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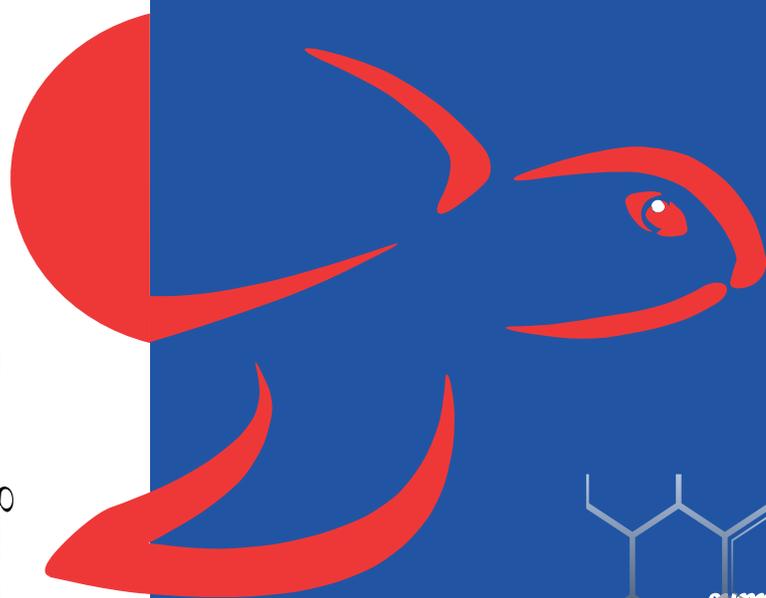
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Cretaceous chelonioid turtles of Northern Eurasia: previous records and new findings

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Chelonioid turtles (superfamily Chelonoidea, the crown and panstem clades Chelonoidea and Pan-Chelonoidea respectively) traditionally unite three families of sea turtles: Cheloniidae, Dermochelyidae, and Protostegidae (Hirayama, 1997, 1998; Joyce et al., 2004). Some authors exclude Protostegidae from Chelonoidea and Pan-Chelonoidea (Joyce, 2007; Parham and Pyenson, 2010), whereas others extend the latter clade to include basal eucryptodiran taxa, such as Xinjiangchelyidae, Sinemydidae and Macrobaenidae (Cadena and Parham, 2015). The oldest chelonioids (in the traditional sense) are known since the Early (protostegids, cheloniids) and Late (dermochelyids) Cretaceous (Hirayama, 1997). The Cretaceous chelonioid records from Northern Eurasia (territory of the former USSR; NE) was recently summarized by Danilov et al. (2017) based on published data. Here we briefly comment on some of these records (1–10; names of taxa are given after Danilov et al., 2017) and report new material (11–20) from this territory.

Abbreviations: AMNH, American Museum of Natural History, New York, USA; IP, Institute of Paleobiology, Tbilisi, Georgia; CYG, Club of Young Geologist, Orsk, Russia; PIN, A.A. Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; ZIN PH, Zoological Institute of the Russian Academy of Sciences, Paleoherpological Collection, St. Petersburg, Russia.

1) *Teguliscapha rossica* Nesson in Nesson et al., 1988 (Protostegidae; Nesson et al., 1988): dentary symphysis with a wide and flat triturating surface (holotype), frontal, opisthotic, nuchal, bridge peripheral, costal, hypoplastron, xiphoplastron, and humerus from Lebedinskii and Stoylenskii quarries (= Gubkin and Staryi Oskol; Averianov, 2002), Belgorod Province, Russia; Sekmenov Formation, upper Albian – lower Cenomanian. The humerus specimen mentioned by Nesson (1987; Nesson et al., 1988) was not found by us. Examination of the type specimens and new materials from the same locality, including maxillae with pronounced labial and lingual ridges, dentaries with narrow triturating surface and sagittal crest, serrated peripheral, T-shaped entoplastron, and humeri, allows us to suggest that the holotype of *T. rossica* belongs to a stem-chelonioid (sensu Parham and Pyenson, 2010), whereas shell elements from the type series and new material belong to a true protostegid, showing similarities with *Rhinochelys* and *Calcarichelys* (see Hooks, 1998).

2) Other materials from NE previously attributed to protostegids (*Teguliscapha* sp. indet. 1 and 2, Protostegidae gen. indet. 1–3; see Danilov et al., 2017) are diagnostic only to the level of Chelonoidea.

3) Dermochelyidae gen. indet. 1 (Dermochelyidae indet.; Averianov, 2002:139): collection ZIN PH 195, shell, scapular and ilial fragments from Lebedinskii and Stoylenskii quarries (Averianov, 2002; see 1 for locality data). This material shows similarity with *Mesodermocheilus undulatus* (Hirayama and Chitoku, 1996) in shape of the iliac blade, broad and robust peripherals with undulated medial border, much expanded between costal ribs, and with recent *Dermocheilus coriacea* and the Chico Formation dermochelyid (lower Campanian of USA; Parham and Stidham, 1999) in the presence of the acromion tubercle on the scapula.

4) *Turgaiscapha kushmurunica* Averianov, 2002 (Dermochelyidae; Averianov, 2002): pygal (holotype) and other shell fragments without surface sculpturing from Kushmurun, Kazakhstan; lower part of the Eginsai Formation, upper Campanian – ?lower Maastrichtian. Hirayama (2006)

suggested considering this taxon as a nomen dubium (Chelonioidea indet.). The anterior neural with surface sculpturing of interconnected ridges, tentatively attributed to *Turgaiscapha kushmurnica* by Averianov (2002), is considered here as Cheloniidae indet. based on similarity with other sculptured cheloniids from the Cretaceous of NE (see 10, 15).

5) Chelonioidea fam. indet. 1 (Chelonioidea fam. gen. et sp. indet.; Nessov and Khosatzky, 1981:77, fig. IV, 11, 12): two bridge peripherals and plastron (?hypoplastron) fragment from Motnya I, Buryatiya, Russia; lower part of the Khilok Formation, Aptian. Given that there are two macrobaenid taxa reported from the same formation (Nessov and Khosatzky, 1981; Skutschas, 2003), this material may belong to macrobaenids as well.

6) Chelonioidea fam. indet. 2 (Knochenbruchstücks von einem Individuum des indetermirnten fossilen Reptils; Kiprijanow, 1883:15–17, 27, Taf. III): storage unknown, proximal part of the humerus from unknown locality, Kursk Province, Russia; “Severischen Osteolith”, Cenomanian. The humerus is poorly preserved, but clearly different in morphology from those of *Teguliscapha rossica*.

7) Chelonioidea fam. indet. 5 (Desmatochelyidae?; Nessov and Udovichenko, 1986:pl. 1, fig. 13; Chelonioidea indet.; Averianov, 2002:141): posterior peripheral from Alymtau, Kazakhstan; Darbaza Formation, lower Campanian? – middle Campanian. This peripheral belongs to a large individual and, as well as additional shell fragments from the same locality (collection ZIN PH 113), bears surface sculpturing made of a net of grooves. Cheloniidae indet. from Alymtau (= Kyrkkuduk II; see Averianov, 2002) was reported without designation of any material. The available turtle material from Alymtau in ZIN PH cannot be attributed to Cheloniidae.

8) Chelonioidea fam. indet. 6 (Chelonioidea indet.; Averianov and Yarkov, 2000:162, fig. 2; Chelonioidea incertae sedis sp. 1; Averianov and Yarkov, 2004:46, figs. 5, 6): frontal, dentaries, shell, and limb bones from Polunino 2, Volgograd Province, Russia; Campanian. Primarily, this material was considered as belonging to “a currently unrecognized group of relatively generalized and large sized protostegids” (Averianov and Yarkov, 2000:163), but later, based on additional material, was reassigned as similar to a cheloniid *Allopleuron* (Averianov and Yarkov, 2004; Karl et al., 2012).

9) Chelonioidea indet. (Averianov, 2002:142): material was not designated; Zhuravlevskii, Kazakhstan; lower part of the Zhuravlevskii Formation, upper Campanian. Material from Zhuravlevskii in IP examined by one of us (ID) consists of peripherals 5 – 7 in articulation, which are similar to those of the macrobaenid *Anatolemys* spp.

10) Testudines subord. indet. 8 (Cryptodira incertae sedis sp. 1; Averianov and Yarkov, 2004:42, figs. 2, 3): fragment of the dentary symphysis, two fragments of the scapula, and a neural with sculpturing made of tubercles and interconnected ridges (all specimens from gigantic individuals) from Rasstrigin 1, Volgograd Province, Russia; Maastrichtian. Additional material of this taxon from the same locality (collection ZIN PH 133) includes several sculptured shell fragments (peripherals and ?costals) from large individuals. Averianov and Yarkov (2004) mentioned similarity of this taxon with *Peritresius ornatus*, a cheloniid turtle from the Maastrichtian of USA, in shell sculpturing, but also noted difference from it in a flat (non-keeled) neural. Here we consider this taxon as a *Peritresius*-like cheloniid.

11) *Teguliscapha* sp. from Saratov (= Lysaya Gora), Saratov Province, Russia; upper Cenomanian: collection ZIN PH 39, dentary symphysis very similar in morphology to the holotype of *Teguliscapha rossica* (see 1). Previous chelonioid material reported from this locality (see Danilov et al., 2017: Chelonioidea fam. indet. 3) included dentaries with narrow triturating surface.

12) Protostegina indet.: collection ZIN PH 244, left maxilla, right jugal, humerus, scapula, several peripherals, and plastral fragments of giant individuals, as well as shell bones from individuals of smaller size, which come from Beloe Ozero, Saratov Province, Russia; Rybushka Formation, Lower Campanian. This material is assigned to protostegids based on large jugal with nearly straight ventral border, and lateral process of the humerus restricted to anterior portion of the shaft (Hirayama, 1997). Absence of the pronounced lingual ridge on the maxilla and shallow

groove on ventral surface of the posterior peripheral suggest attribution to *Protostegina* (Hooks, 1998). The maxilla, jugal and humerus are very similar to those of *Protostega gigas* (AMNH 1503).

13) Chelonioidea indet. from Beloe Ozero (see 12 for locality data): collection ZIN PH 244, large peripheral fragment without clear scute sulci and different in morphology from peripherals of *Protostegina* indet.

14) *Desmatochelys* sp.: complete skull and some postcranial bones in matrix (PIN) from Sengiley locality, Ulyanovsk Province, Russia; lower Aptian. This material is referred to *Desmatochelys* based on large size (skull is about 21 cm in length), similar outline of the skull, large nasal opening facing anteriorly, presence of large nasal bones, and absence of medial contact of prefrontals (see Cadena and Parham, 2015).

15) Cheloniidae indet.: collection ZIN PH 245, fragments of two costals in articulation from Penza, Penza Province, Russia; Campanian – Maastrichtian. This material was mentioned and figured by Nessov (1997:129, pl. 57, fig. 9) as “a girdle bone of a giant sturgeon with a smoothed relief of ridges.” The attribution of this material to turtles is supported by presence of the intercostal suture and remains of two rib thickenings on the internal surface of the specimen.

16) Chelonioidea indet.: collection ZIN PH 246, entoplastron (about 5 cm in length as preserved) from Dmitrievskii, Aktobe Province, Kazakhstan; lower Campanian. The entoplastron is longer than wide, with its posterolateral parts, at life, covered by hyoplastra from the external side that resulted in subtriangular shape of the entoplastron externally.

17) Chelonioidea indet.: collection ZIN PH 247, fragment of costal 1 with estimated medial length of about 6 cm from Karyakino, Saratov Province, Russia; Campanian.

18) Protostegidae indet.: collection ZIN PH 248, right maxilla from Polpino, Bryansk Province; Cenomanian. The maxilla has the same morphology as in the protostegid from Lebedinskii and Stoylenskii quarries (see 1).

19) Chelonioidea indet.: collection ZIN PH 249, peripheral (about 45 mm in length) from Pervomayskoe, Saratov Province, Russia; Cenomanian.

20) Chelonioidea indet.: CYG, complete odd costal (about 22 cm in width) from Izhberda, Orenburg Province, Russia; Campanian.

To summarize, our review demonstrates presence of representatives of stem-chelonioids as well as protostegids, cheloniids, and dermochelyids in the Cretaceous of NE. Stem-chelonioids are represented by *Teguliscapha rossica*, which record is extended to the upper Albian – Cenomanian. Reliable protostegids are known only from the European Russia: *Desmatochelys* sp. from the Aptian (first record for this territory), Protostegidae indet. from the upper Albian – Cenomanian, and *Protostegina* indet. from the Campanian (first record for this territory). Dermochelyids are represented by *Dermochelyidae* gen. indet. 1 from the upper Albian – lower Cenomanian of the European Russia. Probable cheloniids are represented by *Allopleuron*-like forms in the Campanian of the European Russia and *Peritresius*-like forms with sculptured shell in the Campanian – Maastrichtian of the European Russia and Kazakhstan (new record and reinterpretation of the previous records). Available material confirms presence of only one chelonioid taxon in Alymtau (7), two taxa in Beloe Ozero (12, 13), Kushmurun (4), and Saratov (11), and three taxa Lebedinskii and Stoylenskii quarries (1, 3). Some materials primarily assigned to chelonioids (5, 9) more likely belong to macrobaenids. Finally, new materials support cosmopolitanism of *Desmatochelys*, hitherto known from the upper Barremian – lower Aptian of Columbia, upper Cenomanian – Turonian of North America and Japan, and *Protostegina*, hitherto known from the ?Santonian – Campanian of North America and Japan (Hirayama, 1997; Cadena and Parham, 2015)

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