

Review

Aliens and Returnees: Review of Neobiotic Species of Freshwater Mollusks in Siberia from the Kazakhstan Steppe to the Arctic Tundra

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Abstract: (1) This article reviews all available information on the species composition, current distribution, and origins of the neobiotic (non-indigenous and restoring the lost range) freshwater mollusks in Siberia. (2) An extensive literary search has been carried out, and virtually all existing publications of recent decades on the findings of freshwater mollusk species new to Siberia were taken into account. We examined extensive malacological collections of some of Russia's and Kazakhstan's scientific organizations. The core of the examined material is our own observations and collections made in various parts of Siberia and adjacent areas. (3) An annotated checklist of neobiotic species of mollusks reliably recorded in Siberia is presented, and probable mechanisms and "corridors" of infiltration of these species into the region are discussed. Most of the discovered snail species belong to a group popular among aquarists, and their source of introduction is obvious. Another large portion of species infiltrate into the region with the development of fish farming. A classification of species of neobiotic freshwater mollusks of Siberia was proposed and a forecast was made for changes in the Siberian freshwater malacofauna for the coming decades. (4) In our opinion, at present it is possible to accept the newest stage in the genesis of the freshwater malacofauna of Siberia, occurring in conditions specific to the Anthropocene.

Keywords: Mollusca; continental water bodies; non-indigenous species; range restoration; dispersal; Eurasia



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1. Introduction

Until relatively recently, 10–15 years ago, the problem of biological invasions of freshwater mollusks in Siberia was not considered a relevant research topic. Until the beginning of this century, there were practically no publications on this issue. The freshwater malacofauna of the Siberian subcontinent was considered free of alien mollusk species. Two circumstances contributed to this: (1) the almost complete isolation of Siberian water systems from the adjacent river basins, which could serve as a source of non-indigenous species; and (2) the severity of the climate of Siberia, which makes this territory unsuitable for the introduction of such species of mollusks, most of which originate from either tropical regions, or areas of temperate latitudes with a milder climate than Siberia.

Our understanding started to change in the first decade of the 21st century, when the first publications about the discovery of mollusk species new to the region in the water bodies of Siberia began to appear in the scientific literature. These species began to be found in modified water bodies: cooling reservoirs [1–3], long known as “foci” of aquatic invasions in northern latitudes; large artificial reservoirs (the Novosibirsk reservoir [4,5], the Bukhtarma reservoir [6]), and also natural watercourses [7]. The accumulating volume of information on this issue prompted Vinarski et al. [8] to prepare a review paper summarizing all information about alien species of mollusks in Western Siberia, in which the authors also discussed climate and other features that prevent the introductions and invasions of non-indigenous species. Eastern Siberia was left out of consideration by the authors of the review, although information about the presence of non-indigenous mollusks there also appeared in the scientific literature [9,10].

Almost eight years have passed since the publication of the review by Vinarski et al. [8]. Since then, the volume of new information about aquatic mollusk species new to Siberia has grown significantly. In addition to the registration of new species in the malacofauna of Siberia and new localities of previously known species [11–17], there have been works devoted to the ecology of recent migrants in Siberian reservoirs [5,18–21], as well as publications interpreting the problem from a broader point of view, in particular, raising the question of whether all newly registered species must be considered as “real” aliens, or whether one should rather speak about restoring a part of the original range once lost by some of these species, not about introductions and/or invasions in the commonly accepted sense of these terms [16,22].

In this context, the definition of the term “neobiotic mollusk” may be as follows. It is a molluscan species not registered in Siberia until the historical epoch or not found in a given area earlier, despite extensive faunal research, and registered as a new by the current generation of malacologists (i.e., within the last 15–20 years). So, it is believed to have recently settled in this area. As neobiotic mollusks, we consider both non-indigenous species (we also use the equivalent terms, “non-native species”, “alien species”, and “exotic species”) and species that lived in Siberia before the Pliocene-Pleistocene glaciations that are currently restoring their ranges.

This article aims at the synthesis of information on this issue, with consideration of the entire territory of Siberia, and not just its western part, as was done by Vinarski et al. [8]. Siberia is considered by us as a part of Northern Asia located within the basins of rivers flowing into the Arctic Ocean, the largest of which are the basins of the Ob’ (with the Irtysh), Taz, Yenisei, Lena, Yana, Indigirka, and Kolyma rivers. With regard to administrative and political borders, the predominant part of the territory of Siberia belongs to the Russian Federation, and only a relatively small area covering the upper reaches of the Irtysh basin belongs to the territory of the Republic of Kazakhstan. The Yenisei River divides this vast territory into two large parts, traditionally designated as Western Siberia and Eastern Siberia. The territory of the Russian Far East, which is also sometimes referred to as Siberia (in a broad sense), is not considered by us, nor those parts of northwestern China, where the sources of the Irtysh River (the so-called Black Irtysh) are situated. These regions have their own relief, climate, ecological, and economic features, and history of the formation of water bodies and aquatic malacofauna, so they deserve distinct consideration.

We present an annotated checklist of neobiotic species of mollusks reliably recorded in the territory of Western and Eastern Siberia, consider the likely mechanisms and “corridors” of infiltration of these species into the territory of Siberia, and discuss the possible revision of the “non-indigenous” status for some of these recent migrants.

Since the situation with molluscan migrations in the freshwater systems of Siberia is developing rapidly and dynamically, we consider this work only as a preliminary synthesis that allows us to outline the current state-of-the-art in this field of research, and do not pretend to a complete and final resolution of all the topics discussed in this article.

2. Material and Methods

The authors of this paper have studied the neobiotic component of the freshwater fauna of Siberia since early 2000s. The majority of available information on this subject is that obtained during our own research. Thus, the core of the examined material is our own observations and collections made in various parts and drainage basins of Siberia and some adjacent areas (the Urals, Eastern Kazakhstan). The mollusks, both aboriginal and non-native, were collected during our fieldwork following the standard protocols described in the literature [23–26]. In addition, we examined extensive malacological collections of some scientific and educational institutes: the Zoological Institute of the Russian Academy of Sciences, the Laboratory of Macroecology & Biogeography of Invertebrates, St. Petersburg State University (St. Petersburg), the Museum of the Institute of Plant & Animal Ecology, the Ural Branch of the Russian Academy of Sciences (Yekaterinburg), the Zoological Museum of the Institute of Biology, Tyumen State University (Tyumen), and Institute of Zoology of the Republic of Kazakhstan (Almaty).

An extensive literary search was carried out during this research, and virtually all existing publications of recent decades on the findings of freshwater mollusk species new to Siberia were taken into account. References are provided throughout the article.

The identification of collected snails and bivalves was carried out with the use of recent identification keys and manuals [24–28]. The nomenclature of the species and their taxonomic position are given mainly after the Vinarski & Kantor [29] catalog, with corrections, when relevant, after MolluscaBase [30].

The map (Figure 1) was developed by us using QGIS software (Available online: <https://qgis.org/>; accessed on 16 January 2023) with a topographic base from Natural Earth Free Vector and Raster Map Data (Available online: <https://www.naturalearthdata.com/>; accessed on 16 January 2023).

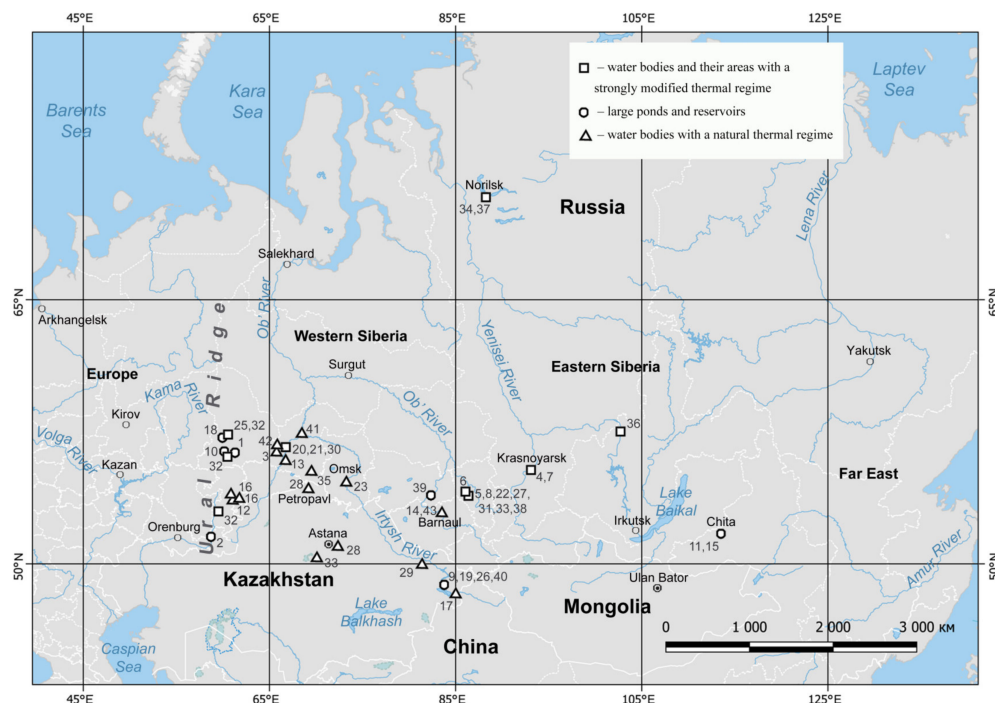


Figure 1. Map of neobiotic freshwater species of Mollusca first occurrences in Siberia. Numbers indicate the localities, which correspond to those in Table 1.

3. Results

Species Composition and Current Distribution of Neobiotic Mollusks of Siberia

Table 1 contains an annotated list of neobiotic mollusks species registered within the borders of Siberia. In total, since 1997, 16 neobiotic species of mollusks (six bivalves and ten

snails) have been registered from Siberia. The bivalves belong to two families, Unionidae and Dreissenidae, whereas the gastropods are members of seven families (Ampullariidae, Lithoglyphidae, Physidae, Planorbidae, Thiariidae, Valvatidae, and Viviparidae).

All bivalve species represent taxa whose native ranges are situated in the temperate and (*Sinanodonta*) subtropical latitudes of Eurasia, whereas, among snails, five alien species of Nearctic (*Ferrissia californica*, *Helisoma anceps*, *Physella acuta*, *Planorbella duryi*) or even Neotropical (*Pomacea canaliculata*) origin have been recorded; their native ranges are also located in the New World. A single species, *Melanoides tuberculata*, may be considered a member of the Old World tropical and subtropical biota. All the snail species listed above belong to a group of mollusks popular among aquarists, and their source of introduction to Siberian waters is obvious.

Most localities of the neobiotic mollusk species known so far are situated within the Ob' River basin (Western Siberia); see Figure 1. The water bodies of Eastern Siberia, on the other hand, remain almost free from neobiotic mollusks. Until 2021, only three localities of neobiotic freshwater mollusks were known from Eastern Siberia: Lake Kenon in Transbaikalia (*Unio pictorum*, *U. tumidus*), the Yenisei River near Krasnoyarsk City (*Sinanodonta lauta*, *S. woodiana*), and the Angara River near Ust'-Ilimsk Town (*Planorbella duryi*); see Table 1 and Figure 1. In July 2021, we discovered a new locality of non-indigenous freshwater snails situated in Noril'sk City, north of the Arctic Circle (GPS coordinates: N 69.3377, E 88.2052). Two species of snails, *Physella acuta* and *Planorbella* sp., were collected in large quantities from Lake Dolgoe (Figure 2B), which serves as a cooling reservoir for the Noril'sk Power Plant. The snails were also found in a warm stream inflowing the lake. The water temperature at the sampling site was +24–26 °C. Arguably, this locality is the northernmost locality of the non-indigenous snails in Siberia and, most probably, it can be considered the northernmost point of their distribution on the global scale. Before this finding, the northern limit of distribution of *Ph. acuta* was situated in the north of European Russia (Kola Peninsula, Lake Imandra; see [31]).

Table 1. A list of neobiotic species of freshwater Mollusca registered in Siberia, with remarks on their distribution and the dates of the first registration in the studied area.

Species	Native Range	Invasive Range	Locality No.	First Finds in Siberia and Neighboring Regions		Coordinates		References
				Date ¹	Site	Latitude	Longitude	
<i>Dreissena polymorpha</i> (Pallas, 1771)	Ponto-Caspian and Aral Sea regions; fresh waters of Balkan Peninsula [32–34]	North America, Europe, Middle and Southern Urals, Western Siberia [17,29]	1	2018	Beloyarsk Reservoir (Pyshma River basin, Middle Urals)	56.8421	61.2780	[35]
			2	2019	Irikliński Reservoir (Ural River basin, Southern Urals)	51.7768	58.7740	[36]
			3	2021	Pyshma River near Tyumen (Tura River basin, Western Siberia)	56.9739	65.3721	[17]
<i>Sinanodonta lauta</i> (E. von Martens, 1877)	Korea, Japan, and the coastal rivers of the South Primorye Region in Russia [37,38]	Ob', Volga and Yenisei basins in Russia, Lake Balkhash basin in Kazakhstan, Borneo [13,14,38,39]	4	2016	Yenisei River at the outlet of the warm water of Krasnoyarsk TPP (Arctic Ocean basin, Eastern Siberia)	55.9892	92.8699	[13]
			5	2019	Cooling reservoir and the channel of the Belovo Power Plant (Inya River basin, Western Siberia)	54.4125 54.4344	86.4643 86.4500	[39]
			6	2019	Inya River just below the Belovo Reservoir (Ob' River basin, Western Siberia)	54.4571	86.4311	[39]

Table 1. Cont.

Species	Native Range	Invasive Range	Locality No.	First Finds in Siberia and Neighboring Regions		Coordinates		References
				Date ¹	Site	Latitude	Longitude	
<i>Sinanodontia woodiana</i> (I. Lea, 1834)	Indochina, China, Korea, and the Amur Basin, Russia [37]	Europe, North America, Central America and Caribbean, Japan, Indonesia, Philippines, Southeast Asia, Central Asia including Kazakhstan and Uzbekistan, Siberia [14,39]	7	2016	Yenisei River at the outlet of the warm water of Krasnoyarsk TPP (Arctic Ocean basin, Eastern Siberia)	55.9892	92.8699	[13]
			8	2019	Cooling reservoir and the channel of the Belovo Power Plant (Inya River basin, Western Siberia)	54.4125 54.4344	86.4643 86.4500	[39]
			9	1997	Bukhtarma Reservoir (Irtysh River basin, Eastern Kazakhstan) ²	49.0259	83.9095	[6,11]
<i>Unio pictorum</i> (Linnaeus, 1758)	Northern, Eastern and Western Europe, European Russia, Western Urals [37]	Middle and Southern Urals, southwest of Western Siberia, upper reaches of the Irtysh River basin (Eastern Kazakhstan) ² , Lake Kenon (Amur Basin, Transbaikalia) [11,16,37]	10	1998	Lake Isetskoye and Verkh-Isetsy Pond (Iset' River basin, Middle Urals)	57.0167 56.8652	60.4667 60.5000	[16,27]
			11	2001	Lake Kenon (Amur River basin, Transbaikalia)	52.0486	113.3726	[9,40]
			12	2002	Uy River in Chelyabinsk region (Tobol River basin, Southern Urals)	54.1167	61.1000	[16]
			13	2007	Tobol River in Tyumen region (Irtysh River basin, Western Siberia)	56.5175	66.3948	[41]
			14	1829	? Barnaul (probably Black Irtysh River basin, see [16])	53.3728?	83.7318?	[16,42]
<i>U. tumidus</i> Philipsson in Retzius, 1788	Northern, Eastern and Western Europe, European Russia, Western Urals, Ural River in Russia and Kazakhstan, upper reaches of the Irtysh River (Eastern Kazakhstan) [16,37]	Southern Urals, extreme southwest of Western Siberia, upper reaches of the Irtysh River (Eastern Kazakhstan), Lake Kenon (Amur Basin, Transbaikalia) [16,37]	15	2001	Lake Kenon (Amur River basin, Transbaikalia)	52.0486	113.3726	[9,40]
			16	2005	Uvel'ka River and Uy River in Chelyabinsk region (Tobol River basin, Southern Urals)	54.0884 54.1000	61.5069 61.1333	[7,16]
			17	2018	Black Irtysh River in East-Kazakhstan region (Irtysh River basin, Eastern Kazakhstan)	47.9000	84.9000	[16,37]
<i>U. crassus</i> Philipsson in Retzius, 1788	Northern, Eastern and Western Europe, European Russia (water bodies of Baltic, Black, Azov, and Caspian Sea drainage basins), Western Urals, Ural River in Russia and Kazakhstan [37]	Unknown ³	18	2006	Pond of Tagil River (Tura River basin, Middle Urals)	57.8000	60.0167	[16]
<i>Borysthemia naticina</i> (Menke, 1845)	Eastern Central Europe, Eastern Europe and Turkey [29]	Southwest of Western Siberia, upper reaches of the Irtysh River (Eastern Kazakhstan) [1,11]	19	2004? 2009	Bukhtarma Reservoir (Irtysh River basin, Eastern Kazakhstan)	49.0259	83.9095	[6,11,18,43]
			20	2005	Cooling reservoir of the Tyumen Heat and Power Plant No. 1 (Tura River basin, Western Siberia)	57.1500	65.6241	[1,18]
<i>Ferrissia californica</i> (Rowell, 1863)	North America: United States, southern Ontario, southern Quebec, southwest of British Columbia [29]	Many European countries, Israel, Syria and south-eastern Asia, southern part of the Western Siberia, Transcaucasia and Central Asia [29]	21	2005	Cooling reservoir of the Tyumen Heat and Power Plant No. 1 (Tura River basin, Western Siberia)	57.1500	65.6241	[1,18]
			22	2010	Cooling reservoir of the Belovo Power Plant (Inya River basin, Western Siberia)	54.4328	86.4647	[3,18]

Table 1. Cont.

Species	Native Range	Invasive Range	Locality No.	First Finds in Siberia and Neighboring Regions		Coordinates		References
				Date ¹	Site	Latitude	Longitude	
<i>Helisoma anceps</i> (Menke, 1830)	North America from Mexico to central Canada [29]	Europe, Middle Urals and Western Siberia [29]	23	1999	Riverbank drifts at Omsk (Irtys River basin, Western Siberia)	54.9912	73.3642	[8,28]
			24	2010	Cooling reservoir of the Belovo Power Plant (Inya River basin, Western Siberia)	54.4328	86.4647	[3,18]
			25	2013	Cooling reservoirs around Nizhny Tagil (Tura River basin, Middle Urals)	57.9105	59.9726	[28]
<i>Lithoglyphus naticoides</i> (C. Pfeiffer, 1828)	Ponto-Azov basin: rivers northwest of the Black Sea [44]	Eastern and Central Europe, European Russia, upper reaches of the Irtys River (Eastern Kazakhstan) [11,29,44]	26	1998	Bukhtarma Reservoir (Irtys River basin, Eastern Kazakhstan)	49.0259	83.9095	[6,11,18]
<i>Melanoides tuberculata</i> (O. F. Müller, 1774)	Africa to Southeast Asia [29]	Australia and New Zealand, North America, South America, Europe and Azores, Western Siberia [29,45–48]	27	2010	Cooling reservoir of the Belovo Power Plant (Inya River basin, Western Siberia)	54.4328	86.4647	[3,18]
			28	1969	Floodplain waterbodies and rivers near Petropavl and Astana (Ishim River basin, Northern Kazakhstan)	54.8765 51.1422	69.1195 71.4047	[49–51]
<i>Physella acuta</i> (Draparnaud, 1805)	North America (Canada, the Great Lakes region and Dakota) [29]	Europe, Asia, Africa, Australia, and South America (the Titicaca Lake), European Russia, Western Siberia and the Russian Far East [29]	29	1979	Upper reaches of the Irtys River basin (East Kazakhstan)	49.9533	82.5941	[52]
			30	2005	Cooling reservoir of the Tyumen Heat and Power Plant No. 1 (Tura River basin, Western Siberia)	57.1500	65.6241	[1,18]
			31	2010	Cooling reservoir of the Belovo Power Plant (Inya River basin, Western Siberia)	54.4328	86.4647	[3,18]
			32	2013	Cooling reservoirs and ponds near Nizhny Tagil, Yekaterinburg and Magnitogorsk (Irtys River and Ural River basins, Southern and Middle Urals)	57.9105 56.8421 53.4075	59.9726 61.2780 58.9784	[28]
			33	2013	Water bodies of the Korgalzhyn Reserve (Ishim River basin and basin of the endorheic lake Tengiz, Northern and Central Kazakhstan)	50.4333	69.1889	[8]
			34	2021	Lake Dolgoye and warm stream inflowing the lake in Noril'sk (Pyasina River basin, Eastern Siberia)	69.3377	88.2052	This study
			35	2022	Swampy oxbow of the Ishim River (Irtys River basin, Western Siberia)	56.0620	69.4772	This study
<i>Planorbella duryi</i> (Wetherby, 1879)	Florida in North America [29]	South America, Hawaii, Northern, Eastern and South Africa, Europe, Northern coast of the Black Sea, Angara River basin [29]	36	2010	Heated stream running from the Ust-Ilimsk Pulp and Paper Plant (Angara River basin, Eastern Siberia)	58.0323	102.7512	[10]
<i>Planorbella</i> sp.	North and South America, northeastern Asia [29]	Widely distributed throughout the world (as aquarium animals, often end up in natural habitats) [29]	37	2021	Lake Dolgoye in Noril'sk (Pyasina River basin, Eastern Siberia)	69.3377	88.2052	This study

Table 1. Cont.

Species	Native Range	Invasive Range	Locality No.	First Finds in Siberia and Neighboring Regions		Coordinates		References
				Date ¹	Site	Latitude	Longitude	
<i>Pomacea canaliculata</i> (Lamarck, 1822)	Southern South America (lower del Plata basin) [53]	South America (other parts), North America, Europe, Asia and many other regions, including Western Siberia [2,53]	38	2002	Cooling reservoir of the Belovo Power Plant (Inya River basin, Western Siberia)	54.4328	86.4647	[2,54]
			39	1990s	Novosibirsk Reservoir (Ob' River basin, Western Siberia)	54.7344	82.8416	[4,5,8]
<i>Viviparus viviparus</i> (Linnaeus, 1758)	Europe except for extreme North and South, Western Transcaucasia [29]	Crimean Peninsula, Western Siberia, Eastern Kazakhstan [19,29]	40	1994	Bukhtarma Reservoir (Irtysh River basin, Eastern Kazakhstan)	49.0259	83.9095	[5,6,11,18]
			41	2009	Oxbow lake near Tobol'sk (Irtysh River basin, Western Siberia)	58.2038	68.2463	[8]
			42	2015	Tura River at Tyumen (Tobol River basin, Western Siberia)	57.1563	65.5395	[12]
			43	2022	Ob' River at Barnaul (Arctic Ocean basin, Western Siberia)	53.3728	83.7318	This study

¹—the dates of the first finds or the dates of the first publications about them are indicated (then they coincide with earlier one in the last column); ²—finds of *U. pictorum* in the upper Irtysh River basin need to be checked, we have no collections or photos of this species from this region, all our finds belong to the species *U. tumidus*; ³—record of *U. crassus* from Lake Kenon [40] was based on erroneous identification and belong to *U. tumidus* see [37].



Figure 2. Some habitats of neobiotic freshwater species of Mollusca in Siberia. (A) The Bukhtarma Reservoir; (B) Lake Dolgoye, Noril'sk City; (C) An oxbow lake of the Irtysh River near Tobol'sk Town; (D) An oxbow lake of the Ishim River south of Ishim Town. Photos: Maxim V. Vinarski.

So far, *Physella acuta* is the most widespread exotic snail species in the freshwater systems of Siberia, known from several points situated in various places of the region. Its patchy distribution is explained by the apparent inability of this species to live in water bodies with an unaltered thermal regime [28,55,56]. On the other hand, reports of findings of this mollusk in natural habitats have occasionally been published since

the late 1960s [8,49,51,52,56]. All these findings were made in the warmest southwestern part of Siberia, whose climatic conditions allow the snails to survive and reproduce. The latest of such findings was made by us in July of 2022, in a swampy oxbow of the Ishim River south of Ishim Town (GPS coordinates: 56.0620 N 69.4772 E) (see Figure 2D). Only a single specimen of *Ph. acuta* was collected from this oxbow, along with other (aboriginal) species of snails. The rarity of these finds underlines the fact that no stable and numerous populations of this snail have been established outside artificially heated habitats on the territory of Siberia so far.

Of the neobiotic bivalve taxa, the most widespread in Siberia are representatives of the genus *Unio*, known from both the western and the eastern part of the region (see Table 1). The history of their appearance and dispersal in Siberia is best documented and well characterizes the complexity and multi-vector ways of distribution. It was assumed that, in the territory of Siberia, mollusks of this genus, once very widespread, disappeared in the Pleistocene [57,58]. Despite this, there were a few references in the literature to the presence of *Unio* in the modern period in Western Siberia [42,59]; summarized in [16]. Since the end of the last century, different species of the genus have been registered both in the upper reaches of the Irtysh basin (Bukhtarma reservoir), and at the junction of the Irtysh and Volga-Kama basins in the Transuralian region [7,27] as well as in Transbaikalia (Lake Kenon). Some of these findings can be explained by human participation in the dispersal of mollusks, and some by the eastward natural expansion of the range [7]. Finally, molecular genetic studies of recent years have shown that some *Unio* are not “aliens” at all, since they disperse from the refugium located in the upper reaches of the Irtysh above Lake Zaisan [16]. Probably, this explains the discovery of *Unio* shells in the Altai region made in 1829 by the participants of the Siberian expedition of Alexander von Humboldt [16,42,60].

Currently, according to our information, mollusks of the genus *Unio*, primarily *U. pictorum*, occur widely in the middle course of the Irtysh River. According to the results of a hydrobiological survey of the Irtysh riverbed within the boundaries of the Russian Federation, conducted in 2022, these bivalves have become quite common in this river near Omsk, as well as upstream, near the border with Kazakhstan (L. Yanygina, unpublished data). In the same year, specimens of *Unio* were collected in the Om’ River (a tributary of the Irtysh) above the city of Omsk (S.I. Andreeva, pers. comm.). Previously, these bivalves were found in the lower reaches of the Tobol River near Tobolsk Town [8], and, in 2021 and 2022, in the tributaries of the Irtysh River flowing from Ural Mountains (Tura, Pyshma, and Iset’ rivers; unpublished data of E. Babushkin & M. Vinarski). Thus, there is reason to believe that the genus *Unio* has practically restored the previously lost part of its range, once located on the territory of the Irtysh River basin.

4. Discussion

4.1. An Analysis of Neobiotic Malacofauna of Siberia

During the Tertiary and Quaternary periods, the territory of Siberia was an arena for large-scale migrations of various species of freshwater animals and even entire faunal complexes. Many groups of mollusks were actively involved in these migrations and faunogenetic processes [58,61–64]. The recent malacofauna of freshwaters of Siberia was formed as a result of climatic perturbations of the Quaternary period. It is considered to be depleted, both at the species and at the generic level, which is explained by the elimination of a large number of taxa that inhabited this territory in the Late Tertiary and Quaternary (during the warmer interglacial stages) time [58,61,65,66].

At present, one can accept the newest stage in the genesis of the freshwater malacofauna of Siberia, occurring in conditions specific to the Anthropocene. First of all, this refers to the factor of human activity, which causes the infiltration of exotic species of tropical or even extra-Eurasian origin into this territory, as well as the impact of global changes on the climate of Siberia [67–69], which probably contribute to the restoration of the North Asian part of the range lost in the Quaternary by some species of mollusks. From this point of view, not all the species presented in Table 1 can be considered non-indigenous in the full

sense of the term. Further genetic studies could clarify this issue [70]. We propose to divide all the species of neobiotic mollusks of Siberia into two groups, of which only one can be called “true aliens”. (Figure 3, Table 2). We are talking about species and genera that have never lived on the territory of Siberia before and have penetrated here solely with the help of humans, most often as a result of unintentional introduction. Natural dispersal has to be excluded, apparently, even for the *Dreissena polymorpha* [17], although this species is a native inhabitant of the Volga basin, geographically adjacent to the Ob’-Irtysh basin.

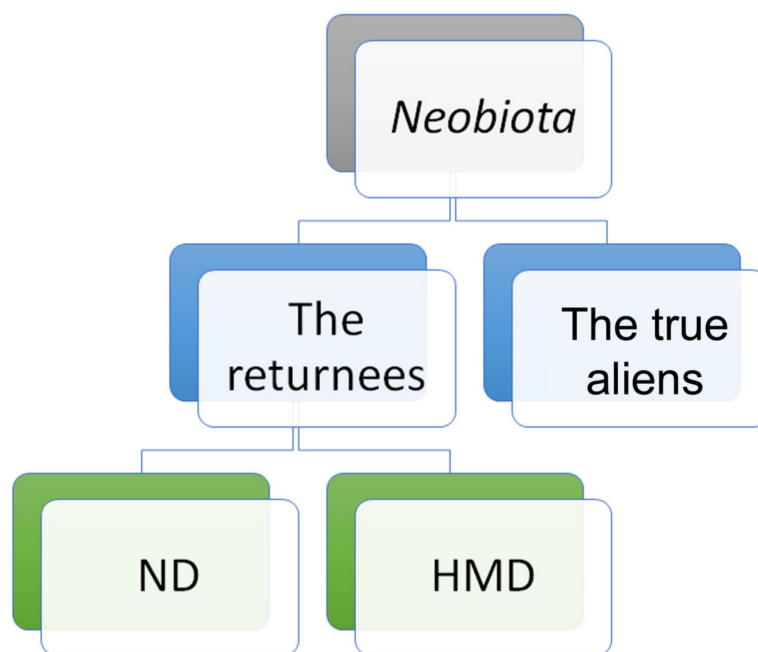


Figure 3. A classification scheme for the newly registered in the fauna of Siberia species of freshwater Mollusca. ND—natural dispersal. HMD—human-mediated dispersal.

Table 2. Classification of species of neobiotic freshwater mollusks in Siberia according to their status in the region*.

True Aliens or Non-Indigenous		The Returnees	
AT	FF	ND	HMD
<i>Ferrissia californica</i> , <i>Melanoides tuberculata</i> , <i>Physella acuta</i> , <i>Helisoma anceps</i> , <i>Planorbella duryi</i> , <i>Planorbella</i> sp., <i>Pomacea canaliculata</i>	<i>Dreissena polymorpha</i> (?), <i>Sinanodonta lauta</i> , <i>S. woodiana</i>	<i>Unio crassus</i> , <i>U.</i> <i>pictorum</i> (partly), <i>U.</i> <i>tumidus</i> (partly)	<i>Borysthenia naticina</i> , <i>Lithoglyphus naticoides</i> , <i>Unio pictorum</i> (partly), <i>U. tumidus</i> (partly), <i>Viviparus viviparus</i>

* Abbreviations: AT—dispersal through aquarium trade; FF—dispersal connected to fish farm stocking; ND—natural dispersal; HMD—human-mediated dispersal.

The second group of neobiotic mollusk species can be considered as “the returnees” currently restoring the North Asian part of their historical range. This can occur both by natural dispersal from the East European water bodies or from some southern refugia, as in the case of the genus *Unio* [7,16,17].

For example, several mollusk species have been recorded in the Ob’ basin, the modern (pre-Anthropocene) range of which is limited to the river basins of Europe. These are *Borysthenia naticina*, *Lithoglyphus naticoides*, *Unio crassus*, and *Viviparus viviparus*. Paleontological data show that all these mollusks inhabited the Ob’ basin until the middle of the Pleistocene and presumably went extinct during the last (Sartan) glaciation, ca. 23,000–10,000 BP.

Modern climate warming creates favorable conditions for the restoration of their area lost during the cooling of the climate [58,61,65,67–69].

The natural and especially human-mediated dispersal of such returnees has the potential to create new invasive species if successful introductions grow out of control and cause ecologic or economic damage. Perhaps the greatest danger is not the returnees themselves, who previously lived in the water bodies of Siberia, but the potential invasions by the accompanying species of aquatic animals, not only mollusks. In the literature on biological invasions, it is customary to define such invasions as intracontinental, contrasting them with the intercontinental ones. The intensity of intracontinental migrations is underestimated, and the number of known instances of these migrations and invasions will likely grow significantly after the widespread introduction of genetic research into environmental monitoring practice [70]. At the same time, such intracontinental migrants can constitute a significant share of the neobiotic species richness and have a negative impact on the recipient ecosystems, becoming invaders. For example, in North America, the proportion of intracontinental invasions averages 14.7% of all registered cases, while in some taxonomic groups this proportion exceeds 50% [71].

In general, the appearance of 75% of neobiotic species in the basins of the Danube and Volga, 57% of species in the basin of the Dnieper River, and 100% of all neobiotic species in the basin of the Ob' River is associated with intracontinental migrations (Figure 4). (Note, this statistic excludes the exotic species not able to establish sustainable populations outside the artificially heated water bodies). The majority of these neobiotic species were represented in the fossil record of the recipient basins, which indicates that the analysis of the paleoarchives can become a useful tool in predicting the modern dispersal of aquatic animals and their invasion potential.

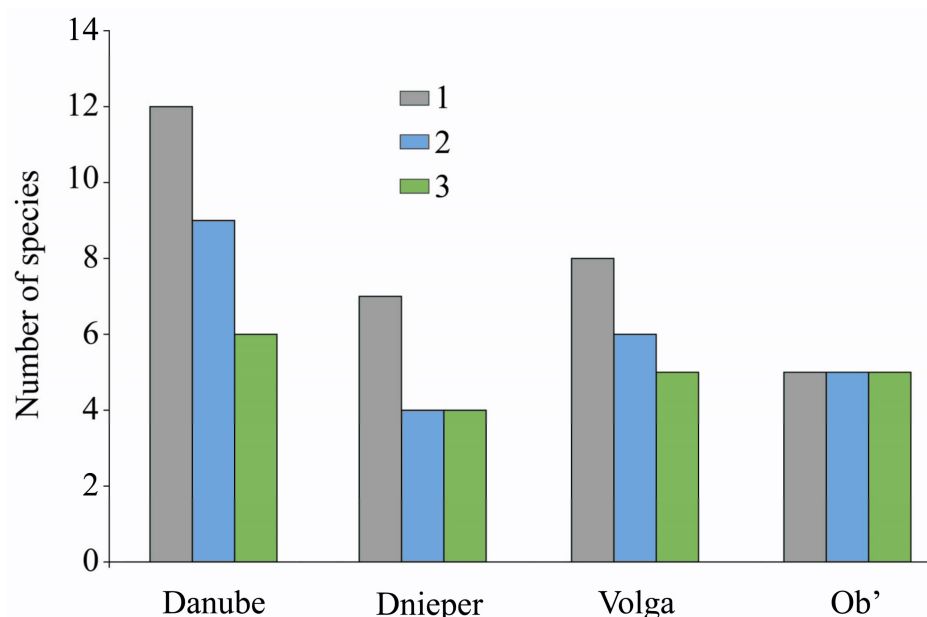


Figure 4. The significance of the intracontinental migrations of mollusks in the formation of the neobiotic malacofauna of some great river basins of Eurasia. 1—The total number of species of neobiotic mollusks registered in water bodies with the natural thermal regime; 2—The number of neobiotic mollusk species of Eurasian origin; 3—The number of neobiotic species of mollusks that inhabited this area in the Pleistocene according to paleolimnological data [72–74]. The numbers are taken from literary data surveyed during this research.

The earliest hotspot of intracontinental molluscan migrations in the territory of the Ob'-Irtys' basin was formed already in the 1990s. It is located in the Bukhtarma reservoir, on the territory of East Kazakhstan (Upper Irtys' basin; see Figure 2A). At least four neobiotic species of snails and bivalves (*Borysthenia naticina*, *Lithoglyphus naticoides*, *Unio*

pictorum, *Viviparus viviparus*) were recorded there for the first time (see Table 1). It is likely that *V. viviparus* entered the ecosystem of the Novosibirsk Reservoir on the Ob' River around the same time. Until now, these reservoirs are the centers of the origin of neobiotic mollusks in this basin: they are characterized not only by a higher species richness of the neobiotic malacofauna, but also by the maximum values of the frequency of occurrence and abundance of such species [19]. In recent years, a similar role has been played by numerous reservoirs located on the eastern macroslope of the Ural Ridge, where a number of non-indigenous species and returnees have already been registered (see Table 1). The functioning of reservoirs as foci of biodiversity of neobionts is mainly associated with the development of fish farms. Due to multi-purpose use, different conditions develop in different parts of the reservoirs; for example, in July 2022, near the discharge of warm water from the Reft Power Plant in the reservoir of the same name (Pyshma River basin, Middle Urals), we found a settlement of global invaders of the genus *Sinanodonta*, which were not previously found in the Irtysh River basin. Among the collected mollusks were very large specimens (shell length >20 cm), which possibly indicates the long-term presence of the mussel in the waterbody. We do not provide information about the find in Figure 1 and Table 1, since species identification based on morphological characters is practically impossible [13,14,37–39], and DNA barcoding data have not yet been obtained. The other parts of the same reservoir are relatively cold, with no *Sinanodonta* individuals found there.

A key issue in the biology of invasions is the search for the causes for the success of introduced species in their conquering of new habitats and regions. An important factor helping to understand these causes is the study of paleoarchives. Paleolimnological data are still used in a very limited way in invasion biology. As a rule, they are used to clarify the time of the beginning of the infiltration to a new territory by a new species [72], and usually data covering the last tens or hundreds of years are used for these purposes. The analysis of more ancient history, spanning tens of thousands and even millions of years, can open up new perspectives in understanding the factors determining the success of invasions and other types of range expansion. For example, analysis of paleolimnological data shows that representatives of all mollusk species naturalized in recent decades in the water bodies of Siberia lived here in the Pleistocene [61,73,74].

The human-mediated dispersal of freshwater mollusk species can significantly accelerate their return to their former habitats, the restoration of the lost parts of their range. The return of species can considerably transform modern aquatic ecosystems and negatively affect the economical use of inland water bodies. For example, the introduction of *Viviparus viviparus* into the Novosibirsk Reservoir is accompanied by an increase in the biomass of zoobenthos to 16 kg/m² due to the neobiotic species [75], which leads to rearrangement of the structure of macroinvertebrate communities, a decrease in their diversity and an increase in density [19]. Huge accumulations of mollusk biomass interfere with the operation of hydraulic structures, and dead mollusks and their empty shells disrupt the recreational use of water reservoirs [75].

From one of the standpoints of theoretical ecology, it can be expected that the “returnees” restore not only their former range, but also the lost niches that remain free. For instance, a preliminary analysis of stable carbon and nitrogen isotopes in the muscles of *V. viviparus* and dominant native gastropods [*Radix auricularia* (Linnaeus, 1758)] showed that the trophic niches of these mollusks in the Novosibirsk Reservoir practically do not overlap (L. Yanygina, unpublished data). If this is also true for other neobiotic mollusks, then their return to the Siberian water bodies can increase the overall diversity of aquatic ecosystems, and complicate food chains and other biotic relationships. This assumption is indirectly supported by the fact that we do not have data on the destructive influence of these species on the recipient freshwater ecosystems of Siberia. But this is a preliminary generalization, and this issue requires special studies. The case of the transforming effect of *V. viviparus* on the ecosystem of the Novosibirsk Reservoir described above remains the only one, and is perhaps not indicative, since artificial reservoirs are a very young type of

habitats that arose only in the historical era, and there were simply no direct analogues to them in Pleistocene.

A special case of intracontinental invasions is a phenomenon that can be referred to as “intra-Siberian invasions”. A striking example of this is the recent—on a scale of the last 100–120 years—introduction of the species *Radix auricularia*, widely distributed in the Palearctic, into the ecosystem of Lake Baikal, which included, almost exclusively, the native mollusk species unique to this waterbody [76–78]. Schniebs et al. [79] undertook the reconstruction of this invasion using methods of molecular and morphological analysis and showed its continuing character. It remains unclear whether the introduction of this mollusk into the Baikal ecosystem is a serious threat to the survival of endemic gastropod species, or whether *R. auricularia* will be able to find and occupy free ecological space, which will not lead to the competitive elimination of the native malacofauna.

4.2. Forecast of Changes in Freshwater Malacofauna of Siberia in the Coming Decades

Currently, it can be predicted that the enrichment of Siberian malacofauna due to the arrival of species of the “returnees” complex will only continue. Paleontological literature shows that neobiotic mollusks that are now restoring their lost range lived in the Pleistocene, together with native species common to the fauna of modern water bodies of Western Siberia and Europe. This may indicate the similarity of environmental conditions in the Pleistocene to those of the present, and increases the likelihood of further, wider distribution of mollusks of the “Pleistocene complex”.

We may make assumptions about groups of mollusks that will, probably, arrive in the freshwater systems of Siberia in the foreseeable future. In our opinion, bivalves of the genus *Corbicula* are the most likely future invaders, primarily the species *C. fluminea* (O.F. Müller, 1774) and *C. fluminalis* (O.F. Müller, 1774), which have long proven their ability to inhabit water bodies of Central and Eastern Europe with a natural thermal regime [26,33,80–82]. Recent studies have shown that these mollusks are able to withstand a decrease in temperature to 0 °C for 9 weeks [83]. When the temperature rises to 16–18 °C (at least 10 degree-days), *C. fluminea* becomes able to reproduce, which allows it to naturalize even in subalpine lakes [84]. The conditions of the European lakes and rivers fully meet these requirements already [83,85]. In the European part of Russia, the corbiculid clams are known from localities lying quite close to the Arctic Circle [82,86], which demonstrates their high tolerance to low temperatures. The territory of Siberia was not a part of the native range of this subtropical genus; however, in the Pleistocene epoch, some species of *Corbicula* were able to disperse into Northern Asia during the warm interstadials, which is well documented in the fossil record [73,74,87]. This indicates the potential for the rapid infiltration, following *Dreissena*, of representatives of the genus *Corbicula*, into the Ob'-Irtysh basin and, probably, to the upper courses of the Amur River basin in the southeastern part of Eastern Siberia.

For Siberia, two species of the family Viviparidae, *Cipangopaludina chinensis* (Gray, 1833) and *Sinotaia quadrata* (Benson, 1842), whose native ranges are situated in the Far East, should also be included in the list of potentially dangerous species of freshwater molluscs, from the point of view of the probability of their introduction. Both species are currently actively conquering the freshwaters of Europe and America, and information about their new findings outside their native range appears annually in the literature [88–93]. Representatives of the genera *Cipangopaludina* and *Sinotaia* are known from the Pliocene-Quaternary deposits of Siberia, and, until the end of the Pleistocene, they lived in the water bodies of Northern Asia together with modern native and neobiotic species [61,73,74].

The neobiotic mollusk species already established in Western Siberia are also likely to broaden their distribution in the region. Considering the evolutionary history of the North Palearctic species of the genus *Unio*, we should expect further expansion of *Unio pictorum* (Linnaeus, 1758) and *U. tumidus* into the water bodies of Western Siberia. The situation with the third European species of the genus, *U. crassus*, remains less clear. This species is considered threatened in a number of European countries, where it has been assigned

a certain conservation status. Perhaps this indicates a reduced adaptive and competitive potential of *U. crassus* compared to *U. pictorum* and *U. tumidus*, and, consequently, its limited opportunities to restore the lost part of its range, located to the east of the Ural Ridge.

The restoration of the lost range should also be expected in the case of *Viviparus viviparus*, already known from a number of points in the territory of the Ob'-Irtysch basin (see Table 1). Given the low number of malacologists and hydrobiologists working in Western Siberia, compared with the vastness of this region, it is not impossible to assume that the real extent of distribution of this snail here is much broader than we know.

Given the high frequency of publication of new findings of *Dreissena polymorpha* in water bodies belonging to the extreme western part of the Irtysch basin [17,35,36], we expect a rapid spread of this invasive bivalve downstream of rivers belonging to the Irtysch basin, and the formation, in the next 10–20 years, of stable foci of zebra mussel invasion at various points of the Irtysch basin on the territory of the West Siberian Plain. Since *D. polymorpha* is well known as a harmful species that has a transformative effect on both recipient ecosystems and a number of spheres of human activity, monitoring the spread of this species is a very urgent task, especially in the regions of southwestern Siberia, for example, in the Tyumen region, where we expect with the greatest probability the formation of new sustainable populations of this mollusk.

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