A TAIL VERTEBRA OF A GIANT SEA TURTLE (TESTUDINES: CHELONIOIDEA) FROM THE UPPER CRETACEOUS DEPOSITS OF THE MALYY PROLOM LOCALITY (RYAZAN PROVINCE, RUSSIA)

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Abstract. The article describes a tail vertebra of a giant sea turtle Chelonioidea indet. From the Upper Cretaceous Malyy Prolom locality (Ryazan Province, Russia; middle Cenomanian – middle Santonian). The tail vertebra, probably IV–X, with a preserved length of 3.8 cm belonged to a turtle comparable in size with the type specimen of the protostegid Archelon ischyros from the Campanian of USA. The proportions of the vertebral centrum suggest that it belonged to a female.

Keywords: *Chelonioidea, turtle, Cretaceous, Dmitrov Formation, Ryazan Province, Russia*

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INTRODUCTION

Remains of sea turtles (superfamily Chelonioidea, or clade Pan-Chelonioidea) from the Cretaceous of European Russia are known from 21 localities (see Danilov et al., 2022: Appendix A). The largest representatives of sea turtles in this territory come from the Upper Albian locality of Akusha, Dagestan (cf. Desmatochelys sp.; Danilov, 2019; Danilov et al., 2020) and the Campanian locality of Beloe Ozero, Saratov Province (Protostega gigas Cope, 1872; Danilov et al., 2022).

In 2021, in a sand quarry on the southwestern outskirts of Maly Prolom village, Shatsky district, Ryazan region, Russia (54°06′ N, 41°69′ E; Fig. 1), one of the authors (A.P. Evsyutkin) found a caudal vertebra of a large reptile. The find comes from a compacted horizon of ferruginous quartz sands with gravel, pebbles, and remains of bivalve mollusks and vertebrates, which belongs to the lower part of the Dmitrov Formation (Middle-Upper Santonian) and lies unconformably on the surface of the Yakhroma Formation (Lower-Middle Cenomanian) (for more details on the geology of the locality, see: Solonin et al., 2021b). Based on materials from this locality, preliminary data on elasmobranch teeth have been previously published, vertebrae and teeth of actinopterygians were mentioned, and teeth of various diapsid reptiles were described: pterosaurs (ornithocheirids), plesiosaurs, ichthyosaurs, and mosasaurids ("aquatic squamates"; Solonin et al., 2020, 2021a, b). Considering the possibility of partial redeposition of vertebrate remains at this locality, the geological age of the complex corresponds to the combined stratigraphic interval of the Yakhroma and Dmitrov Formations (Middle Cenomanian - Middle Santonian), while its individual components may have Cenomanian, Turonian, or Coniacian - Santonian age (Solonin et al., 2020, 2021a, b).

This article describes the aforementioned caudal vertebra of a large reptile, which is attributed to marine turtles (Chelonioidea indet.).

The comparison was carried out in two stages. In the first stage, to determine the systematic position of the vertebra among reptiles, comparisons were made with representatives of various groups of large (similar in vertebrae size) Late Cretaceous reptiles (see Comparison): with the mosasaurid

Prognathodon lutugini (Yakovlev, 1901) from the Krymskoye locality (Campanian), Russia (Grigoriev, 2013), the eusuchian Deinosuchus riograndensis (Colbert and Bird, 1954) from the Aguja Formation (Campanian), USA (Cossette, Brochu, 2020), and titanosaurs Paludititan nalatzensis Csiki et al., 2010, Magyarosaurus dacus (Nopcsa, 1915), Titanosauria indet. and Lithostrotia indet. from several Maastrichtian localities, Romania (Mocho et al., 2023), as well as with marine turtles (superfamily Chelonioidea) in general.

In the second stage, after determining the affiliation with sea turtles, the comparison was made with the following representatives: Allopleuron hofmanni (Gray, 1831) from the Maastricht Formation (Maastrichtian), Netherlands (Mulder, 2003); Archelon ischyros Wieland, 1896 from the Pierre Shale Formation (Campanian), USA (Wieland, 1909); Caretta caretta (L., 1758), recent (Mulder, 2003, Table 39, fig. 2, 3); Chelonia mydas (L., 1758), recent (Mulder, 2003, Table 39, fig. 4); Ctenochelys acris Zangerl, 1953 from the Mooreville Chalk Formation (Santonian–Campanian), USA (Zangerl, 1953b: Table 20, fig. F); Cynocercus incisus Cope, 1872 from an unknown locality, probably the Niobrara Formation (Coniacian–Campanian), USA (Cope, 1875); Mesodermochelys undulatus Hirayama et Chitoku, 1996 from the Lower Sandy Siltstone Formation (lower Maastrichtian), Japan (Hirayama, Chitoku, 1996); Mexichelys coahuilaensis Brinkman et al., 2009 from the Cerro del Pueblo Formation (upper Campanian), Mexico (Brinkman et al., 2009); Protostega gigas Cope, 1872 from the Mooreville Chalk and Niobrara Formations (Coniacian–Campanian), USA, and Rybushka Formation (Campanian), Russia (Cope, 1875; Zangerl, 1953a; Danilov et al., 2022); Toxochelys latiremis Cope, 1873 from several formations (Coniacian–Campanian), USA (Nicholls, 1988) ; Toxochelys moorevillensis Zangerl, 1953 from the Mooreville Chalk Formation (Santonian–Campanian), USA (Zangerl, 1953b).

Specimens mentioned in this article are housed in the following institutions: CMNH – Carnegie Museum of Natural History, Pittsburgh, USA; IRSNB – Royal Belgian Institute of Natural Sciences, Brussels, Belgium; NCB – Netherlands Centre for Biodiversity Naturalis, Leiden, Netherlands; YPM – Peabody Museum of Natural History at Yale University, New Haven, USA; ZIN PH – Zoological Institute of the Russian Academy of Sciences, paleoherpetological collection, St. Petersburg, Russia.

In the description of caudal vertebra elements, the names of morphological structures are given according to A. Romer (Romer, 1956). The taxonomy of turtles follows I.G. Danilov et al. (2017).

Description of the material (fig. 2). ZIN PH 1/291, body of an anterior caudal vertebra. The distal parts of the transverse processes, as well as the areas of the anterior and posterior articular surfaces are rounded. The vertebra is short, slightly dorsoventrally compressed. Nutrient foramina are visible across the entire undamaged surface, especially large ones on the floor of the neural canal. The anterior part of the vertebra is significantly wider than the posterior one due to the expanded areas of articulation with the neural arch and transverse processes. The sutural surfaces for the neural arch are wide; the neural canal is narrow, its width in the middle part is 10 mm. The vertebral body is procoelous. The anterior articular surface is concave, oriented forward and slightly ventrally; its shape when viewed from the front is not entirely clear due to the rounded edges: it could have been oval with dorsoventral compression or hexagonal with rounded corners. The posterior articular surface is strongly convex, its exact shape when viewed from behind is unclear, as its edges are rounded. The transverse processes are connected to the vertebral body by a clearly visible suture. They are located in the anterior part of the vertebral body, oval in cross-section. The exact mediolateral length of the transverse processes is unclear due to rounding, however, judging by the angle between their anterior and posterior edges, they were not very long. The axis of the transverse processes was oriented approximately perpendicular to the axis of the vertebral body. A deep longitudinal groove on the lateral surfaces of the body is not observed. When viewed from the side, the vertebra is concave on the ventral side between the anterior and posterior articular surfaces, and the ventral surface of the posterior part of the vertebra is positioned significantly more ventrally than the anterior part. The preserved area of the ventral surface of the vertebral body is a smooth, approximately rectangular area with no relief structures observed on it. The ventral and lateral surfaces of the vertebra are separated by sharp longitudinal ridge-like bends. The posterior section of the ventral surface of the vertebra, where facets for chevrons might have been, is rounded.

Comparison. The pronounced procoelous bodies and large size of the vertebrae, as in ZIN PH 1/291, among Late Cretaceous reptiles are characteristic of mosasaurids, mentioned from the Maly Prolom locality (Solonin et al., 2021a), eusuchians, caudal vertebrae of most titanosaurs, and posterior cervical and caudal vertebrae of sea turtles. In ichthyosaurs and plesiosaurs, mentioned from this locality (Solonin et al., 2021a), as well as Late Cretaceous dinosaurs not belonging to titanosaurs, the vertebrae do not have a pronounced procoelous shape (Romer, 1956; Skuchas et al., 2015; Averianov, Lopatin, 2020).

If we assume that ZIN PH 1/291 belongs to a mosasaurid, then in shape and general morphology it is most comparable with vertebrae from the trunk and anterior part of the caudal sections (as the transverse processes adjoin the neural arch; Fig. 3, *a, b*). In mosasaurids, haemal arches and transverse processes are simultaneously present only on caudal postpygal vertebrae, but they have a less elongated shape, usually with pear-shaped articular surfaces (Russell, 1967). In any case, ridge-like bends, as in ZIN PH 1/291, are not characteristic of mosasaurid vertebral bodies.

In eusuchians, the transverse processes of caudal vertebrae are dorsoventrally flattened, unlike ZIN PH 1/291 with its wide oval cross-section of transverse processes (Fig. 3, *c*).

Caudal vertebrae of titanosaurs are diverse in shape. The presence of developed transverse processes in ZIN PH 1/291 gives it similarity to the anterior caudal vertebrae of titanosaurs, but these vertebrae (except for the most anterior ones in some species) bear a longitudinal groove on the ventral surface (Averianov, Lopatin, 2020). That is, ZIN PH 1/291 is similar only to the most anterior caudal vertebrae of some titanosaur species (Fig. 3, *d, e*). Dorsoventral compression of the anterior caudal vertebrae is a diagnostic condition of Saltasaurinae, however, Saltasaurinae have dorsoventrally high transverse processes (Salgado et al., 1997; Galina, Otero, 2009). In addition, the posterior part of the vertebral body is displaced ventrally relative to the anterior part, which is not characteristic of titanosaurs. Thus, ZIN PH 1/291 does not belong to titanosaurs.

At the same time, such morphology – a ventrally displaced posterior part of the body is common for caudal vertebrae of turtles, among which only representatives of Chelonioidea reached very large sizes in the Late Cretaceous (Fig. 3, *i*; Hirayama, Chitoku, 1996, Fig. 8, 9). The absence of a keel on the ventral surface of the body indicates that the vertebra cannot be a posterior cervical one. In terms of body length, ZIN PH 1/291 is similar to the caudal vertebra of a female Allopleuron hofmanni (IRSNB 3901), and it is shorter than that of a male of the same species (IRSNB 3668) (Mulder, 2003). The shape of the anterior articular surface of the body of ZIN PH 1/291 could have been oval with dorsoventral compression or hexagonal with rounded corners, as in A. hofmanni and in some caudal vertebrae of Mesodermochelys undulatus, and it differs from the rounded anterior articular surface of the posterior caudal vertebra of Protostega gigas (Zangerl, 1953a, Fig. 54C; Hirayama, Chitoku, 1996, Fig. 8; Mulder, 2003). On the caudal vertebrae of Allopleuron hofmanni (except for the I caudal vertebra NCB 14063), Ctenochelys acris, Cynocercus incisus, and Mesodermochelys undulatus, the transverse processes have a well-defined recess from the anterior edge of the vertebral body (Fig. 3, *j*; Cope, 1875, Table VIII, Fig. 3a, 4a; Zangerl, 1953b, Table 20, Fig. F; Hirayama, Chitoku, 1996, Fig. 8B; Mulder, 2003, Pl. 38). The axis of the transverse processes of ZIN PH 1/291 was oriented approximately perpendicular to the axis of the vertebral body, close to the condition in IV–VI caudal vertebrae of M. undulatus and in the second quarter of the series of caudal vertebrae of modern Caretta caretta and Chelonia mydas (Hirayama, Chitoku, 1996, Fig. 8B; Mulder, 2003, Table 39, Fig. 2–4). No deep longitudinal groove on the lateral surfaces of the body of ZIN PH 1/291 is observed, unlike the smaller of the two described vertebral bodies of Protostega gigas (Cope, 1875, p. 105, Table Pl. XI, Fig. 5b). The preserved area of the ventral surface of the body of ZIN PH 1/291 represents a nearly rectangular smooth platform; no relief structures are observed on it – neither a longitudinal groove, as in Cynocercus incisus (Cope, 1875, Table VIII, Fig. 3a, 4a), nor a ventral keel, as in one of the vertebrae of Protostega gigas (Cope, 1975, p. 105, Pl. XI, Fig. 4b). Similar to ZIN PH 1/291, an extensive area on the ventral surface of the vertebral body, limited laterally by bends, is present on the anterior caudal vertebrae of Allopleuron hofmanni (Fig. 3, *and* ; Mulder, 2003, Table 38, fig. 3).

Measurements, in mm. Length of vertebral body – 38, width with preserved parts of transverse processes – 60; height of anterior articular surface in preserved condition – 22, its width in preserved condition – 26; height of posterior articular surface – 22, its width – 27.

DISCUSSION

Systematic affiliation ZIN PH 1/291. Specimen ZIN PH 1/291 differs from procoelous vertebrae of other large Late Cretaceous reptiles (see Comparison) and corresponds to the caudal vertebrae of turtles based on the following characteristics: ventrally displaced posterior part of the vertebral body; cross-section of transverse processes in the form of a wide oval; presence of an extensive area on the ventral surface of the body, limited laterally by bends. The very large size of ZIN PH 1/291, the associated marine fauna, and the Cretaceous age indicate that this vertebra belonged to a representative of the superfamily Chelonioidea. The Cenomanian–Santonian age of ZIN PH 1/291 suggests its probable affiliation with the family Protostegidae, as giant Cretaceous non-protostegid chelonioids are known only from the Campanian and Maastrichtian (Alienochelys selloumi, Gigantatypus salahi, Leviathanochelys aenigmatica, and Ocepechelon bouyai: Kaddumi, 2006; Bardet et al., 2013; de Lapparent de Broin et al., 2013; Castillo-Visa et al., 2022). Besides them, remains of giant archaic Dermochelyidae indet. have been mentioned from the Albian–Cenomanian of the Lebedinsky and Stoilensky quarries (Averianov, 2002) , but they require additional study (Danilov et al., 2017, 2021; Danilov et al., 2021). Thus, ZIN PH 1/291 is identified as a caudal vertebra of Chelonioidea indet. and possibly belongs to unknown Protostegidae.

Position of ZIN PH 1/291 in the series of caudal vertebrae. The caudal vertebra ZIN PH 1/291 is not the first in the series, as its transverse processes are oriented strictly laterally, not anterolaterally for articulation with the pelvis, which is characteristic of the first caudal vertebra in turtles (Williston, 1925; Romer, 1956; Hoffstetter, Gasc, 1969). It also cannot belong to the posterior part of the series, otherwise the vertebra would have belonged to a turtle of implausibly large size. Considering the orientation of the transverse processes' axis in caudal vertebrae of other marine turtles (see Comparison), it is most likely that it belonged to the middle or posterior part of the anterior half of the series (most likely, IV-X caudal vertebrae).

Sex of the turtle from Maly Prolom. The caudal section of the vertebral column in marine turtles exhibits sexual variation. It is known that in most modern turtles, including chelonioids, the tail is significantly larger and longer in males than in females (Hirayama, Chitoku, 1996). For example, in adult male Chelonia mydas, the tail is on average 1.75 times longer than in females (Mulder, 2003). In addition, adult male marine turtles have large caudal vertebrae with powerful transverse and dorsal processes (Wyneken, 2001). For this reason, pronounced intraspecific differences in the length of caudal vertebrae of Cretaceous chelonioids (Allopleuron hofmanni and Mesodermochelys undulatus) are explained by sexual dimorphism (Hirayama, Chitoku, 1996; Mulder, 2003). The short vertebral body of ZIN PH 1/291, similar in proportions to the caudal vertebrae of a female A. hofmanni IRSNB 3901, suggests that ZIN PH 1/291 may have belonged to a female.

Size of the turtle from Maly Prolom. The length (?) of the IVth-Xth caudal vertebra ZIN PH 1/291 (in its preserved form - 3.8 cm; reconstructed - about 4.0 cm) is the same as that of the IVth and Vth caudal vertebrae of the type specimen of Archelon ischyros YPM 3000 (4.0 cm) with a carapace length of 2 m and a humerus length of 60 cm (Wieland, 1909). In Protostega gigas CMNH 1420, with a humerus length of 34 cm and a carapace length almost half that of Archelon ischyros YPM 3000 (Wieland, 1906, 1909), the length of the Ist caudal vertebra was 3.5 cm. It should be noted that the Ist caudal vertebra of chelonioids is larger than the IVth-Xth caudal vertebrae. Thus, the individual to which the caudal vertebra ZIN PH 1/291 belonged was evidently of similar size to the type specimen of A. ischyros and exceeded the size of Protostega gigas CMNH 1420. These are not the largest specimens of A. ischyros and P. gigas - literature contains data on specimens of A. ischyros with a carapace length of 2.2 m and P. gigas with a carapace length of 2.0 m (Derstler et al., 1993). The length of the IInd and IIIrd caudal vertebrae of the male Allopleuron hofmanni IRSNB 3668 exceeds the length of ZIN PH 1/291, measuring 42 mm, however, the caudal vertebrae of IRSNB 3668 are considerably more elongated than those of the female A. hofmanni IRSNB 3901 (Mulder, 2003) and the chelonioid ZIN PH 1/291. Therefore, the overall size of the individual to which the vertebra ZIN PH 1/291 belonged was evidently larger than that of A. hofmanni IRSNB 3668 with a carapace length of 140 cm and a left humerus length of 28 cm (Hirayama, 1992: Appendix).

Gigantism was a common phenomenon among Cretaceous chelonioids, but most materials about them come from the Campanian and Maastrichtian. Earlier giant chelonioids have been less studied so far, although very large species (Protostegidae inc. sed.) appear in the Valanginian, and those approaching maximum sizes, slightly smaller than the type specimen of Archelon ischyros (Cratochelone berneyi Longman, 1915), appear already in the Late Albian (Kear, 2006; Cadena, Combita-Romero, 2023). In the stratigraphic interval corresponding to the Maly Prolom locality (Cenomanian–Santonian), the known very large chelonioids include protostegids "Protostega" eaglefordensis from the Cenomanian Eagle Ford Shale, USA, and P. gigas from the Coniacian–Campanian of several localities in the USA and from the Campanian of the Beloe Ozero locality in Russia (Zangerl, 1953a; Danilov et al., 2022). Thus, the chelonioid vertebra ZIN PH 1/291 from the middle Cenomanian – middle Santonian of the lower part of the Dmitrov Formation adds to the list of Cretaceous giant chelonioids.

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CONFLICT OF INTERESTS

The authors of this work declare that they have no conflict of interest.

REFERENCES

1. *Danilov I.G.* Paleontological record of marine turtles (Chelonioidea) of Northern Eurasia // Modern herpetology: Problems and solutions. Second international youth conference of herpetologists of Russia and neighboring countries, dedicated to the 100th anniversary of the Department of Herpetology of the Zoological Institute of the Russian Academy of Sciences (St. Petersburg, Russia, November 25-27, 2019). Conference proceedings. St. Petersburg, 2019. P. 45.
2. *Danilov I.G., Lysenko D.P., Bukatkin V.V. et al.* New data on Cretaceous turtles of the Belgorod region // Theoretical and applied aspects of paleontology. Proceedings of the LXVII session of the Paleontological Society. St. Petersburg, 2021. P. 106–107.

3. *Danilov I.G., Syromyatnikova E.V., Sukhanov V.B.* Subclass Testudinata // Fossil vertebrates of Russia and adjacent countries. Fossil reptiles and birds. Part 4 / Eds. Lopatin A.V., Zelenkov N.V. Moscow: GEOS, 2017. P. 27–395.
4. *Danilov I.G., Khapisov O.K., Zverkov N.G.* Discovery of remains of a primitive sea turtle in the Lower Cretaceous of Dagestan // Biogeography and evolutionary processes. Proceedings of the LXVI session of the Paleontological Society of the Russian Academy of Sciences. St. Petersburg: Kartfabrika VSEGEI, 2020. P. 237–238.
5. *Skuchas P.P., Efimov M.B., Rezvyi A.S.* Superorder Crocodyliformes // Fossil vertebrates of Russia and adjacent countries. Fossil reptiles and birds. Part 3 / Eds. Kurochkin E.N., Lopatin A.V., Zelenkov N.V. Moscow: GEOS, 2015. P. 17–45.
6. *Averianov A.O.* Review of Mesozoic and Cenozoic sea turtles from the former USSR // Russ. J. Herpetol. 2002. № 9(2). P. 137–154.
7. *Averianov A.O., Lopatin A.V.* An unusual new sauropod dinosaur from the Late Cretaceous of Mongolia // J. Syst. Palaeontol. 2020. V. 18. Iss. 12. P. 1009–1032. doi: 10.1080/14772019.2020.1716402
8. *Bardet N., Jalil N.E., de Lapparent de Broin F. et al.* Giant chelonioid turtle from the Late Cretaceous of Morocco with a suction feeding apparatus unique among tetrapods // PLOS One. 2013. V. 8(7). e63586. doi:10.1371/journal.pone.0063586
9. *Brinkman D., Aquillon-Martinez M.C., de Leon Dávila C.A. et al.* Euclastes coahuilaensis sp. nov., a basal cheloniid turtle from the late Campanian Cerro del Pueblo Formation of Coahuila State, Mexico // PaleoBios. 2009. № 28(3). P. 76–88.
10. *Cadena E.-A., Combita-Romero D.A.* The onset of large size in Cretaceous marine turtles (Protostegidae) evidenced by new fossil remains from the Valanginian of Colombia // Zool. J. Linn. Soc. 2023. doi:10.1093/zoolinnean/zlad053

11. *Castillo-Visa O., Luján À.H., Galobart À., Sellés A.* A gigantic bizarre marine turtle (Testudines: Chelonioidea) from the Middle Campanian (Late Cretaceous) of South-Western Europe // Sci Rep. 2022. V. 12. № 1. 18322. doi:10.1038/s41598-022-22619-w
12. *Cope E.D.* The Vertebrata of the Cretaceous formations of the West // Report of the U. S. Geol. Surv. Territories. 1875. № 2. P. 1–303.
13. *Cossette A.P., Brochu C.A.* A systematic review of the giant alligatoroid Deinosuchus from the Campanian of North America and its implications for the relationships at the root of Crocodylia // J. Vertebr. Paleontol. 2020. V. 40. № 1. doi: 10.1080/02724634.2020.1767638
14. *Danilov I.G., Lysenko D.P., Bukatkin V.V. et al.* Cretaceous turtles of Belgorod Province (European Russia): Previous records and new findings // Turtle Evolution Symposium. Book of Abstracts. November 10–12, 2021. Publicación Electrónica-Asociación Paleontológica Argentina. 2021. 21(R2): R14.
15. *Danilov I.G., Obraztsova E.M., Arkhangelsky M.S. et al.* Protostega gigas and other sea turtles from the Campanian of Eastern Europe, Russia // Cret. Res. 2022. V. 135: 105196. doi:10.1016/j.cretres.2022.105196
16. *De Lapparent de Broin F., Bardet N., Amaghzaz M., Meslouh S.* A strange new chelonioid turtle from the latest Cretaceous phosphates of Morocco // C. R. Palevol. 2014. V. 13. № 2. P. 87–95.
17. *Derstler K., Leitch A.D., Larson P.L. et al.* The world's largest turtles - The Vienna Archelon (4.6 m) and the Dallas Protostega (4.2 m), upper Cretaceous of South Dakota and Texas // J. Vertebr. Paleontol. 1993. V. 13. P. 33A.
18. *Gallina P.A., Otero A.* Anterior caudal transverse processes in sauropod dinosaurs: morphological, phylogenetic and functional aspects // Ameghiniana. 2009. V. 46. № 1. P. 165–176.

19. *Grigoriev D.V.* Redescription of Prognathodon lutugini (Squamata, Mosasauridae) // Proc. Zool. Inst. RAS. 2013. V. 317(3). P. 246–261.
20. *Hirayama R.* Humeral morphology of chelonioid sea turtles: its functional analysis and phylogenetic implications // Bull. Hobetsu Mus. 1992. № 8. P. 17–57.
21. *Hirayama R., Chitoku T.* Family Dermochelyidae (superfamily Chelonioidea) from the Upper Cretaceous of north Japan // Trans. and Proc. Palaeontol. Soc. Japan. N. ser. 1996. V. 184. P. 597–622.
22. *Hoffstetter R., Gasc J.P.* Vertebrae and ribs of modern reptiles // Biology of the Reptilia. Volume 1. Morphology A. / Eds C. Gans, A. d'A. Bellairs, T.S. Parsons. L.; N. Y.: Acad. Press, 1969. P. 201–310.
23. *Kaddumi H.F.* A new genus and species of gigantic marine turtles (Chelonioidea: Cheloniidae) from the Maastrichtian of the Harrana Fauna-Jordan // PalArch Vertebrate Paleontology. 2006. № 2(1). P. 1–14.
24. *Kear B.P.* Reassessment of Cratochelone berneyi Longman, 1915, a giant sea turtle from the Early Cretaceous of Australia // J. Vertebr. Paleontol. 2006. V. 26. № 3. P. 779–783.
25. *Mocho P., Perez-Garcia A., Codrea V.A.* New titanosaurian caudal remains provide insights on the sauropod diversity of the Hațeg Island (Romania) during the Late Cretaceous // Histor. Biol. 2023. V. 35. № 10. P. 1881–1916.
26. *Mulder E.W.A.* Comparative osteology, palaeoecology and systematics of the Late Cretaceous turtle Allopleuron hofmanni (Gray 1831) from the Maastrichtian type area // Pubicaties van het Natuurhistorisch Genootschap in Limburg. 2003. P. 23–92.
27. *Nicholls E.L.* New material of Toxochelys latiremis Cope, and a revision of the genus Toxochelys (Testudines, Chelonioidea) // J. Vertebr. Paleontol. 1988. V. 8. № 2. P. 181–187.
28. *Romer A.S.* Osteology of the Reptiles. Chicago: Univ. Chicago Press, 1956. 772 p.

29. *Russell D.A.* Systematics and morphology of American mosasaurs // Bull. Peabody Mus. Natur. Hist., Yale Univ. 1967. V. 23. P. 1–237.

30. *Salgado L., Coria R.A., Calvo J.O.* Evolution of titanosaurid sauropods I: Phylogenetic analysis based on the postcranial evidence // Ameghiniana. 1997. V. 34. P. 3–32.

31. *Solonin S.V., Martill D.M., Smith R.E., Vodorezov A.V.* First occurrence of ornithocheirid pterosaur teeth in the Dmitrov Formation (Santonian) of Ryazan Oblast, Russia // Cret. Res. 2021a. V. 127: 104943. doi:10.1016/j.cretres.2021.104943.

32. *Solonin S., Shell R., Vodorezov A., Niedzwiedzki R.* Preliminary report of an Upper Cretaceous elasmobranch fauna from Ryazan Oblast, Russia // Geol. Soc. America Abstracts with Programs. 2020. V. 52. P. 6.

33. *Solonin S.V., Vodorezov A.V., Kear B.P.* Late Cretaceous marine reptiles from Malyy Prolom in Ryazan Oblast, Central Russia // Cret. Res. 2021b. V. 127: 104946. doi:10.1016/j.cretres.2021.104946

34. *Wieland G.R.* The osteology of Protostega // Mem. Carnegie Mus. 1906. № 2. P. 279–298.

35. *Wieland G.R.* Revision of the Protostegidae // Amer. J. Sci. Ser. 4. 1909. № 27(158). P. 101–130.

36. *Williston S.W.* The Osteology of the Reptiles. Cambridge: Harvard Univ. Press, 1925. 300 p.

37. *Wyneken J.* The Anatomy of Sea Turtles. U.S. Department of Commerce NOAA Technical Memorandum NMFS-SEFSC-470. 2001. P. 1–172.

38. *Zangerl R.* The vertebrate fauna of the Selma Formation of Alabama. Part III. The turtles of the family Protostegidae // Fieldiana: Geol. Mem. 1953a. № 3(3). P. 63–133.

39. *Zangerl R.* The vertebrate fauna of the Selma Formation of Alabama. Part IV. The turtles of the family Toxochelyidae // Fieldiana: Geol. Mem. 1953b. № 3(4). P. 145–277.

Figure Captions

Fig. 1. Left – location of Maly Prolom on the geological map of the Shatsky district of the Ryazan region of Russia; center – Shatsky district on the administrative map of the Ryazan region; right – Ryazan region on the administrative map of Russia.

Fig. 2. Caudal vertebra of Chelonioidea indet., ZIN PH 1/291: *a* , *b* – anterior view; *c* – posterior view; *d* , *e* – left lateral view; *f* , *g* – ventral view; *h* , *i* – dorsal view; *b* , *e* , *g* , *i* – explanatory drawings; Russia, Ryazan region, Maly Prolom locality, Upper Cretaceous, Middle Cenomanian – Middle Santonian. Shading in the figures: dark gray – undamaged surface; light gray – damaged surface. Designations: *aas* – anterior articular surface of the centrum, *asa* – sutural surface for the neural arch, *lci* – longitudinal crest-like inflection, *nc* – neural canal, *nf* – nutritive foramen, *pas* – posterior articular surface of the centrum, *stc* – suture between the transverse process and centrum, *tp* – transverse process. Dotted lines indicate reconstructed edges of vertebral elements.

Fig. 3. Vertebrae of Late Cretaceous reptiles: *a, b* – Prognathodon lutugini, trunk vertebra: *a* – lateral view (horizontally mirrored), *b* – ventral view (Grigoriev, 2013, fig. 10H, J); *c* – Deinosuchus riograndensis, caudal vertebra, lateral view (Cossette, Brochu, 2020, fig. 25A); *d, e* – Magyarosuchus dacus, (?) I caudal vertebra: *d* – lateral view, *e* – ventral view (Mocho et al., 2023, fig. 13e, i); *f, g* – Chelonioidea indet., ZIN PH 1/291, anterior caudal vertebra: *f* – lateral view, *g* – ventral view; *h* – Mesodermochelys udulatus, III caudal vertebra, lateral view (Hirayama, Chitoku, 1996, fig. 9B); *i* – Allopleuron hofmanni IRSNB 3901, (?)VIII caudal vertebra, ventral view (Mulder, 2003, pl. 38, fig. 3).

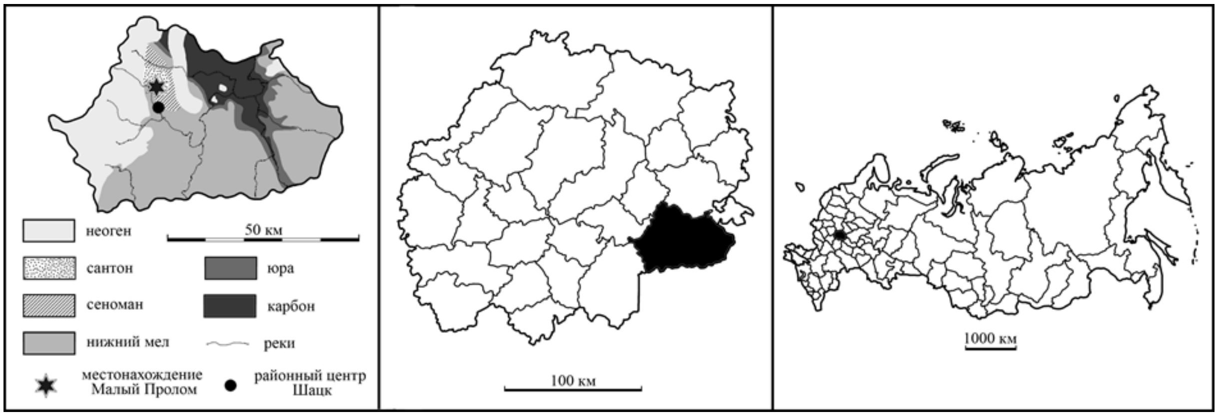
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Fig. 1

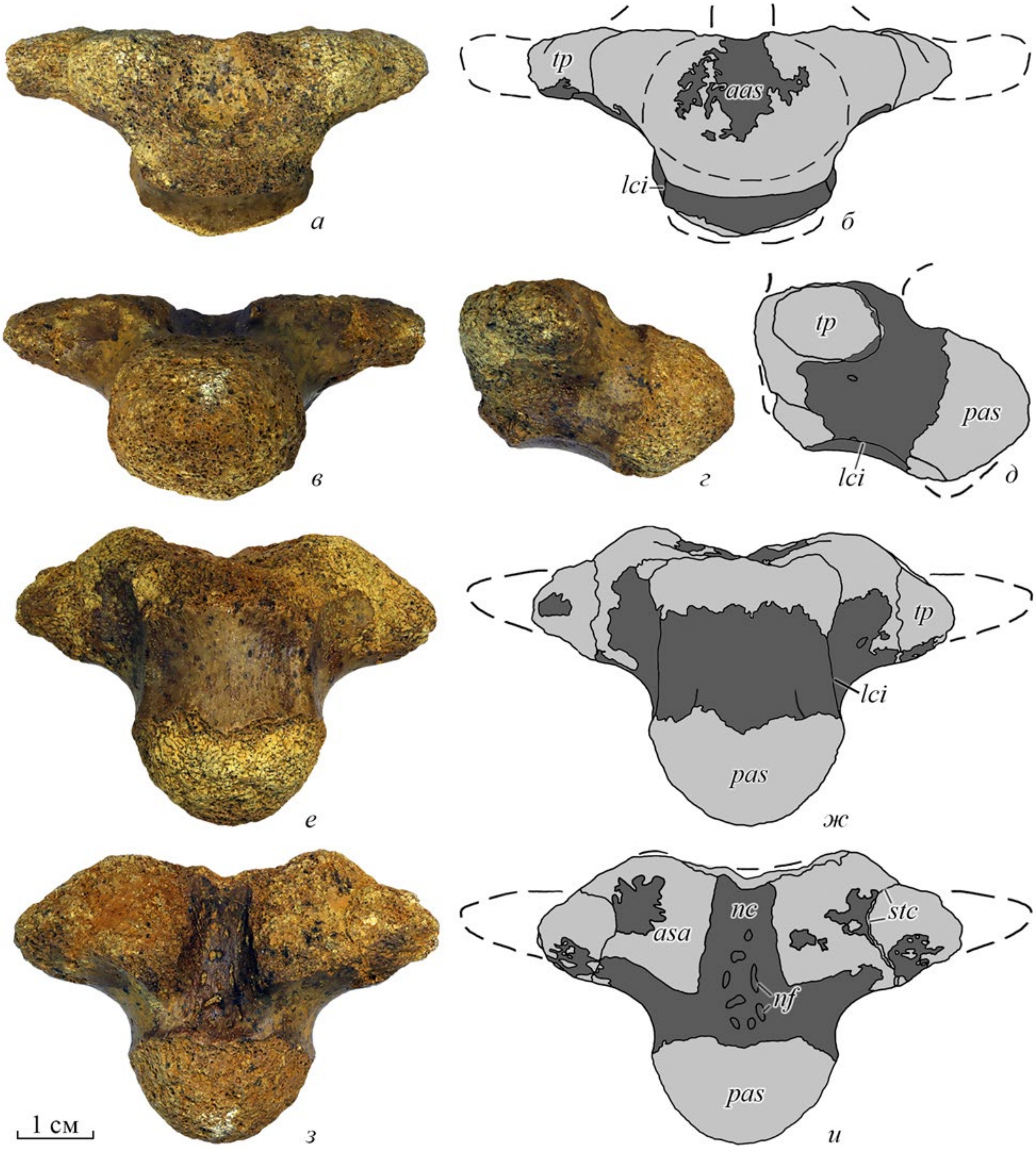

Fig. 2

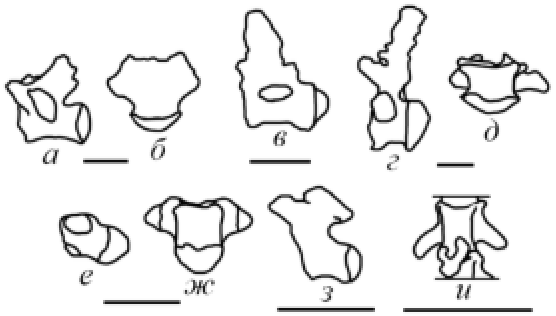

Fig. 3