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...
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-Karatau 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 chondrichthyan species 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 chimaerid taxa from Turonian to Santonian deposits near Saratov city. Averianov & Popov (1995) later named a new species of chimaerid, *Amylodon karamysh*, from Cenomanian 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 chimaerids from the region (which included Shirokyi Karamysh and several localities near Saratov city), and they reported several localities that yielded Cenomanian 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 *Pseudomegalachasma 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 Cretaceous Polunino-2 locality in the Volgograd Oblast, and later Yarkov & Nesov (2000) reported chondrichthyans from the Cenomanian Rykhovo 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., *Elasmopus* 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 *Arbacia capensis*, *Cretalamna appendiculata*, *Eotriatolamia* sp., *Heterodontus* sp., *Pseudoraidas 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.
**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 *Belemnitella mammillata* (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* (Böhm, 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 (*B. mucronata alpha* and *B. mammillata* regional mollusk zones), and strata above the phosphorite are of upper Campanian age (*Hoplitoplacenticeras coesfeldiense*/*B. mucronata* Regional Zone) (Olferiev & Alekseev 2005).
Marine fishes from the Upper Cretaceous of Rybushka Formation, Russia

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 silicate, 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, holocelphants, 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 phosphatic 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 multiple 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 SRT01881 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 (MOM) 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 18-55 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 CS2017 software as part of the production of the figures presented herein. Higher taxonomic rankings follow that of Nelson et al. (2016), and holocelphant tooth plate terminology follows Stahl (1999) and Cecinurri & Ebersole (2014, 2015). The synonyms provided are not intended to be comprehensive and instead reflect taxonomic changes to the identified species.

Systematic Palaeontology

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

Ischyodus bifurcatus Case, 1978a

Material: MMO 1 № 7768-12 (right mandibular), MMO 1 № 7768-13 (left mandibular), MMO 1 № 9273-64 (left mandibular), MNO 1 № 9273-65 (right palatine), MNO 1 № 9273-66 (left palatine), MNO 1 № 9273-67 (right mandibular), MNO 1 № 9273-70 (right mandibular), MNO 1 № 9273-71 (right mandibular), MNO 1 № 9644-8 (left mandibular, Fig. 3A-B), MNO 1 № 9644-9 (right palatine), MNO 1 № 9644-10 (right palatine), MNO 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. rayhassi 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 holoccephalan 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 curved 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-
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 **SELACHI** 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* Siversson, 1989, and *S. turneri* Case, 1987. In addition to these taxa, Cappetta (2012; fig. 306) figured numerous unspeciated *Synechodus* teeth from upper
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 Rybuska 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, monogenetic 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 Rybuska 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)

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 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. bianarticulata* (Wanner, 1902) and *Serratolamna* moroc-
can a (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 of *C. borealis* in the Rybushka Formation.

**Cretalamna cf. C. sarcoportheta** Siversson et al., 2015

**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 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 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. 5G).

**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 Cumba, 2010

**Genus Archaeolamna** Siversson, 1992

**Archaeolamna kop Bingoensis** (Davis, 1890)

**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 (posteriorlateral tooth, robust morphology, Fig. R-S), 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 in our sample, 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 subrecta* (Zhelezko, 1990) *A. arcosa 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 comissure (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* (Gemmelaro, 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**  
**Genus** *Pseudocorax* Priem, 1897

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

**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 Maastrichian 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 (posterior lateral 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) nor 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 labial 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 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 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
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.
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** Taverner, 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 ММО 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 ММО 1 № 10420-54; and 5) on specimen ММО 1 № 10420-55, a tooth on the 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 speculate 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 ММО 1 № 10420-54 and ММО 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 foramina 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. pamphagus as a junior synonym of S. lanciformis, 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 TELECEPHALA 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...
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. 769.

**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. bursaunc* 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 much 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. bursaunc*, *E. dirus*, and *E. libycus*. Specimen UPM 3004 appears to differ from *E. bursaunc* 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. bursaunc* (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. bursaunc* 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](image-url)
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. bursauci*, *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), MNO 1 № 10420-58 (concretion with dentary, premaxilla, and cranial fragments, Fig. 9H-J), UPM 2823 (symphyseal portion of dentary), UPM 2953 (symphyseal portion of dentary), UPM 2917-3017 (premaxilla fragment), UPM 3007 (fragmentary dermopalatine, Fig. 9K), UPM 3012 (premaxilla fragment), UPM 2905 (dentary fragment), UPM 2927 (symphyseal portion of dentary), UPM 2903 (symphyseal portion of dentary), UPM 2904 (symphyseal portion of dentary), UPM 2823 (symphyseal portion of dentary), UPM 2903 (symphyseal portion of dentary), UPM 2904 (symphyseal portion of dentary), UPM 3015 (premaxilla fragment), UPM 3016 (premaxilla fragment), UPM 3017 (premaxilla fragment).

**Description.** Many of the dienty 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 dienty 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 dienty tooth (with more generally occurring on the anterior side). The labial face of the dentary is ornamented with thick ridges that extend antero-posteriorly 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 dientary, 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 antero-posteriorly oriented ridges and has a conspicuous groove that extends antero-posteriorly just below the tooth row. The lingual face of all the dienty 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 antero-posterior 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 antero-posteriorly elongated and dorsi-ventrally 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 antero-posteriorly 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 dienty 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 MNO 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 MNO 1 № 10420-58 represents *E. petrosus* and the remaining, “non-beaded,” dienty 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 antero-posterior length) and almost 90˚ downward angle of the tooth base is reminiscent of dermopalatine
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 specified. 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 Chimaeroidae, 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 Shirokky Karamysh locality within the Saratov Oblast, and by Yarkov & Nesov (2000) from the Campanian Rykhkovo locality in the Volograd 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 (Johnston-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 (Casier 1978a) and Poland (Popov & Machalski 2014).

Averianov & Popov (1995) named *Amylodon karamysh* based on a specimen from the Campanian Shirokky 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 in- dent. 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 chimaeroid species 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), *Callorhinus* (Nesov & Averianov 1996; Olferiev & Alekseev 2005), *Edaphodon* (Glickman 1953; Nesov & Averianov 1996; Popov & Lapkin 2000; Ol- feriev & 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* (Nesov, 1986), *Edaphodon sedgwickii* (Agassiz, 1838), *I. bifurcatus*, and *Lebedidon oskolensis* Nesov & Averianov, 1996 have been identified specifically from Campanian deposits within the Saratov Oblast (Averianov & Glickman 1994; Nesov & Averianov 1996; Aver- ianov & 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 Ry- bushka 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 forma- tions (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 hassel* from Campanian deposits in the area (Averianov & Popov 2014; Grigoriev et al. 2015) and *S. muelleri* (Sintsov 1872; Seltzer & Ivanov 2010) and *Squatina* sp. (Glick- man 1953, 1957, 1958, 1980; Popov & Lapkin 2000) from older Cenomanian deposits. *Squatina* teeth and those of *Cederstroemia* are morphologi-
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Marine fishes from the Upper Cretaceous of Rybushka Formation, Russia (Guinot et al. 2013), and the USA (Siverson 1995). 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 (Sorensen 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*, *Archeolamna*, *Squalicorax*, *Pseudocorax*, and *Eostrotalmonia*. Two *Cretalamna* species, *Cretalamna cf. C. borealis* and *C. cf. C. saroportbatha*, 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 saroportbatha* 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. saroportbatha* 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* 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. saroportbatha*. Olferiev & Alekseev (2005) reported additional Santonian and Campanian *C. appendiculata* specimens from the Mozhzhvelovozhakhnya 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 Berevskaya 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.

*Archeolamna 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 (Meglé 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 Mozhzhevelovrazhnaya 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 (Elliick & 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 (Radwidi 2014), Syria (Bardet et al. 2000), Tunisia (Arambourg 1952), and Alabama (Ikejiri et al. 2013), Arkansas (Becker et al. 2006), California (Weltan & Alderson 1981), Delaware (Lauginger 1988), Georgia (Case & Schwimmer 1988), Kansas (Bice & Shimbata 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, the only other occurrence of *E. subulata* 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 Squatirhina 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. Unspecified 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 (Crossopterygii, Pachyrhizodontidae), Sauracodphalus (Ichthyodectiformes, Saurodontidae), Paralbula (Aulopiformes, Phyllopterygidae), and Enchodus (Aulopiformes, Enchodontidae). Two dentary fragments were identified as Pachyrhizodus sp., and although these are not well enough preserved to be specified, 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-
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; Oroumova et al. 2016). The species has also been reported from Nigeria (Vul-lol & Courville 2014), Patagonia (Bogan & Agnolin 2010), Peru (Gourie-Cavalli et al. 2021), and Sweden (Bazzi et al. 2015), but Gourie-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 palaeobiogeographical 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 segediti* or Eurasia (*Amylodon karamysgh*), 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 palaeofoonas 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 (chondrichthians 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 Cre-talamna saroportheta, Enchodus cf. E. dirus, E. cf. E. gladiolus, E. petrobus, Eostratolamia segedini, E. venusta, Pachyrhizodus sp. Sanrocephalus lanciformis, and Squa-lidorax Morphology 1. In addition, these taxa, along with Cederstromia 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.

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