



Protostega gigas and other sea turtles from the Campanian of Eastern Europe, Russia

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ARTICLE INFO

Article history:

Received 4 January 2022

Received in revised form

5 March 2022

Accepted in revised form 5 March 2022

Available online 12 March 2022

Keywords:

Turtles

Testudines

Pan-Chelonioida

Protostegidae

Protostega

Cretaceous

Russia

ABSTRACT

The Campanian Beloe Ozero locality within the Rybushka Formation in Saratov Province, Russia, produces numerous isolated bones of sea turtles (clade Pan-Chelonioida) identified as belonging to *Protostega gigas*, a giant protostegid, previously reliably known only from the Coniacian – Campanian of North America, and Pan-Chelonioida indet. The *Protostega gigas* specimens described in this paper include bones of the skull (maxillae, jugal, ?quadratojugal, and squamosal), shell (neural, peripherals, and hypoplastron), and appendicular skeleton (scapula and humeri). The material of Pan-Chelonioida indet. demonstrates similarity with different sea turtle taxa of North America and Western Europe: non-*Protostega* protostegids, *Toxochelys* spp., ctenochelyids, dermochelyids, and pan-cheloniids. The estimated size of the *Protostega gigas* specimens from the Beloe Ozero locality well corresponds to those of the largest specimens of this species from North America. *Protostega gigas* from the Beloe Ozero locality represents the first finding of this species outside North America and the first reliable evidence of its cosmopolitanism.

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1. Introduction

Sea turtles (superfamily Chelonioida, the crown and total clades Chelonioida and Pan-Chelonioida respectively) traditionally unite three groups of sea turtles: Cheloniidae, Dermochelyidae, and Protostegidae (Hirayama, 1997, 1998; Raselli, 2018; Evers and Benson, 2019; Evers et al., 2019; Joyce et al., 2021). Some authors exclude Protostegidae from Chelonioida and Pan-Chelonioida (Joyce, 2007; Danilov and Parham, 2008; Sterli, 2010; Parham and Pyenson, 2010; Anquetin, 2012; Anquetin et al., 2015), whereas others extend the latter clade to include basal eucryptodiran taxa, such as Xinjiangchelyidae, Sinemydidae and Macrobaenidae (Cadena and Parham, 2015). In addition, a new clade Ctenochelyidae was recently established within Pan-Chelonioida (Gentry et al., 2019; Joyce et al., 2021).

The Cretaceous record of sea turtles from the European part of the USSR is poorly known (see Appendix A; and reviews: Averianov,

2002; Danilov et al., 2017, 2018; Danilov, 2019). Of 21 records, only eight are based on described and figured materials, whereas others are only mentioned in the literature. Among these latter records, there are materials of *Protostega gigas* Cope, 1872 and Pan-Chelonioida indet. from the Campanian Rybushka Formation of Beloe Ozero, Saratov Province, Russia. These materials were preliminary identified as Protostegina and Chelonioida indet. (Danilov et al., 2018), and later the attribution of the former taxon was specified as *Protostega gigas* (Danilov, 2019). *Protostega gigas* is a giant protostegid turtle previously reliably known only from the Coniacian – Campanian of North America (Fig. 1; see 4. Discussion).

This paper is devoted to the description of the fossil sea turtle material from the Beloe Ozero locality. For geographical and geological setting of this locality as well as for the faunal list of the Rybushka Formation see Averianov and Arkhangelsky (2021).

Institutional Abbreviations – ALAM, Alabama Museum of Natural History, University of Alabama, Tuscaloosa, USA; AMNH, American Museum of Natural History, New York, USA; CM, Carnegie Museum of Natural History, Pittsburgh, USA; FMNH, Field Museum of Natural History, Chicago, USA; FHSM, Sternberg Museum of

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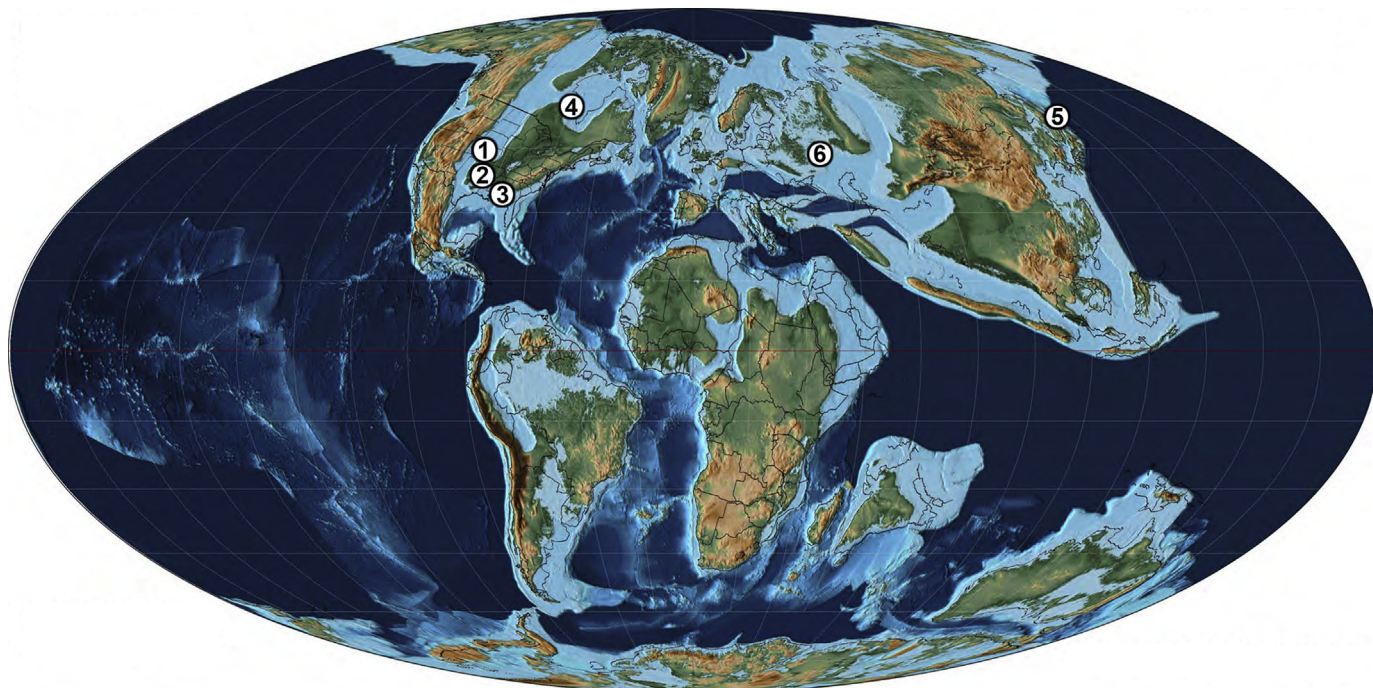


Fig. 1. Distribution of *Protostega*: 1 – Kansas, USA, Niobrara Formation, Coniacian – Campanian (see Zangerl, 1953a); 2 – Arkansas, Brownstown Marl and Marlbrook Marl, Upper Cretaceous (see Zangerl, 1953a); 3 – Alabama, Mooreville Chalk of the Selma Formation, lower-middle Campanian (see Zangerl, 1953a); 4 – Southern Manitoba, Canada, Pembina Member of the Pierre Shale Formation, Campanian (Nicholls et al., 1990); 5 – Iibano-sawa, Katsurazawa, Hokkaido, Japan, upper part? of the Mikasa Formation, middle? Turonian (Hirayama and Chitoku, 1994); 6 – Beloe Ozero locality, Saratov Province, Russia; Rybushka Formation, Campanian (this paper). Paleogeographical map of the early Campanian (80.3 Ma) after Scotese (2013: Map 19).

Natural History at Fort Hays State University, Hays, Kansas, USA; MDM, Morden and District Museum, Morden, Manitoba, Canada; ZIN PH, Paleoherpological collection, Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia.

2. Material and methods

First turtle bones from the Beloe Ozero locality were collected by E.M. Pervushov and M.S. Arkhangelsky in 2001. Additional materials were collected by E.V. Popov in 2003, A.V. Pantelev in 2005, and E.N. Kurochkin in 2006. In 2017–2019, large-scale excavations at this locality were conducted by Saratov State Technical University under licence SRT 01881 PD. All turtle bones described in this paper were found during these excavations. These materials are housed in the collection ZIN PH 244. The same collection contains other turtle bones from the Beloe Ozero locality, which have not been identified yet, and will be described elsewhere.

In addition to the material described below (see Systematic Paleontology), the following Cretaceous pan-chelonoids were used for comparison: *Allopleuron* (orig. *Chelonia*) *hoffmani* (Gray, 1831) from the Maastrichtian – Danian of Netherlands as described by Mulder (2003); *Archelon ischyros* Wieland, 1896 (= *A. marshi* Wieland, 1900) from the lower Campanian – lower Maastrichtian of USA as described by Wieland (1896, 1900a, b, 1903, 1909), and Hay (1908); *Calcarichelys gemma* Zangerl, 1953 from the lower Coniacian – lower Campanian of USA as described by Zangerl (1953a) and Hooks (1998); *Chelosphargis* (orig. *Protostega*) *advena* (Hay, 1908) from the lower Coniacian – lower Campanian of USA as described by Hay (1908) and Zangerl (1953a); *Ctenochelys* (orig. *Toxochelys*) *stenopora* (Hay, 1905) (= *Toxochelys procax* Hay, 1908; = *T. elkader* Hay, 1908; = *Lophochelys natatrix* Zangerl, 1953; = *L. venatrix* Zangerl, 1953; = *Ctenochelys tenuitesta* Zangerl, 1953) from the Coniacian – middle Campanian of USA and United Kingdom,

and Campanian of Germany as described and figured by Hay (1905, 1908), Zangerl (1953b), and Karl and Nyhuis (2012); *Desmatochelys lowi* Williston, 1894 from the upper Cenomanian – upper Turonian of USA as described by Williston (1894), Elliott et al. (1997), Matzke (2007), and Raselli (2018); *D. padillai* Cadena and Parham, 2015 from the upper Barremian-lower Aptian of Colombia as described and figured by Cadena and Parham (2015); *Euclastes* (orig. *Lytoloma*) *wielandi* (Hay, 1908) (= *Osteopygis repandus* Cope, 1868; *Catapleura ponderosa* Cope, 1871; *Lytoloma angusta* Wieland, 1904; *Erquellinesia molaria* Hay, 1908; = *Osteopygis borealis* Hay, 1908; = *Toxochelys atlantica* Zangerl, 1953; = *Dollochelys casieri* Zangerl, 1971; = *Dollochelys coatesi* Weems, 1988; = *Osteopygis roundsi* Weems, 1988; *Osteopygoides priscus* Karl et al., 1998; for other synonyms see Ullmann and Carr, 2021) from the Maastrichtian – Thanetian of European Russia, Morocco and USA as described and figured by Wieland (1904, 1905), Hay (1908), Zangerl (1953b, , 1971), Weems (1988), Karl et al. (1998), Danilov et al. (2018), and Ullmann and Carr, 2021; *Mesodermochelys udulatus* Hirayama and Chitoku, 1996 from the Santonian – lower Maastrichtian of Japan as described by Hirayama and Chitoku (1996); *Porthochelys laticeps* Williston, 1901 from the Coniacian – Santonian of USA as described and figured by Williston (1901) and Zangerl (1953b); *Protostega gigas* Cope, 1872 (= *P. potens* Hay, 1908; = *P. dixie* Zangerl, 1953) from the lower Coniacian – lower Campanian of USA, as described and figured by Cope (1872, 1875), Case (1897), Wieland (1900b, 1906), Williston (1902), Hay (1908), Zangerl (1953a), and Hirayama (1997), and original photographs of the type material (AMNH 1503) from J. Sterli; *Rhinochelys* (orig. *Chelone*) *pulchriceps* (Owen, 1851) (= *Rh. macrorhina* Lydekker, 1889; = *Rh. elegans* Lydekker, 1889; = *Rh. cantabrigiensis* Lydekker, 1889; = *Rh. jessoni* Lydekker, 1889; = *Rh. brachyrhina* Lydekker, 1889; = *Rh. amaberti* Moret, 1935) from the upper Albian – lower Cenomanian of Europe as described and figured by Owen (1851), Lydekker (1889), Scavezzoni and Fischer

(2018), and Evers et al. (2019); *Toxochelys latiremis* Cope, 1873b (= *T. serrifer* Cope, 1875; = *T. brachyrhinus* Case, 1898; = *Porthochelys browni* Hay, 1905; = *Phylemys barberi* Schmidt, 1944; = *Toxochelys weeksi* Collins, 1951) from the Coniacian – Campanian of USA as described and figured by Cope (1873b, 1875), Case (1898), Hay (1905), Schmidt (1944), Collins (1951), Nicholls (1988), Matzke (2009), and Gentry and Ebersole (2018); *Toxochelys moorevillensis* Zangerl, 1953 from the lower Campanian of USA as described and figured by Zangerl (1953b), Nicholls (1988), and Matzke (2009); *Zangerlchelys* (orig. *Catapleura*) *arkansaw* (Schmidt, 1944) from the upper Campanian of USA as described and figured by Schmidt (1944) and Hirayama (2006).

Turtle nomenclature used in this study is phylogenetic (see Joyce et al., 2004, 2021), although traditional (ICZN) nomenclature is also used where relevant.

Anatomical terminology of the turtle skeleton follows Gaffney (1979) for the skull, Zangerl (1969) for the shell, and Hirayama (1992, 1994) for the appendicular skeleton.

3. Systematic paleontology

Testudines Batsch, 1788.

Cryptodira Cope, 1868.

Americhelydia Joyce et al., 2013 (2021).

Pan-Chelonioidea Joyce et al., 2004 (2021).

Protostegidae Cope, 1873a.

Protostega Cope, 1872.

***Protostega gigas* Cope, 1872.**

Figs. 2–4.

Protostegina: Danilov et al., 2018, p. 31; Nelikhov et al., 2018: 114, figs. on pp. 114–118.

Protostega gigas: Danilov, 2019, p. 45.

Referred specimens. ZIN PH: 1/244, left maxilla; 2/244, partial right maxilla; 3/244, right jugal; 4/244, ?partial right quadratojugal; 5/244, partial right squamosal; 6/244, neural; 7/244 and 8/244, bridge peripherals; 9/244, posterior peripheral; 10/244, fragment of the left hypoplastron; 11/244, fragment of the right scapula; 12/244, proximal fragment of the right humerus; 13/244, proximal fragment of the left humerus.

Horizon. Rybushka Formation (Upper Cretaceous, Campanian).

Locality. Beloe Ozero locality, Saratov Province, Russia.

Description. The skull specimens ZIN PH 1/244, 3/244, 4/244, and 5/244 (Fig. 2) belong to large individuals with an estimated skull length of about 60 cm from the tip of the snout to the tip of the squamosal. It cannot be excluded also that all these specimens belong to one individual as they well correspond to each other by size. The specimen ZIN PH 2/244 belongs to a smaller individual with similarly estimated skull length of about 40 cm.

The maxilla ZIN PH 1/244 (Fig. 2A–C) is high with straight anterior (premaxillary) and ventral (labial) borders forming an angle of about 90°. The upper part of the anterior border bears a sheet of bone, which underlies the premaxilla. The contribution to the apertura narium externa is short and located anterodorsally. The prefrontal border is placed dorsally and partially broken off. Posteriorly, the maxilla forms the anteroventral margin of the orbit and a posterior process for the contact with the jugal. Internally, the maxilla has a depression of the fossa nasalis and sutural surfaces for contacts with adjacent elements (premaxilla, prefrontal, vomer, palatine and pterygoid; see Gaffney, 1979: 190), although their precise borders are unclear. The triturating surface of the maxilla is inclined inward (facing medioventrally), narrow, pointing anteriorly and posteriorly and reaching its maximum width in the posterior third. It is slightly concave in cross-section. The labial and

lingual ridges are poorly developed. In its shape and morphology, the maxilla ZIN PH 1/244 is very similar to the maxilla of *Protostega gigas* (AMNH 1503; Hay, 1908: fig. 247; CM P27315; Zangerl, 1953: fig. 31, as *Protostega dixie*).

The partial right maxilla ZIN PH 2/244 (Fig. 2D–F) is poorly preserved and missing most of its borders, except of the posterior 2/3 of the ventral border with triturating surface matching morphology of ZIN PH 1/244.

The right jugal ZIN PH 3/244 (Fig. 2G, H) is roughly triangular in shape. Its anterior process contacted the maxilla under the orbit, the anterodorsal border contributes to the orbit, the posterodorsal process contacted the postorbital, and the posterior border contacted the quadratojugal. The ventral border of the jugal has a very shallow emargination. Internally, the jugal is thickened along the orbital border for about two times the thickness of the rest of the bone. There are no ridges or sutural connections on the internal surface of the bone. The medial process of the jugal is absent. In its shape and morphology the jugal ZIN PH 3/244 is very similar to the jugal of *Protostega gigas* (AMNH 1503; Hay, 1908: fig. 247; CM P27315; Zangerl, 1953: fig. 31, as *Protostega dixie*). The presence of the prominent posterodorsal process of the jugal behind the orbit clearly distinguishes ZIN PH 3/244 from other large bodied protostegids, particularly *Desmatochelys lowii*, in which this process is absent (see Raselli 2018: fig. 5a).

The partial right quadratojugal (?) ZIN PH 4/244 (Fig. 2I, J) is represented by its dorsal portion with a dorsal border for contact with the postorbital and a posterodorsal border for contact with the squamosal. In both contacts, the adjacent bones overlapped the quadratojugal externally by means of deeply interfingering sutures. The preserved portion of the bone is a flat plate with a slight thickening ventrally. The quadratojugal (?) ZIN PH 4/244 is similar to those of *Protostega gigas* (CM P27314, CM P27315; Zangerl, 1953: figs. 30, 31, as *Protostega dixie*).

The partial right squamosal ZIN PH 5/244 (Fig. 2K, L) is missing its anterior, ventral and medial borders. In the central part, the bone has a hole, which, probably, resulted from a bite. Most of the preserved part of the bone is represented by a flat plate participating in the formation of the posterodorsolateral part of the skull roof. The most posterior part of the bone forms an expanded, slightly concave and dorsomedially oriented surface (which, probably, serves as a muscular attachment) continued in a medial process which is not preserved. The squamosal ZIN PH 5/244 is similar in morphology to those of *Protostega gigas* (CM P27314, CM P27315; Zangerl, 1953: figs. 30, 31, as *Protostega dixie*) as well as *Archelon ischyros* (Wieland, 1900a: fig. 1; Hay, 1908: fig. 263), and different from *Desmatochelys lowii* and *D. padillai*, in which the anterior part of the squamosal has a shape of a long band directed anteroventrally (Cadena and Parham, 2015: fig. 6B; Raselli, 2018: fig. 5A).

All shell specimens (ZIN PH 6–10/244; Fig. 3) come from large individuals. The neural ZIN PH 6/244 (Fig. 3A–E) has an irregular shape, wider at anterior (?) end and narrower at posterior (?) end. The anterior end is blunt whereas the posterior one is more pointed with incisions and projections for contact with the subsequent plate. The lateral borders have projections at about mid-length of the neural. The neural keel is well developed making the neural dome-shaped in anterior and posterior views. The ridge is higher at the posterior (?) end. The ventral (internal) surface of the neural is concave bearing breakage from the spiny process. There are no signs of scute sulci on the external surface of the plate. The neural ZIN PH 6/244 is most similar to neural 4 of *Protostega gigas* (CM P27314; Zangerl, 1953a: fig. 35, as *Protostega dixie*).

Two peripherals ZIN PH 7/244 (Fig. 3F–I) and 8/244 (Fig. 3J–M) are roughly rectangular in dorsal view, although their precise medial borders are unclear. The anterior cross-section of ZIN PH 7/244 is

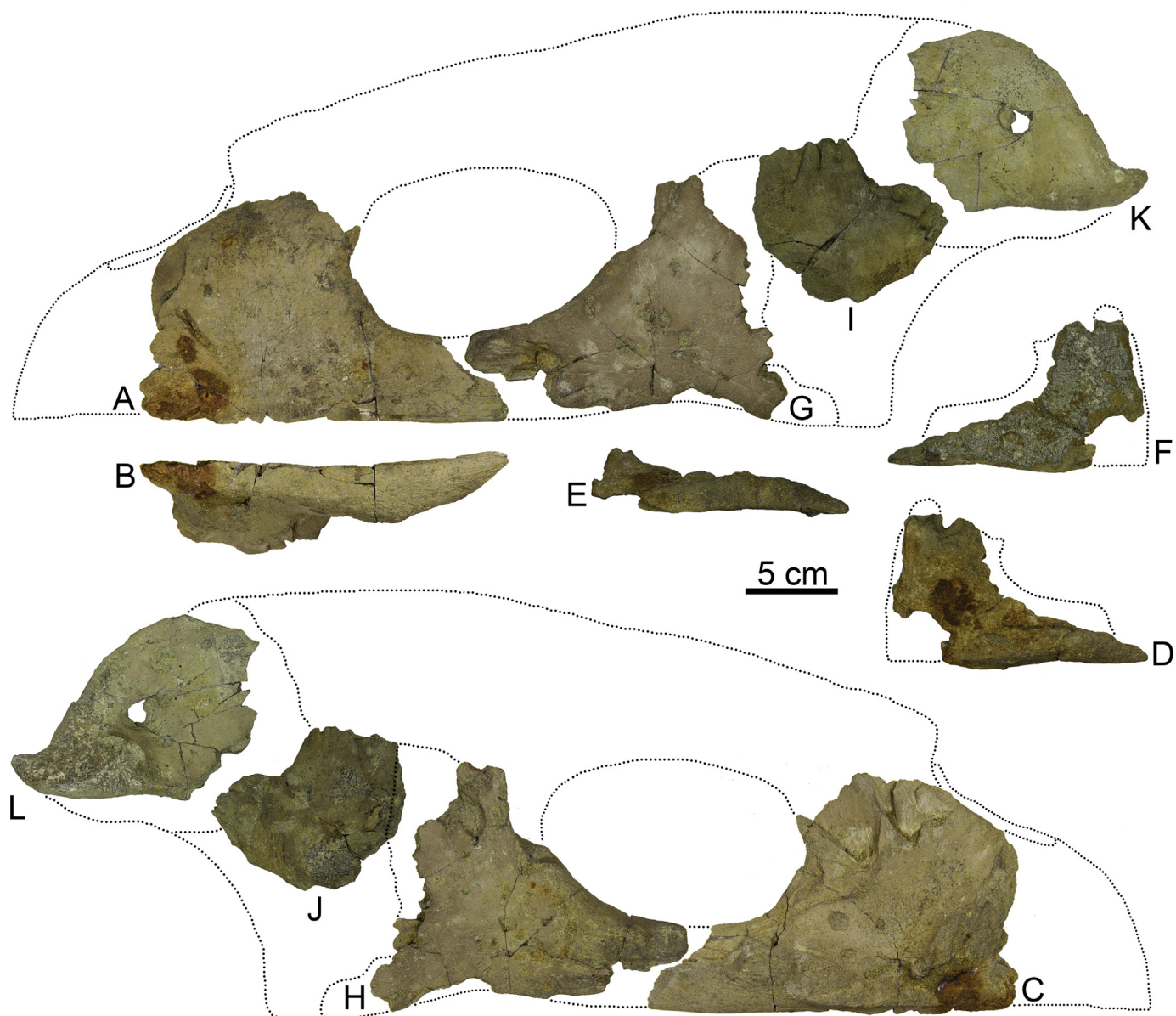


Fig. 2. Skull material of *Protostega gigas* from the Beloe Ozero locality (Saratov Province, Russia; Rybushka Formation, Campanian): A–C – left maxilla ZIN PH 1/244 in lateral (A), ventral (B), and medial (C) views; D–F – partial right maxilla ZIN PH 2/244 in medial (D), ventral (E), and lateral (F) views; G, H – right jugal ZIN PH 3/244 (mirrored) in lateral (G) and medial (H) views; I, J – partial right quadratojugal ZIN PH 4/244 (mirrored) in lateral (I) and medial (J) views; K, L – partial right squamosal ZIN PH 5/244 in lateral (K) and medial (L) views. Dotted lines indicate reconstructed regions.

roughly L-shaped, whereas the posterior one is roughly triangular, suggesting that this is the posterior bridge peripheral, probably, right peripheral 7. The anterior and posterior cross-sections of ZIN PH 8/244 are roughly triangular, suggesting that it comes from a more posterior part of the shell, and, probably, represents left peripheral 8. Externally, ZIN PH 8/244 has a subtriangular bite mark, which is not overgrown by bone and therefore, probably, post-mortem. Scute sulci are absent on both peripherals, although ZIN PH 8/244 has a slight incision at free border in a place where intermarginal sulcus is usually located in turtles. Internally, both peripherals have viscerally opened rib pits, which are rounded in medial view.

The posterior peripheral ZIN PH 9/244 (Fig. 3N–P) is only partially preserved, missing parts of its medial and anterior or posterior borders. The plate is flat, with straight free (lateral) border and fan-shaped medial border. Internally, a shallow groove for free rib is

located in the middle part of plate perpendicular to its free border. The external surface has no scute sulci. In shape and morphology ZIN PH 9/244 is most similar to left peripheral 10 of *Protostega gigas* (CNHM P27314; Zangerl, 1953a: fig. 41C, as *Protostega dixie*).

The fragment of the left hypoplastron ZIN PH 10/244 (Fig. 3Q) represents a posteromedial part of the hypoplastron with the preserved free border at contact with xiphiplastron. The external (ventral) surface of this fragment bears radial striations running from the center of the plate towards its periphery.

The fragment of the right scapula ZIN PH 11/244 (Fig. 4A–C) and proximal fragments of the humeri ZIN PH 12/244 (Fig. 4D–I) and 13/244 (Fig. 4J–O) belong to large individuals. ZIN PH 11/244 is represented by a central portion of the scapula, including the glenoid neck and bases of the acromial and scapular processes; the glenoid articular surface is not preserved. The glenoid neck is not constricted at the base, the glenoid is tetragonal in cross-section,

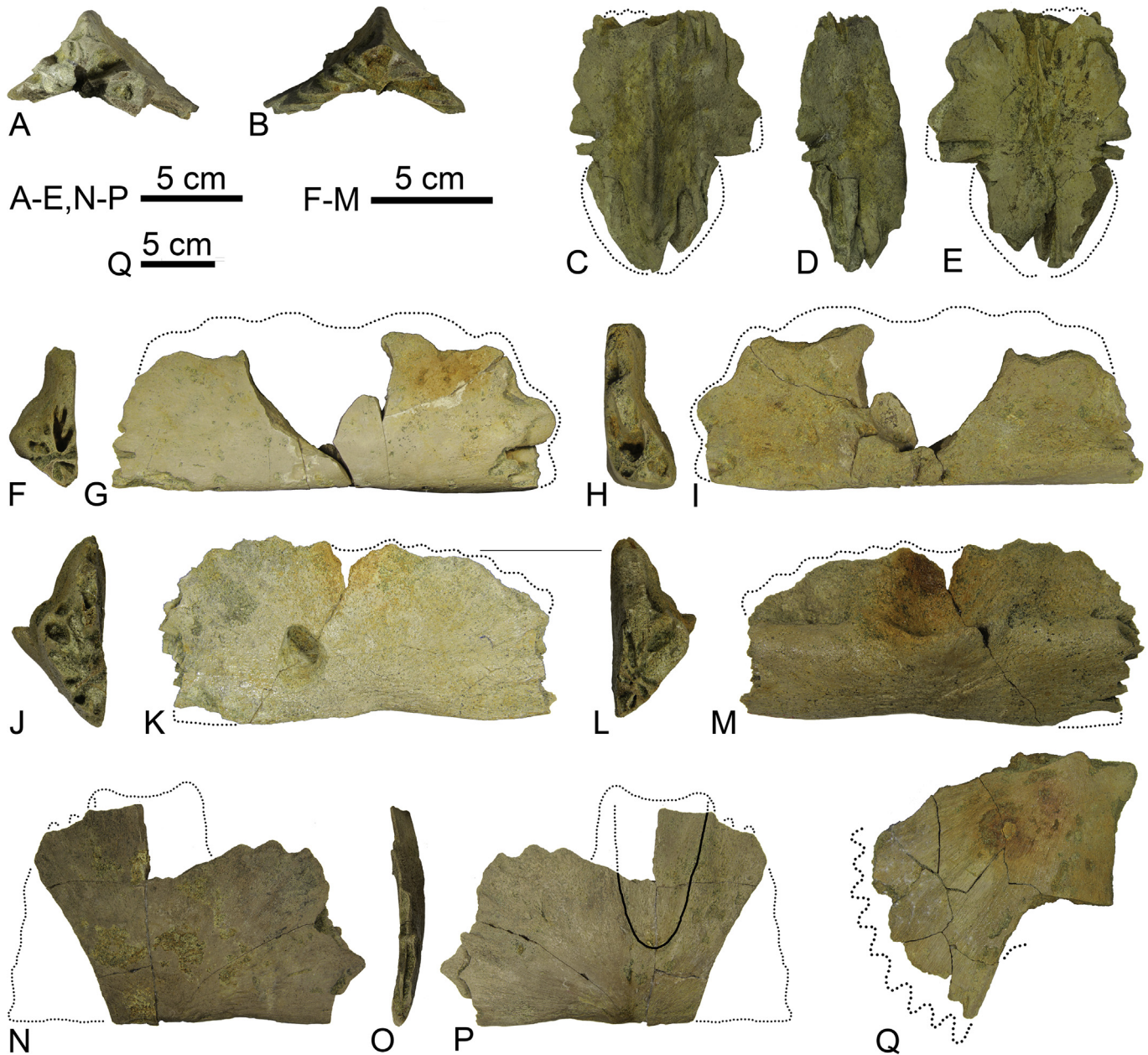


Fig. 3. Shell material of *Protostega gigas* from the Beloe Ozero locality (Saratov Province, Russia; Rybushka Formation, Campanian): A–E – neural ZIN PH 6/244 in posterior (?) (A), anterior (?) (B), dorsal (C), left (?) lateral (D), and ventral (E) views; F–I – bridge peripheral ZIN PH 7/244 in posterior (F), external (G), anterior (H), and internal (I) views; J–M – bridge peripheral ZIN PH 8/244 in posterior (J), external (K), anterior (L), and internal (M) views; N–P – posterior peripheral ZIN PH 9/244 in external (N), anterior or posterior (O), and internal (P) views; Q – fragment of the left hypoplastron ZIN PH 10/244 in ventral view. Dotted lines indicate reconstructed regions.

with its long axis lying in one plane with the processes. The processes are diverging at an angle of about 120° , getting narrower towards distal ends. Both processes are oval-shaped in cross-section. The acromial tubercle is absent. The morphology of the scapula ZIN PH 11/244 is similar to the scapula of *Protostega gigas* (CM P27353; Zangerl, 1953a: fig. 48, as *Protostega dixie*; AMNH 1503).

The proximal fragment of the right humerus ZIN PH 12/244 (estimated length of the humerus is about 290 mm) demonstrates the medial process, which is slightly higher than the humeral head, a partially preserved well developed lateral process, which is restricted to the anterior portion of the shaft, and a small part of the shaft distal from the lateral process. The humeral head is large. The

scar for the m. latissimus dorsi and teres major is shallow and exposed on the middle of the humeral shaft, distal to the humeral head. The scar for the m. coracobrachialis brevis is not observable. The proximal fragment of the left humerus ZIN PH 13/244 (estimated length of the humerus is about 350 mm) is missing part of the shaft distal to the lateral process, which is more complete than in ZIN PH 12/244. The scar for the m. latissimus dorsi and teres major is present, whereas the scar for the m. coracobrachialis brevis is not observable. The bone surface of ZIN PH 13/244 bears numerous traces of post-mortem damage. Both humeri ZIN PH 12/244 and 13/244 look most similar to the humerus of *Protostega gigas* (CM P27452; Zangerl, 1953a: fig. 49, as *Protostega dixie*), and differ from those of its holotype (AMNH 1503) by slender



Fig. 4. Scapular and humeral material of *Protostega gigas* from the Beloe Ozero locality (Saratov Province, Russia; Rybushka Formation, Campanian): A–C – fragment of right scapula ZIN PH 11/244 in posteromedial (A), posterolateral (B), anterolateral (C) views; D–H proximal fragment of the right humerus ZIN PH 12/244 in proximal (D), dorsal (E), anterior (F), ventral (G), and posterior (H) views; I–M – proximal fragment of the left humerus ZIN PH 13/244 in proximal (I), ventral (J), anterior (K), dorsal (L), and posterior (M) views. Dotted lines indicate reconstructed regions.

construction. They differ from the humerus of *Archelon ischyros* by better developed lateral process and narrower waist of the shaft (see Hirayama, 1994: fig. 6g).

Pan-Chelonioida indet.

Figs. 5 and 6.

Referred specimens. ZIN PH: 14/244, fragment of the right maxilla; 15/244, partial left postorbital; 16/244, partial neural; 17/244, anterior suprapygal; 18/244 and 19/244, pygals; 20–22/244, partial costals; 23–28/244, peripherals; 29/244, partial right scapula.

Horizon. Rybushka Formation (Upper Cretaceous, Campanian).

Locality. Beloe Ozero locality, Saratov Province, Russia.

Description. The skull specimens ZIN PH 14/244 and 15/244 (Fig. 5) belong to medium-sized individuals. The fragment of the right maxilla ZIN PH 14/244 (Fig. 5A–D) has a low suborbital portion. The triturating surface is narrowed anteriorly and widened posteriorly with well-developed labial and lingual ridges, of which the former is slightly higher. The preserved medial border did not participate in the formation of the apertura narium interna. In dorsal view, observable are the foramen supramaxillare and the foramen alveolare superius.

The partial left postorbital ZIN PH 15/244 (Fig. 5E–G) is missing its anterior portion. The preserved part of the bone is tetragonal in lateral view, convex externally and concave internally. The dorsal border of the postorbital contacted the parietal, the ventral border contacted the jugal and ?quadratojugal, whereas the posterior border probably was free (contributed to the upper temporal emargination), as it has no signs of a suture.

Among the shell material, there are specimens belonging to medium-sized and large-sized individuals (Fig. 6A–LL).

The neural ZIN PH 16/244 (Fig. 6A–C) is hexagonal shaped, slightly longer than wide with almost equal borders. ZIN PH 16/244 is flat ventrally and convex dorsally and having a bone breakage ventrally indicating a bone connection with a vertebra. The neural has no scute sulcus on the dorsal surface.

The anterior suprapygal ZIN PH 17/244 (Fig. 6D–F) is similar in shape to ZIN PH 16/244, but differs from it in being concave ventrally and keeled (dome-shaped) dorsally and having a smooth ventral surface without bone connection with a vertebra. The suprapygal has no scute sulcus on the dorsal surface.

There are two pygal specimens with different morphology. The pygal ZIN PH 18/244 (Fig. 6G–I) is missing most of its external (dorsal) surface. It is wider than long, narrowed anteriorly and with a small medial (intermarginal) notch posteriorly. Internally, the anterior edge bears a small medial notch, although a contact with the posterior suprapygal, probably, was along entire pygal width as evidenced by its sutured anterior border. There is no scute sulcus either on external or internal surface of the pygal.

The pygal ZIN PH 19/244 (Fig. 6J–M) is complete and has similar proportions to ZIN PH 18/244, from which it differs by smaller size, greater thickness and presence of a midline anterior projection for contact with a posterior suprapygal.

The partial costals ZIN PH 20–22/244 (Fig. 6N–R) have angled medial (neural) borders and reduced ossifications laterally, suggesting presence of large costal-peripheral fontanelles. The lengths of the anteromedial and posteromedial borders of the costals are almost equal, suggesting that the neurals were shortened, like ZIN PH 16/244 described above. In ZIN PH 20/244 and 21/244 (Fig. 6N, O), the ribhead and rib thickening are located in the middle part, whereas in ZIN PH 22/244 (Fig. 6Q) it is moved closer to posterior border of the plate. ZIN PH 20/244 (Fig. 6N) has two round holes near the medial border, which probably represent bite marks. There are no horn sulci on the costals.

The peripherals ZIN PH 23/244 and 24/244 (Fig. 6S–Z) belong to small individuals, whereas ZIN PH 25/244 and 26/244 (Fig. 6AA–HH), to individuals twice as large. The peripherals ZIN PH 23–25/244 (Fig. 6S–DD) represent anterior elements that is evidenced by their shape (long and narrow rectangles with medial thickness increasing towards their posterior border) and absence of rib pits on their medial borders. The free border in ZIN PH 23/244 and 24/244 is straight or slightly convex, whereas in ZIN PH 25/244 it is deeply emarginated at the intermarginal sulcus. In addition, ZIN PH 25/244 has a suture at its posterolateral corner for the intercalary peripheral. ZIN PH 26/244 (Fig. 6EE–HH) represents a posterior peripheral as it has a rib pit at about the center of the medial border and, probably, was wider than ZIN PH 23–25/244, as its medial border is damaged. The free border of ZIN PH 26/244 is deeply emarginated at the intermarginal sulcus, similar to ZIN PH 25/244. ZIN PH 27/244 and 28/244 (Fig. 6II–LL) are incomplete and bear bite marks. In all the peripheral specimens, the sulci are not

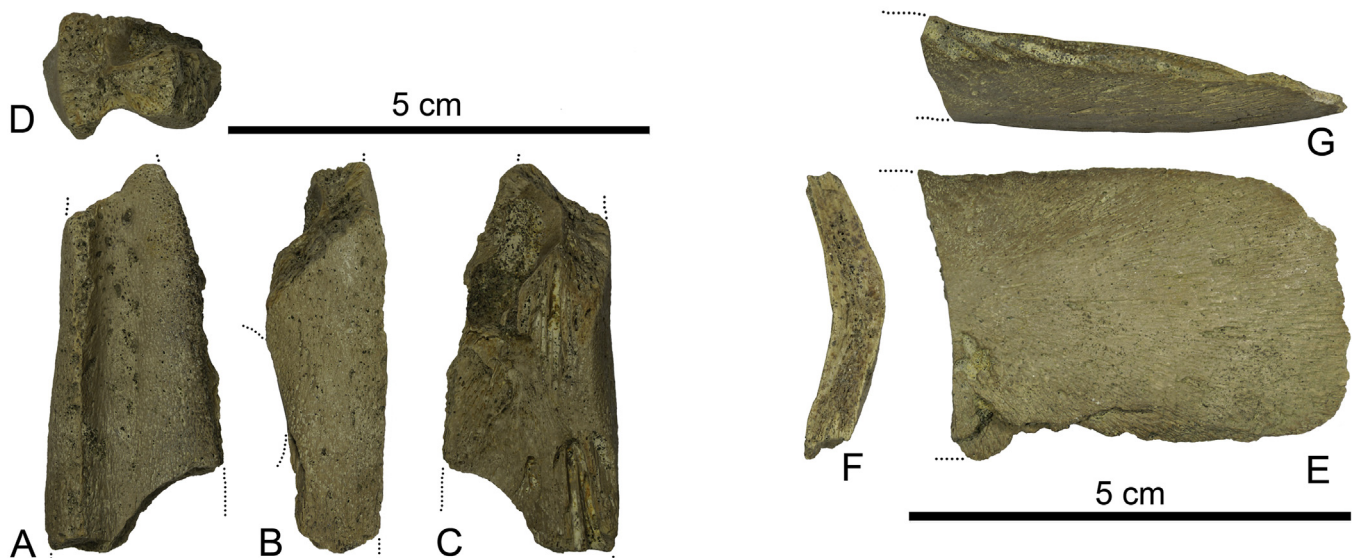


Fig. 5. Skull material of Pan-Chelonioida indet. from the Beloe Ozero locality (Saratov Province, Russia; Rybushka Formation, Campanian): A–D – fragment of the right maxilla ZIN PH 14/244 in ventral (A), right lateral (B), dorsal (C), and anterior (D) views; E–G – partial left postorbital ZIN PH 15/244 in external (lateral) (E), anterior (F), and dorsal (G) views. Dotted lines indicate reconstructed regions.

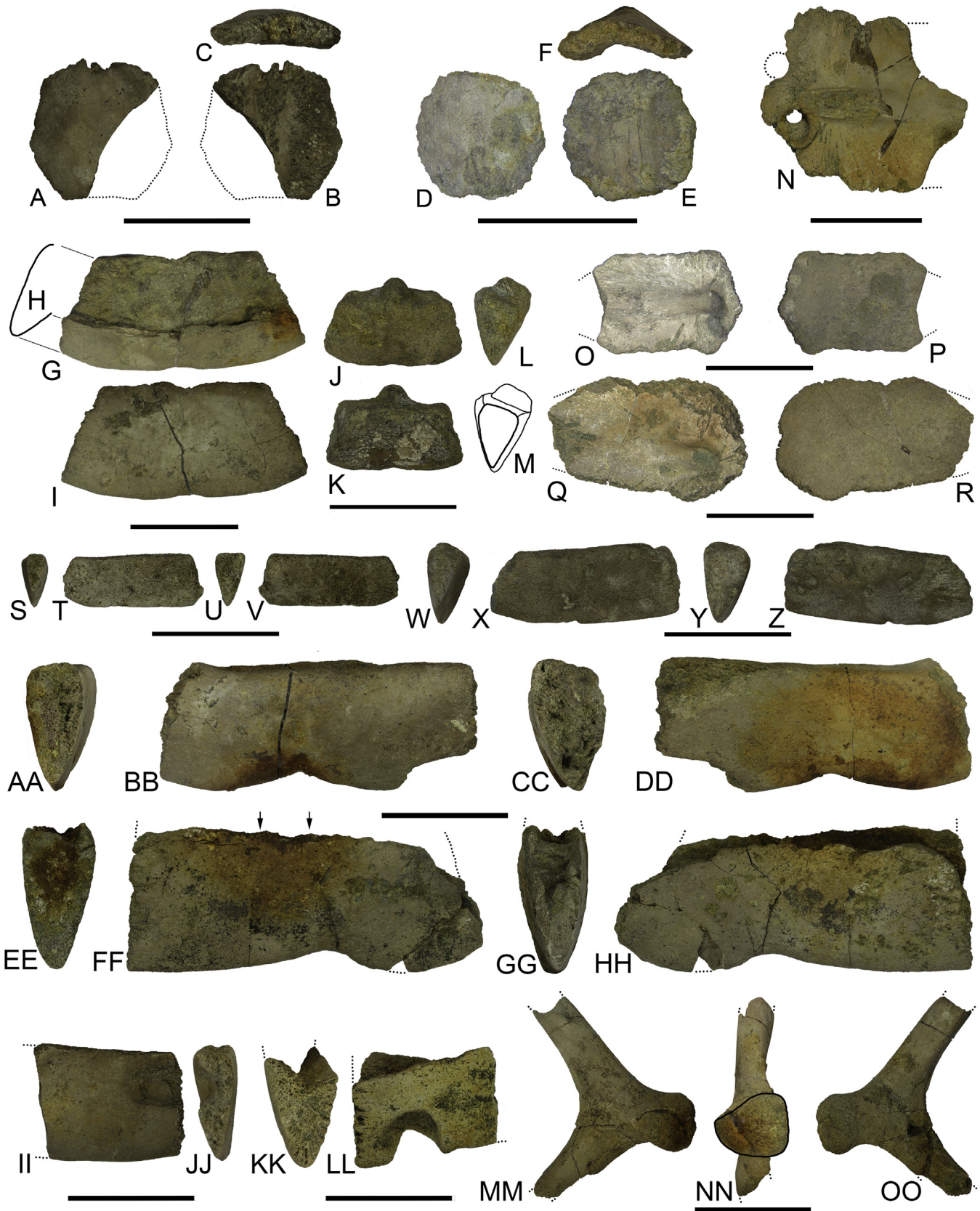


Fig. 6. Postcranial material of *Pan-Chelonioides* indet. from the Beloe Ozero locality (Saratov Province, Russia; Rybushka Formation, Campanian): A–C – partial neural ZIN PH 16/244 in dorsal (A), ventral (B), and anterior (?) (C) views; D–F – anterior supapygal ZIN PH 17/244 in dorsal (D), ventral (E), and anterior (?) (F) views; G–M – pygals ZIN PH 18/244 (G–I) and 19/244 (J–M) in dorsal (G, J), ventral (I, K) and lateral (H, L, M) views; N–R – partial costals ZIN PH 20/244 (N), 21/244 (O, P), and 22/244 (Q, R) in dorsal (P, R) and ventral (N, O, Q) views; S–LL – peripherals ZIN PH 23/244 (S–V), 24/244 (W–Z), 25/244 (AA–DD), 26/244 (EE–HH), 27/244 (II, JJ), and 28/244 (KK–LL) in anterior (S, W, AA, EE, JJ, KK), dorsal (T, Z, BB, HH, II, LL), posterior (U, Y, CC, GG), and ventral (V, X, DD, FF) views; partial right scapula ZIN PH 29/244 in posterior (MM), lateral (NN), and anterior (OO) views. Photographs – all, except H and M (explanatory drawings). Dotted lines indicate reconstructed regions. Arrows on FF indicate position of the rib pit. Scale bars equal 5 cm.

discernible, although the emarginations of the free borders indicate position of the intermarginal sulci.

The partial right scapula ZIN PH 29/244 (Fig. 6MM–OO) is missing distal parts of the acromial and scapular processes. The glenoid neck is slightly constricted at the base, the glenoid is triangular in cross-section, with its long axis perpendicular to the plane of the processes. The processes are diverging at an angle of about 90° and getting narrower towards distal ends. The scapular process is rounded in cross-section, whereas the acromial one is more flattened and triangular in cross-section. The acromial tubercle is absent.)

4. Discussion

4.1. Systematic attribution of the material

The specimens ZIN PH 1–13/244 share large size (larger than in Pan-Chelonioidea indet. from the same locality) and the following features of the Protostegidae: large jugal with nearly straight ventral border, medial process of the jugal absent, lateral process of the humerus restricted to anterior portion of the shaft, deeply interlocking sutures between dermal bones of the skull and shell elements, and, probably, star-shaped hypoplastron (Zangerl, 1953a; Hirayama, 1997; Hooks, 1998; Evers and Benson, 2019). Absence of the pronounced lingual ridge on the maxilla and shallow groove for free rib on ventral surface of the posterior peripheral suggest attribution to the subtribe Protostegina of Hooks (1998) uniting the genera *Archelon* Wieland, 1896 and *Protostega* Cope, 1872. The straight ventral (labial) border of the maxilla, suggesting that the premaxillary beak was only slightly down-curved (unlike *Archelon ischyros*, which has large down-curved beak), well developed keel on the neural (unlike *Archelon ischyros*, which has low and even neural keel), and well developed lateral (radial) process of the humerus (unlike *Archelon ischyros*, in which the radial process of the humerus is reduced to a low ridge) allow assignment of these materials to the genus *Protostega* (Hooks, 1998). Because this genus is currently considered to include only one species – *P. gigas* Cope, 1872 (= *P. potens* Hay, 1908; = *P. dixie* Zangerl, 1953; see Hooks, 1998), and comparison of the new material with the referred material of this species showed their close similarity (see Description), we are confident in assignment of *Protostega* from the Beloe Ozero locality to *P. gigas*. In addition, the age of *Protostega* from the Beloe Ozero locality (Campanian) well corresponds to the known stratigraphic range of *P. gigas* (Coniacian – Campanian; see 4.2. Distribution of *Protostega*). All in all, the described specimens of *Protostega gigas* from the Beloe Ozero locality represent only a small part of the skeleton of this species (Fig. 7).

The specimens ZIN PH 14–29/244 differ from specimens attributed to *Protostega gigas* by smaller size, absence of deeply interlocking sutures between skull bones and shell elements, maxilla with well-developed labial and lingual ridges, postorbital contributing to the upper temporal emargination, hexagonal neurals, absence of viscerally opened rib pits on peripherals, and morphology of the scapula. On the other hand, these specimens demonstrate similarities with different representatives of Cretaceous pan-chelonioids and may belong to several taxa within this group.

The fragment of the right maxilla ZIN PH 14/244 with well-developed labial and lingual ridges (shearing jaws) is similar to some protostegids: *Desmatochelys lowi*, *Rhinochelys* spp., *Chelosphargis advena*, *Calcarichelys gemma*, of which *Rhinochelys*, *Chelosphargis* and *Calcarichelys* are known from the Campanian (Hooks, 1998; Raselli, 2018; Evers et al., 2019). The shearing jaws with well-developed labial and lingual ridges are also known in such

Late Cretaceous pan-chelonioids as *Toxochelys moorevillensis* (Campanian), *Mesodermochelys udulatus* (Maastrichtian) and *Allopleuron hoffmani* (Maastrichtian – Danian) (Zangerl, 1953b; Hirayama and Chitoku, 1996; Mulder, 2003; Parham and Pyenson, 2010).

The partial postorbital ZIN PH 15/244 is somewhat similar to the postorbital of *Chelosphargis advena* (Zangerl, 1953a: fig. 21A, B), which has a straight medial border and contributes to the upper temporal emargination.

The neural (ZIN PH 16/244) and suprapygal (ZIN PH 17/244) specimens are similar to those of *Allopleuron hoffmani* (Mulder, 2003: pls. 6, 7, 22, 24–28, 51) and members of the clade Ctenochelyidae (Gentry, 2018: fig. 15) in being shortened and keeled, although ctenochelyids have additional epineural ossification. Other Cretaceous pan-chelonioids usually have more elongated hexagonal-shaped neurals short sided anteriorly, whereas the shortened neurals are present only in the posterior part of the neural series (see Zangerl, 1953a, b).

The pygal ZIN PH 18/244 is similar in shape to *Porthochelys laticeps* (Zangerl, 1953b: fig. 84), *Toxochelys* spp. (Zangerl, 1953b: figs. 73, 75, 77), and *Zangerlchelys arkansaw* (Schmidt, 1944: fig. 23; Hirayama, 2006: fig. 4), whereas the pygal ZIN PH 19/244 with the midline anterior projection is similar to *Ctenochelys stenopora* (Zangerl, 1953b: fig. 108).

The costal specimens ZIN PH 20–22/244 well correspond to the neural and suprapygal specimens and similar to costals of the clade Ctenochelyidae in almost similar lengths of the anteromedial and posteromedial borders and reduced ossifications laterally (Gentry, 2018: fig. 15).

The peripherals with the emarginations of the free border (ZIN PH 25/244 and ZIN PH 26/244) are similar to those of the members of the clade Ctenochelyidae (Gentry, 2018: fig. 15). The presence of the intercalary peripherals (= epimarginals), similar to ZIN PH 25/244, was reported for *Euclastes wielandi* (as *Lytoloma angusta*) by Wieland (1905: fig. 5).

The scapula ZIN PH 29/244 is similar to those of *Toxochelys latiremis* (Zangerl, 1953b: fig. 72), *Ctenochelys stenopora* (as *Lophochelys natatrix*; Zangerl, 1953b: fig. 91; as *Ctenochelys tenuitesta*; Zangerl, 1953b: fig. 101; as *Ctenochelys stenopora*; Zangerl, 1953b: fig. 111), and *Ctenochelys acris* (Gentry, 2017: fig. 8B, C).

Thus, the non-*Protostega* pan-chelonioid material from the Beloe Ozero locality demonstrates similarity with different sea turtle taxa of North America and Western Europe: non-*Protostega* protostegids, *Toxochelys* spp., ctenochelyids, dermochelyids (*Allopleuron hoffmani*; see Gentry et al., 2019), and pan-chelonioids. Herein, this material is referred to as Pan-Chelonioidea indet. pending new more complete and diagnostic materials from the Beloe Ozero locality.

The described material of *Protostega gigas* and Pan-Chelonioidea indet. suggests overall similarities between the North American, Western European and Russian records of sea turtles in the Campanian.

4.2. Distribution of *Protostega*

Zangerl (1953a) recognized four species in the genus *Protostega*, all from USA: *P. gigas* Cope, 1872 and *P. potens* Hay, 1908 from the Coniacian – lower Campanian Niobrara Formation of Kansas, *P. eaglefordensis* Zangerl, 1953 from the upper Cenomanian Eagle Ford Shale of Texas and *P. dixie* Zangerl, 1953 from the lower-middle Campanian Mooreville Chalk of the Selma Formation of Alabama. In addition, he described material of *Protostega* sp. from the Upper Cretaceous Brownstown Marl and Marlbrook Marl of Arkansas.

Derstler (1988) reported *Protostega* sp. from the uppermost of the middle–upper Campanian Demopolis Chalk of Alabama.

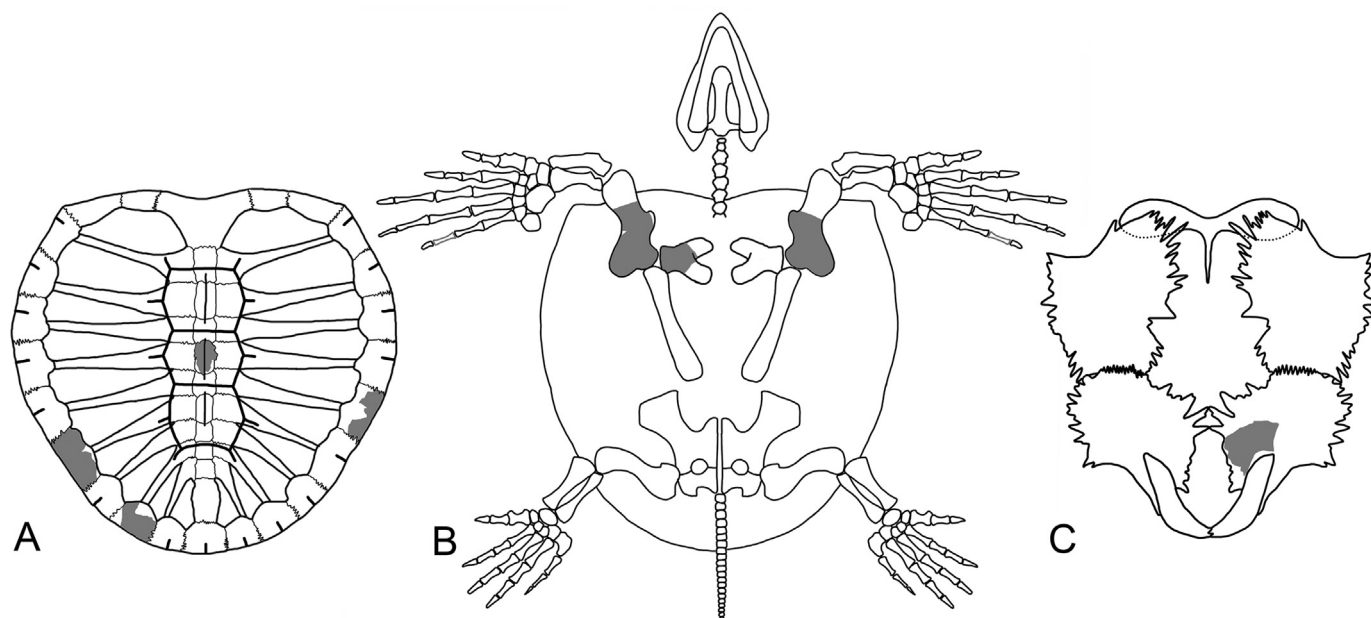


Fig. 7. Reconstructed skeleton of *Protostega gigas* with interpreted positions of the described shell and non-shell postcranial specimens from the Beloe Ozero locality indicated by shaded areas: A – carapace in dorsal view (after Zangerl, 1953a); B – skeleton without plastron in ventral view (after Hirayama, 1997, with modifications); C – plastron in ventral view (after Zangerl, 1953a).

Nicholls et al. (1990) described material of *Protostega* sp. from the lower Campanian Pembina Member of the Pierre Shale of southern Manitoba, Canada.

Hirayama (1997) considered *P. dixie*, *P. potens*, and *Archelon copei* [Wieland, 1909; part] from the Niobrara Formation of Kansas as synonyms of *Protostega gigas*, whereas *P. eaglefordensis* was removed from this genus and considered as “*P. eaglefordensis*”. In addition, he assigned to *P. gigas* material of *Protostega* sp. from Canada (Manitoba), described by Nicholls et al. (1990), and undescribed material of ‘Protostegidae?’ from the middle? Turonian Mikasa Formation of Iibano-sawa, Katsurazawa, Hokkaido, Japan, mentioned by Hirayama and Chitoku (1994). As a result, the distribution of *Protostega gigas* was considered as the ?Santonian – lower Campanian of USA (Kansas, Alabama, and Arkansas), Canada (Manitoba) and Japan (Hokkaido), therefore, being cosmopolitan.

Hooks (1998) moved *Archelon copei* to the genus *Microstega*. Hooks, 1998 and restricted distribution of *Protostega gigas* (= *P. dixie*; = *P. potens*) to the lower Coniacian – lower Campanian of Central and Southeastern USA, apparently overlooking *Protostega* material from Canada and Japan.

Kiernan (2002) mentioned *Protostega* sp. from the Santonian Tombigbee Sand of Alabama.

Everhart (2013) reported finding of a new specimen of *Protostega gigas* (FHSM VP-17979) from the middle Santonian Smoky Hill Chalk of Western Kansas.

Bardet et al. (2014) in a review of Mesozoic marine reptile palaeobiogeography cited Hirayama (1997) in that *Protostega* was probably cosmopolitan, but showed its distribution as restricted to North America only (Hirayama (1997): fig. 5D, circles 2, 4 6; circles 2 and 6 are in wrong position on the map).

Given that material of “*Protostega gigas*” from Japan is undescribed (Hirayama, 1997; pers. comm. to IGD, 2018), *Protostega gigas* from the Beloe Ozero locality represents the first finding of this species outside North America and the first reliable evidence of its cosmopolitanism (Fig. 1).

To summarize, the distribution of *Protostega*, based on all records, should be considered as the Coniacian – Campanian of North

America (Canada, USA) and Campanian of Europe (Russia), whereas the Japanese record needs a confirmation.

4.3. Size of *Protostega*

Cope (1872) restored the total length (head + neck + carapace) of *Protostega gigas* to be 3900 mm based on the skull (AMNH 1503) of 500 mm; the length of the humerus of the same specimen is 300 mm (see Table 1 for measurements). Hay (1895) re-estimated the length of the skull of the same individual as 320 mm (from the snout to the condyle) and 450 mm (the whole length of the skull including the supraoccipital spine), the length of the carapace of another specimen (FMNH UR79) as 3100 mm, neck beyond carapace as 500 mm and as a result, the total length as 3920 mm. Case (1897), based on additional specimen of *Protostega gigas*, which was only slightly smaller than that of Cope's and Hay's specimens, estimated the length of the head, neck and carapace, as 363 mm, 270 mm, and 1640 mm respectively, and therefore the total length of this individual as 2273 mm. The length of the skull of CM 1421, described by Wieland (1906), is 580 mm from the beak to the end of occipital condyle, and the length of its humerus is 340 mm. The length of the carapace of the Wieland's specimen was estimated by Hay (1908) to be about 1100 mm, and its total length, over 2000 mm. At the same time, Hay (1908) estimated the length of the carapace of AMNH 180 (type of *Protostega potens*) to be about 1250 mm; the length of its humerus is 402 mm.

Renger (1935) estimated length of the skull and carapace *Protostega* from the Mooreville Chalk of Alabama to be about 20 inches (508 mm) and 5 feet (1524 mm) respectively, based on a 420 mm long humerus.

The size of other *Protostega gigas* material from Alabama (material of *P. dixie*) can be estimated based on published figures (Zangerl, 1953a): length of the reconstructed skull is estimated to be 650 mm from the beak to end of supraoccipital spine (Zangerl, 1953a: fig. 32) and about 689 mm and 590 mm from the beak to the posterior level of the squamosals in FMNH P27314 and FMNH P27315 (Zangerl, 1953a: figs. 30C and 31) respectively; length of its

Table 1
Some measurements of *Protostega gigas* specimens. “*” means estimated measurement.

| Reference | Specimen | Length, mm | | | | | |
|-----------------------|------------------------------|---------------------------------------|------|----------|---------|-------|--------|
| | | Skull | Neck | Carapace | Humerus | Femur | Total |
| Cope, 1872 | AMNH 1503 | 500* | — | — | 300 | — | 3900* |
| Hay, 1895 | AMNH 1503 | 320 ^a (450 ^b)* | — | — | — | — | 3920* |
| | FMNH UR79 | — | 500* | 3100* | — | — | — |
| Case, 1897 | Larger specimen | 363 ^a * | 270 | 1640* | 348 | 295 | 2273* |
| | Smaller specimen | 197 ^a * | — | — | 190 | — | — |
| Wieland, 1906 | CM 1421 | 580 ^a | — | — | 340 | 270 | — |
| Hay, 1908 | CM 1421 | — | — | 1100* | — | — | >2000* |
| Hay, 1908 | AMNH 180 | — | — | 1250* | 402 | 335 | — |
| Renger, 1935 | ALAM | 508* | — | 1524* | 420 | — | — |
| Zangerl, 1953a | Reconstruction on fig. 18A | — | — | 1690 | — | — | — |
| | Reconstruction on fig. 32 | 650 ^b * | — | — | — | — | — |
| | FMNH P27314 (fig. 30C) | 689 ^c * | — | — | — | — | — |
| | FMNH P27315 (fig. 31) | 590 ^c * | — | — | — | — | — |
| | Reconstruction on fig. 47A | — | — | 1910* | — | — | — |
| | FMNH 27452 (fig. 49) | — | — | — | 363* | — | — |
| Nicholls et al., 1990 | MDM T75.01.06 | — | — | — | — | 280 | — |
| Hirayama, 1997 | Unknown | 600 ^c * | — | 1500* | — | — | 2290* |
| Everhart, 2013 | FHSM VP-17979 | — | — | 800 | — | — | — |
| | FHSM VP-17979 | — | — | — | 180 | — | — |
| This study | ZIN PH 1/244, ZIN PH 3–5/244 | 600 ^c * | — | — | — | — | — |
| | ZIN PH 2/244 | 400 ^c * | — | — | — | — | — |
| | ZIN PH 12/244 | — | — | — | 290* | — | — |
| | ZIN PH 13/244 | — | — | — | 350* | — | — |

^a Length of the skull from the snout to the occipital condyle.
^b Length of the skull from the snout to the supraoccipital spine.
^c Length of the skull from the snout to the end of the squamosal.
^d <http://oceansofkansas.com/ProtostegaDig.html>.

reconstructed carapace is estimated to be about 1910 mm (Zangerl, 1953a: fig. 47); length of the humerus FMNH 27452 is estimated to be about 363 mm (Zangerl, 1953a: fig. 49).

The *Protostega* from Manitoba is smaller than AMNH 180, because the length of the femur from Manitoba is 280 mm, whereas those of AMNH 180 is 335 mm (Hay, 1908).

Hirayama (1997) estimated the maximum length of the carapace of *Protostega gigas* to be 150 cm, but did not indicate the source of this data. In this case, based on reconstruction of the skeleton (Hirayama, 1997: fig. 5A), the skull length and total length (from the tip of the snout to the tip of the tail) are about 60 and 229 cm respectively.



Fig. 8. Hypothetical reconstruction of *Protostega gigas* from the Beloe Ozero locality (Saratov Province, Russia; Rybushka Formation, Campanian), crawling ashore to lay eggs, attacked by two dromaeosaurid theropods, and with an ankylosaur in the background. Painting by Andrey Atuchin.

Everhart (2013) reported 800 mm across the carapace of the *Protostega gigas* specimen (FHSM VP-17979) from the middle Santonian Smoky Hill Chalk of Western Kansas. The humerus of the same specimen is 180 mm long (<http://oceansofkansas.com/ProtostegaDig.html>).

The material of *Protostega gigas* from the Beloe Ozero locality belongs to individuals with the largest skull length of about 600 mm and the largest humerus length of about 350 mm (see Description). These estimations correspond to North American specimens with an estimated carapace length of more than 1100 mm and total length of more than 2000 mm (CM 1421; Wieland, 1906; Hay, 1908; see Table 1). The estimation of the largest skull length of *Protostega gigas* from the Beloe Ozero locality well corresponds to the skull length estimated from the reconstruction of this species presented by Hirayama (1997: fig. 5A) with a maximum carapace length of 1500 mm and an estimated total length of 2290 mm. Thus, the estimated size of the *Protostega gigas* specimens from Europe (the Beloe Ozero locality; Fig. 8) well corresponds to those of the largest specimens of this species from North America.

5. Conclusions

The isolated turtle bones from the Campanian Beloe Ozero locality within the Rybushka Formation in Saratov Province, Russia, belong to sea turtles (Pan-Chelonioida): a giant protostegid *Protostega gigas*, previously reliably known only from the Coniacian – Campanian of North America, and Pan-Chelonioida indet.

Protostega gigas from the Beloe Ozero locality represents the first finding of this species outside North America and the first reliable evidence of its cosmopolitanism.

The estimated size of the *Protostega gigas* specimens from the Beloe Ozero locality well corresponds to those of the largest specimens of this species from North America.

The material of Pan-Chelonioida indet. demonstrates similarity with different sea turtle taxa of North America and Western Europe: non-*Protostega* protostegids, *Toxochelys* spp., ctenochelyids, dermochelyids, and pan-cheloniids.

The described material of sea turtles from the Beloe Ozero locality suggests overall faunal similarities between the North American Western European and Russian records in the Campanian.

Acknowledgments

The authors thank Juliana Sterli for photographs of the type material of *Protostega gigas* used for comparison, Ren Hirayama for information about the material of “*Protostega gigas*” from Japan, and Anthony Melthese for information about additional *Protostega* findings in USA. Two reviewers (Serjoscha Evers and an anonymous) are thanked for useful comments and corrections of the English. The laboratory research by I.G.D., E.M.O. and A.O.A. received support from the Russian Science Foundation (19-14-00020) and the Zoological Institute, Russian Academy of Sciences (project 122031100282-2).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cretres.2022.105196>.