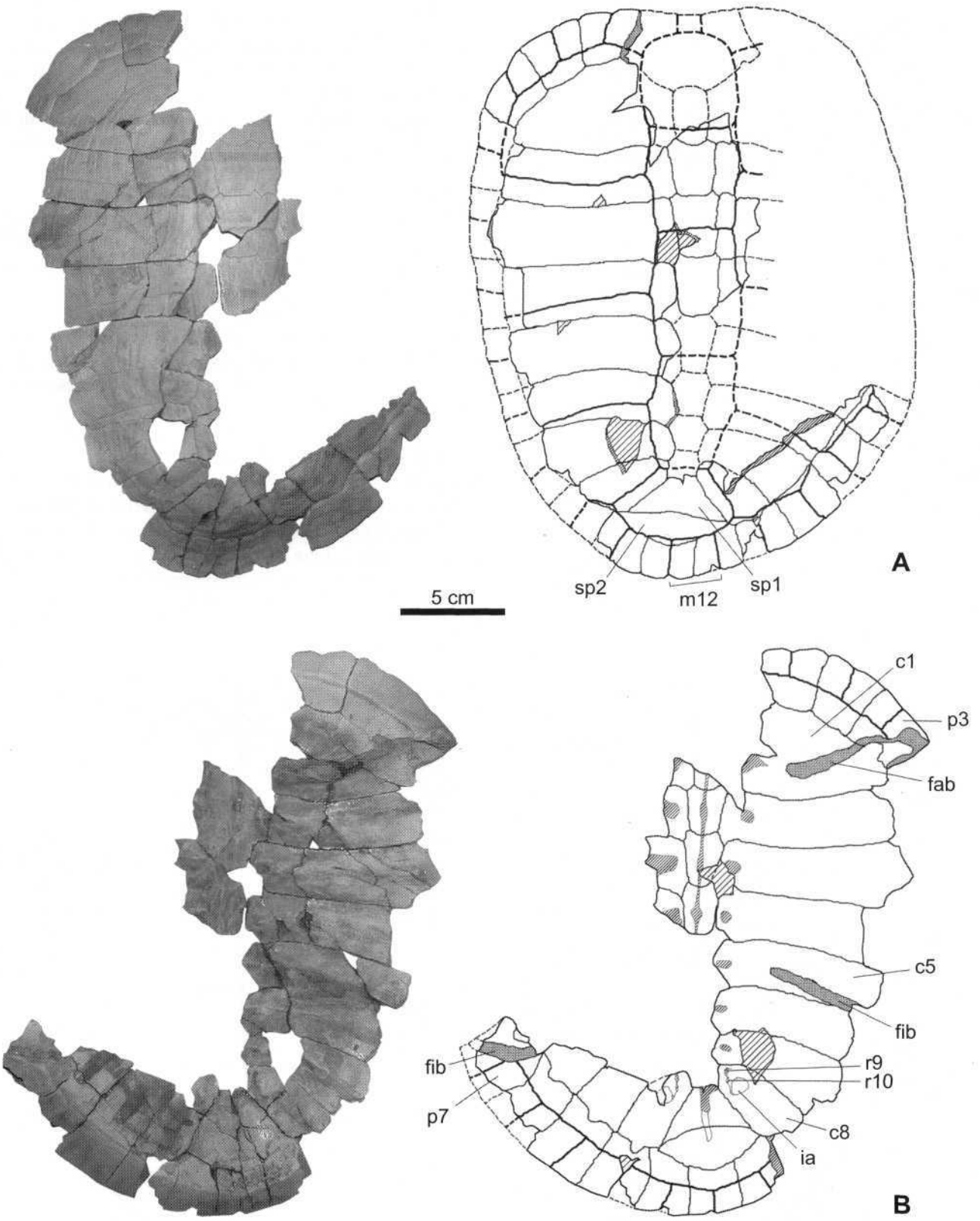

Fig. 2. Carapace of *Gravemys barsboldi*, ZISP PH 1/21. A. dorsal view; B. ventral view. Abbreviations in figures: **ab**, axillary buttress; **abd**, abdominal; **c1**, **c5**, **c8**, costals 1, 5 and 8; **fab**, attachment site for axillary buttress; **fib**, attachment site for inguinal buttress; **ia**, ilial attachment; **ib**, inguinal buttress; **im1**, **im2**, **im3**, **im4**, inframarginals 1–4; **m12**, marginal 12; **msl**, medial sulcus; **mst**, medial suture; **pd**, pelvic attachment site; **p3**, **p6**, **p7**, peripherals 3, 6 and 7; **pect**, pectoral; **r9**, **r10**, rib heads of 9 and 10 thoracic ribs; **sp1**, **sp2**, suprapygals 1 and 2.

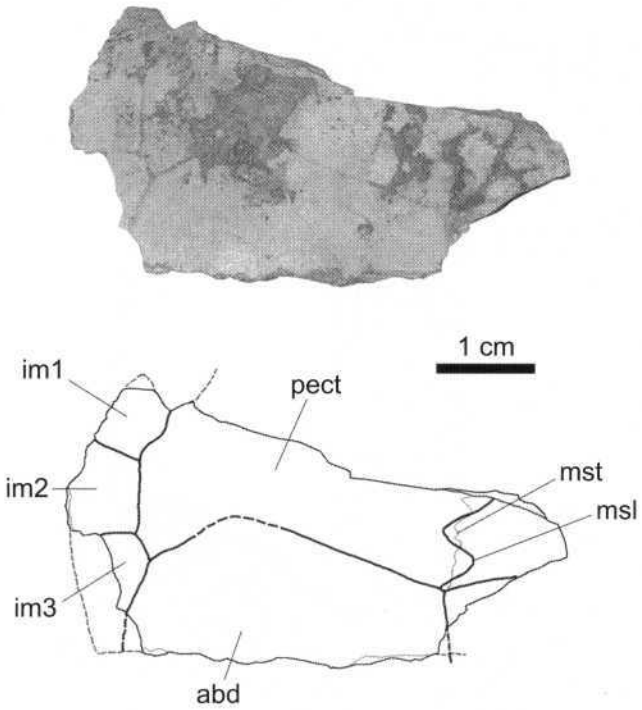

Fig. 3. Fragment of plastron of *Gravemys barsboldi*, ZISP PH 1/24. See Fig. 2 for abbreviations.

the holotype, is trapezoidal, with narrow anterior and wide concave posterior sides, but it is relatively wider than that of the holotype (length is 50% the width in the holotype, and 38% in ZISP PH 1/21). The second suprapygal is in the shape of a biconvex lens, which is longer than in the holotype (length is 26% the width in the holotype, and 44% in ZISP PH 1/21).

The pygal is rectangular and slightly concave anteriorly. The width of the pygal exceeds the length, but it is longer than in the holotype (58% in the holotype , and 68% in ZISP PH 1/21). The free edge of the pygal is slightly convex posteriorly with a distinct medial notch.

The first costal contacts peripherals 1–4, as in the holotype. The axillary buttress is developed in the same manner as in PIN 4064-1 (extends beyond the mid-width of the first costal). It enters the first costal via the third peripheral, without touching the second peripheral. The inguinal buttress extends across 2/3 of the fifth costal width, attaches along its posterior half, and contacts the sixth costal laterally. The sixth costal is thickened along the buttress attachment. Sukhanov and Narmandakh (1983) noted that in PIN 4064-1 the inguinal buttress extends only to the middle of the sixth costal, attaching along its anterior border. My study of this specimen shows that the buttress-costal relationship in PIN 4064-1 are the same as in ZISP PH 1/21.

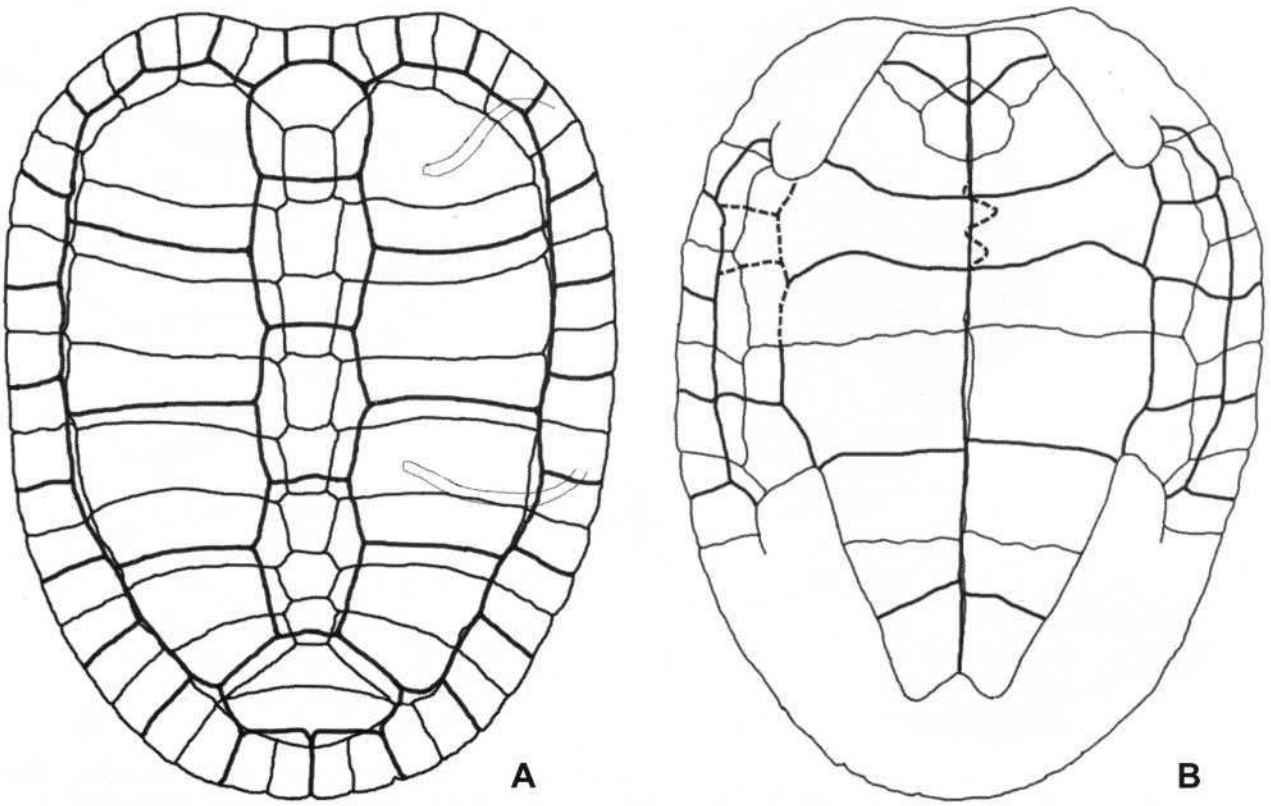

Fig. 4. Reconstruction of the shell of *Gravemys barsboldi:* **A.** dorsal view, thin line shows position of buttresses on the visceral surface of the carapace; **B.** ventral view, the dashed line shows variation in in shape and position of inframarginals and medial sulcus. After Sukhanov and Narmandakh (1983), with modifications. See Fig. 2 for abbreviations.

Among the peculiar peripheral features, it is worth mentioning the presence of a distinct notch on the free edge of peripheral 11 at the sulcus.

In the plastron of ZISP PH 1/21, as in the holotype, there is a characteristic cornice, separating the buttress from the edge of the axillary notch. The gular scales have a greater onlap the entoplastron greater (about 1/3 of length) than in the holotype.

The pleural-marginal sulcus is located in the upper third of peripherals 1-3 and coincides or nearly coincides with the costal-peripheral suture in peripherals 7-9. Peripheral 11 slightly onlaps the eighth costal and peripheral 12 onlaps the second suprapygal for 20% of its length.

As in the holotype, ZISP PH 1/21 has four pairs of inframarginals, whose shape and position almost exactly correspond to the published reconstruction of Sukhanov and Narmandakh (1983, fig. 2). The only exception is that the inframarginal 2 is relatively longer. The pectoral and inframarginal 3 are not in contact in ZISP PH 1/21, as in previously described specimens, whereas they do in ZISP PH 1/24 (Fig. 3). One more peculiarity demonstrated by the latter specimen is the strong sinuosity of the medial sulcus between pectoral scales, that was not noted in the other specimens.

The shell sculpture in ZISP PH 1/21 is the same as in the other specimens. The corrected shell morphology of *Gravemys barsboldi* is shown in the new reconstruction (Fig. 4). Measurements of the described specimens are given in Table 1.

Gravemys hutchisoni sp. nov.
Figure 5.

Mongolemys trufanensis Yeh 1974 (in part), p. 257, Pl. I, fig. 3; 1994 (in part), p. 36, fig. 18.
Mongolemys turfanensis Sun et al. 1992 (in part), p. 30, fig. 34 (lapsus calami).

Holotype and only known specimen—IVPP V4241, complete plastron with bridge peripherals; China, Xinjiang, Turfan (=Turpan), Shisanjianfang, Upper Cretaceous, Subashi Formation (Maastrichtian).

Etymology—The species is named after J. Howard Hutchison, a respected expert on fossil turtles.

Diagnosis—Epiplastron is wider than it is long. The entoplastron is shifted well anterior to the posterior margin of the anterior plastral lobe. Bridge length is 72.5% of the plastron width. Anal notch is weak. Humeral-pectoral sulcus lies anterior to the line connecting the centers of the axillary notches. Pectoral scale expanded medially. Inframarginal scales 3 and 4 are penta- or hexagonal shaped.

Description—The length of the plastron along the midline is 255 mm; maximum length is 261 mm. Its width along the hyo-hypoplastral suture is 158 mm. The gular notch (emargination) is well-developed; its depth is 4 mm. The anal notch is weak, 2 mm in depth. The anterior and posterior plastral lobes are wedge-shaped, narrowing distally. The width of the anterior lobe at its posterior edge is 117 mm, (see also Table 1). The width of the gular projection (width of the lobe in the gular-humeral sulcus) is 69 mm. Width at the hypo-xiphiplastral suture is 85.5 mm; at the femoral-anal sulcus, 60 mm. If the plastral lobes are circumscribed by trapezoids, their length/base ratios are 0.43 and 0.76 for the anterior and posterior lobes respectively (the same ratios in *Gravemys barsboldi* are 0.44 and 0.72 respectively). Ratios of the trapezoid distal width to the base are 0.51 and 0.38 for the anterior and posterior lobes respectively (the same ratios in *Gravemys barsboldi* are 0.43 and 0.37 respectively). The figures show that the anterior lobe is less wedge-shaped (less narrowed distally) in the new species, than in *Gravemys barsboldi*, whereas other proportions of lobes are almost the same in both species. The anterior lobe is shorter and less wedge-shaped, than the posterior one. The bridges are long. Their minimal length makes up 72.5% of the half of the plastral width (in *Gravemys barsboldi*, 60–70 %). Contributions of hyo- and hypoplastron in the bridge length are different: 60 mm for the hyoplastron and 56 mm for the hypoplastron. The bridge parts of the plastron make up less than 1/6 of its width.

Epiplastra are transversely elongated with a spoon-like depression on the dorsal surface. The length of the right epiplastron along the mid-line is 11.5 mm, the maximal length is 27 mm, and the width is 38 mm.

The entoplastron occupies a distal position on the anterior plastral lobe. The ventral distance from its caudal end to the line connecting the centers of the axillary notches is 16 mm. Ventrally, the length of the entoplastron is less than its width (Table 1), whereas dorsally the opposite is true (length is 40.5 mm, width is 31.5 mm). The dorsal surface of the entoplastron bears a longitudinal ridge with acromial pits on each side.

The lengths of the hyoplastra, hypoplastra, and xiphiplastra are all asymmetrical (Table 1). Maximum length of the left hyoplastron is about 108 mm. The base of the axillary buttress extends for 1/4 distance from the free edge of the plastron to the mid-line. The base of the inguinal buttress extends for 1/3 distance from the free edge of the plastron to the mid-line. There is a well developed thickening between bases of inguinal buttresses and also extending from bases of inguinal buttresses along the free edge of the posterior lobe. On the dorsal surface of the xiphiplastron there is a pair of oval-shaped (15 x 9 mm) imprints for contact with the pelvis, oriented along the thickenings of the posterior lobe.

The plastral formula is Gul<Anal<Hum<Pec<Fem<Abd. The gular scales are transversely-oriented and extensively onlap the entoplastron (about 1/4 of its length). The humeral-pectoral sulcus is perpendicular to the mid-line and anterior to the line connecting centers of axillary notches. The pectoral scales are slightly expanded towards the mid-line. The anals are considerably shorter than the femorals (Table 1). There are four pairs of inframarginals. They onlap the peripherals for about 1/3 of their width. The medial border

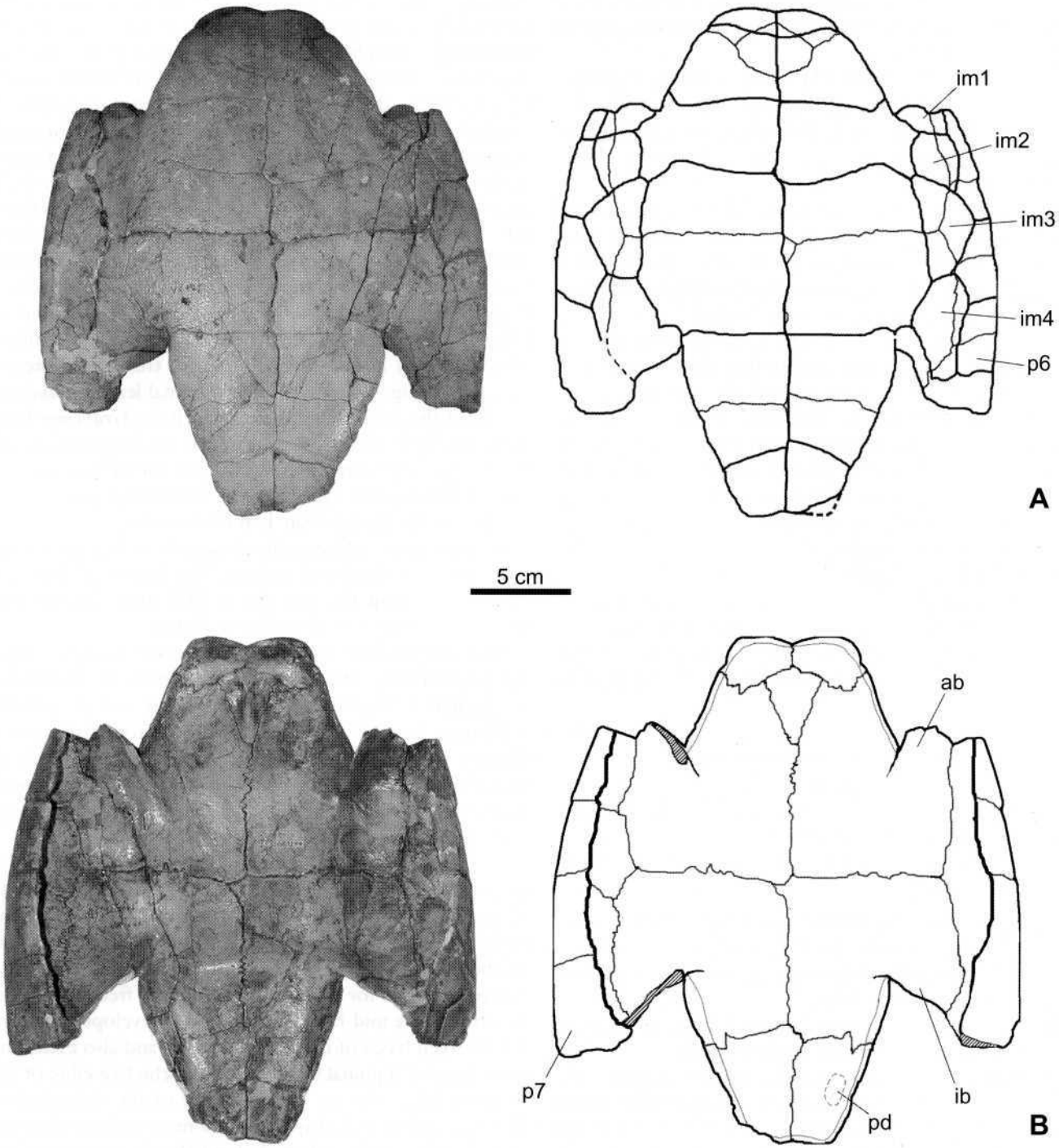

Fig. 5. Plastron of *Gravemys hutchisoni*, IVPP-V4241. **A.** ventral view; **B.** dorsal view. See Fig. 2 for abbreviations.

of the inframarginals is lateral to the line connecting centers of axillary and inguinal notches. The ratio of inframarginal length along its lateral border to width is 0.58, 0.97, 1.26, 1.41 for inframarginals 1–4 respectively (the same ratios in the holotype of *Gravemys barsboldi*: 0.77, 0.96, 1.52, 1.29). The posterior border of the second inframarginal lies on the level of the pectoral-abdominal sulcus. The third inframarginal is elongated, covers hyo-and hypoplastron equally and contacts the pectoral. Its medial border is parallel to the mid-line, and the lateral is wedged between marginals. The length of the fourth inframarginal exceeds its width.

Dorsally, the skin-scale sulcus is separated from the free edge of the anterior plastral lobe by 3 mm, on the anterior (epiplastral) corners by 5 mm, on the base of the posterior lobe for 7 mm, and in the distal parts of the posterior lobe for 3 mm.

Table. 1. Measurements (in mm) of the shells of *Gravemys barsboldi* (Sukhanov and Narmandakh, 1974) and *G. hutchisoni* sp. nov. Measurements of the holotype of *G. barsboldi* and PIN 4064-1 are taken from Sukhanov and Narmandakh (1983). Notations: "~", estimation; "?", element unmeasurable; "–", element not preserved; "d" and "s" designate right and left measurements.

	Gravemys barsboldi			*G. hutchisoni*
Parameters	**Holotype**	**PIN 4064-1**	**ZISP PH 1/21**	**IVPP-V4241**
Carapace (length/width)	~245/~200	~270/~210	~280/?	–
Nuchal (length/width)	34.0/55.0	38.5/53.0	–	–
Neurals (length/width)				
Neural 1	26.5/18.2	27.8/19.6	–	–
Neural 2	21.5/22.0	24.0/23.8	23.2/22.0	–
Neural 3	23.5/20.1	25.1/21.0	26.3/21.1	–
Neural 4	23.0/21.0	23.7/21.0	24.9/19.5	–
Neural 5	21.0/20.8	21.8/19.0	–	–
Neural 6	19.8/20.2	–	–	–
Neural 7	14.2/20.4	–	–	–
Neural 8	18.0/17.8	–	–	–
Suprapygals (length/width)				
Suprapygal 1	19.0/~38.0	–	19.5/50.8	–
Suprapygal 2	>11.0/>42.0	–	24.4/55.2	–
Pygal (length/width)	>20.0/34.6	–	18.0/26.3	–
Costals (width/length proximal/length distal)				
Costal 1	~77.0/25.0/42.0	79.0/28.0/43.0	~81.0/?/46.5	–
Costal 2	~85.0/22.0/29.0	87.0/21.0/25.2	~86.0/23.7/~26.5	
Costal 3	~89.0/24.0/26.0	~92.0/29.0/32.0	97.0/29.5/~31.5	–
Costal 4	86.0/23.0/31.5	~88.0/23.0/29.0	?	–
Costal 5	~82.0/22.5/22.0	~89.0/26.5/29.0	86.0/~28.0/?	–
Costal 6	~72.0/19.6/24.5	–	~73.0/20.1/24.5	–
Costal 7	~58.0/16.0/>24.0	–	59.3/16.6/31.3	–
Costal 8	~46.0/12.0/>27.0	–	47.2/12.0/22.7	–
Peripherals (height/length along the free edge)				
Peripheral 1	26.2/27.7	29.0/29.0	29.8/30.5	–
Peripheral 2	26.9/31.0	30.0/31.0	31.1/31.0	–
Peripheral 3	21.6/31.7	28.2/33.0	27.3/33.0	–
Peripheral 4	22.0/32.0	28.3/35.5	–	31.0/39.0
Peripheral 5	24.6/32.4	29.5/35.5	–	35.0/40.0
Peripheral 6	26.0/37.0	30.7/37.1	–	35.0/41.0
Peripheral 7	?	31.4/37.2	?	36.5/41.0
Peripheral 8	30.7/31.8	–	?	–
Peripheral 9	28.5/30.6	–	30.5/29.6	–
Peripheral 10	26.6/27.0	–	26.2/30.7	–
Peripheral 11	25.0/29.8	–	24.3/27.0	–
Cervical (length/width)	12.0/14.0	13.0/15.0	–	–
Vertebrals (length/width)				
Vertebral 1	40.0/48.0	43.0/46.0	–	–
Vertebral 2	45.0/40.0	48.0/42.0	~51.0/41.5	–
Vertebral 3	47.0/39.0	50.0/40.0	?	–
Vertebral 4	50.0/38.0	–	?	–
Vertebral 5	>40.0/>60.0	–	~44.5/60.0	–

Table. 1. (cont.) Measurements (in mm) of the shells of *Gravemys barsboldi* (Sukhanov and Narmandakh, 1974) and *G. hutchisoni* sp. nov.

	Gravemys barsboldi			*G. hutchisoni*
Parameters	**Holotype**	**PIN 4064-1**	**ZISP PH 1/21**	**IVPP-V4241**
Pleurals (width/length proximal/length distal)				
Pleural 1	>80.0/67.0	75.0/64.0	?/68.0	–
Pleural 2	?/47.0/?	87.0/51.0/68/0	?/53.0/?	–
Pleural 3	?/47.0/49/0	85.0/?/?	?/50.0/~55.0	–
Pleural 4	55.0/29.0/~51.0	–	59.0/32.0/51.0	–
Marginals (height/length along the free edge)				
Marginal 1	23.0/23.0	23.0/20.6	20.6/?	–
Marginal 2	19.0/29.0	20.0/30/0	22.0/31.0	–
Marginal 3	18.0/29.0	20.0/30.0	21.5/28.8	–
Marginal 4	20.0/33.0	21.0/31.0	21.5/?	?
Marginal 5	26.0/33.0	26.0/35.0	–	?
Marginal 6	26.0/33.0	28.0/37.0	–	?
Marginal 7	26.0/~32.0	28.0/40.0	–	?
Marginal 8	?/33.0	27.0/?	?	–
Marginal 9	28.0/31.0	–	28.0/?	–
Marginal 10	26.0/28.0	–	26.6/29.3	–
Marginal 11	25.0/28.0	–	31.8/30.5	–
Marginal 12	20.0/28.0	–	26.6/27.0	–
Plastron (length max./ along the mid-line/width)				
	?/220/150	230/221/155	?	261/255/158
Bridges (minimal length right/left)				
	94.0/~100.0	104.0/108.0	?	116.0/114.0
Anterior lobe (length/width in the humeral-pectoral sulcus)				
	49.0/100.0	50.0/103.0	?	60.0/110.0
Posterior lobe (length/width at base)				
	91.0/90.0	81.0/107.0	?	85.0/103.0
Epiplastron (medial length/ maximal width)				
	~10.0/34.0	15.5/34.0	–	9.0/37.5
Entoplastron (length/width)	~36.0/34.0	29.0/32.5	27.9/?	35.0/40.0
Hyoplastron (medial length)	57.0	58.0	?	78.0d/84.5s
Hypoplastron (medial length)	~71.0	70.0	?	82.5d/72.0s
Xiphiplastron (medial length)	?	49.0	?	52.0d/57.0s
Gulars (medial length)	~20.0	24.0	?	–
Humerals (medial length)	~40.0	31.0	?	36.5
Pectorals (medial length)	27.0	25.0	~32.0	38.0d/42.5s
Abdominals (medial length)	57.0	61.0	?	79.0d/73.0s
Femorals (medial length)	42.0	49.0	?	50.0
Anals (medial length)	40.0	32.0	?	34.5
Inframarginals (length along border with marginals/width)				
Inframarginal 1	17.0/22.0	34.0/29.0	?	15.0/26.0
Inframarginal 2	28.0/29.0	31.0/29.0	?	30.5/31.5
Inframarginal 3	29.0/19.0	34.0/26.0	?	43.0/34.0
Inframarginal 4	40.0/31.0	43.0/35.0	?	52.5/37.0

Peripherals are represented by pairs 4–7. The heights of their ventral plates are less than the heights of their dorsal ones. The contact between the peripherals and the costals is weak and rib pits are open viscerally. The free edge of the bridge peripherals is rounded in cross section. The pleural-marginal sulcus is located close to the costal-peripheral suture.

The surface of the shell is smooth, weak longitudinal ridges are visible only in the area of abdominals, and small pits can be seen along the free edges of the anterior plastral lobe.

DISCUSSION

The most significant characters that distinguish *Gravemys* from other lindholmemydid genera include the presence of four pairs of wide inframarginals that strongly onlap the peripherals, 12th marginals onlap the second suprapygal, large nuchal emargination, and contact of the first costal with four anterior peripherals (Danilov, unpublished manuscript).

The number, shape and position of inframarginals are considered here as rather stable characters appropriate for diagnosing the lindholmemydid genera. For instance, *Mongolemys* Khosatzky and Młynarski, 1971 is invariably characterized by three pairs of wide inframarginals, which do not onlap the peripherals (my personal data, based on examination of more than a hundred specimens). The presence of four pairs of wide inframarginals is apparently primitive as this character is found in the outgroups of testudinoids (trionychoids and turtles of the "macrobaenid" grade).

The new material, described above, shows that, in *Gravemys barsboldi*, the last (12th) pair of marginals onlapped the second suprapygal. Previously, this character was unknown in the lindholmemydids, that are otherwise characterized by low 12th marginals that are restricted to the pygal (Sukhanov, 2000). Among testudinoids, the high 12th marginals characterize the Geoemydidae (=Batagurinae *sensu* McDowell, 1964), with the exception of *Chinemys*, *Notochelys platynota*, *Leucocephalon yuwonoi*, *Geoemyda spengleri*, *Rhinoclemmys pulcherrima* (W. Joyce, pers. com.), the Testudinidae and *Pseudographtemys* Hutchison 1996 from the Oligocene of USA, tentatively referred to the Emydidae (Hutchison 1996). Among the Emydidae (Emydinae *sensu* McDowell, 1964), this character is also present as variation in some individuals of *Chrysemys picta* and *Deirochelys reticularia* (W. Joyce, pers. com). Tall 12th marginals is probably a primitive character for testudinoids, as it is widely distributed outside this group (trionychoids and turtles of the "macrobaenid" grade). Presence of this character state in *Gravemys*, along with four pairs of wide inframarginals, suggests a basal position of this genus within the Lindholmemydidae.

Among the other characters distinguishing *Gravemys*, the big nuchal emargination and contact of the first costal with four anterior peripherals, probably represent autapomorphies of this taxon. The first of them indicates the presence of a relatively big head, whereas the second may be correlated with the unusual anterior widening of the shell.

Gravemys hutchisoni sp. nov. is based on the paratype specimen of *Mongolemys trufanensis* Yeh 1974, which was based on two specimens. The first specimen of *M. trufanensis* (holotype) is represented by an incomplete shell from the Paleocene of Shanshan, Xinjiang; the second one (paratype) is represented by a plastron from the Late Cretaceous of Turfan, Xinjiang (Yeh 1994). The paratype specimen differs from the holotype in proportions of the plastral lobes and shape and position of the inframarginals, which prove its independent specific status. Moreover, both specimens do not belong to *Mongolemys*, because they have four pairs of inframarginals (instead of the three pairs of *Mongolemys*), longer bridges, and different proportions of plastral lobes. On the other hand, the second specimen demonstrates considerable similarity with *Gravemys* in the number and position of inframarginals, the shape of the posterior plastral lobe and its shortened entoplastron. The presence of these characters in this specimen proves its assignment to this genus. *Gravemys hutchisoni* sp. nov. differs from *G. barsboldi* by having a less wedge-shaped anterior plastral lobe, longer bridges, smaller epiplastra, a more anterior position of the entoplastron and the humeral-pectoral sulcus, a weaker anal notch, a longer pectoral scale, and a different shape for the posterior inframarginals. For comparison of the species under discussion see Fig. 6.

The systematic position of *"Mongolemys" trufanensis* is not clear. It displays some similarities with *Paragravemys erratica* Sukhanov et al., 1999 from the Late Cretaceous of Mongolia (Sukhanov et al., 1999) in the configuration of inframarginals (narrowed inframarginals 2 and 3), but differs in the proportions of the plastron. Detailed description of this species and discussion of its systematic position will be given elsewhere.

Identification of the new species of *Gravemys* in the Subashi Formation of China expands the range of this genus, which was known previously only from the Nemegt Formation of Mongolia. Both formations are considered to be Maastrichtian in age (Dong 1995, Shuvalov 2000). Maastrichtian turtle faunas from China and Mongolia are not rich and include, besides *Gravemys*, just a few genera: *Mongolemys* (Lindholmemydidae), *Haichemys* (Haichemydidae), *Mongolochelys* (Mongolochelyidae) and *Amyda* (Trionychidae) in Mongolia (Sukhanov, 2000), and *Nanhsiungchelys* (Nanhsiungchelyidae) and *Amuremys* (Lindholmemydidae) in China (Yeh 1994; Danilov et al. 2002). Thus, *Gravemys* represents a single common genus for the Maastrichtian turtle faunas of China and Mongolia.

Unlike *Mongolemys*, which dominated the Nemegtian Age of Mongolia (Khosatzky and Młynarski, 1971; Sukhanov, 2000) and represented by numerous specimens in the collections, findings of *Gravemys* are very rare. The rarity of *Gravemys* and its morphological peculiarities suggest that it inhabited some special ecological niche, different than that of *Mongolemys* (Danilov 2000). For example, *Gravemys* has a comparatively large nuchal emargination of the carapace that

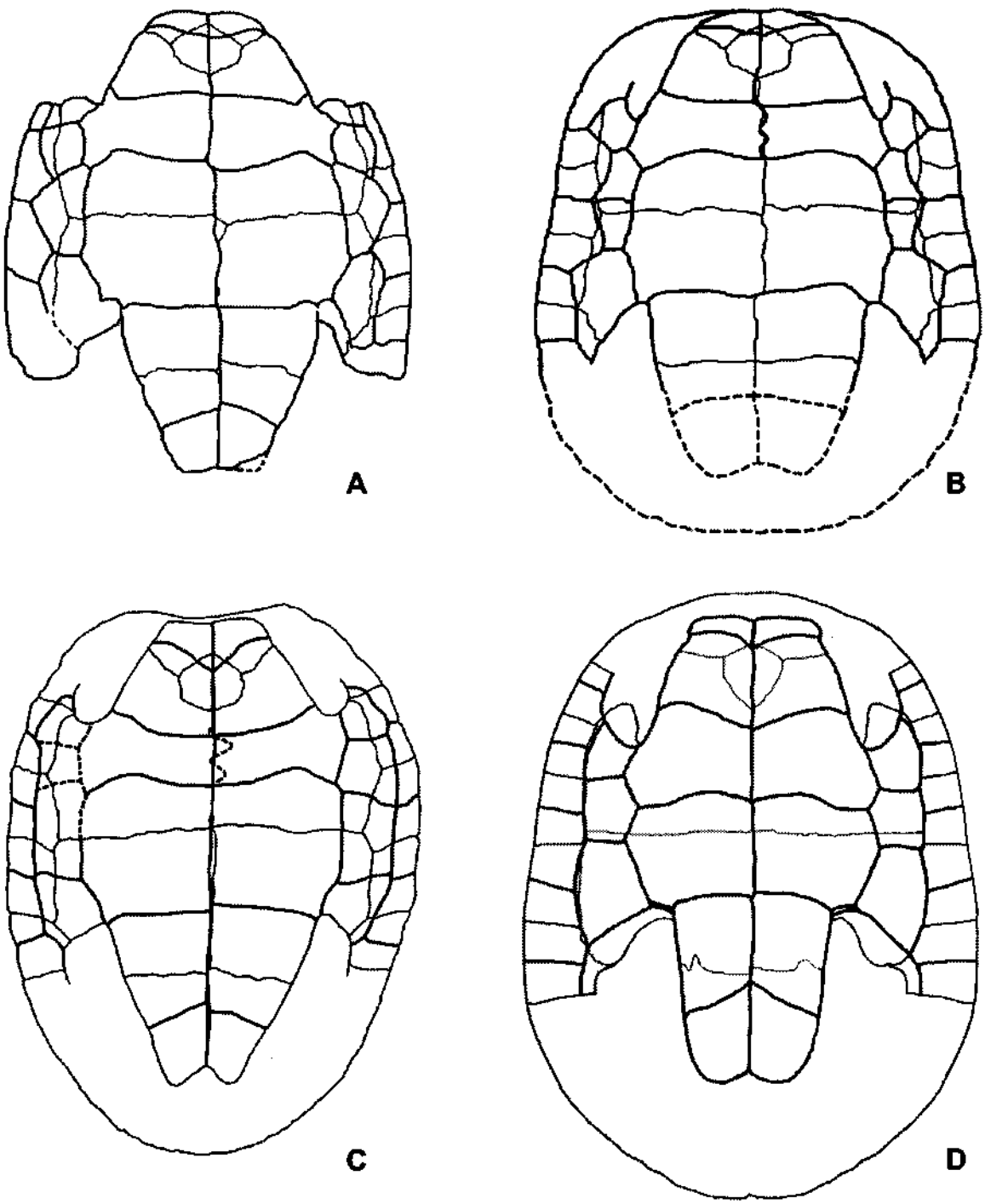

Fig. 6. Shells of some lindholmemydids in ventral view: **A.** *Gravemys hutchisoni* (IVPP-V4241); **B.** "*Mongolemys*" *trufanensis*, (reconstruction, based on IVPP-V4240); **C.** *Gravemys barsboldi* (reconstruction based on several specimens); **D.** *Mongolemys elegans* (reconstruction based on the holotype plastron and several additional specimens).

implies a large head. Also, *Gravemys* has a heavy, thick shell with relatively small openings for limbs, suggesting restricted locomotion. I hypothesize that *Gravemys* was bentophagous and spent much time on subaqueous substrates. The final conclusion about its habits must await discovery of the skull and limb bones.

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