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

3

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## Abstract

Sampling of six horizons of quartz-glaucinite 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, synchodontiforms, 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 pseudoscapnorhynchids 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

## 33 **1. Introduction**

34 Elasmobranchs (sharks, skates, rays and the extinct hybodonts) are mostly represented in the fossil  
35 record by dental remains (Glikman, 1980; Cappetta, 2012). Although known since the Permian  
36 (Ivanov, 2005), neoselachians (shark, skates and rays) remained relatively inconspicuous in marine  
37 ecosystems until the Jurassic when they experienced a series of radiations (Guinot and Cavin,  
38 2016). The Lower Cretaceous is another key period in the neoselachian evolutionary history and  
39 comprises the radiation of different groups including batoids, Carcharhiniformes and especially  
40 Lamniformes (Condamine et al. 2019), a group that comprises today most iconic shark species  
41 occupying specialized ecological niches. Lamniforms reached a high diversity in the Albian, both in  
42 terms of taxic richness and tooth morphologies (Guinot and Cavin, 2016). Despite the importance of  
43 this period in the understanding of elasmobranch evolution and diversity, data on Albian  
44 elasmobranch faunas is relatively scarce. Elasmobranch assemblages of this age are known from  
45 several locations in the world: Lithuania (Dalinkevičius, 1935; Mertiniene, 1975), Western  
46 Australia (Siverson, 1997; Siverson et al., 2018), Gault clay (Ward, 2010) and localities in of  
47 North-East England (Underwood and Mitchell, 1999), North-East France (Biddle, 1993), Russia  
48 and Kazakhstan (Glikman, 1980; Glikman and Averianov, 1998), Texas, USA (Welton and Farish,  
49 1993; Cappetta and Case, 1999; Siverson et al., 2007) and Poland (Siverson and Machalski,  
50 2017).

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

58

## 59 2. Geographical and Geological settings

60

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

86 layers encompass numerous phosphorite concretions that also yielded vertebrate fossils.

87 Burim formation deposits yielding vertebrate remains were found in three ravines on the territory of

88 Kaniv natural reserve (Fig. 1): Pekarskyi (coordinates: 49°42.568'N 31°32.558'E), Melanchyn

89 potik (49°43.325'N 31°30.788'E) and Kholodnyi (49°43.001'N 31°32.381'E). Two layers (E and

90 F) of quartz-glaucinite sands were sampled in Pekarskyi ravine. Layer E in Pekarskyi ravine is

91 correlated to layer E in Melanchyn potik ravine. Brachiopods of the genus *Lingula* and bivalves

92 *?Exogyra* are very common there. Typical feature of *?Exogyra* from this layer is very thick shells,

93 compared to *?Exogyra* from the other layers. This might be due to differences in water depth

94 between the layers, since paleogeographic conditions in this territory were unstable due to frequent

95 transgression and regression events and proximity of a large landmass (Ischenko and Yakushin,

96 2008). This layer lies on silica-cemented sandstones. Vertebrate remains are relatively rare. Layer F

97 in Pekarskyi ravine is characterized by pebbles, naturally rounded fossils and relatively common

98 elasmobranch teeth. Five layers of quartz-glaucinite sands were found in Melanchyn potik, only

99 four of them yielded fossil vertebrate remains. Three of them (A, B and C) are rich in elasmobranch

100 teeth, while layer E is identical to layer E in Pekarskyi ravine. Apart from elasmobranchs,

101 actinopterygian (*Protosphyraena*, Ichthyodectidae indet., *Pachyrhizodus*, Aspidorhynchidae indet.,

102 *Enchodus*, Pycnodontiformes indet., *Hadrodus*) and sauropsid (ichthyosaurs, plesiosaurs and

103 turtles) teeth and/or bones can be occasionally found. The invertebrate fauna of these layers

104 includes thin-shelled morphs of *?Exogyra* bivalves, gastropods of several genera including

105 Patellidae indet., crustaceans, extremely rare cephalopods (a fragment of *Mortoniceras* ammonite

106 and a fragment of unidentified belemnite rostrum) and, unlike layer E, no *Lingula* brachiopods.

107 Only one layer of elasmobranch tooth-bearing sands (layer A) was found in Kholodnyi ravine. Like

108 layers from Melanchyn potik and Pekarskyi ravines, Kholodnyi ravine sands also lay on sandstones,

109 which may contain conifer and occasional vertebrate remains (two shark teeth and several

110 osteichthyan bones were found there). Though, unlike in layer E, no brachiopods had been found in

111 this layer.

112

113 **3. Materials and methods**

114 Fossil elasmobranch teeth were obtained by bulk sampling and sieving using water and, on some  
115 occasions, dry sediment using sieve with 1 mm mesh size. A total of 3,268 elasmobranch teeth were  
116 recovered including 727 teeth from layer A of Melanchyn potik and Kholodnyi ravines; 126 teeth  
117 from layer B of Melanchyn potik; 2264 teeth from layer C in Melanchyn potik; no teeth were found  
118 in layer D of Melanchyn potik; 40 teeth from layer E of Melanchyn potik and Pekarskyi ravine and  
119 111 teeth were collected in layer F of Pekarskyi ravine. All studied specimens are housed in the  
120 Kiev National Natural History Museum of National Academy of Sciences of Ukraine, Geology  
121 department (shorten here to ‘Kiev Museum’) and are numbered NNPM2588-1 to NNPM2588-61.  
122 In addition, specimens illustrated by Rogovich (1861) are housed in the collection of the same  
123 institution.

124

125 **4. Systematic Palaeontology**

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

127 Class Chondrichthyes Huxley, 1880

128 Subclass Elasmobranchii Bonaparte, 1838

129 Cohort Euselachii Hay, 1902

130 Superfamily Hybodontoidae Owen, 1846

131 Family Hybodontidae Owen, 1846

132 Genus *Hybodus* Agassiz, 1837

133 *Hybodus bidentatus* Rogovich, 1861

134 Fig. 2A-D

135 1861 *Hybodus bidentatus* Rogovich, p. 23, pl. 3, fig. 13.

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

138 **Description.** Rogovich’s type specimen (NNPM 391-14; Fig. 2A-B) is an incomplete crown  
139 lacking the distal and mesial edges of the heels. The crown is robust, slightly inclined distally and

140 lingually. Both lingual and labial faces are strongly convex. Very fine cutting edges separate the  
141 labial and lingual faces and run continuously from the apex of the main cusp to the lateral heels.  
142 The heels are moderately high and mesio-distally elongate with at least one distal cusplet that is  
143 well separated from the main cusp by a large concavity. Short striations are present near the base on  
144 the lingual face of the main cusp and cusplets. The labial face bears several long folds that cover up  
145 to 2/3 of the crown's height. The specimen recovered from Melanchyn potik (NNPM 2588-1; Fig.  
146 2C-D) is an incomplete main cusp with similar shape and ornament to the type specimen. Both  
147 specimens are relatively small with main cusps not exceeding 5 mm.

148 **Remarks.** Although incomplete, Rogovich's type and only originally illustrated specimen agrees  
149 with the morphology of *Hybodus* species. Albian *Hybodus* species include *H. molimbaensis* Casier,  
150 1961 from the Aptian-Albian of Democratic Republic of Congo and *H. complanatus* Owen, 1869  
151 from the Upper Greensand of England, but both species are based on dorsal spines (*H. complanatus*  
152 specimen was not illustrated), which makes comparison with Rogovich's species impossible. Teeth  
153 of the latter can be differentiated from *Hybodus* material illustrated by Sweetman et al. (2014) from  
154 the Barremian of the Isle of Wight by their less marked and less numerous labial and lingual  
155 ornament as well as by its more gracile aspect with more elongate main cusp. Other mid-Cretaceous  
156 *Hybodus* species include the Cenomanian *H. eichwaldi* (Kiprijanoff, 1853), based on a dorsal spine.

157

#### 158 **Hybodontoides indet.**

159 Fig. 2E-F

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

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

165 **Remarks.** The crowns recovered display characters of *Merisodonoides* teeth including weak lingual  
166 and stronger labial folds, marked lingual curvature of main cusp and lingually positioned cutting

167 edges (Underwood and Cumbaa, 2010). However, lack of complete specimens precludes accurate  
168 identification of this material.

169

170 Order **Synechodontiformes** Duffin and Ward, 1993

171 Family **Paleospinacidae** Regan, 1906

172 Genus **Synechodus** Woodward, 1888

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

174 Fig. 2G-L

175 1861 *Hybodus kessleri* Rogovich, p. 21, pl. 3, figs 3-5.

176 ?1911 *Synechodus nitidus* Woodward, p. 219, figs 3-4.

177 ?1935 *Synechodus nitidus* Woodward; Dalinkevičius, p. 15, pl. 2, figs 40, 43-49 *non* figs 39, 41-42.

178 ?1999 *Synechodus nitidus* Woodward; Underwood and Mitchell, p. 5, pl. 1, fig. 6.

179

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

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

193 **Remarks.** The systematics of Albian *Synechodus* species is poorly understood despite the presence

194 of several partial articulated skeletal remains from France and England (see Mollen and Hovestadt,  
195 2018 for a review). Currently, seven nominal *Synechodus* species are known from the Albian-  
196 Cenomanian interval. *Synechodus dubrisiensis* (Mackie, 1863) was described from the Zig Zag  
197 Chalk Formation ('Grey Chalk', *Holaster subglobosus* zone, Cenomanian) of Dover (Kent,  
198 England); *S. tenuis* Woodward, 1889 is based on a single illustrated incomplete tooth from the  
199 Lower Greensand (Aptian-lower Albian) of Maidstone (Kent); *S. nitidus* Woodward, 1911 was  
200 erected based on a chondrocranium from the *Holaster subglobosus* zone, Cenomanian of Snodland  
201 (Kent). Other species include *Hybodus bronni* Reuss, 1846 and *Hybodus dispar* Reuss, 1846 both  
202 based on isolated teeth from the Cenomanian (Lower Plänerkalk) of Weisskirchlitz (= Novosedlice,  
203 Czech Republic) as well as *H. subulatus* Rogovich, 1861 and *H. kessleri* Rogovich, 1861 both from  
204 the mid-Cretaceous of Ukraine. Most discussions have focused on the taxonomic status and validity  
205 of *S. dubrisiensis*, *S. nitidus* and *S. tenuis*. The latter has been regarded as a senior synonym of *S.*  
206 *nitidus* (Batchelor and Ward, 1990; Biddle, 1993), while other hypotheses either consider *S. nitidus*  
207 junior synonym of *S. dubrisiensis* (Mollen and Hovestadt, 2018), both *S. nitidus* and *S. tenuis* as  
208 junior synonyms of *S. dubrisiensis* (Ward, 2010) or all three species considered valid (Siversson et  
209 al. 2017). These discrepancies are mainly due to the preservation of the specimens available for  
210 these species. *Synechodus dubrisiensis* is probably the species to which the largest number of  
211 articulated specimens have been referred, including articulated mandibular arches (of which, the  
212 holotype) some including hyoid arches (Woodward, 1886) or postcranial elements (Woodward  
213 1886), as well as a braincase (Maisey, 1985) and associated tooth sets (Woodward, 1888). In  
214 contrast, the holotype of *S. tenuis* is based on a single tooth (Woodward, 1889) and the holotype of  
215 *S. nitidus* [formerly attributed to *S. dubrisiensis* by Woodward (1889)] is represented by an  
216 articulated chondrocranium with associated teeth (Woodward, 1911). The main issue is the  
217 understanding of the intraspecific variability in tooth morphology for these three species. An  
218 articulated *Synechodus* specimen was recently described from the Albian Gault Clay of the  
219 Boulonnais, northern France (Mollen and Hovestadt, 2018). This specimen was reported to display  
220 *S. dubrisiensis*-like latero-posterior teeth with strong reticulate labial ornament but also weakly

221 ornamented (vertical labial folds) anterior teeth that were so far considered representative of *S.*  
222 *nitidus*. This heterodonty was considered as a clue in favor of a synonymy between *S. nitidus* and *S.*  
223 *durbisiensis* (Mollen and Hovestadt, 2018), which would respectively represent anterior and latero-  
224 posterior morphs of the same species. Nevertheless, the species-level assignment of the Boulonnais  
225 specimen is still unclear and it is uncertain whether *S. durbisiensis* also presents this heterodonty. In  
226 addition, differentiating teeth from upper and lower jaws in articulated specimens with associated  
227 teeth is sometimes made difficult by the mixing of teeth from both jaws. Teeth of an articulated  
228 tooth set (BMB 008523) illustrated by Woodward (1888, 1889, 1898, 1911) and studied by one of  
229 us (GG) displays strong reticulate ornament on all files (from parasymphysals to posteriors).  
230 However, it is unclear whether the articulated tooth set belongs to upper or lower jaws (see Mollen  
231 and Hovestadt, 2018). Hence, the hypothesis of a monognathic variation in labial ornament of *S.*  
232 *durbisiensis* teeth remains to be confirmed and, if present, would likely be present in upper or lower  
233 jaws only and/or during ontogeny. *Synechodus tenuis* was erected on the basis of a single  
234 incomplete tooth (Woodward, 1889: pl. 11, fig. 21) of which the sole illustration in labial view has  
235 long hampered precise understanding of the morphology and ornament of the holotype ([PV OR](#)  
236 [9297](#)). This specimen was illustrated by Batchelor and Duffin (in press: Fig. 1G-H) and by Bernard  
237 and Smith (2018) who also illustrated two additional specimens referred as paratypes ([PV OR](#)  
238 [9297a](#) and [PV OR 9297b](#)). Ward (2010) indicated that *tenuis*-like (and *nitidus*-like) teeth are present  
239 in specimen [PV OR 41675](#) (Woodward, 1886; Maisey et al. 2004) referred to *S. durbisiensis*, but  
240 this view has been challenged by Siversson and Machalski (2017). Based on available specimens,  
241 the morphology of the teeth of the type series of *S. tenuis* seems to depart from the variation so far  
242 observed in teeth of type specimens of *S. nitidus* and *S. durbisiensis* and might be better considered  
243 a separate species until revision of the available specimens.

244 Only one of the syntype specimens described by Rogovich (1861) as *Hybodus kessleri* was  
245 recovered in the collections of the Kiev Museum (Fig. 2G-H) and corresponds (original labels  
246 preserved) to the specimen figured in Rogovich (1861: pl. 3, fig. 4). Hence, we designate this

247 specimen (NNPM 391-10) as the lectotype of *Hybodus kessleri* following Article 74 of the ICZN  
248 (1999).. This specimen displays lingually-inclined and slender main cusp and cusplets as well as  
249 nearly smooth labial crown face (only scarce, fine and short ridges at the base of the two mesial-  
250 most cusplets). This morphology is very similar to that of the anterior tooth of the holotype of *S.*  
251 *nitidus* illustrated by Woodward (1912: pl. 46, fig. 3a) and Batchelor and Duffin (in press: Fig. 2F).  
252 The latter authors also noted that some other teeth (from more lateral jaw positions) may also bear  
253 coarse striations, which occasionally bifurcate basally (but not reticulated) and terminate two-thirds  
254 of the way up the central cusp. This type of ornament is also present in lateral teeth reported here  
255 from Kaniv, which are also referred to *S. kessleri* (Fig. 2I-L). The strong degree of similarity  
256 between the Kaniv specimens and the available specimens of *S. nitidus* might suggest synonymy  
257 (the latter would represent a junior synonym of *S. kessleri*). However, considering the confusion  
258 surrounding the validity of the species described from the mid-Cretaceous of England, this decision  
259 is tentative pending revision of dentition of the available *Synechodus* specimens.

260

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

262 Fig. 2M-R

263 1861 *Hybodus subulatus* Rogovich, p. 20, pl. 3, figs 6-11.

264 ?1889 *Synechodus tenuis* Woodward, p. 329, pl. 11, fig.21

265 1935 *Synechodus nitidus* Woodward; Dalinkevičius, p. 15, pl. 2, figs ?39, 41-42 *non* figs 40, 43-49.

266 ?1957 *Synechodus dispar* (Reuss); Glikman, p. 111, pl. 1, figs 1-5.

267 1964 *Synechodus dispar* (Reuss); Glikman, p. 20, pl. 5, figs 5-6.

268 1980 *Synechodus dispar* (Reuss); Glikman, pl. 15, figs 1-3 *non* figs 4-5.

269 **Material.** 91 complete and incomplete teeth including fragmented crowns: 2 from layer F of  
270 Pekarskyi ravine; 3 from layer A of Melanchyn potik ravine; 3 from layer B of Melanchyn potik  
271 ravine; 61 from layer C of Melanchyn potik ravine; 2 from layer E of Melanchyn potik ravine; 20  
272 from Kholodnyi ravine. All figured specimens come from layer C of Melanchyn potik (NNPM

273 2588-5, NNPM 2588-7), except NNPM 2588-6 that comes from layer B.

274 **Description.** Teeth are mostly small - less than 1 cm in height - however, there are some exceptions  
275 as described below. Two morphs can be differentiated. Teeth of the first morph (Fig. 2M-P) have no  
276 ornamentation on the labial face and display poorly pronounced short vertical ridges on the lingual  
277 face. These teeth are sigmoid in lateral view with a labial crown bulge as well as many short and  
278 poorly differentiated cusplets. Some specimens of this morph are extraordinarily large and massive  
279 (several specimens are almost 15 mm wide) and have smaller lateral cusplets compared to the other  
280 morphotypes. The labial crown bulge is hyper-developed especially below the heels. Teeth of the  
281 second morph (Fig. 2Q-R) are almost symmetrical and display a very weak sigmoid profile. These  
282 teeth are relatively labio-lingually compressed and generally no more than 7 mm high. The crown  
283 bears no labial enamel folds but weak vertical ridges on the lingual face and has three to four  
284 elongate cusplets. Cusplets are moderately wide and basally united with each other on each side of  
285 the tooth that reach up to  $\frac{1}{4}$  of the crown height. The root is pseudopolyaulacorhyze, as in the other  
286 morphotype.

287 **Remarks.** Although Rogovich's specimens of *Hybodus subulatus* could not be found in the  
288 collections of the Kiev Museum, the size and morphological variation observed in the specimens  
289 reported here comply with those of the specimens originating from the same area illustrated in  
290 Rogovich (1861) and are thus referred to *S. subulatus* comb. nov. Although none of the syntypes of  
291 *S. subulatus* were found, but we don't consider necessary to designate a neotype among our  
292 sampled specimens because the original illustrated specimens are of sufficient quality with no issue  
293 concerning the stability of nomenclature (ICZN, Art. 75). Lateral teeth from our samplings (Fig.  
294 2M-N), which display flatten and slightly ornamented (short vertical basal ridges) margino-labial  
295 regions as well as numerous incipient and poorly-individualized cusplets, are very similar to the  
296 type specimen of *S. tenuis*. Similarly, the large anterior teeth reported here, which are characterized  
297 by a massive and stubby crown with scalloped labial bulge, labially depressed basal region of the  
298 main cusp and poorly-individualized cusplets are comparable to the paratype of *S. tenuis* ([PV OR](#)  
299 [9297a](#)). It is therefore possible that *S. subulatus* and *S. tenuis* are synonyms but this cannot be

300 ascertained before a thorough revision of mid-Cretaceous *Synechodus* species. Glikman (1957,  
301 1964, 1980) illustrated several *Synechodus* specimens from the Cenomanian of Saratov that he  
302 referred to *S. dispar* (Reuss, 1846). Yet, the original illustrations of *S. dispar* (Reuss, 1846: p. 98,  
303 pl. 24, Figs 27-28) are very difficult to interpret and the possibly secondary anaulacorhize stage of  
304 the root of both specimens, the squared outline of the root lobes, along with the long lingual and  
305 possibly labial vertical ridges rather suggest affinities with lamniforms (e.g. *Scapanorhynchus*).  
306 However, specimens from Saratov include large and bulky anteriors with scalloped basal bulges on  
307 labial crown faces (e.g. Glikman 1964: pl. 5, fig. 5), which are similar to anteriors of *S. subulatus*  
308 (and possibly *S. tenuis*). *Synechodus dispar* specimens of Glikman (1957, 1964, 1980) also include  
309 lateral teeth with more developed cusplets and marked labial ornament made of vertical ridges (e.g.  
310 Glikman 1964: pl. 5, fig. 6) that could fall within the morphological variation of *S. subulatus* (and  
311 possibly *S. tenuis*). However, one specimen illustrated in Glikman (1980: pl. 15, figs 4-5) most  
312 probably belong to a carcharhiniform (e.g. *Protoscyliorhinus*). Contrary to *S. dispar*, the attribution  
313 of *Hybodus bronni* described by Reuss (1846) to the genus *Synechodus* is more likely. However,  
314 the two specimens illustrated by Reuss (1846: pl. 24, fig. 26, pl. 42, fig. 7) have an incomplete root  
315 and the drawings are insufficient to compare their morphology with other known species. This  
316 species, along with *H. dispar*, should be considered *nomina dubia*. Cappetta (2012) illustrated  
317 *Synechodus* teeth from the Santonian of Tyk Butak, Kazakhstan whose anterior teeth (and more  
318 generally teeth from all jaw positions) display the same general morphology as *S. subulatus* but bear  
319 coarser labial ornament, including on cusplets, which suggests that they represent a distinct species.  
320 It is interesting to note, however, that the material from Tyk Butak comprises teeth of the three mid-  
321 Cretaceous morphotypes (*tenuis*-like anteriors, *nitidus*-like laterals, and *dubrisiensis*-like  
322 posteriors). This may favor the hypothesis of a strong heterodonty in some Cretaceous *Synechodus*  
323 as proposed by Ward (2010). Alternatively, the absence of anterior gracile and cuspidate anterior  
324 teeth with reticulate ornament in the Kazakhstan assemblage may indicate that some *Synechodus*  
325 species retained the *dubrisiensis*-like reticulate ornament in posterior teeth only. This hypothesis is  
326 supported by the absence of *dubrisiensis*-like anteriors in our samplings. However, no posterior

327 teeth were found in Kaniv, which is likely due to the coarse mesh sizes used for sieving.

328

329 Order **Hexanchiformes** Buen, 1926

330 Family **Paraorthacodontidae** Glikman, 1958

331 Genus ***Paraorthacodus*** Glikman, 1957

332 ***Paraorthacodus recurvus*** (Trautschold, 1877)

333 Fig. 2S-T

334 1861 *Hybodus dispar* Reuss; Rogovich, p. 22, pl. 3, figs 12-12a.

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

336 1911 *Synechodus* sp.; Priem, p. 14, figs 1-2.

337 1935 *Synechodus recurvus* (Trautschold); Dalinkevičius, p. 17, pl. 2, figs 50-58.

338 1957 *Paraorthacodus recurvus* (Trautschold); Glikman, p. 115, pl. 1, figs 6-13.

339 1977 *Synechodus recurvus* (Trautschold); Gamble, p. 45.

340 1977 *Synechodus recurvus* (Trautschold); Herman, p. 30.

341 1993 *Paraorthacodus recurvus* (Trautschold); Biddle, p. 23, pl. 5, fig. 5.

342 1999 *Paraorthacodus recurvus* (Trautschold); Underwood and Mitchell, p. 6, pl. 1, fig. 7.

343 2010 *Paraorthacodus recurvus* (Trautschold); Ward, p. 282, pl. 52, fig. 9.

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

346 **Description.** Teeth are 1 to 1.5 cm in height. The crown is inclined lingually with coarse labial  
347 ornament consisting of strong parallel and vertical folds that originate from the basal edge to up to  
348 1/4 of the main cusp's height. Labial folds are also present on cusplets where they taper just before  
349 reaching the apex. Fine folds are present on the lower region of the lingual face of the main cusp  
350 and cusplets. The main cusp is bulky with a wide base that is marked by a constriction at the  
351 crown/root edge represented by a high collar. The cutting edges of the main cusp are coarse and  
352 positioned labially. The labial crown face is nearly flat with no labial bulge. Cusplets are rather  
353 gracile and well individualized from the main cusp and from each other by deep notches devoid of

354 enameloid. The root is typically pseudopolyaulacorhize with deep and wide notches on the labial  
355 half of the basal root face. The lingual root face strongly projects lingually.

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

366

367 Order **Squaliformes** Compagno, 1973

368 Family **Squalidae** Bonaparte, 1834

369 Genus ***Protosqualus*** Cappetta, 1977

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

371 Fig. 2U-V

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

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

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

381 would be needed to confirm this attribution.

382

383 Order **Squatiniformes** de Buen, 1926

384 Family **Squatinidae** Bonaparte, 1838

385 Genus *Squatina* Duméril, 1806

386 *Squatina (Cretascyllum) cranei* Woodward, 1888

387 Fig. 2W-X

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

389 1861 *Hybodus marginatus* Rogovich, p. 24, pl. 3 figs 15-16? *non* figs 14, 17-18.

390 2012 *Squatina (Cretascyllum) cranei* Woodward, Guinot et al., p. 532, figs 2-7.

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

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

400 **Remarks.** Teeth found in Kaniv compare well with those of *S. cranei* described by Woodward  
401 (1888) based on a crushed skull from the Sussex chalk (Guinot et al. 2012). There is some degree of  
402 confusion between Albian species *S. cranei* and *S. decipiens*. The latter was described by  
403 Dalinkevičius (1935) from the Cenomanian chalk of Lithuania, who indicated that the only  
404 difference between *S. decipiens* and *S. cranei* was the larger size of the former with no other evident  
405 morphological differences. Guinot et al. (2012) provided evidence that *S. decipiens* is a junior  
406 synonym of *S. cranei*, the former simply representing larger individuals of the same species. In  
407 addition, specimens in the same size range seem to be described by Rogovich (1861) as *Hybodus*

408 *marginatus* from the same locality to the material reported here. However, we did not recover  
409 Rogovich's specimens in the collections of the Kiev Museum.

410

411 Superorder **Galeomorphii** Compagno, 1973

412 Order **Orectolobiformes** Applegate, 1972

413 Family **Hemiscylliidae** Gill, 1862

414 Genus ***Chiloscyllium*** Müller and Henle, 1837

415 ***Chiloscyllium*** sp.

416 Fig. 3A

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

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

423 **Remarks.** This tooth somewhat resembles those of some Cretaceous *Chiloscyllium*, based on  
424 cusplet position relative to the crown and apron's morphology. The fossil record of mid-Cretaceous  
425 hemiscylliids is scarce and is restricted to some representatives of unknown affinities in the Albian  
426 of England reported as *Chiloscyllium* cf. *greeni* and cf. *Hemiscyllium* sp. (Underwood and Mitchell,  
427 1999). Batchelor and Ward (1990) illustrated one tooth assigned to *Chiloscyllium* sp. from the  
428 Aptian of the Hythe Beds in England that agrees with the tooth morphology of extant  
429 representatives of the genus. The crown morphology of the specimen reported here fits that of the  
430 Aptian specimen but the preservation of the Kaniv specimen precludes further comparison.

431

432 **Orectolobiformes incertae fam.**

433 Genus ***Cederstroemia*** Siverson, 1995

434 ***Cederstroemia*** cf. *siverssoni* Guinot, Underwood, Cappetta and Ward, 2013

435

Fig. 3B-C

436 1861 *Hybodus marginatus* Rogovich, p. 24, pl. 3 figs 14, 17 *non* figs 15-16?-18.

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

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

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

459

460 Order **Heterodontiformes** Berg, 1940

461 Family **Heterodontidae** Gray, 1851

462 Genus *Heterodontus* de Blainville, 1816

463 *Heterodontus upnikensis* (Dalinkevičius, 1935)

464 Fig. 3D-E

465 1935 *Cestracion upnikensis* Dalinkevičius, p. 13, pl. 1, figs 29-33.

466 1977 *Heterodontus upnikensis* (Dalinkevičius); Herman, p. 86.

467 1993 *Heterodontus upnikensis* (Dalinkevičius); Biddle, p. 11, pl. 2, figs 2-3.

468 1999 *Heterodontus canaliculatus* (Egerton in Dixon, 1850); Underwood and Mitchell, p. 17, pl. 4,  
469 figs 5-8.

470 2010 '*Heterodontus*' *upnikensis* (Dalinkevičius); Ward, p. 286, pl. 53, fig. 5.

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

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

482 **Remarks.** Original description of this species by Dalinkevičius (1935) includes large anterior teeth  
483 that are very similar to Kaniv specimens as well as lateral teeth that are strongly ornamented and do  
484 not appear to display any characters in common with the anterior teeth (Ward, 2010). In addition to

485 describing *H. upnikensis* teeth from the Jiesia Formation of Lithuania, Dalinkevičius (1935) also  
486 described *H. canaliculatus* teeth from the same Formation and it might be possible that some  
487 laterals assigned to *H. upnikensis* actually belong to this species. A revision of Dalinkevičius'  
488 original material is needed to clarify these attributions. Underwood and Mitchell (1999) reported  
489 anterior and anterolateral teeth from the Albian and Cenomanian of England that were referred to *H.*  
490 *canaliculatus*. However, anterior teeth show similar features to those of *H. upnikensis* and lateral  
491 teeth are smooth or weakly labially ornamented. Biddle (1993) illustrated some anterior and  
492 anterolateral teeth from the Albian of France as *H. upnikensis*, showing similar features to  
493 Underwood and Mitchell's (1999) specimens (absence of cusplets and enamel ornamentation).  
494 However, specimens from the French and English Albian are comparatively smaller than those from  
495 Lithuania and Ukraine. Considering the large size of the latter specimens it is unlikely that *H.*  
496 *upnikensis* represents juveniles of *H. canaliculatus*. However, the part of ontogenetic variation  
497 coupled with questions on the morphology of lateral teeth from the type locality preclude definite  
498 conclusions on the morphological variation and even on the validity of this species (Underwood and  
499 Mitchell, 1999).

500 *Heterodontus* aff. *canaliculatus*

501 Fig. 3F-N

502 1861 *Lamna (Odontaspis) minuta*, Rogovich, p. 52, pl. 7, fig. 22.

503 1861 *Acrodus rugosus* Agassiz; Rogovich, p. 17, pl. 2, fig. 11.

504 **Material.** Two anterior teeth and 33 lateral teeth (21 lateral teeth from Melanchyn potik layer C,  
505 one lateral tooth from layer E, nine lateral teeth from Kholodnyi, two lateral teeth from layer F of  
506 Pekarskyi ravine), all figured specimens come from layer C (NNPM 2588-13 and NNPM 2588-14).  
507 Additional specimen: Rogovich (1861)'s specimen (NNPM 391-1).

508 **Description.** Anterior teeth are cuspidate, up to 5 mm in adult specimens and possess a triangular

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

528 **Remarks.** Adult anterior teeth of *H. aff. canaliculatus* are morphologically close to those of *H.*  
529 *canaliculatus* (Egerton in Dixon, 1850) but differ in having a crown with less broad and more  
530 individualized cusplets as well as narrower concavity in the base edge of the apron. However, the  
531 intraspecific variability of *H. canaliculatus* teeth is imperfectly known and it is unclear whether  
532 these differences are part of intra- or interspecific variation. Similarly, short irregular and sub-  
533 horizontal folds are rarely present on the apron of some anterior teeth of *H. canaliculatus* but some  
534 display entirely smooth crowns, as in the material described here. In addition, lateral teeth of *H. aff.*

535 *canaliculatus* are devoid of median tubercle on the occlusal face whereas this feature is present in  
536 lateral *H. canaliculatus* teeth (Woodward, 1912: pl. 45, figs 1-5), although less marked in the type  
537 specimen (Egerton, 1855). Some lateral teeth from the Albian of Lithuania (Dalinkevičius, 1935)  
538 attributed to *H. upnikensis* might be similar to the specimens described here but the quality of the  
539 original illustrations precludes further comparison with the material from Ukraine. *Lamna*  
540 (*Odontaspis*) *minuta* Rogovich, 1861 was based on a minute juvenile anterior *Heterodontus* tooth  
541 (Fig. 3F-G) attributed here to *H. aff. canaliculatus*. Considering the low systematic value of  
542 juvenile teeth, the taxon name erected by Rogovich (1861) would be better regarded as *nomen*  
543 *dubium*. Another specimen reported by Rogovich (1861: pl. 3, fig. 18) as *Hybodus marginatus*  
544 probably represents an anterior *Heterodontus* tooth in lingual view, but it is unclear whether it more  
545 closely resembles *H. upnikensis* or *H. canaliculatus*. Similarly, Rogovich (1861: pl. 2, fig. 11)  
546 reported the species *Acrodus rugosus* Agassiz, 1939 that most probably represents a lateral tooth of  
547 *H. aff. canaliculatus*.

548

549 Order **Lamniformes** Berg, 1958

550 Family **Anacoracidae** Casier, 1947

551 *Squalicorax* sp.

552 Fig. 3, O-P

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

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

561 **Remarks.** This specimen bears a combination of *Squalicorax* tooth characteristics including a long

562 distal cutting edge and strong distal curvature, a wide distal heel, strong labio-lingual compression  
563 and serrated distal edge of main cusp. However, the preservation of this unique specimen precludes  
564 further identification.

565

566 Family **Archaeolamnidae** Underwood and Cumbaa, 2010

567 Genus *Archaeolamna* Siverson, 1992

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

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

570 1861 *Otodus striatus*, Rogovich, p. 41, pl. 5, fig. 13 *non* fig. 14.

571 ? 1999 *Carcharias* sp. Cumbaa and Tokaryk, p. 61, fig. 5 (pars: upper 3 teeth center right column).

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

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

588 **Remarks.** The species *Otodus striatus* was described by Rogovich (1861: pl. 5, figs 13-14) based

589 on two teeth that were present in the collection of the Kiev museum. Although one tooth (Rogovich,  
590 1861: pl. 5, fig. 14) probably belongs to an undetermined lamniform, the other one (Rogovich,  
591 1861: pl. 5, fig. 13) conforms with the tooth morphology of the material recovered in our sampling  
592 that present both the heterodonty and tooth morphology of *Archaeolamna* species. This latter tooth  
593 (NNPM 391-2) is here designated as the lectotype of *Otodus striatus*. Teeth of *Archaeolamna*  
594 *striata* comb. nov. exhibit some similarities with the Cenomanian *Archaeolamna* ex. gr. *kopingensis*  
595 described by Underwood and Cumbaa (2010) from Canada in having a gracile morphology with  
596 occasional labial enamel folds in upper lateroposterior and posterior teeth. However, teeth from the  
597 Canadian Cenomanian, as well as those from the English Gault Clay (Ward, 2010) have more  
598 developed root lobes and more marked lingual protuberance of the root. Similar gracile specimens  
599 were also figured by Biddle (1993) from the Albian of France as *Archaeolamna kopingensis* that  
600 mostly differ from *A. striata* comb. nov. by their more marked medio-lingual nutritive groove and  
601 might be closely related if not conspecific with *A. striata* comb. nov. Other taxa from the Albian-  
602 Cenomanian interval described as *Archaeolamna*, such as *A. haigi* and *A. aff. kopingensis* reported  
603 by Siversson (1996) and *Archaeolamna* sp. (Vullo et al., 2007) are much more robust than *A. striata*  
604 comb. nov.

605

606 *Archaeolamna* ex. gr. *kopingensis* (Davis, 1890)

607 Fig. 4M-T

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

611 **Description.** Collected specimens display gradient monognathic and dignathic heterodonty. These  
612 teeth are relatively large (up to 15 mm high) and robust with wide triangular main cusp and  
613 cusplets. Cusplets are low and well separated from the main cusp by a notch. In lateral teeth, the  
614 cutting edges of the main cusp can present a marked convexity that forms an incipient cusplet, just  
615 before the notch (e.g., Fig. 4S-T). The basal edge of the main cusp shows no or very weak labial

616 bulge, only a weak depression in the center. A strong lingual protuberance is present, pierced by a  
617 large central foramen. Root lobes are rather short and bulky with rounded labial extremities except  
618 in lateral teeth where they form a sharp angle.

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

625

626 Family **Otodontidae** Glikman, 1964

627 Genus ***Cretolamna*** Glikman, 1958

628 ***Cretolamna*** sp.

629 Fig. 4U-V

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

631 **Description.** These anterior teeth have a gracile, elongate and weakly sigmoid main cusp. Main  
632 cusp can constitute up to  $\frac{3}{4}$  of the tooth height, as in NNPM 2588-30. The main cusp is flanked by a  
633 pair of short, triangular and diverging cusplets separated from the main cusp by a slight notch. The  
634 labial crown base has a central enamel depression. The relatively symmetrical root bears a strong  
635 lingual protuberance devoid of nutrient groove.

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

642

643 Family **Cretoxyrhinidae** Glikman, 1958

644 Genus **Cretoxyrhina** Glikman, 1958

645 **Cretoxyrhina vracconensis** Zhelezko, 2000

646 Fig. 4W-X, Fig. 5

647 1861 *Otodus appendiculatus* (Agassiz) [partim]; Rogovich, p. 39, pl. 5, figs 1-5 *non* figs 6-11.

648

649 1993 *Cretalamna appendiculata* (Agassiz) [partim]; Welton and Farish, p. 103, fig. 2, p. 104,

650 second tooth from the left in the upper jaw.

651 2000 *Pseudoisurus vracconensis* Zhelezko [partim]; Zhelezko, p. 138, pl. 1, figs 3-4 *non* fig. 5

652 (*Cretalamna* sp).

653 2009 *Cretoxyrhina* aff. *vracconensis* (Zhelezko); Ward, p. 291, pl. 54, figs 6-7.

654 2013 *Cretoxyrhina vracconensis* (Zhelezko); Siverson et al., p. 97, figs 4-9.

655 2017 *Cretoxyrhina vracconensis* (Zhelezko); Siverson and Machalski, p. 18, figs 4-9.

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

659 **Description.** Teeth of this species are characterized by triangular crowns with smooth lingual faces,  
660 a pair of broad triangular cusplets and no nutrient groove on the root. Found specimens are rather  
661 large, with anterior teeth sometimes exceeding 4 cm high (e.g., Fig. 5, C-D). In profile view, teeth  
662 are curved labially near the apex. The labial crown face generally has one or two short vertical  
663 bulges in the center near the base. Cusplets are large, rounded, and diverging. They connect to the  
664 main cusp via a thin enameloid band incised by narrow but relatively deep notch. Parasymphyseal  
665 teeth are mesio-distally compressed and have both distally and labially inclined crown. Root lobes  
666 are reduced and oriented. Antermost teeth have a marked and short heel or reduced cusplets and  
667 are mesiodistally compressed. More distal anterior teeth have small cusplets and sometimes thick  
668 dental band. Upper laterals have a slightly distally inclined main cusp. Juvenile teeth have high but  
669 rounded cusplets (e.g., Fig. 5, A-B). Folds on the lingual face of the cusplets may be present in

670 lateroposterior teeth. However, some other teeth attributable to this species have very broad but  
671 triangular and sharp cusplets (e.g., Fig. 4W-X, Fig. 5E-F, and Rogovich's specimen Fig. 5, M-N).  
672 They are similar to the other morphotype in having a protuberance on the root above each cusplet  
673 and a very strong lingual bulge.

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

689

690 Family **Paraisuridae** Herman, 1979

691 *Paraisurus* Glikman, 1957

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

693 Fig. 6A-F

694 1858 *Oxyrhina macrorhiza* Pictet and Campiche, pl. 10, figs 8-10.

695 1861 *Otodus monstrosus* Rogovich, pl. 5, fig. 12.

696 1889 *Oxyrhina macrorhiza* (Pictet and Campiche); Woodward, p. 381.

697 1987 *Paraisurus macrorhiza* (Pictet and Campiche); Cappetta, p. 101, fig. 89D-F.

698 2010 *Paraisurus macrorhizus* (Pictet and Campiche); Ward, pl. 55, fig. 3.

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

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

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

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

718

719 Family *Pseudoscapanorhynchidae* Herman, 1979

720 Genus *Protolamna* Cappetta, 1980

721 *Protolamna* cf. *sokolovi* Cappetta, 1980

722 Fig. 6G-Q

723 ?1861 *Otodus appendiculatus* (Agassiz) [partim], Rogovich, p. 39, pl. 5, figs 6, 10-11 *non* figs 1-5,

724 7-9.

725 **Material.** 40 teeth (three from layer A, 29 from layer C of Melanchyn potik, including NNPM 2588  
726 39-43, three from layer E, two from layer E of Pekarskyi, three from Kholodnyi)

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

736 **Remarks.** Kaniv specimens resemble *Protolamna sokolovi* teeth described in Cappetta (1975,  
737 1980) from the Aptian of France by having no labial ornament in anterior and most lateral teeth,  
738 weak nutrient furrow, similar shape of main cusp and weak lingual ornamentation. However, teeth  
739 of *P. sokolovi* are more robust than Kaniv specimens and display compressed root lobe extremities,  
740 less diverging cusplets and stronger lingual root protuberance in lateral teeth. Kaniv specimens bear  
741 resemblances with teeth of *Protolamna* sp. from Cenomanian of United Kingdom (Guinot et al.,  
742 2013). However, the Cenomanian specimens have pronounced lingual folds and much wider and  
743 more erect cusplets. Specimens from the Albian of Poland reported as *Protolamna* sp. (Siversson  
744 and Machalski, 2017) differ from the teeth described here by their marked labial and lingual face in  
745 most teeth. Teeth of *P. carteri* Cappetta and Case, 1999 from the Cenomanian Woodbine Fm. of  
746 Texas and *P. roanokeensis* from Albian Pawpaw sands of Texas have strong ornamentation on the  
747 lingual crown face and exhibit relatively gracile morphology. Rogovich (1861) reported several  
748 specimens as *Otodus appendiculatus*, some of which (Rogovich, 1861: pl. 5, figs 6, 10-11) showing  
749 a morphology that could fall within the variation found in the material described here, but these  
750 specimens have not been found in the collection of the Kaniv Museum. The tooth that Rogovich

751 (1861: pl. 7, fig. 14) illustrated for his species *Lamna (Odontaspis) ornata* differs in having strong  
752 labial enamel ornamentation and double cusplets on each side of the tooth. Considering the lack of  
753 accurate illustration and likely loss of the type specimen of *Lamna (Odontaspis) ornata*, it is not  
754 possible to assess the identification of this tooth and it is preferable to consider this species *nomen*  
755 *dubium*.

756

757 Genus *Pseudoscapanorhynchus* Herman, 1977

758 *Pseudoscapanorhynchus compressidens* Herman, 1977

759

Fig. 6R-Z

760 1977 *Pseudoscapanorhynchus compressidens* Herman, 192, pl. 7, fig. 8.

761 1991 *Protolamna acuta* Müller and Diedrich, 36, pl. 8, figs 4–6.

762 1999 *Protolamna compressidens* Herman; Cappetta and Case, 25, pl. 12, figs 1, 2.

763 2007 *Pseudoscapanorhynchus compressidens* Herman; Vullo et al., p. 101.

764 2013 *Pseudoscapanorhynchus compressidens* Herman; Guinot et al., p. 639, Fig. 18A-I.

765

766 **Material.** 45 partial and complete teeth (1 from layer A, 1 from layer B, 31 from layer C of

767 Melanchyn potik, including NNPM 2588 44-46, 11 from Kholodnyi).

768 **Description.** Teeth are mostly around 1 cm high and have a strongly sigmoid in profile view and  
769 mesio-distally compressed crown. The lingual crown face is strongly convex, while the labial is  
770 only slightly convex. The labial face is reduced because of the labial position of the cutting edges,  
771 which end before reaching the base of the crown. The labial base of the cusplets usually has two to  
772 three vertical and short parallel wrinkles. Lateral cusplets are elongate, labially positioned relative  
773 to the main cusp and are fully individualized. The basal region of the labial crown face is strongly  
774 mesio-distally compressed in labial view. The root has a strong lingual protuberance with a weak  
775 nutrient furrow. In the teeth positioned closer to jaw symphysis, root lobes are almost completely  
776 merged (e.g., Fig. 6X-Z). No complete lateral teeth have been found – only crowns with partially  
777 preserved roots.

778 **Remarks.** The morphology and size of Kaniv specimens agree with the original description of *P.*  
779 *compressidens* by Herman (1977) based on teeth from Cenomanian to Coniacian sites of Belgium  
780 and France. This species has been reported from numerous Cenomanian-Coniacian localities in  
781 Europe as well as from the Albian of France (Biddle, 1993) as *Leptostyrax macrorhiza* (see Guinot  
782 et al. 2013). Teeth attributed to this species are generally incomplete due to the gracile and elongate  
783 root lobes and cusplets and it is difficult to assess the taxonomical content included in Albian to  
784 Coniacian *P. compressidens*, which might include more than one species.

785

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

787 *Eostriatolamia* Glikman, 1979

788 *Eostriatolamia subulata* (Agassiz, 1843)

789 Fig. 6A'-D'

790 1843 *Lamna (Odontaspis) subulata* Agassiz, vol. 3, p. 206, pl. 37a, figs. 5-6.

791 1861 *Lamna (Odontaspis) subulata* (Agassiz); Rogovich, p. 52, pl. 7, figs 19-21 non fig. 17, 18.

792 1935 *Odontaspis subulata* (Agassiz); Dalinkevičius, pl. III, figs 77-83

793 1977 *Scapanorhynchus subulatus* (Agassiz); Herman, pl. 7, fig. 5.

794 1991 ?*Eostriatolamia subulata* (Agassiz); Müller and Diedrich: p. 29, pl. 21, fig. 1-6.

795 2013 *Eostriatolamia subulata* (Agassiz); Guinot et al., p. 647, figs 21J-R.

796 2017 Carchariidae indet.; Siversson and Machalski, p. 23, Figs 6L-R.

797

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

801 **Description.** Teeth are generally less than 1 cm high with strongly convex lingual face and slightly  
802 convex to flat labial face. Anterior teeth rarely exceed 1 cm, such (e.g., Fig. 6A'-B'). The crown is  
803 sigmoid in profile view. The lingual crown face is finely striated, while the labial face has several  
804 short vertical folds in anterior teeth, and many short folds near the base of the crown in laterals.

805 Ornamentation tends to be more marked on cusplets compared to the main cusp. The basal edge of  
806 the labial crown face bears a marked bulge in anterior teeth, whereas it is less developed in laterals.  
807 The cusplets are elongate, needle-like and slightly curved towards the main cusp. Cusplets are  
808 positioned labially relative to the main cusp – a feature that is more marked in anterior teeth – and  
809 connected to the main cusp via a thin enameloid band. The root bears a generally narrow but  
810 complete nutrient groove in most teeth. The lingual root protuberance is wide but moderately  
811 developed. The distal extremity of the root lobes is slightly labio-lingually compressed.

812 **Remarks.** The species *E. subulata* was described by Agassiz (1843) based on anterior teeth from  
813 the Upper Cretaceous of Germany that might not be conspecific. The absence of precise  
814 stratigraphic data and lack of accurate illustration of original material led Siversson and Machalski  
815 (2017) to consider this species *nomen dubium* and to question the inclusion of this species within  
816 the genus *Eostriatolamia*. Dalinkevičius (1935) reported this species from the Jiesia Formation in  
817 Lithuania and the specimens described here fit the morphology of the Lithuanian specimens, as well  
818 as that of specimens from the Albian of Poland (Siversson and Machalski, 2017) and Cenomanian  
819 of England (Guinot et al. 2013). Rogovich (1861) figured several specimens as *Lamna (Odontaspis)*  
820 *subulata*. However, only specimens on pl. 7, fig. 19-21 are attributable to this species, whereas,  
821 based on the drawings, specimens on fig. 17-18 are more likely to belong to a *Protolamna* species.  
822 Many other reports of this species are questionable (Guinot et al. 2013) and it is preferred here to  
823 limit the included specimens to those mentioned above, pending revision of the species.

824

825 *Eostriatolamia striatula* (Dalinkevičius, 1935)

826

Fig. 6E'-L'

827 1861 *Lamna (Odontaspis) gracilis* (Agassiz); Rogovich, p. 51, pl. 7, figs 15-16a.

828 1935 *Odontaspis (Synodontaspis) striatula* Dalinkevičius; p. 268, pl. 4, figs 84-95.

829 1975 *Carcharias striatula* (Dalinkevičius); Cappetta, p. 122, pl. 1, figs 1-7.

830 1977 *Palaeohypotodus striatula* (Dalinkevičius); Herman, p. 229, pl. 10, fig. 1.

831 1993 *Carcharias striatula* (Dalinkevičius); Biddle, p. 13, pl. 3, figs 3-4.

832 1997 *Carcharias striatula* (Dalinkevičius); Siverson, p. 461, figs. 4T-W.

833 2010 *Eostriatolamia striatula* (Dalinkevičius); Cappetta, fig. 156B.

834 2010 *Carcharias striatula* (Dalinkevičius); Ward, p. 290, pl. 54, figs 1-3.

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

837 **Description.** Teeth are less than 1 cm in height and show monognathic, and possibly dignathic  
838 heterodonty. The crown is slender and slightly mesio-distally compressed, unlike the root that is  
839 only labio-lingually compressed. The main cusp is very slightly sigmoid in profile view. The lingual  
840 crown face is very finely striated, while the base of the labial face only sometimes exhibits short  
841 parallel folds. The labial crown base of some lateral teeth displays a short central bulge (Fig. 6E'-  
842 F'). Lateral cusplets have a slightly wider base relative to the shape of the main cusp and are up to  
843 1/3 of the crown height. The lingual root face bears a sharp and wide bulge. A narrow nutrient  
844 groove is present but weakly marked in some lateral teeth.

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

852

### 853 **Lamniformes indet. 1**

854 Fig. 6M'-N'

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

856 **Description.** The only specimen referred to this species is a lower lateral tooth with a very robust  
857 and wide root and a short symmetrical non-sigmoid main cusp. It is flanked by a pair of gracile and  
858 triangular lateral cusplets. The cusplets are separated from the main cusp by a wide concavity that

859 bears some indentations, which can resemble incipient cusplets. The mesial and distal edges of the  
860 cusplets are made of a sharp blade of enameloid that overhangs the root. The basal region of the  
861 labial crown face displays a short vertical fold in its center. The root has a well-developed lingual  
862 protuberance displaying a small nutritive foramen. The labial root face bears a median depression.  
863 **Remarks.** This specimen bears resemblances with *Archaeolamna* teeth but differs in several ways:  
864 1) root robustness combined with crown gracility; 2) absence of a central labial base enamel  
865 depression, typical of all Kaniv *Archaeolamna* teeth and, instead, presence of a long central fold,  
866 that is more often seen in *Cretoxyrhina vraconensis* from the same locality, suggesting that it might  
867 be a pathological juvenile *Cretoxyrhina* tooth.

868

## 869 **Lamniformes indet. 2**

870 Fig. 6O'-P'

871 1861 *Otodus striatus*, Rogovich, p. 41, pl. 5, fig. 14 *non* fig. 13.

872 ?1861 *Otodus appendiculatus* (Agassiz) [partim], Rogovich, p. 39, pl. 5, fig. 9 *non* figs 1-8, 10-11.

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

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

883 **Remarks.** This specimen was one of the two illustrated specimens that Rogovich (1861) attributed  
884 to *Otodus striatus*. However, unlike the other specimen assigned here to *Archaeolamna striata*, this  
885 specimen exhibits a different morphology with much more elongate and mesio-distally compressed

886 cusps. Elongate cusplets are present in two of the other genera found in the sampled horizons –  
887 *Eostriatolamia* and *Protolamna*. However, the specimen described here is more robust than  
888 *Eostriatolamia* teeth having a large lingual root protuberance. Lateral teeth attributed to *Protolamna*  
889 found in our samples from the Burim formation deposits have a comparable enamel folding pattern  
890 but do not display such a strong distal curvature of the main cusp and differs in the morphology of  
891 the cusplets. Lack of additional material for this morph does not allow to make definite  
892 identification of this specimen. Another specimen illustrated by Rogovich (1861: pl. 5, fig. 9) might  
893 correspond to this taxon.

894

## 895 **5. Discussion**

### 896 **5.1. Geological age of Kaniv elasmobranch fauna**

897 Elasmobranch remains from Kaniv dislocations were previously reported in the literature, but most  
898 of available works on this topic is either outdated (Rogovich, 1861) or provided no descriptions or  
899 illustrations (Glikman 1964; Mertiniene 1975; Glikman 1980; Glikman and Averianov 1998;  
900 Popova et al. 2015). Specimens of Rogovich (1861), Glikman (1964) and Mertiniene (1975) come  
901 from Maryin and Kostyaneckyi ravines (Selyschi village) and from Kaniv city, whereas locations  
902 studied here (Kholodnyi, Pekarskyi and Melanchyn potik ravines) remained undescribed. As of  
903 2018, we were not able to find any exposures of vertebrate-bearing strata in Maryin ravine, it is  
904 likely that they were covered by landslides since the time of Glikman's and Mertiniene's research.  
905 In the Kostyaneckyi ravine, we have not found any Cretaceous exposures either. The only  
906 vertebrates known from this location come from the Eocene Buchak formation (Zvonok, 2011).  
907 Rogovich (1861) published a detailed account of elasmobranch taxa found in the Kaniv Cretaceous,  
908 including the description of eleven new species. Among all Rogovich's illustrated specimens, only  
909 seven were identified in the current collections of the Kiev Museum (Table 1), corresponding to the  
910 following species described by Rogovich (1861): *Otodus monstrosus* (= *Paraisurus macrorhizus*),  
911 *Otodus striatus* (= *Archaeolamna striata* and *Lamniformes* indet. 2), *Lamna minuta* (= *Heterodontus*  
912 aff. *canaliculatus*), *Hybodus bidentatus*, and *Hybodus kessleri* (= *Synechodus kessleri*); along with

913 one specimen originally referred to *Otodus appendiculatus* (= *Cretoxyrhina vracconensis*). All other  
914 specimens were unfortunately lost, including those of the following species described by Rogovich:  
915 *Sphaenonchus* (= *Asteracanthus*) *compressus*, *Hybodus* (= *Polyacrodus*) *parvus*, *Oxyrhina* (=   
916 lamniform indet.) *pygmaea*, *Hybodus* (= *Polyacrodus*) *tuberculatus*, *Lamna* (*Odontaspis*) *ornata* (=   
917 *Protolamna* sp.), *Hybodus* (= *Synechodus*) *subulatus*, and *Hybodus* (= *Cederstroemia* pars.)   
918 *marginatus*. Although none of Rogovich's specimens were found for the species *Asteracanthus*  
919 *compressus*, *Polyacrodus parvus* and *Polyacrodus tuberculatus*, it is preferred to consider these  
920 species names as valid pending further sampling and/or information on the whereabouts of the  
921 missing specimens of Rogovich's collection. Our samplings have resulted in the identification of 22  
922 elasmobranch species (Table 2) represented by 7 different orders: Hybodontiformes,  
923 Synechodontiformes, Squatiniformes, Orectolobiformes, Heterodontiformes, Squaliformes and  
924 Lamniformes, as well as one undetermined lamniform specimen (Lamniformes indet. 1). This  
925 combination of taxa is generally typical of mid-Cretaceous deposits (Guinot et al., 2013; Siversson  
926 and Machalski, 2017). However, some aspects such as absence of batoids and rarity of hybodonts  
927 are somewhat unusual, as discussed below.

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

934 Glikman (1964) described following genera and species: *Squatina* sp., *Paraorthacodus* sp.,  
935 *Synechodus* sp., *Eostriatolamia gracilis*, *Paraisurus macrorhiza*, *Cretoxyrhina* sp., *Notidanus* sp.  
936 and *Scapanorhynchus* sp. Out of this list, only *Notidanus* and *Scapanorhynchus* teeth had not been  
937 found in our samplings. Glikman (1964) also noted that *Gyropleurodus*, *Meristodon*, *Cretaspis*,  
938 *Squalus* and *Polyacrodus* were absent from studied collections. Names for most of these genera are  
939 outdated , however orders to which they belong - heterodontiforms (= *Gyropleurodus*), hybodonts

940 (= *Meristodon* and *Polyacrodus*) and squaliforms (= *Squalus*) have been found in our samplings,  
941 except “*Cretaspis*” (= *Hispidaspis*), though mostly in small amounts. Strangely, no species that  
942 could correspond to *Archaeolamna* - the second most common lamnoid genus in Kaniv - were  
943 mentioned by Glikman (1964).

944 Both Mertiniene (1975) and Glikman (1964) described Kaniv elasmobranch fauna as late Albian in  
945 age, but the lack of illustrations or specimen descriptions made it hard to support their conclusions.  
946 Our samplings, although collected in different locations from those of Mertiniene (1975) and  
947 Glikman (1964), confirm the late Albian age for Kholodnyi, Pekarskyi and Melanchyn potik  
948 ravines: *Paraisurus macrorhizus* is known through Late Aptian to Late Albian, *Cretoxyrhina*  
949 *vracoenensis* occurs in uppermost Albian and lowermost Cenomanian (Siverson et al., 2013;  
950 Zhelezko, 2000). According to Glikman and Averianov (1998), *Eostriatolamia gracilis* and *E.*  
951 *subulata* are chronospecies with *E. gracilis* being an Albian species, whereas morphological  
952 differences between these two taxa are very minor (Glikman, 1964) indicating that their material is  
953 probably conspecific. Although *Eostriatolamia subulata* was initially reported from the  
954 Cenomanian of Lithuania (Dalinkevičius, 1935), reevaluation of these strata led to believe that they  
955 actually are Late Albian in age (Adnet et al., 2008). This species is also extensively described from  
956 Cenomanian of Europe and Asia (Glikman, 1980; Guinot et al., 2013). Glikman (1980) suggested  
957 that the Anacoracidae play an important stratigraphical role because of their higher variation in  
958 serration parameters and general tooth morphology. The anacoracid tooth found in Pekarskyi  
959 ravine, although poorly preserved, displays characteristics of Albian *Squalicorax* species including:  
960 1) longer distal cutting edge and stronger distal curvature; 2) small cusplet on the distal side of the  
961 tooth; 3) crown slightly labio-lingually compressed; 4) coarsely serrated distal side. This specimen is  
962 somewhat similar to *Squalicorax priscoserratus* or *S. pawpawensis* from Texas Pawpaw shale  
963 (Siverson et al., 2007), *Squalicorax* sp. from Poland (Siversson and Machalski, 2017) that are  
964 Albian in age. However, because of the poor preservation of our specimen, it is impossible to  
965 confirm that it actually belongs to one of the named species. Overall, our findings are consistent  
966 with the late Albian or possibly lowermost Cenomanian age of the Burim formation vertebrate-

967 bearing strata, particularly layer C of Melanchyn potik ravine due to greater concentration of  
968 specimens and abundance of *P. macrorhizus* and *C. vracconensis*. For other layers, a similar age can  
969 be inferred based on geographical and stratigraphical proximity to layer C and overall similarity of  
970 the assemblages, which do not show any marked faunal transitions. In addition, all layers other than  
971 A and B are positioned below layer C indicating older age. Layers A and B have a much lower  
972 concentration of specimens but available findings are highly congruent with data from layer C. This  
973 conclusion is also confirmed by paleogeographic studies of the region that constrain the age of the  
974 Burim formation marine deposits to Middle Albian – Cenomanian because in the Aptian and Lower  
975 Albian depositional environment was terrestrial over most of the territory of modern Ukraine  
976 (Menasova and Tymchenko, 2018).

977

## 978 **5.2. Albian elasmobranch faunas**

979 Sharks from the described faunal complex are mostly small, the largest tooth found being about 4  
980 cm high. Large teeth (>1.5 cm) are also very rare (about 4% of the material sampled) and  
981 correspond to the large lamniform genera *Cretoxyrhina* and *Protolamna*. Marine sauropsid teeth are  
982 even less common with only three more or less complete teeth (TS pers. obs.). It is interesting that  
983 the niche of large pelagic predators in Kaniv is monopolized by *Cretoxyrhina*, despite the presence  
984 of large-toothed genera such as *Dwardius* and *Cardabiodon* in contemporary deposits in Europe  
985 (Siverson and Machalski, 2017). According to Siverson et al. (2013), *Dwardius* preferred the  
986 neritic zone, while *Cretoxyrhina* was a more generalist predator. Quartz-glaucinite sand layers in  
987 Kaniv were likely deposited in coastal conditions due to a large amount of broken shell fragments  
988 and occasional brachiopod findings, as well as presence of land plant fossils (mostly various conifer  
989 species, Krochak et al., 2016). Another interesting feature is the absence of hybodont sharks in most  
990 sampled horizons. Hybodonts are known for their tolerance to brackish and freshwater  
991 environments and can represent the largest part of Cretaceous faunas such as in the Lower  
992 Cretaceous Wessex Formation (Sweetman and Underwood, 2006). Most hybodont finds in Kaniv  
993 come from layer F in Pekarskyi ravine (5 teeth, 5.2% of fossil remains). Only a single crown

994 (0.005% of fossil remains) was recovered from Melanchyn potik, layer C. This, along with the  
995 abundance of plant remains, suggest that Kaniv territory in the late Early Cretaceous most likely  
996 consisted of small islands without major freshwater bodies suitable for elasmobranchs, where many  
997 hybodontiforms are thought to raise their youngs (Leuzinger et al., 2015).

998 Other late Albian elasmobranch-bearing localities known from Eastern Europe include Poland  
999 (Siversson and Machalski, 2017) and Lithuania (Dalinkevičius, 1935). Compared to Kaniv fauna,  
1000 the elasmobranch assemblage from Poland has a greater abundance of large lamniforms with the  
1001 genera *Dwardius* and *Cretodus* and *Paraisurus* being much more frequent than in the Burim  
1002 formation. In addition, *Dwardius* teeth are much more common in the Polish assemblage than  
1003 *Cretoxyrhina vracconensis*, whereas the opposite trend can be observed in the Ukrainian Albian. On  
1004 the other hand, the composition of medium-sized lamniform sharks is fairly similar in Poland and  
1005 Ukraine, *Cretolamna* species with elongate anterior teeth are also found in both localities, whereas  
1006 serrated *Squalicorax* teeth are outstandingly rare compared to Albian deposits of United States  
1007 (Siverson et al., 2007). The Polish fauna is also characterized by relatively few taxa represented by  
1008 small-sized teeth with clades such as batomorphs, orectolobiforms, squatiniforms and squaliforms  
1009 being missing from the assemblage, which could be explained by collecting and taphonomic biases  
1010 (Siverson and Machalski, 2017). Collecting bias (use of coarse mesh size for sieving) might also  
1011 explain the absence of batomorphs in our samplings.

1012 Dalinkevičius (1935)'s collections from Upper Albian of Upninkai (Lithuania), on the other hand,  
1013 are very similar to the Kaniv assemblages. Differences between the Lithuanian and Ukrainian  
1014 faunas include the presence of two species of hybodonts in Dalinkevičius (1935)'s samplings, one  
1015 of them being a species of *Acrodus*. Although this genus is absent from our samplings, it is possibly  
1016 present in the Albian fauna from Kaniv since the species *Acrodus affinis* Reuss, 1845 was reported  
1017 by Rogovich (1861). Another species reported by Rogovich (1861), *Acrodus rugosus* (Agassiz,  
1018 1939) more probably corresponds to a lateral tooth of *Heterodontus* (see above). Large lamniforms  
1019 seem to be absent from the Lithuanian assemblage with a single tooth attributable to *C. vracconensis*  
1020 being present (Dalinkevičius, 1935: pl. 5, fig. 107). Overall, species richness seems lower in the

1021 Lithuanian samplings, however it is unknown what biases could have influenced the composition of  
1022 the collections stored in Vilnius university since many of the original Dalinkevičius localities are no  
1023 longer accessible.

1024 Another locality relatively close geographically to Kaniv is Kolbay, Kazakhstan (Kennedy et al.,  
1025 2008). The composition of this ‘Vraconian’ elasmobranch fauna resembles that of Burim formation  
1026 assemblages but differs in the greater abundance of hybodonts and anacoracids and in the presence  
1027 of the genus *Hispidaspis* that is characterized by unusual enamel folding patterns at the base of the  
1028 crown (Glikman, 1980).

1029

### 1030 **Concluding remarks**

1031 Burim formation, Kaniv, Ukraine is one of the few locations in the world containing evidence for  
1032 one of the major adaptive radiations of elasmobranchs. Based on museum specimens originally  
1033 reported by Rogovich (1861) as well as newly sampled material, we provide a detailed account of  
1034 elasmobranch species present in this area during the Upper Albian and revise the status of several  
1035 taxa first mentioned by Rogovich. The taxonomic composition of this fauna supports previously  
1036 limited available paleogeographical and micropaleontological evidence for a late Albian age of the  
1037 sampled vertebrate-bearing stratae. Compared to many other contemporary faunas, the Kaniv  
1038 assemblages are very diverse, consisting of a variety of nectobenthic taxa, very frequent and  
1039 numerous odontaspidiids and macrophagous lamniforms. This study represents the first detailed  
1040 description of a Cretaceous elasmobranch fauna from Ukraine since the 19th century and one of the  
1041 few reports of Cretaceous elasmobranchs from Eastern Europe as a whole.

1042

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1053

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## 1266 **Figure Captions**

1267 Figure 1. Stratigraphic and geographical localisations of sampled horizons. **A**, Upper Albian  
1268 succession of Upper Burim formation deposits, A-F mark layers of coarse-grained quartz-glaucinite  
1269 sands, all of which except layer D contain vertebrate fossils. **B**, map of Kaniv natural reserve with  
1270 the three sampled ravines marked by a red star and original Rogovich's location of Maryin ravine  
1271 marked by a green star; map of Ukraine showing the location of Kaniv is in top right corner. **C**,  
1272 field photo of vertebrate-bearing horizon of layer F in Pekarskyi ravine. [Full page width]

1273 Figure 2. **A-D: *Hybodus bidentatus* comb. nov.** A-B, **Rogovich's type specimen** (NNPM 391-14)  
1274 in A, labial and B, lingual views. C-D, incomplete tooth (NNPM 2588-1) in C, lingual and D, labial  
1275 views, layer C, Melanchyn potik. **E-F: *Hybodontoides* indet.**, incomplete tooth (NNPM 2588-2) in  
1276 E, lingual and F, labial views, layer F, Pekarskyi. **G-L: *Synechodus kessleri* comb. nov.** G-H,  
1277 **Rogovich's type specimen and lectotype**, (NNPM 391-10) in G, labial and H, lingual views. I-J,  
1278 anterolateral tooth (NNPM 2588-3) in I, lingual and J, labial views, layer C, Melanchyn potik. K-L,  
1279 lateroposterior tooth (NNPM 2588-4) in K, labial and L, lingual views, layer C, Melanchyn potik.  
1280 **M-R: *Synechodus dispar*.** M-N, anterolateral tooth (NNPM 2588-5) in M, labial and L, lingual  
1281 views, layer C, Melanchyn potik. O-P, anterior tooth (NNPM 2588-6) in O, lingual and P, labial  
1282 views, layer B, Melanchyn potik. Q-R, anterior tooth (NNPM 2588-7) in Q, labial and R, lingual

1283 views, layer B, Melanchyn potik. **S-T: *Paraorthacodus recurvus***, tooth (NNPM 2588-8) in S,  
1284 labial and T, lingual views, layer C, Melanchyn potik. **U-V: *Protosqualus cf. glickmani***,  
1285 incomplete tooth (NNPM 2588-9) in U, labial and V, lingual views, layer A, Kholodnyi. **W-X:**  
1286 ***Squatina (Cretacyllium) cranei***, tooth (NNPM 2588-10) in W, labial and X, lingual views, layer  
1287 B, Melanchyn potik. Scale bar equals 5 mm. [Full page width]

1288 Figure 3. **A: *Chiloscyllium sp.***, tooth (NNPM 2588-11) in labial view, layer F, Pekarskyi. **B-C:**  
1289 ***Cederstroemia cf. siverssoni***, lateral tooth (NNPM 2588-12) in B, lingual and C, labial views, layer  
1290 F, Pekarskyi. **D-E: ‘*Heterodontus*’ *upnikensis***, anterior tooth (NNPM 2588-15) in D, lingual and E,  
1291 labial views, layer A, Kholodnyi. **F-N: *Heterodontus aff. canaliculatus***. **F-G: Rogovich’s**  
1292 **specimen**, an anterior tooth of a juvenile individual (NNPM 391-1) in F, labial and G, lingual  
1293 views; H-J, adult anterior tooth (NNPM 2588-13) in H, basal, I, lingual and J, profile views, layer  
1294 C, Melanchyn potik; K, lateral tooth (NNPM 2588-14) in occlusal view, layer C, Melanchyn potik;  
1295 L-N, lateral tooth (NNPM 2588-16) in L, occlusal, M, basal and N, lingual views, layer C,  
1296 Melanchyn potik. **O-P: *Squalicorax sp.***, incomplete tooth (NNPM 2588-17) in O, lingual and P,  
1297 labial views, layer F, Pekarskyi. **Q-V: *Archaeolamna striata comb. nov.*** **Q-R: Rogovich’s type**  
1298 **specimen and lectotype**, an upper posterior tooth (NNPM 391-2) in Q, labial and R, lingual views;  
1299 S-T, upper lateral tooth (NNPM 2588-18) in S, lingual and T, labial views, layer C, Melanchyn  
1300 potik; U-V, upper lateroposterior tooth (NNPM 2588-19) in U, labial and V, lingual views, layer C,  
1301 Melanchyn potik. Scale bar equals 5 mm. [Full page width]

1302 Fig. 4. **A-L: *Archaeolamna striata comb. nov.*** A-B, upper anterior tooth (NNPM 2588-20) in A,  
1303 lingual and B, labial views, layer C, Melanchyn potik; C-D, upper anterior tooth (NNPM 2588-21)  
1304 in C, lingual and D, labial views, layer C, Melanchyn potik; E-F, upper lateral tooth (NNPM 2588-  
1305 22) in E, labial and F, lingual views, layer C, Melanchyn potik; G-H, upper anterior tooth (NNPM  
1306 2588-23) in G, lingual and H, labial views, layer C, Melanchyn potik; I-J, upper lateroposterior  
1307 tooth (NNPM 2588-24) in I, lingual and J, labial views, layer C, Melanchyn potik; K-L, upper  
1308 lateroposterior tooth (NNPM 2588-25) in K, lingual and L, labial views, layer C, Melanchyn potik.

1309 **M-T: *Archaeolamna* ex. gr. *kopingensis*.** M-N: lower lateral tooth (NNPM 2588-26) in M, lingual  
1310 and N, labial views, layer C, Melanchyn potik; O-P, lower lateral tooth (NNPM 2588-27) in O,  
1311 lingual and P, labial views, layer C, Melanchyn potik; Q-R, upper antero-lateral tooth (NNPM  
1312 2588-28) in Q, lingual and R, labial views, layer C, Melanchyn potik; S-T, upper lateral tooth  
1313 (NNPM 2588-29) in S, lingual and T, labial views, layer C, Melanchyn potik. **U-V: *Cretolamna***  
1314 **sp.**, lower anterior tooth (NNPM 2588-30) in U, lingual and V, labial views, layer C, Melanchyn  
1315 potik. **W-X: *Cretoxyrhina vracconensis*,** upper anterolateral tooth (NNPM 2588-31) in W, lingual  
1316 and X, labial views, layer C, Melanchyn potik. Scale bar equals 5 mm. [Full page width]

1317 Figure 5. ***Cretoxyrhina vracconensis*.** A-B, upper lateral tooth from a juvenile individual (NNPM  
1318 2588-32) in A, lingual and B, labial views, layer C, Melanchyn potik; C-D, upper anterior tooth  
1319 (NNPM 2588-33) in C, lingual and D, labial views, layer C, Melanchyn potik; E-F, lower lateral  
1320 tooth (NNPM 2588-34) in E, lingual and F, labial views, layer C, Melanchyn potik; G-H, upper  
1321 lateral tooth (NNPM 2588-35) in G, labial and H, lingual views, layer C, Melanchyn potik; I-J,  
1322 upper lateral tooth (NNPM 2588-36) in I, lingual and J, labial views, layer C, Melanchyn potik; K-  
1323 L, parasymphyseal tooth (NNPM 2588-37) in K, lingual and L, labial views, layer C, Melanchyn  
1324 potik; M-N, one of **Rogovich's specimens**, a lower lateral tooth (NNPM 391-37) in M, lingual and  
1325 N, labial views. Scale bar equals 1 cm. [Full page width]

1326 Figure 6. **A-F. *Paraisurus macrorhizus*.** A-C, ?lateral tooth, **Rogovich's specimen** (NNPM 391-  
1327 41) in A, lingual, B, labial and C, lateral views; D-F, ?lateral tooth (NNPM 2588-38) in D, lingual,  
1328 E, labial and F, profile views, layer C, Melanchyn potik. **G-Q: *Protolamna* cf. *sokolovi*.** G-H, upper  
1329 lateral tooth (NNPM 2588-39) in G, labial and H, lingual views, layer C, Melanchyn potik; I-K,  
1330 lower anterior tooth (NNPM 2588-40) in I, lingual, J, labial and K, lateral views, layer E, Pekarskyi;  
1331 L-M, ?upper lateral tooth (NNPM 2588-41) in L, lingual and M, labial views, layer C, Melanchyn  
1332 potik; N-O, lower anterior tooth (NNPM 2588-42) in N, lingual and O, labial views, layer C,  
1333 Melanchyn potik; P-Q, lower ?anterior tooth from an immature individual (NNPM 2588-43) in P,  
1334 lingual and Q, labial views, layer C, Melanchyn potik. **R-Z: *Pseudoscapanorhynchus***

1335 ***compressidens***. R-T, antero-lateral tooth (NNPM 2588-44) in R, lingual, S, labial and T, profile  
1336 views, layer C, Melanchyn potik; U-V, antero-lateral tooth (NNPM 2588-45) in U, lingual, W,  
1337 labial and V, profile views, layer C, Melanchyn potik; X-Z, anterior tooth (NNPM 2588-46) in X,  
1338 lingual, Y, labial and Z, profile views, layer b, Melanchyn potik. **A'-D': *Eostriatolamia subulata***.  
1339 A'-B', lower anterior tooth (NNPM 2588-47) in A', lingual and B', labial views, layer A,  
1340 Kholodnyi; C'-D', lower anterior tooth (NNPM 2588-48) in C', lingual and D', labial views, layer  
1341 C, Melanchyn potik. **E'-L': *Eostriatolamia striatula***. E'-F', ?upper anterior tooth (NNPM 2588-49)  
1342 in E', lingual and F', labial views, layer C, Melanchyn potik; G'-H', upper lateral tooth (NNPM  
1343 2588-50) in G', lingual and H', labial views, layer A, Melanchyn potik; I'-J', ?lower antero-lateral  
1344 tooth (NNPM 2588-51) in I', lingual and J', labial views, layer C, Melanchyn potik; K'-L', lower  
1345 lateral tooth (NNPM 2588-52) in K', lingual and L', labial views, layer C, Melanchyn potik. **M'-**  
1346 **N': *Lamniformes indet. 1***: lower lateral tooth (NNPM 2588-53) in M', labial and N', lingual  
1347 views, layer C, Melanchyn potik. **O'-P': *Lamniformes indet. 2*: Rogovich's specimen**, an upper  
1348 lateral tooth (NNPM 391-3) in O', labial and P', lingual views. Scale bar equals 5 mm. [Full page  
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1359**Table 1.** Summary of the status of species and specimens from the Kaniv area originally reported by Rogovich (1861).

Rogovich's identification	Figures	Status	Revised identification	Specimen number
<i>Hybodus bidentatus</i> Rog.	Pl. 3, Figs 13	Valid	<i>Hybodus bidentatus</i> Rog.	NNPM 391-14 (holotype)
<i>Sphaenonchus compressus</i> Rog.	Pl. 1, Figs 9-10	Pending	<i>Asteracanthus compressus</i> (Rog.)	not found
<i>Hybodus kessleri</i> Rog.	Pl. 3, Figs 3-5	Valid	<i>Synechodus kessleri</i> (Rog.)	NNPM 391-10 (lectotype)
<i>Hybodus marginatus</i> Rog.	Pl. 3, Fig. 18	<i>Nomen dubium</i>	? anterior of <i>Heterodontus</i> sp.	not found
<i>Hybodus marginatus</i> Rog.	Pl. 3, Figs 15-16? non Figs 14, 17-18	-	<i>Squatina (C.) cranei</i> Wood.	not found
<i>Hybodus marginatus</i> Rog.	Pl. 3, Figs 14, 17 non Figs 15-16?-18	-	<i>Cederstroemia cf. siverssoni</i> Gui.	not found
<i>Lamna (Odontaspis) minuta</i> Rog.	Pl. 7, Fig. 22	<i>Nomen dubium</i>	<i>Heterodontus aff. canaliculatus</i>	NNPM 391-1
<i>Otodus monstrosus</i> Rog.	Pl. 5, Figs 12-12a	Junior synonym	<i>Paraisurus macrorhizus</i> (Pic. & Cam.)	NNPM 391-41
<i>Hybodus parvus</i> Rog.	Pl. 3, Figs 1-2	Pending	<i>Polyacrodus parvus</i> (Rog.)	not found
<i>Oxyrhina pygmaea</i> Rog.	Pl. 8, Fig. 13	<i>Nomen dubium</i>	Indetermined lamniform	not found
<i>Otodus striatus</i> Rog.	Pl. 5, Figs 13 non 14	Valid	<i>Archaeolamna striata</i> (Rog.)	NNPM 391-2 (lectotype)
<i>Otodus striatus</i> Rog.	Pl. 5, Figs 14 non 13	-	Lamniformes indet. 2	NNPM 391-3
<i>Hybodus subulatus</i> Rog.	Pl. 3, Figs 6b-11	Valid	<i>Synechodus subulatus</i> (Rog.)	not found
<i>Hybodus tuberculatus</i> Rog.	Pl. 2, Figs 20-21a	Pending	<i>Polyacrodus tuberculatus</i> (Rog.)	not found
<i>Lamna (Odontaspis) ornata</i> Rog.	Pl. 7, Fig. 14	<i>Nomen dubium</i>	<i>Protolamna</i> sp.	not found
<i>Acrodus rugosus</i> Ag.	Pl. 2, Fig. 11		<i>Heterodontus aff. canaliculatus</i>	not found
<i>Acrodus affinis</i> Reu.	Pl. 2, Fig. 12		Indetermined hybodontiform	not found
<i>Hybodus dispar</i> Reu.	Pl. 3, Figs 12-12a		<i>Paraorthacodus recurvus</i> (Trau.)	not found
<i>Carcharodon tenuis</i> Ag.	Pl. 4, Fig. 23		Indetermined lamniform	not found
<i>Carcharodon escheri</i> Ag.	Pl. 4, Figs 21-22		Indetermined lamniform	not found
<i>Otodus appendiculatus</i> Ag.	Pl. 5, Figs 1-5 non Figs 6-11		<i>Cretoxyrhina vracconensis</i> Zhel.	NNPM 391-37
<i>Otodus appendiculatus</i> Ag.	Pl. 5, Fig. 7 non Figs 1-6, 8-11		<i>Archaeolamna?</i>	not found
<i>Otodus appendiculatus</i> Ag.	Pl. 5, Fig. 8-9 non figs 1-7, 10-11		Indetermined lamniform	not found
<i>Otodus appendiculatus</i> Ag.	Pl. 5, Figs 6, 10-11 non Figs 1-5, 7-9		<i>Protolamna cf. sokolovi</i> Capp	not found
<i>Lamna (Odontaspis) subulata</i> Ag.	Pl. 7, Figs 19-21 non Figs 17-18		<i>Eostriatolamia subulata</i> (Ag.)	not found
<i>Lamna (Odontaspis) subulata</i> Ag.	Pl. 7, Figs 17-18 non Figs 19-21		<i>Protolamna</i> sp.?	not found
<i>Lamna (Odontaspis) gracilis</i> Ag.	Pl. 7, Figs 15-16a		<i>Eostriatolamia striatula</i> (Dal.)	not found
<i>Oxyrhina heteromorpha</i> Reu.	Pl. 8, Fig. 12		Indetermined lamniform	not found

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1361 **Table 2.** Distribution of elasmobranch species within the seven sampled horizons of Kholodnyi,

1362 Pekarskiyi and Melanchyn potik ravines. Sampled horizons are arranged in stratigraphic order.

Horizon	Species	Layer A	Layer B	Layer C	Layer E	Layer F
	<i>Hybodus bidentatus</i> Rog.			+		
	Hybodontoides indet.					+
	<i>Synechodus kessleri</i> (Rog.) comb. nov.			+		
	<i>Synechodus subulatus</i> (Rog.) comb. nov.	+	+	+	+	+
	<i>Paraorthacodus recurvus</i> (Trau.)	+	+	+		
	<i>Protosqualus</i> cf. <i>glickmani</i>					+
	<i>Squatina</i> ( <i>C.</i> ) <i>cranei</i> Wood.	+	+			
	<i>Chiloscyllium</i> sp.				+	
	<i>Cederstroemia</i> cf. <i>siverssoni</i>			+		+
	<i>Heterodontus upnikensis</i> (Dal.)					+
	<i>Heterodontus</i> aff. <i>canaliculatus</i>			+	+	+
	<i>Squalicorax</i> sp.					+
	<i>Archaeolamna striata</i> (Rog.) comb. nov.	+	+	+	+	+
	<i>Archaeolamna</i> ex. gr. <i>kopingensis</i> (Dav.)	+	+			+
	<i>Cretolamna</i> sp.			+		
	<i>Cretoxyrhina vracconensis</i> (Zhel.)					?
	<i>Paraisurus macrorhizus</i> (Pic. & Cam.)			+		
	<i>Protolamna</i> cf. <i>sokolovi</i>	+	+	+	+	?
	<i>Pseudoscapanorhynchus compressidens</i> (Her.)	+	+			
	<i>Eostriatolamia subulata</i> (Ag.)	+	+	+	+	+
	<i>Eostriatolamia striatula</i> (Dal.)					+
	Lamniformes indet. 1					+

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