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A review of Neogene and Quaternary pikes of southeastern Europe and a new species from the early Pleistocene of Nogaisk, Ukraine

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The fish genus *Esox* (Teleostei, Esocidae) has been recorded from thirty late Miocene, Pliocene, and Pleistocene localities where forty-one bone-bearing strata are exposed in the territory of Ukraine, Russian Federation, and Republic of Moldova. From eight localities the genus is reported or described for the first time. A detailed description and morphological analysis of the currently available osteological material demonstrates the presence of four species in the studied area: (i) *Esox sibiricus* (late Miocene–early Pliocene); (ii) *Esox moldavicus* (early Pliocene–early Pleistocene); (iii) *Esox nogaicus* sp. nov. (early Pleistocene, Calabrian); (iv) *Esox lucius* (early–middle Pleistocene). The Northern Pike (*Esox lucius*) is recorded for the first time in the early Pleistocene fossil record of southeastern Europe. The new species *E. nogaicus* is characterized by a massive dentary with deep symphysis and the possible presence of a pair of fixed canine-like teeth near the anterior end of the vomer. Such canine teeth are seen also in certain species known only from North America, the extant *Esox masquinongy*, the fossil species *E. columbianus*, and an unnamed Miocene form. However, unlike in *E. nogaicus*, in the three North American species fixed canines also occur anteriorly on the palatines. The Miocene, Pliocene, and Pleistocene pikes from southeastern Europe document a greater diversity of morphologies in the past than exists today in the pike species of Europe. Changes in the predominant species of *Esox* in southeastern Europe are hypothesized to be driven by changing global and regional climates.

Key words: Esociformes, Esocidae, *Esox*, Miocene, Pliocene, Pleistocene, Ukraine, Russia, Moldova.

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Introduction

The genus *Esox* Linnaeus 1758 (i.e., pikes and pickerels) is a group of freshwater fishes known for its duck-billed snout, elongated body and voracious feeding behavior. The family Esocidae (with only one extant genus) has a rich fossil record dating to the Late Cretaceous (Wilson et al. 1992), although all known species are restricted to the Northern Hemisphere. Based on morphological (Nelson 1972; Sytchevskaya 1976; Grande 1999; Grande et al. 2004) and molecular data (López et al. 2000; Grande et al. 2004), species of *Esox* are divided between two subgenera: *Kenoza*, the pickerels, and *Esox*, the pikes. Species within the subgenus *Esox* are restricted to northern latitudes and include the following extant taxa. *Esox lucius* (Northern Pike) exhibits a circumpolar distribution through eastern and central United States, throughout Canada, Europe and into Asia. In eastern and central North America, *Esox masquinongy* (Muskellunge) is also found. Despite their many similarities and partly overlapping distributions, *E. lucius* and *E. masquinongy* display significantly different behavioral traits and developmental trajectories (Burdi and Grande 2010; McCormick et al. in press). In Asia, *Esox reichertii* (Amur Pike) is restricted to the Amur River basin. In Europe, two additional species have been named recently. One recently named species is the Southern Pike *Esox cisalpinus* (Bianco and Delmastro 2011) with junior synonym *E. flaviae* (Lucentini et al. 2011) of Italy. The other recently named species is the Aquitanian Pike *Esox aqui-*

tanicus (Denys et al. 2014) from France. Omitting those two recently named European species, phylogenetic relationships among the extant forms are as follows: [[*E. niger* [*E. americanus americanus*, *E. americanus vermiculatus*]] [*E. masquinongy* [*E. reichertii*, *E. lucius*]]] (Grande et al. 2004). The molecular study of Denys et al. (2014) suggested that both *E. cisalpinus* and *E. aquitanicus* are more closely related to *E. lucius* than to other extant pike species.

Fossil esocids expand the morphological diversity and biogeographic history of the group (Cavender et al. 1970; Gaudant 1979, 2002; Wilson 1980, 1981, 1984; Wilson et al. 1992; Grande 1999; Smith et al. 2000). Late Cretaceous records of Esocidae from North America classified in different genera include *Estesesox* and *Oldmanesox*, the latter being more closely related to *Esox* than the former (Wilson et al. 1992). There are at least twelve nominal species of *Esox* known only as fossils, beginning with *Esox tiemani* Wilson, 1980, from the Paleocene of North America. Two other species, *Esox longkouensis* Chang and Zhou, 2002, late Paleocene or early Eocene of China, and *Esox kronneri* Grande, 1999, early Eocene of North America, are slightly younger. Two relatives of *E. masquinongy* are *Esox columbianus* of Pliocene age (Smith et al. 2000) from southern Washington and a related form referred only to *Esox* sp. from the Miocene of southeastern Oregon (Cavender et al. 1970).

In Europe the skeletal fossil record begins with the Oligocene *E. primaevus* (see Gaudant 1978) and *E. papyraceus* (see Gaudant 1988) and includes the middle Miocene *E. lepidotus* (see Gaudant 1980). *Esox moldavicus* was described from the early Pliocene of Eastern Europe (Sytchevskaya 1974). Diversity of Asian fossil pike species is also high and includes *E. aralensis* from the middle Oligocene–early Miocene, as well as the late Oligocene *E. borealis* and *E. dispar* (see Sytchevskaya 1976). Many remains from the Miocene and Pliocene strata of Western Siberia belong to *Esox sibiricus* (see Sytchevskaya 1974, 1976). In addition, *Esox* aff. *sibiricus* and *Esox* cf. *sibiricus* were defined from the early–middle Pliocene of Western Mongolia and Altai (Sytchevskaya 1976). Lebedev (1959) described *Esox* (*lucius*?) from the late Miocene of the Zaisan locality; however, as clearly stated by Sytchevskaya (1976), these are remains of *E. sibiricus*. Bones of pikes are very numerous in the late Neogene deposits of Eastern Europe and usually determined as *Esox lucius* and *Esox* sp. (see Tarashchuk 1962; Dubrovo and Kapelist 1979; Böhme and Ilg 2003; Kovalchuk 2011, 2015; Kovalchuk et al. 2014a, 2015), but some of them (as is shown below) belong to fossil species (e.g., *E. sibiricus*, *E. moldavicus*, etc.).

The earliest record of extant species of *Esox* in North America might be the palatine tentatively assigned to *E. masquinongy* from the late Miocene of Oregon (Cavender et al. 1970), although a Pliocene fossil from Washington State represents an extinct species (Smith et al. 2000). In Europe *Esox* cf. *lucius* appears first in the Pliocene of Willershausen clay pit in Germany (Gaudant 1997). This species was also described from the late Pleistocene of the Russian Federation (Sytchevskaya et al. 2015). *Esox lucius* has been collected from Pleistocene localities in England (Schreve et al. 2002; Böhme 2010), Germany (Bloos et al. 1991; Böttcher 1994), Hungary (Jánossy 1986), Netherlands (Gaudant 1979), Poland (Pawłowska 1963) and Slovenia (Križnar and Kovalchuk 2016), as well as from the Holocene of Bulgaria (Böhme and Ilg 2003). Bones identified as *Esox* aff. *reichertii* come from the early Pliocene of the Russian Federation (Sytchevskaya 1989).

In southeastern Europe a wealth of esocid fossil material documents the diversity of species of *Esox* represented by fossils. Some of these fossils can be referred to species previously named by Sytchevskaya (1974), and others cannot. This study addresses the morphology and diversity of all of the available fossil esocids from southeastern Europe, for the purpose of clarifying their morphological characteristics, their taxonomy, and their stratigraphic occurrences.

Institutional abbreviations.—NMNHU-P, Department of Paleontology of the National Museum of Natural History, Kyiv, Ukraine.

Other abbreviations.—DDC, diameter of the vomerine canine teeth; DFA, diameter of the fossa articularis; DT, tooth depth; HS, height of dentary symphysis; L, length; LM, maxillar length; LT, tooth length; W, width; WCV, width of the vomerine head; WDF, maximum width of the vomerine dental field; WPSa, width of the anterior part of parasphenoid; WPSp, width of the posterior part of parasphenoid; WS, width of the dentary near the symphysis; WT, tooth width; WTR, width of tooth row.

Geological setting

The fish material described here was recovered by dry screening for microvertebrate fossils. The samples were originally collected during the second half of the twentieth century and the beginning of the twenty-first century to obtain small mammal fossils, described previously by Dubrovo and Kapelist (1979), Krochmal and Rekovets (2010), and Nesin (2013). The fish material comes from thirty localities in the territory of Ukraine, Republic of Moldova, and the Russian Federation (Fig. 1). Forty-one heterochronous bone-bearing strata containing pike remains are dated as late Miocene, Pliocene, and Pleistocene. The ages of the strata were established based on the small mammals (Nesin and Nadachowski 2001; Krochmal and Rekovets 2010) and are consistent with biostratigraphic dates derived from the accompanying fauna (Table 1).

All investigated fish-bearing strata are of alluvial origin, but the accumulations of bones occurred in different water bodies—rivers, lakes, estuaries, and lagoons. Popovo, Lobkovo, Verkhnya Krynitsya, Vasylivka, Novoukrainka, Andreevka, Novopetrovka, and Obukhovka yielded numerous fish bones in gravel lenses, interlayered with fer-

Table 1. Stratigraphic range of investigated localities with pike remains. MN, Mammal Neogene Zone; MIS, Marine Isotope Stage; * remains of *Esox sibiricus* were probably redeposited from the older layer (Popovo 3); + present; – absent. Numbers refer to Fig. 1.

Epoch	Stage		MN/MIS	Age (mya)	Number	Investigated localities	*Esox sibiricus*	*Esox moldavicus*	*Esox nogaicus* sp. nov.	*Esox lucius*	*Esox* spp.
Pleistocene	Middle		MIS 11	0.45	30	Medzhibozh				+	+
			MIS 12–18		29	Bol'shevik 2				–	+
					28	Lysa Gora 1				–	+
					27	Semibalka 1				+	+
				0.77	26	Protopopovka 2				–	+
	Early	Calabrian	MIS 19–20		6	Cherevichne 1				–	+
					25	Kairy				–	+
					24	Nogaisk			+	–	–
					23	Sinyaya Balka				+	+
					22	Nova Etuliya				+	+
				1.80	21	Tiligul					+
		Gelasian	MN 17		1	Popovo 0					+
					1	Popovo 1					+
					1	Popovo 2	+*				+
					18	Kotlovina 3		+			+
				2.58	18	Kotlovina 2		+			+
Pliocene	Kimmerian	Piacenzian	MN 16		8	Verkhnya Krynitsya 1		–			+
					6	Cherevichne 2		+			+
					20	Kryzhanovka		+			–
					19	Zhevakhova Gora		–			+
				3.60	16	Obukhovka 2		–			+
		Zanclean	MN 15		18	Kotlovina 1		–			+
					14	Vinogradovka 2		+			–
					17	Kamenskoe		+			–
					16	Obukhovka 1		+			+
			MN 14	5.33	15	Novopetrovka (= Kuchurgan)	+				+
Late Miocene	Messinian (= Pontian)		MN 13		14	Vinogradovka 1	+				+
				7.25	13	Pontian Lectostratotype	–				+
	Tortonian	Maeotian	MN 12		12	Orekhovka	+				+
					11	Andreevka	–				+
					10	Novoukrainka 1	–				+
					9	Egorovka 1	–				+
					9	Egorovka 2	+				+
					8	Verkhnya Krynitsya 2	+				+
					7	Vasylivka 1	–				+
				9.88	6	Cherevichne 3	+				+
		Late Sarmatian s.l.	MN 11		5	Lobkovo	+				+
					4	Palievo	–				+
					3	Frunzovka 2	–				+
					2	Mykhailivka 2	–				+
				11.0	1	Popovo 3	+				+

ruginized sands and clays (Rekovets and Pashkov 2009; Krochmal and Rekovets 2010; Nesin 2013; Kovalchuk 2013, 2014, 2015). Remains of pikes and other freshwater fish remains from the Mykhailivka locality were obtained from clay and siltstone with interbedded sand, limestone, and gravel lenses (Nesin 2013). The same situation is found at the Frunzovka (Kovalchuk 2015), Palievo (Sinitsa 2008a), Egorovka (Sinitsa 2008b, 2010), Cherevichne (Nesin 2013), Sinyaya Balka (Krochmal and Rekovets 2010). Coarse-grained or fine- to medium-grained crossbedded

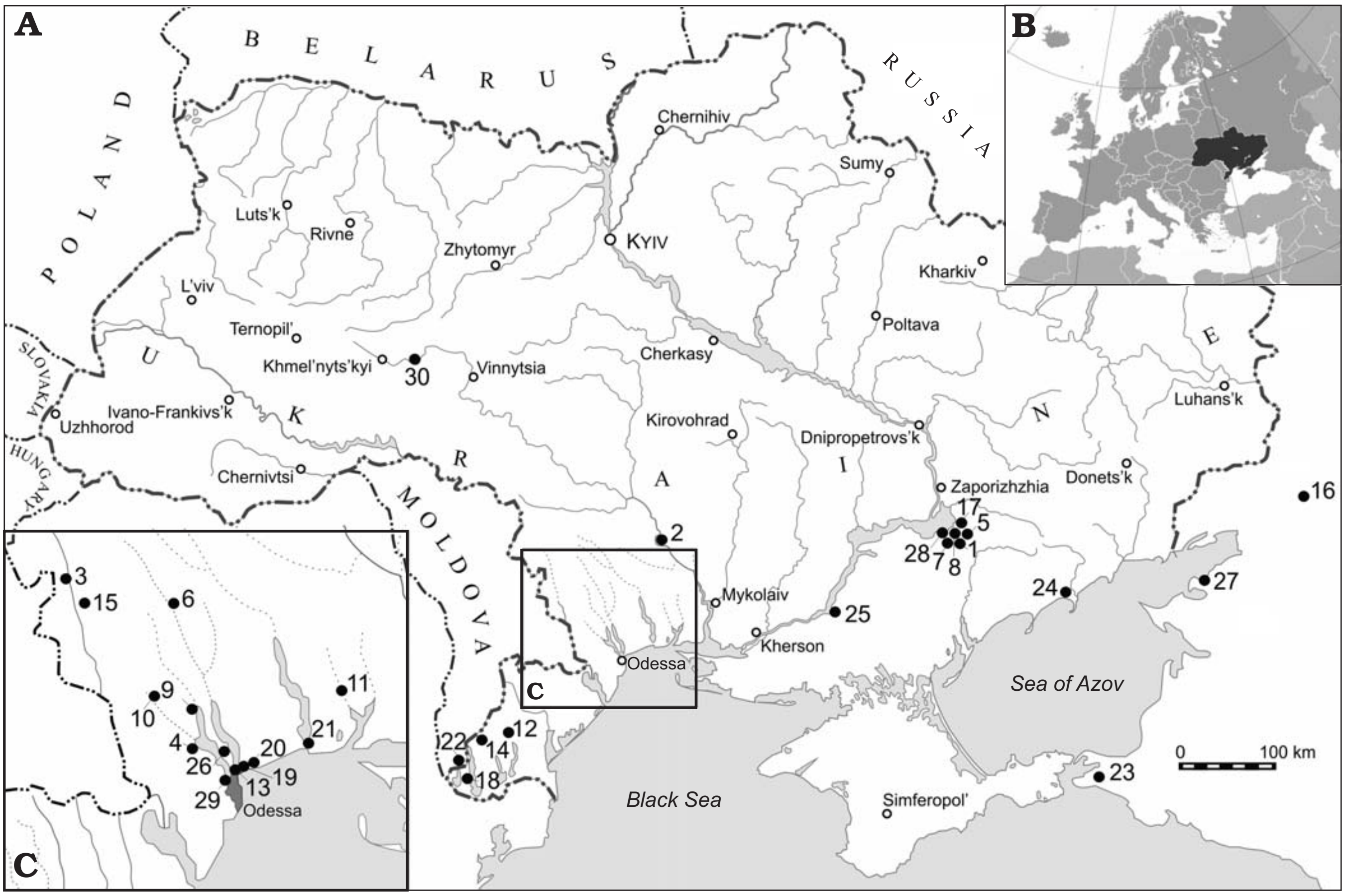


Fig. 1. Map showing location of Ukraine in Europe (**B**). Localities with fossil pike remains in southeastern Europe in Ukraine (**A**), detailed view of area near Odessa (**C**). 1, Popovo; 2, Mykhailivka; 3, Frunzovka; 4, Palievo; 5, Lobkovo; 6, Cherevichne; 7, Vasylivka; 8, Verkhnya Krynitsya; 9, Egorovka; 10, Novoukrainka; 11, Andreevka; 12, Orekhovka; 13, Pontian Lectostratotype; 14, Vinogradovka; 15, Novopetrovka; 16, Obukhovka; 17, Kamenskoe; 18, Kotlovina; 19, Zhevakhova Gora; 20, Kryzhanovka; 21, Tiligul; 22, Nova Etuliya; 23, Sinyaya Balka; 24, Nogaisk; 25, Kairy; 26, Protopopovka; 27, Semibalka; 28, Lysa Gora; 29, Bol'shevik; 30, Medzhibozh.

sand and gravel of the Orekhovka (Nesin 2013), Pontian Lectostratotype (Topachevsky et al. 1988), Vinogradovka (Nesin and Nadachowski 2001; Nesin 2013), Kamenskoe (Tarashchuk 1965), Tiligul, Kryzhanovka, Nogaisk, Kairy, Semibalka (Krochmal and Rekovets 2010), and Lysa Gora (Rekovets et al. 2014) also contain pike remains. Freshwater fish bones of the Kotlovina, Zhevakhova Gora, Nova Etuliya, Protopopovka, Bol'shevik, and Medzhibozh are derived from the layered, partly ferruginized clayey sand and gravel with small carbonate concretions and/or sandstone pebbles (Topachevsky and Nesin 1989; Krochmal and Rekovets 2010; Nesin 2013).

Material and methods

The material under study is represented by disarticulated bones, housed in the Department of Paleontology of the National Museum of Natural History, National Academy of Sciences of Ukraine (collections NMNHU-P No. 27, 29, 33, 35, 37, 38, 41, 42, 45, 53). Comparative material is listed in Appendix 1. Isolated bones were identified based on comparisons with extinct and modern taxa from the literature (Lebedev 1959; Sytchevskaya and Lebedev 1971; Sytchevskaya 1974, 1976, 1980, 1989; Gaudant 1978; Smith et al. 2000). Determination of elements was accomplished using diagnostic features based on comparative observations and literature summaries (Grande 1999; Grande et al. 2004). The taxonomic hierarchy in the systematics section follows Nelson et al. (2016). Correlation of the Eastern Paratethys stages with European Mammal Neogene Zones follows Topachevsky et al. (1997, 1998), as well as Nesin and Nadachowski (2001). General stratigraphic scale of Quaternary deposits (Head et al. 2015) has been used for correlation of the Pleistocene sediments containing pike fossils. The specimens were measured using a digital caliper with 0.1 mm precision. Bone terminology follows Sytchevskaya (1976) and Lepiksaar (1994).

Systematic palaeontology

Subdivision Teleostei Müller, 1845

Order Esociformes Bleeker, 1859

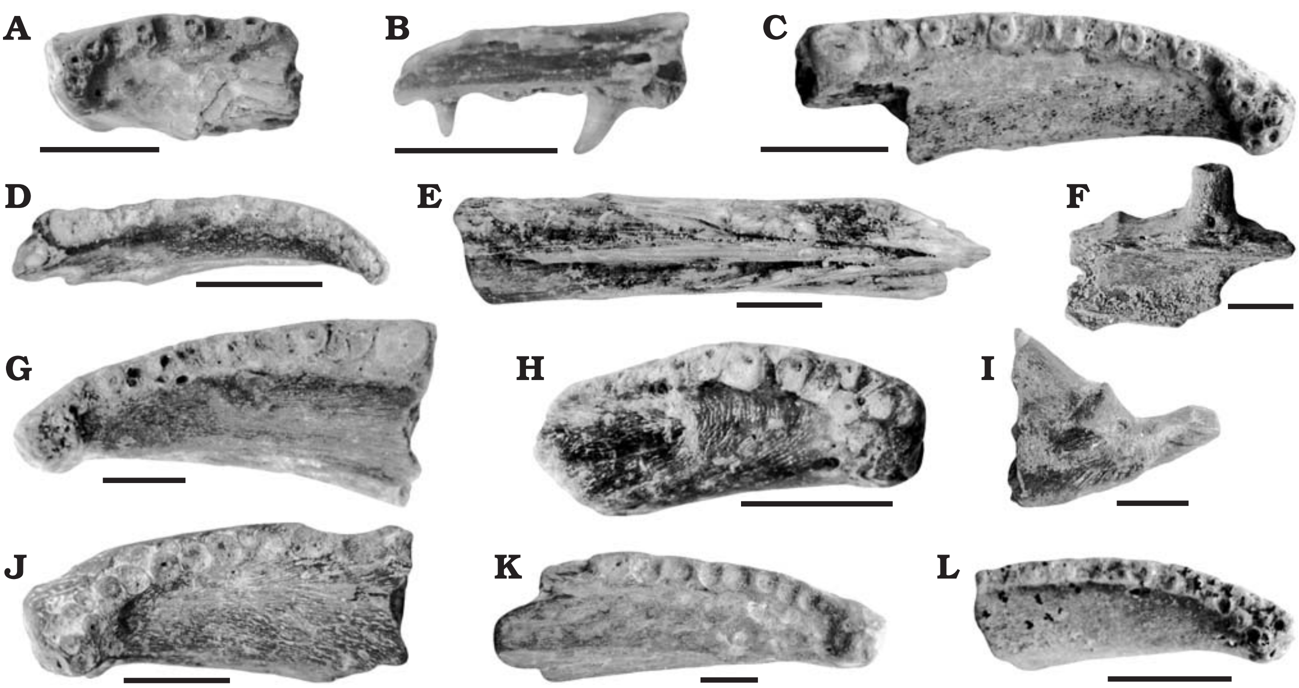


Fig. 2. Isolated elements assigned to a pike *Esox sibiricus* Sytchevskaya, 1976 from Southeastern Europe; late Miocene (A–J), Pliocene (K), and Pleistocene (L). **A**. Right dentary (NMNHU-P 29/1679), Popovo 3, occlusal view. **B**. Dentary fragment with teeth (NMNHU-P 29/1680), Popovo 3, medial view. **C**. Left dentary (NMNHU-P 29/3965), Lobkovo, occlusal view. **D**. Left dentary (NMNHU-P 45/5690), Cherevichne 3, occlusal view. **E**. Parasphenoid (NMNHU-P 29/1033), Verkhnya Krynitsya 2, dorsal view. **F**. Dentary fragment (NMNHU-P 29/1034), Verkhnya Krynitsya 2, lateral view. **G**. Right dentary (NMNHU-P 41/4324), Egorovka 2, occlusal view. **H**. Left dentary (NMNHU-P 41/2847), Orekhovka, occlusal view. **I**. Right articular (NMNHU-P 41/4525), Egorovka 2, lateral view. **J**. Right dentary (NMNHU-P 41/2741), Vinogradovka 1, occlusal view. **K**. Left dentary (NMNHU-P 37/2554), Novopetrovka, occlusal view. **L**. Left dentary (NMNHU-P 29/1583), Popovo 2, occlusal view. C, D, H, I, K, L, anterior to right; A, B, F, G, J, anterior to left; E, anterior towards top. Scale bars 5 mm.

Family Esocidae Rafinesque, 1815

Genus *Esox* Linnaeus, 1758

Type species: *Esox lucius* Linnaeus, 1758, Pleistocene–Recent, Eurasia and North America.

Esox sibiricus Sytchevskaya, 1974

Fig. 2.

1959 *Esox* (*lucius*?); Lebedev 1959: 50, fig. 25.
1971 *Esox* sp.; Sytchevskaya and Lebedev 1971: 49, pl. 1, pl. 2: 5b.
1974 *Esox sibiricus* sp. nov.; Sytchevskaya 1974: 227, pl. 1: 8, pl. 2: 12, pl. 3: 1–4, pl. 4: 1–8.
1976 *Esox sibiricus* Sytchevskaya, 1974; Sytchevskaya 1976: 107, pl. 6: 6–9; 108, figs. 1–11; 109, fig. 8; 110, fig. 1.
1980 *Esox sibiricus* Sytchevskaya, 1974; Sytchevskaya 1980: 201, 202, pl. 9: 8, pl. 10: 1–5.
1989 *Esox sibiricus* Sytchevskaya, 1974; Sytchevskaya 1989: 22–23, pl. 1: 3–11.

Material.—Late Miocene: one left and two right dentaries (NMNHU-P 29/1678–1680, Popovo 3); one left dentary (NMNHU-P 29/3965, Lobkovo); one left dentary (NMNH-P 45/5690, Cherevichne 3); one parasphenoid, three dentary fragments (NMNHU-P 29/1033–1036, Verkhnya Krynitsya 2); one left and three right dentaries, one right articular (NMNHU-P 41/4323–4326, 4525, Egorovka 2); one left dentary (NMNHU-P 41/2847, Orekhovka); one right dentary (NMNHU-P 41/2741, Vinogradovka 1). Early Pliocene: one left dentary (NMNHU-P 37/2554, Novopetrovka); one left dentary (NMNHU-P 29/1583, Popovo 2).

Emended diagnosis.—*Esox sibiricus* differs from other Eurasian taxa by a number of characters: (i) predominance of double tooth row at symphysis of dentary; (ii) narrow and weak dental shelf; (iii) absence of symphysial notch; (iv) very large articular angle (nearly or more than 70°); (v) clearly visible grooves of carotid arteries on parasphenoid; (vi) short and flat facet of maxillar process on palatine.

Description.—The parasphenoid from the Verkhnya Krynitsya 2 locality is presented by caudally extended anterior part (Fig. 2E). The bone is massive; grooves of the carotid arteries are clearly visible. Measurements of the medial part of the parasphenoid are width 5.9 mm, height 3.5 mm, width of anterior medial crest 1.2 mm.

The dentary, which is not deep, has a moderately developed dental shelf, which smoothly rises into the medial wall (Fig. 2A–D, F–H, J–L). Teeth at the symphysis are arranged in two rows, and internal one being better developed. Teeth are completely broken in the fossils, but C-shaped crown bases are visible. There is a gradual increase in their diameter in the direction towards the symphysis. A clear lateral groove separates the anterior edge of the dentary and forms a ventral bulge in the symphysis. The anterior edge of the dentary is straight and thickened at the symphysis. Pores for the sensory canal (Nelson 1972) are clearly visible at the ventral

Table 2. Measurements (in mm) of dentaries of *Esox sibiricus* Sytchevskaya, 1974. N, number of specimens.

Locality	N	Height of dentary symphysis		Width of the dentary near the symphysis		Width of tooth row	
		range	mean	range	mean	range	mean
Popovo 2	1	–	3.6	–	2.3	–	1.5
Novopetrovka	1	–	6.7	–	5.0	–	2.3
Vinogradovka 1	1	–	4.8	–	4.5	–	1.7
Orekhovka	1	–	4.5	–	3.0	–	1.5
Egorovka 2	4	3.1–5.1	4.1	2.2–3.2	3.0	1.1–1.8	1.5
Verkhnya Krynitsya 2	3	3.4–4.6	4.0	2.5–3.6	3.1	1.2–1.7	1.5
Cherevichne 3	1	–	1.9	–	1.4	–	1.3
Lobkovo	1	–	3.8	–	3.1	–	1.6
Popovo 3	3	2.4–5.7	4.1	2.5–4.5	3.1	1.0–2.1	1.5

edge. Two small hook-shaped teeth with rounded crowns are preserved on one dentary from Popovo 3. Measurements of dentaries of *Esox sibiricus* from late Miocene and Pliocene strata of Ukraine are presented in the Table 2.

The articular bone is massive (Fig. 2I), with a high wall (anguloarticular angle is 67°). The posterior process of the bone is elongated, laterally compressed and has a narrow ventral keel. The articular facet is wide (W 4.5 mm; L 6.1 mm), with a thick raised edge. The anteroventral angle is smooth. The height of the bone at the front edge of the articular facet is 7.3 mm.

Remarks.—The described remains from the late Miocene and Pliocene localities of southeastern Europe correspond closely in morphology to those of *Esox sibiricus* from Kazakhstan (Sytchevskaya 1976) and Mongolia (Sytchevskaya 1989). This species is similar to *Esox reichertii* in the structure of the anterior median crest of the parasphenoid. As compared to that in *Esox aralensis*, the dentary of the described species has a smaller dental shelf, a two-row dentition, and lacks a symphysial notch (Sytchevskaya 1976). The limited variety of skeletal elements of *Esox sibiricus* from the described localities (i.e., dentary, parasphenoid and articular bone only) does not allow comparison with some other extinct species. The presence of *Esox sibiricus* in the early Pleistocene strata of Popovo 2 could have been caused by the redeposition of these remains from an older layer (probably Popovo 3).

Stratigraphic and geographic range.—Early Miocene–late Pliocene of Western Siberia; late Miocene–early Pliocene of southeastern Europe.

Esox moldavicus Sytchevskaya, 1974

Fig. 3.

1974 *Esox moldavicus* sp. nov.; Sytchevskaya 1974: 229, pl. 1: 2–6, pl. 2: 10.
1976 *Esox moldavicus* Sytchevskaya, 1974; Sytchevskaya 1976: 110, pl. 9: 2–9.
1980 *Esox moldavicus* Sytchevskaya, 1974; Sytchevskaya 1980: 36–37, pl. 10: 6–9.
2014 *Esox moldavicus* Sytchevskaya, 1974; Kovalchuk et al. 2014b: 51, fig. 7a–c.

Material.—Early Pliocene: one right dentary (NMNHU-P 53/4245, Obukhovka 1); one left and two right dentaries (NMNHU-P 42/513, 532, 1252, Kamenskoe). Late Pliocene: two palatines (NMNHU-P 53/4246, 4247, Obukhovka 2); one left dentary (NMNHU-P 53/4248, Kryzhanovka); one left and one right dentary (NMNHU-P 45/6017, 6018, Cherevichne 2). Early Pleistocene: one left dentary and one palatine (NMNHU-P 41/2452, 2453, Kotlovina 2); two left dentaries and two palatines (NMNHU-P 41/2454–2457, Kotlovina 3).

Emended diagnosis.—*Esox moldavicus* differs from other esocids by (i) the predominance of one-row dentition on dentary; (ii) moderately developed dental shelf; (iii) high articular wall (articular angle more than 60°); (iv) caudally narrowed anterior medial crest on parasphenoid; (v) weakly visible grooves of carotid arteries on parasphenoid; (vi) presence of groove on anterior part of palatine.

Description.—The dentary has a moderately developed shelf, without symphysial notch (Fig. 3A, C–F, H; Table 3). There is one complete tooth row at the symphysis, and a few small teeth in a second row. The profile of the dentary is low, and the ventral bulge near the symphysis is almost not expressed. The ventral keel is narrow, as is especially clearly visible in the symphysial area.

The toothed surface on the *palatine* is short and not concave, extending under the maxillary process. The dorsal surface of the bone is curved. There are four or five rows of small tooth bases on the ventral side of the palatine (Fig. 3B, G). Widths of bones from the Obukhovka 2 are 3.1 and 4.2 mm, and from Kotlovina 2 4.7 mm.

Table 3. Measurements (in mm) of dentaries of *Esox moldavicus* Sytchevskaya, 1974. N, number of specimens.

Locality	N	Height of dentary symphysis		Width of the dentary near the symphysis		Width of tooth row	
		range	mean	range	mean	range	mean
Kotlovina 3	2	2.4; 2.7	–	2.3; 2.5	–	0.9; 2.1	–
Kotlovina 2	1	–	2.2	–	2.6	–	0.9
Cherevichne 2	2	1.4; 2.5	–	0.9; 2.4	–	0.7; 2.0	–
Kryzhanovka	1	–	5.0	–	4.3	–	2.0
Kamenskoe	3	2.5–4.3	3.4	1.7–3.2	2.5	0.9–2.0	1.4
Obukhovka 1	1	–	–	–	–	–	2.7

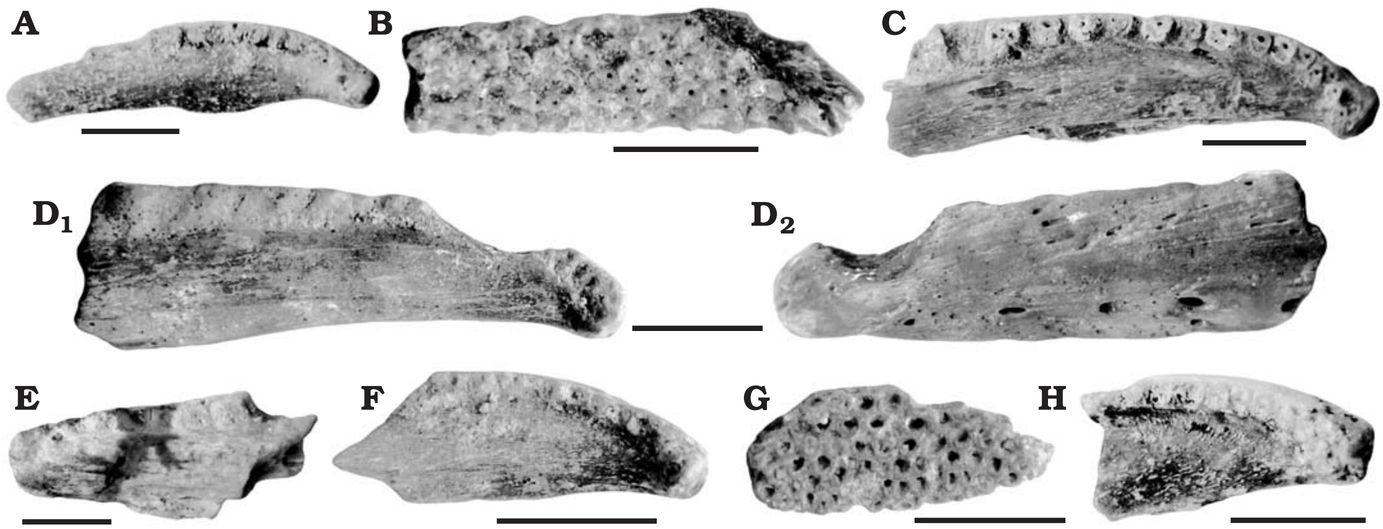


Fig. 3. Isolated elements assigned to a pike *Esox moldavicus* Sytchevskaya, 1974 from Southeastern Europe; Pliocene (A, C–E, G), and Pleistocene (B, F, H). **A**. Left dentary (NMNHU-P 45/6017), Cherevichne 2, occlusal view. **B**. Right palatine (NMNHU-P 41/2556), Kotlovina 3, ventral view. **C**. Left dentary (NMNHU-P 42/513), Kamenskoe, occlusal view. **D**. Left dentary (NMNHU-P 53/4248), Kryzhanovka, occlusal (D_1) and medial (D_2) views. **E**. Right dentary (NMNHU-P 53/4245), Obukhovka 1, occlusal view. **F**. Left dentary (NMNHU-P 41/2452), Kotlovina 2, occlusal view. **G**. Palatine fragment (NMNHU-P 53/4246), Obukhovka 2, ventral view. **H**. Left dentary (NMNHU-P 41/2454), Kotlovina 3, occlusal view. E, D_2, anterior to right; C, D_1, A, F, H, anterior to left; G, B, anterior towards top. Scale bars: E, D, 10 mm; C, G, F, H, B, 5 mm; A, 2 mm.

Remarks.—Described bones are comparable in morphology to those of *Esox moldavicus*. This species resembles *Esox sibiricus* in the structure of the dentigerous surface of the palatine, but differs in the predominance of the one-row dentition at the dentary symphysis. The orientation of the maxillary process on the palatine and the low dentary are similar to those in *Esox lucius*, but differ from features of *E. reichertii* (Sytchevskaya, 1976).

Stratigraphic and geographic range.—Early Pliocene–early Pleistocene of southeastern Europe.

Esox nogaicus sp. nov.

Fig. 4.

Etymology: Derived from the name of the type locality.

Type material: Holotype: NMNHU-P 27/1697, almost complete right dentary (Fig. 4A). Paratypes: NMNHU-P 27/1001, right dentary, NMNHU-P 27/998, left dentary.

Type locality: Nogaisk, Zaporozhye region, Ukraine (Fig. 1).

Type horizon: Calabrian (early Pleistocene).

Material.—NMNHU-P 27/1088–1092, vomers; NMNHU-P 27/1124–1128, frontals; NMNHU-P 27/1129, parietal; NMNHU-P 27/1047–1054, parasphenoids; NMNHU-P 27/1036–1046, maxillae; NMNHU-P 27/1102–1106, 1108, 1110–1115, 1117–1121, palatines; NMNHU-P 27/1012–1021, 1040, quadrates; NMNHU-P 27/1022–1033, 1038, articular bones; NMNHU-P 27/992–995, 997, 1000, 1006, 1007, left dentaries; NMNHU-P 27/1004, 1005, 1008, 1009, 1463, right dentaries; NMNHU-P 27/1093–1096, 1099, hyomandibulars; NMNHU-P 27/1056–1069, ceratohyals; NMNHU-P 27/986–989, 1097, opercular bones; NMNHU-P 27/1035, 1071–1076, 1614, cleithra. All material from the type locality and horizon.

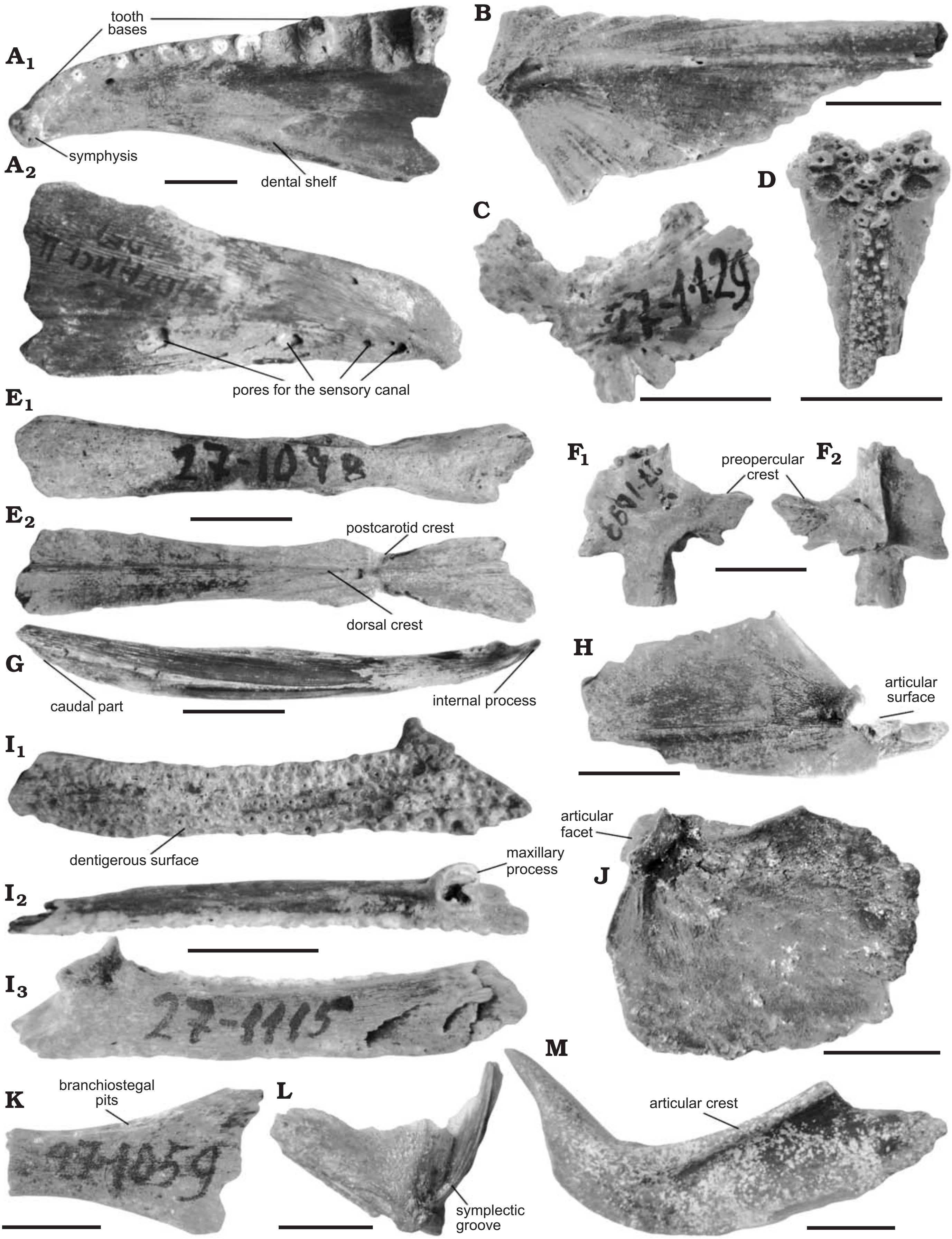
Diagnosis.—*Esox nogaicus* sp. nov. differs from other esocids in the following combination of characters: (i) massive dentary with wide dental shelf and high symphysis; (ii) well-developed antero-ventral crest on frontal; (iii) large angle between horizontal crest and preopercular process of opercle and wide foramen on hyomandibula; (iv) low anguloarticular with wide retroarticular process; (v) long and flat dentigerous surface on palatine; (vi) wide articular crest on cleithrum.

Description.—The dentary (Fig. 4A) is massive, with a well-developed wide dental shelf, a deep symphysis, and uniserial dentition. The anterior (toothed) edge of the dentary is straight and thickened near the symphysis. The oral margin is relatively high. C-shaped tooth bases occupy the anterior two-thirds of the tooth row, with bases of fixed teeth and large replacement pits in the posterior third. A shallow lateral groove divides the anterior edge of the dentary and forms a ventral bulge in the symphysis. On the lateral surface, four pores for the mandibular sensory canal (Nelson 1972) are clearly visible near the ventral edge while, near the tooth row, the trigeminal foramen opens toward the posterior (see Wilson et al. 1992). Measurements of dentaries of the new species are as follows: height of dentary symphysis, 6.6–9.1 mm; width of the dentary near the symphysis, 3.9–5.0 mm; width of tooth row, 4.2–4.5 mm.

The posterior part of the medial suture edge of the frontal (Fig. 4B) is slightly thickened, with a wide sphenotic ledge, a clearly expressed antero-ventral crest, and a narrow side branch of the supraorbital canal. The dorsal surface of the bone is sculptured by radial smooth plates.

The parietal (Fig. 4C) is massive, with a wide posterolateral process and a well-developed ventral crest.

The front edge of the vomer (Fig. 4D) is smooth. The anterior premaxillary process of the vomer forms an angle



A1
tooth bases
symphysis
dental shelf
A2
pores for the sensory canal
B
C
27-1129
D
E1
27-1098
E2
postcarotid crest
dorsal crest
F1
F2
preopercular crest
G
caudal part
internal process
H
articular surface
I1
dentigerous surface
I2
maxillary process
I3
27-1115
J
articular facet
K
branchiostegal pits
L
symplectic groove
M
articular crest

of 115° with the longitudinal axis of the bone. The elongate dental field on the shaft of the vomer is relatively wide (WDF 5.1–6.8 mm) and has numerous very small C-shaped tooth bases. The dental field tapers anteriorly, and connects at a small neck to the triangular anterior dental field on the vomerine head (WCV 11.1–14.3 mm). There are several larger, medial C-shaped tooth bases (DDC 2.3–2.4 mm) on the vomerine head, their sizes increase laterally. A single pair of even larger replacement pits suggests the presence of fixed teeth (Fig. 4D). Similar replacement pits can be seen in several other vomers of *E. nogaicus* sp. nov.

Both anterior and posterior parts of the parasphenoid (Fig. 4E) are long: WPSa 7.3–9.5 mm, WPSp 6.9–8.6 mm. The narrow anterior median crest passes without a neck into the posteriorly extended dorsal medial crest. Carotid grooves are clearly expressed and deepened anteromedially. The angle between the postcarotid crests is about 110–120°.

The upper edge of the hyomandibula (Fig. 4F_1, F_2) and the horizontal crest on the medial surface are almost parallel. The angle between the horizontal crest and the preopercular process is about 120°. There is a deep notch between the wall and the upper edge of the preopercular process.

The maxilla (Fig. 4G) is highly elongated (LM 50.3–61.5 mm), with wider posterior and narrower anterior parts. The short medial process has a rounded tip.

The articular (Fig. 4H) is characterized by a low wall (the anguloarticular angle is 40–45°), an uvular notch of the articular facet (LAF 4.9–5.6 mm), and a wide and elevated retroarticular process. There is an elongated keel at the posteroventral edge of the bone.

The palatine (Fig. 4I) has a large maxillary process with a wide fossa articularis and a small notch beside it. The dentigerous surface is long and flat. There are C-shaped bases from six rows of small, depressible teeth on the ventral surface, the largest bases located anteriorly in the medial row. The width of the bone is in the range 5.7–7.2 mm, DFA 3.2–4.8 mm.

The opercular (Fig. 4J) is flat and almost rectangular, with smooth edges. The articular facet is lenticular.

The massive barbell-shaped ceratohyals (Fig. 4K) are mostly represented by their medial parts with broken ends; they have weekly expressed branchiostegal pits and a wide main shaft.

The quadrate (Fig. 4L) is more or less triangular. The articular condyle is doubled, with medial and lateral lobes, and forms an oblique articulation with the articular bone. In lateral view, the angle between the articular condyle and the body of the quadrate is about 80°. The notch of the anterior edge just above the condyle is narrow and elongated.

The cleithrum (Fig. 4M) is massive and characterized by a wide and well-developed, medially bending articular crest. The width of the main plate is 10.2–12.1 mm.

Remarks.—*Esox nogaicus* sp. nov. is similar to *E. lucius* in the uniserial dentition of the dentary, the well-developed anteroventral crest of the frontal, and in the structure of parietal, vomer, parasphenoid and opercular, but differs in its wider dental shelf and higher dentary symphysis, as well as its lower anguloarticular angle, flat dentigerous surface on palatine, and wider articular crest of the cleithrum. *Esox moldavicus* is close to *E. nogaicus* sp. nov. in the structure of the dentary, but it differs in its weakly visible carotid grooves on parasphenoid, higher anguloarticular angle, and short toothed surface on the palatine. As compared to those in *E. nogaicus* sp. nov. the dentaries of *Esox sibiricus* and *E. reichertii* are characterized by a small and weakly developed dental shelf, two-row dentition, a larger anguloarticular, a relatively short dentigerous surface on the palatine, and a wider articular crest on the quadrate; on the other hand, these species resemble *E. nogaicus* sp. nov. in the structure of the frontal and parasphenoid.

Stratigraphic and geographic range.—Type locality and horizon only.

Esox lucius Linnaeus, 1758

Fig. 5.

Material.—Early Pleistocene: one left cleithrum (NMNHU-P 53/4249, Nova Etuliya); one fragment of cleithrum (NMNHU-P 53/4250, Sinyaya Balka). Middle Pleistocene: one left palatine and two left dentaries (NMNHU-P 53/4253, Semibalka 1); one parasphenoid, two right palatines, two left and six right dentaries (NMNHU-P 53/4254–4264, Medzhibozh).

Emended diagnosis.—*Esox lucius* is characterized by a number of features distinguishing it from other species: (i) only uniserial dentition of dentary; (ii) narrow dental shelf; (iii) presence of symphysial notch; (iv) clearly expressed and anteromedially deepened carotid grooves on parasphenoid; (v) rounded articular facet on palatine; (vi) weakly expressed dorsal crest on cleithrum.

Description.—The posterior part of the parasphenoid and the dorsal medial crest are extended caudally (Fig. 5G). The broad anterior medial crest is well developed. There is a dorsally directed process at the base of the posterior crest. The bone is wide (6.0 mm in the medial part and

← Fig. 4. Isolated elements assigned to a pike *Esox nogaicus* sp. nov. from Southeastern Europe, Nogaisk; Pleistocene. **A**. Holotype, right dentary (NMNHU-P 27/1697), occlusal (A_1) and lateral (A_1) views. **B**. Left frontal (NMNHU-P 27/1124), lateral view. **C**. Left parietal (NMNHU-P 27/1129), dorsal view. **D**. Vomer (NMNHU-P 27/1088), ventral view. **E**. Parasphenoid (NMNHU-P 27/1047), ventral (E_1) and dorsal (E_2) views. **F**. Left hyomandibular (NMNHU-P 27/1093), lateral (F_1) and medial (F_2) views. **G**. Left maxilla (NMNHU-P 27/1036), lateral view. **H**. Right articular (NMNHU-P 27/1024), medial view. **I**. Right palatine (NMNHU-P 27/1115), ventral (I_1), lateral (I_2), and dorsal (I_3) views. **J**. Right opercular (NMNHU-P 27/986), medial view. **K**. Left ceratohyal (NMNHU-P 27/1059), medial view. **L**. Right quadrate (NMNHU-P 27/1012), medial view. **M**. Left cleithrum (NMNHU-P 27/1035), medial view. A_2, G, H, I_1, I_2, M, anterior to right; A_1, B, I_3, J, L, anterior to left; C–F, K, anterior towards top. Scale bars 5 mm.

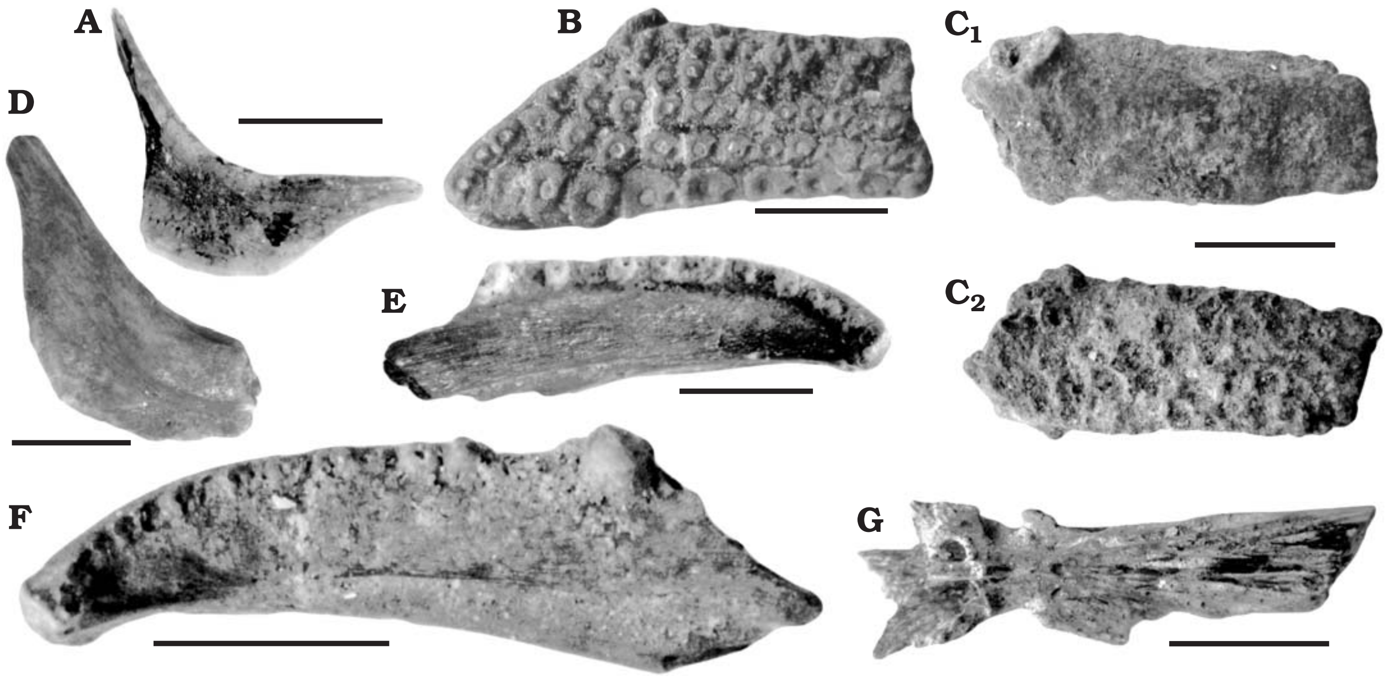


Fig. 5. Isolated elements assigned to the Northern Pike *Esox lucius* Linnaeus, 1758 from Southeastern Europe; Pleistocene. **A**. Left cleithrum (NMNHU-P 53/4249), Nova Etuliya, lateral view. **B**. Left palatine (NMNHU-P 53/4253), Semibalka 1, ventral view. **C**. Right palatine (NMNHU-P 53/4255), Medzhibozh, dorsal view (C_1), ventral view (C_2). **D**. Fragment of cleithra (NMNHU-P 53/4250), Sinyaya Balka, lateral view. **E**. Left dentary (NMNHU-P 53/4387), Semibalka 1, occlusal view. **F**. Right dentary (NMNHU-P 53/4264), Medzhibozh, occlusal view. **G**. Parashenoid (NMNHU-P 53/4254), Medzhibozh, dorsal view. A, D, E, anterior to right; F, anterior to left; B, C, G, anterior towards top. Scale bars: A–F, 5 mm; G, 10 mm.

7.8 mm in the posterior part). Two shallow longitudinal grooves are expressed in the medial part of the ventral side of the bone. There is a large angle between the postcarotid crests.

The dentaries (Fig. 5E, F) are low, with a uniserial dentition of depressible teeth near the symphysis and a narrow dental shelf. Width of the dentary near the symphysis of these bones from Medzhibozh is 1.2–2.9 mm (M 1.5 mm); height of dentary symphysis, 1.9–5.2 mm (M 3.1 mm); and width of tooth row, 1.0–3.1 mm (M 1.9 mm). Dentaries from Semibalka 1 are comparable in size: width of the dentary near the symphysis, 2.2 and 3.0 mm; height of dentary symphysis, 3.8 and 5.6 mm; width of tooth row, 1.6 and 2.0 mm.

The palatine has a rounded fossa articularis and an uvular articular process (Fig. 5B, C). The dentigerous surface is relatively long and concave. There are C-shaped bases from five rows of small depressible teeth on the ventral surface of the bone (the largest of them located in the medial row). The width of the palatine from Semibalka 1 is 7.0 mm, with DFA 3.5 mm.

Cleithra are represented by their caudal parts (Fig. 5A, D). The thickened dorsal crest is weakly expressed. The width of the plate is 6.2 mm for those from Nova Etuliya and 7.2 mm for the cleithrum from Sinyaya Balka.

Remarks.—All described bones are indistinguishable in morphology and size from those of *Esox lucius*.

Stratigraphic and geographic range.—Early Pleistocene–Recent, Eurasia and North America.

Esox spp.

Fig. 6.

Material.—Late Miocene: thirty teeth (NMNHU-P 29/1681–1710, Popovo 3); eleven teeth (NMNHU-P 33/554–564, Mykhailivka 2); one dentary fragment, two teeth (NMNHU-P 41/3015–3017, Frunzovka 2); two teeth (NMNHU-P 41/3472, 3473, Palievo); one palatine fragment and three teeth (NMNHU-P 29/3966–3969, Lobkovo); eight teeth (NMNHU-P 45/5691–5698, Cherevichne 3); one tooth (NMNHU-P 29/3970, Vasylivka 1); two teeth (NMNHU-P 29/1467, 1468, Vasylivka 3); seventy teeth (NMNHU-P 29/1037–1106, Verkhnya Krynitsya 2); twenty-seven teeth (NMNHU-P 41/4498–4524, Egorovka 2); five teeth (NMNHU-P 41/4327–4331, Egorovka 1); one dentary fragment and twenty-four teeth (NMNHU-P 38/1964–1988, Novoukrainka 1); eight teeth, one palatine (NMNHU-P 33/514–522, Andreevka); three teeth (NMNHU-P 41/2848–2850, Orekhovka); ten teeth (NMNHU-P 41/2465–2474, Pontian Lectostratotype); twenty-three teeth (NMNHU-P 41/2742–2764, Vinogradovka 1). Early Pliocene: two teeth (NMNHU-P 37/2555, 2556, Novopetrovka); fourteen teeth (NMNHU-P 53/4265–4278, Obukhovka 1); one tooth (NMNHU-P 42/2458, Vinogradovka 2); five teeth (NMNHU-P 42/2459–2463, Kotlovina 1). Late Pliocene: fifty-nine teeth (NMNHU-P 53/4279–4338, Obukhovka 2); six teeth (NMNHU-P 53/4342–4347, Zhevakhova Gora); one left dentary and four teeth (NMNHU-P 45/6020–6024, Cherevichne 2); fourteen teeth (NMNHU-P 29/626–639,

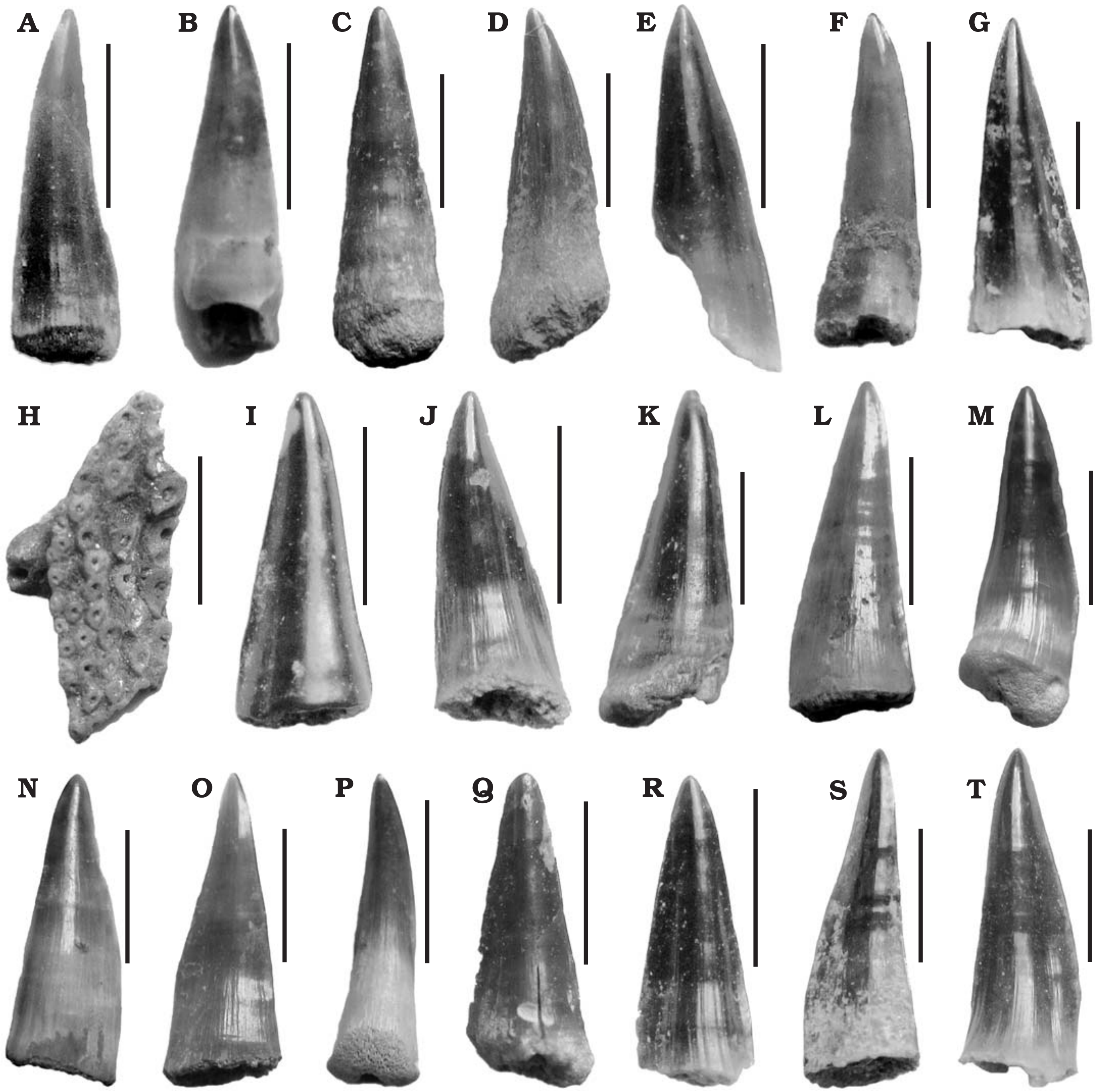


Fig. 6. Isolated elements assigned to a pike *Esox* spp. from Southeastern Europe; late Miocene (A–J), Pliocene (N–Q), and Pleistocene (K–M, R–T). **A**–**G**, **I**–**T**. Tooth, lateral view. **A**. NMNHU-P 41/3472, Palievo. **B**. NMNHU-P 33/561, Mykhailivka 2. **C**. NMNHU-P 29/1708, Popovo 3. **D**. NMNHU-P 29/1045, Verkhnya Krynitsya 2. **E**. NMNHU-P 41/4498, Egorovka 2. **F**. NMNHU-P 41/4329, Egorovka 1. **G**. NMNHU-P 38/1964, Novoukrainka 1. **I**. NMNHU-P 41/2466, Pontian Lectostratotype. **J**. NMNHU-P 41/2742, Vinogradovka 1. **K**. NMNHU-P 53/4395, Bol'shevik 2. **L**. NMNHU-P 29/380, Lysa Gora 1. **M**. NMNHU-P 53/4388, Semibalka 1. **N**. NMNHU-P 42/2458, Vinogradovka 2. **O**. NMNHU-P 53/4281, Obukhovka 2. **P**. NMNHU-P 53/4344, Zhevakhova Gora. **Q**. NMNHU-P 29/627, Verkhnya Krynitsya 1. **R**. NMNHU-P 42/2463, Kotlovina 2. **S**. NMNHU-P 53/4406, Medzhibozh. **T**. NMNHU-P 42/2472, Kotlovina 3. **H**. Left palatine (NMNHU-P 33/517), Andreevka, occlusal view. Scale bars: C, D, H–O, R, S, T, 5 mm; A, B, E, F, P, Q, 4 mm; G, 3 mm.

Verkhnya Krynitsya 1). Early Pleistocene: nine teeth (NMNHU-P 42/2463–2471, Kotlovina 2); forty-seven teeth (NMNHU-P 42/2472–2518, Kotlovina 3); twenty teeth (NMNHU-P 1584–1603, Popovo 2); two teeth (NMNHU-P 29/1533, 1534, Popovo 1); two teeth (NMNHU-P 29/1472, 1473, Popovo 0); one left dentary fragment and eight teeth (NMNHU-P 53/4348–4356, Tiligul); three teeth (NMNHU-P 53/4357–4359, Nova Etuliya); thirteen teeth (NMNHU-P 53/4360–4372, Sinyaya Balka); fourteen teeth (NMNHU-P 53/4373–4386, Kairy); eight teeth (NMNHU-P 45/6025–6032, Cherevichne 1). Middle Pleistocene: ten teeth (NMNHU-P 42/2519–2528, Protopopovka 2); six

Table 4. Measurements (in mm) of jaw teeth of pikes (*Esox* sp.) from the Mio-Pleistocene of southeastern Europe. N, number of specimens.

Locality	n	Tooth length		Tooth width		Tooth		Tooth width / depth
		range	mean	range	mean	range	mean	
Medzhibozh	105	3.2–10.9	7.6	1.5–4.4	2.7	0.9–3.1	1.9	1.4
Bol'shevik 2	6	4.8–11.0	7.3	1.9–3.9	2.9	1.2–3.0	1.9	1.5
Lysa Gora 1	5	4.2–11.1	6.3	1.7–4.3	2.4	1.0–3.3	1.6	1.5
Semibalka 1	6	5.9–12.3	7.5	1.8–3.7	2.7	1.3–2.7	2.1	1.3
Protopopovka 2	10	4.7–8.4	6.1	1.7–2.7	2.3	0.9–2.0	1.4	1.6
Cherevichne 1	8	4.1–7.5	6.2	1.8–3.4	2.6	1.1–1.9	1.6	1.6
Kairy	14	3.1–7.2	5.9	1.4–2.8	2.2	0.8–2.1	1.5	1.5
Sinyaya Balka	13	4.6–8.4	6.9	1.9–3.4	2.6	1.2–2.2	1.7	1.5
Nova Etuliya	3	6.7–7.5	7.1	2.1–3.3	2.6	1.3–1.8	1.6	1.6
Tiligul	8	4.4–7.1	5.8	1.5–2.9	2.2	1.0–2.1	1.6	1.4
Popovo 0	2	5.3; 5.5	–	2.1; 2.5	–	1.2; 1.8	–	1.5
Popovo 1	2	4.3; 5.9	–	1.6; 2.3	–	1.1; 1.6	–	1.4
Popovo 2	20	4.7–10.8	6.9	1.8–4.1	2.5	1.2–2.9	1.8	1.4
Kotlovina 3	47	4.9–12.6	7.9	1.9–4.1	2.9	1.3–3.3	2.1	1.4
Kotlovina 2	9	4.0–8.2	6.2	1.8–3.0	2.4	0.9–2.1	1.6	1.5
Verkhnya Krynitsya 1	14	4.0–8.8	5.9	1.6–3.4	2.2	1.1–2.7	1.6	1.4
Cherevichne 2	4	4.7–8.1	7.0	1.6–2.8	2.4	1.2–1.8	1.6	1.5
Zhevakhova Gora	6	3.5–8.8	5.3	1.3–2.5	1.9	0.7–2.3	1.4	1.4
Obukhovka 2	59	4.0–12.2	7.2	1.7–4.6	2.8	1.0–3.0	1.7	1.6
Kotlovina 1	5	2.8–6.0	4.5	1.4–1.9	1.7	0.8–1.3	1.1	1.5
Vinogradovka 2	1	–	11.4	–	4.5	–	3.2	1.4
Obukhovka 1	14	4.4–11.6	6.2	2.1–4.0	2.3	1.1–3.2	1.6	1.4
Novopetrovka	2	6.2; 7.9	–	2.2; 3.4	–	1.6; 2.2	–	1.5
Vinogradovka 1	23	3.3–9.4	6.0	1.4–3.5	2.2	0.9–2.6	1.7	1.3
Pontian Lectostratotype	10	3.4–8.8	5.7	1.4–3.5	2.3	1.0–2.4	1.6	1.4
Orekhovka	3	3.1–4.2	3.7	1.5–2.1	1.8	0.9–1.2	1.1	1.6
Andreevka	9	5.2–8.3	7.3	2.0–3.6	3.0	1.2–2.3	1.9	1.6
Novoukrainka 1	24	4.6–8.9	6.6	1.7–3.1	2.4	1.1–2.4	1.6	1.5
Egorovka 1	5	3.5–5.2	4.3	1.6–2.0	1.8	1.3–1.5	1.4	1.3
Egorovka 2	27	2.7–7.2	4.6	1.1–2.2	1.6	0.8–1.5	1.1	1.5
Verkhnya Krynitsya 2	70	5.2–9.0	7.3	1.8–3.2	2.7	1.2–2.4	2.0	1.4
Vasylivka 1	1	–	6.6	–	2.1	–	1.5	1.4
Vasylivka 3	2	6.8; 7.6	–	2.3; 2.6	–	1.8; 2.1	–	1.3
Cherevichne 3	8	3.1–6.3	4.8	1.5–2.3	1.9	0.9–1.7	1.2	1.6
Lobkovo	3	5.0–6.6	5.5	1.9–2.6	2.3	1.1–1.5	1.3	1.8
Palievo	2	3.6; 5.6	–	1.6; 1.9	–	1.3; 1.3	–	1.5
Frunzovka 2	2	3.3; 4.7	–	1.3; 1.6	–	0.8; 1.0	–	1.6
Mykhailivka 2	11	3.5–6.7	5.2	1.4–2.1	1.9	1.1–1.6	1.3	1.5
Popovo 3	30	3.7–10.2	7.0	2.2–3.2	2.7	1.5–2.7	1.9	1.4

teeth (NMNHU-P 53/4388–4393, Semibalka 1); five teeth (NMNHU-P 29/380–384, Lysa Gora 1); one palatine fragment and six teeth (NMNHU-P 53/4394–4400, Bol'shevik 2); one hundred and five teeth (NMNHU-P 53/4401–4505, Medzhibozh).

Description.—Palatines from Lobkovo and Bol'shevik 2 are represented by small fragments; their width is 2.4 mm and 5.8 mm, respectively. The toothed surface on the palatine (Fig. 6H) is very long and slightly concave, extending under the maxillary process. The dorsal surface of the bone is somewhat curved. The diameter of the tooth crowns on the palatines averages 0.6 mm.

It is not possible to measure some dentaries because they are fragmentary. WTR of the more complete dentaries varies from 2.1 mm (Frunzovka 2) to 3.1 mm (Novoukrainka 1); the WTR for the dentary from Tiligul (2.2 mm) is close to the smaller one.

Elongate, dagger-shaped jaw teeth (Fig. 6A–G, I–T) are laterally compressed, with slightly curved crowns and rounded bases. Tips of the teeth are sharp and cutting edges are slightly narrowed. Measurements of isolated jaw teeth of pikes are presented in Table 4.

Remarks.—These jaw teeth and other bones undoubtedly belong to the genus *Esox*. Their species attribution is uncertain because of the bones are significant fragmented and the teeth are not diagnostic to species.

Concluding remarks

Pikes were an important element in freshwater fish complexes of southeastern Europe during the late Neogene and Anthropogene. At least three developmental stages for these assemblages (in respect to the presence of certain *Esox* species) can be defined: (i) late Miocene to earliest Pliocene; (ii) early Pliocene to earliest Pleistocene; (ii) early–middle Pleistocene to present.

The first stage is characterized by the wide geographic distribution of *E. sibiricus*. Such a situation, as in the case of *Leobergia* (see Kovalchuk and Murray 2016) and some other freshwater fishes (e.g., catfishes; see Kovalchuk and Ferraris 2016), may be related to the Miocene climatic optimum (Böhme et al. 2008). It can be also explained by a prochoresis of esocids from North America to Asia and Europe, with their subsequent incorporation into local fish complexes.

In the second stage, the later appearance of *E. moldavicus* and the extinction of *E. sibiricus* (as well as other thermophilic species) could have been caused by geographical vicariance and is interpreted here as a response to gradual global climate cooling during the Pliocene and early Pleistocene. The landscape was undergoing major changes associated with the collision of the Afro-Arabian and Eurasian plates causing changes to ocean circulations with the closing of the Tethys, as well as uplift of mountain ranges in Europe (Ivanov et al. 2011). This was also a period of significant climate change with the onset of polar glaciation causing a cooling and drying phase (see Syabryaj et al. 2007; Kovalchuk and Murray 2016 for more details).

Subsequent changes in freshwater fish complexes of southeastern Europe also occurred against the background of significant cooling, which favoured cold-adapted fishes, such as *E. nogaicus* sp. nov. and, finally, *E. lucius*. Similar climatic events have been hypothesized to explain changing geographic and stratigraphic ranges of Cretaceous, Paleogene, and Neogene esocids in North America (Newbrey et al. 2008).

Esox nogaicus sp. nov. presents a distinctive morphology including a stout dentary with deep symphysis and the possible presence of a pair of fixed canine-like teeth near the anterior end of the vomer. Fixed "canine" teeth on the vomer are seen also in certain species known only from North America: the extant *Esox masquinongy*, the related Pliocene fossil species *E. columbianus* Smith, Morgan, and Gustafson, 2000, and an unnamed Miocene form (Cavender et al. 1970). However, the North American species have fixed "canine-like" teeth also anteriomedially on the palatines, unlike *E. nogaicus* sp. nov. which lacks fixed teeth on its palatines.

The Miocene, Pliocene, and Pleistocene pikes from southeastern Europe, taken together, document a greater diversity of morphologies in the past than exists today in the pike species of Europe, and record a series of changes in the predominant esocid species during the Neogene in that region that we hypothesize were driven by climatic change.

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Appendix 1

Comparative material derived from the Field Museum of Natural History (FMNH), Loyola University Chicago Fish Collection (LUC-F), Cornell University Museum of Vertebrates (CU), and NMNHU-P. Specimens are either dried bones and skeletons or cleared and stained (c&s) for bone or for both bone and cartilage. Each number represents an individual specimen.

Esox lucius: FMNH 32734, 9760, 51360, 9964 (dried skeletons); NMNHU-P 1/127, 128, 129, 130, 131, 132, 133, 134, 135, 136, 137, 139, 140, 141, 142, 143, 144, 145, 146, 147, 148, 149, 150, 151, 152, 153, 154, 155, 156, 157, 158, 159, 160, 161, 162, 164, 165, 166, 167, 168, 169, 170, 171, 172, 173, 217 (dried skeletons); NMNHU-P 1/138, 1/163 (c&s).

Esox masquinongy: FMNH 72177 (dried skeleton); CU9118 (c&s).

Esox reichertii: CU 64227, 64228, 64229, 64231 (alcohol and c&s); FMNH 109221.

Esox niger: FMNH 21811 (c&s); LUF 082291-082293 (c&s).

Esox americanus: FMNH 31768 (c&s).

Esox americanus americanus: FMNH 10424 (c&s).

Esox americanus vermiculatus: FMNH 7187 (c&s).