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To cite this version:
Guillaume Guinot, Tymofii Sokolskyi. Elasmobranch (Chondrichthyes) assemblages from the Albian (Lower Cretaceous) of Ukraine. Cretaceous Research, Elsevier, 2021, 117, pp.104603. 10.1016/j.cretres.2020.104603. hal-03406063

HAL Id: hal-03406063
https://hal.archives-ouvertes.fr/hal-03406063
Submitted on 21 Sep 2022

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Elasmobranch (Chondrichthyes) assemblages from the Albian (Lower Cretaceous) of Ukraine

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Abstract

Sampling of six horizons of quartz-glauconite sands in Kaniv dislocations in Ukraine yielded more than three thousand vertebrate specimens, including elasmobranch teeth, chimaera dental plates, actinopterygian and sauropsid teeth and bones. Our study represents the first illustrated and detailed description of elasmobranch teeth from Ukrainian Albian deposits since Rogovich (1861), whose specimens were still preserved in the collections of the Kiev National Natural History Museum of National Academy of Sciences of Ukraine. Twenty-three elasmobranch species belonging to eight orders were identified in our samplings and in some of Rogovich’s material. This paper provides new data on the systematics of Cretaceous elasmobranchs and assesses the taxonomic status of Rogovich’s species. Sampled assemblages include hybodonts, synechodontiforms, hexanchiforms, squaliforms, squatiniforms, orectolobiforms, heterodontiforms and lamniforms. The latter dominate the assemblages, both in terms of species and number of specimens with small odontaspidiid species, early pseudoscapanorhynchids and archaeolamnids as well as large carnivorous sharks *Cretoxyrhina* and *Cretolamna*. Most importantly, *Paraisurus macrorhizus* and *Cretoxyrhina vraconensis* findings indicate a Late Albian age for the sampled deposits, which were so far considered Albian-Cenomanian.

Keywords. Vraconian, Albian, Ukraine, sharks, selachians
1. Introduction

Elasmobranchs (sharks, skates, rays and the extinct hybodonts) are mostly represented in the fossil record by dental remains (Glikman, 1980; Cappetta, 2012). Although known since the Permian (Ivanov, 2005), neoselachians (shark, skates and rays) remained relatively inconspicuous in marine ecosystems until the Jurassic when they experienced a series of radiations (Guinot and Cavin, 2016). The Lower Cretaceous is another key period in the neoselachian evolutionary history and comprises the radiation of different groups including batoids, Carcharhiniformes and especially Lamniformes (Condamine et al. 2019), a group that comprises today most iconic shark species occupying specialized ecological niches. Lamniforms reached a high diversity in the Albian, both in terms of taxic richness and tooth morphologies (Guinot and Cavin, 2016). Despite the importance of this period in the understanding of elasmobranch evolution and diversity, data on Albian elasmobranch faunas is relatively scarce. Elasmobranch assemblages of this age are known from several locations in the world: Lithuania (Dalinkevičius, 1935; Mertiniene, 1975), Western Australia (Siverson, 1997; Siversson et al., 2018), Gault clay (Ward, 2010) and localities in of North-East England (Underwood and Mitchell, 1999), North-East France (Biddle, 1993), Russia and Kazakhstan (Glikman, 1980; Glikman and Averianov, 1998), Texas, USA (Welton and Farish, 1993; Cappetta and Case, 1999; Siversson et al., 2007) and Poland (Siversson and Machalski, 2017).

Here we describe diverse mid-Cretaceous elasmobranch assemblages from the Kaniv National Reserve in central Ukraine, which add to the knowledge on Cretaceous elasmobranch taxonomy, diversity and geographical distribution. Strata yielding the fossil assemblages studied in this work belong to the Burim formation, a local stratigraphic interval spanning the Late Albian-Early Cenomanian interval, starting with Mortoniceras inflatum Zone (Krochak et al., 2016). This study represents the first description of vertebrate remains from this formation since Rogovich (1861), whose original elasmobranch specimens and corresponding species are revised.
2. Geographical and Geological settings

The sampled horizons are located in the Kaniv Natural Reserve near the city of Kaniv, in the Cherkasy Province, central Ukraine (Fig. 1). Cretaceous sections cropping out in the study area are part of Kaniv dislocations, which refer to the effects of tectonics (glaciogenic dislocation) over the Mesozoic successions (Krochak et al., 2016). The Kaniv dislocations belong to the Burim formation and are commonly exposed in many ravines on the territory of Kaniv Natural Reserve lying on top of the Callovian clays (Krochak et al., 2016). The Burim formation was previously considered Albian in age (Krochak et al., 2016), but more recent macrofaunal, foraminiferal and palynological studies suggested an upper Albian-lower Cenomanian age (Ivannik et al., 2014). The lower part of the formation (approximately 20 m) is considered Upper Albian in age and is characterized by the presence of the ammonite species *Mortoniceras inflatum*, which indicates an ammonite zone right before the ‘Vraconian’ according to the stratigraphical data from Central European Basin, which is close to central Ukraine (Marcinowski and Radwanski, 1983; Siversson and Machalski, 2017). The lower part of the formation consists of quartz-glauconite sands with silica cemented sandstone inclusions. Top 40-60 m include greenish-gray quartz-glauconite sands, carbonated sands, silica cemented sandstones and phosphorite concretions. These layers yielded fossil remains of various foraminifera (e.g., *Lingulogavelinella praeformosa, Thalmanninella appenninica*) that suggest a late Albian to early Cenomanian age, including the ‘Vraconian’ stage (Krochak et al., 2016). This upper part of the Burim formation comprises thin (up to 15 cm) layers of coarse-grained quartz-glauconite sands that contain abundant vertebrate remains, such as elasmobranch, chimaeroids, actinopterygian and sauropsid teeth and bones, as well as various invertebrates including broken bivalve shells, gastropods and crustaceans. These layers were likely formed during transgression-regression events with subsequent redeposition from other strata being considered unlikely due to scarcity of remains in the intermediate sequences (Popova et al., 2015). Popova et al. (2015) also considered the possibility of the upper layers being Early Cenomanian in age. However, this hypothesis was based on incorrect identifications of several elasmobranch taxa. Some of the upper
layers encompass numerous phosphorite concretions that also yielded vertebrate fossils.

Burim formation deposits yielding vertebrate remains were found in three ravines on the territory of Kaniv natural reserve (Fig. 1): Pekarskyi (coordinates: 49°42.568’N 31°32.558’E), Melanchyn potik (49°43.325’N 31°30.788’E) and Kholodnyi (49°43.001’N 31°32.381’E). Two layers (E and F) of quartz-glaucnite sands were sampled in Pekarskyi ravine. Layer E in Pekarskyi ravine is correlated to layer E in Melanchyn potik ravine. Brachiopods of the genus *Lingula* and bivalves *Exogyra* are very common there. Typical feature of *Exogyra* from this layer is very thick shells, compared to *Exogyra* from the other layers. This might be due to differences in water depth between the layers, since paleogeographic conditions in this territory were unstable due to frequent transgression and regression events and proximity of a large landmass (Ischenko and Yakushin, 2008). This layer lies on silica-cemented sandstones. Vertebrate remains are relatively rare. Layer F in Pekarskyi ravine is characterized by pebbles, naturally rounded fossils and relatively common elasmobranch teeth. Five layers of quartz-glaucnite sands were found in Melanchyn potik, only four of them yielded fossil vertebrate remains. Three of them (A, B and C) are rich in elasmobranch teeth, while layer E is identical to layer E in Pekarskyi ravine. Apart from elasmobranchs, actinopterygian (*Protosphyraena*, Icthyodectidae indet., *Pachyrhizodus*, Aspidorhynchidae indet., *Enchodus*, Pycnodontiformes indet., *Hadrodus*) and sauropsid (ichthyosaurs, plesiosaurs and turtles) teeth and/or bones can be occasionally found. The invertebrate fauna of these layers includes thin-shelled morphs of *Exogyra* bivalves, gastropods of several genera including Patellidae indet., crustaceans, extremely rare cephalopods (a fragment of *Mortoniceras* ammonite and a fragment of unidentified belemnite rostrum) and, unlike layer E, no *Lingula* brachiopods. Only one layer of elasmobranch tooth-bearing sands (layer A) was found in Kholodnyi ravine. Like layers from Melanchyn potik and Pekarskyi ravines, Kholodnyi ravine sands also lay on sandstones, which may contain conifer and occasional vertebrate remains (two shark teeth and several osteichthyan bones were found there). Though, unlike in layer E, no brachiopods had been found in this layer.
3. **Materials and methods**

Fossil elasmobranch teeth were obtained by bulk sampling and sieving using water and, on some occasions, dry sediment using sieve with 1 mm mesh size. A total of 3,268 elasmobranch teeth were recovered including 727 teeth from layer A of Melanchyn potik and Kholodnyi ravines; 126 teeth from layer B of Melanchyn potik; 2264 teeth from layer C in Melanchyn potik; no teeth were found in layer D of Melanchyn potik; 40 teeth from layer E of Melanchyn potik and Pekarskyi ravine and 111 teeth were collected in layer F of Pekarskyi ravine. All studied specimens are housed in the Kiev National Natural History Museum of National Academy of Sciences of Ukraine, Geology department (shorten here to ‘Kiev Museum’) and are numbered NNPM2588-1 to NNPM2588-61. In addition, specimens illustrated by Rogovich (1861) are housed in the collection of the same institution.

4. **Systematic Palaeontology**

Higher level taxonomy and dental terminology largely follow those of Cappetta (2012).

- **Class** Chondrichthyes Huxley, 1880
- **Subclass** Elasmobranchii Bonaparte, 1838
- **Cohort** Euselachii Hay, 1902
- **Superfamily** Hybodontoidea Owen, 1846
- **Family** Hybodontidae Owen, 1846
- **Genus** *Hybodus* Agassiz, 1837

*Hybodus bidentatus* Rogovich, 1861

Fig. 2A-D

1861 *Hybodus bidentatus* Rogovich, p. 23, pl. 3, fig. 13.

**Material.** One crown fragment (NNPM 2588-1) from layer C of Melanchyn potik and Rogovich’s type specimen (NNPM 391-14).

**Description.** Rogovich’s type specimen (NNPM 391-14; Fig. 2A-B) is an incomplete crown lacking the distal and mesial edges of the heels. The crown is robust, slightly inclined distally and
lingually. Both lingual and labial faces are strongly convex. Very fine cutting edges separate the labial and lingual faces and run continuously from the apex of the main cusp to the lateral heels. The heels are moderately high and mesio-distally elongate with at least one distal cusplet that is well separated from the main cusp by a large concavity. Short striations are present near the base on the lingual face of the main cusp and cusplets. The labial face bears several long folds that cover up to 2/3 of the crown’s height. The specimen recovered from Melanchyn potik (NNPM 2588-1; Fig. 2C-D) is an incomplete main cusp with similar shape and ornament to the type specimen. Both specimens are relatively small with main cusps not exceeding 5 mm.

Remarks. Although incomplete, Rogovich’s type and only originally illustrated specimen agrees with the morphology of *Hybodus* species. Albian *Hybodus* species include *H. molimbaensis* Casier, 1961 from the Aptian-Albian of Democratic Republic of Congo and *H. complanatus* Owen, 1869 from the Upper Greensand of England, but both species are based on dorsal spines (*H. complanatus* specimen was not illustrated), which makes comparison with Rogovich’s species impossible. Teeth of the latter can be differentiated from *Hybodus* material illustrated by Sweetman et al. (2014) from the Barremian of the Isle of Wight by their less marked and less numerous labial and lingual ornament as well as by its more gracile aspect with more elongate main cusp. Other mid-Cretaceous *Hybodus* species include the Cenomanian *H. eichwaldi* (Kiprijanoff, 1853), based on a dorsal spine.

**Hybodontoidea indet.**

Fig. 2E-F

Material. Five crowns (including NNPM 2588-2) from layer F of Pekarskyi ravine.

Description. Teeth of this species are less than 5 mm tall. The basal region of the labial crown face is strongly striated, whereas the lingual face only displays a few fine vertical folds. The crown is biconvex with the cutting edge situated slightly labially. Only two of the crowns found are slightly distally inclined, others are nearly straight.

Remarks. The crowns recovered display characters of *Merisodonoides* teeth including weak lingual and stronger labial folds, marked lingual curvature of main cusp and lingually positioned cutting
edges (Underwood and Cumbaa, 2010). However, lack of complete specimens precludes accurate
identification of this material.

Order **Synechodontiformes** Duffin and Ward, 1993

Family **Paleospinacidae** Regan, 1906

Genus **Synechodus** Woodward, 1888

*Synechodus kessleri* (Rogovich, 1861) comb. nov.

Fig. 2G-L

1861 *Hybodus kessleri* Rogovich, p. 21, pl. 3, figs 3-5.


?1935 *Synechodus nitidus* Woodward; Dalinkevičius, p. 15, pl. 2, figs 40, 43-49 *non* figs 39, 41-42.


**Material.** Twelve complete and incomplete teeth (including NNPM 2588-3 and NNPM 2588-4) from layer C of Melanchyn potik ravine. Additional specimen: Rogovich (1861)’s type specimen NNPM 391-10 (lectotype).

**Description.** All specimens uncovered are under 1 cm high. These teeth have thin, elongate and strongly lingually inclined main cusp and cusplets. Generally, there are four to five lateral cusplets connected to the crown by a thin, sometimes striated enamel band. Cusplets are usually distributed asymmetrically with the distal heel bearing one to two, while the mesial heel can bear two to four, such as in NNPM 2588-3 and NNPM 2588-4 (Fig. 2, I-J, K-L), while Rogovich type specimen NNPM 391-10 (Fig. 2, G-H) is more symmetrical. Labial crown base ornamentation consists of weak parallel vertical folds. Cusplets may reach up to about 1/3-1/4 of the crown height. The root displays a marked and wide lingual protuberance as well as a wide and flat basal face. Lateroposterior teeth have a short and robust crown, with almost conical and markedly distally inclined main cusp, and short ridges near the base of the labial crown face.

**Remarks.** The systematics of Albian *Synechodus* species is poorly understood despite the presence
of several partial articulated skeletal remains from France and England (see Mollen and Hovestadt, 2018 for a review). Currently, seven nominal *Synechodus* species are known from the Albian-Cenomanian interval. *Synechodus dubrisiensis* (Mackie, 1863) was described from the Zig Zag Chalk Formation (‘Grey Chalk’, *Holaster subglobosus* zone, Cenomanian) of Dover (Kent, England); *S. tenuis* Woodward, 1889 is based on a single illustrated incomplete tooth from the Lower Greensand (Aptian-lower Albian) of Maidstone (Kent); *S. nitidus* Woodward, 1911 was erected based on a chondrocranium from the *Holaster subglobosus* zone, Cenomanian of Snodland (Kent). Other species include *Hybodus bronni* Reuss, 1846 and *Hybodus dispar* Reuss, 1846 both based on isolated teeth from the Cenomanian (Lower Plänerkalk) of Weisskirchlitz (= Novosedlice, Czech Republic) as well as *H. subulatus* Rogovich, 1861 and *H. kessleri* Rogovich, 1861 both from the mid-Cretaceous of Ukraine. Most discussions have focused on the taxonomic status and validity of *S. dubrisiensis*, *S. nitidus* and *S. tenuis*. The latter has been regarded as a senior synonym of *S. nitidus* (Batchelor and Ward, 1990; Biddle, 1993), while other hypotheses either consider *S. nitidus* junior synonym of *S. dubrisiensis* (Mollen and Hovestadt, 2018), both *S. nitidus* and *S. tenuis* as junior synonyms of *S. dubrisiensis* (Ward, 2010) or all three species considered valid (Siversson et al. 2017). These discrepancies are mainly due to the preservation of the specimens available for these species. *Synechodus dubrisiensis* is probably the species to which the largest number of articulated specimens have been referred, including articulated mandibular arches (of which, the holotype) some including hyoid arches (Woodward, 1886) or postcranial elements (Woodward 1886), as well as a braincase (Maisey, 1985) and associated tooth sets (Woodward, 1888). In contrast, the holotype of *S. tenuis* is based on a single tooth (Woodward, 1889) and the holotype of *S. nitidus* [formerly attributed to *S. dubrisiensis* by Woodward (1889)] is represented by an articulated chondrocranium with associated teeth (Woodward, 1911). The main issue is the understanding of the intraspecific variability in tooth morphology for these three species. An articulated *Synechodus* specimen was recently described from the Albian Gault Clay of the Boulonnais, northern France (Mollen and Hovestadt, 2018). This specimen was reported to display *S. dubrisiensis*-like latero-posterior teeth with strong reticulate labial ornament but also weakly
ornamented (vertical labial folds) anterior teeth that were so far considered representative of *S. nitidus*. This heterodonty was considered as a clue in favor of a synonymy between *S. nitidus* and *S. durbisiensis* (Mollen and Hovestadt, 2018), which would respectively represent anterior and latero-posterior morphs of the same species. Nevertheless, the species-level assignment of the Boulonnais specimen is still unclear and it is uncertain whether *S. dubrisiensis* also presents this heterodonty. In addition, differentiating teeth from upper and lower jaws in articulated specimens with associated teeth is sometimes made difficult by the mixing of teeth from both jaws. Teeth of an articulated tooth set (BMB 008523) illustrated by Woodward (1888, 1889, 1898, 1911) and studied by one of us (GG) displays strong reticulate ornament on all files (from parasymphyseals to posteriors). However, it is unclear whether the articulated tooth set belongs to upper or lower jaws (see Mollen and Hovestadt, 2018). Hence, the hypothesis of a monognathic variation in labial ornament of *S. dubrisiensis* teeth remains to be confirmed and, if present, would likely be present in upper or lower jaws only and/or during ontogeny. *Synechodus tenuis* was erected on the basis of a single incomplete tooth (Woodward, 1889: pl. 11, fig. 21) of which the sole illustration in labial view has long hampered precise understanding of the morphology and ornament of the holotype (PV OR 9297). This specimen was illustrated by Batchelor and Duffin (in press: Fig. 1G-H) and by Bernard and Smith (2018) who also illustrated two additional specimens referred as paratypes (PV OR 9297a and PV OR 9297b). Ward (2010) indicated that *tenuis*-like (and *nitidus*-like) teeth are present in specimen PV OR 41675 (Woodward, 1886; Maisey et al. 2004) referred to *S. dubrisiensis*, but this view has been challenged by Siversson and Machalski (2017). Based on available specimens, the morphology of the teeth of the type series of *S. tenuis* seems to depart from the variation so far observed in teeth of type specimens of *S. nitidus* and *S. durbisiensis* and might be better considered a separate species until revision of the available specimens.

Only one of the syntype specimens described by Rogovich (1861) as *Hybodus kessleri* was recovered in the collections of the Kiev Museum (Fig. 2G-H) and corresponds (original labels preserved) to the specimen figured in Rogovich (1861: pl. 3, fig. 4). Hence, we designate this
specimen (NNPM 391-10) as the lectotype of *Hybodus kessleri* following Article 74 of the ICZN (1999). This specimen displays lingually-inclined and slender main cusp and cusplets as well as nearly smooth labial crown face (only scarce, fine and short ridges at the base of the two mesial-most cusplets). This morphology is very similar to that of the anterior tooth of the holotype of *S. nitidus* illustrated by Woodward (1912: pl. 46, fig. 3a) and Batchelor and Duffin (in press: Fig. 2F).

The latter authors also noted that some other teeth (from more lateral jaw positions) may also bear coarse striations, which occasionally bifurcate basally (but not reticulated) and terminate two-thirds of the way up the central cusp. This type of ornament is also present in lateral teeth reported here from Kaniv, which are also referred to *S. kessleri* (Fig. 2I-L). The strong degree of similarity between the Kaniv specimens and the available specimens of *S. nitidus* might suggest synonymy (the latter would represent a junior synonym of *S. kessleri*). However, considering the confusion surrounding the validity of the species described from the mid-Cretaceous of England, this decision is tentative pending revision of dentition of the available *Synechodus* specimens.

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**Synechodus subulatus** (Rogovich, 1861 *non* Leriche, 1951) comb. nov.

Fig. 2M-R

1861 *Hybodus subulatus* Rogovich, p. 20, pl. 3, figs 6-11.

?1889 *Synechodus tenuis* Woodward, p. 329, pl. 11, fig. 21

1935 *Synechodus nitidus* Woodward; Dalinkevičius, p. 15, pl. 2, figs ?39, 41-42 *non* figs 40, 43-49.

?1957 *Synechodus dispar* (Reuss); Glikman, p. 111, pl. 1, figs 1-5.

1964 *Synechodus dispar* (Reuss); Glikman, p. 20, pl. 5, figs 5-6.

1980 *Synechodus dispar* (Reuss); Glikman, pl. 15, figs 1-3 *non* figs 4-5.

**Material.** 91 complete and incomplete teeth including fragmented crowns: 2 from layer F of Pekarskyi ravine; 3 from layer A of Melanchyn potik ravine; 3 from layer B of Melanchyn potik ravine; 61 from layer C of Melanchyn potik ravine; 2 from layer E of Melanchyn potik ravine; 20 from Kholodnyi ravine. All figured specimens come from layer C of Melanchyn potik (NNPM
2588-5, NNPM 2588-7), except NNPM 2588-6 that comes from layer B.

**Description.** Teeth are mostly small - less than 1 cm in height - however, there are some exceptions as described below. Two morphs can be differentiated. Teeth of the first morph (Fig. 2M-P) have no ornamentation on the labial face and display poorly pronounced short vertical ridges on the lingual face. These teeth are sigmoid in lateral view with a labial crown bulge as well as many short and poorly differentiated cusplets. Some specimens of this morph are extraordinarily large and massive (several specimens are almost 15 mm wide) and have smaller lateral cusplets compared to the other morphotypes. The labial crown bulge is hyper-developed especially below the heels. Teeth of the second morph (Fig. 2Q-R) are almost symmetrical and display a very weak sigmoid profile. These teeth are relatively labio-lingually compressed and generally no more than 7 mm high. The crown bears no labial enamel folds but weak vertical ridges on the lingual face and has three to four elongate cusplets. Cusplets are moderately wide and basally united with each other on each side of the tooth that reach up to ¼ of the crown height. The root is pseudopolyaulacorhyze, as in the other morphotype.

**Remarks.** Although Rogovich’s specimens of *Hybodus subulatus* could not be found in the collections of the Kiev Museum, the size and morphological variation observed in the specimens reported here comply with those of the specimens originating from the same area illustrated in Rogovich (1861) and are thus referred to *S. subulatus* comb. nov. Although none of the syntypes of *S. subulatus* were found, but we don’t consider necessary to designate a neotype among our sampled specimens because the original illustrated specimens are of sufficient quality with no issue concerning the stability of nomenclature (ICZN, Art. 75). Lateral teeth from our samplings (Fig. 2M-N), which display flatten and slightly ornamented (short vertical basal ridges) margino-labial regions as well as numerous incipient and poorly-individualized cusplets, are very similar to the type specimen of *S. tenuis*. Similarly, the large anterior teeth reported here, which are characterized by a massive and stubby crown with scalloped labial bulge, labially depressed basal region of the main cusp and poorly-individualized cusplets are comparable to the paratype of *S. tenuis* (*PV OR 9297a*). It is therefore possible that *S. subulatus* and *S. tenuis* are synonyms but this cannot be
ascertained before a thorough revision of mid-Cretaceous *Synechodus* species. Glikman (1957, 1964, 1980) illustrated several *Synechodus* specimens from the Cenomanian of Saratov that he referred to *S. dispar* (Reuss, 1846). Yet, the original illustrations of *S. dispar* (Reuss, 1846: p. 98, pl. 24, Figs 27-28) are very difficult to interpret and the possibly secondary anaulacorhize stage of the root of both specimens, the squared outline of the root lobes, along with the long lingual and possibly labial vertical ridges rather suggest affinities with lamniforms (e.g. *Scapanorhynchus*).

However, specimens from Saratov include large and bulky anteriors with scalloped basal bulges on labial crown faces (e.g. Glikman 1964: pl. 5, fig. 5), which are similar to anteriors of *S. subulatus* (and possibly *S. tenuis*). *Synechodus dispar* specimens of Glikman (1957, 1964, 1980) also include lateral teeth with more developed cusplets and marked labial ornament made of vertical ridges (e.g. Glikman 1964: pl. 5, fig. 6) that could fall within the morphological variation of *S. subulatus* (and possibly *S. tenuis*). However, one specimen illustrated in Glikman (1980: pl. 15, figs 4-5) most probably belong to a carcharhiniform (e.g. *Protoscyliorhinus*). Contrary to *S. dispar*, the attribution of *Hybodus bronni* described by Reuss (1846) to the genus *Synechodus* is more likely. However, the two specimens illustrated by Reuss (1846: pl. 24, fig. 26, pl. 42, fig. 7) have an incomplete root and the drawings are insufficient to compare their morphology with other known species. This species, along with *H. dispar*, should be considered *nomina dubia*. Cappetta (2012) illustrated *Synechodus* teeth from the Santonian of Tyk Butak, Kazakhstan whose anterior teeth (and more generally teeth from all jaw positions) display the same general morphology as *S. subulatus* but bear coarser labial ornament, including on cusplets, which suggests that they represent a distinct species.

It is interesting to note, however, that the material from Tyk Butak comprises teeth of the three mid-Cretaceous morphotypes (*tenuis*-like anteriors, *nitidus*-like laterals, and *dubrisiensis*-like posteriors). This may favor the hypothesis of a strong heterodonty in some Cretaceous *Synechodus* as proposed by Ward (2010). Alternatively, the absence of anterior gracile and cuspidate anterior teeth with reticulate ornament in the Kazakhstan assemblage may indicate that some *Synechodus* species retained the *dubrisiensis*-like reticulate ornament in posterior teeth only. This hypothesis is supported by the absence of *dubrisiensis*-like anteriors in our samplings. However, no posterior
teeth were found in Kaniv, which is likely due to the coarse mesh sizes used for sieving.

Order **Hexanchiformes** Buen, 1926

Family **Paraorthacodontidae** Glikman, 1958

Genus **Paraorthacodus** Glikman, 1957

**Paraorthacodus recurvus** (Trautschold, 1877)

Fig. 2S-T

1861 *Hybodus dispar* Reuss; Rogovich, p. 22, pl. 3, figs 12-12a.

1877 *Sphenodus recurvus* Trautschold, p. 335, pl. 5, fig. 4

1911 *Synechodus* sp.; Priem, p. 14, figs 1-2.

1935 *Synechodus recurvus* (Trautschold); Dalinkevičius, p. 17, pl. 2, figs 50-58.

1957 *Paraorthacodus recurvus* (Trautschold); Glikman, p. 115, pl. 1, figs 6-13.

1977 *Synechodus recurvus* (Trautschold); Gamble, p. 45.

1977 *Synechodus recurvus* (Trautschold); Herman, p. 30.

1993 *Paraorthacodus recurvus* (Trautschold); Biddle, p. 23, pl. 5, fig. 5.

1999 *Paraorthacodus recurvus* (Trautschold); Underwood and Mitchell, p. 6, pl. 1, fig. 7.

2010 *Paraorthacodus recurvus* (Trautschold); Ward, p. 282, pl. 52, fig. 9.

**Material.** 21 mostly incomplete teeth (Melanchyn potik: 2 from layer A, 1 from layer B, 12 from layer C, including NNPM2588-8, 1 from layer E; Kholodnyi ravine: 5).

**Description.** Teeth are 1 to 1.5 cm in height. The crown is inclined lingually with coarse labial ornament consisting of strong parallel and vertical folds that originate from the basal edge to up to 1/4 of the main cusp’s height. Labial folds are also present on cusplets where they taper just before reaching the apex. Fine folds are present on the lower region of the lingual face of the main cusp and cusplets. The main cusp is bulky with a wide base that is marked by a constriction at the crown/root edge represented by a high collar. The cutting edges of the main cusp are coarse and positioned labially. The labial crown face is nearly flat with no labial bulge. Cusplets are rather gracile and well individualized from the main cusp and from each other by deep notches devoid of
enameloid. The root is typically pseudopolyaulacorhize with deep and wide notches on the labial half of the basal root face. The lingual root face strongly projects lingually.

**Remarks.** Although incomplete, the teeth recovered in our samplings exhibit several characters (labial and lingual ornament, morphology of cutting edges and cusplets, root vascularization) that are typical of those of *Paraorthacodus recurvus*. This species was described from the Cenomanian of Russia (Trautschold, 1877) and subsequently reported from England (Woodward, 1911) but no precise illustrations were published before Dalinkevičius (1935). Rogovich (1861) illustrated one tooth from Kaniv as *Hybodus dispar*. This specimen was not recovered in the collections of the Kiev Museum but likely belongs to *P. recurvus*. The specimens reported as *Synechodus recurvus* from the Campanian of England (Woodward, 1889, 1911) should probably be included in a different *Paraorthacodus* species but the lack of detail on the original illustrations do not allow a more precise attribution. *Paraorthacodus recurvus* is restricted to the Albian and Cenomanian.

Order **Squaliformes** Compagno, 1973

Family **Squalidae** Bonaparte, 1834

Genus **Protosqualus** Cappetta, 1977

**Protosqualus** cf. *glickmani* Averianov, 1997

Fig. 2U-V

**Material.** One incomplete tooth (NNPM 2588-9) from layer A of Kholodnyi ravine.

**Description.** This incomplete tooth is 4 mm wide. The root is poorly preserved and the mesial part of the crown is lacking. The main cusp is wide and low and strongly inclined distally with a convex mesial edge. The distal heel is fairly high and oblique with an indented outline bearing an incipient cusplet. The basal edge of the labial crown face is irregular in labial view and the apron, although incomplete, is broad and separated from the crown by a wide notch.

**Remarks.** This tooth bears typical characters (irregular basal edge of labial crown face, heel with incipient cusplets, large size) of *P. glickmani*, known from the Albian and Cenomanian of Russia and Lithuania (Dalinkevičius, 1935; Averianov, 1997; Adnet et al. 2008) but additional material
would be needed to confirm this attribution.

Order **Squatiniformes** de Buen, 1926

Family **Squatinidae** Bonaparte, 1838

Genus **Squatina** Duméril, 1806

*Squatina (Cretascyllium) cranei* Woodward, 1888

Fig. 2W-X

For synonymy, see Guinot et al. (2012) and add:


2012 *Squatina (Cretascyllium) cranei* Woodward, Guinot et al., p. 532, figs 2-7.

**Material.** Eight complete or partial teeth: two from layer A (one from Melanchyn potik and one from Kholodnyi), three from layer B (Melanchyn potik), including NNPM 2588-10 and three from layer C (Melanchyn potik).

**Description.** Teeth of this species are under 5 mm high. These teeth have a single cusp which is relatively elongate and may be either straight or slightly lingually and distally inclined. Lingual and sometimes labial faces are convex. Lateral heels are low and bear developed cutting edges running through the extremities of the heels. The apron is triangular or rounded, medium-sized and only slightly extends below the base of the root, as noticeable on NNPM 2588-10 (Fig. 2, W-X). The basal root face has a single foramen in the center.

**Remarks.** Teeth found in Kaniv compare well with those of *S. cranei* described by Woodward (1888) based on a crushed skull from the Sussex chalk (Guinot et al. 2012). There is some degree of confusion between Albian species *S. cranei* and *S. decipiens*. The latter was described by Dalinkevičius (1935) from the Cenomanian chalk of Lithuania, who indicated that the only difference between *S. decipiens* and *S. cranei* was the larger size of the former with no other evident morphological differences. Guinot et al. (2012) provided evidence that *S. decipiens* is a junior synonym of *S. cranei*, the former simply representing larger individuals of the same species. In addition, specimens in the same size range seem to be described by Rogovich (1861) as *Hybodus*
marginatus from the same locality to the material reported here. However, we did not recover Rogovich’s specimens in the collections of the Kiev Museum.

Superorder Galeomorphii Compagno, 1973
Order Orectolobiformes Applegate, 1972
Family Hemiscylliidae Gill, 1862
Genus Chiloscyllium Müller and Henle, 1837

Chiloscyllium sp.

Fig. 3A

Material. One incomplete tooth (NNPM 2588-11) from layer E of Pekarskyi ravine.

Description. This specimen only preserves the crown (lacking the mesial cusplet). The crown is labio-lingually compressed with a broad triangular main cusp oriented lingually and slightly bent towards the commissure. A short and bulky distal cusplet is present, separated from the main cusp by a notch. The cusplet’s apex is oriented about 45° to the main cusp. The apron is short and wide with a rounded lower edge.

Remarks. This tooth somewhat resembles those of some Cretaceous Chiloscyllium, based on cusplet position relative to the crown and apron’s morphology. The fossil record of mid-Cretaceous hemiscylliids is scarce and is restricted to some representatives of unknown affinities in the Albian of England reported as Chiloscyllium cf. greeni and cf. Hemiscyllium sp. (Underwood and Mitchell, 1999). Batchelor and Ward (1990) illustrated one tooth assigned to Chiloscyllium sp. from the Aptian of the Hythe Beds in England that agrees with the tooth morphology of extant representatives of the genus. The crown morphology of the specimen reported here fits that of the Aptian specimen but the preservation of the Kaniv specimen precludes further comparison.

Orectolobiformes incertae fam.

Genus Cederstroemia Siverson, 1995

Cederstroemia cf. siverssoni Guinot, Underwood, Cappetta and Ward, 2013
1861 *Hybodus marginatus* Rogovich, p. 24, pl. 3 figs 14, 17 *non* figs 15-16?–18.

**Material.** Four incomplete teeth: two from layer C (Melanchyn potik), one from layer F (Pekarskyi) – figured as NNPM 2588-12 and one from layer A (Kholodnyi).

**Description.** These teeth are mesio-distally elongate and labio-lingually compressed, a feature that is more marked in lateral teeth, which can reach 1 cm width. The main cusp is low, stubby and bent to the posterior with marked cutting edges that are continuous with those of the heels. Heels are weakly inclined basally with sharp and sinusoidal cutting edges in occlusal view. The lateral extremities of the heels are oriented lingually, as visible on a lateral tooth (Fig. 3B-C). The apron is well developed, wide and lingually oriented. It protrudes labially and overtakes the basal root edge in labial view. The crown lingual protuberance is wide but weak. The root is wider than the crown and displays a sub-rectangular basal face. Numerous foramina open on the lingual root face.

**Remarks.** The material described here closely resembles teeth of *Cederstroemia siverssoni* described by Guinot et al. (2013), which ranges from the Albian to the Turonian. However, as no complete specimens were found in Kaniv, it is preferred to only tentatively refer these specimens to this species. Guinot et al. (2013) also reported teeth attributed to *Cederstroemia cf. siverssoni* from the Cenomanian of England and Coniacian of Northern Ireland that differ from the specimens described here by their broader apron and lower heels. Specimens similar to those reported here were also illustrated by Rogovich (1861: pl. 3 figs 14, 17 *non* figs 15-16?–18) from the same locality, which he assigned to *Hybodus marginatus*. However, Rogovich’s specimens of *Hybodus marginatus* are not preserved in the collections of the Kiev Museum. Considering the heterogeneous series of *Hybodus marginatus*, the lack of sufficiently well-preserved material recovered in this study and in the absence of syntypes in Rogovich’s collections, it is preferred to consider this species name *nomen dubium*.

Order **Heterodontiformes** Berg, 1940

Family **Heterodontidae** Gray, 1851
Genus *Heterodontus* de Blainville, 1816

*Heterodontus upnikensis* (Dalinkevičius, 1935)

Fig. 3D-E

1935 *Cestracion upnikensis* Dalinkevičius, p. 13, pl. 1, figs 29-33.

1977 *Heterodontus upnikensis* (Dalinkevičius); Herman, p. 86.

1993 *Heterodontus upnikensis* (Dalinkevičius); Biddle, p. 11, pl. 2, figs 2-3.

1999 *Heterodontus canaliculatus* (Egerton in Dixon, 1850); Underwood and Mitchell, p. 17, pl. 4, figs 5-8.

2010 ‘*Heterodontus*’ upnikensis’ (Dalinkevičius); Ward, p. 286, pl. 53, fig. 5.

**Material.** Five anterior teeth: 2 from layer C of Melanchyn potik, 3 from Kholodnyi (including NNPM2588-15).

**Description.** These anterior teeth are under 5 mm high and have a robust and smooth crown made of a broad triangular main cusp and a wide and flared apron. The main cusp is biconvex and slightly inclined lingually with marked cutting edges that run continuously until the marginal angles. Lateral cusplets on the crown are either missing or strongly reduced (Fig. 3D-E). The cutting edges are continuous or occasionally present a thickening in the lower part of the main cusp that can form slight protuberances. The apron is strongly flared labially and divided in two marginal regions by a deep and wide concave hollow that reaches the labial base of the main cusp. The labial edge of the hollow presents a concave articular facet. The root is V-shaped with a marked lingual protuberance and developed root branches, the mesial one being wider.

**Remarks.** Original description of this species by Dalinkevičius (1935) includes large anterior teeth that are very similar to Kaniv specimens as well as lateral teeth that are strongly ornamented and do not appear to display any characters in common with the anterior teeth (Ward, 2010). In addition to
describing *H. upnikensis* teeth from the Jiesia Formation of Lithuania, Dalinkevičius (1935) also described *H. canaliculatus* teeth from the same Formation and it might be possible that some laterals assigned to *H. upnikensis* actually belong to this species. A revision of Dalinkevičius’ original material is needed to clarify these attributions. Underwood and Mitchell (1999) reported anterior and anterolateral teeth from the Albian and Cenomanian of England that were referred to *H. canaliculatus*. However, anterior teeth show similar features to those of *H. upnikensis* and lateral teeth are smooth or weakly labially ornamented. Biddle (1993) illustrated some anterior and anterolateral teeth from the Albian of France as *H. upnikensis*, showing similar features to Underwood and Mitchell’s (1999) specimens (absence of cusplets and enamel ornamentation). However, specimens from the French and English Albian are comparatively smaller than those from Lithuania and Ukraine. Considering the large size of the latter specimens it is unlikely that *H. upnikensis* represents juveniles of *H. canaliculatus*. However, the part of ontogenetic variation coupled with questions on the morphology of lateral teeth from the type locality preclude definite conclusions on the morphological variation and even on the validity of this species (Underwood and Mitchell, 1999).

**Heterodontus** aff. *canaliculatus*

Fig. 3F-N

1861 *Lamna (Odontaspis) minuta*, Rogovich, p. 52, pl. 7, fig. 22.

1861 *Acrodus rugosus* Agassiz; Rogovich, p. 17, pl. 2, fig. 11.

**Material.** Two anterior teeth and 33 lateral teeth (21 lateral teeth from Melanchyn potik layer C, one lateral tooth from layer E, nine lateral teeth from Kholodnyi, two lateral teeth from layer F of Pekarskyi ravine), all figured specimens come from layer C (NNPM 2588-13 and NNPM 2588-14).

Additional specimen: Rogovich (1861)’s specimen (NNPM 391-1).

**Description.** Anterior teeth are cuspidate, up to 5 mm in adult specimens and possess a triangular
crown in labial view. The main cusp is bulky and biconvex with marked cutting edges in its lower region. A pair of diverging, rather thin and short lateral cusplets is present, well separated from the main cusp by a notch. The cusplets are united to the margino-labial regions of the apron by a sharp edge of enamoid. The apron is moderately flared and labially protruding with a narrow concavity in its median region. The apron is smooth and overhangs the labial crown face in occlusal view. The lingual crown face is concave in profile view. A well-developed and broad uvula is present, reaching the basal root edge in lingual view. The root is Y-shaped with well-individualized root branches and a protruding medio-lingual region, where a large medio-lingual foramen opens. The margino-lingual edges of the root are concave in basal view. Compared to adult anterior (Fig. 3H-J), a juvenile cuspidate tooth (Rogovich’s specimen NNPM 391-1, Fig. 3F-G) has broader and more triangular cusplets, the lateral cutting edges of which are not individualized form the rest of the crown. The apron is short but protrudes labially with a wide median concavity than in adult anterior teeth. Lateral teeth are mesio-distally elongated with a sigmoid outline in occlusal view. The occlusal face bears a relatively high sigmoidal occlusal crest positioned closer to the lingual side. The median part of the occlusal ridge on is strongly convex. A concave articular facet is present on the lingual crown face. Enamel ornamentation mostly consists of pronounced and not anastomosing ridges that are oriented perpendicular to the transverse crest with some short longitudinal ridges that confer a reticulate pattern near the lingual and labial edges in occlusal view. The anaulacorhize root is asymmetrical in basal view with its mesial part being slightly narrower.

Remarks. Adult anterior teeth of *H. aff. canaliculatus* are morphologically close to those of *H. canaliculatus* (Egerton in Dixon, 1850) but differ in having a crown with less broad and more individualized cusplets as well as narrower concavity in the base edge of the apron. However, the intraspecific variability is of *H. canaliculatus* teeth is imperfectly known and it is unclear whether these differences are part of intra- or interspecific variation. Similarly, short irregular and sub-horizontal folds are rarely present on the apron of some anterior teeth of *H. canaliculatus* but some display entirely smooth crowns, as in the material described here. In addition, lateral teeth of *H. aff.
canaliculatus are devoid of median tubercle on the occlusal face whereas this feature is present in lateral H. canaliculatus teeth (Woodward, 1912: pl. 45, figs 1-5), although less marked in the type specimen (Egerton, 1855). Some lateral teeth from the Albian of Lithuania (Dalinkevičius, 1935) attributed to H. upnikensis might be similar to the specimens described here but the quality of the original illustrations precludes further comparison with the material from Ukraine. Lamna (Odontaspis) minuta Rogovich, 1861 was based on a minute juvenile anterior Heterodontus tooth (Fig. 3F-G) attributed here to H. aff. canaliculatus. Considering the low systematic value of juvenile teeth, the taxon name erected by Rogovich (1861) would be better regarded as nomen dubium. Another specimen reported by Rogovich (1861: pl. 3, fig. 18) as Hybodus marginatus probably represents an anterior Heterodontus tooth in lingual view, but it is unclear whether it more closely resembles H. upnikensis or H. canaliculatus. Similarly, Rogovich (1861: pl. 2, fig. 11) reported the species Acrodus rugosus Agassiz, 1939 that most probably represents a lateral tooth of H. aff. canaliculatus.

Order Lamniformes Berg, 1958
Family Anacoracidae Casier, 1947
Squalicorax sp.

Material. One incomplete tooth (NNPM 2588-17) from layer F of Pekarskyi.

Description. This specimen is a small, 4 mm wide, partially preserved tooth (the apex and entire mesial cutting edge of the crown is lacking) with strong labio-lingual compression. The main cusp is wide and strongly distally inclined. This is well separated from the distal heel by a deep notch. The heel is wide and moderately low with a convex outline. Coarse serrations are present on the basal region of the distal cutting edge of the main cusp, and were possibly present elsewhere on the worn cutting edges. The upper part of root below the labial crown-root margin shows a depression along the entire margin.

Remarks. This specimen bears a combination of Squalicorax tooth characteristics including a long
distal cutting edge and strong distal curvature, a wide distal heel, strong labio-lingual compression and serrated distal edge of main cusp. However, the preservation of this unique specimen precludes further identification.

Family **Archaeolamnidae** Underwood and Cumbaa, 2010

Genus **Archaeolamna** Siverson, 1992

**Archaeolamna striata** comb. nov. (Rogovich, 1861)

(Fig. 3Q-V, Fig. 4A-L)

1861 *Otodus striatus*, Rogovich, p. 41, pl. 5, fig. 13 *non* fig. 14.

? 1999 *Carcharias* sp. Cumbaa and Tokaryk, p. 61, fig. 5 (pars: upper 3 teeth center right column).

**Material.** 702 teeth complete and incomplete teeth (2 from layer E of Pekarskyi; 26 from layer F; 26 from layer A of Melanchyn potik; 11 from layer B; 573 from layer C; 7 from layer E; 57 from Kholodnyi). Specimens NNPM 2588 18-25 come from layer C of Melanchyn potik. Additional specimen: Rogovich (1861)'s specimen NNPM 391-2 (lectotype).

**Description.** Teeth, mostly under 1 cm high for anteriors, found from the type locality display gradient monognathic and dignathic heterodonty. The main cusp is thin and elongate, similar morphology is exhibited by the pair of diverging lateral cusplets. Cutting edges are moderately developed and run continuously from the main cusp to the cusplets with a slight notch between the two (e.g., Fig. 4A-B). The crown is slightly sigmoid in profile view in anterior teeth, while lateral teeth have a flat labial face and have strongly a distally inclined main cusp, especially in upper teeth. The basal part of the labial face of lateroposterior and posterior teeth sometimes bears short vertical folds that occasionally bifurcate (e.g., Fig. 4K-L). In addition, there is often an enamel depression in the labial base center, which is fairly strongly marked in anterior teeth. The root has a well-developed lingual protuberance with a weak nutrient furrow. Root lobes are thin, well-developed and U-shaped, even in laterals. The lingual neck of this tooth type is only slightly narrower in the marginal parts than in the center.

**Remarks.** The species *Otodus striatus* was described by Rogovich (1861: pl. 5, figs 13-14) based
on two teeth that were present in the collection of the Kiev museum. Although one tooth (Rogovich, 1861: pl. 5, fig. 14) probably belongs to an undetermined lamniform, the other one (Rogovich, 1861: pl. 5, fig. 13) conforms with the tooth morphology of the material recovered in our sampling that present both the heterodonty and tooth morphology of *Archaeolamna* species. This latter tooth (NNPM 391-2) is here designated as the lectotype of *Otodus striatus*. Teeth of *Archaeolamna striata* comb. nov. exhibit some similarities with the Cenomanian *Archaeolamna ex. gr. kopinensis* described by Underwood and Cumbaa (2010) from Canada in having a gracile morphology with occasional labial enamel folds in upper lateroposterior and posterior teeth. However, teeth from the Canadian Cenomanian, as well as those from the English Gault Clay (Ward, 2010) have more developed root lobes and more marked lingual protuberance of the root. Similar gracile specimens were also figured by Biddle (1993) from the Albian of France as *Archaeolamna kopinensis* that mostly differ from *A. striata* comb. nov. by their more marked medio-lingual nutritive groove and might be closely related if not conspecific with *A. striata* comb. nov. Other taxa from the Albian-Cenomanian interval described as *Archaeolamna*, such as *A. haigi* and *A. aff. kopinensis* reported by Siversson (1996) and *Archaeolamna* sp. (Vullo et al., 2007) are much more robust than *A. striata* comb. nov.

*Archaeolamna ex. gr. kopinensis* (Davis, 1890)

**Fig. 4M-T**

**Material.** 213 teeth complete and incomplete teeth: 13 from layer F of Pekarskyi; 5 from layer A of Melanchyn potik; 2 from layer B; 193 from layer C. Specimens NNPM 2588 26-29 from layer C of Melanchyn potik.

**Description.** Collected specimens display gradient monognathic and dignathic heterodonty. These teeth are relatively large (up to 15 mm high) and robust with wide triangular main cusp and cusplets. Cusplets are low and well separated from the main cusp by a notch. In lateral teeth, the cutting edges of the main cusp can present a marked convexity that forms an incipient cusplet, just before the notch (e.g., Fig. 4S-T). The basal edge of the main cusp shows no or very weak labial
bulge, only a weak depression in the center. A strong lingual protuberance is present, pierced by a
large central foramen. Root lobes are rather short and bulky with rounded labial extremities except
in lateral teeth where they form a sharp angle.

Remarks. These teeth are much larger and more robust than those of *A. striata*. The teeth described
here are somewhat similar in overall tooth morphology to the Cenomanian specimens from Canada
(Underwood and Cumbaa, 2010) and England (Guinot et al., 2013) included in *A. ex. gr.
*kapingensis*. However, the Kaniv teeth differ in having a less bulged lingual root face. Teeth
described as *A. haigi* from the Cenomanian of Australia (Siversson, 1996) differ in being more
gracile with thinner main cusp and root lobes.

Family **Otodontidae** Glikman, 1964

Genus **Cretolamna** Glikman, 1958

**Cretolamna** sp.

Fig. 4U-V

**Material.** 2 anterior teeth from layer C of Melanchyn potik, including NNPM 2588-30.

**Description.** These anterior teeth have a gracile, elongate and weakly sigmoid main cusp. Main
cusp can constitute up to ¾ of the tooth height, as in NNPM 2588-30. The main cusp is flanked by a
pair of short, triangular and diverging cusplets separated from the main cusp by a slight notch. The
labial crown base has a central enamel depression. The relatively symmetrical root bears a strong
lingual protuberance devoid of nutrient groove.

Remarks. These anterior teeth differ from mid-Cretaceous *Cretolamna* teeth of similar jaw position
(Siversson et al. 2015) in being very gracile and slender. An anterior tooth from the Albian of
Poland (Siversson and Machalski, 2017) reported as *Cretolamna* sp. as well as some specimens
from the upper Albian Pawpaw Formation (Motorola site, see Siverson et al. 2007) in Texas,
reported as *C. appendiculata* (Welton and Farish, 1993) display a comparable morphology and
probably represent a new, unnamed species (Siversson and Machalski, 2017).
Family *Cretoxyrhinidae* Glikman, 1958

Genus *Cretoxyrhina* Glikman, 1958

*Cretoxyrhina vraconensis* Zhelezko, 2000

Fig. 4W-X, Fig. 5

1861 *Otodus appendiculatus* (Agassiz) [partim]; Rogovich, p. 39, pl. 5, figs 1-5 *non* figs 6-11.

1993 *Cretolamna appendiculata* (Agassiz) [partim]; Welton and Farish, p. 103, fig. 2, p. 104, second tooth from the left in the upper jaw.

2000 *Pseudoisurus vraconensis* Zhelezko [partim]; Zhelezko, p. 138, pl. 1, figs 3-4 *non* fig. 5 (Cretalamna sp).

2009 *Cretoxyrhina aff. vraconensis* (Zhelezko); Ward, p. 291, pl. 54, figs 6-7.

2013 *Cretoxyrhina vraconensis* (Zhelezko); Siverson et al., p. 97, figs 4–9.

2017 *Cretoxyrhina vraconensis* (Zhelezko); Siverson and Machalski, p. 18, figs 4-9.

**Material.** 22 complete and almost complete teeth (1 from layer A of Melanchyn potik; 21 from layer C, including NNPM 2588 31-37), 31 isolated cusps (1 from layer A of Melanchyn potik; 29 from layer C; 2 from Kholodnyi).

**Description.** Teeth of this species are characterized by triangular crowns with smooth lingual faces, a pair of broad triangular cusplets and no nutrient groove on the root. Found specimens are rather large, with anterior teeth sometimes exceeding 4 cm high (e.g., Fig. 5, C-D). In profile view, teeth are curved labially near the apex. The labial crown face generally has one or two short vertical bulges in the center near the base. Cusplets are large, rounded, and diverging. They connect to the main cusp via a thin enameloid band incised by narrow but relatively deep notch. Parasymphysial teeth are mesio-distally compressed and have both distally and labially inclined crown. Root lobes are reduced and oriented. Anteriormost teeth have a marked and short heel or reduced cusplets and are mesiodistally compressed. More distal anterior teeth have small cusplets and sometimes thick dental band. Upper laterals have a slightly distally inclined main cusp. Juvenile teeth have high but rounded cusplets (e.g., Fig. 5, A-B). Folds on the lingual face of the cusplets may be present in
lateroposterior teeth. However, some other teeth attributable to this species have very broad but
triangular and sharp cusplets (e.g., Fig. 4W-X, Fig. 5E-F, and Rogovich’s specimen Fig. 5, M-N).
They are similar to the other morphotype in having a protuberance on the root above each cusplet
and a very strong lingual bulge.

Remarks. The morphology of the teeth from Kaniv agrees with that of *C. vraconensis* (see
Siverson et al., 2013 for thorough description) and differs from *C. denticulata* (Glikman 1957) and
*C. mantelli* (Agassiz, 1838) by their developed triangular lateral cusplets in laterals and reduced
cusplets in anteriormost teeth, rounded root lobes and one or two vertical labial bulges on the basal
part of the crown. Rogovich (1861: pl. 5, figs 1-11), illustrated several specimens here referred to
*Otodus appendiculatus* but this series probably comprises several taxa. While the morphology of
the first five specimens agrees with the heterodonty and morphology of *C. vraconensis*, other
specimens more likely belong to *Protolamna* (figs 6, 10-11), possibly *Archaeolamna* (fig. 7) or to
undetermined lamniforms (figs 8-9). Glikman (1964) and Mertiniene (1975) probably described
similar specimens from the Albian of Kaniv (as *Cretoxyrhina* and *Cretalamna appendiculata,*
respectively), but without providing illustrations. Teeth from Albian of Poland (Siversson and
Machalski, 2017) also display similarities with Kaniv teeth, especially those with sharper cusplets.
However, some of the figured teeth are larger and more massive than the Ukrainian specimens. This
is the most abundant large lamniform shark species from Kaniv and is present in all layers where
large lamniform teeth were found.

Family **Paraisuridae** Herman, 1979

**Paraisurus** Glikman, 1957

**Paraisurus macrorhizus** (Pictet and Campiche, 1858)

Fig. 6A-F

1858 *Oxyrhina macrorhiza* Pictet and Campiche, pl. 10, figs 8-10.

1861 *Otodus monstrosus* Rogovich, pl. 5, fig. 12.

1889 *Oxyrhina macrorhiza* (Pictet and Campiche); Woodward, p. 381.
1987 *Paraisurus macrorhiza* (Pictet and Campiche); Cappetta, p. 101, fig. 89D-F.

2010 *Paraisurus macrorhizus* (Pictet and Campiche); Ward, pl. 55, fig. 3.

**Material.** 4 incomplete teeth from layer C of Melanchyn potik, including NNPM 2588-38.

Additional specimen: Rogovich (1861)’s specimen NNPM 391-41.

**Description.** Teeth are up to 15 mm high, and strongly mesio-distally compressed with a strongly convex lingual face and only slightly convex labial face of the main cusp, which is lingually inclined. Ornament is rarely present in the form of fine wrinkles near the lingual base of the main cusp. The center of the labial face is depressed in its base. Cutting edges run on the root in the form of markedly oblique heels. The root is incomplete but shows a very strong lingual protuberance.

**Remarks.** The morphology of the specimens reported here is typical of teeth of the genus *Paraisurus* with mesio-distally compressed crown and root, short lingual crown face, absence of cusplets and extremely developed lingual root bulge. This genus contains six nominal species, the validity of some of them being contestable (Siversson and Machalski, 2017). Sokolov (1978) described the Lower Albian *P. elegans*, the early middle Albian *P. lanceolatus* and the latest Albian (‘Vraconnian’) *P. compressus*. These most probably represent chronospecies, the latter being possibly junior synonym of *P. macrorhizus*. Other nominal species comprise the late Aptian *P. amudarjensis* (Sultanbobo Formation, western Uzbekistan) and Rogovich (1861)’s *Otodus monstrosus*. Rogovich’s holotype and only illustrated specimen of the species *Otodus monstrosus* was recovered in his collections (Fig. 6A-C) and illustrated here. This specimen as well as those from our samplings do not display any characters to differentiate *O. monstrosus* from *P. macrorhizus* and the former should be considered junior synonym of the latter.

Family *Pseudoscapanorhynchidae* Herman, 1979

Genus *Protolamna* Cappetta, 1980

*Protolamna* cf. *sokolovi* Cappetta, 1980

Fig. 6G-Q

?1861 *Otodus appendiculatus* (Agassiz) [partim], Rogovich, p. 39, pl. 5, figs 6, 10-11 *non* figs 1-5,
Material. 40 teeth (three from layer A, 29 from layer C of Melanchyn potik, including NNPM 2588 39-43, three from layer E, two from layer E of Pekarskyi, three from Kholodnyi)

Description. Teeth of this species are relatively large (up to 15 mm high in anterior teeth). The main cusp is elongated, sigmoid in profile view and exhibits folds on the lingual face. Both faces are convex. The labial face is reduced because of labial position of the cutting edges. The cutting edges of lateral cusplets are separated from the well-developed ones of the main cusp by a sharp notch. The labial face of the main cusp is smooth in anterior teeth, whereas it can very occasionally display rare and fine vertical folds in lateral teeth. Cusplets have the shape of the main cusp and are positioned at a 45° angle from the main cusp in anterior teeth (e.g., Fig. 6I-K). The root has a developed lingual protuberance with weak or absent nutrient groove. Intermediate teeth are almost symmetrical, have wider root than anterior teeth and have a striated labial face.

Remarks. Kaniv specimens resemble Protolamna sokolovi teeth described in Cappetta (1975, 1980) from the Aptian of France by having no labial ornament in anterior and most lateral teeth, weak nutrient furrow, similar shape of main cusp and weak lingual ornamentation. However, teeth of P. sokolovi are more robust than Kaniv specimens and display compressed root lobe extremities, less diverging cusplets and stronger lingual root protuberance in lateral teeth. Kaniv specimens bear resemblances with teeth of Protolamna sp. from Cenomanian of United Kingdom (Guinot et al., 2013). However, the Cenomanian specimens have pronounced lingual folds and much wider and more erect cusplets. Specimens from the Albian of Poland reported as Protolamna sp. (Siversson and Machalski, 2017) differ from the teeth described here by their marked labial and lingual face in most teeth. Teeth of P. carteri Cappetta and Case, 1999 from the Cenomanian Woodbine Fm. of Texas and P. roanokeensis from Albian Pawpaw sands of Texas have strong ornamentation on the lingual crown face and exhibit relatively gracile morphology. Rogovich (1861) reported several specimens as Otodus appendiculatus, some of which (Rogovich, 1861: pl. 5, figs 6, 10-11) showing a morphology that could fall within the variation found in the material described here, but these specimens have not been found in the collection of the Kaniv Museum. The tooth that Rogovich
(1861: pl. 7, fig. 14) illustrated for his species Lamna (Odontaspis) ornata differs in having strong labial enamel ornamentation and double cusplets on each side of the tooth. Considering the lack of accurate illustration and likely loss of the type specimen of Lamna (Odontaspis) ornata, it is not possible to assess the identification of this tooth and it is preferable to consider this species nomen dubium.

Genus *Pseudoscapanorhynchus* Herman, 1977

*Pseudoscapanorhynchus compressidens* Herman, 1977

Fig. 6R-Z

1977 *Pseudoscapanorhynchus compressidens* Herman, 192, pl. 7, fig. 8.

1991 *Protolamna acuta* Müller and Diedrich, 36, pl. 8, figs 4–6.

1999 *Protolamna compressidens* Herman; Cappetta and Case, 25, pl. 12, figs 1, 2.

2007 *Pseudoscapanorhynchus compressidens* Herman; Vullo et al., p. 101.

2013 *Pseudoscapanorhynchus compressidens* Herman; Guinot et al., p. 639, Fig. 18A-I.

**Material.** 45 partial and complete teeth (1 from layer A, 1 from layer B, 31 from layer C of Melanchyn potik, including NNPM 2588 44-46, 11 from Kholodnyi).

**Description.** Teeth are mostly around 1 cm high and have a strongly sigmoid in profile view and mesio-distally compressed crown. The lingual crown face is strongly convex, while the labial is only slightly convex. The labial face is reduced because of the labial position of the cutting edges, which end before reaching the base of the crown. The labial base of the cusplets usually has two to three vertical and short parallel wrinkles. Lateral cusplets are elongate, labially positioned relative to the main cusp and are fully individualized. The basal region of the labial crown face is strongly mesio-distally compressed in labial view. The root has a strong lingual protuberance with a weak nutrient furrow. In the teeth positioned closer to jaw symphysis, root lobes are almost completely merged (e.g., Fig. 6X-Z). No complete lateral teeth have been found – only crowns with partially preserved roots.
Remarks. The morphology and size of Kaniv specimens agree with the original description of *P. compressidens* by Herman (1977) based on teeth from Cenomanian to Coniacian sites of Belgium and France. This species has been reported from numerous Cenomanian-Coniacian localities in Europe as well as from the Albian of France (Biddle, 1993) as *Leptostyrax macrorhiza* (see Guinot et al. 2013). Teeth attributed to this species are generally incomplete due to the gracile and elongate root lobes and cusplets and it is difficult to assess the taxonomical content included in Albian to Coniacian *P. compressidens*, which might include more than one species.

Family **Odontaspidae** *s.l.* Müller and Henle, 1839

*Eostriatolamia* Glikman, 1979

*Eostriatolamia subulata* (Agassiz, 1843)

Fig. 6A’-D’

1843 *Lamna (Odontaspis) subulata* Agassiz, vol. 3, p. 206, pl. 37a, figs. 5-6.

1861 *Lamna (Odontaspis) subulata* (Agassiz); Rogovich, p. 52, pl. 7, figs 19-21 non fig. 17, 18.

1935 *Odontaspis subulata* (Agassiz); Dalinkevičius, pl. III, figs 77-83

1977 *Scapanorhynchus subulatus* (Agassiz); Herman, pl. 7, fig. 5.

1991 ?*Eostriatolamia subulata* (Agassiz); Müller and Diedrich: p. 29, pl. 21, fig. 1-6.

2013 *Eostriatolamia subulata* (Agassiz); Guinot et al., p. 647, figs 21J-R.

2017 *Carchariidae* indet.; Siversson and Machalski, p. 23, Figs 6L-R.

Material. About 2000 complete and incomplete teeth (122 from layer A of Melanchyn potik, 105 from layer B, 1231 from layer C, including NNPM 2588-48, 17 from layer E; 4 from layer E, 61 from layer F of Pekarskyi; 460 from Kholodnyi, including NNPM 2588-47).

Description. Teeth are generally less than 1 cm high with strongly convex lingual face and slightly convex to flat labial face. Anterior teeth rarely exceed 1 cm, such (e.g., Fig. 6A’-B’). The crown is sigmoid in profile view. The lingual crown face is finely striated, while the labial face has several short vertical folds in anterior teeth, and many short folds near the base of the crown in laterals.
Ornamentation tends to be more marked on cusplets compared to the main cusp. The basal edge of the labial crown face bears a marked bulge in anterior teeth, whereas it is less developed in laterals. The cusplets are elongate, needle-like and slightly curved towards the main cusp. Cusplets are positioned labially relative to the main cusp – a feature that is more marked in anterior teeth – and connected to the main cusp via a thin enameloid band. The root bears a generally narrow but complete nutrient groove in most teeth. The lingual root protuberance is wide but moderately developed. The distal extremity of the root lobes is slightly labio-lingually compressed.

Remarks. The species *E. subulata* was described by Agassiz (1843) based on anterior teeth from the Upper Cretaceous of Germany that might not be conspecific. The absence of precise stratigraphic data and lack of accurate illustration of original material led Siversson and Machalski (2017) to consider this species *nomen dubium* and to question the inclusion of this species within the genus *Eostriatolamia*. Dalinkevičius (1935) reported this species from the Jiesia Formation in Lithuania and the specimens described here fit the morphology of the Lithuanian specimens, as well as that of specimens from the Albian of Poland (Siversson and Machalski, 2017) and Cenomanian of England (Guinot et al. 2013). Rogovich (1861) figured several specimens as *Lamna (Odontaspis) subulata*. However, only specimens on pl. 7, fig. 19-21 are attributable to this species, whereas, based on the drawings, specimens on fig. 17-18 are more likely to belong to a *Protolamna* species. Many other reports of this species are questionable (Guinot et al. 2013) and it is preferred here to limit the included specimens to those mentioned above, pending revision of the species.

*Eostriatolamia striatula* (Dalinkevičius, 1935)

Fig. 6E’-L’

1861 *Lamna (Odontaspis) gracilis* (Agassiz); Rogovich, p. 51, pl. 7, figs 15-16a.

1935 *Odontaspis (Synodontaspis) striatula* Dalinkevičius; p. 268, pl. 4, figs 84-95.

1975 *Carcharias striatula* (Dalinkevičius); Cappetta, p. 122, pl. 1, figs 1-7.

1977 *Palaeohypotodus striatula* (Dalinkevičius); Herman, p. 229, pl. 10, fig. 1.

1993 *Carcharias striatula* (Dalinkevičius); Biddle, p. 13, pl. 3, figs 3-4.
1997 *Carcharias striatula* (Dalinkevičius); Siverson, p. 461, figs. 4T-W.

2010 *Eostriatolamia striatula* (Dalinkevičius); Cappetta, fig. 156B.

2010 *Carcharias striatula* (Dalinkevičius); Ward, p. 290, pl. 54, figs 1-3.

**Material.** 45 teeth, 36 from layer C, including NNPM 2588 49-52, 9 from layer A of Melanchyn potik.

**Description.** Teeth are less than 1 cm in height and show monognathic, and possibly dignathic heterodonty. The crown is slender and slightly mesio-distally compressed, unlike the root that is only labio-lingually compressed. The main cusp is very slightly sigmoid in profile view. The lingual crown face is very finely striated, while the base of the labial face only sometimes exhibits short parallel folds. The labial crown base of some lateral teeth displays a short central bulge (Fig. 6E’-F’). Lateral cusplets have a slightly wider base relative to the shape of the main cusp and are up to 1/3 of the crown height. The lingual root face bears a sharp and wide bulge. A narrow nutrient groove is present but weakly marked in some lateral teeth.

**Remarks.** The morphology of the specimens reported here agrees with that of the type specimens described by Dalinkevičius (1935) from the Jiesia Formation in Lithuania. This species has been reported from several localities in the middle-late Albian (Dalinkevičius, 1935; Landemaine, 1991; Biddle, 1993; Cappetta, 2010; Ward, 2010) and late Aptian (Cappetta, 1975) of Europe as well as from the Albian of the Southern Hemisphere (Siverson, 1997). Similar specimens from Kaniv were figured by Rogovich (1861) as *Lamna (Odontaspis) gracilis* but they were not recovered in the collections of the Kiev Museum.

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**Lamniformes indet. 1**

*Fig. 6M’-N’*

**Material.** One complete tooth from layer C of Melanchyn potik, NNPM 2588-53.

**Description.** The only specimen referred to this species is a lower lateral tooth with a very robust and wide root and a short symmetrical non-sigmoid main cusp. It is flanked by a pair of gracile and triangular lateral cusplets. The cusplets are separated from the main cusp by a wide concavity that
bears some indentations, which can resemble incipient cusplets. The mesial and distal edges of the
cusplets are made of a sharp blade of enameloid that overhangs the root. The basal region of the
labial crown face displays a short vertical fold in its center. The root has a well-developed lingual
protuberance displaying a small nutritive foramen. The labial root face bears a median depression.

Remarks. This specimen bears resemblances with *Archaeolamna* teeth but differs in several ways:
1) root robustness combined with crown gracility; 2) absence of a central labial base enamel
depression, typical of all Kaniv *Archaeolamna* teeth and, instead, presence of a long central fold,
that is more often seen in *Cretocyrrhina vraconensis* from the same locality, suggesting that it might
be a pathological juvenile *Cretocyrrhina* tooth.

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**Lamniformes indet. 2**

Fig. 6O’-P’

1861 *Otodus striatus*, Rogovich, p. 41, pl. 5, fig. 14 *non* fig. 13.

?1861 *Otodus appendiculatus* (Agassiz) [partim], Rogovich, p. 39, pl. 5, fig. 9 *non* figs 1-8, 10-11.

Material. One tooth from original Rogovich collection, NNPM 391-3.

Description. This specimen is a small lateral tooth lacking root lobes. The main cusp is strongly
bent distally and slightly sigmoid in profile view. The distal cusplet is thin, elongate and does not
display distal curvature as in the main cusp. The mesial cusplet lacks its upper half but the lower
one exhibits similar morphology to the distal cusplet. The basal part of both lingual and labial
crown faces exhibits ornament made of vertical parallel folds. While these are very faint on the
lingual face, folds are more marked on the labial face and few of them run higher up on the crown.
Enamel on the labial face forms a basal extension with a slight depression in the middle. The lingual
root face does not show evidences of a nutrient groove and exhibits a moderately pronounced and
wide lingual protuberance.

Remarks. This specimen was one of the two illustrated specimens that Rogovich (1861) attributed
to *Otodus striatus*. However, unlike the other specimen assigned here to *Archaeolamna striata*, this
specimen exhibits a different morphology with much more elongate and mesio-distally compressed
cusps. Elongate cusplets are present in two of the other genera found in the sampled horizons—
*Eostriatolamia* and *Protolamna*. However, the specimen described here is more robust than
*Eostriatolamia* teeth having a large lingual root protuberance. Lateral teeth attributed to *Protolamna*
found in our samples from the Burim formation deposits have a comparable enamel folding pattern
but do not display such a strong distal curvature of the main cusp and differs in the morphology of
the cusplets. Lack of additional material for this morph does not allow to make definite
identification of this specimen. Another specimen illustrated by Rogovich (1861: pl. 5, fig. 9) might
correspond to this taxon.

5. Discussion

5.1. Geological age of Kaniv elasmobranch fauna

Elasmobranch remains from Kaniv dislocations were previously reported in the literature, but most
of available works on this topic is either outdated (Rogovich, 1861) or provided no descriptions or
illustrations (Glikman 1964; Mertiniene 1975; Glikman 1980; Glikman and Averianov 1998;
Popova et al. 2015). Specimens of Rogovich (1861), Glikman (1964) and Mertiniene (1975) come
from Maryin and Kostyaneckyi ravines (Selyschi village) and from Kaniv city, whereas locations
studied here (Kholodnyi, Pekarskyi and Melanchyn potik ravines) remained undescribed. As of
2018, we were not able to find any exposures of vertebrate-bearing strata in Maryin ravine, it is
likely that they were covered by landslides since the time of Glikman’s and Mertiniene’s research.
In the Kostyaneckyi ravine, we have not found any Cretaceous exposures either. The only
vertebrates known from this location come from the Eocene Buchak formation (Zvonok, 2011).
Rogovich (1861) published a detailed account of elasmobranch taxa found in the Kaniv Cretaceous,
including the description of eleven new species. Among all Rogovich’s illustrated specimens, only
seven were identified in the current collections of the Kiev Museum (Table 1), corresponding to the
following species described by Rogovich (1861): *Otodus monstrosus* (=*Paraisurus macrorhizus*),
*Otodus striatus* (=*Archaeolamna striata* and Lamniformes indet. 2), *Lamna minuta* (=*Heterodontus*
aff. *canaliculatus*), *Hybodus bidentatus*, and *Hybodus kessleri* (=*Synechodus kessleri*); along with
one specimen originally referred to *Otodus appendiculatus* (=*Cretoxyrhina vraconensis*). All other specimens were unfortunately lost, including those of the following species described by Rogovich: *Sphaenonchus (= Asteracanthus) compressus*, *Hybodus (= Polyacrodus) parvus*, *Oxyrhina (= lamniform indet.) pygmaea*, *Hybodus (= Polyacrodus) tuberculatus*, *Lamna (Odontaspis) ornata (= Protolamna sp.)*, *Hybodus (= Synechodus) subulatus*, and *Hybodus (= Cederstroemia pars.) marginatus*. Although none of Rogovich’s specimens were found for the species *Asteracanthus compressus*, *Polyacrodus parvus* and *Polyacrodus tuberculatus*, it is preferred to consider these species names as valid pending further sampling and/or information on the whereabouts of the missing specimens of Rogovich’s collection. Our samplings have resulted in the identification of 22 elasmobranch species (Table 2) represented by 7 different orders: Hybodontiformes, Synechodontiformes, Squatiniformes, Orectolobiformes, Heterodontiformes, Squaliformes and Lamniformes, as well as one undetermined lamniform specimen (Lamniformes indet. 1). This combination of taxa is generally typical of mid-Cretaceous deposits (Guinot et al., 2013; Siversson and Machalski, 2017). However, some aspects such as absence of batoids and rarity of hybodonts are somewhat unusual, as discussed below.

Elasmobranch taxa reported from Kaniv by Mertiniene (1975) included: *Squatina muelleri*, *Synechodus dispar*, *Gyropleurodus canaliculatus*, *Meristodon sp.*, *Paraorthacodus recurvus*, *Cretolamna appendiculata*, *Odontaspis subulata*, *O. macrohizus*, *Scapanorhynchus raphiodon*. Because of no illustrative material, it is impossible to know which of the elasmobranch taxa reported here did Mertiniene (1975) name ‘*Cretolamna appendiculata*’ and ‘*Scapanorhynchus raphiodon*’. Analogues of all other species had been found by the authors.

Glikman (1964) described following genera and species: *Squatina sp.*, *Paraorthacodus sp.*, *Synechodus sp.*, *Eostriatolamia gracilis*, *Paraisurus macrorhiza*, *Cretoxyrhina sp.*, *Notidanus sp.* and *Scapanorhynchus sp.*. Out of this list, only *Notidanus* and *Scapanorhynchus* teeth had not been found in our samplings. Glikman (1964) also noted that *Gyropleurodus*, *Meristodon*, *Cretaspis*, *Squalus* and *Polyacrodus* were absent from studied collections. Names for most of these genera are outdated, however orders to which they belong - heterodontiforms (=*Gyropleurodus*), hybodonts
(=Meristodon and Polyacrodus) and squaliforms (=Squalus) have been found in our samplings, except “Cretaspis” (=Hispidaspis), though mostly in small amounts. Strangely, no species that could correspond to Archaeolamna - the second most common lamnoid genus in Kaniv - were mentioned by Glikman (1964).

Both Mertiniene (1975) and Glikman (1964) described Kaniv elasmobranch fauna as late Albian in age, but the lack of illustrations or specimen descriptions made it hard to support their conclusions. Our samplings, although collected in different locations from those of Mertiniene (1975) and Glikman (1964), confirm the late Albian age for Kholodnyi, Pekarskyi and Melanchyn potiki ravines: Paraisurus macrorhizus is known through Late Aptian to Late Albian, Cretoxyrhina vraconensis occurs in uppermost Albian and lowermost Cenomanian (Siverson et al., 2013; Zhelezko, 2000). According to Glikman and Averianov (1998), Eostriatolamia gracilis and E. subulata are chronospecies with E. gracilis being an Albian species, whereas morphological differences between these two taxa are very minor (Glikman, 1964) indicating that their material is probably conspecific. Although Eostriatolamia subulata was initially reported from the Cenomanian of Lithuania (Dalinkevičius, 1935), reevaluation of these strata led to believe that they actually are Late Albian in age (Adnet et al., 2008). This species is also extensively described from Cenomanian of Europe and Asia (Glikman, 1980; Guinot et al., 2013). Glikman (1980) suggested that the Anacoracidae play an important stratigraphical role because of their higher variation in serration parameters and general tooth morphology. The anacoracid tooth found in Pekarskyi ravine, although poorly preserved, displays characteristics of Albian Squalicorax species including: 1) longer distal cutting edge and stronger distal curvature; 2) small cusplet on the distal side of the tooth; 3) crown slightly labio-lingually compressed; 4) coarsely serrated distal side. This specimen is somewhat similar to Squalicorax priscoserratus or S. pawpawensis from Texas Pawpaw shale (Siverson et al., 2007), Squalicorax sp. from Poland (Siversson and Machalski, 2017) that are Albian in age. However, because of the poor preservation of our specimen, it is impossible to confirm that it actually belongs to one of the named species. Overall, our findings are consistent with the late Albian or possibly lowermost Cenomanian age of the Burim formation vertebrate-
bearing strata, particularly layer C of Melanchyn potik ravine due to greater concentration of specimens and abundance of *P. macrorhizus* and *C. vraconensis*. For other layers, a similar age can be inferred based on geographical and stratigraphical proximity to layer C and overall similarity of the assemblages, which do not show any marked faunal transitions. In addition, all layers other than A and B are positioned below layer C indicating older age. Layers A and B have a much lower concentration of specimens but available findings are highly congruent with data from layer C. This conclusion is also confirmed by paleogeographic studies of the region that constrain the age of the Burim formation marine deposits to Middle Albian – Cenomanian because in the Aptian and Lower Albion depositional environment was terrestrial over most of the territory of modern Ukraine (Menasova and Tymchenko, 2018).

5.2. Albian elasmobranch faunas

Sharks from the described faunal complex are mostly small, the largest tooth found being about 4 cm high. Large teeth (>1.5 cm) are also very rare (about 4% of the material sampled) and correspond to the large lamniform genera *Cretoxyrhina* and *Protolamna*. Marine sauroptid teeth are even less common with only three more or less complete teeth (TS pers. obs.). It is interesting that the niche of large pelagic predators in Kaniv is monopolized by *Cretoxyrhina*, despite the presence of large-toothed genera such as *Dwardius* and *Cardabiodon* in contemporary deposits in Europe (Siversson and Machalski, 2017). According to Siverson et al. (2013), *Dwardius* preferred the neritic zone, while *Cretoxyrhina* was a more generalist predator. Quartz-glauconite sand layers in Kaniv were likely deposited in coastal conditions due to a large amount of broken shell fragments and occasional brachiopod findings, as well as presence of land plant fossils (mostly various conifer species, Krochak et al., 2016). Another interesting feature is the absence of hybodont sharks in most sampled horizons. Hybodonts are known for their tolerance to brackish and freshwater environments and can represent the largest part of Cretaceous faunas such as in the Lower Cretaceous Wessex Formation (Sweetman and Underwood, 2006). Most hybodont finds in Kaniv come from layer F in Pekarskyi ravine (5 teeth, 5.2% of fossil remains). Only a single crown
(0.005% of fossil remains) was recovered from Melanchyn potik, layer C. This, along with the abundance of plant remains, suggest that Kaniv territory in the late Early Cretaceous most likely consisted of small islands without major freshwater bodies suitable for elasmobranchs, where many hybodontiforms are thought to raise their youngs (Leuzinger et al., 2015).

Other late Albian elasmobranch-bearing localities known from Eastern Europe include Poland (Siversson and Machalski, 2017) and Lithuania (Dalinkevičius, 1935). Compared to Kaniv fauna, the elasmobranch assemblage from Poland has a greater abundance of large lamniforms with the genera *Dwardius* and *Cretodus* and *Paraisurus* being much more frequent than in the Burim formation. In addition, *Dwardius* teeth are much more common in the Polish assemblage than *Cretoxyrhina vraconensis*, whereas the opposite trend can be observed in the Ukrainian Albian. On the other hand, the composition of medium-sized lamniform sharks is fairly similar in Poland and Ukraine, *Cretolamna* species with elongate anterior teeth are also found in both localities, whereas serrated *Squalicorax* teeth are outstandingly rare compared to Albian deposits of United States (Siverson et al., 2007). The Polish fauna is also characterized by relatively few taxa represented by small-sized teeth with clades such as batomorphs, orectolobiforms, squatiniforms and squaliforms being missing from the assemblage, which could be explained by collecting and taphonomic biases (Siverson and Machalski, 2017). Collecting bias (use of coarse mesh size for sieving) might also explain the absence of batomorphs in our samplings.

Dalinkevičius (1935)’s collections from Upper Albian of Upninkai (Lithuania), on the other hand, are very similar to the Kaniv assemblages. Differences between the Lithuanian and Ukrainian faunas include the presence of two species of hybodonts in Dalinkevičius (1935)’s samplings, one of them being a species of *Acrodus*. Although this genus is absent from our samplings, it is possibly present in the Albian fauna from Kaniv since the species *Acrodus affinis* Reuss, 1845 was reported by Rogovich (1861). Another species reported by Rogovich (1861), *Acrodus rugosus* (Agassiz, 1839) more probably corresponds to a lateral tooth of *Heterodontus* (see above). Large lamniforms seem to be absent from the Lithuanian assemblage with a single tooth attributable to *C. vraconensis* being present (Dalinkevičius, 1935: pl. 5, fig. 107). Overall, species richness seems lower in the
Lithuanian samplings, however it is unknown what biases could have influenced the composition of the collections stored in Vilnius university since many of the original Dalinkevičius localities are no longer accessible.

Another locality relatively close geographically to Kaniv is Kolbay, Kazakhstan (Kennedy et al., 2008). The composition of this ‘Vraconian’ elasmobranch fauna resembles that of Burim formation assemblages but differs in the greater abundance of hybodonts and anacoracids and in the presence of the genus *Hispidaspis* that is characterized by unusual enamel folding patterns at the base of the crown (Glikman, 1980).

**Concluding remarks**

Burim formation, Kaniv, Ukraine is one of the few locations in the world containing evidence for one of the major adaptive radiations of elasmobranchs. Based on museum specimens originally reported by Rogovich (1861) as well as newly sampled material, we provide a detailed account of elasmobranch species present in this area during the Upper Albian and revise the status of several taxa first mentioned by Rogovich. The taxonomic composition of this fauna supports previously limited available paleogeographical and micropaleontological evidence for a late Albian age of the sampled vertebrate-bearing stratae. Compared to many other contemporary faunas, the Kaniv assemblages are very diverse, consisting of a variety of nectobenthic taxa, very frequent and numerous odontaspidiids and macrophagous lamniforms. This study represents the first detailed description of a Cretaceous elasmobranch fauna from Ukraine since the 19th century and one of the few reports of Cretaceous elasmobranchs from Eastern Europe as a whole.

**Acknowledgements**

The authors would like to thank Volodymyr Grytsenko from Kiev National Natural History Museum of National Academy of Sciences of Ukraine (NNPM) for providing access to historical collections of Rogovich, Lilia Popova of Kyiv National University (KNU) and Kaniv Natural Reserve staff for helping to get access to the localities in Kaniv and providing useful information on
the assemblages and to George Sokolskyi (Kyiv Polytechnic University), Oleg Solonyi, Anton
Pyankov, Ihor Kenduikhov and Yulia Tyhonravova from KNU for assistance with specimen
collection from 2013 to 2018. This work benefited from comments made by E. Popov, J.
Amalfitano and the Editor on an earlier version of the manuscript. First author (TS) benefitted from
Karsh International Scholarship Enrichment funding program of Duke University.

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**Figure Captions**

Figure 1. Stratigraphic and geographical localisations of sampled horizons. A, Upper Albian succession of Upper Burim formation deposits, A-F mark layers of coarse-grained quartz-glaucnite sands, all of which except layer D contain vertebrate fossils. B, map of Kaniv natural reserve with the three sampled ravines marked by a red star and original Rogovich’s location of Maryin ravine marked by a green star; map of Ukraine showing the location of Kaniv is in top right corner. C, field photo of vertebrate-bearing horizon of layer F in Pekarskyi ravine. [Full page width]

views, layer B, Melanchyn potik. **S-T:** *Paraorthacodus recurvus*, tooth (NNPM 2588-8) in S, labial and T, lingual views, layer C, Melanchyn potik. **U-V:** *Protosqualus cf. glickmani*,

incomplete tooth (NNPM 2588-9) in U, labial and V, lingual views, layer A, Kholodnyi. **W-X:** *Squatina (Cretaccyllium) cranei*, tooth (NNPM 2588-10) in W, labial and X, lingual views, layer B, Melanchyn potik. Scale bar equals 5 mm.

**Figure 3.** A: *Chiloscyllium sp.*, tooth (NNPM 2588-11) in labial view, layer F, Pekarskyi. **B-C:** *Cederstroemia cf. siverssoni*, lateral tooth (NNPM 2588-12) in B, lingual and C, labial views, layer F, Pekarskyi. **D-E:** ‘*Heterodontus’ upnikensis*, anterior tooth (NNPM 2588-15) in D, lingual and E, labial views, layer A, Kholodnyi. **F-N:** *Heterodontus aff. canaliculatus*. **F-G:** Rogovich’s *specimen*, an anterior tooth of a juvenile individual (NNPM 391-1) in F, labial and G, lingual views; H-J, adult anterior tooth (NNPM 2588-13) in H, basal, I, lingual and J, profile views, layer C, Melanchyn potik; K, lateral tooth (NNPM 2588-14) in occlusal view, layer C, Melanchyn potik; L-N, lateral tooth (NNPM 2588-16) in L, occlusal, M, basal and N, lingual views, layer C, Melanchyn potik. Scale bar equals 5 mm.

**Figure 4.** A-L: *Archaeolamna striata comb. nov.* A-B, upper anterior tooth (NNPM 2588-20) in A, lingual and B, labial views, layer C, Melanchyn potik; C-D, upper anterior tooth (NNPM 2588-21) in C, lingual and D, labial views, layer C, Melanchyn potik; E-F, upper lateral tooth (NNPM 2588-22) in E, labial and F, lingual views, layer C, Melanchyn potik; G-H, upper anterior tooth (NNPM 2588-23) in G, lingual and H, labial views, layer C, Melanchyn potik; I-J, upper lateroposterior tooth (NNPM 2588-24) in I, lingual and J, labial views, layer C, Melanchyn potik; K-L, upper lateroposterior tooth (NNPM 2588-25) in K, lingual and L, labial views, layer C, Melanchyn potik.

Figure 5. *Cretoxyrhina vraconensis*. A-B, upper lateral tooth from a juvenile individual (NNPM 2588-32) in A, lingual and B, labial views, layer C, Melanchyn potik; C-D, upper anterior tooth (NNPM 2588-33) in C, lingual and D, labial views, layer C, Melanchyn potik; E-F, lower lateral tooth (NNPM 2588-34) in E, lingual and F, labial views, layer C, Melanchyn potik; G-H, upper lateral tooth (NNPM 2588-35) in G, labial and H, lingual views, layer C, Melanchyn potik; I-J, upper lateral tooth (NNPM 2588-36) in I, lingual and J, labial views, layer C, Melanchyn potik; K-L, parasymphyseal tooth (NNPM 2588-37) in K, lingual and L, labial views, layer C, Melanchyn potik; M-N, one of Rogovich’s specimens, a lower lateral tooth (NNPM 391-37) in M, lingual and N, labial views. Scale bar equals 1 cm. [Full page width]


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- vertebrate fossils
- phosphatic concretions
- quaternary siltstones
- coarse-grained sands
- quartz-glaucocnite sands with sandstone inclusions

Kaniv Natural Reserve
Melanchyn potik
Maryin
Kholodnyi
Pekarskyi

Forested area

A
B
Kholodnyi

Upper Albian
Burin formation (upper part)

1 m

Kholodnyi
Melanchyn potik
Pekarskyi

0.5 m