

# European River Lamprey *Lampetra Fluviatilis* in the Upper Volga: Distribution and Biology

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## Research

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# Abstract

After the construction of the Volga Hydroelectric Station and other dams, migration routes of the Caspian lamprey were obstructed. The ecological niches vacated by this species attracted another lamprey of the genus *Lampetra* to the Upper Volga, which probably came from the Baltic Sea via the system of shipways developed in the 18<sup>th</sup> and 19<sup>th</sup> centuries. Based on collected samples and observations from sites in the Upper Volga basin, we provide diagnostic characters of adults, and information on spawning behavior. Silver coloration of *Lampetra fluviatilis* was noted for the first time and a new size-related subsample of “large” specimens was delimited, in addition to the previously described “dwarf”, “small” and “common” adult resident sizes categories. The three water systems: the Vyshnii Volochek, the Tikhvin and the Mariinskaya, are possible invasion pathways, based on the migration capabilities of the lampreys. Dispersal and colonization of the Caspian basin was likely a combination of upstream and downstream migrations. First, the lampreys migrated upstream along the rivers of the Baltic basin until they reached the water-parting line, followed by mostly downstream dispersal into rivers of the Caspian basin. Dispersal in the Volga River was similar, in accordance with the migration cycle of this opportunistic lamprey species.

## Introduction

Four genera of lampreys (Petromyzontiformes) occur in the central part of the eastern Europe (European part of Russia, Fig. 1). Representatives of the genera *Lampetra* (the Northeast Atlantic Ocean and the rivers of Europe) and *Lethenteron* (drainages of the White and Barents seas of the Arctic Ocean) are represented by both migrant (anadromous, potamodromous) and freshwater (the so-called resident) ecological forms. The genus *Caspiomyzon* (the Caspian Sea and the rivers of its northern, western, and southern watersheds) includes anadromous lampreys only, while the genus *Eudontomyzon* (rivers of the Black and Azov seas) currently comprises only freshwater forms [1–8].

Before the construction of the Volga Hydroelectric Station (1958), the Volga river system was almost entirely populated by the Caspian lamprey *Caspiomyzon wagneri*, an anadromous species, which does not form freshwater populations or satellite (paired) freshwater species [7,9]. These lampreys used to go up the Volga as far as the city of Kalinin (now Tver) and the mouth of the Tvertsa River [10]. The migration routes were later obstructed by the dams in the Upper Volga (the section of the Volga between the source and the confluence with the Oka River) and then blocked entirely after the construction of the Volga Hydroelectric Station. Only single specimens of the Caspian lamprey were noted upstream of the station's dam, in the Volgograd Reservoir [11], and it is absent further upstream, in the Saratov Reservoir [12]. The ecological niches vacated by the Caspian lamprey attracted representatives of other lamprey genera: *Lampetra* from the Baltic Sea basin and *Eudontomyzon* from the Azov-Black Sea basin [4,13]. This became possible owing to the anthropogenic modification of the river network expressed in the construction of shipways. The modification went on for more than three centuries resulting in the connection of the basins of five seas: the White, the Baltic, the Caspian, the Black Sea and the Sea of Azov.

The anadromous form of the European river lamprey *Lampetra fluviatilis* inhabits the basins of the North, the Baltic, and the Mediterranean Sea. The freshwater form of the European river lamprey, traditionally referred to as the European brook lamprey *Lampetra planeri*, has been repeatedly registered in the Upper Volga, i.e. in the Caspian Sea basin, in the middle and the second half of the 20<sup>th</sup> century [10,14–20]. There are reasons to believe that the invasion of the European river lamprey into the Volga River has been associated with the development of inland shipping and the network of shipways in the 18<sup>th</sup>–19<sup>th</sup> centuries. The Upper Volga is thus of special interest for studies dealing with the dispersal of hydrobionts. It is connected with rivers of the Baltic Sea basin by three hydrological systems of shipways and with rivers of the White Sea basin by one hydrological system. Two navigable waterways from the Baltic Sea and one from the White Sea connect with the Rybinsk Reservoir, which is the zone of “accumulation of invaders” as well as the area of intergradation of the northern and the Ponto-Caspian hydrobionts [21].

The freshwater form of the European river lamprey is currently included in the fish fauna lists of the Rybinsk Reservoir with the status of a rare species decreasing in numbers [21–23]. Researchers from the Institute for Biology of Inland Waters of the Russian Academy of Sciences (IBIW RAS) note that the lamprey does not occur in the reservoir itself [21], surviving as small local populations in the tributaries [23]. Other experts from the same institute question the presence of the European river lamprey in the system of the Rybinsk Reservoir [24,25]. However, there is no detailed information about the distribution of the European river lamprey in the Rybinsk Reservoir and in the Upper Volga in general. Moreover, characteristics of its local populations are also unknown.

The aim of our study was to establish whether representatives of the order Petromyzontiformes occur in the rivers of the Upper Volga basin and to reconfirm the taxonomic position of lampreys from the Upper Volga basin. A second objective was to analyze invasion pathways and dispersal mechanisms of lampreys from the Baltic Sea to the Upper Volga basin.

## Results

Based on the analysis of the satellite images and the literature information [26–29], we calculated the distances between locations of lamprey samples and the Volga-Baltic water-parting line (Table 1).

Table 1

Extrapolated distances of dispersal of the European river lamprey *Lampetra fluviatilis* along the rivers of the Upper Volga basin

Site	Water course	Coordinates of the capture site	Distance (km) from the water-parting line, <u>downstream</u> upstream
1	Vysochinsky Stream	58°17'06.00" N, 35°31'22.74" E	<u>226</u> 185.8
2	Saragozha River	58°16'24.14" N, 35°36'03.11" E	<u>226</u> 151
3	Kamenka River	58°11'56.24" N, 37°51'24.83" E	<u>369</u> 15
4	Tunoshonka River	57°32'31.82" N, 40°06'57.54" E	<u>612</u> 1.3
5	Vyazma River	56°28'46.63" N, 35°49'17.18" E	<u>245</u> 62
6	Malaya Dubenka River	56°51'13.66" N, 33°14'42.71" E	<u>188</u> 348
Note: the distances were calculated for the Tikhvin water system (1–4) and the Vyshnii Volochek water system (5–6). Site numbers as on the Fig. 1.			

## Reconfirmation of the taxonomic status

The external attributes and dentition allowed us to confirm that the adult specimens and larvae were European river lamprey *Lampetra fluviatilis*: cloaca is posterior to the origin of the second dorsal fin, under its first half. Oral papillae very small, of uniform size along the entire perimeter of oral disc. Eyes dorsolateral. Teeth blunt in most specimens (Fig. 3). Exolateral rows without dentition. Three rows of right and three rows of left endolaterals. Second rows of endolaterals always with three cusps. Supraoral lamina with two unicuspid teeth separated by bridge without dentition. Marginal cusps of infraoral lamina larger than inner ones, usually bicuspid (sometimes asymmetric). In total, 6–10 cusps on infraoral lamina. Anterior rows bearing 0–2 teeth; if teeth present, 0–7 anterior teeth in the first row. Posterior teeth absent. Trunk myomeres 58–77 in number. Relative size (% of the body length) in specimens with total length 123–151 mm: prebranchial length – 8.6–13.9; branchial length – 9.0–15; trunk length – 45.9–56.4; tail length – 25.2–31.4; disc length – 4.5–6.7.

Coloration of the lampreys from the Vysochinsky Stream was dark dorsally and silvery on lateral sides, which is characteristic of juvenile European river lamprey during downstream migration (Fig. 4a). Coloration of males and females from the Kamenka River and males from the Saragozha River was dark brown dorsally and light on the ventral side (Fig. 4b, c). Females from the Saragozha River were olive or light brown on the dorsal side, olive or sandy on lateral sides. Dorsal part of the branchial area colored, ventral part light, oral disc not pigmented. Despite the coloration of the specimens from the Vysochinsky Stream, all the lampreys had well-expressed secondary sexual characteristics and developed reproductive products.

## Discussion

The coloration of adults from the studied populations was diverse. Lampreys from the Saragozha and the Kamenka were, in general, colored similarly to adults of the European river lamprey from various rivers of Europe [3,7,30]. The coloration of adults from the Vysochinsky Stream deserves a special discussion. Their silvery coloration is characteristic of post-metamorphic juveniles (transformers, macrophthalmia) during their downstream migration [31–33]. Sperone et al. [34] found what they took to be the southernmost resident population of the European river lamprey (they call it the European brook lamprey *L. planeri*) in the Lao River (Calabria, Italy). They caught two such specimens on October, 26 2018 with an electrofisher (total length 170 and 175 mm). It is clear from the photo of the specimen with the silvery coloration (P. 133, and the figure in [34]) that it is not an adult but a post-metamorphic immature specimen (secondary sexual characteristics are absent). Most probably, it was a smolt of the European river lamprey. Of the other resident species of *Lampetra*, silvery coloration was also noted for *Lampetra aepyptera* [7]. It is unclear if the silvery coloration of lampreys is associated with their migratory activity and why lampreys from the Vysochinsky Stream do not lose this coloration upon maturation. These questions might open avenues for further research and the need for genetic analysis of archived specimens.

According to Renaud [7], the resident form of the European river lamprey (*L. planeri sensu* Renaud 2011) has a maximum total length 170 mm. Kucheryavyi et al. [35] grouped them according to length: “dwarf” (78–83 mm), “small” (90–104 mm) and “common” (107–140 mm). Following these definitions, the lampreys from the Kamenka River were classified as “small” (n = 1) and “common” (n = 4). All adults from the Saragozha River were “common” (n = 7). In the Vysochinsky Stream, 63% (n=19) of the lampreys were “common”, while 37% (n=11) were attributed to a new subsample, “large” (>141 mm). Lampreys like these have been recorded from northwestern Scotland (in the Endrick River, a tributary of the Loch Lomond – [36]) and in isolated populations in Spain (the Deva-Cares system) and Portugal (the rivers Esmoris and Vouga) [37,38].

One of the hypotheses explaining the presence of the landlocked lampreys (e.g. resident European river lamprey in the Upper Volga or lake form of sea lamprey *Petromyzon marinus* in the Lake Ontario) assumes the impact of global climate changes on the ichthyofauna 70–10 thousand years ago. Lawrie [39] and Smith [40] believe that the sea lamprey inhabiting the lake and its drainages is a relict

Pleistocene population in North America. Dorofeev et al. [41] and Slynko and Tereshchenko [23] suggest that the retreat of the Valdai glaciation in Europe under the influence of the global warming (12–10 thousand years ago) resulted in the formation of numerous periglacial lakes and other water bodies of glacial origin. Owing to this, the entire Ponto-Caspian basin was populated by fish species of the Arctic freshwater and boreal-submontane faunistic complexes. The European river lamprey belongs to the latter. This is how the presence of the European river lamprey in the tributaries of the Upper Volga, the Ivankovo, the Uglich and the Rybinsk Reservoir is explained by Slynko and Tereshchenko [23].

If the European river lamprey had inhabited the Upper Volga for > 11000 years, its local populations would have mixed resulting in homogeneous phenotypes. In contrast, lampreys from the Vysochinsky Stream, the Saragozha River, and the Kamenka River show diverse phenotypes (Fig. 4). These water courses are located close to each other, are not separated by physical barriers, and have similar hydrological characteristics (all of them are lowland rivers). The observed differences indicate a recent invasion of the European river lamprey into this region. Therefore, we forward the invasion hypothesis (entry of the European river lamprey into the system of the Volga River via manmade shipways). Extremely low numbers of the European river lamprey in the entire Upper Volga are likely a consequence of the construction of dams for hydroelectric, which caused limnification of the river and a decrease in the abundance of rheophilic species, including lampreys.

In the early 18<sup>th</sup> century the Caspian, Baltic and White Sea basins were not yet connected (Fig. 5). Shipways connecting the Upper Volga with the Baltic basin started with construction of the Vyshnii Volochek water system (1708, here and below we give the year of the completion of earthworks and construction activities on the artificial canals connecting the rivers. Practically, the basins of different seas became connected after that. Officially, the water systems in question were opened later (max. 6 years later), one of the reasons was the need to build sluices for the passage of ships). This was followed by the Tikhvin water system (1805), and by the Mariinskaya water system (1808), which is now called the Volga-Baltic water system [26,28,29]. The North Dvina water system in 1828 connected the Caspian and the White sea basins [27]. The development of the system of shipways opened new water courses, along which various hydrobionts including fish and cyclostomes have been dispersing for more than 300 years. Their dispersal along the Volga was unimpeded until the construction of the first dam, the Upper Volga Beishlot (1843), which has separated the lakes of the Upper Volga from the rest of the river. The dispersal pathways along the Upper Volga were blocked altogether after the construction of hydroelectric stations near Ivankovo (1937), Uglich (1940), Rybinsk (1941) and Nizhny Novgorod (1955).

The Volga River system is now one of the major invasion corridors of Europe. According to Konovalov et al. [42], hydrobionts mainly disperse from the Caspian basin northwards, to the Baltic basin (i.e., Volga pikepech *Sander volgensis*, blue bream *Ballerus ballerus*, wels catfish *Silurus glanis*) and the White Sea basin (i.e. sterlet *Acipenser ruthenus*, spined loach *Cobitis taenia*). This, probably, was made possible not only by the shipways but also because global warming causing northward displacement of a number of the species [43]. Dispersal in the opposite direction has been noted for fewer fish species, mainly due to their small adult sizes and short life cycle [44]. It may also be associated with the regulation of the run-off

of the Volga River, which results in an increase in the water temperature, low oxygen conditions, a change in the water mineralization, demands on spawning substrate, and growing eutrophication [21].

The Tikhvin water system is closer than the other two to the system of the Saragozha River and to the Kamenka River. The Vyshnii Volochek water system is situated in direct proximity of the Vyazma River, the Malaya Dubenka River, the Malaya and the Bolshaya Kosha rivers, the Shutinka Stream and the sites of collection of the European river lamprey in the studies by Viktorov [19], Viktorov et al. [20] and Nezdolii & Kirillov [15]. We consider these two systems of shipways as the most probable invasion pathways of the European river lamprey from the Baltic to the Caspian basin in the corresponding parts of the distribution. However, distance cannot be the only criterion in this matter. To ascertain the pathways used by the European river lamprey for the invasion in the Caspian basin, phenogeographic studies are necessary.

The foregoing reasoning about the colonization pathways opened due to the human activity closely resembles the process underway in the North American Laurentian Great Lakes. While the situation with the Lake Ontario remains a topic of debate, the remaining invasion pathways are clear to most researchers. Sea lamprey (*Petromyzon marinus*) has spread throughout the system of the lakes due to the construction of channels, which has made it possible to bypass Niagara Falls. It took only 25 years for sea lamprey to get to the farthest Lake Superior [49]. Of note is that as both sea and European river lamprey penetrate more deeply into these freshwater systems, they reduce their adult sizes and fecundity, producing parasitic lake forms. The European river lamprey goes further to produce a nonparasitic resident form [3], which after metamorphosis has no need of feeding and can disperse wider and inhabit more types of habitats.

Anadromous lampreys are quite capable of covering the distances mentioned above during one upstream migration [3]. For instance, the presence of an anadromous lamprey from the Gdovka River in the collection of the Museum of the Zoological Institute of the Russian Academy of Sciences (ZISP 25430–25433) indicates that the European river lamprey could migrate upstream the Narva River and cross Lake Peipus, covering in total more than 3000 km. In water-abundant years, lampreys in the Luga River overcome the Kingisepp and the Sabsk rapids and entered the tributaries of the Luga, e.g. the Krupa River, ascending 150 km upstream (ZISP 26437; 26438).

A possible scenario of the dispersal of the European river lamprey into the Upper Volga, based on the evidence from the Tikhvin water system, is as follows. Anadromous lamprey adults were noted in the Syas River [50]. Berg (ZISP 39080; 42976) and Ivanova-Berg (ZISP 42977) ascertained the presence of adults of the lake form in that river. This means that anadromous lampreys could have migrated upstream from the Baltic Sea along the Syas River up to the upper reaches of the Tikhvinka River, i.e. up to the water-parting line (457.3 km). For the lake form of lampreys from Lake Ladoga this way is 271.3 km long.

Earthworks on the Tikhvin water system were completed in 1805 [29], heralding the connection between the Baltic and the Caspian basin. After that, anadromous, lake adults (or resident adults from the Syas

and the Tikhvinka) could cross the water-parting line and start migrating along the Volga slope. Further downstream dispersal along the rivers of the Tikhvin water system and the Volga River was achieved by the larval stages. Primary dispersal in the form of downstream migration is shown for lampreys aged 0+ [51,52], while downstream migration of older ammocoetes has been repeatedly recorded in various rivers throughout the year. During downstream migrations lampreys can cover considerable distances (tens of kilometers) over a short period of time. This means that it could take as little as several decades for the species to disperse across the Upper Volga. Upstream dispersal into rivers such as the Saragozha, the Kamenka and the Tunoshonka could be performed both by the resident adults and by the larvae of the European river lamprey [53].

Thus, the mechanism employed by the European river lamprey for colonization of the Caspian basin was a combination of upstream and downstream migrations. At the first stage, the lampreys migrated upstream along the rivers of the Baltic basin until they reached the water-parting line. Reaching and crossing the water-parting line became possible owing to the anthropogenic interference: the construction of sluices on the rivers (allowing lampreys to navigate up the rapids) and on the water-parting line, and the opening of shipways. The second stage was represented by mass, mostly downstream migrations along the rivers of the Caspian basin. Dispersal along the system of the Volga River was also a combination of upstream and downstream migrations in accordance with the migration cycle of the European river lamprey.

The European river lamprey – a species capable of long-term and long-distance migrations both upstream and downstream – could disperse across the Caspian basin along corridors of anthropogenic origin. Considerable morphological diversity of its local populations reported in our study provides evidence for this hypothesis. The diversity of lampreys from the Vysochinsky Stream, the Saragozha River and the Kamenka River is probably associated with the fact these young (not more than 60 generations) local populations formed from a handful of pioneering adults.

## Material And Methods

**Animals.** This study is based on the analysis of our own material: collections of lamprey larvae and adult lampreys during spawning as well as observations of the lamprey distribution in the Upper Volga (central European Russia, Fig. 1). All animals were captured and taken from the environment in accordance with guidelines approved by Institute of Ecology and Evolution, Russian Academy of Sciences. The lamprey larvae in all the rivers were caught in shallow areas with the help of a Kinalev net (8-mm rebar frame 50×70 cm with knotless del 80 cm depth, mesh size 2.5 mm). Captured lampreys were immobilized with MS-222 solution (50 mg/l), photographed, and placed in 4% isotonic solution of formaldehyde. The material was deposited in the collection of the Laboratory for Behaviour of Lower Vertebrates of Institute of Ecology and Evolution (deposition numbers: sample from the Vysochinsky Stream and its tributary, IEE 190515001; sample from the Saragozha River, IEE 19051502; sample from the Kamenka River, IEE 18051501; sample from the Tunoshonka River, IEE 14070501; sample from the Malaya Dubenka River, IEE 20063001, IEE 20063002; sample from the Malaya Kosha River, IEE 12073001; sample from the

Bolshaya Kosha River, IEE 13051202; sample from the Volga River, IEE 13070002). Data from the fish collection of the Zoological Institute of the Russian Academy of Sciences (St Petersburg, ZISP) were also used.

Spawning of lampreys was documented in a nameless tributary of the Vysochinsky Stream, in the Saragozha River on May, 15 2019 and in the Kamenka River on May, 15 2018 (Fig. 2). Collections and observations of lamprey larvae were made in the Tunoshonka River on July, 05 2014, in the Vyazma River on June, 13 2014, and in the Malaya Dubenka River on June, 30 2020. According to communications of the researchers from the Laboratory for Behaviour of Lower Vertebrates of A.N. Severtsov Institute of Ecology and Evolution (B.P. Legky, D.Yu. Nazarov, M.P. Ostrovsky, I.K. Popova), adults of the resident form of the European river lamprey were observed to spawn in different years in the Shutinka Stream, the Malaya Kosha River and the Bolshaya Kosha River, which are the tributaries of the Volga in the upper reaches. A resident adult was also caught in the Volga near the town of Konakovo.

Habitats in the Upper Volga basin. The Vysochinsky Stream and its nameless tributary are, respectively, the 5<sup>th</sup> and the 6<sup>th</sup> order tributaries of the Rybinsk Reservoir. These streams connect with the reservoir through Lake Kremino and the rivers Kremennitsa, Saragozha and Mologa. The Vysochinsky Stream is 12.3 km long, while its nameless tributary is 8.3 km long. Both begin in boggy areas. The Vysochinsky Stream is 5 m wide, its tributary is 1–2 m wide, and their depth is 10–30 cm. The substrate is pebbly gravel with a little sand and few particles up to 30–40 cm in diameter. Upstream and downstream from the spawning area the bottom is clay-covered, with organic debris. Silty grounds suitable for the lamprey larvae are nearly absent. The water is transparent and water temperature at the time of this study was 11°C.

The Saragozha River is a 2<sup>rd</sup> order tributary of the Rybinsk Reservoir. It flows from Lake Pavlovskoe, and is 53 km long. Together with the Vysochinsky Stream, the Saragozha belongs to a vast fluvio-lacustrine system, which also includes Lake Ilovets, the Ilovets River, Lake Zastizhskoe, Lake Obretinskoe, the Zhelezinka River, etc. The width of the examined section of the river is ~15 m, the depth is 0.5–1 m, with pools up to 2 m deep. The bottom is sandy, with occasional small pebbly areas. It was in these pebbly areas that the lampreys were observed to spawn. The water has a light brownish (peaty) color and water temperature was 12°C at the time of sampling.

The Kamenka River is the 2<sup>nd</sup> order tributary of the Rybinsk Reservoir. Its length is 14 km. The Kamenka River is a tributary of a large river, the Sit, into which it flows at a distance of 13 km from the reservoir. We examined a 2-km-long section of this river, situated at a distance of 1.25 km from the river mouth. At this location, the river is 10–12 m wide and depth varies from 30 cm to 1.8 m. The bottom is pebbly gravel, with numerous ratchels and boulders. Small and shallow inwashes of fallen leaves were noted in some places. The water has a light brownish (peaty) color and water temperature was 17°C at the time of sampling.

The Tunoshonka River (51 km long) is a first-order tributary of the Volga River (Gorky Reservoir). It was examined in the lower reaches, where it is 30 m wide or even wider. Shallow areas with a depth of 20–50 cm alternate with deeper pools ( $\geq 2$  m). Substrate is silty-sandy, with middle-sized pebble in some places. The Vyazma River, which is a 2<sup>nd</sup>-order tributary of the Volga River (Ivankovo Reservoir), is 43 km long. Near its mouth the Vyazma is 5–10 m wide and 20–50 cm deep. The bottom is smooth and stony. The Malaya Dubenka River (14 km long) drains into the Upper Volga Reservoir (Volgo lake). The lowermost 2–2.5 km of the river is a bay of the lake with no current, silty substrate, and abundant aquatic vegetation. Lamprey larvae were caught in the middle section where there was sandy/ pebble substrate, 0.5 m water depth and channel width of ~5m.

Cartography, meta- and digital data. Distances concerning the water bodies of the Baltic basin and the tributaries of the Upper Volga given in this paper were measured based on satellite images or topographic maps and are as near as possible to the actual ones. In the few instances when the distances were taken from the literature, the references are given.

Coastline on the figures in this study is based on SHP Small scale data [54]. Layer of the marine basins is developed on database Hydrosheds [55] and Interactive database of the World's river basins [56], water features established by the use of database HydroSheds [57], analysis of topographic maps and satellite imagery of Google Maps and Google Earth. Species area outlined on [1,58–62]. The historical map representing the state of the discussed water systems is created on the material of the historical GIS for the spatial history of the Russian Empire by Kelly O'Neill "Canvas Empire" [63], on Kashin [26], Shirokova et al. [28,29], and *Otsenka kachestva vody...* [27].

## Declarations

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## Conflicts of interest/Competing interests

Authors declare no conflict of interest

## Availability of data and material (data transparency)

Samples designated IEE are stored in collection of lampreys in Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russia. Samples designated ZISP are stored in the fish collection of the Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia.

Distances measured based on satellite images of public sources Google Earth and Google Maps.

# Authors' contributions

AOZ: Field works, maps analysis, historical data analysis, MS

AVKu: specimens' morphology, description, figures, MS

AVKo: maps analysis, distances, figures, MS

NVP: statistics, MS

DSP: MS

All authors gave final approval for publication.

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## Figures

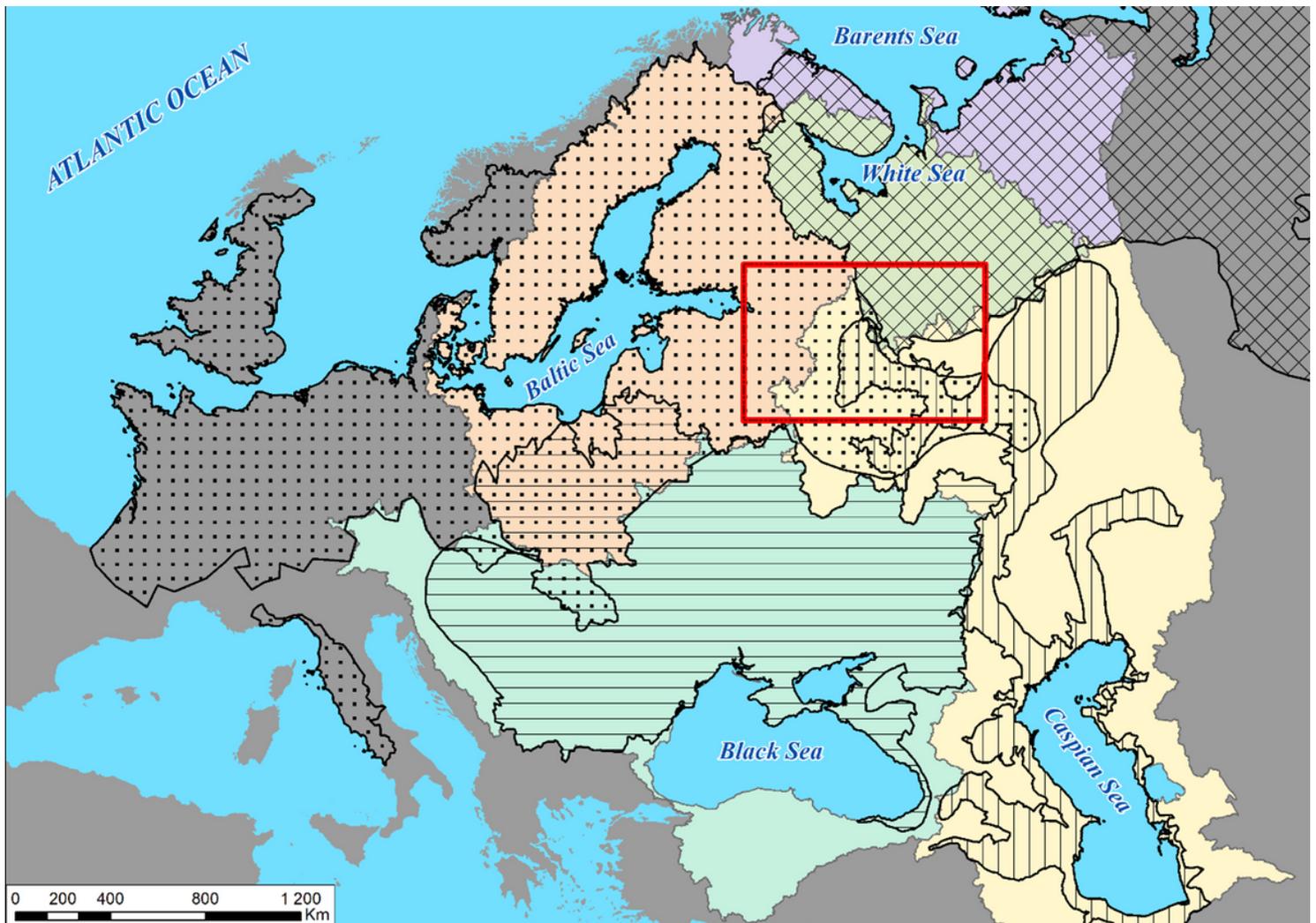


Figure 1

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**Figure 2**

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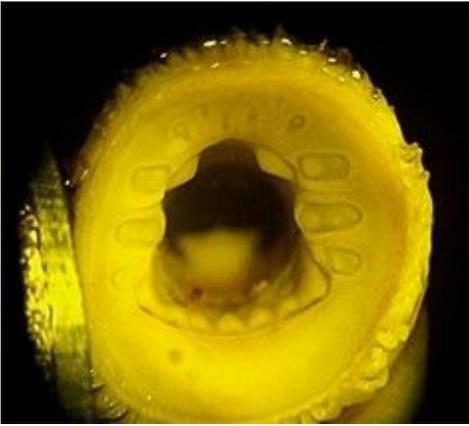


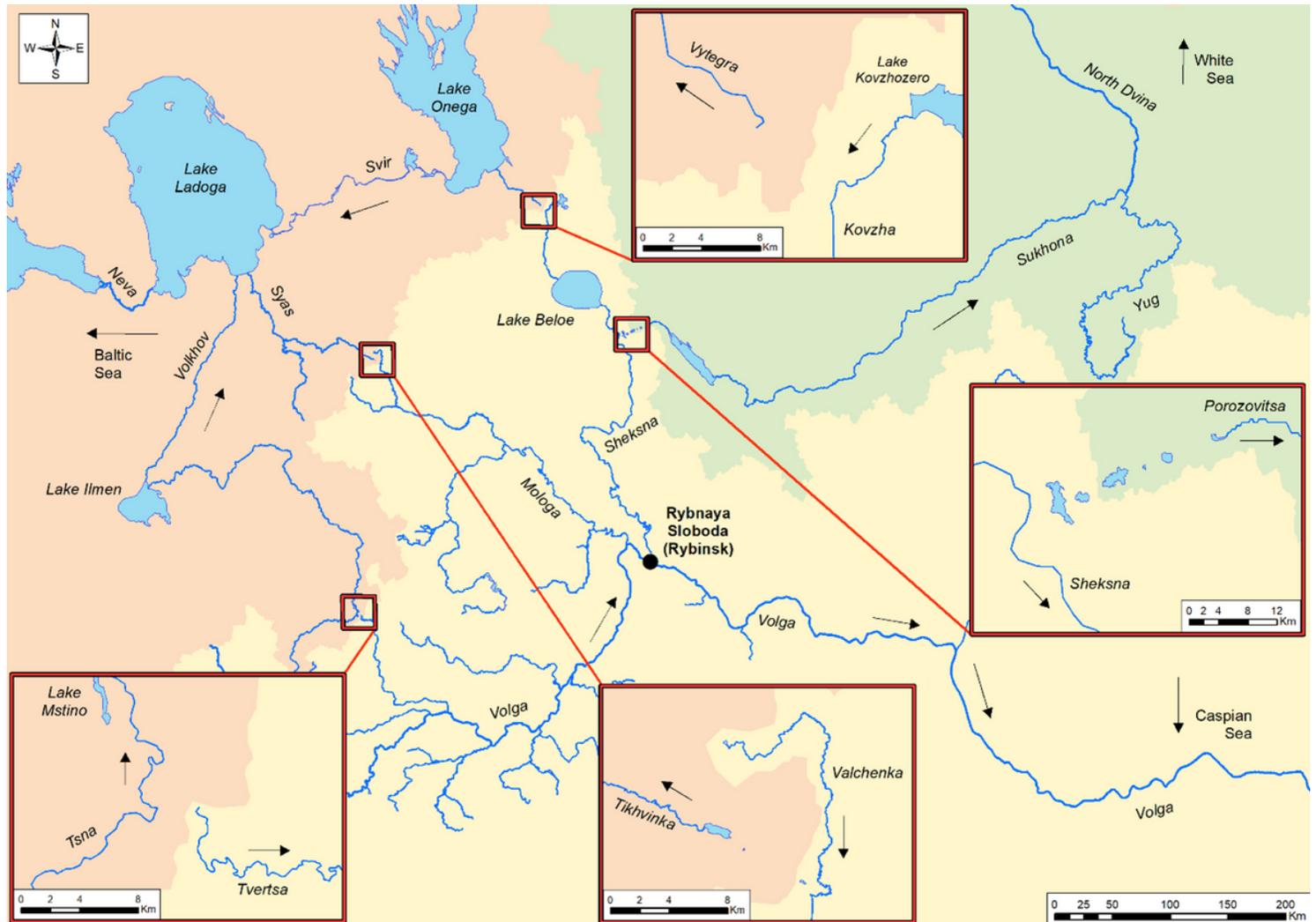
Figure 3

Oral disc of the European river lamprey *Lampetra fluviatilis* (Kamenka River)



Figure 4

External appearance of adults of the European river lamprey *Lampetra fluviatilis* from the Vysochinsky Stream (a), Saragozha (b), and Kamenka (c) rivers



**Figure 5**

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