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A NEW LINDHOLMEMYDID TURTLE (TESTUDINES: LINDHOLMEMYDIDAE) FROM THE BAYN SHIRE FORMATION (LATE CRETACEOUS) OF MONGOLIA

Vladimir B. Sukhanov,[1] Igor G. Danilov,[2] and Pagam Narmandakh[3]

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Paragravemys erratica gen. et sp. nov. is described from the lower part of the Bayn Shire Formation (late Cretaceous, Cenomanian – Turonian) of Mongolia. This new genus differs from other lindholmemydids by unique pattern of inframarginals which include two wide and two narrow scutes on each side and by a sinuous medial sulcus on the plastron. Unlike known lindholmemydids with four pairs of inframarginals (with possible exception of *Elkemys*) the third inframarginal in the new genus is restricted to the hypoplastron.

Key words: *Paragravemys erratica*, Lindholmemydidae, turtles, Cretaceous, Bayn Shire Formation, Mongolia.

INTRODUCTION

Turtles from the late Cretaceous of Mongolia are unevenly studied. Most of them are described from the Djadokhta and Nemegt Formations (Campanian – Maastrichtian), whereas turtles from the Bayn Shire Formation (Cenomanian – Santonian), especially in the lower part of the section (Cenomanian – Turonian), are much less known and represented mainly by fragmentary remains (Shuvalov and Čkhikvadze, 1975; Sukhanov, in press). In contrast, turtle assemblages of the Cenomanian – Santonian interval are well-represented in Middle Asia (Nessov, 1984, 1997).

A partial plastron of a new turtle from Shine-Us-Khuduk locality (lower part of the Bayn Shire Formation) of Eastern Mongolia, collected by one of the authors (Pagam Narmandakh), is described below. This turtle was mentioned in the list of fossil tutrles of Mongolia (Narmandakh, 1991) under the name *Gravemys erratica*. Reinvestigation of this material by the first two authors resulted in conclusion that it represents new genus and species *Paragravemys erratica* gen. et sp. nov. The assignment of this genus to the family Lindholmemydidae is based on the presence of a complete row of inframarginals (primitive character) and well developed plastral buttresses which contact the costals [advanced character of testudinoids according to Gaffney and Meylan (1988)]. Thus, lindholmemydids are considered here to be paraphyletic group for which no synapomorphy is currently recognized.

Abbreviations. IG) Collection of the Paleontology and Stratigraphy Department, Institute of Geology, Mongolian People's Republic.

SYSTEMATIC PALEONTOLOGY

Order Testudines Linnaeus, 1758
Parvorder Eucryptodira Gaffney, 1975
Suborder Polycryptodira Gaffney and Meylan, 1988
Family Lindholmemydidae Čkhikvadze, 1970
Genus *Paragravemys*, gen. nov.

Type species. *Paragravemys erratica*, sp. nov.

Etymology. Named after "para" (Greek) — "close to" and *Gravemys*.

Diagnosis. Middle-sized turtles (length of the shell about 20 cm) with well developed buttresses (the posterior buttresses extend inward from the free borders of the hinder lobe about one third the distance to the midline). The bridge is slightly elevated above

[1] Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya ul. 123, Moscow, Russia.

[2] Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1, 199034, St. Petersburg, Russia. E-mail: dig@herpet.zin.ras.spb.ru.

[3] Institute of Geology, Academy of Sciences of the Mongolian People's Republic, Ulan Baator, Mongolia.

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the plastron plane and makes little contribution to the height of the shell. Four pairs of inframarginals of which the first and the fourth are wide and the second and the third are narrow. The third inframarginal is restricted to the hypoplastron. The inframarginals occur mainly on the plastron but can partially come to peripherals. The medial sulcus of the plastron is sinuous. The entoplastron is relatively big (occupies more than 1/2 length of the anterior lobe of the plastron), crossed by gulo-humeral sulcus. The sculpture of the plastron weakly developed.

Comparison. This taxon differs from *Lindholmemys* Riabinin, 1935 from the late Cretaceous of Asia by the number and shape of inframarginals (*Lindholmemys* has three pairs of inframarginals with point contacts), by the less developed buttresses, by a larger entoplastron (in *Lindholmemys* it occupies less than 1/2 length of the anterior lobe (see Nessov and Khosatzky, 1980: Fig. 2*b*). It is similar to *Lindholmemys* in low elevation of the bridge parts of the plastron. However, some specimens of *Lindholmemys* demonstrates sinuous mid-sulcus of the plastron (our data) like the new genus.

The new genus differs from *Tsaotanemys* Bohlin, 1953 from the Cretaceous of Kansu, China, by the shape and probably by the number of inframarginals (according to reconstruction of the plastron of *Tsaotanemys* (see Bohlin, 1953: Fig. 62, Pl. VII, Fig. 11), it has four pairs of narrow inframarginals of which the third is coming to the hyoplastron), by the shape of the anterior lobe of the plastron, by a relatively bigger entoplastron, and by the more anterior position of the humero-pectoral sulcus.

The new genus differs from *Mongolemys* Khosatzky et Młynarski, 1971 from the late Cretaceous of Mongolia[4] by the number and shape of inframarginals [*Mongolemys* has three pairs of wide inframarginals instead of three to four pairs mentioned in the original description (Khosatzky and Młynarski, 1971)], by stronger buttresses, by the wider lobes of the plastron, by its bigger entoplastron, by the low elevation of the bridge parts of the plastron, by longer bridges (distance between axillary and inguinal notches), and by a sinuous mid-plastral sulcus.

[4] According to our data, *Mongolemys* includes at least two species from the late Cretaceous of Mongolia: *Mongolemys elegans* Khosatzky et Młynarski, 1971 and *Mongolemys* sp. nov. Other species usually assigned to this genus (Sukhanov, in press) probably represent different genera and are compared with the new genus separately.

The new genus differs from *Elkemys* Čkhikvadze, 1976, based on *Mongolemys australis* Yeh, 1974 from the Paleocene of Guangdong Province, China by the shape and probably by the number of inframarginals (Yeh 1974, 1994) mentioned four pairs of inframarginals, of which the third is restricted to the hypoplastron like in the new genus, however, Čkhikvadze (1987) considered *Elkemys* to have only three pairs of inframarginals), by having an entoplastron that is not not crossed by humero-pectoral sulcus, and by the shape of the anterior lobe of the plastron. Like the new genus, *Elkemys* has relatively big entoplastron.

The new genus differs from *Gravemys* Sukhanov et Narmandakh, 1983 from the late Cretaceous of Mongolia by shape and position of inframarginals lying mainly on the plastron, by the shape of the plastral lobes (*Gravemys* has wider basements of the lobes, the lobes are more narrowed distally), by the wider bridge parts of the plastron and by their lower elevation, by wider axillary and inguinal notches, by shorter bridges, by equal contribution of the hyo- and hypoplastra to the bridge length [hyoplastron makes bigger contribution to the bridge length in *Gravemys* (Sukhanov and Narmandakh, 1983)], by the shape of the entoplastron (shortened in *Gravemys*), by the orientation of buttresses, by the less strong buttresses, by the sinuous mid-plastral sulcus.

Comparison with the genus *Khodzhakulemys* Danilov, 1999 based on *Mongolemys occidentalis* Nessov, 1984 from the mid-Cretaceous of Uzbekistan (Danilov, 1999) is difficult to provide due to inadequate material. *Khodzhakulemys* has a distinct sculpture on the shell which is not observed in the new genus.

Comparison with "*Mongolemys*" *planicostatus* (Riabinin, 1930) from the late Cretaceous of Amur basin (China) is impossible to provide due to inadequate material on *"M." planicostatus*.

The new genus differs from "*Mongolemys*" *tatarinovi* Sukhanov et Narmandakh, 1976 from the late Paleocene of Mongolia by a different shape of inframarginals (the third inframarginal comes to hyoplastron in "*Mongolemys*" *tatarinovi* (Sukhanov and Narmandakh, 1976), by the low elevation of bridge parts of the plastron, by a shorter bridge, by a less wide anterior lobe of the plastron, by stronger buttresses, and by sinuous mid-plastral sulcus.

The new genus differs from "*Mongolemys*" *reshetovi* Sukhanov et Narmandakh, 1976 from the Pa-

leocene of Mongolia by a different number and shape of inframarginals.

The new genus differs from "*Mongolemys*" *trufanensis* Yeh, 1974 from the Upper Cretaceous — Paleocene deposits of Xinjiang, China, by the shape and probably by the number of inframarginals (Yeh, 1994) and by sinuous mid-sulcus.

Remarks. The number and shape of inframarginals are considered here to be good features for distinguishing genera of the Lindholmemydidae. This is proved by stable number and invariable shape of inframarginals in *Mongolemys* s. s. (three pairs of wide inframarginals occupying lateral thirds of the hyo- and hypoplastra) and in a new undescribed genus of "*Mongolemys*"-like turtle from the Paleocene of Mongolia (three pairs of narrow inframarginals, occupying lateral fourths of the hyo- and hypoplastra).

As represented only by partial plastron, *Paragravemys* does not display features which allow to determine its certain relationships with other lindholmemydids. The presence of the four pairs of inframarginals is probably primitive for Polycryptodira, as it occurs in xinijangchelyids, macrobaenids (Sukhanov, in press), and thus cannot be used to unite *Paragravemys* with any of lindholmemydids. On the other hand, *Paragravemys* demonstrates new unique inframarginal pattern which include two relatively wide and two narrow inframarginals which occupy mainly plastral part of the bridge. Morever, unlike known four-inframarginal lindholmemydids (with possible exception of *Elkemys*) it has third inframarginal restricted to the hypoplastron, whereas usually (*Gravemys*, "*Mongolemys*" *tatarinovi*) the third inframarginal is relatively longer and overlaps the hyoplastron to anterior half of its length.

Included species. The type species only.

Locality and horizon. Shine-Us-Khuduk locality in Eastern Gobi, 30 km ENE from the town of Sain-Shand, lower part (Cenomanian – Turonian) of the Bayn Shire Formation.

Paragravemys erratica sp. nov

Holotype. IG 25/114. Partial plastron with sutured fragments of III – IV peripherals. Shine-Us-Khuduk locality in Eastern Gobi, 30 km ENE from the town of Sain-Shand, lower part (Cenomanian – Turonian) of the Bayn Shire Formation.

Etymology. Named after "erraticus" (Latin) — roaming, in respect to sinuous nature of mid-plastral sulcus.

Description. A partial plastron with fragments of III – VI left peripherals (Fig. 1). Both epiplastra, the lateral parts of the right hyo- and hypoplastron, the rear parts of the xipiplastra are broken off. The length of the preserved specimen is 175 mm. The estimated length of the plastron is about 200 mm. The estimated width of the plastron at the hyo-hypoplastral suture is about 140 mm. The ventral surface appears to be almost flat. The bridge is only sligthly elevated above the plane of the plastron, thus the plastral contribution to the shell height is small. The small plastral contribution is demonstrated also by *Lindholmemys*, whereas *Gravemys* and especially *Mongolemys* have more elevated lateral parts of the plastron (Sukhanov and Narmandakh, 1983: Fig. 4). The bridge, as well as the axillary and inguinal notches, are wider than in *Gravemys*. Probably this is due to relatively narrower (than in *Gravemys*) lobes of the plastron. The distance is about 100 mm between axillary notches and 88 mm between inguinal notches. The anterior lobe is 83 mm and 60 mm wide as estimated by the width of the left hyoplastron at the humero-pectoral sulcus and epi-hyoplastral suture respectively. The width of the anterior lobe at the humero-pectoral sulcus is about 105 % of the greatest length of the hyoplastron (this ratio is 105% in *Mongolemys* and 115% in *Gravemys*). The contribution of the hyoplastron to the length of the anterior lobe is about 45% of the greatest length of the hyoplastron (these ratio is 50 and 37% in *Mongolemys* and *Gravemys*, respectively). Thus, the anterior lobe in *Paragravemys* is relatively shorter than in *Mongolemys* and longer than in *Gravemys*. The posterior lobe is 85 and 76 mm wide at the abdomino-femoral sulcus and at the hypo-xiphiplastral suture respectively. Both lobes are relatively wider distally than they are in *Gravemys*. The lateral borders of the posterior lobe are slightly convex, similar to *Lindholmemys* (lateral borders of the posterior lobe are more parallel in *Mongolemys* and stronger inclined to the mid-line in *Gravemys*). The minimum length of the bridge (distance between axillary and inguinal notches) is 83 mm, that makes about 125% of the half of the plastron width (this ratio is 100 – 110, 115, and 130% in *Mongolemys*, *Lindholmemys*, and *Gravemys*, respectively). The distance between basements of the axillary buttresses is about 70 mm and that between inguinal buttresses is about 50 mm. The base of the

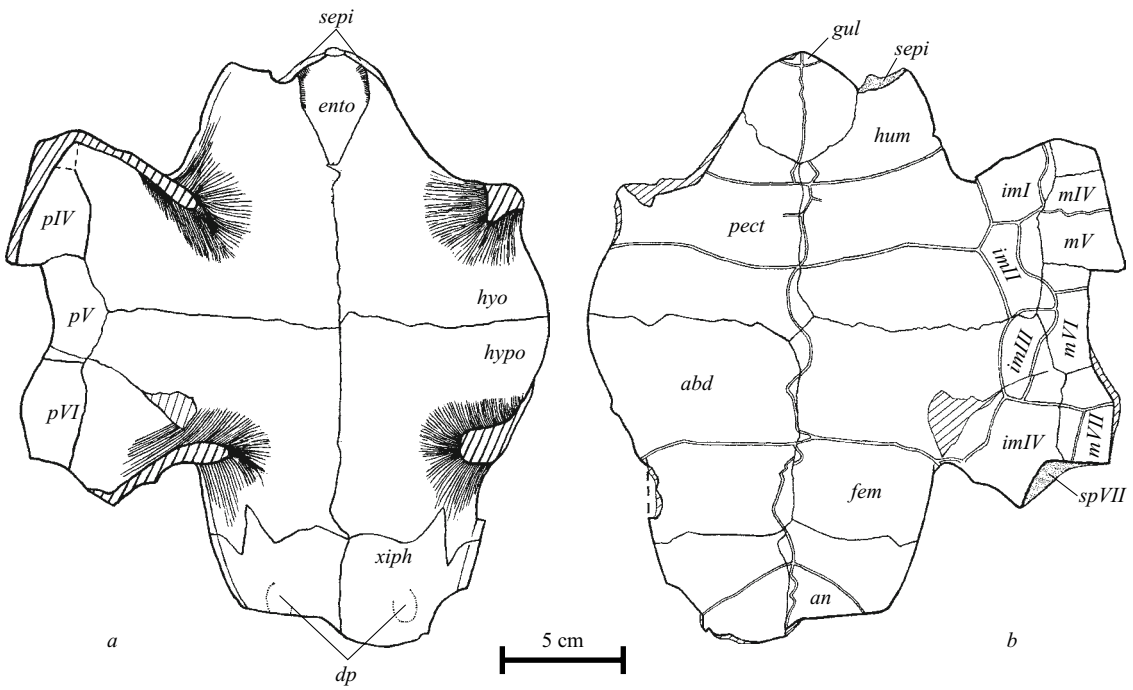

Fig. 1. The partial plastron with fragments of III – VI left peripherals of *Paragravemys erratica* gen. et sp. nov, specimen IG 25/114. *a*) Ventral view; *b*) dorsal view. Cross-hatched area represents broken parts of the plastron; dotted area represents sutures. Abbreviations: *abd*) abdominal; *an*) anal; *dp*) depressions for contact with the pelvis; *ento*) entoplastron; *fem*) femoral; *gul*) gular; *hum*) humeral; *hyo*) hyoplastron; *hypo*) hypoplastron; *imI – IV*) inframarginal I – IV; *mIV – VII*) marginal IV – VII; *pect*) pectoral; *pIV – VI*) peripherals IV – VI; *sepi*) sutures for the epiplastra; *spVII*) suture for peripheral VII; *xiph*) xiphiplastron.

anterior buttress is directed anterolaterally and form an angle of 50° with the midline (this angle in *Gravemys* is 30° due to the more anteriorly directed bases). They extend inward from the free border of the anterior lobe about one fourth the distance to the midline. The base of the posterior buttress is almost perpendicular to the midline and extends inward from the free border of the posterior lobe about one third the distance to the midline (the base of the posterior buttress extends inward from the free border of the posterior lobe more than one third the distance to the midline in *Lindholmemys* and *Gravemys* and about one fourth in *Mongolemys*). In posterior view the inguinal buttress is directed dorsolaterally, forming an angle of about 115 – 120° with the plastron plane (this angle is about 100° in *Gravemys* and *Lindholmemys* and 150° in *Mongolemys*). The same angle for the axillary buttresses can only be estimated since the buttresses are broken off very close to their bases. It is about about 130° (about 100 and 130° in *Gravemys* and *Mongolemys*, respectively, at the basement of the buttress, but distally the buttress changes its direction to more vertical). Viewed from sagittal section the axillary buttress is directed anterodorsally. The internal angle with the plastron plane is about 130°. The inguinal buttress is directed posterodorsally and forms an angle with the plane of the plastron of 120°. These angles in *Gravemys* are about 125 and 85° for the axillary and inguinal buttress, respectively. In *Gravemys* the inguinal buttress is directed anterodorsally if viewed from sagittal section. In *Mongolemys* the comparable angles are 130° for both buttresses. All these measurements show that the buttresses in the new genus directed more vertically than in *Mongolemys*, but less vertically than in *Gravemys* and *Lindholmemys*. The intermediate degree of buttress development is also demonstrated by the degree of extension of the buttresses inward from the free borders of lobes to the midline. The low elevation of the bridge parts of the plastron, comparatively long bridges, and orientation of the buttresses may have allowed for large pulmonary chambers in the new genus. The degree to which buttresses come to the costals can be estimated, but seems to be about half the length of the corresponding costals.

The entoplastron is relatively large, occupying more than half the length of the anterior lobe and its posterior border lies very close to the axillary notches. Viewed externally, the entoplastron is almost round, 33 mm long and 33 mm wide. Viewed internally it is elongated drop-shaped, 39 mm long and 21 mm wide. The posterolateral borders of the entoplastron are overlayed by the hyoplastra, that resulted in the drop-shape from internal view. There is a pair of tuberosities for the acromial processes of the scapulae on its internal surface close to the anterior border. The entoplastron is wedged between epiplastra by its anterior corner, which bears a broken process to overlay the interepiplastral suture. The thickness of the anterior border of the entoplastron is 5.5 mm.

The left hyoplastron is 45.5 mm long along the midline and the right is 53.0 mm. They are almost flat, due to the low elevation of the bridge. The anterolateral corner of the hyoplastron is slightly raised close to the suture with the epiplastron. Anteromedially the hyoplastra overlay the posterolateral borders of the entoplastron. The anterior border, which contacts with the epiplastron, is directed almost perpendicular to the midline. Viewed dorsally it bears a scar from the overlaying posterior process of the epiplastron. The thickness of the hyoplastra between anterior buttresses is 10.2 mm, but there is no distinct transverse thickening.

The left hypoplastron is 62.5 mm long and the right is 60.0 mm along the midline. Unlike *Gravemys*, the hyoplastra and hypoplastra have equal contribution to the bridge length. There is transverse thickening between inguinal buttresses (thickness of the bulge is 11.2 mm). There is a thickening along the free border of the hypoplastron posterior to the basement of the inguinal butress (thickness of this bulge in the hypo-xiphiplastral suture is 8.7 mm). The free border of the hypoplastron is rounded in cross-section, its thickness is 4.6 mm. The hypo-xiphiplastral suture almost perpendicular to the midline with Z-shaped curvature close to the free border, which is more developed internally.

The xiphiplastra are incomplete posteriorly. Centered on their dorsal surface there is a pair of oval-shaped depressions (12 × 7 mm) for contact with the pelvis. Such depressions lie closer to the free border of the xiphiplastra in *Mongolemys*.

Only parts of the III – IV peripherals are present on the left side of the specimen. The III – V peripherals contact hyoplastron and the V – VI contact hypoplastron. There is a suture for contact with the VII peripheral on the left hypoplastron.

The gular scutes barely come to the entoplastron (less than in *Gravemys*). The preserved part of the gulo-humeral sulci indicates that they were directed more perpendicular to the midline, like in *Lindholmemys*. The humero-pectoral sulci slightly curved posteriorly, lie closer to the axillary notches than in *Mongolemys*, but not as far back as in *Gravemys*. The pectorals are slightly shorter medially than laterally. The abdominals are almost square-shaped, slightly broadened lateraly on the contact with inframarginals (II – IV). The abdomino-femoral sulcus is almost straight, it forms anterior border of the posterior lobe. The femoro-anal sulci directed postero-lateraly with strong inclination posteriorly.

There are four inframarginals visible on the left side of the plastron. They occupy the lateral portions of the hyo- and hypoplastra, occupying 25% of their width. They partially overlap peripherals. *Gravemys* also has four pairs of inframarginals but they overlap the peripherals for the half of their width. Four pairs of inframarginals which do not overlap the peripherals are known also in "*Mongolemys*" *tatarinovi*, but like *Gravemys* and unlike *Paragravemys*, the third inframarginal in this genus comes to the hyoplastron and not restricted to hypoplastron. The shape of the inframarginals in *Paragravemys* is also different from other lindholmemydids.

The first iframarginal is almost square-shaped, relatively short, occupies the anterior third of the bridge part of the hyoplastron and does not overlap the peripherals. It contacts the pectoral medially, inframarginal II and marginal V posteriorly, marginal IV laterally. The second inframarginal is narrow, elongated, broadened posteriorly, occupies more than half the length of the bridge part of the hyoplastron and overlaps peripheral V by its posterolateral corner. It contacts the pectoral and abdominal medially, inframarginal I anteriorly, inframarginal III posteriorly and marginals, and V and VI laterally. The third inframarginal is similar in shape to the second but broadened anteriorly, overlapping peripheral V. It occupies anterior half of the bridge length of the hypoplastron and does not come to hyoplastron. It contacts inframarginal II anteriorly, abdominals medially, inframarginal III posteriorly, marginal VI laterally. The quadrangular fourth inframarginal is the biggest, and occupies the posterolateral part of the bridge and overlaps peripherals VI and VII. It contacts abdomi-

TABLE 1. Measurements (in mm) of IG 25/114, *Paragravemys erratica* gen. et sp. nov.

Plastron (length/width)	?/140*
Plastral bridges (minimal length)	83
Anterior lobe (width at the humero-pectoral sulcus)	83*
Anterior lobe (width at the epi-hyoplastral suture)	60*
Posterior lobe (width at the abdomino-femoral sulcus)	85
Posterior lobe (width at the hypo-xiphiplastral suture)	76
Entoplastron (length/width) externally	33/33
Entoplastron (length/width) internally	39/21
Hyoplastron (medial length; left/right)	45.5/53.0
Hypoplastron (medial length; left/right)	62.5/60.0
Humerals (medial length)	34.5
Pectorals (medial length)	24.5
Abdominals (medial length)	50
Femorals (medial length)	40.5
Inframarginals (medial length/maximal width):	
I	12.5/22.0
II	28/16
III	23/15
IV	21.5/31.0

* Estimation.

nal medially, inframarginal III and marginal VI anteriorly and marginal VII laterally.

The medial sulcus of the plastron is sinuous posterior to the entoplastron. There are short additional sulci branching from the mid-sulcus in the humerals and pectorals.

Sculpture of the plastron is weakly developed, it is represented with weak longitudinal ridges in the abdominals and by tubercles in the pectoral and humeral.

Measurements of the plastron are given in Table 1.

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