



New data on lindholmemydid turtle *Lindholmemys* from the Late Cretaceous of Mongolia

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Reinvestigation of a fragmentary lindholmemydid turtle from a Mongolian locality Sheeregeen Gashoon (late Turonian–Santonian) suggested reassignment to *Lindholmemys martinsoni* Čkhikvadze, 1975. This restricts the stratigraphic range of the genus *Mongolemys*, to which the specimen was originally assigned. Additionally, new morphological data on *L. martinsoni* have been gathered and are presented in this paper. The Lindholmemydidae are considered here as a paraphyletic group uniting primitive testudinoids (all of which are known from Cretaceous to Paleocene of Asia). Their shell morphology is characterized by well developed plastral buttresses, which contact costal bones (synapomorphy of testudinoids, see Gaffney & Meylan 1988) and by complete (uninterrupted) row of inframarginal scutes (primitive character).

Lindholmemys martinsoni is based on the incomplete shell and shell fragments from the Sheeregeen Gashoon locality in Trans-Altai Gobi, Mongolia which can be correlated with the upper part of the Bayn Shire Formation (late Turonian–Santonian) of Eastern Gobi Desert (Shuvalov & Čkhikvadze 1975). A more complete specimen of this species is known from the Usheen Khuduk locality in Eastern Gobi (Shuvalov & Čkhikvadze 1979). However, some important characters of *L. martinsoni* (pygal morphology, the shape and number of the suprapygals) have remained unknown.

A nearly complete carapace and a broken plastron of one individual from the Sheeregeen Gashoon locality, ZPAL MgCh/71 was described as *Mongolemys* sp. (Młynarski & Narmandach 1972). This description was incomplete and incorrect in some respects. According to Młynarski & Narmandach (1972) the Sheeregeen Gashoon *Mongolemys* sp. differs from the geologically younger *Mongolemys elegans* Khosatzky & Młynarski, 1971 from the Nemegt Formation (Maastrichtian) of Mongolia only by the dermal sculpturing. However, some other distinctive characters of ZPAL MgCh/71 are visible on the published figure (Młynarski & Narmandach 1972: fig. 2) and were even mentioned in the description (the presence of nuchal emargination, wide neurals and narrow central scutes).

Additional preparation of the ZPAL MgCh/71 reveals other important features such as the plastral buttresses strongly developed and the first thoracic rib considerably shortened. Altogether, these characters allow us to refer this specimen to *Lindholmemys martinsoni* Čkhikvadze, 1975. The new specimen gives information on nuchal and pygal morphology and the number and shape of suprapygals in *L. martinsoni*.

Institutional abbreviations. — IP, Institute of Paleobiology, Georgian Academy of Sciences, Tbilisi; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

Lindholmemydidae Čkhikvadze, 1975

Lindholmemys Riabinin, 1935

Lindholmemys martinsoni Čkhikvadze, 1975

Figs. 1–4.

Mongolemys sp.; Młynarski & Narmandach 1972: pp. 97–98, fig. 2.

Lindholmemys martinsoni Čkhikvadze, 1975; Shuvalov & Čkhikvadze 1975: pp. 226–227, figs. 4–6; Shuvalov & Čkhikvadze 1979: pp. 73–74, pl. I: 2, pls. III, IV.

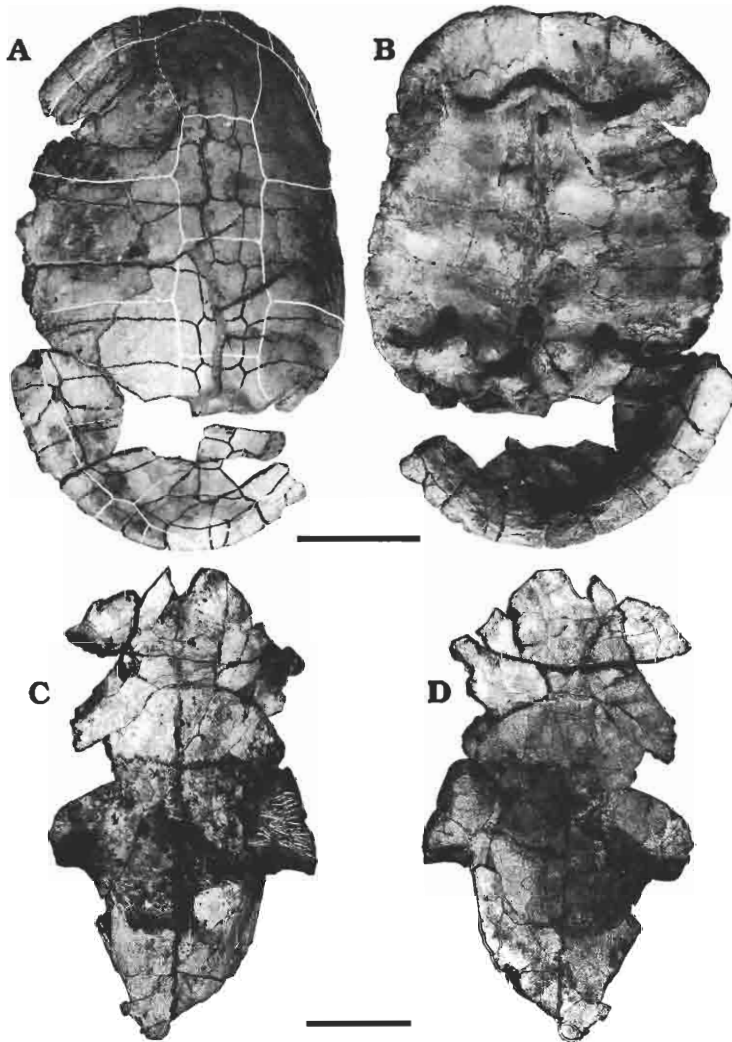


Fig. 1. *Lindholmemys martinsoni* Čkhikvadze, 1975, ZPal MgCh/71, carapace in dorsal (A) and ventral (B) views. Arrows show distal ends of buttresses. Plastron in dorsal (C) and ventral (D) views. Scale bars 5 cm.

Holotype: IP Mg-6-17, central part of the carapace and fragmentary plastron; Sheeregeen Gashoon, Trans-Altai Gobi, Mongolia; 'Sheeregeen Gashoon beds', equivalent to the upper part of the Bayn Shire Formation, late Turonian–Santonian (Shuvalov & Čkhikvadze 1975).

Referred specimens: ZPAL MgCh/71, a fragmentary carapace and plastron from the same locality as the holotype; IP 11-11-1, a fragmentary shell; Usheen Khuduk locality, Eastern Gobi, Mongolia, the upper part of the Bayn Shire Formation, late Turonian–Santonian.

Description. — ZPAL MgCh/71 consists of a fragmentary carapace (Fig. 1A, B) without left peripherals IV–VI and right peripherals IV–IX and of a plastron (Fig. 1C, D) lacking epiplastra, entoplastron and lateral parts. The length of the shell is 193 mm. The estimated length of IP Mg-6-17 is 200–250 mm (Shuvalov & Čkhikvadze 1975), and the length of IP 11-11-1 is 220–230 mm. The carapace of ZPAL MgCh/71 is elongated, oval-shaped, wider, unserrated posteriorly, and with a small nuchal emargination anteriorly. It is more domed than in *Mongolemys* and less domed than in

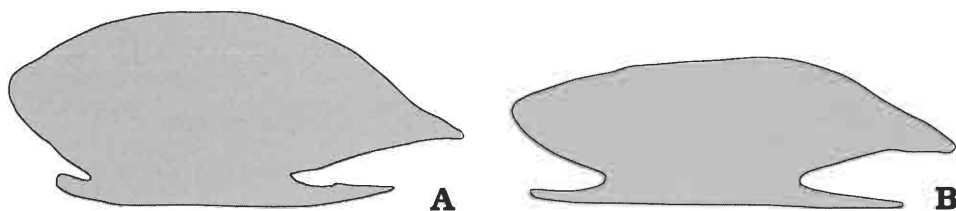


Fig. 2. **A.** *Lindholmemyx elegans* Riabinin, 1935, lateral outline of the shell, after Riabinin (1935). **B.** *Lindholmemyx martinsoni* Čkhikvadze, 1975, ZPal MgCh/71, lateral outline of the shell.

Lindholmemyx elegans Riabinin, 1935 (Fig. 2) from the Late Cretaceous of Kizylkum Desert (Riabinin 1935), which is a type species of the genus. The shell bones are thick, especially in the plastron. The sculpture of the shell is not clear because of surface damage. In IP 11-11-1 there are slight ridges and tubercles within the pleurals, neurals, and abdominals and growth lines are present on the neurals. The plates of the carapace are strongly sutured. There are no costal-peripheral fontanelles even in the posterior part of the carapace, whereas the bigger (225 mm) shell of *L. elegans* has well developed costal-peripheral fontanelles (Riabinin 1935).

The nuchal is relatively wide with its anterolateral border almost equal to the posterolateral one. The small nuchal emargination is restricted to the nuchal. The small nuchal emargination was mentioned in IP 11-11-1 and also present in *L. elegans*, but absent in *Mongolemys*. The neural I is elongated oval-shaped. The following neurals (II–VIII) are hexagonal short-sided anteriorly. Among them the neural VI represented only by its anterior part and the VII by its posterior part. The ratios of the neural lengths to their widths are 1.71 (I), 1.33 (II), 1.47 (III), 1.38 (IV), 1.13 (V). In IP 11-11-1 these ratios are 1.62 (I), 1.28 (II), 1.38 (III), 1.35 (IV), 1.21 (V), 0.97 (VI), 0.71 (VII). There are two suprapygals. The first suprapygal is trapezoid-shaped, widened and concaved posteriorly. The posterior width of the plate exceeds its length. The second suprapygal is wide, lens-shaped, with convex anterior and posterior borders. It contacts the pygal, peripheral XI, and has point contacts with the peripheral X. The pygal is trapezoid-shape with its anterior border wider than the posterior one, its length is 41% of its width. In *L. elegans* the pygal is more narrow, its length is 66% of its width. The central V overlays the pygal to more extent than in *L. elegans*, thus the posterior border of the central V is closer to the free border of the carapace. A notch in the posterior border of the pygal is absent, whereas a little notch is present in *L. elegans*.

The costal I contacts peripherals I–III. The estimated length of the anterolateral border of the costal I is 43 mm, the contacts with peripherals I–III are 12, 18, and 16 mm respectively. The maximum width of the costal I is in the medial third of its length. The axillary buttress reaches lateral two thirds of the length of the costal I. The first thoracic rib is strongly shortened, shorter than in *Mongolemys*, its distal end reaches about medial one fourth of the costal I length. The contact of the first thoracic rib with the costal I is triangle-shaped, widened medially and tapering laterally. The first thoracic rib is continued into the strong costal ridge. The thickness of the costal I is sharply decreased anteriorly from this ridge and more gradually posteriorly to it. The costal II has almost parallel anterior and posterior borders which are slightly curved (the anterior border is concave and the posterior is convex). In contrast, the costal III has concave anterior and posterior borders. The remaining costals (IV–VIII) are convex anteriorly and concave posteriorly. All the costals are wider distally than proximally. The inguinal buttress contacts mainly the posterior part of the costal V, along its suture with the costal VI. The costal VI is thickened at the suture with the costal V. The inguinal buttress occupies the lateral two thirds of the length of the costal V. The costal VIII bears an elongated thickening for the contact with the ilium.

The peripherals I and II are not high, their length along the free border is exceeding their height. The peripheral I is considerably narrowed medially, its medial length is about 50% of its lateral length. The free border of the anterior peripherals is rounded, not raised as in *Mongolemys*, and in the peripheral I it is wedge-shaped in the cross-section. The lengths of peripherals VIII and IX are almost equal to their heights, i.e. the posterior peripherals are relatively higher than the anterior ones. The anterior border in peripherals IX–XI is higher than the posterior one. Peripherals X and XI are relatively lower than peripheral IX.

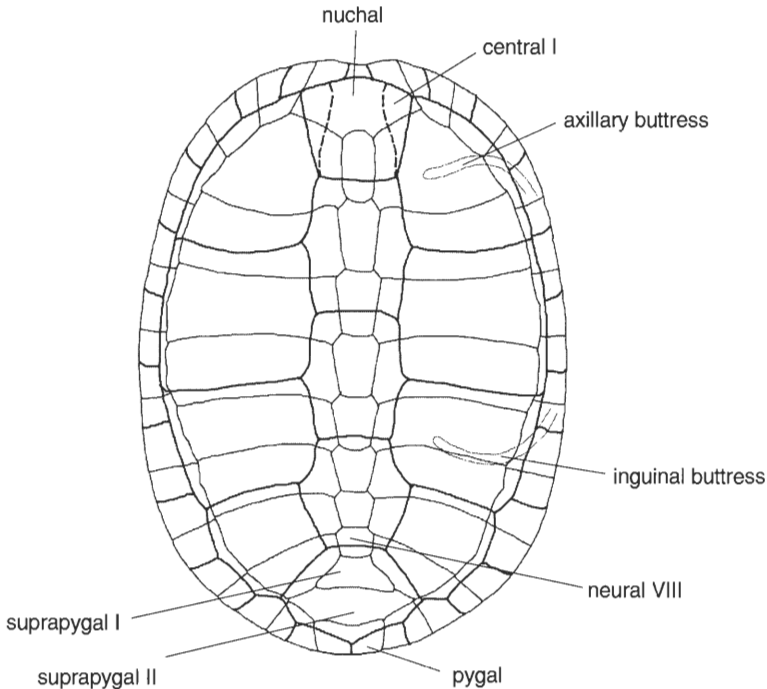


Fig. 3. *Lindholmemys martinsoni* Čkhikvadze, 1975, carapace in dorsal view. Reconstruction from several specimens. Variations in the shape of central I is shown by dashed line.

The shape of the precentral can not be certainly determined because of the bone surface damage. However, there is no reason to regard this scute absent, as was assumed by Mlynarski and Narmandach (1972). It was probably trapezoid, like in IP 11-11-1. The central I is wider anteriorly than posteriorly, its lateral borders are convex. The maximum width of the scute anteriorly (about 37 mm) is slightly more than its length (35 mm). It is narrow, restricted to nuchal and does not contact the marginals II. In IP 11-11-1 the central I is narrower, its lateral borders concave anteriorly and convex posteriorly. In IP Mg-6-17 the central I is widened anteriorly. The centrals II and III are narrow, their greatest width is 81 and 87% of their lengths respectively. The anterior width of these scutes is 58 and 67% of their length respectively. In IP 11-11-1 the corresponding centrals relatively narrower: the greatest width of the centrals II and III is 74 and 70% and their anterior width is 53 and 42% of their length respectively. As estimated from the figure (Shuvalov & Čkhikvadze 1975: fig. 5), the maximum and anterior width of the central III in IP Mg-6-17 is 82 and 52% of its length respectively, closer to ZPAL MgCh/71. The mentioned differences in the relative width of the centrals seems to be age correlated, the larger specimen having narrower centrals. In the holotype of *L. elegans*, which probably represents a young specimen (Nessov & Khosatzky 1980), the centrals are relatively much wider. The maximum width of centrals I–III in *L. elegans* is 136, 100, and 88% of the length of corresponding centrals, respectively. The anterior width of the first and second centrals is 69 and 68% of the length of corresponding centrals, respectively. The central V is relatively wider than the anterior ones. Its lateral corners overlay the peripherals X, and its posterior corner comes close to the posterior border of the carapace.

The anterior marginals overlay lateral two thirds of the corresponding peripherals. The height of the anterior marginals is about 50% of their length. The height of the marginals IV–VII is unknown in ZPAL MgCh/71. In IP 11-11-1, the pleural-marginal sulcus lies on peripherals IV–VII very close to the costal-peripheral suture. The posterior marginals (VIII and IX) come closer to the costal-peripheral suture than the anterior ones. The marginals XI reach costal-peripheral suture. The marginals XII are low and become lower towards the mid-line.

Table. 1. Measurements (in mm) of the shell of *Lindholmemys martinsoni*; '~', estimation; '?', element is impossible to measure; '-', element is absent from the material.

Parameters	ZPAL MgCh/71	IP 11-11-10
Carapace (length/width)	193/?	~230/?
Nuchal (length/width)	25.0/44.0	31.8/47.5
Neurals	(length/width)	
I	24.0/14.0	26.7/16.5
II	20.5/15.4	21.8/17.0
III	~22.0/15.0	25.0/18.0
IV	~18.0/~13.0	22.0/16.3
V	17.0/~15.0	21.8/18
VI	?/~15.0	15.8/16.3
VII	?	12.5/17.5
VIII	?	-
Suprapygal I (length/width)	11.0/27.5	-
Suprapygal II (length/width)	14.5/43.4	-
Pygal (length/width)	10.0/24.3	-
Costals	(length/proximal width/distal width)	
I	~51.0/?/?	?
II	~62.0/21.0/22.5	77.0/22.0/27.5
III	68.0/22.0/26.0	83.0/26.7/31.2
IV	66.5/18.0/24.0	85.5/20.0/30.0
V	55.0/17.0/19.0	?/22.0/18.4
VI	?	?/16.8/22.0
VIII	?/?/17.0	-
Peripherals	(length/height)	
I	~22.0/17.0	24.0/23.8
II	22.0/18.0	29.2/23.4
III	-	29.5/21.2
IV	-	29.5/21.2
V	-	31.0/20.5
VI	-	29.7/23.0
VII	-	28.0/23.8
VIII	~21.0/~22.0	-
IX	~22.0/~20.0	-
X	20.5/16.0	-
XI	17.5/15.0	-
Precentral (length/height)	?	?/11.4
Centrals	(length/maximum width/anterior width)	
I	?	39.7/28.0/?
II	43.0/35.0/25.0	43.4/32.3/23.2
III	~39.0/~34.0/~26.0	48.0/33.5/20.2
IV	?/?/~26.0	?/38.0/27.6
V	?/46.0/?	-
Pleurals	(proximal length/distal length)	
I	~50.0/?	-
II	~41.0/?	-
Marginals	(length/height)	
I	?/12.0	-
II	?/12.0	-
III	?/12.0	-
Posterior lobe of the plastron (length/width)	~54.0/58.0	-
Entoplastron (length/width)	-	26.5/27.5
Hypoplastron (medial length)	51.0	?
Hypoplastron (medial length)	52.0	?
Xiphiplastron (medial length)	~34.0	?
Humerals (medial length)	?	35.0
Pectorals (medial length)	?	12.5
Abdominals (medial length)	?	59.0
Femorals (medial length)	31.0	35.0
Anal (medial length)	27.0	?

The plastron is concave along the mid-line. The bridges are broken off, their length can be estimated as about 70–72 mm. The axillary buttress contacts the anterior half of the peripheral III, barely touches the peripheral II and comes to the internal surface of the costal I, reaching lateral two thirds of its length. The inguinal buttress contacts the peripheral VII, comes to the costal V close to the suture with the costal VI and reaches about lateral two third of its length.

Anteriorly in the plastron, the contact area between the hyoplastra and the entoplastron is preserved, though the entoplastron is lacking. The distance between the notch for the entoplastron and level of the axillary notches is about 15 mm. The width of the posterior lobe of the plastron is 58 mm, its length is about 54 mm. The posterior lobe has slight waist at the base (marked by abdominal-femoral sulcus). Thus, the inguinal notches are directed anteromedially. The bases of the inguinal buttresses extend inward from the free border about one third the distance to the mid-line. The hyoplastron and hypoplastron are equal in mid-line length. The thickness of the hyoplastron and hypoplastron in the midline between the buttresses is 8 mm. The thickness of the plastron on the hypoplastron-xiphiplastron suture is 6 mm. The xiphiplastra bear oval depressions centered on their dorsal surface for contact with the pelvis. Similar depressions present also in *L. elegans*. The femoral-anal sulcus is directed posterolaterally from the mid-line. The position of other sulci cannot be determined in ZPAL MgCh/71. In IP 11-11-1 the pectoral-abdominal sulcus is strongly curved, and like in IP Mg-6-17, the abdominal-femoral sulcus restricts the posterior lobe anteriorly; it is almost straight, slightly curved in its lateral part.

Discussion. — Reinvestigation of ZPAL MgCh/71 showed that its previous assignment to *Mongolemys* cannot be supported. ZPAL MgCh/71 differs from *Mongolemys* by the strongly developed buttresses, considerably shortened first thoracic rib, narrower first central scute, presence of nuchal emargination. These characters suggested reassignment of ZPAL MgCh/71 to *Lindholmemyx*.

According to Čkhikvadze (Shuvalov & Čkhikvadze 1975), *L. martinsoni* differs from *L. elegans* by lacking the costal-peripheral fontanelles, having the pectoral-abdominal sulcus more curved, anal notch developed more strongly, and central scutes more elongated. The presence of two of these characters (absence of the costal-peripheral fontanelles and relatively elongated centrals) can be seen in ZPAL MgCh/71 and thus it is referred to *L. martinsoni*. The shape of the anal notch and plastral sulci are impossible to establish in ZPAL MgCh/71. However, reinvestigation of the *L. elegans* holotype and additional materials does not confirm differences between *L. elegans* and *L. martinsoni* in the shape of anal notch and plastral sulci pattern.

Sukhanov & Narmandakh (1983) mentioned presence of the nuchal emargination in *L. martinsoni*, as a character distinctive from *L. elegans*. However, *L. elegans* also has a nuchal emargination, which can be seen on the holotype and new materials. A weak nuchal emargination is visible also in *L. gravis* (Nessov & Khosatzky, 1980: fig. 2b). The pygal is considerably wider in *L. martinsoni* than in *L. elegans*. Thus, its shape could be a specific character of *L. martinsoni*. This character is unknown in *L. gravis*. Riabinin (1935) considered *L. elegans* as having probably one suprapygal. The reexamination of the type and new materials indicates presence of two suprapygals in *L. elegans* species as well as in *L. martinsoni*. According to Nessov & Khosatzky (1980), *L. martinsoni* differs from *L. gravis* by the absence of growth lines in the carapace and by wider central I. Growth lines are absent in ZPAL MgCh/71, but they are present in IP 11-11-1. The central I in ZPAL MgCh/71 (and probably also in IP Mg-6-17) is wider anteriorly, but it is narrowed anteriorly in IP 11-11-1. Thus, the shape of the central I is variable in *L. martinsoni*. The same can be seen also in *L. elegans*.

In summary, *L. martinsoni* differs from *L. elegans* by the absence of costal-peripheral fontanelles, wider pygal, less domed carapace (Fig. 2) and more elongated centrals. Differences between *L. martinsoni* and *L. gravis* are unclear. New reconstruction of the carapace of *L. martinsoni* is given in the Fig. 3. The temporal distribution of the genus *Mongolemys* was considered to be Cenomanian–Late Paleocene (Nessov & Krassovskaya 1984; Sukhanov & Narmandakh 1976). Sukhanov and Narmandakh (1974) mentioned *Mongolemys* sp. from the Early Cretaceous of Mongolia, but this material has not been published. Recently the oldest described species of *Mongolemys*, *M. occidentalis* Nessov, 1984 from the early Cenomanian of Uzbekistan, was referred to a separate genus *Khodzha-kulemys* (Danilov 1999), which is not closely related to *Mongolemys*. Reinterpretation of *Mongole-*

mys sp. from the Shereegeen Gashoon locality (late Turonian–Santonian) as *L. martinsoni*, further restricts the lower limit of *Mongolemys* temporal distribution.

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