MARINE FISHES (CHONDRICHTHYES, HOLOCEPHALI, ACTINOPTERYGII) FROM THE UPPER CRETACEOUS (CAMPANIAN) RYBUSHKA FORMATION NEAR BELOE OZERO, SARATOV OBLAST, RUSSIA

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Abstract. A diverse fish paleofauna occurs in the upper Campanian portion of the Rybushka Formation exposed near Saratov city in the Saratov Oblast, Russia. Twenty taxa have been identified, including two holocephalans (*Ischyodus bifurcatus* and *Amylodon karamysh*), twelve elasmobranchs (*Synechodus* sp., *Cederstroemia* sp., *Cretalamna* cf. *C. borealis*, *C.* cf. *C. sarcoportheta*, *Archaeolamna kopingensis*, *Eostriatolamia segedini*, *E. venusta*, *Pseudocorax laevis*, *Squalicorax kaupi*, *Squalicorax* Morphology 1, Squalidae indet., and *Squatirhina* sp.), and six teleosts (*Pachyrhizodus* sp., *Saurocephalus lanciformis*, *Paralbula casei*, *Enchodus* cf. *E. dirus*, *E.* cf. *E. gladiolus*, and *E. petrosus*). Many of these taxa are new to the Campanian fish record of Russia, and the assemblage demonstrates that there is significant taxonomic overlap between the Rybushka Formation paleofauna and that of North America.

INTRODUCTION

The Volga Federal District, one of eight federal districts that form the Russian Federation, is bounded on the east by the Ural Federal District and on the west by the Northwestern, Central, and Southern Federal Districts (Fig. 1A). The Volga Federal District essentially comprises the area of land encompassing the drainage basin of the Volga River, the longest river in Europe, and herein we refer to this area as the Volga region. The Volga Federal District consists of 14 smaller subdivisions of land (oblasts), with the Saratov Oblast occurring in the southwest corner of the District (Fig. 1B). The Volga River divides the Saratov Oblast into eastern and

Fig. 1 - Geographic maps of western Russia. A) map of western Russia showing the location of the Volga Federal District. B) geopolitical map of the Volga Federal District showing the location of the Saratov Oblast. C) map of the Saratov Oblast showing the location of the study area. D) enlargement of area within the rectangle of C showing the location of the Beloe Ozero locality and its proximity to the city of Saratov.

western parts, and the city of Saratov is located on the western bank of the river (Fig. 1C). This area is known for the abundance of Late Cretaceous marine vertebrate fossils that occur.

Paleontological investigations of Late Cretaceous vertebrates within the Volga region date back more than a century. Sintsov (1872) described vertebrate fossils, including 16 elasmobranch taxa,

that were derived from Cenomanian deposits in the Saratov Oblast near Saratov city. Sintsov (1899) later reported an additional five Late Cretaceous cartilaginous and bony fishes from phosphorite sandstones and sands in the vicinity of Saratov city. Glickman (1953, 1957, 1958, 1980) conducted additional and extensive investigations of Cenomanian phosphorite deposits near the city of Saratov, collecting over 10,000 elasmobranch teeth that were attributed to 13 taxa. Averianov (1996) documented a new shark species, *Paracorax unilateralis*, from the Santonian-Campanian Kikino locality in the Penza Region, and Popov & Lapkin (2000) described a new shark species, *Galeorhinus glickmani*, from Cenomanian deposits near Saratov city (and they provided a list of other chondrichthyans occurring at the locality). Fossils of the bony fish *Pycnodus* sp. were reported by several authors from deposits of the same age in the Volga region (Glickman 1953; Nesov & Averianov 1996; Popov 2016).

Glickman (1953), Nesov & Averianov (1996), and Popov (2016) reported approximately 400 *Ischyodus* and *Edaphodon* (Callorhinchidae) tooth plates from the Saratov Oblast, and Averianov & Glickman (1994) subsequently described several chimaeroid taxa from Turonian to Santonian deposits near Saratov city. Averianov & Popov (1995) later named a new species of chimaeroid, *Amylodon karamysh*, from Campanian deposits at the Shirokyi Karamysh locality, and they listed six elasmobranch taxa from the site. Soon after, Nesov & Averianov (1996) provided a brief overview of Cretaceous chimaeroids from the region (which included Shirokyi Karamysh and several localities near Saratov city), and they reported several localities that yielded Campanian chondrichthyan remains.

More recent studies have documented additional chondrichthyan taxa from other parts of the Volga region, including the Penza and Volgograd oblasts. Shimada et al. (2015) named *Pseudomegachasma casei* from Cenomanian to Santonian deposits (but likely reworked from the Cenomanian) in both the Saratov and Penza oblasts. Nesov & Averianov (1996) reported the occurrence of the chimaeroids *Amylodon* sp., *Ischyodus* sp., and *Edaphodon* sp. from the Campanian Polunino-2 locality in the Volgograd Oblast, and later Yarkov & Nesov (2000) reported chondrichthyans from the Campanian Rychkovo locality in the Volgograd Oblast, which included seven elasmobranch taxa. Finally, Popov & Biriukov (2015) and Biriukov (2016, 2018) reviewed 13 Cenomanian

localities in the Volga region (including sites from the Penza, Saratov, and Volgograd oblasts) that had yielded seven elasmobranch taxa.

Our study focuses on fossil fish remains that were collected from a site near Beloe Ozero in the Saratov Oblast, southwest of Saratov city (Fig. 1D). This locality was first mentioned by Ochev (1976), who reported a plesiosaur rostrum from the site. Although Ochev (1976) did not specify the exact location of the Beloe Ozero locality, the site was rediscovered in 2001 by a team of paleontologists from Saratov State Technical University, which included one of the present authors (MSA). Subsequent geological investigations revealed the exposures at the Beloe Ozero locality to belong to the Rybushka Formation, which is of Campanian age (Olferiev & Alekseev 2005; Seltzer & Ivanov 2010).

Other past investigations of the Rybushka Formation in the Saratov Oblast documented a rather varied assortment of vertebrates from the unit, including plesiosaurs (Arkhangelsky et al. 2007; Pervushov et al. 1999; Zverkov et al. 2017), mosasaurs (Pervushov et al. 1999; Grigoriev et al. 2015), pterosaurs (Averianov et al. 2005, 2008, 2016; Averianov & Arkhangelsky 2020, 2021; Averianov & Popov 2014), turtles (Arkhangelsky 1999; Danilov et al. 2018; Pervushov et al. 1999), birds (Panteleyev et al. 2004; Zelenkov et al. 2017), and the chimaeroids *Amylodon karamysh*, *Edaphodon* sp., *Elasmodus* sp., and *Ischyodus bifurcatus*. These investigations indicated that the vertebrate fauna of the Rybushka Formation is much more diverse than previously documented, as numerous bony fishes and some elasmobranchs were listed but not described in detail. Among the fish taxa previously reported from this locality are *Archaeolamna kopingensis*, *Cretalamna appendiculata*, *Eostriatolamia* sp., *Heterodontus* sp., *Pseudocorax laevis*, *Squalicorax kaupi*, *Squatina hassei*, and *Squatirhina* sp., and undescribed members of the Enchodontidae (Averianov & Popov 2014; Grigoriev et al. 2015; Olferiev & Alekseev 2005; Seltzer & Ivanov 2010; Zverkov et al. 2017).

Presented herein is the first comprehensive evaluation of the cartilaginous and bony fish fauna from the Rybushka Formation, based on our investigation of the Beloe Ozero locality (Fig. 1D). We provide a detailed overview of the geology at the locality, detailed descriptions and illustrations of representative remains of each taxon, pertinent taxonomic notes, and discussion on the palaeobiogeographical implications of this fossil fish fauna.
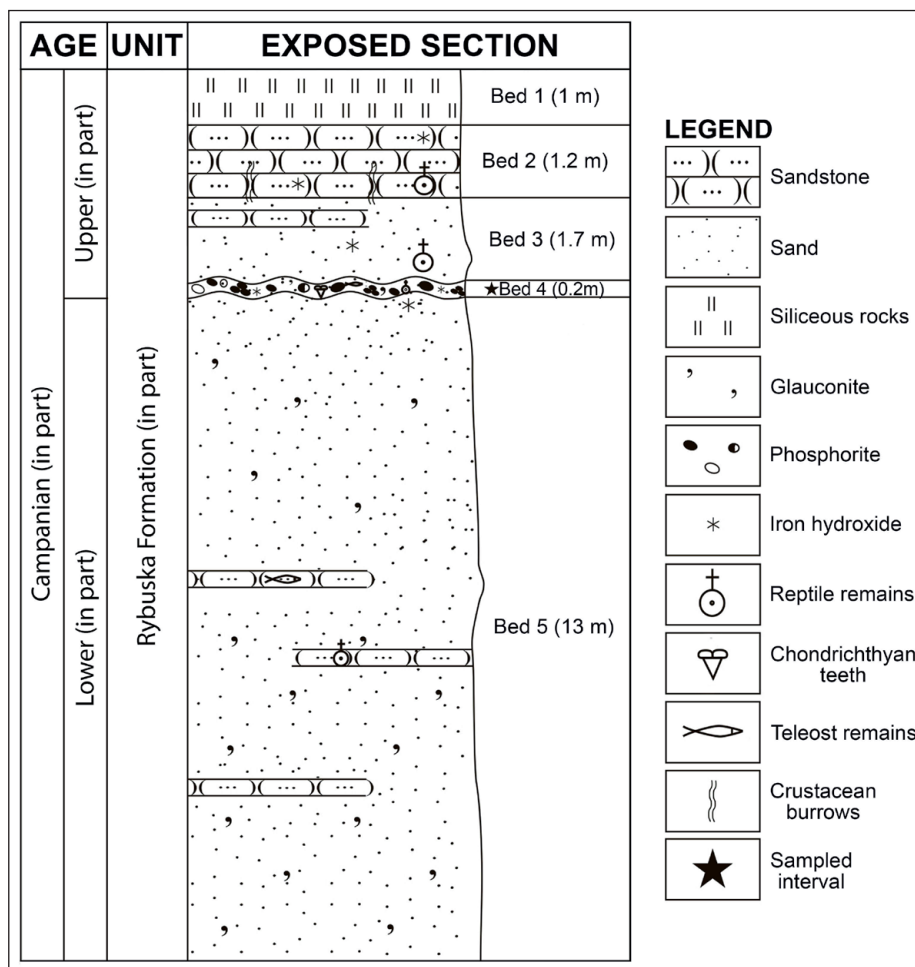
Fig. 2 - Generalized stratigraphic section of the Rybushka Formation based on exposures at the Beloe Ozero locality, Saratov Oblast, Russia.

GEOLOGICAL SETTING

The Beloe Ozero locality is located in the Lysogorsky District, one of 38 municipal districts within the Saratov Oblast. The Beloe Ozero locality is approximately 78 km southwest of Saratov city, 2 km east of Beloe Ozero village, and 7 km south of the confluence of the Medveditsa and Karamysh rivers (Fig. 1D). The western part of the Volga region, colloquially known as the "right bank," is a hilly plain crossed by numerous ravines, in which Upper Cretaceous sandstones, siltstones, marls, and silicious rocks crop out. These Campanian strata are exposed at the Beloe Ozero locality, on the right side of the "Golyi" ravine, which extends approximately 4 km to the southeast of Beloe Ozero.

The geologic exposures at the Beloe Ozero locality consist predominantly of the lower to upper Campanian Rybushka Formation. In the Saratov Region, the Rybushka Formation overlies the upper Santonian Mezinolapshinovka Formation and underlies the upper Campanian Ardymsk Formation. The Rybushka Formation ranges from 16 to 60 m in thickness and is comprised of beds consisting of sand, glauconitic sand and sandstones, and a thin phosphorite horizon occurs in the upper part (Fig. 2). The formation has yielded a plethora of macro-invertebrates, including the belemnites *Belemnellocamax mammillatus* (Nilsson, 1826) and *Belemnitella mucronata* (von Schlotheim, 1813) (Seltzer & Ivanov 2010), the ammonite *Hoplitoplacenticeras* sp., the bivalves *Oxytoma psilomonica* Ivanov, 1993, *O. tenuicostata* (Roemer, 1841), *Cataceramus balticus* (Bőhm, 1907), and *C. regularis* (d'Orbigny, 1845) and benthic foraminifers of the *Cibicidoides aktulagayensis* (Vasilenko, 1950) Subzone of the *Brotzenella monterelensis* (Marie, 1941) Regional Zone (Olferiev et al. 2004, 2007; Olferiev & Alekseev 2005). Based on these biostratigraphic markers, the part of the Rybushka Formation below the phosphorite was deposited during the lower Campanian (*Belemnitella mucronata alpha* and *Belemnellocamax mammillatus* regional mollusk zones), and strata above the phosphorite are of upper Campanian age (*Hoplitoplacenticeras coesfeldiense/ Belemnitella mucronata* Regional Zone) (Olferiev & Alekseev 2005).

At the Beloe Ozero locality, we documented several facies changes within the Rybushka Formation section, which are presented in Fig. 2 as five distinct beds. In descending order, the beds include:

Bed 1. Dark gray to light gray clayey silicite, with a small admixture of fine-grained glauconitic quartz sand. The contact with the underlying layer is sharp (1 m).

Bed 2. Greenish-gray, calcareous, glauconitic, fine-grained quartz sandstone. Molds of crustacean burrows, oriented sub-perpendicular to bedding, occur at the base. The contact with the underlying bed is gradational. Rare poorly phosphatized bones of marine reptiles and fishes occur in this interval (1.2 m).

Bed 3. Greenish-gray, glauconitic, medium-grained quartz sand. Dark brown phosphorite inclusions up to 2 cm in size, and ferruginous inclusions up to 10 cm in size are common and occur throughout the bed. Rare, weakly phosphatized bones of marine reptiles and fishes occur at the base of the bed (1.5 m).

Bed 4. Phosphorite horizon bone bed consisting of brown and dark brown, somewhat sandy, irregularly shaped phosphatic nodules up to 3.5 cm in size. Along strike, phosphate inclusions are not uniformly distributed, forming lenticular aggregations in places. The bed is occasionally stained by brownish-red iron hydroxide deposits. Rare, silicified dolomite pebbles up to 8 cm in diameter occur. The bed is loosely consolidated to indurated, with the cementing material being ferruginous and psammitic components. The lower surface of the bed is uneven and pit-like. Fossils of elasmobranchs, holocephalans, teleost fishes, and marine reptiles are common. Selachian coprolites reach lengths of up to 8 cm (0.2 m).

Bed 5. Greenish-gray, glauconitic, medium-grained quartz sand. Bed ranges from highly indurated to poorly consolidated. Light brown, rounded phosphate pebbles, up to 1 cm in size, are rare. Some portions of the bed are stained brown by iron hydroxide deposits. Rare weakly phosphatized bones of marine reptiles and fish are found in poorly consolidated sandstone lenses (13 m).

MATERIAL AND METHODS

All of the specimens documented herein were collected in the headwaters of the "Golyi" ravine at the Beloe Ozero locality in the Lysogorsky District of the Saratov Oblast (Fig. 1). Collected on mul-

tiple occasions between 2015-21, the specimens were obtained from an abandoned quarry that was formerly mined for quartz sandstones. All of the fossils discussed below were collected from the phosphorite horizon (Bed 4; Fig. 2) of the Rybushka Formation. At the site, earth moving equipment was used to grade the outcrops down to Bed 4, and specimens were manually extracted from this phosphorite layer. Some of our material was obtained through processing bulk matrix from Bed 4 with sieves from 1 mm (minimum) to 5 mm (maximum) mesh sizes. The collection of specimens was carried out in accordance with license SRT 01881 PD that was issued to the Saratov State Technical University. Several specimens in our sample are imbedded in concretions. These specimens were partially prepared to show the external morphology of the specimen; however, they were not entirely removed from the concretion due to the fragility of the elements and to preserve the semi-articulated nature of several specimens.

Larger macrofossils were cleaned with water and deposited in the collections of the Museum of the World Ocean (MMO) in Kaliningrad, the Undory Paleontological Museum (UPM) in Undory village (Ulyanovsk Oblast), and Saratov State Technical University (SSTU). Fossils were photographed with a Nikon D5200 DSLR with an 18-105 mm lens, a Canon 450 D DSLR with an 18-55 mm lens, a Canon EOS 2000 D DSLR (Macro AF Auto extension tube set DG, Kenko Company for macro photography). All photographs were rendered in Adobe Photoshop CC2017 software as part of the production of the figures presented herein. Higher taxonomic rankings follow that of Nelson et al. (2016), and holocephalan tooth plate terminology follows Stahl (1999) and Cicimurri & Ebersole (2014, 2015). The synonyms provided are not intended to be comprehensive and instead reflect taxonomic changes to the identified species.

SYSTEMATIC PALAEONTOLOGY

Class **CHONDRICHTHYES** Huxley, 1880
Subclass **HOLOCEPHALI** Bonaparte, 1831
Superorder **Holocephalimorpha** (*sensu* Nelson et al., 2016)
Order **Chimaeriformes** Obruchev, 1953
Suborder **Chimaeroidei** Patterson, 1965
Family Callorhinchidae Garman, 1901
Genus *Ischyodus* Egerton, 1843

Ischyodus bifurcatus Case, 1978a

Fig. 3A-D

Material: MMO 1 № 7768-12 (right mandibular), MMO 1 № 7768-13 (left mandibular), MMO 1 № 9273-64 (left mandibular), MMO 1 № 9273-65 (right palatine), MMO 1 № 9273-66 (left palatine), MMO 1 № 9273-67 (right mandibular), MMO 1 № 9273-70 (right mandibular), MMO 1 № 9273-71 (right mandibular), MMO 1 № 9644-8 (left mandibular, Fig. 3A-B), MMO 1 № 9644-9 (right palatine), MMO 1 № 9644-10 (right palatine), MMO 1 № 9644-11 (right palatine), UPM 2826 (right palatine), UPM 2827 (right mandibular), UPM 2828 (left palatine), UPM 2888 (left mandibular), UPM 2889 (right mandibular), UPM 2890 (left mandibular), UPM 2891 (right mandibular), UPM 2892 (left mandibular), UPM 2893 (left palatine), UPM 2909 (left palatine), UPM 2910 (left palatine), UPM 2911 (right palatine, Fig. 3C-D), UPM 2912 (left mandibular), UPM 2913 (left mandibular), UPM 2914 (right palatine), UPM 2915 (left palatine), UPM 2929 (left palatine), UPM 2930 (right mandibular).

Description. The anterior, more mesial end of palatine tooth plates is rather narrow, but the plates are expanded posteriorly (in the distal direction), resulting in a roughly triangular oral/aboral outline. The symphyseal surface is rather high, vertical, and constitutes the entire lingual margin of the plate. The posterior portion of the labial margin is flared into a wing-like projection. Four tritors occur on the oral surface, with the anterior and posterior inner tritors being located near the symphysis (Fig. 3C). An outer tritor occurs along the labial margin of the plate, and a middle tritor is between the outer and posterior inner tritors. In aboral view (Fig. 3D), an elongated furrow extends from just behind the anterior tip to the distal end of the plate.

The anterior end of the mandibular plates is extended into a beak-like projection. The labial margin is very concave between the beak tip and a conspicuous medially located prominence, as well as between the medial prominence and a more posterior, distal prominence (Fig. 3B). The symphyseal margin is uniformly convex. The outer surface of the plate is weakly convex apico-basally but concave mesio-distally. There are four main tritors (Fig. 3A), including a laminated tritor at the beak. The labial margin bears two tritors, with the anterior outer tritor located on the medial prominence, and the posterior outer tritor on the distal prominence. The middle tritor comprises much of the inner (oral) surface of the plate, and it has a bifurcated anterior margin. There may also be a narrow but elongated inner tritor located between the middle tritor and symphyseal margin.

Remarks. Although vomerine tooth plates are part of our chimaeroid sample, only palatine and mandibular plates could be confidently identified generically. *Ischyodus* palatine plates are easily distinguished from those of *Edaphodon*, which has been reported from the Saratov Region (Averianov & Glickman 1994; Popov 2016), by having four tritors instead of three, with the fourth tritor being expressed as numerous circular pads or an elongated structure along the labial margin of the plate (Case 1978a; Cicimurri & Ebersole 2014). *Ischyodus* mandibular plates are labiolingually thinner and the anterior beak is generally shorter compared to *Edaphodon* mandibulars. Additionally, whereas the mandibular plates of *Ischyodus* connected to each other along the convex ventral margin, *Edaphodon*

mandibulars articulated with each via a vertical, flat, and elongated symphyseal surface (Stahl & Parris 2004; Cicimurri & Ebersole 2014, 2015). The *I. bifurcatus* mandibular plate is also characterized by a bifid middle tritor. Cicimurri & Ebersole (2014, 2015) discussed the morphological variation of the tooth plates and tritors of both *Ischyodus bifurcatus* and *I. dolloi*, respectively, and they discussed how the plates articulated and occluded with each other.

An additional species of *Ischyodus* that can have a bifid middle tritor, *I. rayhasii* Hoganson & Erickson 2005, has been reported from Maastrichtian strata that accumulated within the northern part of the Western Interior Seaway in the USA (Hoganson & Erickson 2005; Hoganson et al. 2015). This taxon, which was identified from the Saratov Region by Hoganson et al. (2015), was placed into a "*Ischyodus bifurcatus* species group" by Johnson-Ransom et al. (2018). The mandibular plate of *I. rayhassi* from the USA may be distinguished from *I. bifurcatus* reported from the Campanian (Alabama) and Maastrichtian (New Jersey) by having a more elongated lower branch of the middle tritor that extends up to the anterior end of the anterior outer tritor. In contrast, the upper and lower prongs of the *I. bifurcatus* middle tritor are of roughly equal length, and they extend up to, but not far beyond, the posterior end of the anterior outer tritor (Case 1978a; Case & Schwimmer 1992; Cicimurri & Ebersole 2014).

Two additional holocephalan genera, *Elasmodus* and *Amylodon*, have been reported from the Saratov region (Averianov & Glickman 1994; Averianov & Popov 1995). Like *Edaphodon*, *Elasmodus* palatine plates may have three tritor pads (Gurr 1962; Averianov 2001), but palatines of the latter taxon differ from both *Edaphodon* and *Ischyodus* by having a laminated tritor along the symphyseal margin. *Elasmodus* mandibular plates differ from those of *I. bifurcatus* by having an a single large, elliptical middle tritor and numerous small laminated tritor pads along the labial margin (Gurr 1962; Averianov 2001; Cicimurri & Ebersole 2015). On palatine and mandibular plates of *Ischyodus* and *Edaphodon*, only the symphyseal/beak tritor is laminated. The differences between *Amylodon* and *I. bifurcatus* are discussed in detail below.

Family Rhinchochimaeridae Garman, 1901
Genus *Amylodon* Storms, 1894

Amylodon karamysh Averianov and Popov, 1995
Fig. 3E-F

Material: MMO 1 № 10420-49 (right mandibular plate).

Description. The specimen measures 8 cm from the broken mesial end to the distal angle. The plate has a roughly triangular outline in labial/lingual view. The upper portion of the plate is straight, whereas the lower portion curves sharply medially. The anterior end of the plate is formed into a beak-like structure (although the tip is damaged). The labial margin is rather sharp and straight except for a slight medial prominence. Tritor tissue is exposed along the labial edge, between the beak and the prominence. The distal margin is convex. The symphyseal margin is convex along its length, and the symphysis itself is thick (uniform along length), vertical, and flat. The outer surface of the plate is rather rough (Fig. 3F), but the inner surface is very smooth and devoid of tritors (Fig. 3E).

Remarks. Specimen MMO 1 № 10420-49 is morphologically identical to the type specimen of *Amylodon karamysh* described by Averianov & Popov (1995). Their holotype, from the Shirokyi Karamysh locality in the Saratov Oblast, was derived from the same lithostratigraphic unit as MMO 1 № 10420-49. The one, perhaps insignificant, difference between the two specimens is that MMO 1 № 10420-49 lacks elongated medial tritors.

Averianov & Popov (1995) indicated that the *Amylodon* mandibular plate performed a shearing function, a hypothesis that we concur with based on the sharp-edged, tritor-reinforced nature of the labial margin. This is similar to the morphology of the oral margin of vomerine tooth plates described below, and it is likely that *Amylodon* palatine and mandibular plates acted together to slice prey (Stahl 1999). Cicimurri & Ebersole (2014, 2015) have also discussed the shearing aspect of the vomerine plate and mandibular beak tritor in both *Edaphodon* and *Ischyodus*. If the holotype (left mandibular) and MMO 1 № 10420-49 were articulated, they would connect along the thickened and flat symphysis to form a narrow, U-shaped structure. The reduction to absence of tritors on the oral surface of *Amylodon* suggests that this taxon did not consume hard-shelled prey like *Ischyodus* (Cicimurri & Ebersole 2014, 2015). The unusual plate morphology and lack of tritors on the oral surface of MMO 1 № 10420-49 distinguishes *A. karamysh* from *Ischyodus*, *Edaphodon*, and *Elasmodus* mandibular plates.

Chimaeroidei indet.
Fig. 3G-K

Material: MMO 1 № 9273-69 (right vomerine, Fig. 3G-H), MMO 1 № 9273-72 (dorsal spine, Fig. 3I-K), MMO 1 № 9273-73 (dorsal spine), MMO 1 № 9644-7 (dorsal spine), UPM 2829 (right vomerine), UPM 2830 (dorsal spine), UPM 2902 (dorsal spine), UPM 2928 (dorsal spine), UPM 2946 (dorsal spine), UPM 3013/3014 (dorsal spine).

Description. In labial/lingual view, the vomerine plates have a somewhat rectangular or trapezoidal outline (Fig. 3H). The symphyseal margin is convex and forms a mesial angle with the labial margin. The symphyseal margin extends to a dorsal projection, and the dorsal margin is concave. The oral portion of the labial margin is a thin ridge, but the post-oral portion is thicker and extends dorsally to roughly parallel the symphyseal margin. In oral view, the outer surface of the plate is convex, whereas the inner surface is concave. There are several rod-like tritors exposed on the oral surface of the labial margin. The symphyseal surface is thick and flat (Fig. 3G).

The dorsal fin spines are very elongated structures that are widest basally but gently tapering apically. In anterior view they are straight, but in lateral view they are posteriorly curved, particularly closer to the apex, which is blunt. The anterior face is very convex and may bear a straight medial ridge that parallels the spine height (Fig. 3I), and the lateral faces are weakly to moderately convex. These surfaces bear networks of fine, closely spaced, parallel vertical ridges that are discontinuous to continuous (Fig. 3J). The posterior face is flat and bears a medially located, vertical furrow that becomes wider towards the spine apex. Most of the spine fragments bear two rows of denticles, with each denticle being basally curving and positioned directly opposite those in the opposing row. On the lower portion of the spine, the denticle rows are located closer to the midline, but towards the apex they migrate to the lateral edges of the spine (Fig. 3K). Denticles appear to have been lacking at the spine base.

Remarks. The vomerine plates are not taxonomically informative beyond Chimaeroidei because similar-looking structures have been at-
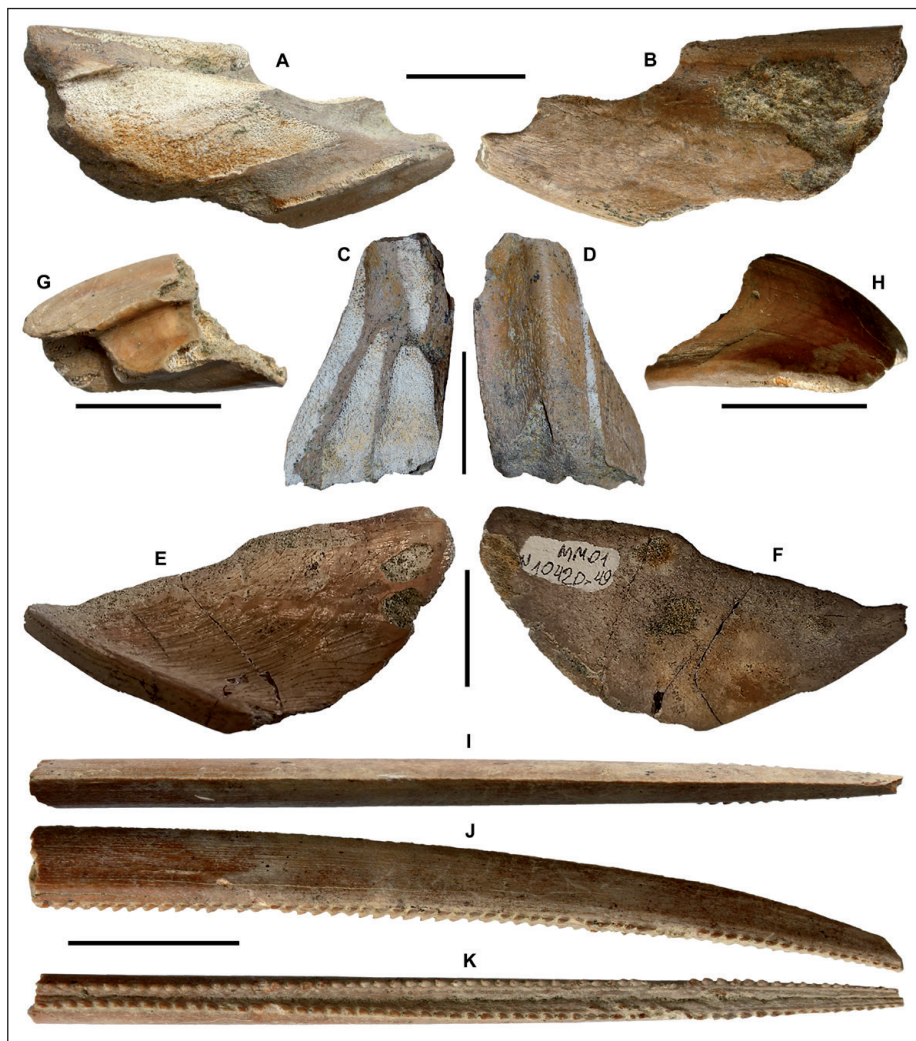
Fig. 3 - Chimaeriformes remains from the Beloe Ozero locality in the Saratov Oblast, Russia. A–B) MMO 1 № 9644-8, *Ischyodus bifurcatus*, left mandibular plate: A, lingual view; B, labial view. C–D) UPM 2911, *Ischyodus bifurcatus*, right palatine plate: C, oral view; D, aboral view. E–F) MMO 1 № 10420-49, *Amylodon karamysh*, right mandibular plate: E, lingual view; F. labial view. G–H) MMO 1 № 9273-69, Chimaeriformes indet., right vomerine plate: G, lingual view; H, labial view. I–K) MMO 1 № 9273-72, Chimaeriformes indet., dorsal fin spine: I, anterior view; J, left lateral view; K, posterior view. All scale bars represent 2 cm.

tributed to *Edaphodon* and *Ischyodus* (Cicimurri & Ebersole 2014, 2015). Although we did not identify any *Edaphodon* material in our sample, the genus has been reported from older Cenomanian deposits in the region (Glickman 1953; Nesov & Averianov 1996; Popov & Lapkin 2000), and we therefore only identify the vomerine plates to the subordinal level. The thick, flat symphyseal surface indicates a very close connection between the vomerine plates, and the oral portion of the labial margin likely formed a shearing surface with the mandibular beak (Cicimurri & Ebersole 2014, 2015).

The fin spines appear to be relatively ubiquitous among the Chimaeroidei, and we cannot confidently assign them to any of the genera that have been reported from Cretaceous strata of the region. The specimens within our sample do not differ appreciably from each other, and we cannot determine if more than one taxon is present.

Subclass **EUSELACHII** Hay, 1902
Infraclass **ELASMOBRANCHII** Bonaparte, 1838
Division **SELACHII** Cope, 1871
Superorder **Galeomorphi** Compagno, 1973
Order **Synechodontiformes** Duffin and Ward, 1993
Family Palaeospinacidae Regan, 1906
Genus *Synechodus* Woodward, 1888

Synechodus sp.
Fig. 4A-F

Material: UPM 2976 (lateral tooth, Fig. 4C-D), UPM 2977 (anterolateral tooth, Fig. 4E-F), UPM 2978 (posterolateral tooth, Fig. 4A-B).

Description. UPM 2977 (Fig. 4E-F) is an anterolateral tooth measuring 7 mm as preserved (the distal side is damaged). The crown bears a tall and

sharply tapering main cusp that is flanked by high lateral shoulders. The shoulders are oblique to the main cusp height. The main cusp is very slightly distally inclined, with the mesial side being oblique and slightly concave, whereas the distal side is vertical and straight. There are three mesial lateral cusplets that decrease in size basally. The distal shoulder is broken but two proximal lateral cusplets are preserved, both of which are larger than the corresponding mesial cusplets (Fig. 4E). A smooth cutting edge extends across the main cusp and lateral cusplets. The labial crown ornamentation consists of fine longitudinal ridges across the entire width, with ridges extending to just below the lateral cusplets and up to one-half the main cusp height (Fig. 4E). The labial crown foot is straight. In lingual view the crown shoulders are very low, and the main cusp appears isolated from the lateral cusplets. The cusp faces are more convex than they are labially, but the ornamentation is much reduced. The root is poorly preserved.

UPM 2976 (Fig. 4C-D) is a lateral tooth measuring 9 mm in crown width. In labial view the crown has a roughly triangular outline, and there is a broad-based, distally inclined main cusp (incompletely preserved) that lacks cutting edges. The main cusp is flanked by mesial and distal shoulders that are oblique to the main cusp height. The mesial shoulder is elongated and bears five cusplets that decrease in size basally, whereas the distal shoulder is shorter and smooth except for a single cusplet adjacent to the main cusp base (Fig. 4D). The primary lateral cusplets are rather tall, sharply pointed, and well-separated from the main cusp. Labial crown ornamentation consists of robust vertical ridges that are primarily located on the mesial and distal heels, and these ridges do not reach the lateral cusplet apices. The ornament fades medially and apically, and these areas of the crown are smooth (Fig. 4C). The crown foot is deeply concave. The labial and lingual faces of the cusp and cusplets are convex, and lingual ornament is restricted to the mesial and distal shoulders. The root is not preserved.

UPM 2978 (Fig. 4A-B) is a posterolateral tooth measuring approximately 11.5 mm in labio-lingual width. The specimen has a broad-based but low, distally inclined main cusp that is flanked by elongated mesial and distal shoulders. The shoulders are somewhat perpendicular to the main cusp height, and each bears lateral cusplets.

The mesial shoulder is more elongated and bears four low and widely separated cusplets that decrease in size basally, whereas the distal shoulder is shorter and bears only two cusplets (Fig. 4B). In labial view, the crown foot is sinuous, broadly concave, but becomes convex along the mesial shoulder. A smooth cutting edge extends along the main cusp and lateral cusplets. The labial crown ornamentation consists of robust sinuous longitudinal ridges across the entire face (Fig. 4A). These ridges vary in height, and none reach the apices of the main cusp or lateral cusplets. Lingual ornamentation is indistinct on the main cusp and limited to the lower half. The labial face overhangs the root, which is low and nearly as wide as the crown. The root is lingually directed with four distinct nutritive grooves (particularly on the distal side) that are each penetrated by a nutritive foramen.

Remarks. The teeth in our sample can be distinguished from those of the morphologically similar *Paraorthacodus* (Hexanchiformes) by their low root, thickened labial crown foot that overhangs the root, and rather small lateral cusplets with respect to overall tooth size. In addition, the lateral cusplets on the teeth in our sample are broadly united basally, a characteristic not seen on *Paraorthacodus* teeth. Based on the shared similarities among the three specimens in our sample, we believe the variation represents heterodonty within a single species rather than multiple taxa. We consider UPM 2977 to represent a more anterior tooth file based on its nearly vertical main cusp and symmetrical appearance (given that the mesial shoulder is incomplete) in labial view. UPM 2976 is believed to be from a more lateral file because of its broader main cusp and asymmetrical appearance, with the main cusp being distally inclined and the mesial shoulder being longer (with more cusplets) compared to the distal shoulder. UPM 2978 is regarded as a distal lateral tooth because it is similar to teeth in the distal one-half of a *Synechodus dubrisiensis* (Mackie, 1863) dentition described by Woodward (1911).

Several Late Cretaceous *Synechodus* species have been named in the literature, including *S. dereki* Cappetta et al., 2020, *S. dispar* (Reuss, 1846), *S. dubrisiensis*, *S. filipi* Siversson et al., 2016, *S. lerichei* Herman, 1977, *S. nitidus* Woodward, 1911, *S. perssoni* Siverson, 1989, and *S. turneri* Case, 1987. In addition to these taxa, Cappetta (2012; fig. 306) figured numerous unspeciated *Synechodus* teeth from upper
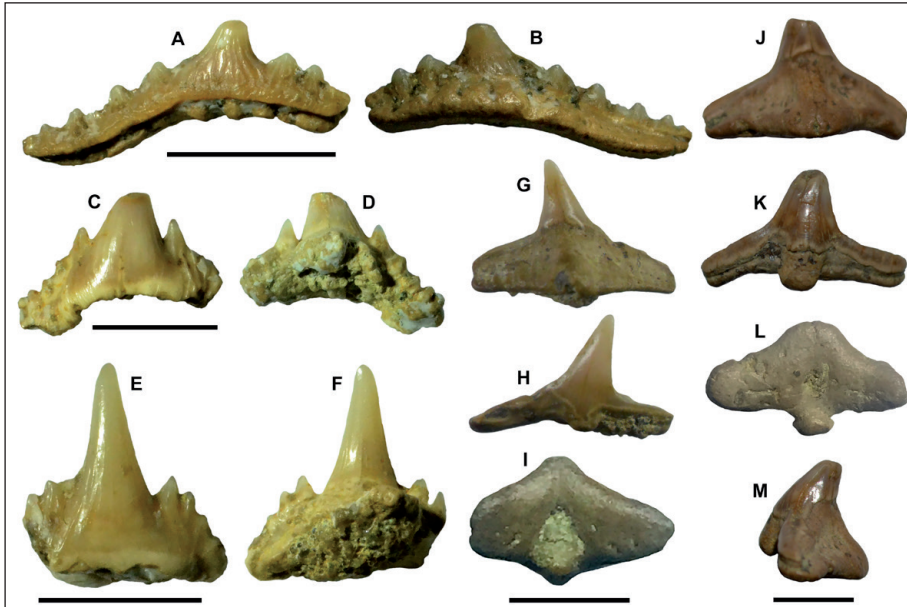
Fig. 4 - *Synechodus* sp. and *Cederstroemia* sp. teeth from the Beloe Ozero locality in the Saratov Oblast, Russia. A–B) UPM 2978, *Synechodus* sp., posterolateral tooth: A, labial view; B, lingual view. C–D) UPM 2976, *Synechodus* sp., lateral tooth: C, labial view; D, lingual view. E–F) UPM 2977, *Synechodus* sp., anterolateral tooth: E, labial view; F, lingual view. G–I) UPM 2994, *Cederstroemia* sp., G, lingual view; H, labial view; I, basal view. J–M) UPM 2991, *Cederstroemia* sp., J, lingual view; K, labial view; L. basal view; M, distal view. All scale bars represent 5 mm.

Santonian deposits in Kazakhstan. Unfortunately, our sample of *Synechodus* teeth is limited to three specimens, two of which are incompletely preserved, and the other is from a more generic lateral position. Therefore, with limited knowledge of the morphological variation within the Rybushka Formation taxon, we cannot properly compare our specimens to those of previously described *Synechodus* species.

Order **Orectolobiformes** Applegate, 1974
Family Orectolobidae Jordan and Fowler, 1903
Genus *Cederstroemia* Siverson, 1995

Cederstroemia sp.
Fig. 4G-M

Material: UPM 2933 (tooth), UPM 2934 (tooth), UPM 2990 (tooth), UPM 2991 (tooth, Fig. 4J-M), UPM 2992 (tooth), UPM 2993 (tooth), UPM 2994 (tooth, Fig. 4G-I), UPM 2995 (tooth), UPM 2996 (tooth).

Description. The largest specimen measures 13 mm in crown width. The crown of each specimen consists of a triangular cusp that is flanked by elongated mesial and distal shoulders (Fig. 4H, K). The labial and lingual faces of the cusp are convex to varying degrees, with the lingual face always being more convex than the labial face. The cusp is lingually curved and may be distally inclined, depending on the jaw position. The mesial and distal shoulders are up to one-third the height of the cusp and are thin labiolingually. These heels are rather

straight and may be perpendicular or oblique to the cusp height, and they vary in length depending on the jaw position and the side of the cusp they are on (i.e., mesial vs. distal). The labial face is characterized by an elongated, basally directed protuberance that is located at the base of the cusp. The crown enameloid is smooth. A continuous, smooth cutting edge extends across the lateral shoulders and cusp. In basal view, the root has a triangular outline, the basal attachment surface is conspicuously concave, and a large foramen is centrally located (Fig. 4I, L). This foramen opens labially into a wide channel. In profile the root extends well beyond the lingual crown foot, and its oral surface is oblique to the cusp height (Fig. 4M). This morphology results in a steeply inclined surface from the base of the cusp. There is a small foramen located at the most convex part of the lingual root margin (Fig. 4G, J).

Remarks. Although most of the specimens in our sample are incompletely preserved, monognathic heterodonty is evident. Specimens from more anterior jaw positions are roughly symmetrical, with a vertical cusp and oblique lateral heels of similar length. Teeth from more lateral positions have a distally inclined cusp, and the mesial shoulder is often longer and more contiguous with the cusp, whereas the shorter distal heel is roughly perpendicular to cusp height. Towards the commissure the crown width and distal crown inclination increases, but the cusp height decreases.

Cederstroemia was originally included within the hypodigm of another orectolobiform shark, *Cretorectolobus* Case, 1978b. The Rybushka Forma-

tion specimens lack the cuspidate lateral shoulders that occur on *Cretorectolobus* (Case 1978b; Siverson 1995). Although *Cederstroemia* teeth are morphologically similar to *Squatina*, they differ by having higher lateral shoulders, a strongly oblique root profile, a more elongated and parallel-sided labial protuberance, and holaulocorhize root (on some specimens). It is difficult to compare our small and incompletely preserved sample to the teeth of the several nominal *Cederstroemia* species that have been described. However, the Rybushka Formation specimens are not dissimilar from *C. triangulata* which was originally reported from the Campanian of Montana (Siverson 1995).

Order **Lamniformes** Garman, 1885
Family Otodontidae Glikman, 1964
Genus *Cretalamna* Glikman, 1958

Cretalamna cf. ***C. borealis*** (Priem, 1897)
Fig. 5A-D

1897 *Lamna borealis* - Priem, p. 40, pl. 1, fig. 4.
1980 *Cretalamna borealis* - Glickman, pl. 10, fig. 12, pl. 21, figs. 1-5.

Material: UPM 2791 (upper anterior tooth), UPM 2942 (upper lateral tooth, Fig. C-D), UPM 2943 (upper anterior tooth, Fig. 5A-B).

Description. Upper anterior teeth have a tall, triangular, and erect main cusp that is only slightly distally inclined (Fig. 5A-B). The mesial and distal cutting edges are smooth and continuous along the main cusp, slightly concave near the base but weakly convex near the apex. The labial face of the main cusp is flat, but the lingual face is strongly convex, and the crown enameloid is smooth. There is a single pair of diminutive lanceolate lateral cusplets that are nearly completely disconnected from the main cusp. The lateral cusplets are divergent and have convex medial and lateral edges. The root is high in lingual view, is separated from the main cusp enameloid by a chevon-shaped dental band and has a robust protuberance extending mesiodistally across the face (Fig. 5A). A lingual nutritive groove is lacking, and no nutritive foramina are preserved on the two specimens examined. The root is bilobate, with lobes slightly divergent and rounded. The mesial root lobe is conspicuously longer and slightly narrower than the distal lobe, but the distal lobe is more labiolingually compressed. The interlobe area is deep and U-shaped.

The upper lateral tooth has a triangular main cusp that is lower, narrower, and more distally inclined than that of the anterior teeth (Fig. 5C-D). The mesial cutting is edge rather straight but becomes slightly convex at the apex, whereas the distal cutting edge is concave near the base but somewhat convex towards the apex. A single pair of large lateral cusplets flank the main cusp. Lateral cusplets are broadly triangular, diverging, with smooth cutting edges. The lateral edges of the cusplets are concave but the medial edges are convex. The root is not as high as on the anterior files and the lingual protuberance is also not as pronounced (Fig. 5C). The root lobes are broad, somewhat rectangular, slightly divergent, labiolingually compressed, and have slightly scalloped basal edges. The interlobe area is shallow and U-shaped.

Remarks. Teeth with the morphology described above have historically been assigned to *Cretalamna appendiculata* (Agassiz, 1843). However, Siversson et al. (2015) recently demonstrated that this species had become a "waste-basket" taxon, and *C. appendiculata sensu stricto* is currently geographically and temporally restricted to the Turonian of England. Siversson et al.'s (2015) reevaluation of Cenomanian to Campanian *Cretalamna* teeth from around the world indicated that the genus is much more diverse than previously thought, prompting them to erect a number of new species. We have tentatively recognized two of these species in the Rybushka Formation.

The upper anterior teeth described above (UPM 2791 and UPM 2943) exhibit several characteristics in common with those of *Cretalamna borealis* described and figured by Siversson et al. (2015; fig. 9a-c), including a narrow and distally inclined main cusp, lanceolate and divergent lateral cusplets, elongated and rounded mesial root lobe, and a pronounced and mesiodistally elongated lingual root protuberance. The upper lateral tooth (specimen UPM 2942) is similar to those illustrated in Siversson et al. (2015; fig. 9d-e) by having a short, mesiodistally narrow and distally hooked main cusp, and weakly scalloped root lobes. The presence of a single pair of lateral cusplets distinguishes these teeth from species like *C. biauriculata* (Wanner, 1902) and *Serratolamna moroc-*

cana (Arambourg, 1935), and the combination of characteristics described above allows us to separate these teeth from the other nominal Santonian to Maastrichtian species (see Siversson et al. 2015; Ebersole & Ehret 2018). Although our specimens are morphologically similar to teeth of *C. borealis* as described and figured by Siversson et al. (2015), we only tentatively assign them to this species because of our small sample size (n=3). Additional specimens from other jaw positions are needed to help corroborate the occurrence *C. borealis* in the Rybushka Formation.

Cretalamna cf. *C. sarcoportheta* Siversson et al., 2015
Fig. 5E-J

Material: MMO 1 № 9273-14 (lower anterior tooth), MMO 1 № 9273-14 (anterior tooth, Fig. 5E-F), MMO 1 № 9273-17 (upper lateral tooth, Fig. 5I-J), MMO 1 № 9273-18 (lower lateral tooth), MMO 1 № 9273-19 (upper anterior tooth), MMO 1 № 9273-24 (lower lateral tooth), MMO 1 № 9273-25 (upper lateral tooth), MMO 1 № 9273-26 (upper lateral tooth, Fig. 5G-H), UPM 2793 (lower anterior tooth), UPM 2801 (upper anterior tooth), UPM 2932 (upper anterior tooth), UPM 3001 (lower anterior tooth).

Description. Upper anterior teeth have a tall, erect and broadly triangular main cusp (Fig. 5E). The mesial cutting edge is slightly convex and, depending on the anterior file, the distal cutting edge can be convex or slightly concave. The lingual face of the main cusp is strongly convex and with smooth enameloid, whereas the labial face is weakly convex and short enameloid wrinkles occur at the crown base on some specimens. The main cusp is flanked by a single pair of diverging, lanceolate lateral cusplets (Fig. 5H, J). The root is robust and has a strong lingual protuberance. A shallow nutritive foramen occurs on the lingual root face on some teeth. The root lobes are rounded and the mesial lobe is often mesiodistally wider and longer than the distal lobe (Fig. 5F). The interlobe area is deep and U-shaped. The lower anterior teeth differ from those in the upper anterior files by having straighter mesial and distal cutting edges. The lateral teeth have a lower and mesiodistally wider main cusp (Fig. 5I) compared to anterior files. The upper lateral teeth have a main cusp that is more distally inclined than those in the lower lateral files. The basal edges of the root lobes are scalloped on some specimens. The interlobe area on lateral teeth is shallower than that of teeth in the anterior files (Fig. 5 G).

Remarks. The teeth we assigned to *Cretalamna* cf. *C. sarcoportheta* differ from the *Cretalamna* cf. *C. borealis* teeth in our sample by having a mesiodistally wider main cusp and a more robust root. Many of the teeth in our sample are ablated and have a damaged crown and/or root. Due to the poor preservation of many of these teeth, they are only tentatively assigned to this taxon.

For the sake of completeness, we mention several additional teeth in our sample (i.e., SGTU MEZ № 4-128, UPM 2805, UPM 2955, UPM 2957, UPM 2960) that are herein assigned to *Cretalamna*. However, the specimens are either poorly preserved or otherwise do not possess features of either of the two species we believe occur in the Rybushka Formation.

Family Archaeolamnidae Underwood and Cumbaa, 2010
Genus *Archaeolamna* Siverson, 1992

Archaeolamna kopingensis (Davis, 1890)
Fig. 5K-R

1890 *Odontaspis kopingensis* - Davis, p. 390, pl. 38, figs. 27, 28.
1992 *Archaeolamna kopingensis* Siverson - p. 531, pl. 2, figs. 1-15.

Material: MMO 1 № 7768-2 (anterior tooth), MMO 1 № 7768-3 (lateral tooth, Fig. 5M-N), MMO 1 № 9273-15 (lateral tooth, Fig. 5 O-P), MMO 1 № 9273-21 (lateral tooth), MMO 1 № 9273-23 (lateral tooth), MMO 1 № 9273-27 (posterolateral tooth, robust morphology, Fig. Q-R), MMO 1 № 9273-30 (anterior tooth), SGTU MEZ № 4/127 (anterior tooth), UPM 2792 (lateral tooth), UPM 2795 (anterior tooth), UPM 2796 (lateral tooth), UPM 2797 (anterior tooth, Fig. 5K-L), UPM 2798 (anterior tooth), UPM 2800 (lateral tooth), UPM 2802 (anterior tooth), UPM 2803 (anterior tooth), UPM 2804 (lateral tooth), UPM 2810 (lateral tooth), UPM 2811 (anterior tooth), UPM 2940 (anterior tooth), UPM 2944 (anterior tooth), UPM 2945 (anterior tooth).

Description. Anterior teeth have a tall and triangular main cusp that is both distally inclined and curving (Fig. 5L). The lingual crown face is strongly convex but the labial face ranges from flat to slightly convex, and both crown faces are smooth. The main cusp is flanked by a single pair of tall, triangular, sharply pointed, diverging lateral cusplets. The cutting edges are smooth and extend across the main cusp and lateral cusplets. The root is bilobate and bears a pronounced lingual protuberance (Fig. 5K). No nutritive groove is developed, but one or more nutritive foramina are usually present. The root lobes are elongated, rather narrow,

rounded, divergent, and the interlobe area is deep and U-shaped. The main cusp on the upper anterior teeth is generally more distally inclined or hooked than those in the lower anterior files.

Lateral teeth are mesiodistally wider and have a lower main cusp and shallower interlobe area compared to anterior teeth. The upper lateral files have a distally hooked main cusp (Fig. 5N), whereas those on the lower lateral teeth have a main cusp with a slight distal inclination (Fig. 5P). Moreover, the lower lateral teeth have a wider crown base than those in the upper files. All lateral teeth bear a single pair of tall, sharply pointed, diverging lateral cusplets (Fig. 5M, O, Q). Larger teeth from upper lateral files, located closer to the commissure, bear short but distinct plications along the labial crown base (Fig. 5R).

Remarks. The Rybushka Formation *Archaeolamna* teeth are morphologically similar to the *Cretalamna* teeth in our sample, but differ by having a hooked appearance, a much more robust lingual root protuberance, taller cusplets in comparison to the height of the main cusp, longer and narrower root lobes, a deeper interlobe area, and large upper posterolateral teeth with distinct labial ridges. Two *Archaeolamna* morphotypes appear to be present in our sample, including robust and gracile (*sensu* Underwood & Cumbaa 2010). Teeth of the robust morphotype are larger in overall size and have a wider crown base than those of the gracile morphotype in equivalent files. Some robust upper posterolateral teeth may also have short enameloid plications along the labial crown foot (see Fig. 5R),

Several nominal Santonian to Maastrichtian *Archaeolamna* species and subspecies have been described, including *A. aduncata* (Zhelezko, 1990), *A. aduncata suberecta* (Zhelezko, 1990) *A. arcuata orica* (Zhelezko, 1990), *A. kopingensis* (Davis, 1890), *A. kopingensis judithensis* Siverson, 1992, and *A. kopingensis kopingensis* Siverson, 1992. The three taxa erected by Zhelezko (1990) were all derived from Santonian deposits in Kazakhstan, and their validity is questioned. The occurrences of all three are based only on the type specimens, and the figured syntypes (Zhelezko 1990, pl. 10, figs. 1-25; pl. 11, figs. 1-5) all appear to fall within the morphological range of *A. kopingensis* (see Underwood & Cumbaa 2010, text-figs. 3-4). Siverson (1992) erected the subspecies *A. kopingensis judithensis* and *A. kopingensis kopingensis* based on specimens from the Campanian of

Montana and Wyoming, USA, and the Campanian of Sweden, respectively. Siverson (1992) noted that there was morphological overlap between the two taxa, and he regarded them as geographically separated subspecies of *A. kopingensis*. Of these two subspecies, the Rybushka Formation specimens more closely resemble those of *A. kopingensis kopingensis* from Sweden because the main cusp, especially on the anterior teeth, is not as broad as those of *A. kopingensis judithensis* (see Siverson 1992, pl. 2, figs. 19-20). Underwood & Cumbaa (2010) recognized gracile and robust morphotypes within their sample of *A. kopingensis* teeth from the Cenomanian of Canada. Those authors also suggested that the gracile morphotype represented teeth of mature male individuals, whereas the robust morphotype represented those of female and immature individuals. Both robust and gracile morphologies appear to occur in the Rybushka Formation sample, and we consider this to represent intraspecific variation rather than two morphologically similar species within the same deposit. We identify the teeth as *A. kopingensis* but refrain from assigning them to a subspecies.

Family Anacoracidae Casier, 1947
Genus *Squalicorax* Whitley, 1939

Squalicorax kaupi (Agassiz, 1843)
Fig. 5S-V

1843 *Corax kaupi* - Agassiz, p. 225, pl. 26a, figs. 25-34, pl. 26, figs. 4-8.
1975 *Squalicorax kaupi* - Cappetta and Case, p. 8, pl. 7, figs. 17-29.

Material: MMO 1 № 9273-20 (tooth), SGTU MEZ № 41-26 (tooth, Fig. 5S-T), UPM 2799 (tooth, Fig. 5U-V).

Description. The largest specimen measures 17 mm in mesio-distal width. The labial face of each specimen is flat, the lingual face is convex, and both crown faces are smooth. The mesial cutting edge is moderately to strongly convex, and it intersects with the distal cutting edge apically to form a sharply pointed apex. The distal cutting edge ranges from erect to distally inclined, and straight to slightly convex. The distal cutting edge forms an oblique to acute angle (depending on jaw position) with a short distal heel. The distal heel is straight to convex and extends to the distal edge of the tooth. The apex of the cusp is distally directed in all tooth positions, with the degree of inclination increasing

towards the commissure (compare Fig. 5S to Fig. 5U). All cutting edges are coarsely serrated. The largest serrations on the mesial edge occur medially, but they are finer basally and apically. On the distal cutting edge, serrations are largest on the lower half but become finer apically. The root is labiolingually thin, high lingually, and generally forms a U-shaped junction with the crown foot. The root is bilobate, with the lobes being short, divergent, and with rounded extremities. The mesial lobe of anterior teeth is mesiodistally narrower than the corresponding distal lobe (Fig. 5T). The interlobe area is wide and U-shaped (Fig. 5V), and a low root protuberance occurs on the lingual face that is not clearly demarcated from the remainder of the root.

Remarks. The teeth in our sample are morphologically similar to several other Campanian *Squalicorax* species, including *S. bassanii* (Gemmellaro, 1920), *S. kaupi* (Agassiz, 1843), *S. pristodontus* (Agassiz, 1835) and *S. yangaensis* (Dartevelle & Casier, 1943). The Rybushka Formation teeth differ from those of *S. bassanii* and *S. yangaensis* by having a more broadly convex mesial cutting-edge that lacks the slight concavity near the crown base. The distinctive "petal-shaped" anterior tooth morphology of *S. bassanii* and *S. yangaensis* is also lacking within our sample. The Rybushka Formation teeth differ from *S. pristodontus* by being smaller in overall size, having mesial serrations that are not mesially hooked, and by the sharp angular intersection of the distal cutting edge and distal heel (which is rounded to contiguous on *S. pristodontus* teeth). These characteristics fall within the morphological range of *S. kaupi*, and the Rybushka Formation teeth are assigned to this taxon. We note here that we consider *S. lindstromi* (Davis, 1890) to be a *nomen dubium*, as Davis (1890) did not provide a differential diagnosis between this taxon and *S. kaupi*, and he could not rule out the possibility that the morphologies occurred within the same mouth.

Squalicorax Morphology 1
Fig. 5W-X

Material: UPM 2931 (tooth).

Description. Specimen UPM 2931 is similar in overall morphology to the *S. kaupi* teeth described above, but it exhibits some notable differences. Although specimen UPM 2931 has a damaged mesial root lobe, the crown is well preserved. The lower two-thirds of the mesial cutting edge is evenly convex, however the upper third is nearly straight and is uniquely inset from the remainder of the cutting edge (Fig. 5W). The distal cutting edge is straight apically but strongly convex basally, where it transitions into a short and rounded distal heel. Both mesial and distal crown edges are coarsely serrated, with the largest serrations occurring on the lower two-thirds of the mesial cutting edge (Fig. 5X). The serrations on the upper-third of the mesial edge are finer and approximately the same size as those that occur on the distal edge and distal heel. Both the labial and lingual crown faces are slightly convex and have smooth enameloid. The root is slightly higher on the lingual face than on the labial face. Although the basal edge of the distal root lobe is damaged, it appears as if it was rounded. The mesial root lobe is not preserved. The interlobe area is shallow and U-shaped.

Remarks. The distinctly inset apical portion of the mesial edge on specimen UPM 2931 is unique among the various known *Squalicorax* species (see Cappetta 2012; Siversson et al. 2019). Although this specimen may represent an aberrant or pathological *S. kaupi* tooth, teeth with this distinct crown morphology have been observed in upper Santonian and Campanian deposits in the Gulf Coastal Plain of the USA (JAE, personal observation). This suggests that UPM 2931 represents a unique and undescribed species of *Squalicorax*, however, we refrain from naming this morphology because our Rybushka Formation sample consists only of a single specimen. Additional specimens are needed to further elucidate the taxonomy of this tooth.

Family Pseudocoracidae Cappetta, 2012
Genus *Pseudocorax* Priem, 1897

Pseudocorax laevis (Leriche, 1906)
Fig. 5Y-Z

1906 *Pseudocorax affinis* var. *laevis* - Leriche, 81.
1929 *Pseudocorax laevis* - Leriche, p. 223.

Material: UPM 2998 (lateral tooth).

Description. Specimen UPM 2998 measures approximately 1 cm in mesiodistal width and 7 mm in apicobasal height. The main cusp is triangular and is highly distally inclined. The cusp base is broad

but tapers apically to a sharp point. The mesial edge of the main cusp is slightly convex, whereas the distal edge is convex towards the apex and concave near the base (Fig. 5Z). The distal cutting edge is separated from a rounded distal heel by a distinct notch. A low and rounded mesial heel is not well delineated from the mesial edge of the main cusp. The cutting edge is smooth and continuous across the crown. The lingual face of the crown is convex, whereas the labial face is flat. The mesial and distal edges of the crown slightly overhang the root. The root lobes are sub-rectangular, slightly divergent, and separated by a shallow and U-shaped interlobe area. The mesial lobe is slightly wider than the distal lobe, and a faint nutritive groove is visible on a low lingual protuberance (Fig. 5Y).

Remarks. Three *Pseudocorax* species have been reported from Santonian through Maastrichtian deposits elsewhere, including the Maastrichtian *P. affinis* (Münster in Agassiz, 1843) and the Coniacian-Campanian species *P. granti* Cappetta & Case, 1975 and *P. laevis* (see Cappetta 2012; Jambura et al. 2021). Hamm & Shimada (2007) concluded that *P. granti* is a junior synonym of *P. laevis*, and we assign specimen UPM 2998 to *P. laevis* because it appears conspecific to the type specimens as described and figured by Leriche (1906). *Pseudocorax laevis* teeth lack the serrated cutting edges that are characteristic of *P. affinis* teeth.

Family *Incertae sedis*
Genus *Eostriatolamia* Glikman, 1980

Eostriatolamia segedini Glikman and Zhelezko in Zhelezko, 1977
Fig. 5AA-DD

Material: MMO 1 № 7768-1 (anterior tooth), MMO 1 № 9273-28 (anterior tooth), MMO 1 № 9273-29 (lower lateral tooth), UPM 2806 (anterior tooth), UPM 2808 (upper lateral tooth, Fig. 5CC-DD), UPM 2935 (anterior tooth, Fig. 5AA-BB), UPM 2941 (anterior tooth), UPM 2971 (lateral tooth), UPM 2972 (lateral tooth), UPM 2979 (anterior tooth), UPM 2980 (anterior tooth), UPM 2981 (anterior tooth), UPM 2982 (anterior tooth), UPM 2983 (anterior tooth), UPM 2984 (anterior tooth), UPM 2985 (anterior tooth), UPM 2986 (anterior tooth), UPM 2987(posterolateral tooth), UPM 2988 (anterior tooth), UPM 2989 (anterior tooth), UPM 2999 (anterior tooth).

Description. Anterior teeth have a tall and very narrowly triangular main cusp that is slightly distally inclined on most specimens (Fig. 5BB). The cutting edges are sub-parallel, with the distal edge being rather straight apically but strongly convex at the base. The mesial cutting edge is slightly convex apically and convex at the base. The lingual face of the main cusp is strongly convex, and very faint longitudinal ridges occur at the crown base on some teeth. The labial face ranges from flat to slightly convex, and weak enameloid plications occur along the crown base on some specimens. The main cusp is flanked by a single pair of small, divergent cusplets that vary in shape. They are short and recurved on teeth near the jaw symphysis, but on anterolateral teeth the cusplets are taller, broader, and more triangular. The root is bilobate with elongated, rather pointed, divergent lobes, and the interlobe area is V-shaped. There is a pronounced lingual protuberance that is bisected by a deep nutritive groove (Fig. 5AA).

The lateral teeth have a tall and triangular main cusp that can be slightly inclined (i.e., lower lateral files) or distally hooked (i.e., upper lateral files). On upper lateral teeth, the mesial cutting edge of the main cusp is relatively straight, whereas the distal edge is straight apically but concave at the cusp base. On lower lateral teeth, both cutting edges are slightly convex apically and concave basally. The lingual face of the main cusp is strongly convex, but the labial face is weakly convex. Short enameloid plications are visible along the labial crown foot (Fig. 5DD), and extremely faint lingual striations occur along the base of the main cusp on some specimens. The main cusp is flanked by two distinct pairs of sharply pointed lateral cusplets, with the medial pair being two times or more taller than the distal pair (Fig. 5CC). The base of the distal cusplets is largely united to the base of the medial cusplets. The mesial and distal cutting edges are continuous and extend across the lateral cusplets. The root lobes are shorter, labiolingually thinner, and more divergent than those of anterior teeth. A deep nutritive groove occurs on a lingual root protuberance. The interlobe area is always V-shaped and ranges from deep to shallow.

Remarks. *Eostriatolamia segedini* was named by Glikman & Zhelezko in Zhelezko (1977) for Santonian teeth from Kazakhstan. However, this species was neither described nor figured in the original publication and was therefore a *nomen nudum*. According to Cappetta (2012), this species was later validated by Zhelezko (1987, figs 9-10), who provided the first illustrations of the taxon. We concur

with Zhelezko (1977, 1987) and Cappetta (2012) that *E. segedini* (particularly the lateral teeth) represents a distinct *Eostriatolamia* species, and we therefore provided a formal description for the morphology (above). However, it should be noted that a search for the *E. segedini* type specimens was conducted by one of the present authors (SVS). Unfortunately, this search did not prove fruitful, and it is believed the type specimens were housed in the private collection of the late Victor Zhelezko (and not in a scientific collection) and have subsequently been lost.

Because the *E. segedini* type specimens cannot be accounted for, the descriptions we provide for this taxon are based on specimens in our Rybushka Formation sample. However, additional information on this taxon was gleaned from our examination of figured *E. segedini* teeth recovered from the type locality. Zhelezko (1987, figs 9-10) provided line drawings of the *E. segedini* type specimens, which included an anterior tooth that was figured in labial view, and a lateral tooth shown in both labial and lingual views. Cappetta (2012, fig. 236k-m) later provided a photograph of a *E. segedini* lateral tooth that was also collected from the type locality. As far as the present authors are aware, these are the only *E. segedini* teeth previously figured in the literature. The lateral teeth illustrated by Zhelezko (1987) and Cappetta (2012) exhibit some distinctive commonalities, including a distally hooked and triangular main cusp, and two pairs of lateral cusplets. In addition, the specimen shown by Cappetta (2012, fig. 236) clearly possesses distinctive labial plications. Neither Zhelezko (1977) or Zhelezko (1987) provided detailed descriptions of *E. segedini*, and the statements that were made about the teeth of this taxon are contradictory. For example, Zhelezko (1977:17) noted that the teeth are between 12-14 mm in height, have "ribbing" at the base of the labial crown face, striae along the lingual crown base, and lateral cusplets are present. Zhelezko (1987:126), however, stated that *E. segedini* teeth are between 12-13.5 mm in height, have a relatively expanded crown, and, as a rule, vertical ribs are absent on the labial face. Later, Glikman & Averianov (1998) discussed (but unfortunately did not figure) a number of *Eostriatolamia* teeth from the *E. segedini* type locality and noted that the teeth had a narrower main cusp compared to *E. venusta*, and that there are two pairs of lateral cusplets, lingual longitudinal ridges, and labi-

al plications are sometimes present at the base of the lateral cusplets. This latter statement, combined with Zhelezko's (1977, 1987) observations regarding the presence or absence of labial "ribbing," indicates that the occurrence of this characteristic is variable within the *E. segedini* dentition. Intraspecific variation within this taxon is also suggested by the specimens figured by Zhelezko (1987, figs 9-10), which possess two pairs of lateral cusplets on the lateral tooth but only a single pair on the anterior tooth. Also of interest, Zhelezko (1987) alludes to the presence of labial and lingual ornamentation on teeth of other *Eostriatolamia* taxa he illustrated (see figs. 4b, 6b, 11a, 12, 14b), but shows no such features on the *E. segedini* teeth he figured (figs. 9-10). Nevertheless, several lateral teeth in our Rybushka Formation sample appear to be conspecific to the tooth illustrated by Cappetta (2012), which shows clear labial plications, and these teeth are therefore assigned to *E. segedini*. These teeth have a triangular and distally hooked main cusp, two pairs of lateral cusplets, conspicuous labial plications at the crown base, and occasionally very faint enameloid plications along the lingual crown base. It is this unique combination of characteristics that separates these lateral teeth from those of the other recognized *Eostriatolamia* species (see Zhelezko 1987; Glikman & Averianov 1998; Cappetta 2012).

The only prior illustration of an *E. segedini* anterior tooth is that shown in Zhelezko (1987, fig. 9), which is a small line drawing of a specimen in labial view. Unfortunately, this illustration provides little detail of the morphology of the anterior teeth, nor does it allow us to sufficiently differentiate them from those of the other *Eostriatolamia* species. Therefore, our diagnosis of *E. segedini* anterior teeth is based on specimens in our Rybushka Formation sample. These anterior teeth are assigned to *E. segedini* based on their association with confirmed *E. segedini* lateral teeth. The teeth have a single pair of lateral cusplets, and the specimens in our sample indicate a lateral cusplet morphology that grades from short and recurved on the anterior-most teeth to those that are taller, broader, and more triangular on the teeth in the anterolateral files. Although the anterior teeth never have more than a single pair of lateral cusplets, the cusplets on the anterolateral teeth are morphologically very similar to the primary cusplets on the lateral teeth, indicating that they belong to the same tax-

on. These teeth are dissimilar to *E. venusta* (Leriche, 1906) anterior teeth that also occur in our sample, particularly in the narrowness of the crown base (see below) and by having a taller and narrower main cusp.

Eostriatolamia venusta (Leriche, 1906)
Fig. 5EE-HH

1906 *Lamna venusta* - Leriche, p. 86.
1977 *Plicatolamna? venusta* - Herman, p. 206, pl. 8, fig. 5.
1980 *Eostriatolamia venusta* - Glickman, p. 120.

Material: MMO 1 № 9273-31 (upper lateral tooth, Fig. 5GG-HH), MMO 1 № 9273-32 (upper lateral tooth), UPM 2807 (lateral tooth), UPM 2809 (anterior tooth), UPM 2936 (upper lateral tooth), UPM 2937 (lower lateral tooth), UPM 2938 (anterior tooth, Fig. EE-FF), UPM 2973 (lower lateral tooth), UPM 2974 (upper lateral tooth), UPM 2975 (anterior tooth), UPM 3000 (upper lateral tooth).

Description. Anterior teeth have a broadly triangular, symmetrical main cusp. The mesial and distal cutting edges are convex at the base, but otherwise straight and gradually tapering to form a sharply pointed apex. The labial face ranges from flat to slightly convex, whereas the lingual face is strongly convex. Faint enameloid plications occur along the labial crown base (Fig. 5FF), and faint vertical ridges are visible at the base of the lingual face. The main cusp is flanked by a single pair of small, triangular and divergent lateral cusplets. The root is bilobate, with lobes being highly divergent and rounded basally. A deep nutritive groove occurs on a pronounced lingual root boss (Fig. 5EE). The interlobe area is deep and U-shaped.

The lateral teeth are similar to those in the anterior positions but have a much lower main cusp and wider crown base. The single pair of lateral cusplets is also comparatively much shorter in height (Fig. 5GG). Lateral teeth positioned closer to the jaw symphysis are apico-basally taller than they are wide, whereas those positioned near the commissure are mesiodistally wider than they are tall. Upper lateral teeth have a distally inclined main cusp, whereas those in the lower lateral files have an erect and symmetrical main cusp. The labial and lingual ornamentation is less conspicuous on lateral teeth and is absent on teeth situated closer to the jaw commissure. The interlobe area on the lateral teeth is often V-shaped and is shallow (Fig. 5HH) compared to anterior teeth.

Remarks. Glickman & Averianov (1998) and Cappetta (2012) recognized six species of *Eostriatolamna*, four of which have a stratigraphic range from the Campanian through Maastrichtian. These include *E. holmdelensis* (Cappetta & Case, 1975), *E. lerichei* (Glikman & Zhelezko in Zhelezko, 1977), *E. segedini*, and *E. venusta* (Leriche, 1906). *Eostriatolamia holmdelensis* was originally reported from the upper Campanian of New Jersey, and teeth of this species, much like those of the Albian to Cenomanian *E. gracilis* (Agassiz, 1843), *E. striatula* (Dalinkevicius, 1935), and *E. subulata* (Agassiz, 1843), differ significantly from the Rybushka Formation *Eostriatolamia* specimens by having robust and elongated longitudinal ridges on the lingual crown face (see Cappetta & Case 1975, pl. 6, figs 10-21; Glikman & Averianov 1998, figs 4-5).

The teeth described herein differ from those assigned to *E. segedini* (see above) by having a broader crown base and by only having a single pair of lateral cusplets on the lateral teeth. Our sample is comparable to material of *E. lerichei* and *E. venusta*, but in a comparison of these two species, Glickman & Averianov (1998) noted that *E. lerichei* teeth from the Campanian of Kazakhstan were practically identical to the *E. venusta* teeth from the Santonian-Campanian of Europe. Despite appearing to be conspecific, Glickman & Averianov (1998) argued that the morphological similarity between the two taxa did not preclude them from representing two distinct species. However, due to the lack of clear distinguishing features between the two species, we view them as being conspecific and assign the Rybushka Formation specimens to *E. venusta*, as this name has priority over *E. lerichei*.

Superorder **Squalomorphi** (*sensu* Nelson et al., 2016)
Series **Squalida** (*sensu* Nelson et al., 2016)
Order **Squaliformes** Goodrich, 1909
Family Squalidae de Blainville, 1816

Gen. et sp. indet.
Fig. 6A-D

Material: UPM 2814 (dorsal fin spine, Fig. 6A-B), UPM 2815 (dorsal fin spine, Fig. 6C-D).

Description. Both fin spines measure approximately 5.5 cm in height. In lateral view the
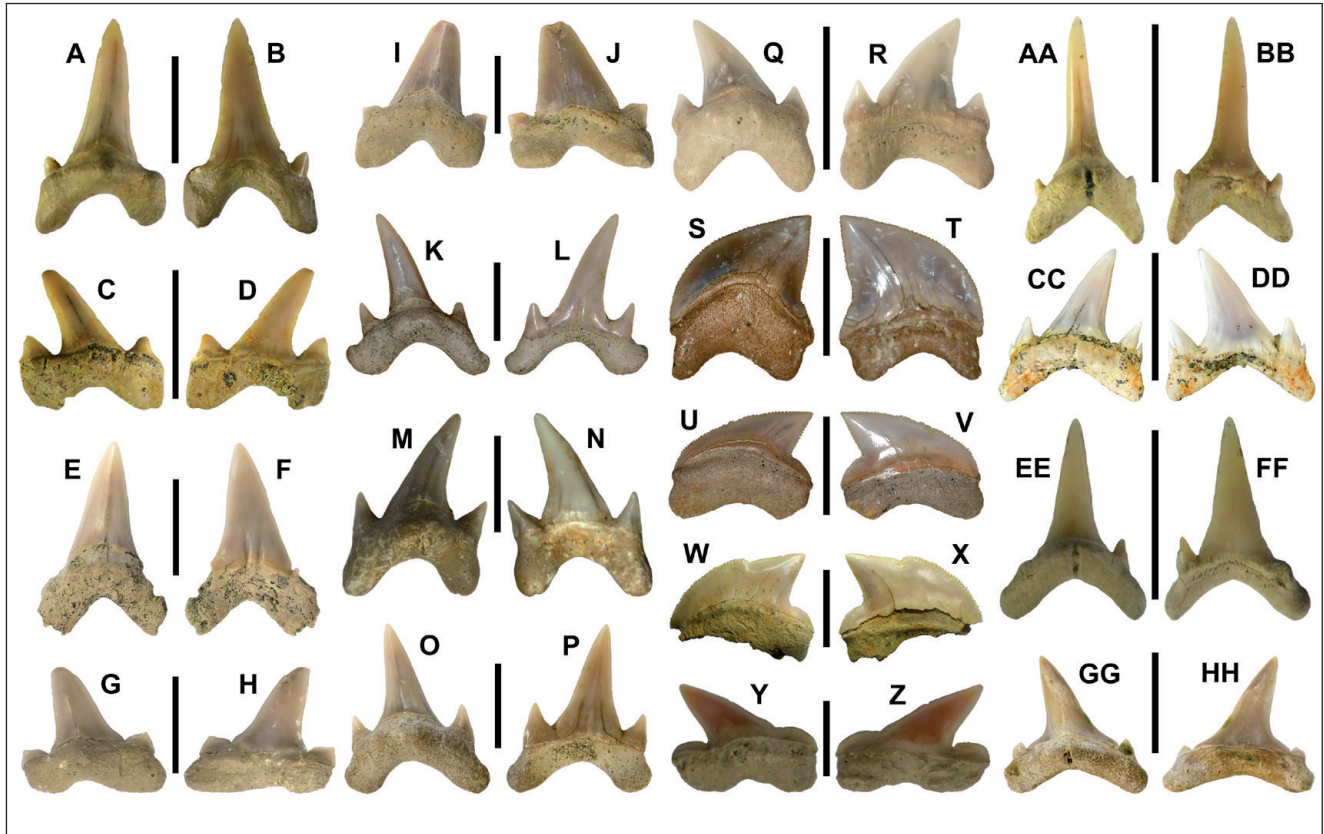
Fig. 5 - Lamniformes teeth from the Beloe Ozero locality in the Saratov Oblast, Russia. A–B) UPM 2943, *Cretalamna* cf. *C. borealis*, upper left anterolateral tooth: A, lingual view; B, labial view. C–D) UPM 2942, *Cretalamna* cf. *C. borealis*, upper right lateral tooth: C, lingual view; D, labial view. E–F) MMO 1 № 9273-14, *Cretalamna* cf. *C. sarcoportheta*, lower right anterior tooth: E, lingual view; F, labial view. G–H) MMO 1 № 9273-26a, *Cretalamna* cf. *C. sarcoportheta*, upper right posterolateral tooth: G, lingual view; H, labial view. I–J) MMO 1 № 9273-17, *Cretalamna* cf. *C. sarcoportheta*, upper left anterolateral tooth: I, lingual view; J, labial view. K–L) UPM 2797, *Archaeolamna kopingensis*, anterolateral tooth: K, lingual view; L, labial view. M–N) MMO 1 № 7768-3, *Archaeolamna kopingensis*, upper left lateral tooth: M, lingual view; N, labial view. O–P) MMO 1 № 9273-15, *Archaeolamna kopingensis*, lower left lateral tooth: O, lingual view; P, labial view. Q–R) MMO 1 № 9273-27, *Archaeolamna kopingensis*, upper right posterolateral tooth, robust morphology: Q, lingual view; R, labial view. S–T) SGTU MEZ № 41-26, *Squalicorax kaupi*, tooth: S, lingual view; T, labial view. U–V) UPM 2799, *Squalicorax kaupi*, posterolateral tooth: U, lingual view; V, labial view. W–X) UPM 2931, *Squalicorax* Morphology 1, tooth: W, lingual view; X, labial view. Y–Z) UPM 2998, *Pseudocorax laevis*, tooth: Y, lingual view; Z, labial view. AA–BB) UPM 2935, *Eostriatolamia segedini*, anterior tooth: AA, lingual view; BB, labial view. CC–DD) UPM 2808, *Eostriatolamia segedini*, lateral tooth: CC, lingual view; DD, labial view. EE–FF) UPM 2938, *Eostriatolamia venusta*, anterior tooth: EE, lingual view; FF, labial view. GG–HH) MMO 9273-31, *Eostriatolamia venusta*, lateral tooth: GG, lingual view; HH, labial view. All scale bars represent 1 cm, except Y–Z which is 0.5 cm.

spines are posteriorly recurved, with a convex anterior margin and concave posterior margin. The lateral edges are slightly convex. The spines are thickest at the base but gradually taper to a sharp apex. The spines are internally hollow and have a sub-triangular transverse cross-section. The anterior face of the spine bears a bluntly pointed carina extending the entire height of the spine. On the posterior face, a concave sulcus extends the entire height of the spine (Fig. 6B, D). On specimen UPM 2815, enameloid covers a majority of the trunk but is absent at the apex and at the base (Fig. 6A). On specimen UPM 2814, enameloid covers the apex and the trunk, but is absent at the base (Fig. 6C). Although enameloid is absent within the posterior sulcus, it does occur along the lateral margins of the sulcus. On specimen UPM 2815, faint annuli are visible that extend anteroposteriorly across the enameloid-covered portion of the spine. Specimen UPM 2814 differs from UPM 2815 by having a conspicuous medial swelling along the anterior edge (Fig. 6A).

Remarks. The morphological similarity of the two dorsal fin spines in our sample suggest they belong to the same taxon. Among extant elasmobranchs, dorsal fin spines occur on members of the families Heterodontidae, Squalidae and, occasionally, Echinorhinidae (Maisey 1979). Based on the morphology of the sulcus and enameloid covering on the trunk, the Rybushka Formation spines are morphologically comparable to those of extant *Heterodontus*

and *Squalus*. However, the posterior curvature of the Rybushka Formation specimens is more consistent with the condition of extant *Squalus* spines, whereas those of extant *Heterodontus* are much straighter (see Maisey 1979, fig. 2). Moreover, the sulcus margins on the Rybushka Formation specimens exhibit a slight overlapping of the enameloid onto the dentine walls, a phenomenon also occurring on extant *Squalus* spines (see Maisey 1979, fig. 2e). This contrasts with the sulcal margins on extant *Heterodontus* spines, which are entirely enameloid-covered (see Maisey 1979, fig. 2f).

Cappetta (2012) recognized three genera of Cretaceous Squalidae - *Centrosqualus*, *Protosqualus*, and *Squalus*. Unfortunately, the Cretaceous species within these genera are known almost exclusively from teeth, and their dorsal fin spine morphologies are unknown. Because it is unclear as to which genus or species the Rybushka Formation spines belong, they are herein assigned to an undetermined taxon of Squalidae.

Squalomorphi indet.
Fig. 6E-F

Material. UPM 2822 (vertebral centrum), UPM 2894 (vertebral centrum, Fig. 6E-F), UPM 2895 (vertebral centrum), UPM 2906 (vertebral centrum), UPM 2920 (vertebral centrum).

Description. The centra are slightly dorsoventrally compressed, making them mediolaterally wider than tall (Fig. 6E), with greatest width between 3 cm and 4.5 cm. The anterior and posterior faces of the centrum are slightly concave and smooth, a shallow notochord depression occurs at the center of both faces, and numerous concentric growth annuli are visible. The vertebrae are thick, with some exceeding 1.5 cm in greatest anteroposterior thickness. The lateral edges of the vertebrae range from smooth to having slight rugosities. Paired circular fossae occur dorsally and/or ventrally (Fig. 6F) that are attachment surfaces for neural and/or hemal arches.

Remarks. The dorsoventrally compressed morphology of the centra differs from those of centra of Galeomorphi, which are more circular in outline. Although vertebrae with this compressed morphology have been observed in both extant and extinct squalomorphs (i.e., *Squatina*, see Mollen et al. 2016), this generalized morphology is shared amongst several different taxa within this order.

Division **BATOMORPHI** (Cappetta, 1980)
Order **Rajiformes** Berg, 1940
Family *Incertae sedis*
Genus *Squatirhina* Casier, 1947

Squatirhina sp.
Fig. 6G-J

Material: UPM 2997 (tooth, Fig. 6G-J).

Description. The crown measures nearly 6 mm in width and 4.5 mm in height as preserved (the crown apex is damaged), and in occlusal view it has a triangular outline. The crown is dominated by a slightly distally inclined cusp (Fig. 6G) that is strongly lingually inclined and curved (Fig. 6H). The cusp is predominantly formed by the labial face, which is highly convex anteriorly but becomes flatter at the mesial and distal sides. The posterior margin of the labial face is abrupt and sharp-edged, and this edge becomes obsolete basally. The lingual face is flat apically but becomes more convex basally, where it extends as a narrow protuberance onto the root. The mesial and distal sides of the crown base are low, laterally expanded, and perpendicular to the cusp height. A very low but broad and sharp-edged cusplet occurs on each side of the cusp, close to the lingual crown margin (Fig. 6I). These cusplets are not connected to the edge of the main cusp. The medial portion of the labial crown foot is extended into a broad, squared, strongly basally curved protuberance. The crown enameloid is smooth. The root is imperfectly preserved, but it is low and bears a pair of margino-lingual foramina. In basal view, the root is bisected medially by a nutritive groove that bears a central foramen, and basal attachment surfaces of each root lobe are flat and heart-shaped (Fig. 6J). Although the root extends beyond the lingual crown margin, it does not extend to the labial or lateral crown margins.

Remarks. Specimen UPM 2997 exhibits the salient features that allow us to identify it as *Squatirhina*. However, it is difficult to speciate the single specimen available to us because the nominal species that have been attributed to the genus exhibit monognathic and apparently gynandric heterodonty (Casier 1947; Vullo 2005; Guinot et al. 2012). Specimen UPM 2997 may represent a male individual because it bears a distinctive cusp (see Guinot et al. 2012). As several Late Cretaceous species have

Fig. 6 - Squalomorphi and Batomorphi remains from the Beloe Ozero locality in the Saratov Oblast, Russia. A–B) UPM 2814, Squalidae indet., dorsal fin spine: A, left lateral view; B. posterior view. C–D) UPM 2815, Squalidae indet., dorsal fin spine: C, left lateral view; D. posterior view. E–F) UPM 2894, Squalomorphi indet., vertebra: E, anterior view; F, dorsal view. G–J) UPM 2997, *Squatirhina* sp., tooth: G, labial view; H, mesial view; I. lingual view; J, basal view. K–L) UPM 2825, Batomorphi indet., dermal denticle: K, apical view; L, profile view. Scale bars are 2 cm in A–D, 5 mm in G-J, 1 cm in E-F, K-L.

been reported from Europe, including *Squatirhina* sp. from the Cenomanian of the Saratov Oblast (Popov & Biriukov 2015), additional material is necessary for us to ascertain morphological variation and accurately identify the species represented by UPM 2997.

Batomorphi indet.
Fig. 6K-L

Material: UPM 2825 (dermal denticle, Fig. 6K-L).

Description. The dermal denticle has a roughly circular apical outline, with irregular margins (Fig. 6K). In profile view, the specimen has a short, medially positioned, recurved triangular cusp (Fig. 6L). The apex of the cusp is covered with smooth enameloid. The denticle is thickest medially but thins towards the margins. The basal attachment surface is slightly convex but otherwise featureless.

Remarks. This thorn-like dermal denticle is similar to those occurring along the midline of the body and tail of many extant rays (see Cappetta 2012). Unfortunately, this dermal denticle morphology is shared among many families, genera, and species of rays, and we therefore cannot identify it with certainty beyond Batomorphi.

Class **OSTEICHTHYES** Huxley, 1880
Subclass **ACTINOPTERYGII** (*sensu* Goodrich, 1930)
Unranked **NEOPTERYGII** Regan, 1923
Division **TELEOSTEOMORPHA** Arratia et al., 2004
Subdivision **TELEOSTEI** Müller, 1845
Order **Crossognathiformes** Taverne, 1989
Family Pachyrhizontidae Cope, 1872
Genus *Pachyrhizodus* Dixon, 1850

Pachyrhizodus sp.
Fig. 7

Material: MMO 1 № 10420-54 (right dentary fragment, Fig. 7A-C), MMO 1 № 10420-55 (anterior portion of right dentary, Fig. 7D-E).

Description. Specimen MMO 1 № 10420-54 (Fig. 7A-C) is a fragment of a right dentary. This specimen measures approximately 12.5 cm in anteroposterior length and 1.5 cm in greatest labio-lingual width as preserved. In occlusal view (Fig. 7A), the specimen has an evenly convex labial margin and a relatively straight lingual margin (although the anterior one-third of the lingual margin is damaged and not well preserved). The

lingual margin bears a single row of tightly packed tooth bases and alveoli. The largest tooth base measures approximately 1 cm in diameter and is located towards the posterior end of the element. The more anteriorly positioned tooth bases are smaller and range between 0.2 and 0.5 cm in diameter. The tooth bases range from circular to oval in outline and have a hollow pulp cavity. The teeth are pleurodont and are set into shallow alveoli. The labial face of the dentary exhibits some irregular pitting (due to erosion) but is otherwise featureless. Unfortunately, no additional characteristics can be discerned from the labial face because the anterior, posterior, occlusal, and ventral edges are not entirely preserved. However, in lingual view, a thick bony ridge beneath the tooth row extends anteroposteriorly along nearly the entire length of the bone (Fig. 7B).

Specimen MMO 1 № 10420-55 (Fig. 7D-E) is the anterior portion of a right dentary. Unfortunately, this specimen is both crushed and embedded in a concretion, and only the occlusal and labial surfaces are taxonomically informative. In occlusal view, the specimen has an evenly convex lingual margin (Fig. 7D). The anterior end of the dentary is represented by a sub-rounded and laterally expanded symphysis. The labial margin is lined with five prominent tooth bases that are separated by four wide and concretion-filled alveoli. A sixth tooth base can be seen at the anterior-most end of the symphysis. The tooth bases are circular, have a flared base and hollow pulp cavity, and are pleurodont while also being partially embedded in shallow alveoli. The labial face is convex both anteroposteriorly and dorsoventrally (Fig. 7E). The exposed portions of the bone are smooth and featureless.

Remarks. Although the two dentaries in our sample are not well preserved, they can be assigned to *Pachyrhizodus* because they possess the following combination of characteristics: 1) the tooth bases range from circular to oval in occlusal outline and have a hollow pulp cavity; 2) the tooth bases are robust and, although pleurodont, embedded in shallow alveoli; 3) the tooth row consists of a combination of tightly-packed tooth bases and alveoli that are arranged into a single row; 4) a thick bony ridge occurs beneath the tooth row on the lingual face of MMO 1 № 10420-54; and 5) on specimen MMO 1 № 10420-55, a tooth on the
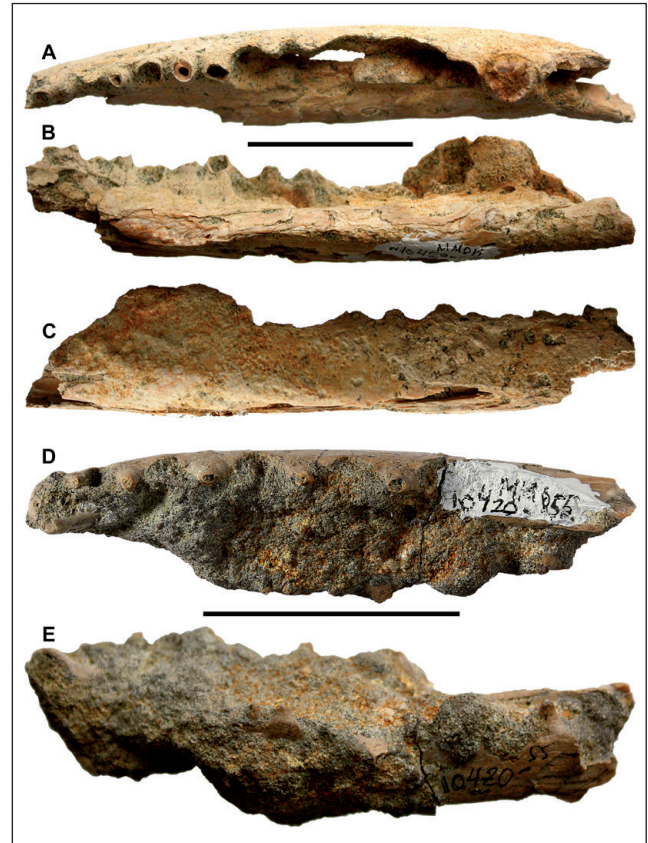

Fig. 7 - *Pachyrhizodus* sp. remains from the Beloe Ozero locality in the Saratov Oblast, Russia. A–C) MMO 1 № 10420-54, right dentary fragment: A, occlusal view; B, lingual view; C, labial view. D–E) MMO 1 № 10420-55, anterior portion of right dentary: D, occlusal view; E, labial view. Both scale bars represent 4 cm.

symphysis is positioned lingual to the main tooth row (Fig. 7D).

Unfortunately, the incomplete and poor preservation of the two *Pachyrhizodus* elements from the Rybushka Formation does not allow us to speciate them with certainty. However, of the numerous *Pachyrhizodus* species that have been named (see Applegate 1970; Shimada & Fielitz 2006; Shimada 2015; Stewart & Hackel 2015), the tooth bases on specimens MMO 1 № 10420-54 and MMO 1 № 10420-55 are too large and robust to be referred to *Pachyrhizodus minimus* Stewart, 1899, and all teeth appear to lack carinae as occur on the teeth of *P. leptopsis* Cope, 1874. Although this indicates that the Rybushka Formation specimens belong to one of the other species within the genus, better preserved material is needed to make this determination.

Order **Ichthyodectiformes** Bardack and Sprinkle, 1969
Family Saurodontidae Stewart, 1900
Genus *Saurocephalus* Harlan, 1824

Saurocephalus lanciformis Harlan, 1824
Fig. 8A-D

Material: MMO 1 № 10420-50 (partial dentary, Fig. 8A-B), MMO 1 № 10420-51 (partial dentary), MMO 1 № 10420-52 (partial dentary, Fig. 8C-D), UPM 2899 (partial dentary).

Description. In lingual view, the dentary has a straight oral margin that is slightly angled posteriorly. The symphyseal margin is preserved on one specimen (UPM 2899), and it intersects the oral margin at approximately an 80° angle. The anterior two-thirds of the oral margin is straight, whereas the posterior one-third is slightly convex. The oral margin is lined with a single row of tightly packed teeth. The teeth have a lanceolate labial/lingual outline, with convex and sharp anterior and posterior carinae (Fig. 8C). The labial and lingual crown faces are evenly convex (Fig. 8A). In occlusal view, the teeth are slightly rotated clockwise in the tooth row such that the anterior edge of any given tooth overlaps the posterior edge of the preceding tooth. The teeth are erupted at various heights across the tooth row. The dentary is labiolingually compressed, and the labial and lingual faces are flat. Although the labial face is unornamented, the lingual face has a shallow furrow that extends anteroposteriorly below the tooth row (Fig. 8B, D). This furrow contains a single row of regularly spaced, deep foramina.

Remarks. The teeth preserved on the dentary fragments in our sample are morphologically similar to those of *Saurodon* and *Saurocephalus* from the Western Interior and Gulf Coastal Plain of the U.S.A. The dental elements of these taxa are similar but can be easily differentiated by the occurrence of "key-hole"-shaped lingual foramina being positioned just below the teeth on *Saurodon*. On *Saurocephalus*, the foraminae are cylindrical and reside within a furrow located below the tooth row (as seen on the Rybushka Formation specimens).

Numerous nominal *Saurocephalus* species occur in the historical literature, including *S. arapahovius* Cope, 1872, *S. broadheadi* (Stewart, 1898a), *S. dentatus* Stewart 1898a, *S. ferox* Stewart 1898b, *S. goodeanus* (Cope, 1877), *S. lanciformis* Harlan, 1824, *S. pamphagus* Hay, 1899, *S. phlebotomus* Cope, 1870, *S. pygmaeus* (Loomis, 1900), *S. woodwardii* Davies, 1878, and *S. xiphirostris* Stewart, 1898b. These species were reviewed by Shimada & Fielitz (2016), who designated *S. arapahovius*, *S. dentatus*, *S. goodeanus*, and *S. pamphagus* as junior synonyms of *S. lanciformis*, and *S. broadheadi*, *S. ferox*, *S. phlebotomus*, and *S. xiphirostris* as conspecific with the closely related *Saurodon leanus* (Hays, 1830). Stewart (1999) referred *S. pygmaeus* to a new genus, *Prosaurodon*, noting that this taxon has more cylindrical teeth than *S. lanciformis*, and it lacks a lingual row of foramina beneath the tooth rows on the dentary, maxilla, and premaxilla. Some questions have arisen regarding the validity of *S. woodwardii* (see Bardack & Sprinkle 1969; Friedman 2012) and whether it is also a junior synonym of *S. lanciformis*. Regardless, photographs of the *woodwardii* holotype (NHM 42979) illustrated by Friedman (2012, fig. 4) show that the teeth have straighter anterior and posterior edges than those on *S. lanciformis*, resulting in a more triangular, as opposed to lanceolate, outline. The teeth of specimen NHM 42979 appear to be finely serrated, a characteristic noted by Woodward (1901), whereas the cutting edges on *S. lanciformis* teeth are smooth. The Rybushka Formation dentaries have lanceolate, unserrated teeth, and we therefore refer them to *S. lanciformis*.

Supercohort **Teleocephala** de Pinna, 1996
Cohort **Elopomorpha** Greenwood et al., 1966
Order **Elopiformes** Sauvage, 1875
Family Phyllodontidae Dartevelle and Casier, 1943
Genus *Paralbula* Blake, 1940

Paralbula casei Estes, 1969
Fig. 8E-G

Material: MMO 1 № 10420-61 (basibranchial tooth plate with teeth).

Description. The anterior and posterior ends of MMO 1 № 10420-61 are missing, but as preserved, this basibranchial plate measures 32 mm in anteroposterior length and 15 mm in greatest mediolateral width. The posterior end of the plate is mediolaterally wider than the anterior end. Overall, the occlusal surface appears slightly convex, but the central portion of the plate is obscured by matrix (Fig. 8E). Numerous circular to sub-circular

Fig. 8 - Teleost remains from the Beloe Ozero locality in the Saratov Oblast, Russia. A–B) MMO 1 № 10420-50, *Saurocephalus lanciformis*, left dentary fragment: A, labial view; B, lingual view. C–D) MMO 1 № 10420-52, *Saurocephalus lanciformis*, right dentary fragment: C, labial view; D, lingual view. E–G) MMO 1 № 10420-61, *Paralbula casei*, basibranchial plate: E, oral view; F, close-up of teeth; G, aboral view. All scale bars represent 2 cm.
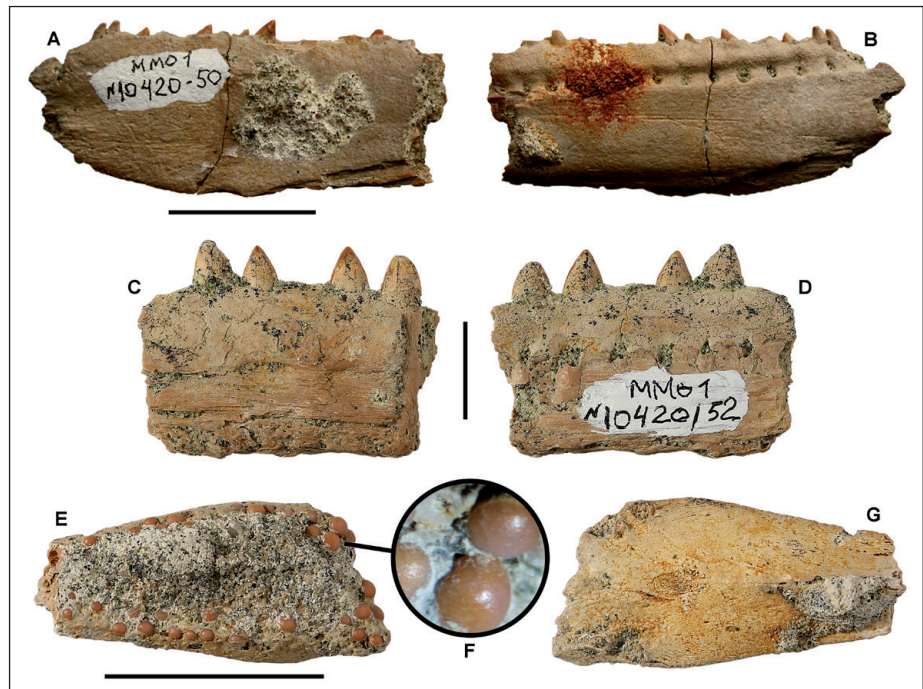
teeth are visible around the periphery of the plate (Fig. 8F) and likely occur on the matrix-covered portion. The occlusal surface of the teeth is evenly convex, and the enameloid appears to extend to the tooth base on nearly all visible specimens. The tooth enameloid on unworn teeth is ornamented with a granular texture. The aboral surface is convex (Fig. 8G) and ornamented with fine concentric ridges that resemble a fingerprint pattern, and a distinct ridge extends down the midline on the anterior half.

Remarks. Two species of *Paralbula* have a temporal range during the Late Cretaceous, including *Paralbula casei* Estes, 1969 and *Paralbula marylandica* Blake, 1940 (Estes 1969; Schein et al. 2011). According to Estes (1969), these species are readily differentiated by the ornamentation on their teeth. The crown enameloid of *P. casei* teeth has a unique granular ornamentation, whereas *Paralbula marylandica*, which has a range extending into the Paleogene (see Ebersole et al. 2019), has teeth with smooth enameloid. The granular ornamentation on *P. casei* teeth is very susceptible to wear, so worn or abraded teeth may appear to have smooth enameloid. However, unworn teeth located along the periphery of specimen MMO 1 № 10420-61 exhibit granular ornamentation (see Fig. 8F), leading us to refer the specimen to *P. casei*.

Unranked **Clupeocephala** Patterson and Rosen, 1977
Cohort **Euteleostei** Rosen, 1985
Superorder **Cyclosquamata** Rosen, 1973
Order **Aulopiformes** Rosen, 1973
Suborder **Alepisauroidei** (*sensu* Nelson et al., 2016)
Superfamily Alepisauroidea (*sensu* Davis, 2010)
Family Enchodontidae (*sensu* Nelson et al., 2016)
Genus *Enchodus* Agassiz, 1835

Enchodus cf. *E. dirus* (Leidy, 1857)
Fig. 9A-B

1857 *Phasganodus dirus* - Leidy, p. 2.
1900 *Enchodus dirus* - Stewart, p. 376.

Material: UPM 3004 (dermopalatine tooth).

Description. This tooth measures approximately 1.5 cm in height and 4 mm in greatest anteroposterior width. In labial and lingual views, the tooth has a sigmoidal outline and tapers apically to a point (Fig. 9A). The labial and lingual faces are evenly convex, and faint lingual enameloid striations are visible at the crown base. The tooth has a sharp anterior cutting edge (Fig. 9B), whereas the posterior edge is evenly rounded. The tooth has a symmetrical, teardrop-shaped cross section.

Remarks. *Enchodus* is a diverse genus comprised of 24 to 30 recognized species (see Goody 1976; Chalifa 1996; Forey et al. 2003; Silva & Gallo 2011; Holloway et al. 2017). Of these, more than a dozen species of *Enchodus* have been described from Santonian through Maastrichtian deposits around the world, including *E. bursauxi* Arambourg, 1952, *E. dirus* (Leidy, 1857), *E. elegans* Dartevelle & Casier, 1949, *E. faujasi* Agassiz, 1843, *E. ferox* Leidy, 1855, *E. gladiolus* (Cope, 1872), *E. lamberti* Arambourg & Joleaud, 1943, *E. lewesiensis* (Mantell, 1822), *E. libycus* (Quass, 1902), *E. oliverai* Maury, 1930, *E. petrosus* Cope, 1874, *E. shumardi* Leidy, 1856, *E. subaequilateralis* Cope, 1885, *E. tineidae* Holloway et al., 2017, and *E. zinensis* Chalifa, 1996 (see Goody 1976; Chalifa 1996; Forey et al. 2003; Silva & Gallo 2011; Holloway et al. 2017). Unfortunately, a number of these species were named for extremely fragmentary material consisting of isolated dental bones and/or teeth, and it is likely that several of these taxa are *nomina nuda*. Although several *Enchodus* species have been named from nearly complete skeletons (see Chalifa 1996; Fielitz & Gonzalez-Rodriguez 2010; Schein et al. 2013), such examples are extremely rare. Due to the incomplete and fragmentary nature of most of the *Enchodus* material collected, speciation is generally based on morphological differences between (well-preserved) dermopalatine bones and dermopalatine teeth (see Arambourg 1954; Goody 1976; Parris et al. 2007).

The Rybushka Formation dermopalatine tooth represented by UPM 3004 has been tentatively identified as *E. dirus* because, although it has a sigmoidal profile reminiscent of dermopalatine teeth of *Enchodus* cf. *E. gladiolus* (see below), it lacks the post-apical barb that is characteristic of the latter taxon. At least three other *Enchodus* species have sigmoidal dermopalatine teeth, including *E. bursauxi*, *E. dirus*, and *E. libycus*. Specimen UPM 3004 appears to differ from *E. bursauxi* and *E. libycus* by being less robust and anteroposteriorly narrower at the crown base (see Arambourg 1952: pl. 33). Whereas posterior basal striations are absent on *E. bursauxi* (see Arambourg 1952: pl. 33, figs. 24-36), these occur on UPM 3004 and the dermopalatine teeth of *E. dirus* and *E. libycus* (Arambourg 1952; Goody 1976). Although the robust nature of *E. libycus* dermopalatine teeth might indicate that UPM 3004 belongs to *E. dirus*, it cannot be ruled out that this characteristic reflects ontogeny. As far as the present authors are

aware, there are no published characteristics to definitively differentiate isolated dermopalatine teeth of *E. dirus* from *E. libycus*. However, because *E. bursauxi* and *E. libycus* are regarded as Maastrichtian taxa (Quass 1902; Arambourg 1952), UPM 3004 is tentatively assigned to *E. dirus* due to its occurrence elsewhere in stratigraphically equivalent (Campanian) deposits (Goody 1976; Parris et al. 2007).

Enchodus cf. *E. gladiolus* (Cope, 1872)
Fig. 9C-D

1872 *Cimolichthys gladiolus* - Cope, p. 353.
1875 *Phasgnodus gladiolus* - Cope, p. 235.
1976 *Enchodus gladiolus* - Goody, p. 103, pl. 1, figs. 11-12, pl. 3, fig. 3.

Material: UPM 2813 (dermopalatine tooth, Fig. 9C-D), UPM 2948 (dermopalatine tooth).

Description. Specimen UPM 2813 is the best preserved of the two teeth in the sample. This specimen measures approximately 3.2 cm in apicobasal height and 9 mm in anteroposterior width (across the crown base). The tooth base includes remnants of the dermopalatine bone. In labial or lingual views, the tooth has a slightly sigmoidal anterior edge that is strongly convex near the base but slightly concave near the apex. The lower three-fourths of the posterior edge is slightly concave, but the remainder is a convex cutting edge that terminates in a post-apical barb (Fig. 9C). The labial and lingual crown faces are nearly equally convex, and both are ornamented with extremely faint vertical striations. A single cutting edge extends the length of the anterior edge (Fig. 9D). The presence of an anterior carina and the lack of a posterior carina below the post-apical barb gives the tooth a teardrop-shaped cross-section. Specimen UPM 2948 is morphologically similar to UPM 2813, but due to ablation no ornamentation is preserved on the labial or lingual crown faces, and the post-apical barb is only partially preserved.

Remarks. Specimen UPM 2813 possesses the salient features of *E. gladiolus* dermopalatine teeth known from the Western Interior and Gulf Coastal Plain of the USA. These features include a sigmoidal labial or lingual outline, faint labial and lingual striations, an anterior carina, a post-apical barb, and a teardrop-shaped cross-section (Parris et al. 2007). According to Goody (1976), several Old World *Enchodus* species have "*gladiolus* type" dermo-

palatine teeth, including *E. elegans*, *E. lamberti*, and *E. crenulatis*. Although all three of these taxa have dermopalatine teeth with a post-apical barb, those of *E. elegans* have two offset carinae (like that on *E. petrosus*), and those of *E. lamberti* and *E. crenulatis* have serrated cutting edges (Goody 1976). Three other species, *E. bursauxi*, *E. dirus*, and *E. lybicus*, have laterally compressed and sigmoidal dermopalatine teeth like *E. gladiolus*, but of these taxa only *E. gladiolus* teeth have a post-apical barb (see Arambourg 1952; Goody 1976; Green 1913). Specimens UPM 2813 and UPM 2948 bear a post-apical barb and are tentatively identified as *E. gladiolus*, but confirmation of the occurrence of this species in the Rybushka Formation must await the discovery of more complete material.

Enchodus petrosus Cope, 1874
Fig. 9E-G

Material: UPM 2824 (dermopalatine tooth, Fig. 9E-F), UPM 2950 (dermopalatine tooth), UPM 2952 (dermopalatine with partial tooth, Fig. 9G), UPM 3005 (partial dermopalatine tooth), UPM 3009 (dermopalatine tooth).

Description. In labial view, the dermopalatine bone (UPM 2952) has a sub-rectangular outline (Fig. 9G). Not including the tooth, the anteroposterior length of this dermopalatine is approximately 27 mm and the dorsoventral height is 12 mm. The ventral margin is broadly V-shaped, with the anterior part of the margin being slightly longer than the posterior part. The posterior edge is convex and marked by a rounded, triangular, posteroventrally extended ectopterygoid process, and a rounded and upturned postero-dorsal projection. Anterior to the postero-dorsal projection, the remainder of the dorsal margin is irregularly convex. The anterior margin is straight and anterodorsally slanted. The ventral portion of the anterior margin is contiguous with the anterior part of the dermopalatine tooth. The dorsal portion of the anterior margin is marked by a rounded and anteriorly directed ethmoid process. The ethmoid process is positioned above the median portion of the dermopalatine tooth. A wide and deep maxillary groove extends from the anterior half of the dorsal margin to the posterior half of the ventral margin, and the anterior edge of the maxillary groove is positioned over the posterior edge of the tooth. Both labial and lingual faces of the dermopalatine bone are convex, but the dorsal

features on the lingual face cannot be discerned because they are obscured by matrix. Only the base of the dermopalatine tooth is preserved, which has two offset carinae, one that is positioned anteromedially and the other posterolaterally. The anterior edge of the tooth is slightly convex and smooth, whereas the posterior part of the tooth is strongly convex and bears faint longitudinal striations. The dermopalatine tooth is anteriorly projected with the posterior margin forming an approximately 110° angle with the ventral margin of the dermopalatine.

Of the four isolated dermopalatine teeth, specimen UPM 2824 is the most complete. This tooth is slender and tall, measuring approximately 21 mm in height. The tooth has a slightly sigmoidal profile and possesses anteromedial and posterolateral carinae (Fig. 9E). The anterior face of the tooth is slightly convex, whereas the posterior face is strongly convex and has faint striations near the base (Fig. 9F). The strong convexity of the posterior face results in a D-shaped cross section. Specimens UPM 2950, UPM 3005, and UPM 3009 are incomplete but exhibit the characteristics described above.

Remarks. A combination of characteristics allows us to assign the dermopalatine bone (UPM 2952) to *E. petrosus*, including: 1) a dermopalatine tooth with anteromedial and posterolateral carinae (as opposed to anterior and/or posterior carinae) and distinct posterior striations at the crown base; 2) the anteroposterior length of the dermopalatine is twice the height; 3) the anterior edge of the maxillary groove is positioned over the posterior edge of the tooth; and 4) the ethmoid process is positioned over the medial portion of the tooth. This combination of characteristics appears to be unique to *E. petrosus* (Parris et al. 2007) and not known to occur on any of the other described species (although for taxa like *E. tineidae*, the dermopalatine is not preserved or visible).

The isolated dermopalatine teeth in our sample possess the characteristics observed on *E. petrosus* teeth from North America, including anteromedial and posterolateral carinae, distinct lingual striations at the crown base, strongly convex posterior face, and weakly convex anterior face. These dermopalatine teeth have two carinae, whereas *E. dirus* and *E. gladiolus* have one, and they are not slender and needle-like as are those of *E. shumardi*. Although Goody (1976) mentions several Old World

taxa with "*petrosus* type" teeth (i.e., *E. longidens*, *E. marchesetti*, and *E. lewisiensis*), we refer them to *E. petrosus* because of their morphology and co-occurrence within the Rybushka Formation with an *E. petrosus* dermopalatine (UPM 2952).

Enchodus spp.
Fig. 9H-M

Material: MMO 1 № 10420-53 (symphyseal portion of dentary, Fig. 9M), MMO 1 № 10420-56 (symphyseal portion of dentary), MMO 1 № 10420-58 (concretion with dentary, premaxilla, and cranial fragments, Fig. 9H-J), UPM 2823 (symphyseal portion of dentary), UPM 2903 (symphyseal portion of dentary), UPM 2904 (symphyseal portion of dentary), UPM 2905 (dentary fragment), UPM 2917 (concretion with dermopalatine?, Fig. 9L), UPM 2927 (symphyseal portion of dentary), UPM 2953 (premaxilla fragment), UPM 3007 (fragmentary dermopalatine, Fig. 9K), UPM 3012 (premaxilla fragment), UPM 3015 (premaxilla fragment), UPM 3016 (premaxilla fragment), UPM 3017 (premaxilla fragment).

Description. Many of the dentary fragments are well preserved, but most are represented only by the symphyseal portion. All have a convex ventral edge and two or more pointed anteroventral projections. Nearly all the specimens have a single large dentary tooth (or tooth base) located just behind the symphysis on the anterior half of the dorsal margin (Fig. 9M). This tooth lacks enameloid and is slightly angled anteriorly on most specimens. Small pointed or blunt processes occur on the dorsal margin of the dentary, just anterior and posterior to the large dentary tooth (with more generally occurring on the anterior side). The labial face of the dentary is ornamented with thick ridges that extend anteroposteriorly across the element (Fig. 9I). On one specimen (MMO 1 № 10420-58, Fig. 9J), the ridges are ornamented with beaded enameloid. Specimen UPM 2905 is the medial portion of a dentary, and it has a single line of short triangular teeth that are deeply set into the bone. The labial face of the bone is ornamented with anteroposteriorly oriented ridges and has a conspicuous groove that extends anteroposteriorly just below the tooth row. The lingual face of all the dentary fragments is generally smooth.

UPM 3007 appears to be an incomplete and worn dermopalatine based on its L-shaped outline in labial view (Fig. 9K). It is small and measures approximately 1 cm in greatest anteroposterior length. Only the base of the dermopalatine tooth is preserved, and no discernible features are present.

Specimen UPM 2917 is a concretion that contains teleost remains. Although most of the elements are not exposed, what appears to be a partially preserved dermopalatine and tooth is visible (Fig. 9L). The lateral edge of this partial dermopalatine is smooth and featureless, however, an elongated tooth extends ventrally from the element. This tooth is long, straight, and needle-like, and appears to be greater in height than the length of the dermopalatine.

Specimens UPM 2953, UPM 3012, and UPM 3015-3017 are premaxillary fragments. These fragments are anteroposteriorly elongated and dorsoventrally narrow. A single row of short, triangular teeth deeply set into the bone lines the ventral margin. The labial surface is ornamented with a series of anteroposteriorly extended ridges, whereas the lingual face is smooth and largely featureless.

Remarks. Several Rybushka Formation specimens are herein assigned to *Enchodus* because they have one or more characteristics that align them with this genus. Although these specimens do not preserve the characteristics necessary for species assignment, they likely belong to one of the three Rybushka Formation species described above. For example, the dentary fragments are all ornamented with labial ridges, a characteristic that is shared among *E. ferox*, *E. gladiolus*, *E. petrosus*, and *E. tineidae*, but absent on *E. dirus* and *E. shumardi* (Goody 1976; Green 1913; Parris et al. 2007; Holloway et al. 2017). Specimen MMO 1 № 10420-58 is of interest because it has labial ornamentation consisting of ridges that are covered with beaded enameloid. Although Parris et al. (2007) noted the presence of beaded enameloid on the dentaries of *E. petrosus* (and absence on *E. gladiolus*), it is unclear if this ornamentation occurs on any of the other *Enchodus* species. We identified *E. gladiolus* and *E. petrosus* based on other elements, and it is possible that specimen MMO 1 № 10420-58 represents *E. petrosus* and the remaining, "non-beaded," dentary fragments belong to *E. gladiolus*.

The two small dermopalatine fragments (UPM 2917, UPM 3007) are of interest because they may represent a fourth *Enchodus* species within the Rybushka Formation, *E. shumardi*. Although specimen UPM 3007 is worn and lacks a dermopalatine tooth, the small size of the element (1 cm in anteroposterior length) and almost 90° downward angle of the tooth base is reminiscent of dermopalatine

Fig. 9 - *Enchodus* remains from the Beloe Ozero locality in the Saratov Oblast, Russia. A–B) UPM 3004, *Enchodus* cf. *E. dirus*, right dermopalatine tooth: A, lingual view; B, anterior view. C–D) UPM 2813, *Enchodus* cf. *E. gladiolus*, right dermopalatine tooth: C, lingual view; D, anterior view. E–F) UPM 2824 *Enchodus petrosus*, right dermopalatine tooth: E, labial view; F, posterior view. G) UPM 2952, *Enchodus petrosus*, left dermopalatine in lingual view. H–J) MMO 1 № 10420-58, *Enchodus* sp., cranial elements in matrix: H, left premaxilla in labial view; I, left dentary in labial view; J, close-up of labial ornamentation. K) UPM 3007, *Enchodus* sp., left dermopalatine in lingual view. L) UPM 2917, *Enchodus* sp., right dermopalatine (in matrix) in labial view. M) MMO 1 № 10420-53, *Enchodus* sp., anterior portion of right dentary in labial view. Scale bars represent 1 cm in A–G and L–M, 2 cm in H–J, and 5 mm in K.

bones of *E. shumardi* from the Gulf Coastal Plain of the USA (JAE, pers. observ.). Specimen UPM 2917 is difficult to interpret because it is embedded within a concretion and only visible in lateral view. Nevertheless, if this specimen indeed represents a dermopalatine, the presence of a slender and needle-like tooth that is taller than the anteroposterior length of the dentary are characteristics unique to *E. shumardi* (Goody 1976; Parris et al. 2007). Due to the poor preservation of these two specimens, we refrain from attributing them to *E. shumardi* until better-preserved material from the Rybushka Formation is recovered.

The premaxillary elements represented by specimens UPM 2953, UPM 3012, and UPM 3015-3017 are too fragmentary to be speciated. Although the short, triangular, and deeply rooted teeth are consistent with *Enchodus*, toothed premaxillaries are nearly ubiquitous among the many named species. However, the presence of labial ornamentation on specimens like UPM 2953 indicate they could represent *E. gladiolus* or *E. petrosus*. Both species have ornamented premaxillaries and both have been identified in the Rybushka Formation based on other remains.

DISCUSSION

We examined 226 fossil fish remains that were collected from the Rybushka Formation at the Beloe Ozero locality south of Saratov city, Saratov Oblast. Twenty unequivocal taxa were identified, including two chimaeroids, 12 elasmobranchs, and six teleosts. Nine orders and 13 families of fish taxa are represented, with three taxa of uncertain familial placement. Numerous specimens in our sample could not be identified beyond Chimaeroidei, Batomorphi, Galeomorphi, or Teleostei and could represent additional genera or species. A review of these taxa and the paleobiogeographic implications of the fish fauna are discussed below.

Review of the fossil fishes from Beloe Ozero locality

At least two chimaeroids were identified in our sample, including *Ischyodus bifurcatus* and *Amylodon karamysh*. Tooth plates of *I. bifurcatus* are very common in our sample, and a wide morphological range of palatine and mandibular plates is represented. This taxon was previously identified from the Rybushka Formation in the Saratov Oblast

by Averianov & Popov (2014) and Grigoriev et al. (2015), and elsewhere within the formation by Olferiev & Alekseev (2005). Additional specimens that were tentatively assigned to this taxon were reported by Averianov & Popov (1995) from the Campanian Shirokyi Karamysh locality within the Saratov Oblast, and by Yarkov & Nesov (2000) from the Campanian Rychkovo locality in the Vologograd Oblast. *Ischyodus bifurcatus* was originally named from upper Cretaceous deposits in New Jersey, and subsequent investigations in the USA have confirmed the taxon in Alabama (Cicimurri & Ebersole 2014), Arkansas (Case 1978a), California (Johnson-Ransom et al. 2018), Delaware (Case 1978a), Georgia (Case & Schwimmer 1992), Mississippi (Manning & Dockery 1992), Montana (Case 1978a), and North Carolina (Robb 1989). Outside of the USA and Russia, *I. bifurcatus* has been reported from Belgium (Case 1978a) and Poland (Popov & Machalski 2014).

Averianov & Popov (1995) named *Amylodon karamysh* based on a specimen from the Campanian Shirokyi Karamysh locality. However, the specimen we report herein is the first to be identified from the Rybushka Formation at the Beloe Ozero locality. Olferiev & Alekseev (2005) also documented this taxon from the Rybushka Formation, and it was later reported from the Saratov Oblast by Averianov & Popov (2014) and Grigoriev et al. (2015). A specimen assigned to *Amylodon* sp. was reported by Nessov & Averianov (1996) from the Campanian Polunino-2 locality in the Volgograd Oblast. Cretaceous occurrences of this enigmatic taxon outside of Russia are limited to Sweden (Johnson-Ransom et al. 2018).

Several vomerine plates and dorsal fin spines in our sample are assigned to Callorhinchoidei indet. Although these elements may belong to *A. karamysh* or *I. bifurcatus*, the morphology of the palatines, vomerines, and dorsal spines of *A. karamysh* have yet to be formally described, and the Rybushka Formation elements lack the diagnostic characteristics necessary to be assigned to any of the known Cretaceous chimaeroids reported from the region. In addition to *Amylodon* and *Ischyodus*, various other chimaeroid genera have been identified from Cretaceous deposits in the Volga region, including *Belgorodon* (Nesov & Averianov 1996), *Callorhinchus* (Nesov & Averianov 1996; Olferiev & Alekseev 2005), *Edaphodon* (Glickman 1953; Nesov

& Averianov 1996; Popov & Lapkin 2000; Olferiev & Alekseev 2005; Averianov & Popov 2014; Grigoriev et al. 2015; Popov 2016), *Elasmodectes* (Olferiev & Alekseev 2005), *Elasmodus* (Averianov & Glickman 1994; Olferiev & Alekseev 2005; Averianov & Popov 2014; Grigoriev et al. 2015), and *Lebedidon* (Nesov & Averianov 1996). Of these, *A. karamysh*, *Belgorodon bogolubovi* (Nessov, 1986), *Edaphodon sedgwickii* (Agassiz, 1838), *I. bifurcatus*, and *Lebedidon oskolensis* Nessov & Averianov, 1996 have been identified specifically from Campanian deposits within the Saratov Oblast (Averianov & Glickman 1994; Nesov & Averianov 1996; Averianov & Popov 2014; Grigoriev et al. 2015). The number of Campanian chimaeroid taxa previously reported from the Saratov Oblast suggests that the diversity of this group is likely greater in the Rybushka Formation than our sample indicates.

Three teeth in our sample have been identified as *Synechodus* sp. Two *Synechodus* taxa have been previously reported from Cenomanian deposits within the Saratov Oblast, including specimens assigned to *Synechodus* sp. (Glickman 1953, 1957, 1958, 1980) and *S. dispar* (Olferiev & Alekseev 2005; Popov & Lapkin 2000; Seltzer & Ivanov 2010). Additional *Synechodus* records from the Volga region include *S. hesbayensis* Casier, 1943 from the upper Santonian Sokolovskaya Formation, and *S. lerichei* Herman, 1977 from the Santonian Sokolovskaya and Maastrichtian Bereslavka formations (Olferiev & Alekseev 2005). *Synechodus* has a long stratigraphic range (lower Triassic to lower Paleocene; Cappetta 2012) with various Cretaceous species being reported from deposits in Asia, Europe, and North America (Cappetta 2012).

Nine teeth of *Cederstroemia* sp. were identified, and this taxon represents the only member of the Orectolobiformes in our sample. The only other occurrence of this taxon in the region (*Cederstroemia* sp.) was reported from Cenomanian deposits in the Saratov region (Popov & Lapkin 2000). However, several fossil *Squatina* species have been previously reported from the Saratov Oblast, including *Squatina hassei* from Campanian deposits in the area (Averianov & Popov 2014; Grigoriev et al. 2015) and *S. muelleri* (Sintsov 1872; Seltzer & Ivanov 2010) and *Squatina* sp. (Glickman 1953, 1957, 1958, 1980; Popov & Lapkin 2000) from older Cenomanian deposits. *Squatina* teeth and those of *Cederstroemia* are morphologi-

cally similar, and it is possible that the aforementioned reports instead belong to this latter taxon. Unfortunately, we could not verify these previously reported *Squatina* specimens because they were not described nor figured, and their whereabouts are unknown. Five *Cederstroemia* species have been named from Lower and Upper Cretaceous deposits, and members of this genus have been reported from Belgium (Herman 1977), France (Guinot et al. 2013), Sweden (Sørensen et al. 2013), Ukraine (Sokolskyi & Guinot 2021), the United Kingdom (Guinot et al. 2013), and the USA (Siverson 1995).

Lamniformes are well represented in our Rybushka Formation sample. Eight unequivocal taxa were identified within the genera *Cretalamna*, *Archaeolamna*, *Squalicorax*, *Pseudocorax*, and *Eostriatolamia*. Two *Cretalamna* species, *Cretalamna* cf. *C. borealis* and *C.* cf. *C. sarcoportheta,* are tentatively identified from the Beloe Ozero locality. *Cretalamna borealis* was previously identified from the Rybushka Formation in the Saratov Oblast by Olferiev & Alekseev (2005) and Zverkov et al. (2017). Averianov & Popov (1995) reported *C. borealis* teeth from Campanian deposits at the Shirokyi Karamysh locality, and Yarkov & Nesov (2000) reported additional specimens from the Campanian Rychkovo locality in the Volgograd Oblast. Reports of *C. borealis* are scarce, and outside of Russia this species has only been reported from Santonian to Campanian deposits in Belgium, Japan, Sweden, Uzbekistan, and Delaware in the USA (Siversson et al. 2015).

Cretalamna sarcoportheta was named by Siversson et al. (2015) for teeth from Campanian deposits in Sweden, and additional specimens have since been identified from the Campanian of Belgium, France, and Texas in the USA (Siversson et al. 2015; Condamine et al. 2019). Although our Rybushka Formation specimens represent the first occurrence of *C. sarcoportheta* in Russia, several Campanian specimens reported from the Saratov Oblast were identified as *C. appendiculata* (Averianov & Popov 2014; Grigoriev et al. 2015). Siversson et al. (2015) determined that *C. appendiculata* had become a waste-basket taxon, with verified *C. appendiculata senso stricto* teeth being confined to the Turonian of England. Thus, the *Cretalamna* teeth reported by Averianov & Popov (2014) and Grigoriev et al. (2015) likely belong to a different taxon, possibly *C. borealis* and/or *C. sarcoportheta.* Olferiev & Al-

ekseev (2005) reported additional Santonian and Campanian *C. appendiculata* specimens from the Mozhzheveloovrazhnaya and Sokolovskaya formations in the Volga Region, and Seltzer & Ivanov (2010) reported this taxon from Cenomanian deposits in the Saratov Region. Moreover, Yarkov & Nesov (2000) reported *Cretalamna lata* among the Campanian taxa from the Rychkovo locality in the Volgograd Oblast, and Olferiev & Alekseev (2005) reported this species from the Maastrichtian Bereslavka Formation in the Volga Region. These latter reports need to be reevaluated in order to determine the true diversity of Santonian to Maastrichtian *Cretalamna* in the region.

Archaeolamna kopingensis is one of the more abundant taxa in our sample, with 22 specimens identified. Averianov & Popov (2014) and Grigoriev et al. (2015) previously reported *A. kopingensis* teeth from the Rybushka Formation in the Saratov Oblast, and Popov & Biriukov (2015) listed this taxon among those derived from early to middle Cenomanian deposits in the Volga Region. Underwood & Cumbaa (2010) mentioned the presence of *A. kopingensis* in Russia, but noted they were mislabeled as other species. Unfortunately, these specimens were not figured, and their locality and stratigraphic unit are unknown. Outside of Russia, *A. kopingensis* has been reported from Australia (Siverson 1996), Canada (Peng et al. 2001), France (Biddle 1993), Germany (Ladwid 2000), Italy (Amalfitano et al. 2020), Kazakhstan (Kennedy et al. 2008), Scandinavia (Davis 1890), Sweden (Siverson 1992), Ukraine (Sokolskyi & Guinot 2021), and the United Kingdom (Ward 2010), and Alabama (Ciampaglio et al. 2013), Colorado (Shimada et al. 2006), Iowa (Gormon et al. 2014), Kansas (Shimada & Martin 2008), Nebraska (Meglei et al. 2013), New Jersey (Callahan et al. 2014), and New Mexico (Williams 2006) in the USA.

Two *Squalicorax* taxa were identified in our sample, including *S. kaupi* and a single tooth assigned to *Squalicorax* Morphology 1. *Squalicorax kaupi* has previously been reported from the Rybushka Formation in the Saratov Oblast by Averianov & Popov (2014) and Grigoriev et al. (2015), and Zverkov et al. (2017), and Yarkov & Nesov (2000) reported this species from the Campanian Rychkovo locality in the Volgograd Oblast. Olferiev & Alekseev (2005) reported *Squalicorax* cf. *santonicus*

teeth from the Santonian Mozhzheveloovrazhnaya and Sokolovskaya formations, but these specimens should be reevaluated to determine if they instead belong to *S. kaupi*.

Squalicorax kaupi had a nearly circumglobal distribution, as specimens have been reported from Algeria (Arambourg 1952), Angola (Antunes & Cappetta 2002), Brazil (da Silva 2007), Congo (Dartevelle & Casier 1959), Denmark (Elicki & Magnus 2012), Egypt (Bazzi et al. 2021), France (Guinot et al. 2013), Germany (Diedrich & Scheer 2015), Iberian Peninsula (Pereda-Suberbiola et al. 2015), Israel (Retzler et al. 2013), Jordan (Mustafa et al. 2002), Lebanon (Signeux 1959), Lithuania (Dalinkevicius 1935), Madagascar (Gottfried et al. 2001), Morocco (Ambroggi & Arambourg 1951), Netherlands (van de Geyn 1937), Poland (Noetling 1885), Spain (Corral et al. 2021), Sweden (Ladwid 2014), Syria (Bardet et al. 2000), Tunisia (Arambourg 1952), and Alabama (Ikejiri et al. 2013), Arkansas (Becker et al. 2006), California (Welton & Alderson 1981), Delaware (Lauginiger 1988), Georgia (Case & Schwimmer 1988), Kansas (Bice & Shimada 2016), Maryland (Garcia & Hippensteel 2012), Mississippi (Manning & Dockery 1992), Montana (Case 1978b), New Jersey (Cappetta & Case 1975), New Mexico (Williams 2006), North Carolina (Case et al. 2017), South Dakota (Wiese et al. 2004), Texas (Schubert et al. 2017), and Wyoming (Wiese et al. 2004) in the USA.

The tooth assigned to *Squalicorax* Morphology 1 appears to represent an undescribed taxon. However, additional specimens are needed to confirm this hypothesis. Similar teeth have been observed by the senior author (JAE) in Santonian and Campanian deposits in Alabama in the USA.

A single *Pseudocorax laevis* tooth was identified in our sample. This species was previously reported from the Rybushka Formation in the Saratov Oblast by Averianov & Popov (2014) and Grigoriev et al. (2015), and Averianov & Popov (1995) reported *P. laevis* teeth from Campanian deposits at the Shirokyi Karamysh locality. Outside of Russia, *P. laevis* teeth have been reported from Belgium (Leriche 1927), France (Biddle 1988), Germany (Schnrider & Ladwig 2013), Spain (Corral et al. 2011), Lithuania (Dalinkevicius 1935), and Sweden (Sørensen et al. 2013), and Alabama (Ciampaglio et al. 2013), Kansas (Hamm & Shimada 2007), and Texas (Hamm & Cicimurri 2011)

in the USA. Olferiev & Alekseev (2005) reported *Pseudocorax affinis* among the taxa derived from the Maastrichtian Bereslavka Formation in the Volga Region. Teeth of this species differ from those of *P. laevis* by having serrated cutting edges. This tooth needs to be reevaluated to determine if it represents *P. affinis* or *P. laevis*.

We identified two species of *Eostriatolamia*, *E. segedini* and *E. venusta*, in our sample. These specimens represent the first confirmed occurrences of both species in the Rybushka Formation in the Saratov Oblast, as well as from the Cretaceous of Russia in general. Averianov & Popov (2014) and Grigoriev et al. (2015) reported unspeciated *Eostriatolamia* teeth from the same unit and location, and these may belong to one or both of these species. A third species, *E. subulata*, was reported by Olferiev & Alekseev (2005) from the Rybushka Formation and lower Santonian Mozhzheveloovrazhnaya Formation in the Volga region, and by Averianov & Popov (1995) from Campanian deposits at the Shirokyi Karamysh locality. These teeth should be reevaluated to determine if they instead belong to *E. segedini* or *E. venusta*. *Eostriatolamia subulata* teeth have also been reported from Cenomanian deposits in the Volga Region, as well as Saratov and Volgograd oblasts (Popov & Lapkin 2000; Olferiev & Alekseev 2005; Popov & Biriukov 2015). Outside of Russia, the only other occurrence of *E. segedini* is from the type locality in Kazakhstan (Glikman & Averianov 1998). *Eostriatolamia venusta*, on the other hand, is more widely distributed and has been reported from Australia (Kemp 1991), Belgium (Leriche 1927), Germany (Albers & Weiler 1964), Greenland (Bendix-Almgreen 1969), and the Netherlands (Herman 1977).

Two dorsal fin spines in our sample are identified as belonging to a member of the Squalidae (Squaliformes). Although these spines could not be assigned to a genus or species, they nonetheless represent the first confirmed occurrence of this family from the Rybushka Formation in the Saratov Oblast. Averianov & Popov (2014) and Grigoriev et al. (2015) reported dorsal spines from the same formation that they referred to *Heterodontus* sp. However, due to the morphological similarity of extant *Heterodontus* dorsal spines to those of extant *Squalus*, the specimens reported by Averianov & Popov (2014) and Grigoriev et al. (2015) should

be reexamined to determine if they instead belong to Squalidae. Popov & Lapkin (2000) listed *Squalus* sp. among the species derived from Cenomanian deposits near the city of Saratov, representing the only other known occurrence of a Cretaceous member of the Squalidae from the region. Several dorso-ventrally compressed vertebrae were identified in our sample that belong to an unidentified member of the Squalomorphi. Unfortunately, the generalized morphology of these vertebrae prohibits a more refined identification.

Ablated teeth and cylindrical vertebral centra in our sample could not be identified beyond Galeomorphi. Although these elements may belong to one or more of the species identified within our study, they could belong to other taxa. More completely preserved and/or more diagnostic material is needed for accurate taxonomic determination.

A single tooth of *Squatirhina* sp. occurs in our Rybushka Formation sample. Unspeciated *Squatirhina* teeth have also been reported by Averianov & Popov (2014) and Grigoriev et al. (2015) from Campanian deposits in the Saratov Oblast, and Popov & Lapkin (2000) listed this taxon within Cenomanian deposits in the area. Although *Squatirhina* is the only ray to be identified from any Campanian and Cenomanian deposits in the area, our Rybushka Formation sample contains a dermal denticle that is referred here to Batomorphi indet. Although this denticle might belong to *Squatirhina*, it could belong to an unknown batoid within the formation. Five named *Squatirhina* species have been reported from Late Cretaceous to Paleocene deposits in Asia (Kennedy et al. 2008), Eurasia (Popov & Lapkin 2000; Averianov & Popov 2014; Grigoriev et al. 2015), and Europe (Guinot et al. 2012).

We identified four teleost genera in our Rybushka Formation sample, including *Pachyrhizodus* (Crossognathiformes, Pachyrhizodontidae), *Saurocephalus* (Ichthyodectiformes, Saurodontidae), *Paralbula* (Elopiformes, Phyllodontidae), and *Enchodus* (Aulopiformes, Enchodontidae). Two dentary fragments were identified as *Pachyrhizodus* sp., and although these are not well enough preserved to be speciated, they are significant because they represent the first confirmation of *Pachyrhizodus* from the Rybushka Formation in the Saratov Oblast (and very likely the Cretaceous of Russia in general). This genus appears to have had a near circumglob-

al distribution during the Cretaceous, as specimens have been identified from Australia (Bartholomai 1969), Europe (Forey 1977), Mexico (Giersch et al. 2010), New Zealand (Wiffen 1983), and various states in the USA (Stewart 1900; Applegate 1970; Shimada & Fielitz 2006).

Four dentary fragments belong to *Saurocephalus lanciformis*. These elements are easily identified based on the morphology of their lanceolate teeth and the conspicuous line of lingual foramina that occurs below the tooth row. Reports of *Saurocephalus* outside of North America are sparse but the genus has been confirmed from Europe and the Middle East (Bardack & Sprinkle 1969; Kaddumi 1999). As far as the present authors are aware, the Rybushka Formation specimens represent the first occurrence of the genus and species in Russia.

An incomplete basibranchial plate of *Paralbula casei* represents the only member of Phyllodontidae in our sample. This taxon was named by Estes (1969) for a fragmentary basibranchial plate collected from the Maastrichtian of New Jersey, and it has since been confirmed from various Cretaceous localities in both Canada and the USA (Estes 1969; Schein et al. 2011). Occurrences of *P. casei* outside of North America are rare, with the only known occurrence being from Ypresian (lower Eocene) deposits in the United Kingdom (Estes 1969). Therefore, the Rybushka Formation specimen reported herein represents only the second occurrence of *P. casei* outside of North America and the first Cretaceous record of this species outside of Canada and the USA.

Three *Enchodus* taxa were identified in our Rybushka Formation sample, including *Enchodus* cf. *E. dirus*, *Enchodus* cf. *E. gladiolus*, and *E. petrosus*, all of which represent first occurrences of these taxa from Russia. Additional remains in our sample assigned to *Enchodus* spp. may belong to one or more additional species (i.e., *E. shumardi*), but the fossils are not well enough preserved to make more accurate determinations. Averianov & Popov (2014) reported unspeciated members of the Enchodontidae within the Rybushka Formation at the Beloe Ozero locality, and Sintsov (1899) reported both *E. faujasi* Agassiz, 1843 and *E. halocyon* Agassiz, 1835 from phosphorite deposits in the Saratov Oblast. Unfortunately, the whereabouts of these latter specimens is unknown, and we could not confirm the occurrence of these species.

Published occurrences of *E. dirus* are limited to reports from various localities in North America (Goody 1976; Silva & Gallo 2011) and a single occurrence in Greece (Cavin et al. 2012). However, the presence of *E. dirus* in the Rybushka Formation is based on a single dermopalatine tooth that is only tentatively referred to this species. Our sample of *E. gladiolus* consists of isolated dermopalatine teeth, but the species was relatively common in North America (Cope 1872; Goody 1976; Cumbaa & Murray 2008; Cumbaa et al. 2010; Jansen et al. 2012; Nagrodski et al. 2012; Gallardo et al. 2013; Carbot-Chanona & Than-Marchese 2013; Ouroumova et al. 2016). The species has also been reported from Nigeria (Vullo & Courville 2014), Patagonia (Bogan & Agnolin 2010), Peru (Gouiric-Cavalli et al. 2021), and Sweden (Bazzi et al. 2015), but Gouiric-Cavalli et al. (2021) indicated that occurrences outside of North America should be viewed as tentative. We concur with this assessment because most occurrences of *E. gladiolus* are based on isolated dermopalatine teeth. Such is the case in our Rybushka Formation sample (n=2), and these specimens are only tentatively referred to this species. The occurrence of *E. petrosus* in the Rybushka Formation is based on three isolated dermopalatine teeth and two dermopalatines with *in situ* teeth. Of the *Enchodus* species we identified from the Rybushka Formation, those of *E. petrosus* are the only ones that are assigned with confidence because the identification is based on both teeth and dermopalatine bones. Prior reports of *E. petrosus* are limited to Canada, Mexico, and the USA (Goody 1976; Thurmond & Jones 1981; Case & Schwimmer 1988; Shimada & Fielitz 2006; Schein & Lewis 2007; Parris et al. 2007; Cumbaa & Murray 2008; Carbot-Chanona & Than-Marchese 2013).

Several teleost teeth, vertebrae, and cranial elements in our sample could not be identified due to their preservation or our lack of comparative material. However, the teeth and cranial elements do not appear to belong to any of the teleost taxa we identified during our study, indicating that bony fish diversity in the Rybushka Formation is greater than presented herein.

Palaeobiogeographic implications of the Beloe Ozero fish fauna

This study represents the first description of a marine fish complex from the Cretaceous of Russia. In total, 20 unequivocal holocephalan (n=2), elasmobranch (n=12), and teleost (n=6) taxa were identified, all of which contribute to our understanding of the palaeobiogeograpical distributions of these fishes. From a geographical perspective, the Beloe Ozero locality resides in western Russia and is considered a part of Europe. The Rybushka Formation fish palaeofauna is of interest because it is comprised of taxa shared with every other continent except Antarctica. Only two of the 20 taxa we identified are endemic to Europe (*Eostriatolamia segedini*) or Eurasia (*Amylodon karamysh*), whereas the other 18 taxa also occur in Africa (3 in common with Rybushka Formation), Asia (7 in common), Australia (3 in common), North America (15 in common), South America (2 in common), and Oceania (1 in common).

The substantial overlap of the Rybushka Formation fish taxa with species in North America (15 of 20, 75%) suggests an east-west dispersal event of marine fishes occurred between Europe and North America during the Late Cretaceous. This dispersal event coincides with the opening of the Atlantic Ocean, beginning approximately 130 Ma, starting in the south but extending to the north Atlantic by the Santonian Stage approximately 84 Ma (Fitton and Larsen 2001). Our Rybushka Formation sample indicates that the formation of the northern Atlantic Ocean eliminated east-west geographical barriers, thereby facilitating dispersal of marine taxa between North America and Eurasia during the Santonian and Campanian.

The significant taxonomic overlap between North American and Rybushka Formation fish paleofaunas may also be indicative of a collection bias. Our sample of 226 fish fossils was largely surface collected, resulting in a sample that is biased towards larger remains visible to the naked eye. Additionally, vertebrate remains smaller than 1 mm (smallest mesh sized used during screen washing) are not represented. Many of the specimens belong to fishes that are known from elsewhere to have attained body lengths of one meter or longer, and it is likely that these medium- to large-sized fishes could more easily travel between North America and Eurasia than their smaller-sized counterparts. Future sampling for micro-remains in the Rybushka Formation may increase the known fish diversity within this lithostratigraphic unit and provide a more accurate reflection of vicariance (endemism) versus dispersal between continents.

Conclusions

This report is the result of our examination of 226 fish fossils recovered from the upper Campanian Rybushka Formation at the Beloe Ozero locality in the Saratov Oblast of western Russia. This study represents the first comprehensive description of a marine fish complex (chondrichthyans and actinopterygians) from the Upper Cretaceous (or Cretaceous in general) of Russia. A total of 20 unequivocal taxa were identified, including two chimaeroids, 12 elasmobranchs, and six teleosts. Nine taxa identified in our sample represent first occurrences in the fossil record of Russia, including *Cretalamna sarcoportheta*, *Enchodus* cf. *E. dirus, E.* cf. *E. gladiolus*, *E. petrosus*, *Eostriatolamia segedini*, *E. venusta*, *Pachyrhizodus* sp. *Saurocephalus lanciformis*, and *Squalicorax* Morphology 1. In addition, these taxa, along with *Cederstroemia* sp. and Squalidae indet., represent first occurrences within the Rybushka Formation. The taxa in our sample demonstrate a considerable taxonomic overlap (15 of 20) with those that occur in North America, indicating a Late Cretaceous east-west dispersal event between North America and Europe, possibly corresponding with the opening of the northern Atlantic Ocean during the Santonian (~84 mya). Additional sampling of the Rybushka Formation at the Beloe Ozero locality for well-preserved macro- and micro-remains could result in the discovery of new species and elucidate the taxonomy of some of the species in our sample, furthering our understanding of the marine fish diversity in the Volga region during the Campanian.

References

Agassiz L. (1835) - Recherches Sur Les Poissons Fossiles, 4th livraison. Imprimerie de Petitpierre, Neuchatel: 33-52.

Agassiz L. (1838) - Recherches sur les poissons fossiles, 11th livraison (November 1838). Petitpierre et Prince (text) and H. Nicolet (plates), Neuchâtel, 3: 73-140.

Agassiz L. (1843) - Recherches sur les poissons fossiles, 15th and 16th livraisons (March 1843). Jent and Gassmann, Soleure (text) and H. Nicolet (plates), Neuchâtel, 3: 157-390.

Albers H. & Weiler W. (1964) - Eine Fischfauna aus der oberen Kreide von Aachen und neuere Funde von Fischresten aus dem Maestricht des angrenzenden belgisch-holländischen Raumes. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 120: 1-33.

Amalfitano J., Giusberti L., Fornaciari E. & Carnevale G. (2020) - Upper Cenomanian fishes from the Bonarelli Level (OAE2) of northeastern Italy. *Rivista Italiana di Paleontologia e Stratigrafia*, 126(2): 261-312.

Ambroggi R. & Arambourg C. (1951) - Sur le Maestrichtien et l'Eocène inférieur de la vallée du Sous (Sud-Marocain). *Comptes Rendus de l'Académie des Sciences*, 232: 170-171.

Antunes M.T. & Cappetta H. (2002) - Sélaciens du Crétacé (Albien-Maastrichtien) d'Angola. *Palaeontographica, Abt. A*, 264(5-6): 85-146.

Applegate S.P. (1970) - The vertebrate fauna of the Selma Formation of Alabama, Part VIII, the fishes. *Fieldiana Geology Memoirs*, 3(8): 1-72.

Applegate S.P. (1974) - A revision of the higher taxa of Orectoloboids. *Journal of the Marine Biological Association of India*, 14(2): 743-751.

Arambourg C. (1935) - Note préliminaire sur les vertébrés fossiles des phosphates du Maroc. *Bulletin de la Société géologique de France,* 5(5): 413-439.

Arambourg C. (1952) - Les vertébrés fossiles des gisements de phosphates (Maroc-Algérie-Tunisie). *Notes et Mémoires du Service Géologique du Maroc*, 92: 1-372.

Arambourg C. (1954) - Les poisons crétacés du Jebel Tselfat (Maroc). *Notes du Service Géologique du Maroc, Notes et Mémoires*, 118: 1-188.

Arambourg C. & Joleaud L. (1943) - Vertébrés fossils du basin du Niger. *Bulletin de la Direction de Mines, Dakar*, 7: 27-84.

Arkhangelsky M.S. (1999) - Finds of turtle remains in the Upper Cretaceous of the Lower Volga region. *Proceedings of the Geological Faculty of SSU and Research Institute of Geology of SSU* [*Trudy Geologicheskogo Faculteta SGU i NII Geologii SGU*], 1999: 42-144 [in Russian].

Arkhangelsky M.S., Averianov A.O. & Pervushov E.M. (2007) - Short-necked plesiosaurs of the family Polycotylidae from the Campanian of Saratov Region. *Paleontological Journal*, 6(41): 656-660.

Arratia G., Scasso R.A. & Kiessling W. (2004) - Late Jurassic fishes from Longing Gap, Antarctic Peninsula. *Journal of Vertebrate Paleontology*, 24(1): 41-55.

Averianov A.O. (1996) - Additions to the Selachian fauna of the Russian Cretaceous. 2. A new species of *Paracorax* Cappetta, 1977 (Chondrichthyes: Anacoracidae). *Zoosystematica Rossica*, 6(1/2): 315-316.

Averianov A.O. (2001) - Systematics of the Cretaceous-Paleogene chimaeroid fish of the genus *Elasmodus* (Chondrichthyes, Holocephali). *Paleontological Journal*, 35(3): 289-300.

Averianov A.O. & Arkhangelsky M.S. (2020) - A large pteranodontid pterosaur from the Late Cretaceous of Eastern

Europe. *Geological Magazine*, 2020: 1-13.

Averianov A.O. & Arkhangelsky M.S. (2021) - *Pteranodons* of Russia. *Priroda*, 3: 30-37. [in Russian]

Averianov A.O., Arkhangelsky M.S. & Merkulov S.M. (2016) - An azhdarchid humerus (Pterosauria, Azhdarchidae) from the Upper Cretaceous of Saratov Region. *Paleontological journal*, 4(50): 414-417.

Averianov A.O., Arkhangelsky M.S. & Pervushov E.M. (2008) - A new Late Cretaceous Azhdarchid (Pterosauria, Azhdarchidae) from the Volga Region. *Paleontological Journal*, 6(42): 634-642.

Averianov A.O., Arkhangelsky M.S., Pervushov E.M. & Ivanov A.V. (2005) - A new record of an azhdarchid (Pterosauria: Azhdarchidae) from the Upper Cretaceous of the Volga Region. *Paleontological Journal*, 4(39): 433-439.

Averianov A.O. & Glickman L.S. (1994) - Remains of chimaeras (Chondrichthyes, Holocephali) from the "sponge horizon" of the upper Cretaceous of Saratov. *Paleontological Journal*, 2: 119-122 [in Russian].

Averianov A.O. & Popov E.V. (1995) - A new species of chimaeroid fish from the Upper Cretaceous of the Saratov Region, Russia. *Palaeontology*, 38(3): 659-664.

Averianov A.O. & Popov E.V. (2014) - A pterosaurian vertebra from the Upper Cretaceous of the Saratov Region. *Paleontological Journal*, 48(3): 326-329.

Bardack D. & Sprinkle G. (1969) - Morphology and relationships of saurocephalid fishes. *Fieldiana Geology*, 16(12): 297-340.

Bardet N., Cappetta H., Pereda Suberbiola X., Mouty M., Al-Maleh A.K., Ahmad A.M., Khrata O. & Gannoum N. (2000) - The marine vertebrate faunas from the Late Cretaceous phosphates of Syria. *Geological Magazine*, 137(3): 269-290.

Bartholomai A. (1969) - The Lower Cretaceous elopoid fish *Pachyrhizodus marathonensis* (Etheridge Jnr). In: Cambell, K.S.W. (Ed.) - Stratigraphy and Paleontology; essays in honour of Dorothy Hill 249-263. Australian National University Press, Canberra.

Bazzi M., Einarsson E. & Kear B.J. (2015) - Late Cretaceous (Campanian) actinopterygian fishes from the Kristianstad Basin of southern Sweden. In: Kear B.J., Lindgren J., Hurum J.H., Milan J. & Vajda V. (Eds) - Mesozoic Biotas of Scandinavia and its Arctic Territories. *Geological Society of London, Special Publications*, 434: 1-327.

Bazzi M., Campione N.E., Kear B.P., Pimiento C. & Ahlberg P.E. (2021) - Feeding ecology has shaped the evolution of modern sharks. *Current Biology*, 31: published online 5 October. https://doi.org/10.1016/j.cub.2021.09.028

Becker M.A., Chamberlain J.A. & Wolf G.E. (2006) - Chondrichthyans from the Arkadelphia Formation (Upper Cretaceous: upper Maastrichtian) of Hot Spring County, Arkansas. *Journal of Paleontology*, 80(4): 700-716.

Bendix-Almgreen S.E. (1969) - Notes on the Upper Cretaceous and Lower Tertiary fish faunas of northern West Greenland. *Meddelelser fra Dansk Geologisk Forening*, 19(2): 204-217.

Berg L.S. (1940) - Classification of fishes, both recent and fossil. *Travaux de l'Institut Zoologique de l'Academie des Sciences de l'URSS*, 5(2): 85-517.

Bice K.N. & Shimada K. (2016) - Fossil marine vertebrates from the Codell Sandstone Member (middle Turonian) of the Upper Cretaceous Carlile Shale in Jewell County, Kansas, USA. *Cretaceous Research*, 65: 172-198.

Biddle J.P. (1988) - Contribution à l'étude des Sélaciens du Crétacé supérieur. Découverte d'une faune remaniée au Sud-Ouest du Bassin de Paris. SAGA Information, Paris, 7 pp.

Biddle J.P. (1993) - Les Elasmobranches de l´Albien inférieur et moyen (Crétacé inférieur) de la Marne et de la Haute-Marne (France). *Belgian Geological Survey, Professional Paper: Elasmobranches et Stratigraphie*, 264: 191-240.

Biriukov A.V. (2016) - Cenomanian elasmobranchs (Chondrichthyes) of the Volga region: diversity and biostratigraphic significance. Chernomorpress, Simferopol: 67-69 [in Russian].

Biriukov A.V. (2018) - On the stratigraphic significance of elasmobranchs (Chondrichthyes, Elasmobranchii) in the Cenomanian of the Volga River Basin (right bank). *Izvestiya of Saratov University, New series, Earth Science*, 18(1): 27-40 [in Russian].

Blainville H.M.D. de. (1816) - Prodrome d'une nouvelle distribution systématique du règne animal. *Bulletin des Sciences, par la Société Philomatique de Paris*, 8: 105-124.

Blake S.F. (1940) - *Paralbula*, a new fossil fish based on dental plates from the Eocene and Miocene of Maryland. *Journal of the Washington Academy of Sciences*, 30: 205-209.

Bogan S. & Agnolin F.L. (2010) - Primera ictiofauna marina del Cretácico Superior (Formación Jaguel, Maastrichtiano) de la provincia de Río Negro, Argentina. *Papéis Avulsos de Zoologia*, 50(12): 175-180.

Bőhm J. (1907) - Über *Inoceramus cripsi* Mant. *Zeitschrift der Deutschen Geologischen Gesellschaft, Monatsberichte*, 59: 113-114.

Bonaparte C.L. (1831) - Saggio di una distribuzione metodica degli animali vertebrati. Pesci, Roma, 78 pp.

Bonaparte C.L. (1838) - Selachorum tabula analytica. *Nuovi Annali della Science Naturali Bologna*, 1(2): 195-214.

Callahan W.R., Mehling C.M., Denton R.K. & Parris D.C. (2014) - Vertebrate paleontology and stratigraphy of the Late Cretaceous Holmdel Park Site, Monmouth County, New Jersey. *Dakoterra*, 6: 163-169.

Cappetta H. (1980) - Les Sélaciens du Crétacé supérieur du Liban. II. Batoïdes. *Palaeontographica Abt. A*, 168(5-6): 149-229.

Cappetta H. (2012) - Chondrichthyes Mesozoic and Cenozoic Elasmobranchii: Teeth. In: Schultze. H.-P. (Ed) - Handbook of Paleoichthyology, Volume 3E. Gustav Fischer Verlag, Münchin, 512 pp.

Cappetta H. & Case G.R. (1975) - Contribution à l'étude des Sélaciens du groupe Monmouth (Campanien-Maestrichtien) du New Jersey. *Palaeontographica Abt. A*, 151(1-3): 1-46.

Cappetta H., Morrison K. & Adnet S. (2020) - A shark fauna from the Campanian of Hornby Island, British Columbia, Canada: an insight into the diversity of Cretaceous deep-water assemblages. *Historical Biology*, 33(8): 1121-

1182.

Carbot-Chanona G. & Than-Marchese B.A. (2013) - Presencia de *Enchodus* (Osteichthyes: Aulopiformes: Enchodontidae) en el Maastrichthiano (Cretácico Tardío) de Chiapas, México. *Paleontología Mexicana*, 63(2): 8-16.

Case G.R. (1978a) - *Ischyodus bifurcatus*, a new species of chimaeroid fish from the upper Cretaceous of New Jersey. *Géobios*, 11: 21-29.

Case G.R. (1978b) - A new selachian fauna from the Judith River Formation (Campanian) of Montana. *Palaeontographica, Abt. A*, 160(1-6): 176-205.

Case G.R. (1987) - A new selachian fauna from the Late Campanian of Wyoming (Teapot Sandstone Member, Mesaverde Formation, Big Horn Basin). *Palaeontographica, Abt. A*, 197(1-3): 1-37.

Case G.R. Cook T.D., Sadorf E.M. & Shannon K.R. (2017) - A late Maastrichtian selachian assemblage from the Peedee Formation of North Carolina, USA. *Vertebrate Anatomy Morphology Palaeontology*, 3: 63-80.

Case G.R. & Schwimmer D.R. (1988) - Late Cretaceous fish from the Blufftown Formation (Campanian) in Western Georgia. *Journal of Paleontology*, 62(2): 290-301.

Case G.R. & Schwimmer D.R. (1992) - Occurrences of the chimaeroid *Ischyodus bifurcatus* Case in the Cusseta Formation (Upper Cretaceous, Campanian) of Western Georgia and its distribution. *Journal of Paleontology*, 66(2): 347-350.

Casier E. (1943) - Contributions à l'étude des poissons fossiles de la Belgique. III. Quelques espèces nouvelles ou peu connues du Landénien marin. *Bulletin du Musée Royal d'Histoire Naturelle de Belgique*, 19(35): 1-16.

Casier E. (1947) - Constitution et évolution de la racine dentaire des Euselachii. I. Note préliminaire. *Bulletin du Musée Royal d'Histoire Naturelle de Belgique*, 23(13): 1-15.

Cavin L., Alexopoulos A. & Piuz A. (2012) - Late Cretaceous (Maastrichtian) ray-finned fishes from the island of Gavdos, southern Greece, with comments on the evolutionary history of the aulopiform teleost *Enchodus. Bulletin de la Société Géologique de France*, 187: 561-572.

Chalifa Y. (1996) - New species of *Enchodus* (Aulopiformes: Enchodontidae) from the Northern Negev, Israel, with comments on evolutionary trends in the Enchodontoidei. In: Arratia G. & Viohl G. (Eds) - Mesozoic Fishes - Systematics and Paleoecology: 349-367. Verlag Dr. Friedrich Pfeil, München.

Ciampaglio C.N., Cicimurri D.J., Ebersole J.A. & Runyon K.E. (2013) - A note on Late Cretaceous fish taxa recovered from stream gravels at site AGr-43 in Greene County, Alabama. *Bulletin Alabama Museum of Natural History*, 31(1): 84-97.

Cicimurri D.J. & Ebersole J.A. (2014) - Late Cretaceous chimaeroids (Chondrichthyes: Holocephali) from Alabama, USA. *PaleoBios*, 31(2): 1-14.

Cicimurri D.J. & Ebersole J.A. (2015) - Paleocene chimaeroid fishes (Chondrichthyes: Holocephali) from the eastern United States, including two new species of *Callorhinchus. PaleoBios*, 32(1): 1-29.

Condamine F.L., Romieu J. & Guinot G. (2019) - Climate cooling and clade competition likely drove the decline of lamniform sharks. *Proceedings of the National Academy of Sciences of the United States of America*, 116(41): 20584-20590.

Compagno L.J.V. (1973) - Interrelationships of living elasmobranchs. *Zoological Journal of the Linnean Society*, 53(1): 15-61.

Cope E.D. (1870) - On the Saurodontidae. *Proceedings of the American Philosophical Society*, 11: 529-538.

Cope E.D. (1871) - Observations on the systematic relations of the fishes. *The American Naturalist*, 5: 579-593.

Cope E.D. (1872) - On the families of fishes of the Cretaceous formations in Kansas. *Proceedings of the American Philosophical Society*, 12: 327-357.

Cope E.D. (1874) - Review of the Vertebrata of the Cretaceous Period found west of the Mississippi River. *Bulletin of the United States Geological and Geographical Survey of the Territories, First Series*, 2: 3-48.

Cope E.D. (1875) - The vertebrata of the Cretaceous formations of the west. United States Geological Survey of the Territories, Washington, D.C., 303 pp.

Cope E.D. (1877) - On some new or little known reptiles and fishes of the Cretaceous of Kansas. *Proceedings of the American Philosophical Society*, 17: 176-181.

Cope E.D. (1885) - A contribution to the vertebrate paleontology of Brazil. *Proceedings of the American Philosophical Society*, 23(121): 1-21.

Corral J. C., Baedet N., Pereda Suberbiola X. & Arz J.A. (2011) - Depredadores marinos (osteíctios, selacios y mosasaurios) en el Campaniense de la Cuenca Vasco-Cantábrica. In: XXVII Jornadas Sociedad Española de Palaeontological, Sabadell, 5-8 octubre de 2011. *Palaeontology i evolució Memoria especial,* 5: 83-87.

Corral J.C., Berreteaga A., Poyato-Ariza F.J., Bardet N., Cappetta H., Floquet M., Astibia H., Badiola A. & Pereda Suberbiola X. (2021) - Stratigraphy, age, and vertebrate palaeontology of the latest Cretaceous Quintanilla la Ojada locality (Basque-Cantabrian Region, northern Spain): a synthesis. *Comptes Rendus Palevol*, 20(7): 91-117.

Cumbaa S.L. & Murray A.M. (2008) - New Late Cretaceous pachyrhizodontid and enchodontoid fishes and associated ichthyofauna from the Northwest Territories, Canada. In: Arratia G., Schultze H.-P. & Wilson M.V.H. (Eds) - Mesozoic Fishes 4 - Homology and Phylogeny: 229-256. Verlag Dr. Friedrich Pfeil, München, 502 pp.

Cumbaa S.L., Shimada K. & Cook T.D. (2010) - Mid-Cretaceous vertebrate faunas of the Western Interior Seaway of North America and their evolutionary, paleobiogeographical, and paleo ecological implications. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 195: 199-214.

Dalinkevicius J.A. (1935) - On the fossil fishes of the Lithuanian Chalk. I. Selachii. *Mémoires de la Faculté des Sciences de l'Université de Vytautas le Grand*, 9: 243-305.

Danilov I.G., Obraztsova E.M., Arkhangelsky M.S., Ivanov A.V. & Averianov A.O. (2018) - Cretaceous chelonioid turtles of Northern Eurasia: previous records and new findings. *Turtle Evolution Symposium, Waseda University, Japan*, May 26-27: 30-33.

Dartevelle E. & Casier E. (1943) - Les poissons fossiles du Bas-

Congo et des régions voisines. *Annales du Musée du Congo Belge, Sér. A*, 2(1): 1-200.

Dartevelle E. & Casier E. (1949) - Les poissons fossils du Bas-Congo et des régions voisines. *Annales du Muséum de Congo Belge, Sér. A*, 2(2): 205-255.

Dartevelle E. & Casier E. (1959) - Les poissons fossiles du Bas-Congo et des régions voisines. *Annales du Musée du Congo Belge, Sér. A*, 2(3): 257-568.

Davis J.W. (1890) - On the fossil fish of the Cretaceous formations of Scandinavia. *Scientific Transactions of the Royal Dublin Society*, 2(4): 363-434.

Davis M.P. (2010) - Evolutionary relationships of the Aulopiformes (Euteleostei: Cyclosquamata): a molecular and total evidence approach. 431-470. In: Nelson J.S. (Ed) - Origin and Phylogenetic Interrelationships of Teleosts. Verlag Dr. Friedrich Pfeil, München, 480 pp.

Davies W. (1878) - II.-On the nomenclature of *Saurocephalus lanciformis* of the British Cretaceous deposits: with description of a new species (*S. woodwardii*). *Geological Magazine*, 5(6): 254-261.

Diedrich C.G. & Scheer U. (2015) - Marine vertebrates from the Santonian coastal carbonates of northwestern Germany - a tool for the reconstruction of a Proto- North Sea Basin intertidal dinosaur-exchange bridge. *Open Geosciences*, 7(1): 342-361.

Dixon F. (1850) - The geology and fossils of the Tertiary and Cretaceous formations of Sussex. Longman, Brown, Green, and Longmans, London, 469 pp.

Duffin C.J. & Ward D.J. (1993) - The Early Jurassic palaeospinacid sharks of Lyme Regis, southern England. *Belgian Geological Survey, Professional Paper: Elasmobranches et Stratigraphie*, 264: 53-101.

Ebersole J.A., Cicimurri D.J. & Stringer G.L. (2019) - Taxonomy and biostratigraphy of the elasmobranchs and bony fishes (Chondrichthyes and Osteichthyes) of the lower-to-middle Eocene (Ypresian to Bartonian) Claiborne Group in Alabama, USA, including an analysis of otoliths. *European Journal of Taxonomy,* 585: 1-274.

Ebersole J.A. & Ehret D.J. (2018) - A new species of *Cretalamna sensu stricto* (Lamniformes, Otodontidae) from the Late Cretaceous (Santonian-Campanian) of Alabama, USA. *PeerJ*, 6: e4229. https://doi.org/10.7717/peerj.4229

Egerton P. (1843) - On some new species of fossil chimaeroid fishes, with remarks on their general affinities. *Proceedings of the Geological Society of London*, 4(94): 153-157.

Elicki O. & Magnus M. (2012) - *Squalicorax kaupi* Agassiz, 1843, (Chondrichthyes, Lamniformes) and *Echinocorys gravesi* Agassiz & Desor, 1847, (Echinoidea, Holasteroida) from the late Cretaceous of Bornholm (Denmark). *Freiberger Forschungshefte*, C542: 55-64.

Estes R. (1969) - Studies on fossil phyllodont fishes, interrelationships and evolution in the Phyllodontidae (Albuloidei). *Copeia*, 1969(2): 317-331.

Fielitz C. & González-Rodriguez K.A. (2010) - A new species of *Enchodus* (Aulopiformes: Enchodontidae) from the Cretaceous (Albian to Cenomanian) of Zimapán, Hidalgo, México. *Journal of Vertebrate Paleontology*, 30: 1343-1351.

Fitton G. & Larsen L.M. (2001) - The geological history of the North Atlantic Ocean. 9-27. In: Fellows-Jensen G. (Ed.) - Denmark and Scotland: the cultural and environmental resources of small nations. Joint symposium of the Royal Society of Edinburgh and the Royal Danish Academy of Sciences and Letters held in Copenhagen 15th-18th September 1999, 256 pp.

Forey P.L. (1977) - The osteology of *Notelops* Woodward, *Rhacolepis* Agassiz and *Pachyrhizodus* Dixon (Pisces: Teleostei). *Bulletin of the British Museum (Natural History), Geology*, 28(2): 125-204.

Forey P.L., Yi L., Patterson C. & Davies C.E. (2003) - Fossil fishes from the Cenomanian (Upper Cretaceous) of Namoura, Lebanon. *Journal of Systematic Palaeontology*, 1: 227-330.

Friedman M. (2012) - Ray-finned fishes (Osteichthyes, Actinopterygii) from the type Maastrichtian, the Netherlands and Belgium. In: Jagt J.W.M., Donovan S.K. & Jagt-Yazykova E.A. (Eds) - Fossils of the type Maastrichtian (Part 1). *Scripta Geologica Special Issue*, 8: 113-142.

Gallardo C., Shimada K. & Schumacher B.A. (2013) - A new Late Cretaceous marine vertebrate assemblage from the Lincoln Limestone Member of the Greenhorn Limestone in southeastern Colorado. *Transactions of the Kansas Academy of Science*, 115(3-4): 107-116.

Garcia W.J. & Hippensteel S.P. (2012) - Chondrichthyan and osteichthyan material from Elizabethtown, NC, and Bowie, MD, and the fish fauna of the Campanian-Maastrichtian of eastern North America. *Journal of Vertebrate Paleontology*, 32(1): 99.

Garman S. (1885) - *Chlamydoselachus anguineus* Garm. - A living species of cladodont shark. *Bulletin of the Museum of Comparative Zoology at Harvard College*, 12(1): 1-35.

Garman S. (1901) - Genera and families of the chimaeroids. *Proceedings of the New England Zoölogical Club*, 2: 75-77.

Gemmellaro M. (1920) - Ittiodontoliti Maëstrichtiani di Egitto. *Atti della Accademia di Scienze, Letter e Arti di Palermo*, 7: 149-204.

Giersch S., Frey E., Stinnesbeck W. & González A.H. (2010) - *Pachyrhizodus caninus* Cope, 1872 (Teleostei, Crossognathiformes) from the early Turonian of Vallecillo (Mexico). *N. Jb. Geol. Paläont. Abh.*, 258: 219-228.

Glickman L.S. (1953) - Upper Cretaceous vertebrates of the Saratov region. Preliminary data. *Uchenye zapiski Saratovskogo Universiteta*, 38: 51-54 [in Russian].

Glickman L.S. (1957) - Taxonomic significance of the accessory teeth of sharks of the families Lamnidae and Scapanorhynchidae. *Trudy geol. Muz. A.P. Karpinskogo» Akad. Nauk S.S.S.R.,* 1: 103-109 [in Russian].

Glickman L.S. (1958) - Rates of evolution in lamnoid sharks. *Doklady Akademii Nauk SSSR*, 123(3): 568-571 [in Russian].

Glickman L.S. (1964) - Sharks of Paleogene and their stratigraphic significance. Nauka Press, Moscou, 229 pp. [in Russian].

Glickman L.S. (1980) - Evolution of Cretaceous and Cenozoic lamnoid sharks. Nauka Press, Moscou, 248 pp. [in Russian].

Glickman L.S. & Averianov A.O. (1998) - Evolution of the Cretaceous lamnoid sharks of the genus *Eostriatolamia*. *Paleontological Journal*, 32(4): 376-384.

Goodrich E.S. (1909) - Vertebrata craniate, fasc. 1. Cyclostomes and fishes. In: Lankester R. (Ed.) - A treatise on zoology, part 9. Adam and Charles Black, London, 518 pp.

Goodrich E.S. (1930) - Studies on the structure & development of vertebrates. Macmillan, London, 837 pp.

Goody P.C. (1976) - *Enchodus* (Teleostei, Enchodontidae) from the Upper Cretaceous Pierre Shale of Wyoming and South Dakota with an evaluation of the North American enchodontid species. *Palaeontographica Abteilung A: Palaeozoologie- Stratigraphie*, 152(4-6): 91-112.

Gorman K.L., Shimada K. & Witzke B.J. (2014) - Late Cretaceous Marine Fishes from the Basal Greenhorn Limestone in Western Iowa. *Transactions of the Kansas Academy of Science*, 117(1-2): 91-99.

Gottfried M.D., Rabarison J.A. & Randriamiarimanana L.L. (2001) - Late Cretaceous elasmobranchs from the Mahajanga Basin of Madagascar. *Cretaceous Research*, 22(4): 491-496.

Gouiric-Cavalli S., Cione A., Tineo D., Pérez L., Iribarne M., Allcca Torres M. & Pioré D. (2021) - The first Peruvian record of *Enchodus* (Actinopterygii, Aulopiformes, Enchodontidae) in the Upper Cretaceous Vivian Formation. *Andean Geology*, 48(2): 303-315.

Green W.R. (1913) - A description of the specimens of the teleostean genus *Enchodus* in the University of Kansas Museum. *The University of Kansas Science Bulletin*, 7: 71-107.

Greenwood P.H., Rosen D.E., Weitzman S.H. & Meyers G.S. (1966) - Phyletic studies of teleostean fishes, with a provisional classification of living forms. *Bulletin of the American Museum of Natural History*, 131(4): 341-455.

Grigoriev D.V., Arkhangelsky M.S. & Merkulov S.M. (2015) - A record of *Clidastes propython* Cope (Squamata, Mosasauridae) in the Upper Cretaceous of the Saratov region (Russia). *Paleontologicheskii zhurnal*, 5: 512-520.

Guinot G., Underwood C.J., Cappetta H. & Ward D.J. (2012) - Batoids (Elasmobranchii: Batomorphii) from the British and French Late Cretaceous. *Journal of Systematic Paleontology*, 10(3): 445-474.

Guinot G., Underwood C.J., Cappetta H. & Ward D.J. (2013) - Sharks (Elasmobranchii: Euselachii) from the Late Cretaceous of France and the UK. *Journal of Systematic Palaeontology*, 11(6): 589-671.

Gurr P.R. (1962) - A new fish fauna from the Woolwich Bottom Bed (Sparnacian) of Herne Bay, Kent. *Proceedings of the Geologist's Association*, 73: 419-447.

Hamm S.A. & Cicimurri D. J. (2011) - Early Coniacian (Late Cretaceous) selachian fauna from the basal Atco Formation, lower Austin Group, north central Texas. *Paludicola*, 8(3): 107-127.

Hamm S.A. & Shimada K. (2007) - The Late Cretaceous anacoracid shark, *Pseudocorax laevis* (Leriche), from the Niobrara Chalk of western Kansas. *Transactions of the Kansas Academy of Science*, 110(1/2): 44-52.

Harlan R. (1824) - On a new fossil genus of the order Enalio sauri, (of Conybeare). *Journal of the Academy of Natural Sciences of Philadelphia, Series 1*, 3(2): 331-337.

Hay O.P. (1899) - On one little known and one hitherto unknown species of *Saurocephalus*. *American Journal of Science*, 4(7): 299-304.

Hay O.P. (1902) - Bibliography and catalogue of the fossil vertebrata of North America. *Bulletin of the United States Geological Survey*, 179: 1-868.

Hays I. (1830) - Description of a fragment of the head of a new fossil animal, discovered in a marl pit, near Moorestown, New Jersey. *Transactions of the American Philosophical Society, Series 2*, 3(18): 471-477.

Herman J. (1977) - Les Sélaciens des terrains Néocrétacés et Paléocènes de Belgique et des contrées limitrophes. Eléments d'une biostratigraphie intercontinentale. *Mémoires pour servir à l'explication des Cartes géologiques et minières de la Belgique*, 15: 1-401.

Hoganson J.W. & Erickson J.M. (2005) - A new species of *Ischyodus* (Chondrichthyes: Holocephali: Callorhynchidae) from upper Maastrichtian shallow marine facies of the Fox Hills and Hell Creek Formations, Williston Basin, North Dakota, USA. *Palaeontology*, 48(4): 709-721.

Hoganson J.W., Erickson J.M. & Everhart M. J. (2015) - *Ischyodus rayhaasi* (Chimaeroidei; Callorhinchidae) from the Campanian-Maastrichtian Fox Hills Formation of northeastern Colorado, USA. *Transactions of the Kansas Academy of Science*, 118(1-2): 27-40.

Holloway W.L., Claeson K.M., Sallam H.M., El-Sayed S., Kora M., Sertich J.J. W. & O'Connor P.M. (2017) - A new species of the neopterygian fish *Enchodus* from the Duwi Formation, Campanian, Late Cretaceous, western desert, Central Egypt. *Acta Palaeontologica Polonica*, 62(3): 603-611.

Huxley T.H. (1880) - On the application of the laws of evolution to the arrangement of the Vertebrata, and more particularly of the Mammalia. *Proceedings of the Zoological Society of London*, 1880: 649-662.

Ikejiri T., Ebersole J.A., Blewitt H.L. & Ebersole S.M. (2013) - An overview of Late Cretaceous vertebrates from Alabama. *Bulletin Alabama Museum of Natural History*, 31(1): 46-66.

Ivanov A.V. (1993) - *Oxytoma* of Santonian and Campanian of the Saratov Volga region. *Voprosy stratigrafii paleozoya, mezozoya i kajnozoya.Izdatel'stvo Saratovskogo universiteta*, 8: 149-156 [in Russian].

Jambura P.L., Stumpf S. & Kriwet J. (2021) - Skeletal remains of the oldest known pseudocoracid shark *Pseudocorax kindlimanni* sp. nov. (Chondrichthyes, Lamniformes) from the Late Cretaceous of Lebanon. *Cretaceous Research*, 125: 104842. https://doi.org/10.1016/j.cretres.2021.104842

Jansen K.R., Shimada K. & Kirkland J.I. (2012) - Fossil fish fauna from the uppermost Graneros Shale (Upper Cretaceous: middle Cenomanian) in southeastern Nebraska. *Transactions of the Kansas Academy of Science*, 115(3-4): 145-152.

Johnson-Ransom E.D., Popov E.V., Deméré T.A. & Shimada K. (2018) - The Late Cretaceous chimaeroid fish, *Ischyodus bifurcatus* Case (Chondrichthyes: Holocephali), from California, USA, and its paleobiogeographical significance. *Paleontological Research*, 22(4): 364-372.

Jordan D.S. & Fowler H.W. (1903) - A review of the Elasmobranchiate fishes of Japan. *Proceedings of the United States National Museum*, 26(1324): 593-674.

Kaddumi H.F. (2009) - Saurodontids (Ichthyodectiformes: *Saurocephalus*) of Harrana with a description of a new species from the late Maastrichtian Muwaqqar Chalk Marl Formation. In: Fossils of the Harrana Faunaand the adjacent areas: 215-231. Publications of the Eternal River Museum of Natural History, Amman, 324 pp.

Kemp N.R. (1991) - Chapter 15: Chondrichthyans in the Cretaceous and Tertiary of Australia. *Vertebrate Palaeontology of Australasia*, 1991:497-568.

Kennedy W.J., King C. & Ward D.J. (2008) - The upper Albian and lower Cenomanian succession at Kolbay, eastern Mangyshlak (southwest Kazakhstan). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Science de la Terre*, 78: 117-147.

Ladwid J. (2000) - Haizähne aus dem Obercampan von Kronsmoor. *Teil 2 Der Geschiebesammler*, 33: 77-90.

Ladwid J. (2014) - Haizähne der Art *Squalicorax kaupi* (Agassiz, 1843) (Lamniformes, Anacoracidae) aus Ignaberga (Schonen, Schweden). *Arbeitskreis Paläontologie Hannover*, 42: 101-103.

Lauginiger E.M. (1988) - Cretaceous fossils from the Chesapeake and Delaware Canal: A guide for students and collectors. *Geological Survey, University of Delaware, Special Publication*, 18: 1-61.

Leidy J. (1855) - Indications of twelve species of fossil fishes. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 7: 395-397.

Leidy J. (1856) (published 1857) - Description of two Ichthyodorulites. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 8: 11-12.

Leidy J. (1857) - Notices on some remains of extinct fishes. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 9: 167-168.

Leriche M. (1906) - Contribution à lètude des poisons fossils du Nord de la France et des regions voisines. *Mémoires de la Société géologique du Nord*, 5: 1-430.

Leriche M. (1927) - Les Poissons du Crétacé marin de la Belgique et du Limbourg hollandais (note préliminaire). Les résultats stratigraphiques de leur étude. *Bulletin de la Société Belge de Géologié, de Paléontologie et d'Hydrologie*, 37(3): 199-299.

Leriche M. (1929) - Les poissons du Crétacé marin de la Belgique et du Limbourg hollandais. Note préliminaire. Les résultats stratigraphique de leur étude. *Bulletin of the Society of Belge Geology*, 37:199-299.

Loomis F. B. (1900) - Die anatomie und die verwandtschaft der Ganoid- und Knochen-fische aus der Kreide-Formation von Kansas, U.S.A. *Palaeontographica*, 46: 213-283.

Mackie S.J. (1863) - On a new species of *Hybodus* from the lower chalk. *Geologist*, 6: 332-347.

Maisey J.G. (1979) - Finspine morphogenesis in squalid and heterodontid sharks. *Zoological Journal of the Linnean Society*, 66(2): 161-183.

Manning E.M. & Dockery D.T. III. (1992) - A guide to the Frankstown vertebrate fossil locality (Upper Cretaceous), Prentiss County, Mississippi. *Mississippi Department of Environmental Quality Office of Geology Circular*, 4: 1-43.

Mantell G.A. (1822) - The fossils of the South Downs or illustrations of the geology of Sussex. Lupton Relfe, London, 327 pp.

Marie P. (1941) - Les Foraminifères de la craie à *Belemnitella mucronata* du Bassin de Paris. *Mémoires du Muséum National d'Histoire Naturelle de Paris, Nouvelle Série*, 12: 1-296.

Maury C.J. (1930) - O Cretaceo do Parahyba do Norte. Brazil. *Monographie do Serviço Geológico e Mineralógico*, 8: 1-305.

Meglei A.D., Shimada K. & Kirkland J.I. (2013) - Fossil Vertebrates from the Middle Graneros Shale (Upper Cretaceous: Middle Cenomanian) in Southeastern Nebraska. *Transactions of the Kansas Academy of Science*, 116(3-4): 129-135.

Mollen F.H., van Bakel B.W.M. & Jagt J.W.M. (2016) - A partial braincase and other skeletal remains of Oligocene angel sharks (Chondrichthyes, Squatiniformes) from northwest Belgium, with comments on squatinoid taxonomy. *Contributions to Zoology*, 85(2): 147-171.

Müller J. (1845) - Über den Bau und die Grenzen der Ganoiden, und über das natürliche System der Fische. *Archiv für Naturgeschichte*, 11(1): 91-141.

Mustafa H.A., Case G.R. & Zalmout I.S. (2002) - A new selachian fauna from the Wadi Umm Ghudran Formation (Late Cretaceous) - Central Jordan. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 226(3): 419-444.

Nagrodski M., Shimada K. & Schumacher B.A. (2012) - Marine vertebrates from the Hartland Shale (Upper Cretaceous: Upper Cenomanian) in southeastern Colorado, USA. *Cretaceous Research*, 37: 76-88.

Nelson J.S., Grande T.C. & Wilson M.V.H. (2016) - Fishes of the World, Fifth Edition. John Wiley & Sons, Inc., New York, 707 pp.

Nessov L.A. (1986) - Mesozoic and Early Paleogene birds of the USSR and some questions of the early history of the class. *The study of birds of the USSR, their protection and rational use,* 1986: 104-106. [in Russian].

Nessov L.A. & Averianov A.O. (1996) - Ancient *Chimaera*-like fish of Russia, Ukraine, and Kazakhstan. I. Some ecological features of chimaeras and an overview of locations. *Vestnik SPbGU*, 1(7): 11-19 [in Russian].

Nilsson S. (1826) - Om de mångrummiga snäckor som förekomma i kritformationen i Sverige. *Kongliga Vetenskaps-Academiens Handlingar*, 1825: 329-343.

Noetling F. (1885) - Die Fauna des samländischen Tertiärs. *Abhandlungen zur geologischen Specialkarte von Preussen und den Thüringischen Staaten*, 6(3): 1-218.

Obruchev D.V. (1953) - Izuchenie edestid y raboty A. P. Karpinskogo. *Trudy Paleontologičeskogo Instituta, Akademiya Nauk SSSR* , 45: 1-85 [in Russian].

Ochev V.G. (1976) - A new plesiosaur from the upper Cretaceous of the Penza region. *Paleontologicheskii Zhurnal*, 2: 135-138 [in Russian].

Olferiev A.G. & Alekseev A.S. (2005) - Stratigraphic chart of the Upper Cretaceous deposits of the East Europe Platform: explanatory note. *Paleontologicheskogo Instituta Akademii Nauk SSSR, Moscow,* 1 pp. [in Russian].

Olferiev A.G., Alekseev A.S., Beniamovski V.N., Vishnevskaya V.S., Ivanov A.V., Kopaevich L.F., Pervushov E.M., Seltser V.B., Kharitonov V.M. & Shcherbinina E.A. (2004) - The Mezino-Lapshinovka reference section of the upper Cretaceous and problems of Santonian- Campanian boundary in Saratov area near the Volga River. *Stratigraphy and Geological Correlation*, 12(6): 603-636.

Olferiev A.G., Alekseev A.S., Beniamovski V.N., Vishnevskaya V.S., Ivanov A.V., Kopaevich L.F., Pervushov E.M., Seltser V.B., Kharitonov V.M. & Shcherbinina E.A. (2007) - Upper Cretaceous deposits in the northwest of Saratov Oblast. Part 1: Litho- and biostratigraphic analysis of the Vishnevoe section. *Stratigraphy and Geological Correlation*, 15(6): 610-655.

d'Orbigny A. (1843-47) - Paléontologie Française. Description zoologique et géologique de tous les animaux mollusques et rayonnés fossiles de France. *Terrains Crétacés*, 3: 237-489.

Ouroumova O., Shimada K. & Kirkland J.I. (2016) - Fossil marine vertebrates from the Blue Hill Shale Member (Middle Turonian) of the Upper Cretaceous Carlile Shale in northeastern Nebraska. *Transactions of the Kansas Academy of Science*, 119(2): 211-221.

Panteleyev A.V., Popov E.V. & Averianov A.O. (2004) - New record of *Hesperornis rossicus* (Aves, Hesperornithiformes) in the Campanian of Saratov Province, Russia. *Paleontological Research,* 8: 115-122.

Parris D.C., Grandstaff B.S. & Gallager W.C. (2007) - Fossil fish from the Pierre Shale Group (Late Cretaceous): Clarifying the biostratigraphic record. 99-109. In: Martin J.E. & Parris D.C. (Eds) - The Geology and Paleontology of the Late Cretaceous Marine Deposits of the Dakotas. *Geological Society of America Special Paper*, 427: 1-256.

Patterson C. (1965) - The phylogeny of the chimaeroids. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences*, 249(757): 101-219.

Patterson C. & Rosen D.E. (1977) - Review of the ichthyodectiform and other Mesozoic teleost fishes and the theory and practice of classifying fossils. *Bulletin of the American Museum of Natural History*, 158: 83-172.

Peng J., Russell A.P. & Brinkman D.B. (2001) - Vertebrate microsite assemblages (exclusive of mammals) from the Foremost and Oldman formations of the Judith River group (Campanian) of Southeastern Alberta: an illustrated guide. *Provincial Museum of Alberta Natural History, Occasional Paper*, 25: 1-54.

Pereda-Suberbiola X., Corral J.C., Astibia H., Badiola A., Bardet N., Berreteaga A., Buffetaut E., Buscalioni A.D., Cappetta H., Cavin L., Diez Diaz V., Gheerbrant E., Murelaga X., Ortega F., Pérez-Garcia A., Poyoto-Ariza F.J., Rage J.-C., Sanz J.L. & Torices A. (2015) - Late Cretaceous continental and marine vertebrate assemblages of the Laño Quarry (Basque-Cantabrian Region, Iberian Peninsula): an update. *Journal of Iberian Geology*, 41: 101-124.

Pervushov E.M., Arkhangelsky M.S. & Ivanov A.V. (1999) - Catalogue of localities of marine reptiles in the Jurassic and Cretaceous deposits of the Lower Volga region. College, Saratov, 230 pp. [in Russian].

Pinna M.C.C. de. (1996) - Teleostean monophyly. In: Stiassny M.L.J., Parenti L.R. & Johnson G.D. (Eds) - Interrelationships of Fishes: 147-162. Academic Press, San Diego.

Popov E.V. (2016) - An Annotated Bibliography of the Soviet Palaeoichthyologist Leonid Glickman (1929-2000). *Proceedings of the Zoological Institute RAS*, 320(1): 25-49.

Popov E.V. & Biriukov A.V. (2015) - Early and middle Cenomanian elasmobranchs from the Volga Region, Russia. *Abstracts with Programs, Society for Vertebrate Paleontology, 75th Annual Meeting in Dallas, Texas, USA, October 14-16,* 2015: 197.

Popov E.V. & Lapkin A.V. (2000) - A new shark species of the genus *Galeorhinus* (Chondrichthyes, Triakidae) from the Cenomanian of the Lower Volga River Basin. *Paleontological Journal*, 34: 72-75.

Popov E.V. & Machalski M. (2014) - Late Albian chimaeroid fishes (Holocephali, Chimaeroidei) from Annopol, Poland. *Cretaceous Research*, 47: 1-18.

Priem M.F. (1897) - Sur des dents d'élasmobranches de divers gisements sénoniens (Villedieu, Meudon, FoIx-les-Caves). *Bulletin de la Société géologique de France*, 3(25): 40-56.

Quass A. (1902) - Beiträge zur Kenntnis der Fauna der Obersten Kreidebildungen in der Libyschen Wüste. *Palaeontographica*, 30(2): 153-336.

Regan C.T. (1906) - Descriptions of some new sharks in the British Museum collection. *Annals and Magazine of Natural History, Series 7*, 18(65): 435-440.

Regan C.T. (1923) - The skeleton of *Lepidosteus*, with remarks on the origin and evolution of the lower neopterygian fishes. *Proceedings of the Zoological Society of London*, 1923(1-2): 445-461.

Retzler A., Wilson M.A. & Avni Y. (2013) - Chondrichthyans from the Menuha Formation (Late Cretaceous: Santonian-Early Campanian) of the Makhtesh Ramon region, southern Israel. *Cretaceous Research*, 40: 81-89.

Reuss A.E. (1846) - Die Versteinerungen der böhmischen Kreideformation. Mit Abbildungen der neuen oder weniger bekannten Arten. *Abtheilung*, 2: 1-148.

Robb A.J. (1989) - The Upper Cretaceous (Campanian, Black Creek Formation) fossil fish fauna of Pheobus Landing, Bladen County, North Carolina. *Mosasaur*, 4: 75-92.

Roemer F.A. (1841) - Die Versteinerungen des Norddeutschen Kreidegebirges. *Mit sechszehn lithographirten Tafeln. Hahn'schen, Hofbuch-handlung,* 1840: 49-145.

Rosen D.E. (1973) - Interrelationships of higher euteleostean fishes. In: Greenwood P.H., Miles R.S. & Patterson C. (Eds) - Interrelationships of fishes: 397-513. Academic Press, London, 536 pp.

Rosen D. E. (1985) - An essay on euteleostean classification. *American Museum Novitates*, 2827: 1-57.

Sauvage H.E. (1875) - Essai sur la faune ichthyologique de la périod Liasique suivi d'une notice sur les poissons du Lias de Vassy, deuxième mémoire. *Bibliothèque de l'École des Hautes Études, Section des Sciences Naturelles*, 14: 1-24.

Schein J.P., Grandstaff B.S., Gallagher W.B., Poole J.C. & Lacovara K. J. (2011) - *Paralbula* in North America, revisiting and enigmatic Campanian - Late Paleocene Teleost with

hope for new insights. *The Geological Society of America Abstracts with Programs*, 43 (1): 87.

Schein J.P., Parris D.C., Poole J.C. & Lacovara K.J. (2013) - A nearly complete skull of *Enchodus ferox* (Antinopterygii, Alupiformes) from the Upper Cretaceous Ripley Formation of Lowndes County, Alabama. *Bulletin Alabama Museum of Natural History*, 31(1): 78-83.

Schein J.P. & Lewis R.D. (2007) - Actinopterygian fishes from Upper Cretaceous rocks in Alabama, with emphasis on the teleostean genus *Enchodus*. *Paludicola*, 6(2): 41-86.

Schlotheim E.F. von. (1813) - Beiträge zur Naturgeschichte der Versteinerungen in geognostischer Hinsicht. In: Leonhard C.C. (Ed.) - *Leonhard's Taschenbuch für die gesammte Mineralogie mit Hinsicht auf die neuesten Entdeckungen*, 1(7): 1-134.

Schneider C. & Ladwig J. (2013) - Fossilien aus dem Campan von Hannover - Fische (Pisces). In: Arbeitskreis Paläontologie Hannover: Fossilien aus dem Campan von Hannover 257-270.

Schubert J.A., Wick S.L. & Lehman T.M. (2017) - An Upper Cretaceous (middle Campanian) marine chondrichthyan and osteichthyan fauna from the Rattlesnake Mountain sandstone member of the Aguja Formation in West Texas. *Cretaceous Research*, 69: 6-33.

Seltzer V.B. & Ivanov A.V. (2010) - Atlas of Late Cretaceous ammonites the Volga Region near Saratov. Knizhn. Dom "Universitet", Moscow, 152 pp. [in Russian].

Shimada K. (2015) - Body form and paleoecology of the large Late Cretaceous bony fish, *Pachyrhizodus caninus*. *Cretaceous Research*, 52: 286-291.

Shimada K. & Fielitz C. (2006) - Annotated checklist of fossil fishes from the Smoky Hill Chalk of the Niobrara Chalk (Upper Cretaceous) in Kansas. In: Lucas S.G. & Sullivan R. (Eds) - Late Cretaceous vertebrates from the Western Interior. *New Mexico Museum of Natural History and Science Bulletin*, 35: 193-213.

Shimada K. & Martin D.J. (2008) - Fossil fishes from the basal Greenhorn Limestone (Upper Cretaceous: late Cenomanian) in Russell County, Kansas. *Fort Hays Studies Special Issue*, 2: 89-103.

Shimada K., Popov E.V., Siversson M., Welton B.J. & Long D.J. (2015) - A new clade of putative plankton-feeding sharks from the Upper Cretaceous of Russia and the United States. *Journal of Vertebrate Paleontology*, 35(5): e981335. https://doi.org/10.1080/02724634.2015.981335

Shimada K., Schumacher B.A., Parkin J.A. & Palermo J.M. (2006) - Fossil marine vertebrates from the lowermost Greenhorn Limestone (Upper Cretaceous: Middle Cenomanian) in southeastern Colorado. *Journal of Paleontology*, 80(63): 1-45.

Signeux J. (1959) - Contributions à la stratigraphie et la paléontologie du Crétacé et du Nummulitique de la marge NW de la Péninsule Arabique. A: Poissons et reptiles marins. *Notes et Mémoires sur le Moyen-Orient*, 7: 223-228.

Silva C.M. da. (2007) - Os vertebrados da Bacia da Paraíba: Cretáceo Superior-Paleoceno, Nordeste do Brasil. Unpublished PhD dissertation, Universidade Federal de Pernambuco, 150 pp.

Silva H.M.A. & Gallo V. (2011) - Taxonomic review and phylogenetic analysis of Enchodontoidei (Teleostei: Aulopiformes). *Anais da Academia Brasileira de Ciências*, 83(2): 483-511.

Sintsov I.F. (1872) - Jurassic and Cretaceous fossils of Saratov Province. Materialy dlya geologii Rossii, Tom 4. Tipografiya Imperatorskoj Akademii nauk, Sankt-Peterburg, 127 pp. [in Russian].

Sintsov J. (1899) - Notizen uber die Jura-Kreide-und Neogen-Ablagerung der Gouvernements Saratow, Simbirsk, Samara und Orenburg. "Ekonomische" Buch-u. Steindruckerei, Odessa, 112 pp.

Siverson M. (1989) - Palaeospinacid selachians from the Late Cretaceous of the Kristianstad Basin, Skåne, Sweden. Unpublished PhD dissertation, University of Lund, 24 pp.

Siverson M. (1992) - Biology, dental morphology and taxonomy of lamniform sharks from the Campanian of the Kristianstad Basin, Sweden. *Palaeontology*, 35(3): 519-554.

Siverson M. (1995) - Revision of *Cretorectolobus* (Neoselachii) and description of *Cederstroemia* n. gen., a Cretaceous carpet shark (Orectolobiformes) with a cutting dentition. *Journal of Paleontology*, 69(5): 974-979.

Siverson M. (1996) - Lamniform sharks of the mid Cretaceous Alinga Formation and Beedagong Claystone, Western Australia. *Palaeontology*, 39(4): 813-849.

Siversson M., Cook T.D., Cederström P. & Ryan H.E. (2016) - Early Campanian (Late Cretaceous) squatiniform and synechodontiform selachians from the Åsen locality, Kristianstad Basin, Sweden. *Geological Society, London, Special Publications*, 434: 251-275.

Siversson M., Cook T.D., Ryan H.E., Watkins D.K., Tatarnic N.J., Downes P.J. & Newbrey M.G. (2019) - Anacoracid sharks and calcareous nannofossil stratigraphy of the mid-Cretaceous "upper" Gearle Siltstone and Haycock Marl in the lower Murchison River area, Western Australia. *Alcheringa*, 43(1): 85-113.

Siversson M., Lindgren J., Newbrey M.G., Cederström P. & Cook T.D. (2015) - Cenomanian-Campanian (Late Cretaceous) mid-palaeolatitude sharks of *Cretalamna appendiculata* type. *Acta palaeontologica Polonica*, 60(2): 339-384.

Sokolskyi T. & Guinot G. (2021) - Elasmobranch (Chondrichthyes) assemblages from the Albian (Lower Cretaceous) of Ukraine. *Cretaceous Research*, 117: 104603. https://doi.org/10.1016/j.cretres.2020.104603

Sørensen A.M., Surlyk F. & Lindgren J. (2013) - Food resources and habitat selection of a diverse vertebrate fauna from the upper lower Campanian of the Kristianstad Basin, southern Sweden. *Cretaceous Research*, 42: 85-92.

Stahl B.J. (1999) - Handbook of Paleoichthyology, Vol. 4: Chondrichthyes III. Holocephali. Verlag Dr. Friedrich Pfeil, München, 164 pp.

Stahl B.J. & Parris D.C. (2004) - The complete dentition of Edaphodon mirificus (Chondrichthyes: Holocephali) from a single individual. *Journal of Paleontology,* 78(2): 388-392.

Stewart A. (1898a) - A contribution to the knowledge of the ichthyic fauna of the Kansas Cretaceous. *Kansas Univer-*

sity Quarterly, 7(1): 22-29.

Stewart A. (1898b) - Some notes on the genus *Saurodon* and allied species. *Kansas University Quarterly*, 7(4): 177-186.

Stewart A. (1899) - *Pachyrhizodus minimus*, a new species of fish from the Cretaceous of Kansas. *Kansas University Quarterly* 8: 37-38.

Stewart A. (1900) - Teleosts of the Upper Cretaceous. *The University Geological Survey of Kansas, Topeka*, 4: 257-403.

Stewart J.D. (1999) - A new genus of Saurodontidae (Teleostei: Ichthyodectiformes) from Upper Cretaceous rocks of the Western Interior of North America. In Arratia G. & Schultze H-P. (Eds) - Mesozoic Fishes 2 - Systematics and Fossil Record 335-360. Verlag Dr. Friedrich Pfeil, München.

Stewart J.D. & Hackel M. (2005) - A review of *Pachyrhizodus* species from the USA, with comments on those of other countries. In: Poyato-Ariza F.J. (Ed.) - Fourth international meeting on Mesozoic fishes - Systematics, Homology, and Nomenclature, extended abstracts: 235-238, Madrid.

Storms R. (1894) - Troisième note sur les poissons du terrain rupélien. *Bulletin de la Société Belge de Géologié, de Paléontologie et d'Hydrologie*, 8: 67-82.

Taverne L. (1989) - *Crossognathus* Pictet, 1858 du Cretace Inferieur de l'Europe et systematique, paleozoogeographie etbiologie des Crossognathiformes nov. ord. (Teleosteens) du Cretace et du Tertiaire. *Palaeontographica (A)*, 207: 79-105.

Thurmond J.T. & Jones D.E. (1981) - Fossil vertebrates of Alabama. University of Alabama Press, Tuscaloosa, 244 pp.

Underwood C.J. & Cumbaa S.L. (2010) - Chondrichthyans from a Cenomanian (Late Cretaceous) bonebed, Saskatchewan, Canada. *Palaeontology*, 53(4): 903-944.

van de Geyn W. (1937) - Les élasmobranches du Crétacé marin du Limbourg Hollandais. *Natuurhistorisch Maandblad Maestricht*, 26: 16-21, 28-33, 42-53, 56-60, 66-69.

Vasilenko V.P. (1950) - Foraminifera of the Paleocene of the central part of the Dniepr-Donets Basin. Microfauna of the USSR. *Proceedings of the Oil Research Geological Institute*, 4: 177-224.

Vullo R. (2005) - Selachians from the type Campanian area (Late Cretaceous), Charentes, western France. *Cretaceous Research*, 26: 1-24.

Vullo R. & Courville P. (2014) - Fish remains (Elasmobranchii, Actinopterygii) from the Late Cretaceous of the Benue Trough, Nigeria. *Journal of African Earth Sciences*, 97: 194-206.

Wanner J. (1902) - Die fauna der obersten weissen Kreide der libyschen Wüste. *Palaeontographica*, 30(2): 91-152.

Ward D.J. (2010) - Sharks and rays. In: Young J. R., Gale A. S., Knight R. I. & Smith A. B. (Eds) - Field Guide to Fossils Number 12, Fossils of the Gault Clay, London: 275-299.

Wiese F., Čech S., Ekrt B., Košťákd M., Mazuch M. & Voigt S. (2004) - The Upper Turonian of the Bohemian Cretaceous Basin (Czech Republic) exemplified by the Úpohlavy working quarry: integrated stratigraphy and palaeoceanography of a gateway to the Tethys. *Cretaceous Research*, 25(3): 329-352.

Welton B.J. & Alderson J.M. (1981) - A preliminary note on the Late Cretaceous sharks of the Chatworth Formation at Dayton Canyon, Simi Hills, Los Angeles County, California. In: Squires R.L. & Colburn I.P. (Eds) - Simi Hills Cretaceous Turbidites, Southern California, Pacific Section: 53-57. Society of Economic Paleontologists and Mineralogists, Fall Field Trip Guidebook.

Whitley G.P. (1939) - Taxonomic notes on sharks and rays. *Australian Zoologist*, 9(3): 227-262.

Wiffen J. (1983) - The first record of *Pachyrhizodus caninus* Cope (Order Clupeiformes) from the Late Cretaceous of New Zealand. *New Zealand Journal of Geology and Geophysics*, 26(1): 109-119.

Williams S.C. (2006) - Late Cretaceous selachian biostratigraphy in New Mexico. Unpublished M.S. thesis, University of New Mexico, Albuquerque, 117 pp.

Woodward A.S. (1888) - On the Cretaceous selachian genus *Synechodus. Geological Magazine*, decade 3(5): 496-499.

Woodward A.S. (1901) - Catalogue of fossil fishes in the British Museum (Natural History), Part IV. Trustees of the British Museum (Natural History), London, 636 pp.

Woodward A.S. (1911) - The fossil fishes of the English Chalk. Part VI. *Monograph of the Palaeontographical Society London*, 64: 185-224.

Yarkov A.A. & Nessov L.A. (2000) - New finds of remains of hesperonithiform birds Hesperonithiformes in the Volgograd region. *Russkij ornitologicheskij zhurnal*, 94: 3-12 [in Russian].

Zelenkov N.V., Panteleyev A.V. & Yarkov A.A. (2017) - New finds of hesperornithids in the European Russia, with comments on the systematics of Eurasian Hesperornithidae. *Paleontological Journal*, 51(5): 547-555.

Zhelezko V.I. (1977) - Stratigraphy and fossil sharks of the Upper Cretaceous deposits of West Kazakhstan. *Rotaprint Geotekhnika*, 1977: 1-31 [in Russian].

Zhelezko V.I. (1987) - Les sélaciens du Santonien et du Campanien inférieur de l'Oural méridional et des Mugodzhars. *Acad. Nauk CCCP*, 1987: 117-130 [in Russian].

Zhelezko V.I. (1990) - (Pisces (Selachii)). Upper Cretaceous deposits of southern post-Urals (region of the upper Tobol River. *Uralian Branch of the Academy of Sciences of USSR, Sverdlovsk*, 1990: 122-133 [in Russian].

Zverkov N.G., Averianov A.O. & Popov E.V. (2017) - Basicranium of an elasmosaurid plesiosaur from the Campanian of European Russia, *Alcheringa: An Australasian Journal of Palaeontology*, 42(4): 528-542.