

Middle Eocene cartilaginous fishes (Vertebrata: Chondrichthyes) of the Dnieper–Donets Basin, northern Ukraine

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ABSTRACT

Marine basins that existed in present-day Ukraine during the Eocene harboured various groups of cartilaginous and bony fishes, reptiles, aquatic birds, and marine mammals. Fish remains from Paleogene deposits of Kyiv and its vicinities were first collected and described by O.S. Rogovich in the mid-19th century. Here we have carried out a re-examination of chondrichthyan fossils from Rogovich's collection and evaluated several later records, all of which were recovered from middle Eocene deposits. In total, 88 specimens represented by teeth, vertebrae, and other skeletal elements were analysed and described. As a result, the sample revealed to a single chimaeriform species (*Edaphodon bucklandi*), and 12 shark and two ray taxa, respectively. Ten sharks were identified to species level, whereas the rays could be identified only at higher systematic ranks (Myliobatidae, Myliobatiformes). Several nomenclatural changes are proposed here, including the synonymisation of *Carcharodon megalotis*, *C. lanceolatus*, *C. productus*, *Lamna cuspidata*, *L. denticulata*, *L. compressa*, *L. (Odontaspis) hispida*, *L. lata*, *Oxyrhina brevidens*, and *O. biflens* with more recently proposed taxa. Seven species erected by Rogovich (*Galeocерdo paradoxus*, *Otodus microtus*, *Lamna elegans*, *Oxyrhina falcata*, *Oxyrhina leptodon*, *Chomatodus dubius*, and *Hybodus helophorus*) are suggested to most likely be *nomina dubia*. Many identified taxa represent the epi- and mesopelagic fishes and only a relatively small number of them belong to benthopelagic, demersal, and bathydemersal forms. The studied sample is of important historical and scientific value and substantially contribute to the understanding of the palaeodiversity of Eocene marine ecosystems that existed in present-day Ukraine and generally in Eastern Europe.

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INTRODUCTION

The Paleogene was a period of major global changes in both marine environments and biota. It was characterised by the continuous break-up of the supercontinent of Laurasia and opening the Norway–Greenland Sea of the North Atlantic and its connection with the Paleoarctic ocean. At that time, the Neo-Tethys has been closed because of collision of the African and Indian plates with the Eurasian plate, Australia separated from Antarctica, and the Circum-Antarctic current emerged. Warmhouse climate changed to global coolhouse climate disrupted by short time hyperthermal and cooling/glaciation events (e.g., Zachos et al., 2001; Prothero, 2021; Speijer et al., 2020). The K–Pg boundary extinction event left the deep-sea realm seemingly unaffected while causing a significant biodiversity loss among pelagic marine vertebrates and durophagous demersal feeders on the continental shelf (Patterson, 1993; Kriwet and Benton, 2004; Sibert and Norris, 2015; Adnet et al., 2020; Guinot and Condamine, 2023).

As a result, new ecosystems with new ecological niches, favouring new faunistic compositions within food webs, appeared, leading to exceptional radiation and diversification among vertebrates,

including fishes. At the Paleocene–Eocene boundary, volcanism and orogeny triggered an enhanced supply of greenhouse gases into the atmosphere leading to the rise of sea surface temperatures and sea level, ocean deoxygenation, and changes in Earth's carbon cycle (Jenkyns, 2003; Zachos et al., 2008; Miller et al., 2009; Sluijs et al., 2014; Hessler et al., 2017; Dykan et al., 2018). The organic flux into the deep sea collapsed, but a subsequent major biochemical recovery may have contributed to the creation of new evolutionary opportunities for a wide range of marine organisms (D'Hondt, 2005). The Paleocene–Eocene Tethyan realms, similarly to reef ecosystems, harboured biodiversity hotspots of vertebrates in the warm and shallow marine environments (Guinot and Cavin, 2016).

The marine basin of the Dnieper–Donets depression that existed in the territory of present-day northern Ukraine during most of the Eocene, namely in the early Ypresian, Lutetian, Bartonian, and Priabonian stages, connected the basins located to the east (Turan and Siberian Seas) and west (North Sea) (Ronov and Khain, 1961; Savytska, 1996; Beniamovskii, 2005, 2007; Akhmetiev, 2010; Vasilieva, 2018). This created favourable conditions for the development of diverse

vertebrate assemblages (Bosboom et al., 2017 and references therein).

A large number of Eocene taxa of various vertebrate groups have been reported from this basin, including elasmobranchs (Glickman, 1964; Udovichenko and Nesson, 1987; Udovichenko, 2006, 2009), bony fishes (Bannikov, 2010; Bratishko, 2011, 2013), sea turtles (Averianov, 2002; Danilov et al., 2011; Zvonok, 2011; Zvonok et al., 2013; Zvonok and Danilov, 2017), crocodiles (Zvonok and Skutschas, 2011; Kuzmin and Zvonok, 2021), snakes (Snetkov and Bannikov, 2010; Zvonok and Snetkov, 2012), aquatic birds (Averianov et al., 1990; Mayr and Zvonok, 2011, 2012; Zvonok et al., 2015; Zvonok and Gorobets, 2016; Dobrovolsky, 2023; Dobrovolsky and Gorobets, 2023), and marine mammals (Gol'din et al., 2012; Gol'din and Zvonok, 2013; Gol'din et al., 2014; Averianov and Zvonok, 2021; Davydenko et al., 2021).

Fish remains from Paleogene deposits of Kyiv and its vicinities were first described by Afanasii [Opanas] Semenovych Rogovich (1813–1878), who was a professor at Saint Volodymyr Imperial University (now Taras Shevchenko National University of Kyiv, Ukraine). Rogovich assembled a large collection of fossils from different regions of present-day Ukraine and described most of them in a series of papers (Rogovich, 1861, 1870, 1875a, 1875b). The taxonomic identity of Jurassic and Cretaceous fish specimens from this collection were previously revised (Kovalchuk and Anfimova, 2020; Kovalchuk et al., 2022). However, remains of middle Eocene sharks, rays, and chimaeras from the so-called 'blue brick clays' in the vicinity of Vyshhorod near Kyiv, which were initially reported by Rogovich (1861), have remained largely ignored for more than 150 years despite major taxonomic revisions of many of the taxa.

The aim of this study, therefore, is to carry out a thorough examination of chondrichthyan fossils from O.S. Rogovich's collection and to describe several later records from coeval deposits to clarify the taxonomic composition of the chondrichthyan assemblage that existed in the Dnieper–Donets Basin of northern Ukraine during the middle Eocene (Kyiv time).

NOTES ON THE HISTORY OF O.S. ROGOVICH'S FOSSIL COLLECTION

During the Paleogene, most of the area of present-day Ukraine was covered by sea. For many decades, our knowledge on Eocene chondrichthyans that existed in the Dnieper–Donets Basin was based on materials described by

Rogovich from his fossil collection. According to the minutes of meeting of the Council of the Physics and Mathematics Faculty at Saint Volodymyr Imperial University dated to 22 November 1869, this collection was acquired for the mineralogical cabinet in the same year for a significant amount of money (2000 silver rubles; about 18 grams of silver in 1 ruble; O. Kozlov, pers. comm., 2021). Professor Kostiantyn Matviyovych Feofilaktov (1818–1901), head of the mineralogical cabinet, especially singled out the collection of fish remains, which included 440 specimens, 'both because of its completeness and rarity, and the excellent preservation of specimens' (Archive of the Department of Geology at the National Museum of Natural History (NMNHU-G), National Academy of Sciences of Ukraine). Feofilaktov considered the amount of money to be paid for the collection 'very moderate' and noted that 'through the acquired collection, the palaeontological department of the mineralogical cabinet will obtain not only a significant local collection of fossils, but also a unique one among those of both Russian and foreign cabinets' (Archive NMNHU-G). Unfortunately, the collection was subsequently divided into several parts and transferred to different institutions in Kyiv, Moscow, and Saint Petersburg (see Zvonok and Averianov, 2017 for more details). The part of the collection that remained in Kyiv was first relocated to the Academy of Sciences and was housed at the Institute of Geological Sciences (Zvonok and Danilov, 2017). Later it was transferred to the Institute of Zoology and subsequently it became part of the scientific collections of the NMNHU-G, National Academy of Sciences of Ukraine. The nomenclature of chondrichthyan taxa described by Rogovich was revised by Capetta (2006) and Pollerspöck and Straube (2022), but the specimens have not been re-examined in detail.

MATERIAL AND METHODS

In total, 88 remains of sharks, rays, and chimaeras represented by isolated teeth, dental plates, and vertebrae were studied. Of them, 83 specimens are part of Rogovich's collection, and the other five specimens represented by isolated vertebrae were collected later, in the 1960s, from coeval deposits at the construction site of the Zoloti Vorota station of the Kyiv Metro (Figure 1). Isolated teeth are the most numerous remains (62 specimens), followed by vertebrae ($n = 21$), four chimaeroid tooth plate fragments and a single caudal spine of a ray. The specimens from Rogovich's collection come from middle Eocene deposits of Vysh-

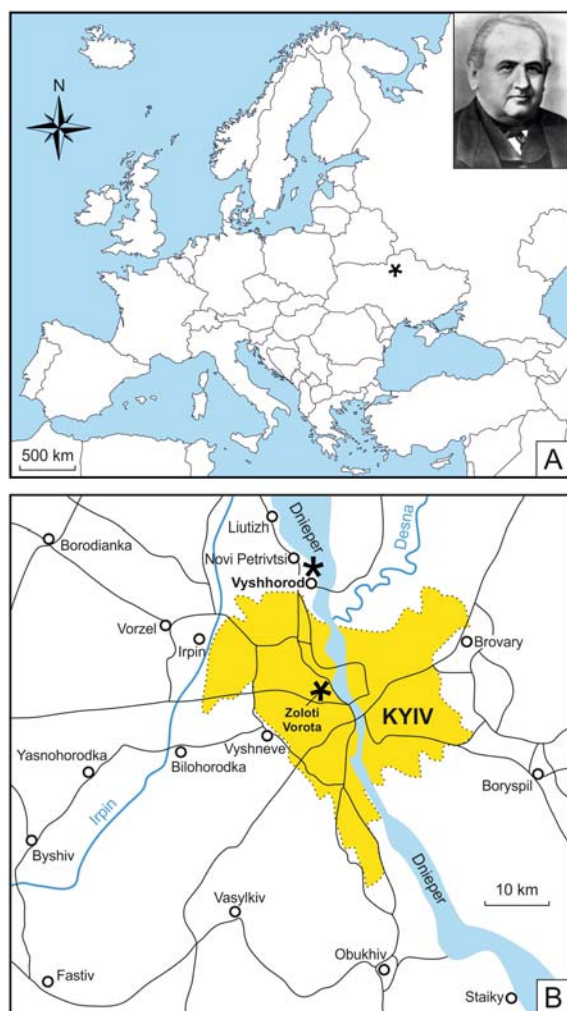


FIGURE 1. Studied localities (indicated by asterisks) on the map of Europe (A), with a portrait of Opanas Semenovych Rogovich, and on the schematic map of Kyiv and its vicinities (B).

horod and are housed in NMNHU-G, whereas shark vertebrae of the same age from Zoloti Vorota are deposited in the Department of Palaeontology at the National Museum of Natural History, National Academy of Sciences of Ukraine, Kyiv (NMNHU-P, collection PI). The fossils were identified using diagnostic features based on descriptions mostly taken from literature sources (e.g., Cappetta, 2012) and on information provided by the shark reference database compiled by Pollerspöck and Straube (2022). The taxonomic hierarchy and descriptive terminology follow Stahl (1999), Stahl and Parris (2004), and Cicimurri and Ebersole (2015) for chimaeroids, and Cappetta (2012) for sharks and rays. X-ray images of shark vertebrae were taken with VATEL Alpha 1 in the

veterinary clinic Vetmedservice (National University of Life and Environmental Sciences of Ukraine, Kyiv).

GEOLOGICAL SETTING

All the material described herein was derived from the Kyiv Formation, the type formation of the middle Eocene Kyiv regional stage (upper Lutetian–Bartonian) of northern Ukraine. The deposits of the Kyiv regional stage are exposed in the western and south-western parts of the East European Platform. In the northern part of Ukraine, the sediments representing this stage are widespread within the Dnieper–Donets Depression, the Pripyat Depression, the Ukrainian Shield, on adjacent slopes of the Voronezh Anticline, and outskirts of the Donetsk Basin (Figure 2). In older reports (from the late nineteenth century), the Kyiv Formation was usually described as the ‘Kiev Stage’ (see Table 1 in Zosimovich and Shevchenko, 2014 for more details).

The Kyiv Formation in the northern part of Ukraine is comprised of (in ascending order) a horizon of yellowish-greenish-grey coarse and fine-grained phosphorite sands, a clay-marl member, and a member of non-carbonate clays (Ryabokon, 2002; Zosimovich and Shevchenko, 2014, 2015). The Kyiv Formation is now considered to be of middle Eocene (upper Lutetian–Bartonian) age (Figure 2): the horizon of phosphorite sands and the clay-marl member represent the late Lutetian stage, whereas the member of non-carbonate clays is dated to the Bartonian (Zosimovich and Shevchenko, 2015).

Nowadays, fish remains, mainly shark teeth, in the vicinities of Kyiv are known from two stratigraphic levels: the first of them is confined to the interval from the upper part of the horizon of phosphorite sands up to the lowest part of the clay-marl member, and the second one is from the ‘phosphorite plate’ (the upper part of the Kyiv Formation) of local distribution between the marls and non-calcareous silty clays in Pyrohiv quarry (Udovichenko and Nessonov, 1987; Bratishko, 2011). Most of the fish specimens were recovered by O.S. Rogovich from the first stratigraphic level – marls and clays in the former quarry of the Eismann’s brickworks near Vyshhorod (50°35' N, 30°29' E; Figure 1).

The shark vertebrae found during earthworks at the construction site of the Zoloti Vorota metro station in Kyiv (50°26' N, 30°30' E; Figure 1) come from a depth of 110 m. Using standard approaches (Bugrova, 2005), the following foraminifera were identified in the rock sample from the cavities in

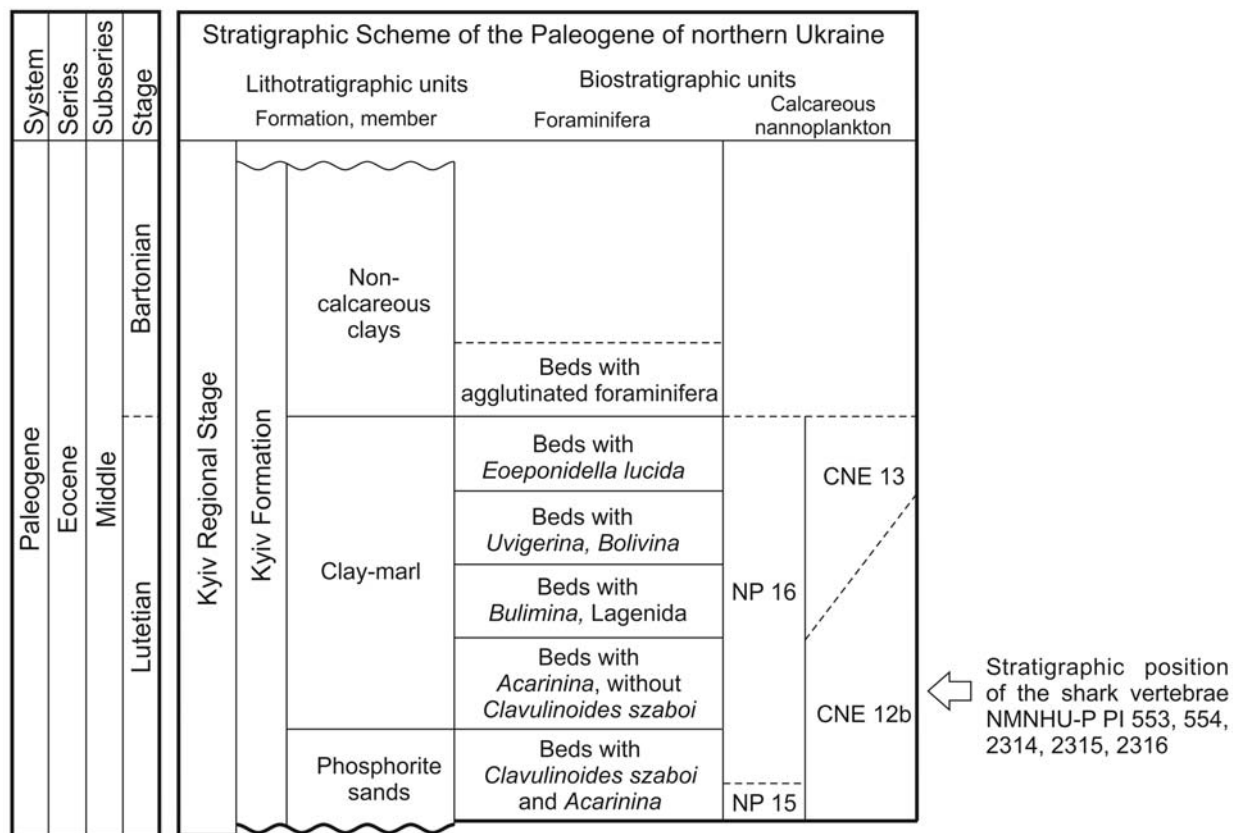


FIGURE 2. Stratigraphy of the Kyiv Formation section in the Kyiv area. The regional stratigraphic scheme of the Paleogene of northern Ukraine is presented after Zosimovich and Shevchenko (2014, 2015); foraminiferal biostratigraphy of the section follows Ryabokon (2002); Musatov and Ryabokon (2017); calcareous nannoplankton biostratigraphy is presented after Savitska (1996), Solyanik (2009), and Musatov and Ryabokon (2017).

these vertebrae: *Acarinina medizai* (Toumarkin et Bolli, 1975), *A. aff. A. rohri* (Brönnimann et Bermudez, 1953), *A. rugosoaculeata* Subbotina, 1953, *Bolivina pussilla* Schwager, 1866, *Bulimina aksuatica* Morozova, 1936, *Cibicides karpaticus* Mjatluk, 1950, *C. tenellus* (Reuss, 1865), *Dentalina approximata* Reuss, 1866, *Epistominella vitrea* Parker, 1953, *Globocassidulina globosa* (Hantken, 1875), *Guttulina problema* d'Orbigny, 1846, *Gyroidinoides octocameratus* (Cushman et Hanna, 1927), *Gyroidinoides soldanii* (d'Orbigny, 1826), *Heterolepa eocaena* (Gümbel, 1870), *Pseudohastigerina micra* (Cole, 1927), *Siphonodosaria annulifera* (Cushman et Bermudez, 1936), *Spiroplectammina cariniformis* Morozova, 1939, *Spiroplectammina guembeli* Hagn, 1956, *Quinqueloculina ludwigi* Reuss, 1866, *Turritina alsatica* Andreae, 1884, and *Trifarina budensis* (Hantken, 1875).

The assemblage of small benthic foraminifera extracted from the sample is characteristic for the lower, carbonated part of the Kyiv Formation. The assemblage of planktonic foraminifera—*A. mediz-*

zai, *A. rugosoaculeata*, *A. aff. A. rohri*, and *Pseudohastigerina micra*—indicates that the sample containing *Acarinina* without *Clavulinoides szaboi* comes from layers of the lower part of the clay-marl member of the Kyiv Formation, just above the horizon of phosphorite sands (Ryabokon, 2002). Based on the planktonic foraminifera, these layers are of late Lutetian age and correspond to the chronostratigraphic level of zones E10–E11 of the zonal planktonic foraminiferal scale (Speijer et al., 2020). According to Solyanik (2009), Musatov (2020), and Musatov and Ryabokon (2017), these layers belong to the time from the first common (abundant) appearance of *Discoaster bifax* and *Blackites gladius*, accompanied with *Nannotetrina fulgens*, to the abundant and large *Reticulofenestra umbilica* ($\geq 14 \mu\text{m}$), representing the upper part of zone CNE12b (Agnini et al., 2014; Ogg et al., 2016) or the lowest part of Zone NP16. In terms of geological history, the deposition of the lower part of Kyiv Formation broadly corresponds to the climatic (hyperthermal) 'C19r

event' dated at 41.5 Ma, representing the late Lutetian Thermal Maximum (LLTM) (Westerhold et al., 2018; Ryabokon, 2021). It was a short period of warming by approximately 2°C of deep-sea waters of the South Atlantic, which is of interest due to its coincidence with the highest means of insolation for the past 45 million years. Consequently, the accumulation of these layers (i.e., the rocks comprising shark vertebrae from Zoloti Vorota) directly preceded the LLTM (Speijer et al., 2020).

SYSTEMATIC PALAEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880
Subclass HOLOCEPHALI Bonaparte, 1832
Order CHIMAERIFORMES Obruchev, 1953
Family CALLORHINCHIDAE Garman, 1901
Genus *EDAPHODON* Buckland, 1838
Edaphodon bucklandi Agassiz, 1843

Figure 3

- 1843 *Edaphodon bucklandi*; Agassiz, p. 351-352, pl. 40d, figs. 1-4, 9-12, 19-24.
1843 *Edaphodon eurygnathus*; Agassiz, p. 352.
1848 *Edaphodon Bucklandii* [sic] Ag.; Giebel, p. 378.
1848 *Edaphodon eurygnathus* Ag.; Giebel, p. 379.
1850 *Edaphodon eurygnathus*; Dixon, p. 111, pl. 10, figs. 18, 19, 22; pl. 12, fig. 5.
1850 *Edaphodon Bucklandi* [sic]; Dixon, p. 111, pl. 10, figs. 20, 21.
1861 *Edaphodon Bucklandii* [sic] Ag.; Rogovich, p. 60, pl. I, figs. 5, 6.
1861 *Edaphodon eurygnathus* Ag.; Rogovich, p. 61, pl. VIII, figs. 18, 19.
1891 *Edaphodon bucklandi*, Agassiz; Woodward, p. 80-81.
1901 *Edaphodon Bucklandi* [sic] Agassiz; Priem, p. 485.
1902 *Edaphodon Bucklandi* [sic] Agassiz, 1843; Leriche, p. 35, pl. I, fig. 51.
1905 *Edaphodon Bucklandi* [sic] Agassiz, 1843; Leriche, p. 137-140, figs. 18, 19.
2012 *Edaphodon bucklandi* Agassiz, 1843; Diedrich, p. 19, fig. 14.19.

Material. Three right palatinal fragments, NMNHU-G 391/114, 391/138/1-2; one left mandibular fragment, NMNHU-G 391/115, Vyshhorod.

Description. Palatine tooth plates (Figure 3A–C) are robust and broad, with a stepped oral surface. NMNHU-G 391/138/1 bears three tritors, of which the posterior inner one is the largest and broadest

(albeit partly destroyed in its distal part), reaching 12.6 mm in width. It is separated from the anterior inner tritor with a narrow groove and smoothly tapers anteriorly. The outer tritor is elongated and well separated from both inner ones with a deep valley, and its anterior end lies at the level of the middle part of the anterior inner tritor. Two inner tritors are preserved in NMNHU-G 391/114, which is more than twice as large as in NMNHU-G 391/138/1. The length of the anterior and posterior inner tritors is 21.7 and 26.6 mm, and their width is 14.3 and 23.6 mm, respectively. The mandibular tooth plate (Figure 3D) with a broad symphyseal surface is also robust. The median tritor occupies more than two-thirds of the lingual surface, has irregular oval shape, and is separated from the posterior border of the symphysis with a narrow band. The anterior outer tritor is triangular with rounded edges, and it is much smaller and lies below the median tritor. Numerous vertical tubules are visible at the cross section of both tritors.

Remarks. The specimens from Vyshhorod were assigned to the genus *Edaphodon* based on the number of tritors on palatine tooth plates (Woodward, 1891; Stahl, 1999; Stahl and Parris, 2004; Cicimurri and Ebersole, 2015). Albeit being partly broken, they are similar in gross morphology (shape, size, and orientation of tritors, morphology of the labial margin) to those of *E. bucklandi* erected by Agassiz (1843) from the Eocene of England. Rogovich (1861) identified two of the specimens described (NMNHU-G 391/114, 391/115) as *E. bucklandi*, and two others he assigned to another species, *E. eurygnathus* Agassiz, 1843. The latter is no longer valid because it was synonymised with *E. bucklandi* by Woodward (1891:80) as the 'differences between the palatine teeth of this species and those of the so-called *E. eurygnathus* are solely due to the imperfect state of preservation of the type specimens of the latter.' Apart from England, *E. bucklandi* is recorded from the Paleocene and Eocene of Belgium (Leriche, 1902, 1905; Casier, 1943; Dobbels, 1994), as well as from the Eocene of France (Priem, 1901, 1908; Leriche, 1906), Germany (Giebel, 1848; Diedrich, 2012) and Morocco (Case and Herman, 1973). An *Edaphodon* fossil, represented by a left mandibular fragment with morphological traits similar to those in *E. bucklandi*, was also reported from the late Eocene of North America (Parmley and Cicimurri, 2005). It is similar to NMNHU-G 391/115 in having a broad, flat symphyseal surface, a large medium tritor, and an anterior outer tritor of similar shape and punctuate surface pattern.

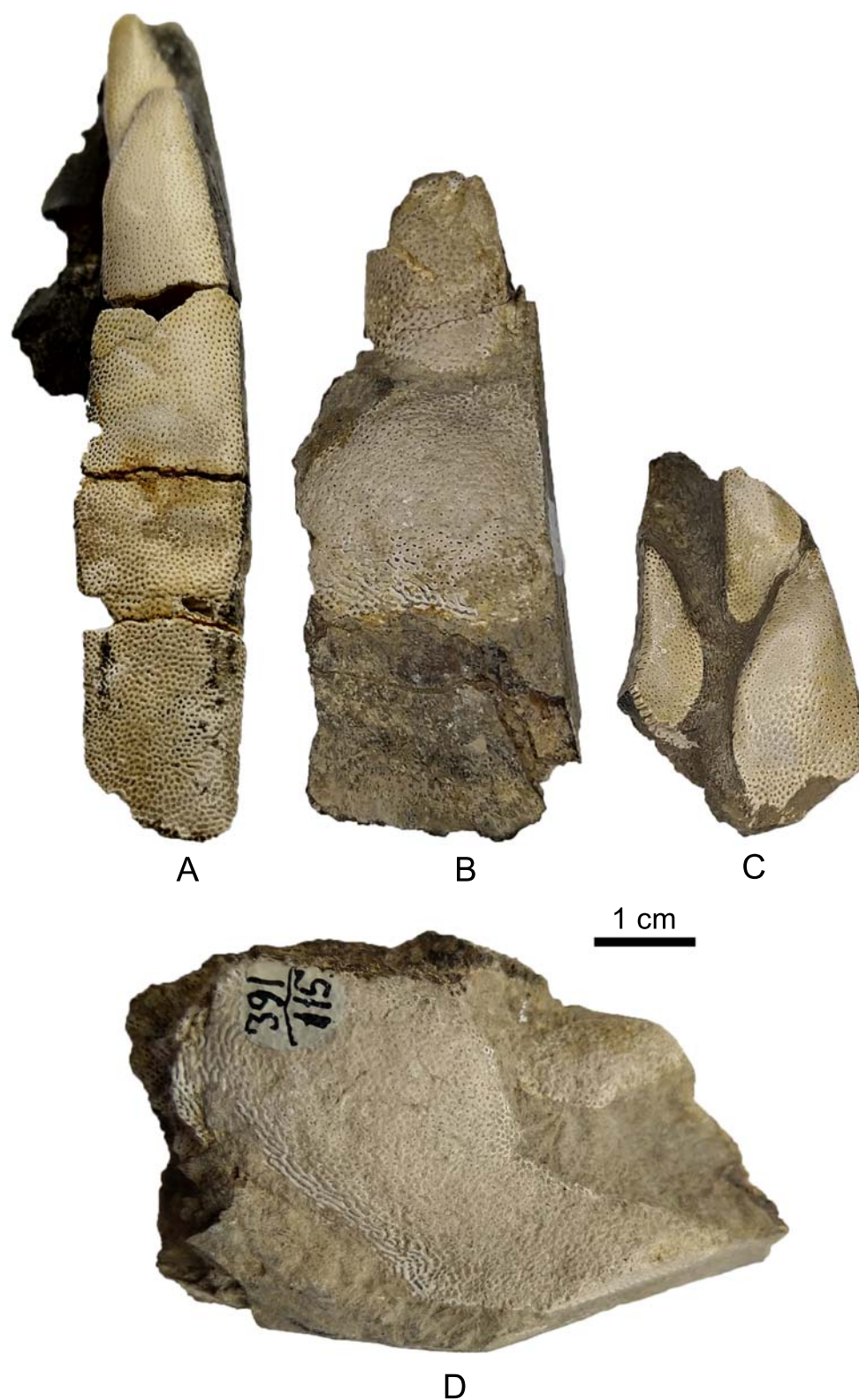


FIGURE 3. Chimaera (*Edaphodon bucklandi*) remains from the middle Eocene deposits of Vyshhorod: **A-C** – palatine fragments NMNHU-G 391/138/1 (**A**), NMNHU-G 391/114 (**B**), and NMNHU-G 391/138/2 (**C**); **D** – left mandibular fragment NMNHU-G 391/115.

Subclass ELASMOBRANCHII Bonaparte, 1838
 Cohort NEOSELACHII Compagno, 1970
 Order HEXANCHIFORMES Buen, 1926
 Family HEXANCHIDAE Gray, 1851
 Genus *HEXANCHUS* Rafinesque, 1810
Hexanchus agassizi Cappetta, 1976
 Figure 4A–C

- 1861 *Notidanus microdon* Ag.; Rogovich, p. 29, pl. III, figs. 25, 26.
- 1886 *Notidanus serratissimus* Ag.; Woodward, p. 216, pl. VI, figs. 24, 26.
- 1899 *Notidanus serratissimus* Ag.; Woodward, p. 6, pl. I, fig. 7.
- 1928 *Notidanus serratissimus* Ag.; Menner, p. 294, pl. X, fig. 1.
- 1964 *Notidanus serratissimus* Ag.; Glickman, p. 157, pl. VI, fig. 5-5a; pl. XXVI, fig. 22.
- 1966 *Notidanus serratissimus* Ag.; Casier, p. 44, pl. 1, figs. 10-12.
- 1967 "*Nodidanus*" *serratissimus* Ag.; Pledge, p. 140, pl. 1, fig. 2.
- 1976 *Hexanchus agassizi* nov. sp.; Cappetta, p. 553-554, pl. 1, figs. 5-8.
- 1979 *Hexanchus agassizi* Cappetta, 1976; Ward, p. 114-115, pl. 2, figs. 1, 2.
- 2005 *Hexanchus agassizi* Cappetta, 1976; Mustafa et al., p. 405-406, figs. 3-5.
- 2006 *Hexanchus agassizi* Cappetta; Malyshkina, pl. 12, fig. 4.
- 2006 *Hexanchus* cf. *agassizi* Cappetta, 1976; Udovichenko, p. 203, pl. I, fig. 1.
- 2012 *Hexanchus agassizi* Cappetta, 1976; Cappetta, p. 92-93, fig. 82.
- 2012 *Hexanchus agassizi* Cappetta, 1976; Zalmout et al., p. 74, fig. 3A.
- 2013 *Hexanchus agassizi* Cappetta, 1976; Otero et al., fig. 5.1-6.
- 2013 *Hexanchus agassizi* Cappetta, 1976; Schultz, p. 23-24, pl. 4, figs. 4a, b, 5.
- 2016 *Hexanchus agassizi* Cappetta, 1976; Szabó and Kocsis, p. 38-40, figs. 14-17.
- 2017 *Hexanchus agassizi* Cappetta, 1976; Zalat et al., p. 204, pl. 1, fig. 15.
- 2021 *Hexanchus agassizi* Cappetta, 1976; Adnet et al., p. 44, fig. 12.1-12.2.

Material. One upper left anterolateral tooth, NMNHU-G 391/21/2; two lower (left and right) lateral teeth, NMNHU-G 391/21/3, 391/21/4, Vyshhorod.

Description. The upper anterolateral tooth (Figure 4A) is 8.7 mm long mesiodistally and 8.3 mm high.

The root is robust and wide, it has a striated ornamentation on its lingual face, and a shallow longitudinal groove on the smooth labial face. There is a long and sharp central cusp oriented posteriorly to the tooth base. A small lateral cusplet is separated from the central cusp with a deep arcuate notch. Edges of the central cusp and the cusplet are laterally compressed.

The lower lateral teeth (Figure 4B–C) are also small (11.9 and 11.3 mm wide), about two times wider than high. The root is compressed labiolingually with a concave mesial edge and bears numerous small foramina on both the labial and lingual faces. There are eight to nine cones (including the acrocone) decreasing in height distally. The acrocone is slightly more developed than the first accessory cone; its mesial edge is serrated near the base in one of the specimens, whereas it is smooth in the second tooth. The L2/L3 ratio (see Adnet, 2006a for details) is 0.8 and 0.9, that is, L2<L3 in both cases. The number of cusps per tooth width equals 7.3 and 7.5.

Remarks. The teeth are morphologically identical to and metrically close to those in *Hexanchus agassizi* Cappetta, 1976. The specimens described are somewhat similar to those in *Notorynchus primigenius* (Agassiz, 1843) but differ by their smaller size and having more numerous accessory cones. The estimated length of the body (based on lower lateral teeth), following the equations in Compagno (1984) and Adnet (2006a), could have reached 129 and 136 cm. *Hexanchus agassizi* had a worldwide distribution during the Eocene (Cappetta, 2012). The presence of this species (also under the name *Notidanus serratissimus* Agassiz, 1843) is documented in the Eocene fossil record of Europe (Woodward, 1886, 1899; Casier, 1966; Cappetta, 1976; Ward, 1979; Dutheil, 1991; Adnet, 2006a; Adnet et al., 2008), Asia (Menner, 1928; Glickman, 1964; Case et al., 1996; Zhelezko and Kozlov, 1999; Mustafa et al., 2005; Malyshkina, 2006), Africa (Dartevelle and Casier, 1943; Zalmout et al., 2012; Zalat et al., 2017), South and North America (Case, 1981; Otero et al., 2013), and Australia (Pledge, 1967; Kemp, 1978). Adnet (2006a) considered *H. agassizi* to be the only lower–middle Eocene species of *Hexanchus*, whereas other taxa described from coeval deposits (*Hexanchus collinsonae* Ward, 1979 and *Hexanchus hookeri* Ward, 1979) may represent different ontogenetic stages of this species.

Genus *NOTORYNCHUS* Ayres, 1855
Notorynchus kemp Ward, 1979
 Figure 4D–E

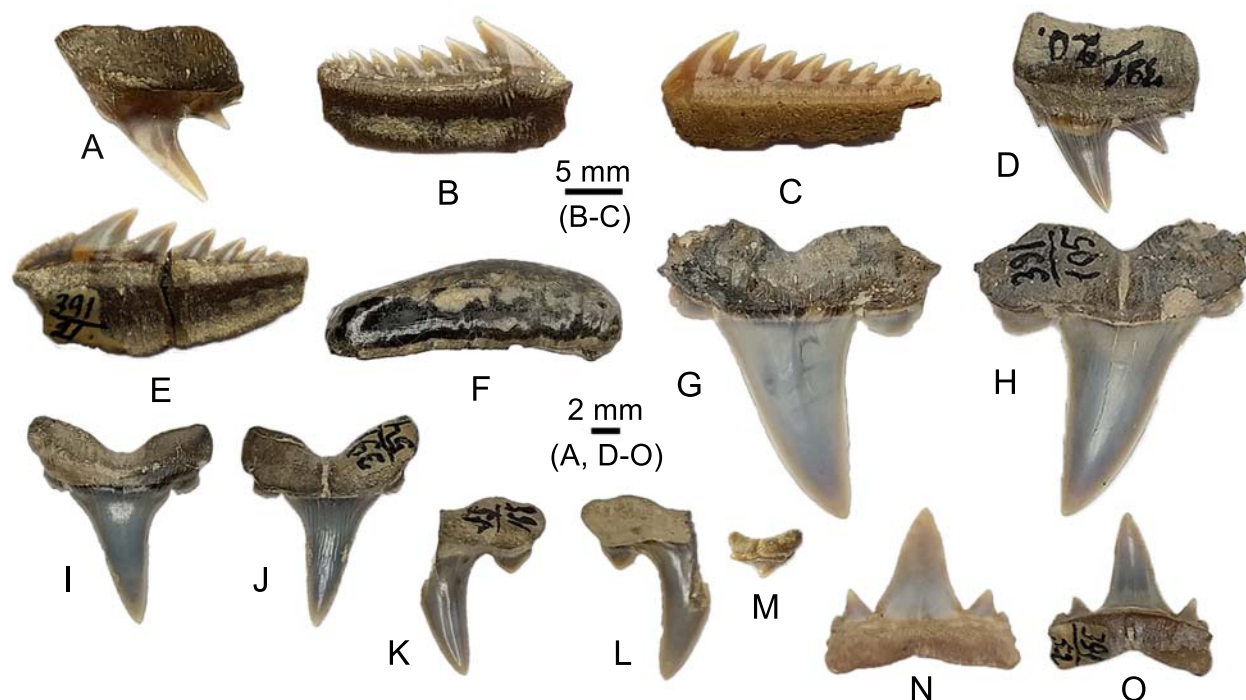


FIGURE 4. Hexanchiform, heterodontiform and lamniform shark teeth from the middle Eocene deposits of Vyshhorod: **A-C** – *Hexanchus agassizi* Cappetta, 1976, upper anterolateral tooth NMNHU-G 391/21/2 (**A**), lower lateral teeth NMNHU-G 391/21/3 (**B**) and NMNHU-G 391/21/4 (**C**); **D-E** – *Notorynchus kemp* Ward, 1979, upper anterolateral tooth NMNHU-G 391/20 (**D**), lower lateral tooth NMNHU-G 391/21/1 (**E**); **F** – *Heterodontus* sp., lateral tooth NMNHU-G 391/6; **G-M** – *Striatolamia macrota* (Agassiz, 1843), upper lateral teeth NMNHU-G 391/105 (**G-H**), NMNHU-G 391/54 (**I-J**), NMNHU-G 391/55 (**K-L**), upper posterior tooth NMNHU-G 391/92 (**M**); **N-O** – *Brachycarcharias lerichei* (Casier, 1946), lower lateral tooth NMNHU-G 391/52. Lingual view in **A**, **H**, **J-K**, **M**, and **O**, labial view in **B-G**, **I**, **L**, and **N**.

- 1861 *Notidanus serratissimus* Ag.; Rogovich, p. 29, pl. III, figs. 23, 24.
 1912 *Notidanus primigenius* Ag.; Savtchenko, p. 168-170, pl. XIII, figs. 11, 12.
 1979 *Notorynchus kemp* sp. nov.; Ward, p. 121-122, pl. 3, figs. 4-7.
 1999 *Notorhynchus kemp*; Zhelezko and Kozlov, pl. 32, figs. 4a-9b, pl. 34, figs. 1-6.
 2006 *Notorhynchus kemp* Ward, 1979; Udovichenko, p. 204, pl. I, fig. 5.

Material. One upper left anterolateral tooth, NMNHU-G 391/20; one lower left lateral tooth, NMNHU-G 391/21/1, Vyshhorod.

Description. The upper anterolateral tooth (Figure 4D) is quite large, 15.6 mm wide and 18.0 mm high, with an erect, convex crown inclined distally and possessing a complete cutting edge. The root is wide, compressed labiolingually, and wedge-shaped in anterior view (the lingual surface is steeply inclined towards the root base); its mesial and apical edges form a right angle. There is a single weakly serrated mesial cusplet and two sepa-

rated distal cusplets, the first of which is almost two times shorter than the main cusp.

The lower lateral tooth (Figure 4E) is 24.8 mm wide and 12.3 mm high. Its crown is labiolingually compressed and mesiodistally extended with an acrocone followed by six gradually decreasing lateral cusplets angled posteriorly. There are eight or nine small denticles increasing in size apically on the mesial edge of the main cusp.

Remarks. The specimens described were assigned to the genus *Notorynchus* based on the presence of denticles on the mesial edge of the main cusp of lower lateral teeth (Applegate, 1965; Kocsis, 2007) and a characteristic shape of the upper anterolateral tooth (Cappetta, 2012). These teeth resemble those in *Notorynchus kemp* Ward, 1979, in overall morphology and size. The teeth of *N. serratissimus* (Agassiz, 1843) are considerably smaller, have relatively coarser mesial cusplets as well as less numerous, larger, and less curved distal cusplets (Ward, 1979). As compared to *N. kemp* Ward, 1979, *N. primigenius* is characterised by larger tooth size, coarser mesial cusplets, rela-

tively larger, more pointed, and upright main cusp and distal cusplets (Ward, 1979). The specimens considered differ from *N. cepedianus* (Péron, 1807) in having a smaller overall tooth size and more erect cusplets. *Notorynchus kemp* ranged from the middle to late Eocene, being restricted to Zones NP 15–17 (Ward, 1979; Udovichenko, 2006). This species originally was described from the Bartonian of England (Ward, 1979), and later its remains were also found in Kazakhstan (Zhelezko and Kozlov, 1999) and Ukraine (Udovichenko, 2006).

Order HETERODONTIFORMES Berg, 1937

Family HETERODONTIDAE Gray, 1851

Genus *HETERODONTUS* Blainville, 1816

Heterodontus sp.

Figure 4F

1861 *Acrodus kioviensis* n. sp.; Rogovich, p. 17, pl. II, figs. 4–10.

Material. Two lateral teeth, NMNHU-G 391/6, 391/7, Vyshhorod.

Description. The teeth are asymmetrical, equal in size, reaching 2 cm in length. The crown is low (up to 5 mm), with one cutting edge being straight, while the others are slightly convex and wrinkled. The occlusal surface is smooth due to abrasion. There are poorly developed radial folds that converge in the central part of the crown. The basal surface of the root is flat.

Remarks. Seven isolated teeth were collected and described by Rogovich (1861) from the Eocene deposits of Vyshhorod. A new species—*Acrodus kioviensis*—was erected based on these specimens, only two of which are now present in the collection of NMNHU-G. Nevertheless, the teeth share some diagnostic characters of heterodontiform sharks (in particular, the genus *Heterodontus*) albeit resemble those in acrodontids due to a dental convergence (Cappetta, 2012). Representatives of the family Acrodontidae existed in Mesozoic seas and went extinct no later (if not earlier) than the Paleocene (Cook and Ramsdell, 1991). We refrain from assigning the specimens considered to a particular species, although we assume that this should be *Heterodontus vincenti* (Leriche, 1905) or another morphologically similar Eocene representative of this genus.

Order LAMNIFORMES Berg, 1937

Family MITSUKURINIDAE Jordan, 1898

Genus *STRIATOLAMIA* Glickman, 1964

Striatolamia macrota (Agassiz, 1843)

Figure 4G–M

- 1843 *Otodus macrotus* n. sp.; Agassiz, p. 273, pl. 32, figs. 29, 30.
- 1843 *Lamna elegans* n. sp.; Agassiz, p. 289, pl. 35, figs. 1–7; pl. 37a, figs. 58, 59.
- 1861 *Otodus macrotus* Ag.; Rogovich, p. 43, pl. V, figs. 16–22.
- 1861 *Lamna compressa* Ag.; Rogovich, p. 46, pl. V, figs. 29–30a.
- 1861 *Oxyrhina brevidens*; Rogovich, p. 57, pl. VIII, figs. 11, 11a.
- 1874 *Otodus striatus*; Winkler, p. 8, pl. 1, figs. 7–9.
- 1895 *Odontaspis macrota* var. *rossica*; Jaekel, p. 11, pl. 1, figs. 8–17; pl. 2, figs. 8–10.
- 1901 *Odontaspis macrota*; Eastman, p. 105, pl. 14, fig. 4.
- 1901 *Lamna striata* n. sp.; Priem, p. 484, pl. 11, figs. 29, 30.
- 1905 *Odontaspis macrota*; Leriche, p. 75.
- 1912 *Otodus macrotus* Ag.; Savtchenko, p. 173–174, pl. XIII, figs. 7–10.
- 1912 *Oxyrhina brevidens* Rog.; Savtchenko, p. 181.
- 1928 *Odontaspis macrota* Ag.; Menner, p. 301–302.
- 1942 *Odontaspis macrota striata* var. *semistriata*; Leriche, p. 13–14, pl. 1, figs. 6–8.
- 1964 *Striatolamia macrota* (Agassiz, 1843); Glickman, p. 120–121, 124–126, 143–144, pl. XIII, figs. 1–3, 5, 7–9, 14; pl. XXIII, figs. 12, 13, 15, 16.
- 1964 *Striatolamia rossica prima*; Glickman, p. 124, 128, 172, 182, pl. XXIV, figs. 1–9.
- 1964 *Striatolamia rossica usakensis*; Glickman, p. 124, 126, 148–149, 172, 177–178, pl. VII, figs. 3, 4; pl. XII, figs. 9–13, 16–18; pl. XIII, figs. 2–6, 11, 13.
- 1964 *Striatolamia rossica rossica*; Glickman, p. 121, 124, 126, 172, 178, pl. XI, figs. 9–13; pl. XII, figs. 3–8, 14–15.
- 1968 *Striatolamia macrota*; Applegate, p. 32–36, pls. 1–3.
- 1985 *Striatolamia macrota* (Agassiz, 1843); Bor, p. 92, pl. 2, figs. 9–11.
- 1987 *Striatolamia macrota* (Agassiz); Cappetta, p. 90, fig. 80A–E.
- 1988 *Odontaspis* (*Synodontaspis*) *macrota* (L. Agassiz, 1843); Bauzá and Gómez Pallero, p. 123–126, fig. 2.14–2.21.
- 1988 *Striatolamia macrota* (Agassiz); Nolf, p. 110, pl. 27.

- 1999 *Striatolamia macrota* (Agassiz, 1843); Zhelezko and Kozlov, p. 131-135, pl. 9, figs. 1-3; pl. 10; pl. 11, figs. 1-4; pl. 57; pl. 58, figs. 1-5, 7-10; pl. 59; pl. 60, figs. 7, 9.
- 2000 *Striatolamia macrota* (Agassiz); Cunningham, pl. 2, fig. 2; pl. 5, figs. 2, 4; pl. 6, figs. 2, 4; pl. 7, fig. 2; pl. 8, fig. 2; pl. 9, fig. 2; pl. 10, fig. 2; pl. 11, fig. 2; pl. 12, fig. 2; pl. 13, fig. 2; pl. 14, fig. 2; pl. 15, fig. 2; pl. 16, fig. 2; pl. 17, fig. 2.
- 2006 *Striatolamia macrota* (Agassiz); Malyshkina, pl. 6, fig. 1; pl. 10, figs. 1-4.
- 2006 *Striatolamia macrota* (Agassiz); Udovichenko, p. 202, pl. I, fig. 13.
- 2012 *Striatolamia macrota* (Agassiz, 1838); Cappetta, p. 189-190, fig. 178.
- 2012 *Striatolamia macrota* (Agassiz, 1843); Die-drich, p. 16, fig. 12.
- 2013 *Striatolamia macrota* (Agassiz, 1843); Malyshkina et al., pl. 13, figs. 2, 3.
- 2013 *Striatolamia macrota* (Agassiz, 1843); Otero et al., fig. 4.19-4.26.
- 2014 *Striatolamia macrota* (Agassiz, 1843); Carlsen and Cuny, p. 43-45, fig. 3G-L.
- 2019 *Striatolamia macrota* (Agassiz, 1843); Ebersole et al., p. 32-37, fig. 11.
- 2019 *Striatolamia macrota* (Agassiz, 1843); Trif et al., p. 8-10, figs. 5.5-7', 10-11.
- 2021 *Striatolamia macrota* (Agassiz, 1843); Adnet et al., p. 28-29, fig. 2.2-2.4.
- 2022 *Striatolamia macrota* (Agassiz, 1843); Trif et al., fig. 5G-O.

Material. Two upper lateral teeth, NMNHU-G 391/54, 391/105; one lower lateral tooth, NMNHU-G 391/55; one upper posterior tooth, NMNHU-G 391/92, Vyshhorod.

Description. Lateral teeth (Figure 4G–L) with triangular labiolingually flattened crowns are quite large or moderate-sized, and their height varies from 12.6 to 21.5 mm and width from 14.2 to 20.2 mm. Both upper and lower teeth are recognised in the series according to the curvature of the labial side of their crowns (Cunningham, 2000). The labial surface of the upper teeth is nearly straight from the base of the enameloid to the crown tip, whereas that of the lower teeth is slightly convex. There is a main cusp with a distal inclination and two shovel-shaped cusplets on the crown of each lateral tooth. The lingual face is ornamented with weak parallel striations reaching the middle of the crown. The striations are better pronounced in upper lateral teeth and less developed or absent in

the lower lateral teeth described herein. The blade-like cutting edges are complete in all specimens regardless of their position in the jaw.

The upper posterior tooth (Figure 4M) has a very low and wide crown, and its total height is 3.4 mm and maximum width is 6.4 mm. The labial side of the crown is straight. There is a semi-circular ridge with numerous thin vertical striations on the lingual side of the crown. The distal lateral denticle retains its definition from the crown, but the mesial lateral denticle is shoulder-like (*sensu* Cunningham, 2000:10). The root is notched labially, whereas its lingual side is swollen and is divided in the middle by a deep vertical furrow. The shallow interspace between the root lobes is V-shaped. The enameloid on the lingual surface is strongly striated.

Remarks. The lateral teeth described are similar in morphology and size to those in *Striatolamia macrota* (Agassiz, 1843). This species was widely distributed in Europe and Asia during the Ypresian, Lutetian, and Bartonian (Cappetta, 2012). The presence of *S. macrota* in the fossil record of Ukraine was documented by Zhelezko and Kozlov (1999) and Udovichenko (2006). Eight species of the genus *Striatolamia* are now considered to be valid (Pollerspöck and Straube, 2022), including two Paleocene taxa (*Striatolamia* ex gr. *S. whitei* (Arambourg, 1952), *S. striata* (Winkler, 1874)) and two Eocene species from the territory of Ukraine (Zhelezko and Kozlov, 1999). *Striatolamia sibirica* Zhelezko in Zhelezko and Kozlov (1999) was represented in the Dnieper–Donets Basin during the Bartonian. The specimens considered differ from those of *S. sibirica* in having larger roots, thicker crowns, and cusplets more isolated from the main cusp (Zhelezko and Kozlov, 1999). According to Ebersole et al. (2019), there are no appreciable differences between the teeth of *S. macrota* and *S. striata*, and these taxa therefore could be part of a species complex that cannot be differentiated morphologically. As compared to the specimens considered here, the teeth of the Bartonian/Ypresian species *Striatolamia tchelkarensis* are much larger and more robust, and have a less pronounced lingual ornamentation (Malyshkina, 2021).

Rogovich (1861) described and figured a new species of the genus *Oxyrhina*—*O. brevidens*—from ‘blue clay near Kyiv.’ The specimen considered is part of the type series (syntype), while the other ‘few teeth’ mentioned in the original description were subsequently lost. Savtchenko (1912), when analysing shark remains from the Eocene of

Mangyshlak, used the material from Rogovich's collection for comparison. He concluded that one specimen from his own collection was almost identical morphologically to that of *Oxyrhina brevidens*. This species is represented in the database by Pollerspöck and Straube (2022) but placed in the genus *Striatolamia*, probably because of the presence of characteristic (albeit weak) striation on the lingual side of the crown. We suggest that the specimen initially described by Rogovich (1861) as *O. brevidens* in fact represents the upper left posterior tooth of *S. macrota*. It is very similar to the one figured by Cunningham (2000: pl. 10, fig. 2, upper row, second from the left).

Family ODONTASPIDIDAE Müller and Henle,
1838

Genus *BRACHYCARCHARIAS* Cappetta and Nolf,
2005

Brachycarcharias lerichei (Casier, 1946)
Figure 4N–O

- 1861 *Otodus macrotus* Ag. (partim); Rogovich, p. 43, pl. V, fig. 23.
- 1946 *Lamna lerichei* n. sp.; Casier, p. 80, pl. 2, fig. 7a-b.
- 1988 *Lamna lerichei* Casier; Nolf, pl. 30, figs. 2-11.
- 1990 *Lamna lerichei* Casier; Kemp et al., p. 9, pl. 3, figs. 9, 10.
- 2005 *Brachycarcharias lerichei* (Casier, 1946); Cappetta and Nolf, p. 241-242, pl. 2.
- 2012 *Brachycarcharias lerichei* (Casier, 1946); Diedrich, p. 19, fig. 14.1-14.6.
- 2013 *Brachycarcharias lerichei* (Casier, 1946); Clayton et al., fig. 2L.
- 2016 *Brachycarcharias lerichei* (Casier, 1946); Cappetta and Case, pl. 3, figs. 8-22.
- 2018 *Brachycarcharias lerichei* (Casier, 1946); Marramà et al., p. 291, fig. 4.
- 2019 *Brachycarcharias lerichei* (Casier, 1946); Ebersole et al., p. 39-41, fig. 13.
- 2022 *Brachycarcharias lerichei*; Perez, p. 635, fig. 4A-B.

Material. One lower lateral tooth, NMNHU-G 391/52, Vyshhorod.

Description. The lateral tooth has a triangular crown; its height reaches 14.0 mm, and its width is 14.3 mm. The main cusp is slightly inclined distally and has an accentuated apex. There are two pairs of triangular lateral cusplets, the first of which is considerably larger than the second one. The crown surface is smooth and devoid of ornamentation. The root is holaulacorhize with a V-shaped

interlobe area. There is a shallow nutritive groove on the lingual root protuberance.

Remarks. The specimen described here is identical in morphology and size to teeth of *Brachycarcharias lerichei* (Casier, 1946). It differs from the respective teeth of other species of this genus in their smaller overall size, narrower main cusp, and smaller lateral cusplets (see Ebersole et al., 2019, for more details). In addition, the specimen considered differs from those of the coeval *Brachycarcharias atlasi* (Arambourg, 1952) in the absence of faint striations at the lingual crown base. The lateral teeth of *Hypotodus* have smaller and less divergent cusplets compared to *B. lerichei*. The latter species is characterised by less hooked lateral teeth with larger lateral cusplets than those in *Jaekelotodus* (Ebersole et al., 2019). In addition, the surface of the lateral teeth of *Striatolamia macrota* is ornamented, their lateral cusplets are blunt, and the root lobes are slightly wider. *Brachycarcharias lerichei* was distributed across the Northern Hemisphere during the early Paleogene (Marramà et al., 2018; Ebersole et al., 2019).

Genus *JAEKELOTODUS* Menner, 1928
Jaekelotodus trigonalis (Jaekel, 1895)
Figure 5A–F

- 1861 *Lamna cuspidata* Ag.; Rogovich, p. 46, pl. VI, figs. 7-14b.
- 1861 *Lamna denticulata* Ag.; Rogovich, p. 47, pl. VI, figs. 15-23.
- 1895 *Hypotodus trigonalis* n. sp.; Jaekel, pl. 1, figs. 6, 7.
- 1912 *Lamna (Odont.) crassidens* Ag. 1843; Savtchenko, p. 177-178, pl. XIII, figs. 20-23.
- 1928 *Iekelotodus trigonalis* (Iek.); Menner, p. 315.
- 1964 *Jaekelotodus trigonalis* (Jaekel) *minor* Gluckman; Glickman, p. 137, pl. XVIII, figs. 32, 33, 40-42, 44, 45; pl. XIX, figs. 1-3.
- 1964 *Jaekelotodus trigonalis* (Jaekel) *medius* Gluckman; Glickman, p. 137, pl. XIX, figs. 4, 5, 7, 8, 11-13, 18.
- 1964 *Jaekelotodus trigonalis trigonalis* (Jaekel); Glickman, pl. XIX, figs. 15-17, 20-22.
- 1988 *Hypotodus trigonalis* (Jaekel); Nolf, p. 114, pl. 29, figs. 1, 2.
- 1994 *Jaekelotodus trigonalis* (Jaekel, 1895); Zhelezko and Kozlov, p. 110-112, pl. 1, figs. 1-2; pl. 2, figs. 1-3; pls. 37-39.
- 2005 *Jaekelotodus trigonalis* (Jaekel, 1895); Cappetta and Nolf, p. 247, pl. 6, figs. 1-4.

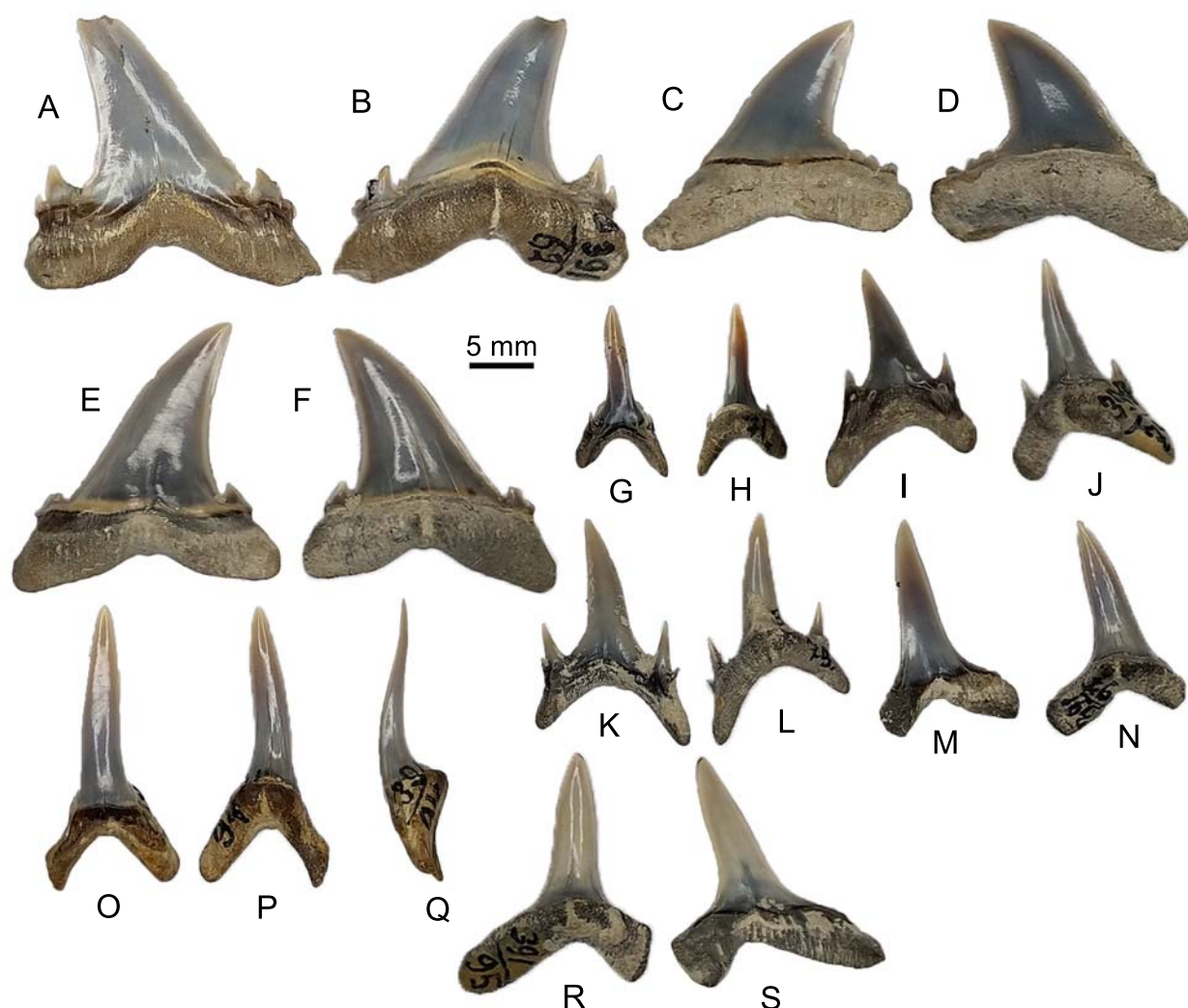


FIGURE 5. Lamniform shark teeth from the middle Eocene deposits of Vyshhorod: **A-F** – *Jaekelotodus trigonalis* (Jaekel, 1895), lateral teeth NMNHU-G 391/62 (**A-B**), NMNHU-G 391/139/1 (**C-D**), NMNHU-G 391/139/2 (**E-F**); **G-H** – *Mennerotodus* cf. *M. parmelei* Cicimurri, Ebersole and Martin, 2020, lower anterior tooth NMNHU-G 391/71; **I-L** – *Odontaspis winkleri* Leriche, 1905, anterolateral tooth NMNHU-G 391/74 (**I-J**); lateral tooth NMNHU-G 391/79 (**K-L**); **M-S** – *Isurolamna affinis* (Casier, 1946), anterolateral tooth NMNHU-G 391/97 (**M-N**), anterior tooth NMNHU-G 391/94 (**O-Q**), lateral tooth NMNHU-G 391/95 (**R-S**). Labial view in **A, C, E, G, I, K, M, O, and S**, lingual view in **B, D, F, H, J, L, N, P, and R**, mesial view in **Q**.

2006 *Jaekelotodus trigonalis* (Jaekel); Malyshkina, p. 99, pl. 9, figs. 3-5.

2006 *Jaekelotodus trigonalis* (Jaekel); Udovichenko, p. 202, pl. I, fig. 10.

2012 *Jaekelotodus trigonalis* (Jaekel, 1895); Cappetta, p. 200, fig. 189.

2012 *Jaekelotodus trigonalis* (Jaekel, 1895); Diedrich, p. 15, fig. 11.11-11.15.

2022 *Jaekelotodus trigonalis*; Perez, p. 635, fig. 4C.

Material. Six lateral teeth, NMNHU-G 391/62, 391/139/1-5, Vyshhorod.

Description. The teeth (Figure 5A–F) measure from 16.9 to 20.0 mm apicobasally (mean 19.0 mm) and from 19.5 to 21.5 mm mesiodistally (mean 20.2 mm). The main cusp is broad, with a curved tip, and has a concave, V-shaped cavity on its labial surface. Cutting edges are complete and progress into broad triangular primary cusplets. Secondary cusplets are also present, but they are smaller. Both pairs of cusplets are turned towards the main cusp, which has irregular and variably strong serrations near the base. On some of the specimens considered here, there are accessory denticles between the main cusp and lateral cus-

plets. The roots are massive and thickened labiolingually. The labial root surface is convex while the lingual is concave.

Remarks. The specimens described resemble those of *Jaekelotodus trigonalis* in overall morphology, although they are somewhat smaller. The teeth of Ypresian species (*J. londonensis* Zhelezko, 1994 and *J. borystenicus* Glickman, 1964) have larger, narrower, and more erect crowns. *Jaekelotodus trigonalis* differs from *J. robustus* (Leriche, 1921) in having higher, sharper, and more lateral cusplets, as well as a less pronounced furrow at the top of the root (Cappetta and Nolf, 2005). It differs from the teeth of *Hypotodus verticalis* (Agassiz, 1843) by having complete cutting edges of the main cusp, which extend to the lateral cusplets. We need to stress that our identification is somewhat tentative: these specimens may also belong to or include similar odontaspid taxa, such as *Mennerotodus*, *Tethylamna*, or *Brachycarcharias*.

Genus *MENNEROTODUS* Zhelezko, 1994
Mennerotodus cf. *M. parmleyi* Cicimurri, Ebersole and Martin, 2020
Figure 5G–H

1861 *Lamna* (*Odontaspis*) *Hoppei* [sic] Ag.; Rogovich, p. 49, pl. VII, figs. 3–10.

Material. One lower anterior tooth, NMNHU-G 391/71; one anterolateral tooth, NMNHU-G 391/88, Vyshhorod.

Description. The anterior tooth (Figure 5G–H) is quite small; it reaches 13.0 mm apicobasally and 7.4 mm mesiodistally. The main cusp is narrow, triangular, and slightly inclined distally. Cutting edges are sharp, smooth, and do not reach the base of the main cusp. There is a single pair of short, conical cusplets at the crown base. The labial face of the main cusp is smooth and flat while the lingual face is convex. Root lobes are elongated and almost of equal length.

The lateral tooth is much smaller, 6.5 mm high and 5.3 mm wide. It is morphologically similar to the anterior tooth, albeit has a shorter and relatively broader main cusp, cutting edges extending to the crown base, and root lobes are shorter but wider and more widely separated.

Remarks. The teeth resemble those of *Mennerotodus* Zhelezko, 1994, and their morphological characteristics fit well into the emended diagnosis of this genus provided by Cicimurri et al. (2020). The specimens from Vyshhorod are close in overall morphology to teeth assigned to *Mennerotodus parmleyi* from the middle Eocene of the USA, but we only tentatively assign them to this species con-

sidering the absence of denticles between the cutting edges and lateral cusplets (which are characteristic for this species according to Cicimurri et al., 2020) and the small size of the studied sample. *Mennerotodus parmleyi* differs from *M. glueckmani* Zhelezko, 1994 from the middle Eocene of Kazakhstan in having much smaller teeth and the presence of a single pair of lateral cusplets on lateral teeth (Cicimurri et al., 2020). It further differs from the Paleocene (Danian) *M. mackayi* Cicimurri et al., 2020 in having a more conspicuous and extensively developed denticulation and a greater crown–root height ratio (Cicimurri et al., 2020).

Genus *ODONTASPIS* Agassiz, 1838
Odontaspis winkleri Leriche, 1905
Figure 5I–L

- 1861 *Lamna* (*Odontaspis*) *hispida* Rog.; Rogovich, p. 50, pl. VII, figs. 11, 12.
- 1905 *Odontaspis winkleri* sp. nov.; Leriche, p. 74, p. 117, pl. 6, fig. 1–12.
- 1912 *Odontaspis winkleri* [sic] Ler. 1904; Savtchenko, p. 178–179.
- 1928 *Oxyrhina hopei* Ag.; Menner, p. 303, pl. X, figs. 7, 8.
- 1946 *Odontaspis* (*Synodontaspis*) *winkleri* Leriche, 1905; Casier, p. 72, pl. 2, fig. 6.
- 1966 *Odontaspis* (*Synodontaspis*) *winkleri* Leriche, 1905; Casier, p. 72, pl. 5, figs. 1–4.
- 1985 *Odontaspis winkleri* Leriche, 1905; Bor, p. 91, pl. 2, fig. 8.
- 1987 *Odontaspis winkleri* Leriche; Cappetta, p. 89, fig. 79A–D.
- 1988 *Odontaspis winkleri* Leriche; Nolf, pl. 26, figs. 1–12.
- 2005 *Odontaspis winkleri* Leriche, 1905; Cappetta and Nolf, p. 248.
- 2006 *Odontaspis winkleri* (Leriche); Udovichenko, p. 202, pl. I, figs. 11, 12.
- 2012 *Odontaspis winkleri* Leriche, 1905; Cappetta, p. 204, fig. 192A–D.
- 2012 *Otodus winkleri* Leriche, 1905; Diedrich, p. 19, fig. 14.11.
- 2014 *Odontaspis* cf. *winkleri* Leriche, 1905; Carlsen and Cuny, p. 54, fig. 9G–L.
- 2016 *Odontaspis winkleri* Leriche, 1905; Cappetta and Case, p. 49, pl. 2, fig. 6.
- 2016 *Odontaspis winkleri* Leriche, 1905; Malyshkina and Ward, p. 53, fig. 3N, O.
- 2019 *Odontaspis winkleri* Leriche, 1905; Ebersole et al., p. 52–53, fig. 18.

Material. Two anterior teeth, NMNHU-G 391/83; one anterolateral tooth, NMNHU-G 391/74; three lateral teeth, NMNHU-G 391/76, 391/79, 391/82, Vyshhorod.

Description. The teeth (Figure 5I–L) vary in size from 10.9 to 17.3 mm apicobasally and from 9.1 to 12.5 mm mesiodistally. The crown is slender and has a smooth surface. In addition to a narrow and pointed main cusp, there are two pairs of very sharp cusplets, which are fused by their bases and differ in size: the inner ones are high (up to 4 mm) and circular at the base while the outer cusplets are vestigial. Cutting edges are not serrated and do not reach the crown base. The root is massive, usually arcuate, and has two relatively long lobes with rounded tips. Its labial face is concave, whereas the lingual face is convex and bears a deep nutritive groove.

Remarks. The specimens considered are similar in morphology and size to those in *Odontaspis winkleri* originally described by Leriche (1905). They differ from those of other odontaspidids by high and cylindrical lateral cusplets, incomplete cutting edges in anterior teeth, and well-pronounced folds at the base of the labial side in lateral teeth (Ebersole et al., 2019). *Odontaspis winkleri* is well represented in the Eocene fossil record of Europe (Leriche, 1905; Casier, 1946, 1966; Bor, 1985; Nolf, 1988; Adnet 2006b; Dutheil et al., 2006; Udovichenko, 2006; Eeckhaut and De Schutter, 2009; Rayner et al., 2009; Cappetta, 2012; Diedrich, 2012; Carlsen and Cuny, 2014), Asia (Savtshenko, 1912; Menner, 1928; Malyshkina and Ward, 2016), and North America (Cappetta and Case, 2016; Ebersole et al., 2019).

Family LAMNIDAE Bonaparte, 1835

Genus *ISUROLAMNA* Cappetta, 1976

Isurolamna affinis (Casier, 1946)

Figure 5M–S

- 1861 *Oxyrhina biflexa* n. sp.; Rogovich, p. 55, pl. VIII, figs. 4, 5.
- 1912 *Oxyrhina biflexa* Rog.; Savtchenko, p. 180, pl. XIII, figs. 28, 33, 39.
- 1928 *Oxyrhina biflexa* Rog.; Menner, p. 306.
- 1946 *Odontaspis hopei* var. *affinis*; Casier, p. 65, pl. 2, fig. 11b-c.
- 1950 *Lamna affinis* (Casier); Casier, p. 17.
- 1966 *Lamna affinis* (Casier); Casier, p. 80, pl. 5, figs. 7-14.
- 1976 *Isurolamna affinis* (Casier, 1946); Cappetta, p. 555-556, pl. 2, figs. 1-8.
- 2012 *Isurolamna affinis* (Casier, 1946); Cappetta, p. 217, fig. 203A-G.

2012 *Isurolamna affinis* (Casier, 1946); Diedrich, p. 19, fig. 14.10.

2014 *Isurolamna affinis* (Casier, 1946); Carlsen and Cuny, p. 46, fig. 4A-G.

2021 *Isurolamna affinis* (Casier, 1946); Adnet et al., p. 31-33, fig. 4.5-4.6.

Material. Three anterior teeth, NMNHU-G 391/94, 391/99, 391/100; one anterolateral tooth, NMNHU-G 391/97; three lateral teeth, NMNHU-G 391/95, 391/140/1-2, Vyshhorod.

Description. The anterior teeth (Figure 5O–Q) measure from 16 to 17 mm apicobasally. The crown is slender and moderately inclined lingually. The lingual face is strongly convex, and the labial face is almost flat with a median depression near the crown-root junction. The enameloid is smooth on both faces, and the cutting edges reach the base of the crown. There is only a main cusp without cusplets, and both mesial and distal sides of the crown are smooth. The root with an arcuate basal edge shows two rounded lobes, which are broken and therefore it is not possible to measure the angle between them. There is a round foramen on the lingual protuberance.

The anterolateral tooth (Figure 5M–N) is similar in morphology and size to the anterior ones (measuring 16.5 mm apicobasally and 11.1 mm mesiodistally), although it has a wider main cusp. The root consists of two lobes differing in size and the degree of roundness.

The lateral teeth (Figure 5R–S) measure from 10.5 to 18.4 mm apicobasally and from 10.8 to 16.0 mm mesiodistally. The crown is triangular, inclined distally, and flattened labiolingually. There are two doubled triangular cusplets that are well separated from the main cusp in lingual view, although they are absent in one specimen (as in the case of anterior and anterolateral teeth). One of the root lobes is shorter and rectangular, whereas the other one is longer and has a rounded edge. The basal root edge is arcuate, and the angle between the root lobes equals 100°.

Remarks. The genus *Isurolamna* has characteristic heterodonty: anterior and anterolateral teeth of its representatives are of isuroid morphology, whereas the lateral teeth are morphologically similar to those in certain lamnids (Cappetta, 1976). Of the three species known so far from the Eocene of Europe and Asia (Adnet et al., 2021), the specimens described in this study are the most similar to those of *I. affinis* (Casier, 1946). These teeth differ from *I. inflata* Leriche, 1905 in lacking lateral cusplets, and they are much smaller than those of *I. bajarunasi* Glickman and Zhelezko, 1985 from the

middle Eocene of Kazakhstan (see Adnet et al., 2021 for details). Udovichenko (2006) noted the presence of the latter species in the middle Eocene of Hradyzk (Ukraine). We assume that the specimen depicted there should rather be assigned to *I. affinis*. It is, however, possible that teeth of taxa such as *Anomotodon* may be mixed in this sample.

Genus *MACRORHIZODUS* Cappetta, 1976
Macrorhizodus praecursor (Leriche, 1905)
 Figure 6A–H

- 1861 *Lamna lata* Rog.; Rogovich, p. 49, pl. VII, figs. 1-2a.
- 1861 *Oxyrhina Desorii* [sic] Ag.; Rogovich, p. 54, pl. VIII, figs. 1-3.
- 1905 *Oxyrhina desori praecursor*; Leriche, p. 128.
- 1928 *Oxyrhina desori* Sismonda; Menner, p. 304, pl. X, figs. 28-31.
- 1928 *Oxyrhina desori* mut. *praecursor* Leriche; Menner, p. 305.
- 1942 *Oxyrhina praecursor americana*; Leriche, p. 45, pl. 3, figs. 6-13.
- 2002 *Cosmopolitodus praecursor*; Mustafa and Zalmout, p. 82, pl. 1, figs. 7-11.
- 2005 *Cosmopolitodus praecursor* (Leriche, 1905); Mustafa et al., p. 408-409, figs. 14-20.
- 2006 *Isurus praecursor* (Leriche); Udovichenko, p. 202, pl. I, fig. 16.
- 2011 *Macrorhizodus praecursor* (Leriche, 1905); Underwood et al., p. 54, fig. 4C, D.
- 2012 *Macrorhizodus praecursor* (Leriche, 1905); Cappetta, p. 221-222, fig. 207.
- 2012 *Isurus praecursor* (Leriche, 1905); Diedrich, p. 15, fig. 11.1-11.10.
- 2012 *Macrorhizodus praecursor* (Leriche, 1905); Zalmout et al., p. 76, fig. 4A-V.
- 2013 *Macrorhizodus praecursor* (Leriche, 1905); Otero et al., fig. 3.28-3.34.
- 2013 *Macrorhizodus praecursor* (Leriche, 1905); Malysheva et al., pl. 13, fig. 7.
- 2017 *Macrorhizodus praecursor* (Leriche, 1905); Zalat et al., p. 207; pl. 1, fig. 5.
- 2019 *Macrorhizodus praecursor* (Leriche, 1905); Ebersole et al., p. 56-58, fig. 20.
- 2019 *Macrorhizodus praecursor* (Leriche, 1905); Trif et al., p. 8, fig. 5.1-5.4.
- 2021 *Macrorhizodus praecursor* (Leriche, 1905); Adnet et al., p. 31, fig. 4.1-4.4.
- 2021 *Macrorhizodus praecursor* (Leriche, 1905); Zouhri et al., p. 125, fig. 2H-K.

2022 *Macrorhizodus praecursor* (Leriche, 1905); Perez, p. 635, fig. 4L, M.

Material. One anterior tooth, NMNHU-G 391/101; one anterolateral tooth, NMNHU-G 391/103, Vyshhorod; one additional anterior tooth, NMNHU-G 391/68, and one additional anterolateral tooth, NMNHU-G 391/69, also from Vyshhorod, tentatively identified to this taxon.

Description. NMNHU-G 391/101 (Figure 6A–B) is quite large, although the crown is broken at the tip; therefore, it is not possible to measure its apico-basal height. The main cusp is stout, has a lingual inclination in profile, and is not accompanied by any cusplets. Both the labial and lingual faces of the crown are smooth and convex. The cutting edges extend from the apex to the crown base. The robust root ends with lanceolate lobes, one of which is partly broken.

NMNHU-G 391/68 (Figure 6C–D) represents a crown broken at the base near its junction with the root. The crown is triangular and reaches 19.4 mm mesiodistally. Its labial face is almost flat, whereas the lingual face is convex. The cutting edges extend to the crown base.

NMNHU-G 391/103 (Figure 6E–F) measures 23.8 mm apicobasally and 17.6 mm mesiodistally. The triangular cusp is shorter than that in the anterior tooth. The root lobes with slightly pointed tips are unequal in length. There is a weak lingual protuberance on the root.

NMNHU-G 391/69 (Figure 6G–H) measures 22.8 mm apicobasally and ca. 20.5 mm mesiodistally. It is preserved better, albeit its root is broken. The cusp is asymmetrical and lateral cusplets are absent. Both the mesial and distal cutting edges are convex.

Remarks. The specimens described are morphologically similar to those in *Macrorhizodus praecursor* and fit well into the diagnosis of this species. *Macrorhizodus praecursor* had a worldwide distribution during the middle and late Eocene (Cappetta, 2012; Adnet et al., 2021). However, the taxonomic identification of NMNHU-G 391/68 and NMNHU-G 391/69 is tentative because of their poor state of preservation, particularly due to the absence of roots.

Family OTODONTIDAE Glickman, 1964
 Genus *OTODUS* Agassiz, 1838
Otodus (*Carcharocles*) sp.
 Figures 6I–P, 7A–M

- 1861 *Carcharodon megalotis* Ag.; Rogovich, p. 36, pl. IV, figs. 14-16b.

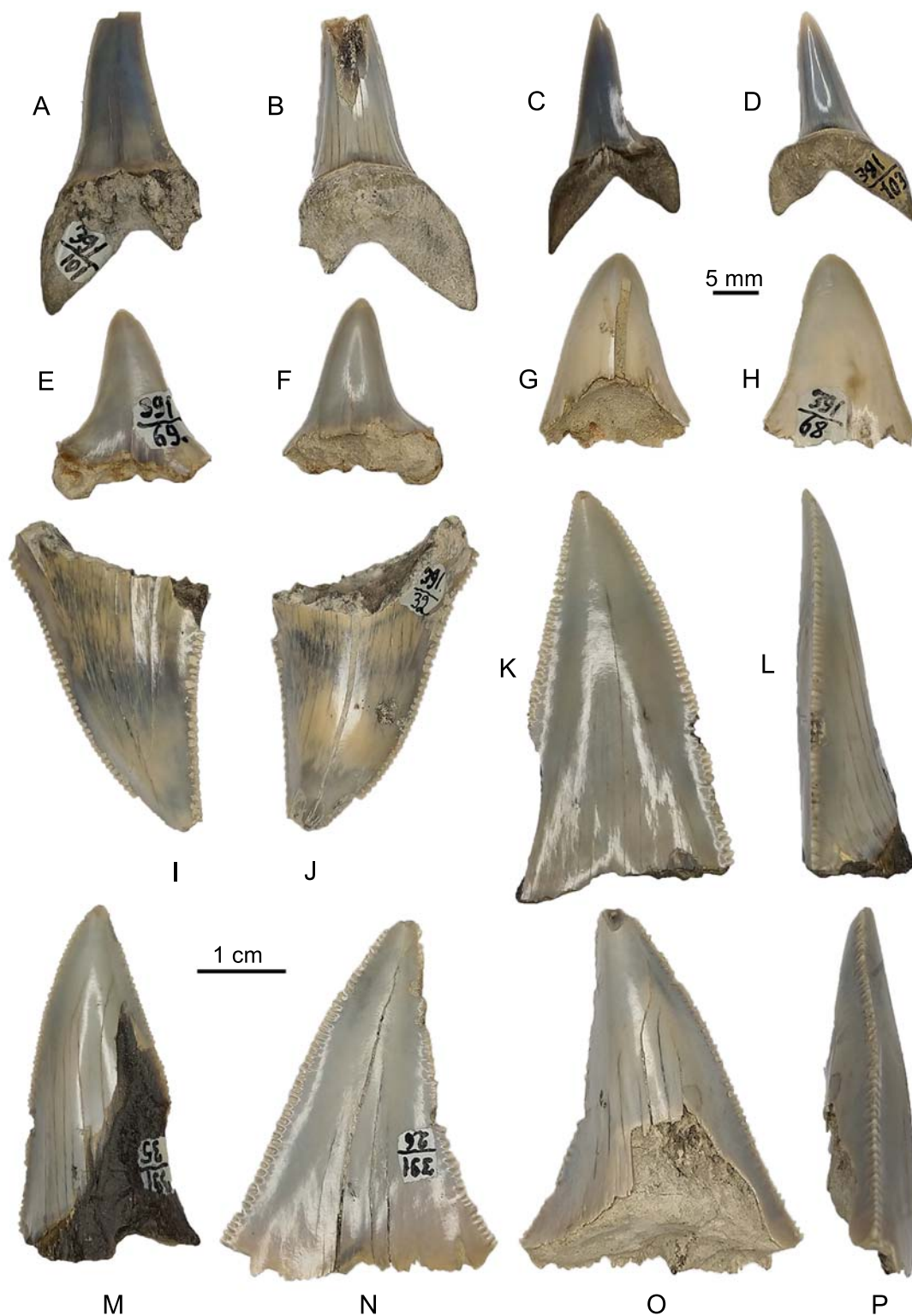


FIGURE 6. Lamniform shark teeth from the middle Eocene deposits of Vyshhorod: **A-H** – *Macrorhizodus praecursor* (Leriche, 1905), anterior teeth NMNHU-G 391/101 (**A-B**), anterolateral teeth NMNHU-G 391/103 (**C-D**), 391/69 (**E-F**), anterior tooth NMNHU-G 391/68 (**G-H**); **I-P** – *Otodus (Carcharocles)* sp., upper lateral tooth NMNHU-G 391/32 (**I-J**), lower anterolateral teeth, NMNHU-G 391/35 (**K-M**), lower anterolateral tooth NMNHU-G 391/26 (**N-P**). Labial view in **A, C, E, G, I, K, and N**, lingual view in **B, D, F, H, J, M, and O**, mesial view in **L and P**.

1861 *Carcharodon lanceolatus* Ag.; Rogovich, p. 37, pl. IV, fig. 17; pl. 9, figs. 58, 58a.

1861 *Carcharodon productus* Ag.?; Rogovich, p. 37, pl. IV, figs. 18, 19.

Material. One upper lateral tooth, NMNHU-G 391/32; three lower anterolateral teeth, NMNHU-G 391/26, 391/29, 391/35, Vyshhorod; five isolated vertebrae, NMNHU-P PI 553, PI 554, PI 2314, PI 2315, PI 2316, Zoloti Vorota.

Description. The anterolateral and lateral teeth (Figure 6I–P) are large and wide, triangular or lanceolate in shape; all the specimens are broken near the crown-root junction. The total height of the crown is in the range of 39.1–46.8 mm with the maximum width of about 30 mm. Both crown faces are smooth; the lingual face is convex and the labial one is flat. The cutting edges are irregularly serrated with saw-like serrations from the rounded crown apex to the base.

The vertebrae specimens (Figure 7A–M) are represented by robust, well-calcified, disk-shaped centra, where the smallest one (NMNHU-P PI 554) measures 64 mm in diameter and 29 mm in anteroposterior length; the largest one (NMNHU-P PI 2314) measures 88 mm in diameter and 32 mm in anteroposterior length. They are characterised as 'lamnoid vertebrae' (Applegate, 1967) by exhibiting many radiating calcified lamellae (asterospondylic) connecting the two primary cones of unperforated amphicoelous calcification (corpora calcarea) (for terminology, see Ridewood, 1921; Newbrey et al., 2015). The walls of the pairs of circular to oval foramina for the basidorsal and basiventral cartilages (Welton and Farish, 1993) make direct contact with the corpora calcarea. Both articular surfaces exhibit many concentric growth bands.

Remarks. The tooth specimens from Vyshhorod are identical in morphology and size to those of *Otodus* (*Carcharocles*) *auriculatus* from the Eocene of Europe, Asia, and North America (e.g., Savtchenko, 1912; Glickman, 1964; Nolf, 1988; Zhelezko and Kozlov, 1999; Cappetta, 2012; Carlsen and Cuny, 2014; Maisch et al., 2015; Adnet et al., 2021). Zhelezko and Kozlov (1999) reported on the presence of a specific subspecies—*Otodus auriculatus auriculatus* (Blainville, 1818)—occurring in the Lutetian of Ukraine, Kazakhstan, and Central Asia. It differs from *Otodus auriculatus disauris* (Agassiz, 1843) in the presence of regular serrations on the cutting edges. While the state of preservation of the material described in this study is insufficient for identifying it closer than to genus level, the merit of such subspecies concept for the genus *Otodus* is uncertain.

The specimens considered are represented by broken crowns only, therefore we do not speculate them. The five isolated vertebrae likely represent the same taxon due to their similar morphology and belong to a lamniform based on their 'lamnoid' type (see above). The tentative identification is based on their large vertebral sizes that precludes to be any other known lamniform taxa from the Eocene, and the fact that their morphology does not contradict with that of previously described vertebrae of *O. auriculatus* (Ehret and Ebersole, 2014).

Lamniformes indet.

Figure 8A–M

1861 Shark vertebrae; Rogovich, p. 63, pl. IX, figs. 6-6b, 11-16.

Material. Seven vertebrae, NMNHU-G 391/118, 391/119, 391/120, 391/121, 391/122, 391/136, 391/137, Vyshhorod.

Description. NMNHU-G 391/118, 391/119, 391/120, 391/121, and 391/122 represent five of the six vertebral centra that are considered to have come from a single vertebral column, which were found near Vyshhorod (Rogovich, 1861), whereas NMNHU-G 391/136 and 391/137 represent isolated vertebrae. All the vertebrae are represented by gracile but well-calcified, unperforated, amphicoelous centra with several thin radiating calcified lamellae. Their articular surfaces are circular ranging up to 44.1 mm in diameter and 19.4 mm in anteroposterior length (based on NMNHU-G 391/136). The walls of the pairs of robust circular to oval foramina for the basidorsal and basiventral cartilages make direct contact with the corpora calcarea. Many faint concentric growth bands are present on both articular surfaces of the vertebrae considered.

Remarks. The seven vertebrae described here exhibit a generally similar morphology, but whether all of them are conspecific cannot be ascertained. Similarly to the vertebrae of *Otodus* (*Carcharocles*) sp. (see above), the entire surface of the intermedialia (i.e., the body of each centrum between both sides of corpora calcarea) is rough because of the terminal edges of the radiating calcified lamellae, indicating that they are of 'lamnoid type' (see above). They differ from all other elasmobranch vertebrae described below by the surface of the intermedialia being either largely smooth or massive in appearance (except for the oval foramina for the basidorsal and basiventral cartilages) or having laterally oblong (non-circular) articular surfaces. However, because they are isolated finds

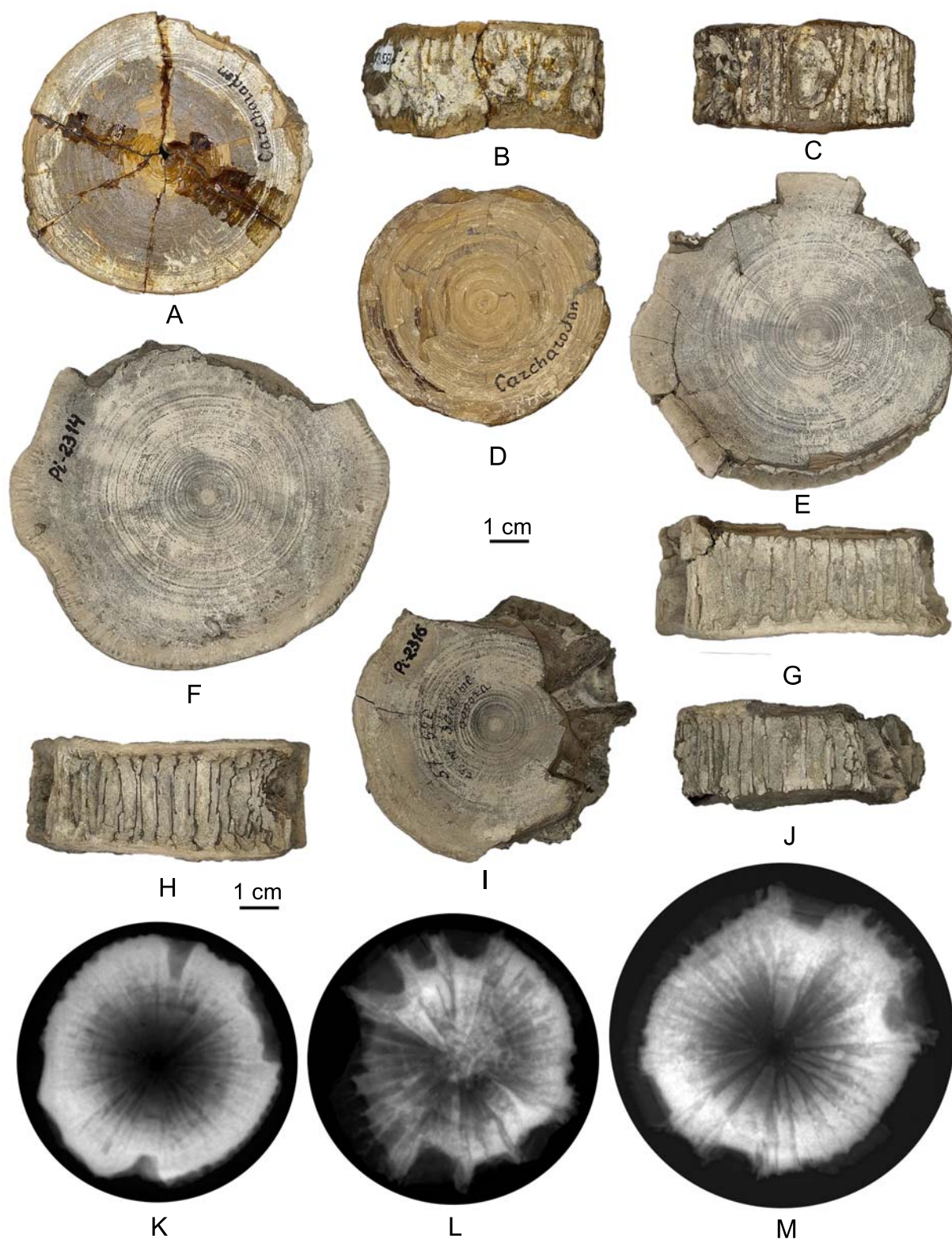


FIGURE 7. Vertebrae of *Otodus* (*Carcharocles*) sp. from the middle Eocene deposits of Zoloti Vorota (Kyiv): **A-B** – NMNHU-P PI 553; **C-D, K** – NMNHU-P PI 554; **E-F** – NMNHU-P PI 2314; **G-H, M** – NMNHU-P PI 2315; **I-J, L** – NMNHU-P PI 2316. Anterior view in **A, C, E, G,** and **I**, lateral view in **B, D, F, H,** and **J**. X-ray images are those in **K-M** (not to scale).

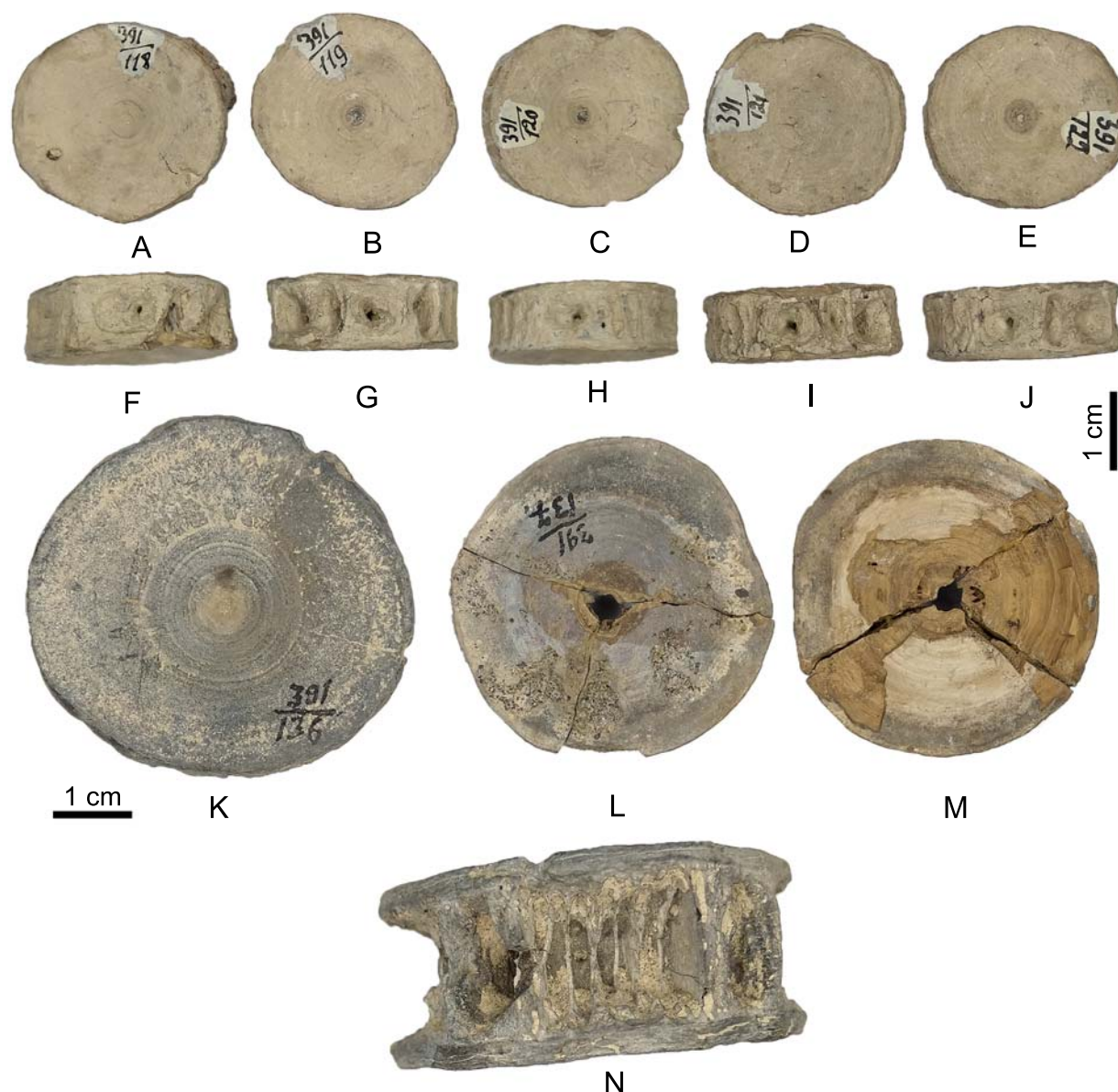


FIGURE 8. Lamniform vertebrae (Lamniformes indet.) from the middle Eocene deposits of Vyshhorod: **A, F** – NMNHU-G 391/118; **B, G** – NMNHU-G 391/119; **C, H** – NMNHU-G 391/120; **D, I** – NMNHU-G 391/121; **E, J** – NMNHU-G 391/122; **K** – NMNHU-G 391/136; **L-N** – NMNHU-G 391/137. Anterior view in **A-E** and **K-L**, posterior view in **M**, lateral view in **F-J** and **N**.

with no associated teeth, their exact taxonomic identity beyond 'Lamniformes indet.' is uncertain.

Order CARCHARHINIFORMES Compagno, 1973
Family CARCHARHINIDAE Jordan and Evermann, 1896

Genus *PHYSOGALEUS* Cappetta, 1980

Physogaleus secundus (Winkler, 1876)

Figure 9

1861 *Galeocерdo minor* Ag.; Rogovich, p. 30, pl. IV, figs. 1-7.

1876 *Trigonodus secundus* n. sp.; Winkler, p. 16-48, pl. 2, figs. A-F.

1905 *Physodon secundus* (Winkler); Leriche, p. 189, pl. 8, figs. 6, 17, 18.

1912 *Galeocерdo minor* Ag.; Savtchenko, p. 170–171, pl. XIII, figs. 13-15.

1980 *Physogaleus secundus* (Winkler, 1876); Cappetta, p. 37, pl. 5.

1985 *Striatolamia macrota* (Agassiz, 1843); Bor, p. 95, pl. 3, figs. 3-8.

- 2002 *Physogaleus secundus* (Winkler, 1874); Dutheil et al., p. 758, fig. 4F, G.
- 2006 *Physogaleus secundus* (Winkler); Malyshkina, pl. 7, figs. 7-8.
- 2012 *Physogaleus secundus* (Winkler, 1876); Cappetta, p. 313-315, fig. 297.
- 2014 *Physogaleus* cf. *secundus* Winkler, 1876; Carlsen and Cuny, p. 61-62, fig. 14.
- 2019 *Physogaleus secundus* (Winkler, 1876); Ebersole et al., p. 95-98, fig. 34.
- 2019 *Physogaleus secundus* Winkler, 1876; Trif et al., p. 7-8, fig. 4.5-4.11.

Material. Three upper lateral teeth NMNHU-G 391/24/2-4, one lower anterolateral tooth NMNHU-G 391/24/1, one lower lateral tooth, NMNHU-G 391/24/5, Vyshhorod.

Description. The anterolateral tooth (Figure 9B) is quite large measuring 9.4 mm mesiodistally, 9.0 mm apicobasally, and 4.1 mm labiolingually. It has a slender and sigmoidal main cusp. The lingual face of the crown is convex, and the labial face is almost flat. The mesial cutting edge is long and faintly serrated near the base, whereas the distal edge is shorter and bears two rounded cusplets. The root has a lingual protuberance and deep central furrow.

The lateral teeth (Figure 9A, C) range in size from 7.8 to 9.9 mm mesiodistally (mean 8.6 mm), from 5.2 to 5.9 mm apicobasally (mean 5.6 mm), and from 2.2 to 2.5 mm labiolingually (mean 2.3 mm). The lower lateral tooth (Figure 9C) is slightly larger than the upper lateral ones. The sigmoidal crowns are angled distally. The mesial and distal edges of the main cusp are smooth. The base of the mesial cutting edge is slightly serrated, and there are four coarse triangular cusplets at the base of the distal cutting edge. The lingual and labial tooth surfaces are convex and the labial one overhangs the root. The root has a large lingual protuberance with a deep nutritive groove. The rectilinear basal root surface is nearly flat or slightly concave.

Remarks. The teeth are identical in morphology and size to those of *Physogaleus secundus*. The latter differs from other species of the genus in tooth size, cusp width, development of cusplets, and morphology of the cutting edge (Carlsen and Cuny, 2014; Ebersole et al., 2019; Trif et al., 2019). In particular, the teeth of *P. secundus* can be differentiated from those in the coeval species *Physogaleus alabamensis* (Leriche, 1942) by the number and strength of the mesial and distal denticles (Ebersole et al., 2019). The remains of *P. secundus*

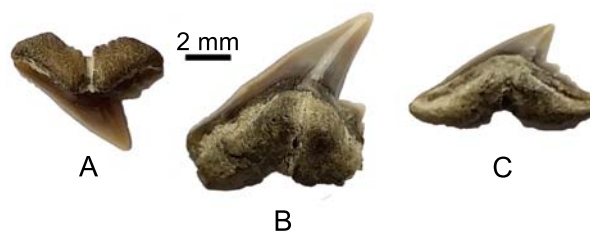


FIGURE 9. Teeth of *Physogaleus secundus* (Winkler, 1876) from the middle Eocene deposits of Vyshhorod: **A** – upper lateral tooth NMNHU-G 391/24/2; **B** – lower anterolateral tooth NMNHU-G 391/24/1; **C** – lower lateral tooth NMNHU-G 391/24/5, all in lingual view.

are known from the Eocene of Europe (Leriche, 1905; Bor, 1985; Dutheil et al., 2002; Cappetta, 2012; Carlsen and Cuny, 2014; Trif et al., 2019), Asia (Malyshkina, 2006), and North America (Maisch et al., 2015; Ebersole et al., 2019). It should be emphasised that Rogovich (1861) described a series of carcharinid teeth from Vyshhorod that he identified as *Galeocerdo minor*. This taxon originally was erected and figured by Agassiz (1835; Agassiz, 1833–1843, vol. 3, p. 232, pl. 26a, figs. 64-66, pl. 26, figs. 15-21) under the name *Galeus minor*. Woodward (1889) considered *Galeocerdo minor* to be valid but questioned its generic attribution. Although the locality and age of the original sample were unknown, Agassiz (1843) assumed that it probably came from Tertiary deposits of the Swiss Molasse Basin. *Galeocerdo minor* was reported from the Eocene of Belgium, England, the USA, and from the Miocene of France (Woodward, 1889). In addition, Savtchenko (1912) documented the remains of this taxon in the Eocene of Mangyshlak (Kazakhstan). It is noteworthy that the latter was the last published reference to *Galeocerdo minor* in the literature. It is figured in the database compiled by Pollerspöck and Straube (2022) as *Physogaleus minor* (Agassiz, 1835). We cautiously assume that *P. minor* and *P. secundus* could be conspecific, although such a revision is beyond the scope of our present study.

Order MYLIOBATIFORMES Compagno, 1973

Family MYLIOBATIDAE Bonaparte, 1838

Myliobatidae gen. et sp. indet.

Figure 10A-F

- 1861 *Myliobates toliapicus* Ag.; Rogovich, p. 12, pl. 2, figs. 14, 22.

Material. Nineteen teeth, NMNHU-G 391/3, Vyshhorod.

Description. The teeth (Figure 10A–F) are hexagonal and mesiodistally elongated. The root consists of thin, uniformly narrow lobes, fused at the tip, and

oriented perpendicular to the crown in the form of a comb. The crown overhangs the root, and it is separated from it by a sharp transverse ridge on the labial side and has a respective recess on the lingual side. It consists of a thin enameloid layer, the surface of which is either straight or convex. There are faint longitudinal ridges and numerous nutritive foramina on the transverse edges of the crown.

Remarks. The series of teeth described above was assigned to the family Myliobatidae based on several characters, including hexagonal shape, mesiodistal elongation, and the presence of multiple nutritive grooves (Cappetta, 2012). We refrain from assigning these fragmentary specimens to a particular genus due to the poor state of their preservation. In addition, the recent molecular divergence estimated by Villalobos-Segura and Underwood (2020) indicates that myliobatid genera did not diverge until the Neogene. Thus, Paleogene forms seemingly represent stem members of their respective lineages and cannot be assigned to any extant genera.

Myliobatiformes indet.
Figure 10G-I

- 1843 *Myliobates Owenii* [sic]; Agassiz, p. 331, pl. 45, figs. 11-13.
1861 *Myliobates Owenii* [sic] Ag.; Rogovich, p. 11, pl. I, fig. 7.
1912 *Myliobates Owenii* [sic] Ag.; Savtchenko, p. 167, pl. XIII, fig. 4.
1912 *Myliobates* sp.; Savtchenko, p. 167-168, pl. XIII, figs. 1-3.
2019 Myliobatinae indet. 2; Trif et al., p. 13-14, fig. 7.13-7.15.
2021 Myliobatiformes indet.; Szabó et al., p. 391, pl. IX, figs. J'-M'.
2022 Myliobatiformes indet.; Trif et al., fig. 9A-C.

Material. One broken caudal spine, NMNHU-G 391/2, Vyshhorod.

Description. The flattened caudal spine (Figure 10G-I) is large with a preserved length of 14.6 cm and maximum width of 2.0 cm. It is broken into three fragments of different sizes. The spine gradually tapers towards the distal tip. Both lateral edges at a distance of about 4 cm from the base bear short sawtooth barbs that are proximally curved and increase in size to the tip. Both dorsal and ventral surfaces of the spine are striated and covered by irregular grooves parallel to each other. In addition, there are two longitudinal ridges on the ventral side of the spine.

Remarks. Rogovich (1861) initially identified this specimen as *Myliobates Owenii* [sic], and, in fact, it

looks identical to those figured by Agassiz (1843, pl. 45, figs. 11-13). However, *M. owenii* is now recognised a *nomen dubium* because it was erected based on the caudal spine and not on dentition (Pollerspöck and Straube, 2022). According to Hovestadt and Hovestadt-Euler (2013) and Trif et al. (2022), caudal spines of Myliobatiformes have little diagnostic value and therefore we leave the specimen considered here in open nomenclature.

Elasmobranchii indet.

Figure 11

- 1861 *Lamna* (vertebrae); Rogovich, p. 62, pl. IX, figs. 2, 3, 5.
1861 Shark vertebrae; Rogovich, p. 63, pl. IX, figs. 7, 8.

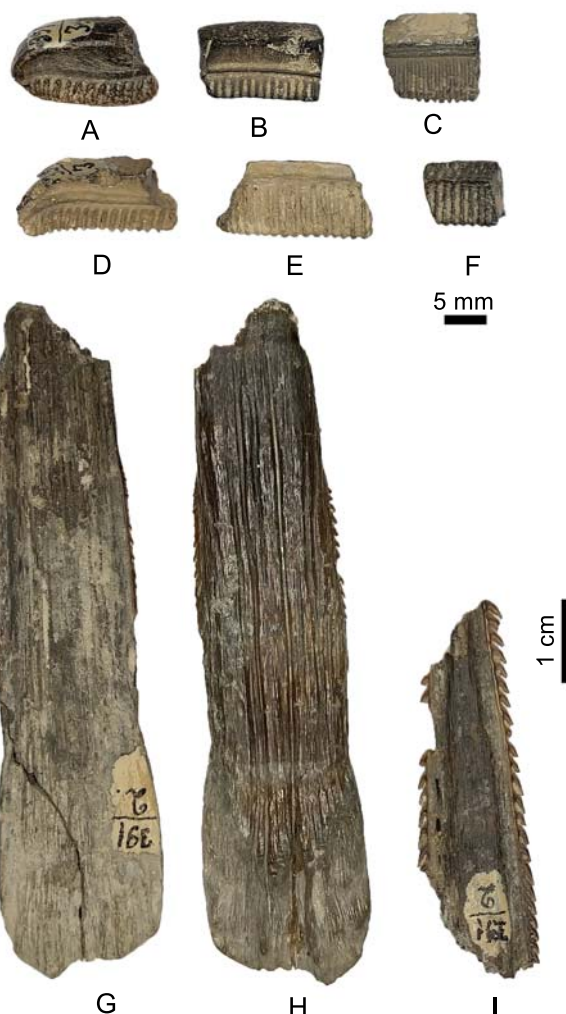


FIGURE 10. Myliobatiform remains from the middle Eocene deposits of Vyshhorod: **A-F** – Myliobatidae gen. et sp. indet., teeth NMNHU-G 391/3/1-6; **G-I** – Myliobatiformes indet., caudal spine NMNHU-G 391/2, represented by three fragments.

Material. Nine vertebrae, NMNHU-G 391/125, 391/126, 391/127, 391/129, 391/130, 391/131, 391/133, 391/134, 391/135, Vyshhorod.

Description. The vertebrae are represented by well-calcified, unperforated, amphicoelous centra with a variable range of sizes but quite similar in overall morphology.

Remarks. Because of the wide range of size and morphological variations observed among the nine vertebrae, they most certainly represent multiple taxa. For example, NMNHU-G 391/126, 391/129, 391/130, 391/131, 391/133, 391/134, and 391/135 may belong to the same taxon because they exhibit laterally oblong articular surfaces, but the articular surfaces are circular in NMNHU-G 391/125 and 391/127. However, they cannot be interpreted as Lamniformes because their intermedialia does not exhibit any noticeable radiating calcified lamellae. The slight dorsoventral compression observed in these vertebrae may indicate that they belong to a batoid, but we conservatively describe them here as *Elasmobranchii* indet. They may belong to one or more of the aforementioned taxa in this study, and their exact taxonomic identifications are difficult because they are not accompanied by any teeth, which have higher diagnostic value.

DISCUSSION

Palaeogeographic Features of the Dnieper–Donets Basin

The Paleogene marine basin that existed in the area of present-day Ukraine was the successor of the Cretaceous Ocean. During the Cretaceous, the southern and western regions of the East European Platform, as well as the Ukrainian Shield,

subsided, sea-level rose, and by the Turonian–Coniacian only a few islands remained above the water (Kraeva et al., 1960; Ivanik et al., 2013; Kyselevych and Kovalchuk, 2021; Kovalchuk et al., 2022; Amadori et al., 2023). Following the uplift of the north-western and part of the southern regions of the East European Platform during the Cretaceous–Paleogene boundary, these and adjacent regions began to submerge again in the Paleogene. Palaeoceanographic changes, the opening and closing of seaways, have had a major impact on faunal exchange between different marine basins. Rögl (1998) considered these factors as major driving forces in the evolution of marine ecosystems. During the Eocene, marine waters filled the Pripyat Fault and the Dnieper–Donets depression, and the area of present-day Ukraine from the middle Lutetian was covered by sea, with only a few islands within the Ukrainian Shield and Near-Azov Massif remaining above the water (Ronov and Khain, 1961). During the middle Eocene, the Dnieper–Donets Basin was part of the Trans-European sub-latitudinal marine corridor between the North Sea and marine basins in the Northern Near-Black Sea region, the Crimea–Caucasus region, and the Scythian Plate (Figure 12). These basins were also connected with the Turan Sea of the north-eastern Peri-Tethys and with the Siberian Sea through the Turgai Strait in the east, as well as with Tethyan basins in the south (e.g., see Ronov and Khain, 1961; Savytska, 1996; Beniamovskii, 2005, 2007; Akhmetiev, 2010; Vasilieva, 2018).

Such an extensive network of interconnected bodies of water facilitated the dispersal of marine organisms, including sharks, rays, and chimaeras. At the time of the accumulation of phosphorite sands, the shallow-marine, neritic Dnieper–Donets Basin in the Kyiv region was well-aerated and had normal salinity (Sokolov, 1986; Savytska, 1996; Shevchenko, 2000, 2002; Ryabokon and Shevchenko, 2001). Shallow-dwelling taxa prevailed among the calcareous nannoplankton, including equatorial-tropical and subtropical forms, which suggests a high surface water temperature (Savytska, 1996). The rich benthic fauna was represented by solitary and colonial corals, bryozoans, and stenohaline and stenothermic molluscs (Sokolov, 1986).

The progressive transgression led to the accumulation of a marl-clayey series in a deep marine, middle-outer neritic basin as suggested by the presence of calcareous nanoplankton characteristic of a deep-sea shelf (Savytska, 1996). This is also indicated by the ratio of phytoplankton

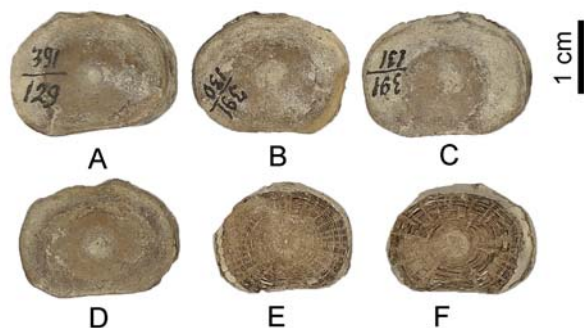


FIGURE 11. Elasmobranchian vertebrae (*Elasmobranchii* indet.) from the middle Eocene deposits of Vyshhorod: **A, D** – NMNHU-G 391/129; **B, E** – NMNHU-G 391/130; **C, F** – NMNHU-G 391/131. Anterior view in **A–C**, posterior view in **D–F**.

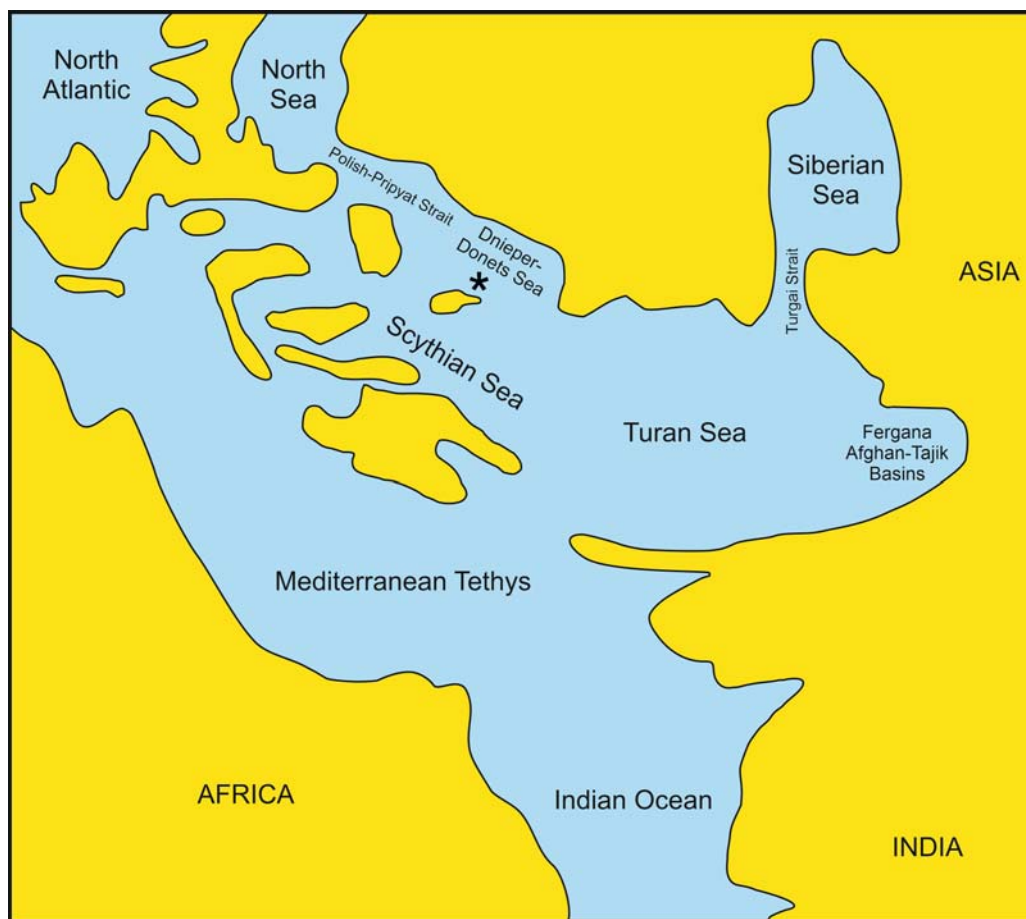


FIGURE 12. Palaeogeographic map of the Peri-Tethyan area during the middle Eocene (after Bosboom et al., 2017, modified). The studied region is indicated with an asterisk.

groups, and many oceanic dinocysts (Shevchenko, 2000, 2002).

Middle Eocene chondrichthyans of the Dnieper–Donets Basin

Our knowledge on the taxonomic composition of cartilaginous fishes in the middle Eocene marine ecosystem of the Dnieper–Donets Basin has long been based on the faunal list published by Rogovich (1861). Based on the fossils collected from the Vyshhorod locality, O. S. Rogovich identified 29 chondrichthyan taxa, including two species of chimaeras, 24 sharks, and three rays. As mentioned above, some specimens described by him were subsequently lost or (less likely) transferred to other institutions; those are remains of eight species (either valid or synonymised), mostly of lamniform sharks, but also *Myliobatis striatus* Buckland, 1836 (Table 1). This material is not available and thus cannot be considered in further discussion.

The revision of the remaining part of the sample has resulted in a consolidated faunal list com-

prising a single chimaeriform species (*Edaphodon bucklandi*), 12 shark and one or two ray taxa. Of the latter two groups, 10 sharks are identified to species level, whereas rays are only identified to order and family ranks (Myliobatiformes, Myliobatidae). Shark remains belong to representatives of the orders Hybodontiformes, Hexanchiformes, Lamniformes, and Carchariniformes. Because of the poor preservation and/or lack of reliable diagnostic characters, vertebral centra from Rogovich's collection and those recovered from Zoloti Vorota are all described in open nomenclature (Lamniformes indet. and Elasmobranchii indet., respectively).

When comparing the original and revised lists of taxa, it becomes clear that only two species were identified accurately in the original publication (Rogovich, 1861), whereas the other taxa have been either synonymised or re-assigned to other genera or even families. The explanation for the considerable number of erroneous taxonomic assignments by O.S. Rogovich is that Agassiz

TABLE 1. The list of chondrichthyan fishes of the Dnieper–Donets Basin published by Rogovich (1861) in the original order compared to the one presented in this paper. Taxa that were identified by O.S. Rogovich correctly (albeit subsequently synonymised) are highlighted in bold. Question mark indicates the material originally assigned to the given species but now absent in the collection.

Old taxonomic assignments (Rogovich, 1861)	Valid name (Pollerspöck and Straube, 2022)	Revised taxonomic assignments (this paper)
Chimaeras		
<i>Edaphodon Bucklandii</i>	<i>Edaphodon bucklandi</i>	<i>Edaphodon bucklandi</i>
<i>Edaphodon eurygnathus</i>	<i>Edaphodon bucklandi</i>	<i>Edaphodon bucklandi</i>
Sharks		
<i>Acrodus kioviensis</i>	<i>Acrodus kioviensis</i>	<i>Heterodontus</i> sp.
<i>Notidanus serratissimus</i>	<i>Notorynchus serratissimus</i>	<i>Hexanchus agassizi</i>
<i>Notidanus serratissimus</i>	<i>Notorynchus serratissimus</i>	<i>Notorynchus kemp</i>
<i>Notidanus microdon</i>	<i>Hexanchus microdon</i>	<i>Hexanchus agassizi</i>
<i>Galeocerdo minor</i>	<i>Physogaleus minor</i>	<i>Physogaleus secundus</i>
<i>Galeocerdo paradoxus</i>	<i>Physogaleus latus</i>	?
<i>Carcharodon megalotis</i>	<i>Otodus (Carcharocles) auriculatus</i>	<i>Otodus (Carcharocles)</i> sp.
<i>Carcharodon lanceolatus</i>	<i>Otodus (Otodus) obliquus</i>	<i>Otodus (Carcharocles)</i> sp.
<i>Carcharodon productus</i>	<i>Otodus (Megaselachus) megalodon</i>	<i>Otodus (Carcharocles)</i> sp.
<i>Otodus macrotus</i>	<i>Striatolamia macrota</i>	<i>Striatolamia macrota</i>
<i>Otodus macrotus</i> (partim)	<i>Striatolamia macrota</i>	<i>Brachycarcharias lerichei</i>
<i>Otodus microtus</i>	<i>Isurus microtus</i>	?
<i>Lamna elegans</i>	<i>Striatolamia macrota</i>	?
<i>Lamna compressa</i>	<i>Striatolamia macrota</i>	<i>Striatolamia macrota</i>
<i>Lamna cuspidata</i>	<i>Carcharias cuspidatus</i>	<i>Jaekelotodus trigonalis</i>
<i>Lamna denticulata</i>	<i>Carcharias cuspidatus</i>	<i>Jaekelotodus trigonalis</i>
<i>Lamna lata</i>	<i>Cretalamna appendiculata</i>	<i>Macrorhizodus praecursor</i>
<i>Lamna (Odontaspis) Hoppei</i>	<i>Hypotodus verticalis</i>	<i>Mennerotodus</i> cf. <i>M. parmleyi</i>
<i>Lamna (Odontaspis) hispida</i>	<i>Odontaspis hispida</i>	<i>Odontaspis winkleri</i>
<i>Oxyrhina biflora</i>	<i>Isurolamna biflexa</i>	<i>Isurolamna affinis</i>
<i>Oxyrhina Desorii</i>	<i>Oxyrhina desori</i>	<i>Macrorhizodus praecursor</i>
<i>Oxyrhina falcata</i>	<i>Macrorhizodus falcata</i>	?
<i>Oxyrhina leptodon</i>	<i>Carcharodon hastalis</i>	?
<i>Oxyrhina brevidens</i>	<i>Oxyrhina brevidens</i>	<i>Striatolamia macrota</i>
<i>Chomatodus dubius</i>	<i>Chomatodus dubius</i>	?
<i>Hybodus helophorus</i>	<i>Squatina helophora</i>	?
Rays		
<i>Myliobates striatus</i>	<i>Myliobatis striatus</i>	?
<i>Myliobates Owenii</i>	[nomen nudum]	<i>Myliobatiformes</i> indet.
<i>Myliobates toliapicus</i>	<i>Myliobatis toliapicus</i>	<i>Myliobatidae</i> gen. et sp. indet.

(1833–1843) was the only reference source he used in his study, and he had no comparative materials in his possession. These incorrect taxonomic identifications were later replicated without revision by other researchers, although nomenclatural changes of several taxa described by Rogovich were introduced by Capetta (2006), presumably

based on the images of the corresponding specimens published in Rogovich's monograph. Our findings confirm and amend these earlier revisions. In particular, 'species' *sensu* Rogovich (1861) such as *Carcharodon megalotis*, *C. lanceolatus*, and *C. productus* belong to a single taxon, *Otodus (Carcharocles)* sp. The specimens of '*Lamna cus-*

pidata and '*L. denticulata*' were re-identified here as *Jaekelotodus trigonalis*. At the same time, we assume that the teeth assigned by Rogovich (1861) to *Notidanus serratissimus* represent two different species—*Hexanchus agassizi* and *Noto-rhynchus kempī*. Another important issue is that characters used by O.S. Rogovich to describe new species (e.g., *Acrodus kioviensis*) are now considered not diagnostic enough due to their wide range of variation. In the light of our findings, such species names, including those created for the lost specimens, that is, *Galeocерdo paradoxus* (Rogovich, 1861, pl. IV, figs. 10, 11), *Otodus microtus* (Rogovich, 1861, pl. V, figs. 24-27), *Lamna elegans* (Rogovich, 1861, pl. IV, figs. 10, 11), *Oxyrhina falcata* (Rogovich, 1861, pl. VII, figs. 24, 25), *Oxyrhina leptodon* (Rogovich, 1861, pl. VIII, figs. 9, 10), *Chomatodus dubius* (Rogovich, 1861, pl. I, fig. 8), and *Hybodus helophorus* (Rogovich, 1861, pl. III, figs. 19, 20), are most likely *nomina dubia*. We conclude that *Lamna compressa* and *Oxyrhina brevidens* erected by Rogovich (1861) should indeed be synonymised with *Striatolamia macrotia*. Another name, *Lamna (Odontaspis) hispida*, also should be regarded a synonym of *Odontaspis winkleri*. In addition, we synonymise *Lamna lata* and *Oxyrhina biflens* with *Macrorhizodus praecursor* and *Isurolamna affinis*, respectively. The latter conclusion is based on direct examination of the specimens by the authors, and it corroborates the assumption previously made by Cappetta (2006).

Certainly, the analysed sample does not fully reflect the taxonomic diversity of the middle Eocene chondrichthyan assemblage in this part of the Dnieper–Donets Basin, and thus palaeoecological reconstructions based only on these materials would substantially be biased. Little is known about the collecting approach, which is not described in detail by Rogovich (1861). Most likely, the teeth, vertebrae, and other skeletal elements (such as fragments of the caudal spine) were collected by hand and the bone-bearing rock was not sieved or screen-washed. The presence of individual small teeth in the collection is therefore considered rather accidental. Nonetheless, the studied sample of fishes is of important historical and scientific

value and contributes to the understanding of the palaeodiversity of Eocene marine ecosystems that existed in present-day Ukraine and, more widely, in Eastern Europe.

Most taxa identified in the present study represent the epi- and mesopelagic assemblage and only a relatively small number of them represent benthopelagic (*Edaphodon bucklandi*, Myliobatidae gen. et sp. indet.) and demersal or bathydemersal forms (*Hexanchus agassizi*, *Noto-rhynchus kempī*). These chondrichthyans inhabited shallow, warm waters (up to 200 m depth but most likely to 100 m) and were confined to the continental shelf. Their remains could have been transported by currents over some distance and deposited in a deeper marine environment. Further studies based on a more comprehensive sample are needed to shed more light on the structure of palaeocommunities in middle Eocene marine ecosystems of Ukraine.

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