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A NEW GENUS OF LINDHOLMEMYDID TURTLE (TESTUDINES: TESTUDINOIDEA) FROM THE LATE CRETACEOUS OF THE AMUR RIVER REGION, RUSSIA

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New material of *Mongolemys planicostatus* (Riabinin, 1930), known formerly by a single first costal plate from the Upper Cretaceous of the Amur River Region, allow us to recognize it as a separate genus of lindholmemydids, *Amuremys* gen. nov. *Amuremys* is probably closely related to *Mongolemys* and *Lindholmemys*.

Key words: *Amuremys*, Lindholmemydidae, turtles, Late Cretaceous, Amur River Region

The Late Cretaceous vertebrate assemblage of the Amur River Region of Eastern Russia, include several groups of dinosaurs, crocodiles and turtles, has been intensively studied during last decades (Moiseenko et al., 1997; Nessov, 1997; Bolotsky, 2000). Historically, investigators have been attracted mainly by the dinosaurs (Riabinin, 1930; Bolotsky and Moiseenko, 1988; Bolotsky and Kurzanov, 1991), whereas other groups of reptiles are less studied. This is specially true of the Amur turtles, which are known by two families — Lindholmemydidae, represented by a single species of ambiguous systematic position (see below), and Trionychidae, represented by undetermined specimens (Moiseenko et al., 1997). The first work devoted to fossil turtles from Amur was published by A. N. Riabinin (1930), who described a new species of trionychid, *Aspideretes planicostatus* on the basis of a single shell fragment (the first costal). Nessov (1981) showed that this plate could not belong to a trionychid, due to the presence of sulci and a plastral buttress attachment scar, features that are not characteristic for trionychids (Sukhanov, 1964; Meylan, 1987). Nessov (1981) assigned this species to the genus *Mongolemys* of the family Dermatemydidae. After revision of the Dermatemydidae (Shuvalov and Chkhikvadze, 1975; Nessov, 1977; Sukhanov and Narmandakh, 1983; Sukhanov, 2000), *Mongolemys* was placed within the extinct family Lindholmemydidae. Lindholmemydidae unites primitive testudinoid turtles from the Cretaceous to Paleocene of Asia and characterized by presence of additional inframarginal scales (Sukhanov, 2000; Danilov, 2001). Despite the fact that a single carapace plate can not show the presence of additional inframarginals, the Amur turtle was referred to the Lindholmemydidae, because it is the only group of the Mesozoic turtles in Asia, with contact of the plastral buttresses with the costal plates of the carapace [testudinoid synapomorphy (Gaffney and Meylan, 1988)].

The assignement of the Amur turtle to the genus *Mongolemys* is more questionable. It is based on the general appearance of the first costal, although some differences (considered as specific) in more rough sculpturing and more developed buttresses have been mentioned (Nessov, 1981). Taking into cosideration diversity of linholmemydids and the low diagnostic value of the first costal plate, the taxonomic determination should be regarded as unfounded (Sukhanov, 2000). Moreover, the description of the type species

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of *Mongolemys* (*M. elegans*), provided by Khosatzky and Młynarski (1971), is inadequate to characterize the genus (Sukhanov and Narmandakh, 1976). To date, eight species have been assigned to *Mongolemys* (Khosatzky and Młynarski, 1971; Yeh, 1974a, 1974b; Sukhanov and Narmandakh, 1974, 1976; Nessov, 1981; Nessov and Krassovskaya, 1984), though not all of them are valid congeners (Sukhanov, 2000). Three species of *Mongolemys* have been split off into their own genera (Chkhikvadze, 1976; Sukhanov and Narmandakh, 1983; Danilov, 1999). Finally, Chkhikvadze (1976) synonimizes *Mongolemys* with *Tsaotanemys*. Under such conditions the taxonomic position of "*Mongolemys*" planicostatus could not be resolved without additional material on Amur turtles and information on variation of other better known species of Lindholmemydidae.

New materials of "*Mongolemys*" *planicostatus*, described herein, were collected by Yu. Bolotsky and I. Donchenko in Kundur locality in the Amur River Basin (Moiseenko et al., 1997; Bolotsky, 2000). Age of this locality is considered as Early Maastrichtian on the basis of pollen assemblages (Markevich, Bugdaeva, 2001). New materials allow us to make a more complete description of the species. Specifically, the presence of three pairs of inframarginals proves its attribution to the Lindholmemydidae. Within Lindholmemydidae this character is shared by *Mongolemys* (sensu stricto) and *Lindholmemys*. More detailed comparison with these genera shows phylogenetic distinctiveness of "*Mongolemys*" *planicostatus* and allows us to recognize it as a separate genus.

Abbreviations. ANHM, Amur Natural Historical Museum (Blagoveshchensk, Russia); PIN, Paleontolgical Institute, Russian Academy of Sciences (Moscow, Russia); CCMGE, Chernyshev's Central Museum of Geological Exploration (St. Petersburg, Russia); ZISP PH, Paleoherpetological collection, Zoological Institute, Russian Academy of Sciences (St. Petersburg, Russia).

Amuremys, gen nov.

Type species. *Aspideretes planicostatus* Riabinin, 1930; Late Cretaceous, Amur River Region.

Etymology. Name of the genus from Amur river and "emys" (Greek) — a turtle.

Diagnosis. A turtle with a shell of 20 – 30 cm length. Shell bones thick. Nuchal emargination weak. Nuchal plate with a transverse thickening passing into the anterior peripherals. First neural shortened. Free margin of anterior peripherals upraised. Buttresses moderately developed (intermediate between conditions in *Mongolemys* and *Lindholmemys*). Inguinal buttress attaches along the posterior border of the costal V. Trace of the first thoracic rib shortened. Plastral proportions as in *Mongolemys*. Cervical scale

TABLE 1. Comparison of Some Shell Characters in *Amuremys planicostata*, *Mongolemys elegans*, and *Lindholmemys elegans*

Characters	*Amuremys planicostata*	*Mongolemys elegans*	*Lindholmemys elegans*
Nuchal emargination	Weak	Absent	Weak
Anterior width/maximum width of the nuchal	0.77	0.90	0.64
Transverse thickening of the nuchal	Strong	Weak	Absent
Neural I	Shortened	Not shortened	Not shortened
Cervical scale	Relatively small, square-shaped	Relatively small, widened rectangle	Relatively big, trapezoid
First vertebral scale	Widened anteriorly, with a waist, goes on to peripherals I, does not reach marginals II	Widened anteriorly, no waist, goes on to peripherals I, reach marginals II	Narrowed anteriorly, no waist, does not go on to peripherals I, does not reach marginals II
Trace of first thoracic rib	Short	Long	Short
Buttresses	Moderate	Weak	Strong
Anterior peripherals	Upraised	Upraised	Not upraised
Hyoplastron proportions	Relatively wide	Relatively wide	Relatively narrow
Inframarginal scales	Wider than in *Lindholmemys*, but narrower than in *Mongolemys*, cover about 1/2 of the hyoplastral bridge	Wide, first scale covers 1/3 – 1/2 of the hyoplastral bridge	Narrow, first scale covers about 1/3 of the hyoplastral bridge
Shell bones	Thick	Thin	Thick or thin
Shell surface	With well developed sculpture	With or without sculpture	Without sculpture

relatively small, square. First vertebral scale widened anteriorly with a waist in its anterior part, overlaps first peripherals but does not reach second marginals. Last pair of marginals low. Three (?) pairs of elongated inframarginals. Their width is about 25% of the half of the plastron width. First inframarginal covers about half of the bridge part of hyoplastron. Shell surface sculpture consists of pronounced tubercles and ridges.

Content. One species.

Comparison. *Amuremys* differs from all genera of Lindholmemydidae with known number of inframarginals, besides *Mongolemys* and *Lindholmemys*, by presence of three pairs of inframarginals arranged in complete (uninterrupted) rows; from *Mongolemys* and *Lindholmemys* (see Table 1) — by structure of nuchal, shape of cervical, shortened neural, degree of buttress development, waist of the first vertebral, shape of sutural surfaces of the anterior peripherals, shape of inframarginals, well developed sculpturing; from *Mongolemys* — by stronger buttresses, shorter first thoracic rib, thicker shell bones, absence of contact between first vertebral and second marginal scales, narrower inframarginals; from *Lindholmemys* — by weaker buttresses, proportions of the hyoplastron, wider inframarginals; from *Khodzhakulemys* with unknown number of inframarginals (Danilov, 1999) — by shape of sutural surfaces of the anterior peripherals, not shortened first peripheral, shape of cervical and first vertebral scales.

Distribution. Late Cretaceous (Maastrichtian) of the Amur River Region.

Amuremys planicostata (Riabinin) comb. nov.[3]

Aspideretes planicostatus: Riabinin, 1930, Table I; *Mongolemys planicostatus*: Nessov, 1981:69, Fig. III, 1; Nessov, 1987, Pl. II, Fig. 1*a*, *b*; "*Mongolemys*" *planicostatus*: Danilov, 1999:66; Sukhanov, 2000:354.

Holotype. CCMGE 12/3413, right first costal; Upper Cretaceous, Yuliangze Formation (Early-Middle Maastrichtian); Belyie Kruchi locality, Amur River Basin, Heilongiang Province, China.

Material. The new material includes about 100 specimens, represented mainly by fragmentary plates (see **Appendix**); Upper Cretaceous, lower part of Udurchukan Svita (Early Maastrichtian); Kundur locality, Amur River Region, Russia.

[3] The species name is corrected in accordance with feminine gender of the generic name (International Code of Zoological Nomenclature, 4th ed., art. 31).

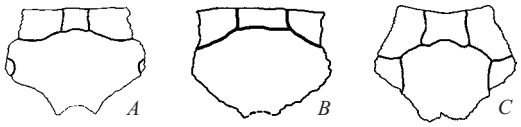


Fig. 1. Nuchal (reconstruction): *A*, *Amuremys planicostata* (based on ANHM 2/461); *B*, *Mongolemys elegans* (based on PIN, without number); *C*, *Lindholmemys elegans* (based on ZISP PH 106/7).

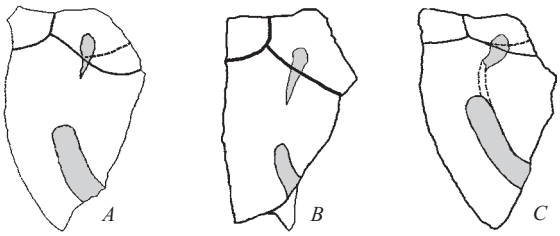


Fig. 2. Morphology of the first costal (reconstruction based on several specimens): *A*, *Amuremys planicostata*; *B*, *Mongolemys elegans*; *C*, *Lindholmemys elegans*. The dashed line shows variants of position of the lateral sulcus of the first vertebral scale. Places of attachment of the axillary buttress and first thoracic rib on the inner surface of the plate are filled with gray color.

Diagnosis. Same as for the genus.

Description. Nuchal (Fig. 1*a*; Plate 2, *1*). The nuchal of *Amuremys planicostata* by shape resembles *Lindholmemys elegans* (Fig. 1*c*). The anterior border is almost straight, indicating weak nuchal emargination. In *Lindholmemys* the anterior border of the nuchal is concave, whereas in *Mongolemys* it is convex. The ratios of the plate width to length (1.51) and anterior border width to maximum width (0.77) are within the limits of variation of these parameters in *Lindholmemys elegans* (1.25 – 1.72 and 0.51 – 0.77, respectively) although the simple means differ (1.49 and 0.64, respectively, $N = 7$). In *Mongolemys elegans* the nuchal (Fig. 1*b*) is always relatively wider anteriorly (ratio of the anterior width to maximum width is about 0.90) and thinner, than in *Lindholmemys*. The ratio of the nuchal width to length in *Mongolemys elegans* varies from 1.31 to 1.38, the simple mean is 1.35, $N = 2$. A distinguishing feature of the nuchal in *Amuremys planicostata* is its transverse thickening, approximately one third length of the plate from the anterior border. This thickening is

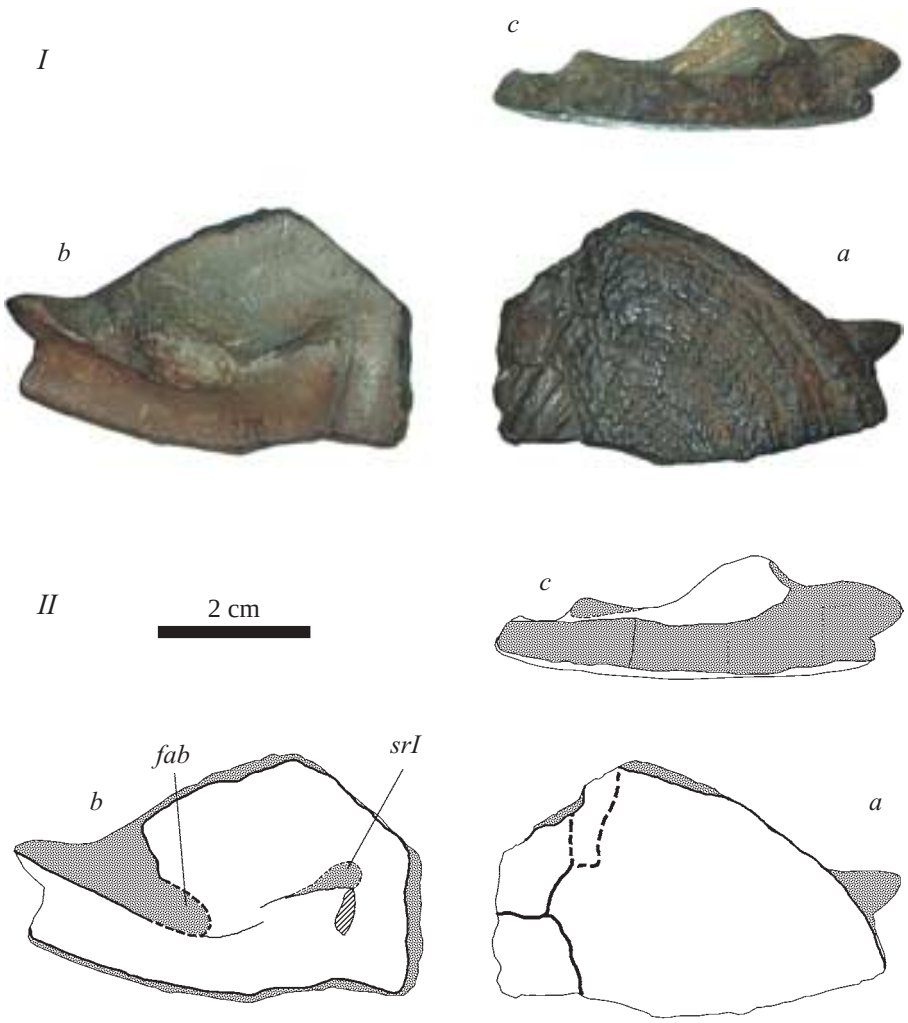


Plate 1. Holotype of *Amuremys planicostata* (Riabinin, 1930), the right costal I (CCMGE 12/3413): external (*a*), internal (*b*), and anterior (*c*) views. The dashed lines show variants of position of the lateral border of the first vertebral scale.

readily visible in the shape of the sutural surfaces of the first peripherals (Plate 2, *2 –4*), which have a characteristic vaulting. The discribed thickening is absent in *Lindholmemys*. The free edge of the plate is upraised laterally, which also serves to distinguish it from *Lindholmemys*. In *Mongolemys elegans* the plate is considerably thinner, the transverse thickening is weaker than in *Amuremys*, but the free edge is upraised like in *Amuremys* (Plate 2, *5*).

Arrangement of the sulci on the nuchal also distinguish *Amuremys planicostata* from *Lindholmemys*. The cervical scale is quadrangular, its length is slightly less than width and makes out 22% of the nuchal length. In *Lindholmemys* the cervical is usually trapezoid and relatively bigger, its length makes out 1/2 – 1/3 length of the plate. In *Mongolemys elegans* the cervical is usually in shape of wide rectangle, it makes out 20% of the nuchal length. Lateral corners of the nuchal in *Amuremys planicostata* are sligthly covered with first pleurals (Plate 2, *6*). In *Lindholmemys* these scales overlap the plate more strongly, whereas in *Mongolemys* they do not reach nuchal.

External surface of the nuchal in *Amuremys planicostata* is sculptured with longitude ridges in the

TABLE 2. Measurements of the Specimens of *Amuremys planicostata* (Riabinin, 1930)

Parameters	*Amuremys planicostata*	
Nuchal:	**ANHM 2/461**	
Length midline/width maximum	34.0/51.5	
Sides length: anterior/antero-lateral/postero-lateral/posterior	39.5/23.0/24.5/15.0	
Thickness: in central part/laterally/posteriorly	6.5/9.0/4.0	
Neural I	**ANHM 2/468**	
Length/width/ratio	20.0/16.2/1.23	
Neural III	**ANHM 2/540**	
Length/width/ratio	17.5/13.2/1.30	
Neural VI	**ANHM 2/565**	
Length/width/ratio	9.2/10.3/0.89	
Neural VII	**ANHM 2/479**	
Length/width/ratio	14.2/19.5/0.73	
Suprapygal II:	**ANHM 2/466**	
Length/width/ratio	16.8/39.5/0.43	
Sides length: anterior/antero-lateral/postero-lateral/posterior	28.5/9.0 /13.5/17.5	
Thickness anteriorly/posteriorly	5.4/6.0	
Pygal	**ANHM 2/740**	**ANHM 2/736**
Length midline/length maximum/width	11.0/15.0/22.9	12.0/18.0/~25.0
Costal I:	**ANHM 2/460**	**CCMGE 12/3413**
Width/length/ratio	38.0/~63.0/0.59	31.0/50.3/0.62
Length of the buttress fossa (% of the plate length)	~27.0 (43%)	23 (45%)
Thickness anteriorly (medially/laterally)	5.0/13.5	4.5/10.5
Thickness posteriorly (medially/laterally)	7.5/4.0	5.7/3.5
Thickness of the costal ridge	13.5	16.0
Peripheral I:	**ANHM 2/497**	**ANHM 2/568**
Length/height	26.0/22.0	26.0/23.5
Thickness anteriorly/posteriorly	8.0/9.0	9.3/11.0
Height of pleural-marginal sulcus anteriorly/in intermarginal sulcus/posteriorly	11.5/10.0/~11.5	~13.5/13.0/~15.0
Peripheral V:	**ANHM 2/491**	
Plastral part: length/height	29.5/23.5	
Peripheral VIII:	**ANHM 2/557**	
Length/height	23.0/~30.0	
Thickness anteriorly/posteriorly	17.2/13.0	
Peripheral X:	**ANHM 2/485**	
Length/height	23.0/20.0	
Thickness anteriorly/posteriorly	7.0/5.7	
Height of pleural-marginal sulcus anteriorly/in intermarginal sulcus/posteriorly	13.5/11.0/14.0	
Peripheral XI:	**ANHM 2/737**	
Length/height	?/27.0	
Thickness anteriorly/posteriorly	9.5/6.5	
Height of pleural-marginal sulcus anteriorly/in intermarginal sulcus/posteriorly	21.0/12.5/?	
Entoplastron:	**ANHM 2/475**	
Length/width externally	~20/19.5	
Length/width internally	?/15.8	
Thickness anteriorly/posteriorly	4.0/4.8	
Hyoplastron:	**ANHM 2/555**	**ANHM 2/556**
Length midline/maximum	~45.0/65.5	?/?
Width posteriorly/in humeral-pectoral sulcus	58.0/~40.0	?
Contribution to bridge length	33.0	44.0
Cervical:	**ANHM 2/461**	
length/width anteriorly/posteriorly	7.5/10.0/10.5	
Inframarginal I:	**ANHM 2/555**	**ANHM 2/556**
Length along contact with marginals/width	20.0/12.5	29.0/18.5

Note: ~, approximate measurement; ?, non-measured. All measurements in mm.

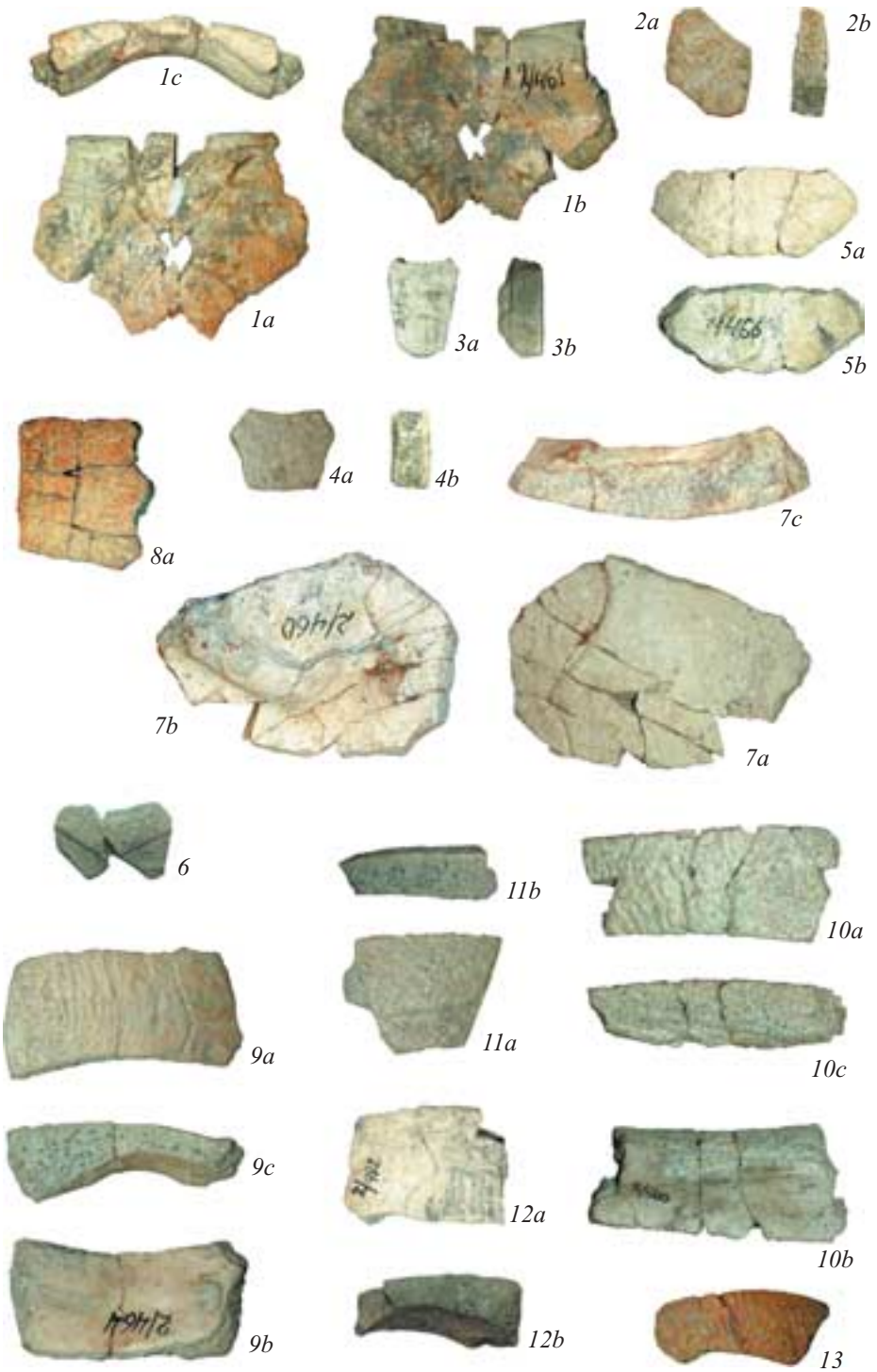
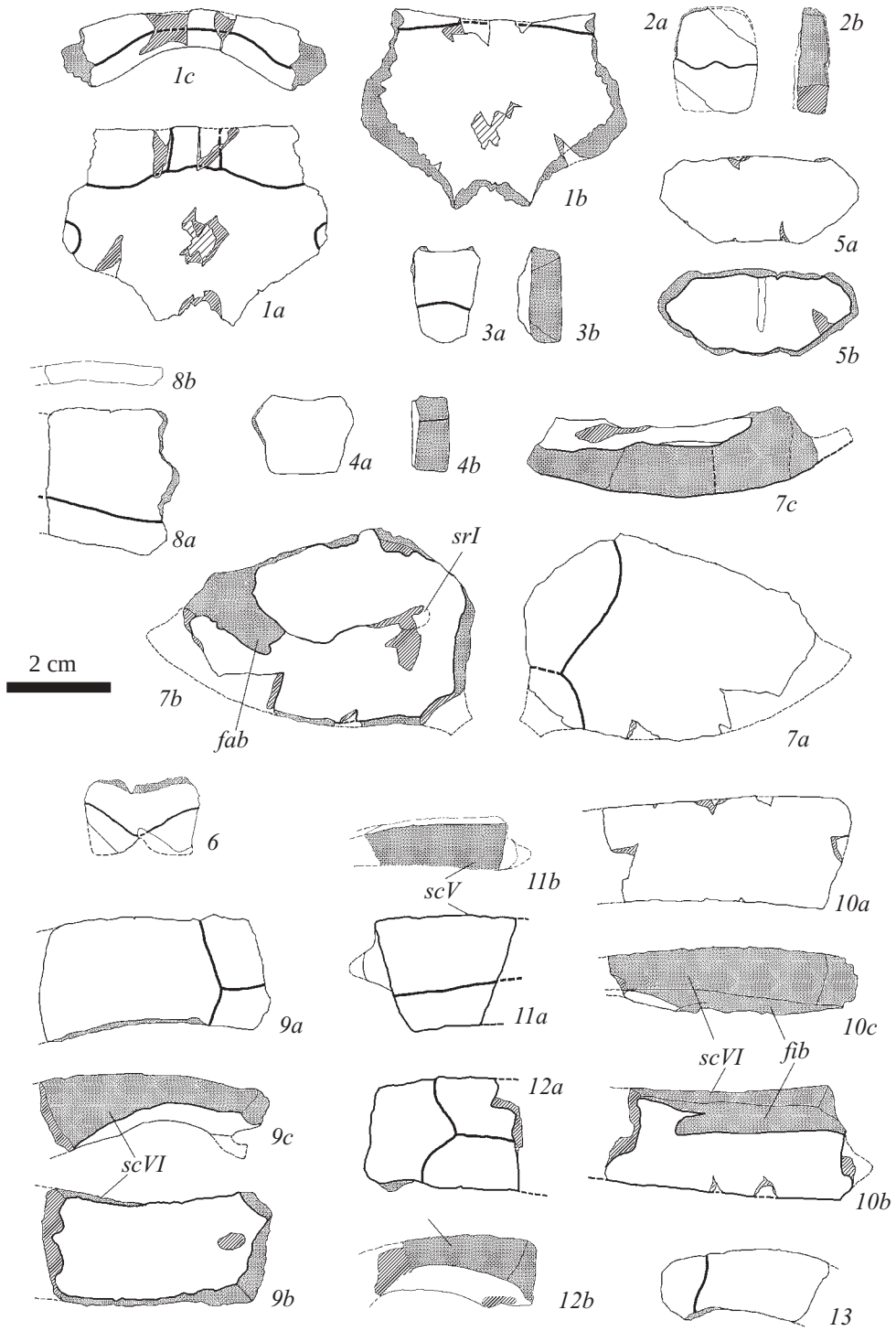
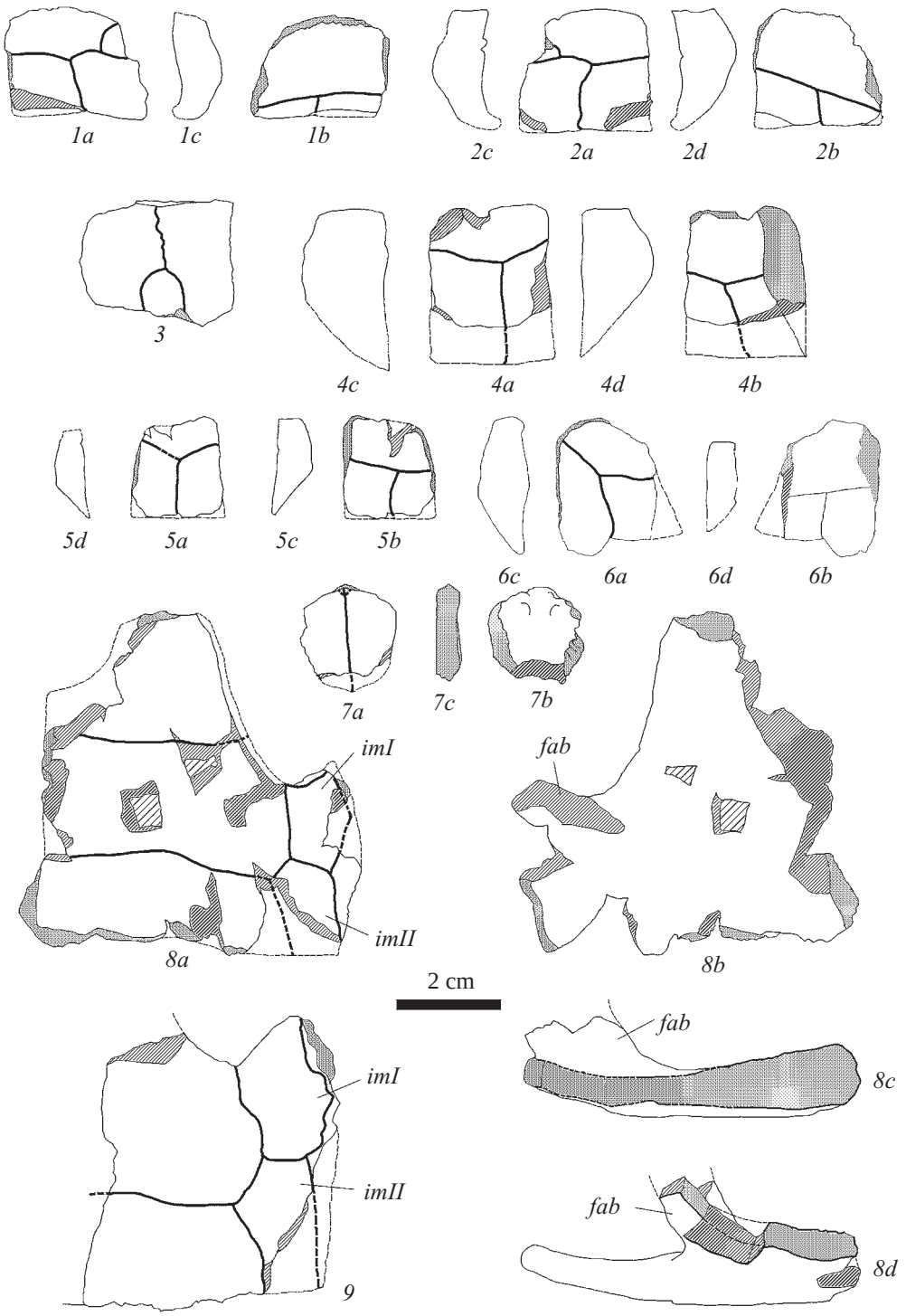


Plate 2. Shell bones of *Amuremys planicostata* (Riabinin, 1930). *1*, Nuchal (ANHM 2/461): external (*1a*), internal (*1b*), and anterior (*1*c) views; *2*, neural I (ANHM 2/468): external view (*2a*) and view from left side (*2b*); *3*, neural III (ANHM 2/540): external view (*3a*) and view from left side (*3b*); *4*, neural VII (ANHM 2/479): external view (*4a*) and view from left side (*4b*); *5*, suprapygal II (ANHM 2/466): external (*5a*) and internal (*5b*) views; *6*, pygal (ANHM 2/740) in external view; *7*, right costal I (ANHM 2/460): external (*7a*), internal (*7b*), and anterior (*7*c) views; *8*, lateral part of the right costal IV (ANHM 2/552): external (*8a*) and posterior (*8b*) views; *9*, medial part of



the left costal V (ANHM 2/464): external (*9a*), internal (*9b*), and posterior (*9c*) views; *10*, lateral part of the right costal V (ANHM 2/506): external (*10a*), internal (*10b*), and posterior (*10c*) views; *11*, lateral part of the left costal VI (ANHM 2/503): external (*11a*) and anterior (*11b*) views; *12*, medial part of the right costal VI (ANHM 2/492): external (*12a*) and anterior (*12b*) views; *13*, right costal VII (ANHM 2/481), external view. **Abbreviations:** *fab*, attachment site for axillary buttress (= buttress fossa); *fib*, attachment site for inguinal buttress; *scV*, *scVI*, sutural surfaces for contact with costals V, VI; *srI*, scar of the first thoracic rib.

Plate 3. Shell bones of *Amuremys planicostata* (Riabinin, 1930): *1*, Right peripheral I (ANHM 2/497): external (*1a*) and internal (*1b*) views, view of the anterior sutural surface (*1c*); *2*, Left peripheral I (ANHM 2/568): external (*2a*) and internal (*2b*) views, views of anterior (*2c*) and posterior (*2d*) sutural surfaces; *3*, plastral lobe of peripheral V (ANHM 2/491), external view; *4*, left peripheral VIII (ANHM 2/557): external (*4a*) and internal (*4b*) views, views of anterior (*4c*) and posterior (*4d*) sutural surfaces; *5*, right peripheral X (ANHM 2/485): external (*5a*) and internal (*5b*) views, views of anterior (*5c*) and posterior (*5d*) sutural surfaces; *6*, left peripheral XI (ANHM



2/737): external (*6a*) and internal (*6b*) views, views of anterior (*6c*) and posterior (*6d*) sutural surfaces; *7*, entoplastron (ANHM 2/475): external (*7a*) view, internal (*7b*) view, and view from left side (*7c*); *8*, left hyoplastron (ANHM 2/555): external (*8a*), internal (*8b*), posterior (*8c*), and left (*8d*) views; *9*, fragment of the left hyoplastron (ANHM 2/556), external view. **Abbreviations:** *imI*, *imII*, inframarginals I – II; for other abbreviations see Plate 2.

area of the first vertebral and by ridges parallel to the free edge in the areas of the first marginals.

Neurals (Plate 3, *2 – 4*). The first neural is a shortened quadrangle with convex sides. The ratio of the first neural length to width is 1.23, considerably less than in *Lindholmemys elegans* (minimum 1.37, mean 1.53, $N = 12$) and *Mongolemys elegans* (mean 1.76, $N = 4$). The remaining neurals are hexagonal, casque-shaped and short-sided anteriorly. There are no differences in their morphology from the neurals of *Lindholmemys*.

Suprapygals (Plate 3, *5*). The new material provides one suprapygal II available (ANHM 2/466). The outline of this bone is a wide hexagon (length/width ratio 0.43). The anterior border is wider than the posterior one and anterolateral borders less than posterolateral ones. Thickness of the suprapygal II increases posteriorly. There is a scar for vertebrae attachment visible on the inner surface of the plate. Absence of scale sulci on the suprapygal indicate a low pair of marginals XII (i.e., marginals XII do not overlap suprapygal II).

Pygal (Plate 3, *6*). In dorsal view the pygal is a wide quadrangle with concave anterior border and strongly notched posterior one. Marginals XII reaching 2/3 of the pygal length (height) laterally. Medially vertebral V scale almost reach the free edge of the plate.

Costals (Plates 1; 2, *7 – 13*). New specimens of the first costals (Plates 1; 2, *7*) allow to us to expand the characteristics of this element, represented formerly by holotype (CCMGE 12/3413). The new specimens differ from the holotype by the following features: thickening of the costal ridge less, lateral sulcus of the first vertebral scale crosses nuchal border more laterally (although position of this sulcus in the holotype is questionable, see Plate 1), and the absence of growth lines. Comparison of the first costal of *Amuremys* with *Mongolemys* and *Lindholmemys* demonstrates considerable differences from both genera. The length of the buttress fossa in *Amuremys planicostata* makes up about 45% of the plate length, which is more than in *Mongolemys elegans* (about 30%) and less than in *Lindholmemys elegans* (about 60%). The scar of the first thoracic rib in *Amuremys planicostata* is relatively short, like in *Lindholmemys elegans*, whereas in *Mongolemys elegans* it is more elongated. Position of the lateral sulcus of the first vertebral scale in *Amuremys planicostata* could be variable, as was mentioned above. In *Lindholmemys elegans* its position also variable, including variants noted in *Amuremys*, whereas in *Mongolemys elegans*

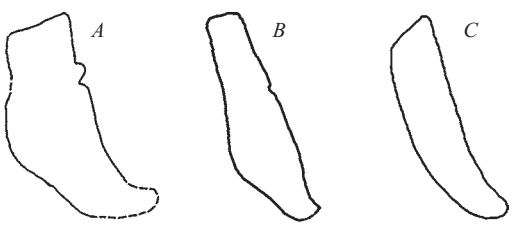


Fig. 3. Shape of the anterior sutural surface of the first peripheral: *A*, *Amuremys planicostata* (ANHM 2/568); *B*, *Mongolemys elegans* (PIN); *C*, *Lindholmemys elegans* (ZISP PH 125/7).

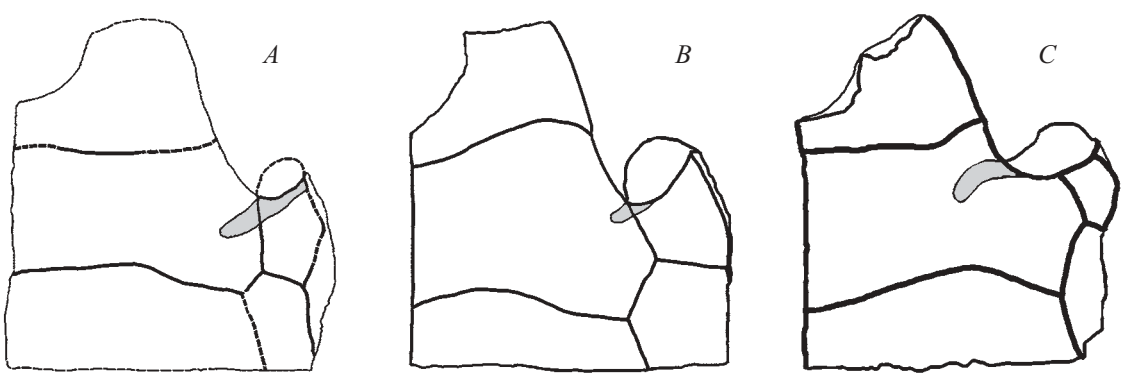


Fig. 4. Morphology of the hyoplastra: *A*, *Amuremys planicostata* (based on ANHM 2/555); *B*, *Mongolemys elegans* (based on holotype); *C*, *Lindholmemys elegans* (based on several specimens). The position of the axillary buttress basements on the internal surface of the hyoplastron filled with gray color.

it is placed more laterally, crossing border between first costal and first peripheral. Sculpturing of the first costal in *Amuremys* is represented by elongated tubercles arranged either in ridges perpendicular to posterior border of the plate (ANHM 2/460) or along the growth lines (CCMGE 12/3413) in the area of the pleural scale. The latter type of sculpturing could be a juvenile character. In *Lindholmemys elegans* shell surface usually is smooth, whereas in *Mongolemys elegans* it could be covered by tubercles and ridges in adults.

Costal IV (Plate 2, *8*) is thin, with a weakly pronounced free rib and rib ridge. This could indicate weakened contact with peripherals and late obliteration of the costal-peripheral fontanneles. Costal V (Plate 2, *9*) is thickened along the posterior border for attachment with inguinal buttress. The reconstructed length of the buttress fossa is about 45% of the plate length.

Costal VI (Plate 2, *11*, *12*) does not contact the inguinal buttress, although thickened along anterior border.

Costal VII (Plate 2, *13*) has typical morphology compared to *Mongolemys* and *Lindholmemys*.

The costals are sculptured with tubercles in lateral parts of pleural scales and by ridges perpendicular to intercostal sutures in their medial parts.

Peripherals (Plate 3, *1 – 6*). The first peripheral (Plate 2, *1*, *2*) exhibits an upraised free edge and thickenning parallel to the free edge. Both peculiarities are reflected in the shape of sutural surfaces (Plate 3, *1c*, *2c*). A marginal scale covers the lateral half of the plate. Anteriorly the plate is slightly covered by the first vertebral scale, which remains separated from the second marginal. The described sulcus pattern is present in three available specimens, proving the stability of this character. Sculpturing of the first peripheral is represented by tubercles in the area of the anterior marginal scale, by oblique ridges directed posterolaterally in the area of posterior marginal scale and by ridges perpendicular to the pleural-marginal sulcus in the area of the pleural scale.

A fragment of peripheral V (Plate 3, *3*) demonstrates overlapping of the plastral lobe by an inframarginal scale (? II).

Peripheral VIII (Plate 3, *4*) does not contact the inguinal buttress. The marginal scale covers about 2/3 of its external surface.

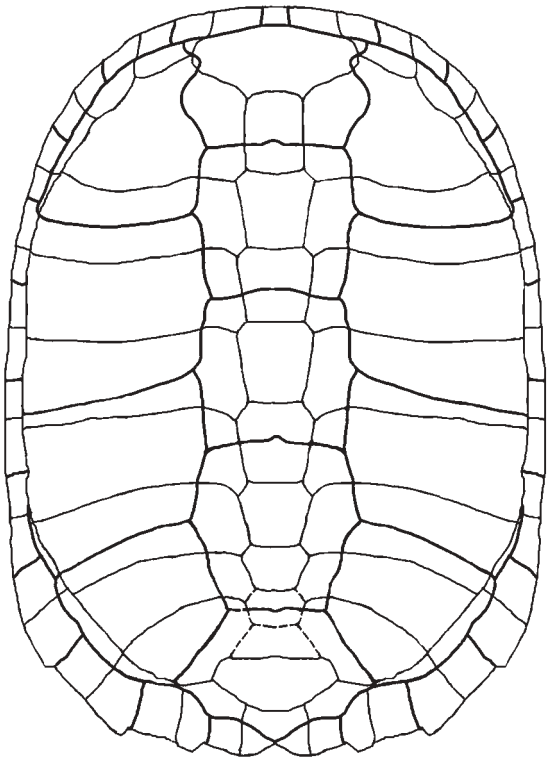


Fig. 5. Reconstruction of the carapace of *Amuremys planicostata* based on separate plates.

Peripheral X (Plate 3, *5*) has no peculiarities compared to *Mongolemys* and *Lindholmemys*.

Peripheral XI (Plate 3, *6*) has a notch in its posterior border. Together with the pygal notch, the posterior notch indicates serration of the posterior margin of the carapace.

Comparison of the peripherals of *Amuremys planicostata* with *Mongolemys* and *Lindholmemys* (Fig. 3) reveals similarity with the *Mongolemys* in the upraised edge of anterior peripherals and in presence of the thickening, though this latter character is less-developed in *Mongolemys*.

Scalation of the carapace (Fig. 5). According to available material, the general pattern of scalation of the carapace in *Amuremys* resembles other lindholmemydids. The shape of the first vertebral scale can be established based on morphology of the nuchal, first costal and first peripheral. The first vertebral was widened anteriorly and slightly overlapped peripherals, although did not reach marginals II. There is a peculiar waist in the anterior portion of the scale.

Lindholmemys is characterized by the first vertebral narrowed anteriorly, not extended besides the nuchal. In *Mongolemys* first vertebral is strongly widened anteriorly, reaching second marginals. Certain proportions of vertebral scales (i.e., width/length ratio etc.) could not be established due to fragmentary nature of the material.

Entoplastron (Plate 3, *7*). The entoplastron has no specific peculiarities. It is hexagonal externally and diamond-shaped internally (ratio of internal width to external one 0.81). The length of the plate is about equal to its width. Gulars enter the anterior tip of the entoplastron. Sculpture is absent. A similar structure of the entoplastron is demonsrated by *Mongolemys* and *Lindholmemys*.

Hyoplastron (Plate 3, *8*, *9*). The ratio of the hyoplastron width posteriorly (along the hyoplastron — hypoplastron suture) to its maximum length in *Amuremys planicostata* (ANHM 2/555) is 0.91. In *Mongolemys elegans* (holotype) it is 0.92, whereas in *Lindholmemys elegans* (holotype) it is about 0.80. The ratio of the width of the anterior lobe of the hyoplastron (distance from the top of the inguinal notch to medial border of the hyoplastron) to the hyoplastron width is 0.75 in *Amuremys planicostata* (ANHM 2/555). This same ratio is 0.69 and 0.84 in *Mongolemys elegans* (holotype) and *Lindholmemys elegans* (holotype), respectively. In *Amuremys*, the basement of the axillary buttress is weaker than in *Lindholmemys elegans*, but stronger than in *Mongolemys elegans*. The angle formed by buttress basement and midline (viewed from above) is about 60°. This is similar to *Mongolemys elegans* and unlike *Lindholmemys elegans* where the angle is about 30°. Thus, by proportions of hyoplastron *Amuremys planicostata* is more similar to *Mongolemys*, than to *Lindholmemys*. However, the hyoplastron of *Amuremys* differs from the hyoplastron of *Mongolemys* by virtue of its stronger buttress, wider anterior lobe and thicker bone and from the hyoplastron of *Lindholmemys* by its width, narrower anterior lobe, weaker buttress and different orientation of the buttress base.

There are two inframarginals visible on the hyoplastron. The first (most anterior) one and anterior part of the second. Their medial borders lie at about the level of inguinal notch or even more medially. The lateral borders of the inframarginals lie along the suture with the peripherals. As it was noted above, some overlapping of the peripherals is also possible. The lengths of both scales exceed their widths (width/length ratio for the first inframarginal equals 0.68 in ANHM 2/555 and 0.66 in ANHM 2/556). The first inframarginal scale covers approximately half of the hyoplastral bridge (distance from the axillary notch top to the posterior border of the hyoplastron). The ratio of scale width to hyoplastral width (ANHM 2/555) is about 0.25. For comparison, in *Mongolemys elegans* length of the first and second inframarginals only slightly more than width and the first scale covers from 1/3 to 1/2 of the hyoplastral bridge, the ratio of the scales width to hyoplastral width is about 0.30; in *Lindholmemys elegans* length of the first scale equals the width, the scale covers about 1/3 of the hyoplastral bridge, and the ratio of the scales width to hyoplastral width is about 0.20. It should be mentioned however, that shape and relative size of inframarginals could be quite variable in *Lindholmemys* (unpublished data).

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Appendix.
List of material examined

Amuremys planicostata

Nuchals: ANHM 2/461, 2/754, 2/755. **Neurals:** ANHM 2/468, 2/802, neural I; ANHM 2/540, neural III; ANHM 2/747, neural IV; ANHM 2/479, 2/795, neurals VII; ANHM 2/788, neural VIII. **Suprapygal II:** ANHM 2/466. **Pygals:** ANHM 2/736, 2/740. **Costals:** CCMGE 12/3413, ANHM 2/460, 2/761, right costals I; ANHM 2/465, 2/470, 2/476, 2/494, 2/496, 2/546, 2/561, 2/571, 2/588, 2/766, fragmentary costals I; ANHM 2/464, 2/469, 2/471, 2/506, 2/549, 2/559, fragmentary costals V; ANHM 2/463, 2/483, 2/492, 2/541, 2/547, 2/597, fragmentary costals VI; ANHM 2/481, 2/786, costals VII; ANHM 2/797, costal VIII; ANHM 2/488, 2/503, 2/530, 2/532, 2/552, 2/554, 2/562, 2/587, 2/814, fragmentary even costals; ANHM 2/482, 2/543, 2/549, 2/553, 2/582, 2/818, fragmentary odd costals; ANHM 2/504, 2/511, 2/523, 2/572, 2/573, 2/578, 2/581, 2/591, 2/600, fragmentary costals. **Peripherals:** ANHM 2/480, 2/497, 2/563, 2/568, 2/842, peripherals I; ANHM 2/743, peripheral II; ANHM 2/491, 2/499, 2/589, fragmentary bridge peripherals (? V); ANHM 2/472, 2/474, 2/525, 2/557, 2/744, fragmentary peripherals VIII; ANHM 2/485,

2/601, 2/742, 2/756, peripherals IX or X; ANHM 2/501, 2/737, peripherals XI; ANHM 2/527, fragmentary peripheral. **Entoplastron:** ANHM 2/475. **Hyoplastra:** ANHM 2/555, left hyoplastron; ANHM 2/467, 2/487, 2/493, 2/495, 2/556, 2/566, fragmentary hyoplastra; ANHM 2/490, 2/524, fragmentary hypoplastra. **Plastra indet.:** ANHM 2/473, 2/486, 2/489, 2/498, 2/502, 2/505, 2/516, 2/558, 2/567, 2/585.

Lindholmemys elegans:

Shell: holotype CCMGE 34/12175. Nuchals: ZISP PH 106/7, 107/7, 108/7, 114/7, 121/7, 161/7, 397/7. **Neurals:** ZISP PH 635/7, 637/7, 642/7, neurals I; ZISP PH 693/7, 702/7, neurals III; ZISP PH 737/7, 750/7, neuralsVII. **Suprapygal II:** ZISP PH 11/7. **Costals:** ZISP PH 1/7, 4/7, 54/7, 55/7, 63/7, costals I; ZISP PH 549/7, 551/7, costals V; ZISP PH 518/7, 523/7, costals VI. **Peripherals:** ZISP PH 125/7, 128/7, 402/7, peripherals I; ZISP PH 305/7, 313/7, 319/7, peripherals VIII. Entoplastra: ZISP PH 34/7, 35/7. **Hyoplastra:** ZISP PH 441/7, 442/7, 443/7, 447/7, 460/7.

Mongolemys elegans:

Shells: holotype PIN 551-422 (= ZISP PH T/M-46.1), ZISP PH T/M 47.1, Zpal MgCh/21, PIN 4699-3, 4693-16. **Separate plates** (PIN, without numbers): 2 nuchals, 1 costal I, 2 peripherals I, 1 peripheral VIII, 3 entoplastra.