Limnologica 90 (2021) 125903

Contents lists available at ScienceDirect

Limnologica

journal homepage: www.elsevier.com/locate/limno

European freshwater mussels (*Unio* spp., Unionidae) in Siberia and Kazakhstan: Pleistocene relicts or recent invaders?

E.S. Babushkin[a,b,c,*], M.V. Vinarski[a,d], A.V. Kondakov[a,e], A.A. Tomilova[e], M.E. Grebennikov[f], V.A. Stolbov[g], I.N. Bolotov[a,e]

[a] *Laboratory of Macroecology & Biogeography of Invertebrates, Saint-Petersburg State University, Universitetskaya Emb., 7/9, 199034, Saint-Petersburg, Russia*
[b] *Surgut State University, Lenina Ave., 1, 628403, Surgut, Russia*
[c] *Tyumen Scientific Center, Siberian Branch of the Russian Academy of Sciences, Malygina St., 86, 625026, Tyumen, Russia*
[d] *Omsk State Pedagogical University, 14 Tukhachevskogo Emb., 644099, Omsk, Russia*
[e] *N. Laverov Federal Center for Integrated Arctic Research, Ural Branch of the Russian Academy of Sciences, Northern Dvina Emb., 23, 163000, Arkhangelsk, Russia*
[f] *Institute of Plant and Animal Ecology, Ural Branch of the Russian Academy of Sciences, 8 marta St., 202, 620144, Yekaterinburg, Russia*
[g] *Tyumen State University, Volodarskogo St., 6, 625003, Tyumen, Russia*

ARTICLE INFO

Keywords:
Bivalves
Ob' River basin
Range recovery

ABSTRACT

Unionidae is a species-rich family of large freshwater mussels with an almost worldwide distribution. In many regions of the world, these mussels are imperiled. Northern Asia, excluding the Far East, is an excellent example of a region with a sharply impoverished fauna of the Unionidae as recently thought with one native species. Since the end of the 19th century, two freshwater mussel species of the genus *Unio* (*U. pictorum* and *U. tumidus*) were repeatedly recorded in Siberia. In the course of this study, these finds are confirmed both morphologically and genetically, the number of known occurrences of these mussels in the waterbodies of Asiatic Russia and Kazakhstan has drastically increased, and the third species, globally endangered *U. crassus*, was found in the Ob' River basin. The unique *U. tumidus* haplotype discovered from the Upper Irtysh River basin is of probable relic origin, which may indicate the presence of a Pleistocene refugium there. Due to natural environmental changes during the last century, several genera of freshwater Mollusca that previously inhabited Western Siberia, but went completely extinct in the Pleistocene, have started to recover the North Asiatic part of their former ranges. The case of *Unio* is exceptional since the recovery of its lost range goes not exclusively with the humans' help but also involves the natural mechanisms of dispersal and range extension, and also because these mussels are disappearing in other parts of the world and are placed in the IUCN Red List of Threatened Species.

1. Introduction

The Unionidae Rafinesque, 1820 (freshwater mussels, naiads) is a species-rich family of large freshwater bivalves with an almost worldwide distribution. In many regions of the world these mollusks are imperiled that explains the increasing interest in their taxonomy, biogeography, and conservation (see Ferreira-Rodríguez et al., 2019; Graf and Cummings, 2021a; Lopes-Lima et al., 2018, 2017 and references therein). Certain parts of the world such as North America and Southeast Asia are biodiversity hotspots for this group, with hundreds of endemic species, whereas the Unionidae fauna of several other regions is rather poor (Araujo et al., 2018; Bogan, 2008; Bogan and Roe, 2008; Bolotov et al., 2020; Graf and Cummings, 2021a, b, 2019; Lopes-Lima et al., 2018). Siberia, excluding the Amur River basin, is an excellent example of a region with a sharply impoverished fauna of the family Unionidae. The latest integrative revision of the Unionidae of Russia (Bolotov et al., 2020) showed that only one native species, the Duck Mussel *Anodonta anatina* (Linnaeus, 1758), inhabits the vast territory of Siberia.

However, this situation characterizes only the Holocene epoch. In the Neogene, Siberia was inhabited by a rich and taxonomically diverse naiad fauna, with many endemic genera and species (Bogachev, 1961; Lindholm, 1932a, 1932b; Maderni, 1990; Zykin, 2012, 1979). Starobogatov (1970) and Zykin (2012, 1979) classified these taxa as closely allied to the living South Asian genera and, thus, considered this extinct North Asian fauna as a derivative of the Sino-Indian zoogeographic

* Corresponding author at: Surgut State University, Lenina Ave., 1, 628403, Surgut, Russia.
E-mail address: babushkines@gmail.com (E.S. Babushkin).

https://doi.org/10.1016/j.limno.2021.125903
Received 21 May 2021; Received in revised form 8 July 2021; Accepted 9 July 2021
Available online 21 July 2021

complex. This rich and largely endemic faunal assemblage was completely exterminated during the Pleistocene, most likely due to a sharp climate cooling, although alternative hypotheses have been put forward, including one explaining the unionid extinction in Siberia by the impact of some unidentified epidemic, like the "crayfish plague" (Bogachev, 1966; Maderni, 1974).

It was believed until recently that freshwater mussels of the genus *Unio* Philipsson in Retzius, 1788, widely distributed in Europe, the Near East, and Northern Africa, are absent in the recent fauna of Siberia (Starobogatov, 1970; Starobogatov et al., 2004; Zhadin, 1952). Nevertheless, a few occasional reports of *Unio* mussels in the Ob' River basin (Western Siberia) can be found in historical literary sources (von Martens, 1875; Mozley, 1936). These references will be discussed below. In 2003, information on *Unio* species records from the Ob' Basin appeared in the catalog of the malacological collection of the Institute of Plant and Animal Ecology, Ural Branch of the Russian Academy of Sciences (Khokhutkin et al., 2003), that became the first confirmation of the presence of *Unio* mussels in Siberia in the recent literature. Khokhutkin et al. (2003) published a list of sites at which the mollusks were collected with their geographic coordinates but, unfortunately, no images of shells were provided, and the issue of *Unio* mussels' dispersal east of the Ural Ridge was not discussed.

Later on, and quite independently of Khokhutkin et al. (2003), Andreyeva et al. (2009) reported the occurrence of *Unio* mussels in the rivers of the eastern slope of the Ural Ridge, which hydrographically belong to the Ob' basin. According to the authors, these finds reflect the ongoing process of the westward expansion of the genus' range, and the further dispersal of *Unio* mussels over the Western Siberian Plain is to be expected.

Most recently, Klishko et al. (2017) discussed the records of *Unio* species in Transbaikalia (Eastern Siberia), in Lake Kenon, which serves as a cooling reservoir for the thermal power station in the city of Chita. In 2009–2013 the first records of *Unio* mussels from the Bukhtarma Reservoir, located in East Kazakhstan, in the upper courses of the Irtysh River, were published (Devyatkov, 2013, 2009; Yanygina, 2016). The samples were tentatively identified as *Unio pictorum* (Linnaeus, 1758). The authors of the cited papers believe that these occurrences reflect the unintentional introduction that took place during the stocking of the reservoir with fish (see, for example, Yanygina, 2016). Later on, the presence of the genus *Unio* in the upper reaches of the Irtysh River in Kazakhstan was genetically confirmed by Bolotov et al. (2020). A recent study of the infestation of unionid mussels by parasitic mites *Unionicola* (Acari: Unionicolidae) in the south of Western Siberia, in which *U. pictorum* samples were examined (Stolbov and Voronova, 2019), also must be mentioned here.

This increasing body of primary distribution data indicates that *Unio* mussels are currently not only present but also much more widespread in Siberia than it was assumed not so long ago. At the same time, some Palearctic species of freshwater mussels are known to be disappearing in certain parts of the world and even included in the IUCN Red List of Threatened Species. Furthermore, the perceived view of the complete extermination of this genus in Northern Asia may turn out to be unfounded.

In this paper, we summarize and analyze all the information available to date on the distribution of the genus *Unio* in Siberia and the Upper Irtysh River basin, based on the extensive search through accessible literature, the examination of museum collections as well as the results of our own fieldwork made in various regions of Russian and Kazakhstan located east of the Ural Ridge. We aimed at elucidating both the origin and relationships of *Unio* mussels from Siberia and the Upper Irtysh River basin. Another goal was to trace, as far as possible, the dispersal of mollusks of this genus eastward of the Ural Ridge during historical time.

2. Material and methods

The primary material for this study was the collections of unionid mussels housed in scientific institutions of Russia, as well as the samples of these mollusks collected by us from watercourses and waterbodies of the Urals, Siberia, and East Kazakhstan (Fig. 1).

We studied, either morphologically or genetically (or both), 421 specimens of *Unio* mussels (Table 1). Museum specimens of *Unio* collected in Siberia were studied at the Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia (ZIN hereafter), Museum of the Institute of Plant and Animal Ecology of the Ural Branch of the Russian Academy of Sciences, Yekaterinburg, Russia (IPAE hereafter), and the Zoological Museum of the Institute of Biology, Tyumen State University, Tyumen, Russia (BITSU hereafter). The first of these institutions holds the largest collection of continental mollusks in Russia, the history of which dates back to the first half of the 19th century (Vinarski, 2010). The historical significance of this collection can hardly be overestimated since it stores materials on the Russian malacofauna, collected by several generations of Russian and foreign malacologists. It contains, among others, the oldest known historical sample of Siberian *Unio* mussels collected in 1829 by the expedition of A. von Humboldt and K. Ehrenberg (see below).

IPAE is the largest repository of malacological collections made in watercourses and waterbodies of the Urals and adjacent areas. This institution keeps mollusk samples from habitats located both in the western and eastern slopes of the Ural Ridge, covering all bioclimatic zones which are present in the region. The formation of this collection began in the 1950s and, during the 1990–2000s, it was replenished most intensively (Khokhutkin et al., 2003). IPAE collection documents both the species content and geographical distribution of the terrestrial and aquatic malacofauna of the Urals and some other regions for the period of the last 50–60 years, which allows one to trace trends in mollusk species' dispersal and abundance.

Own samplings of freshwater mussels, discussed in this paper, were carried out during 2007–2020 in the parts of the Ob' River basin situated within the boundaries of Chelyabinsk, Sverdlovsk, Tyumen, and Omsk regions of Russia as well as in the upper course of the Irtysh River (so-called "Black Irtysh") in East Kazakhstan. Mussels were collected by hands or by dredging; soft tissues (if available) were fixed in 96 % ethanol and subsequently processed in a laboratory. The voucher specimens are kept in BITSU, IPAE, Russian Museum of Biodiversity Hotspots of the Federal Center for Integrated Arctic Research of the Ural Branch of the Russian Academy of Sciences, Arkhangelsk, Russia (RMBH hereafter), Malacological Collection of the senior author (MCB hereafter), and in the Laboratory of Macroecology & Biogeography of Invertebrates, Saint-Petersburg State University, Saint-Petersburg, Russia (LMBI hereafter) (for detailed information see Table 1).

For the species identification, we used the data of some publications on the taxonomy of unionid mussels (Bolotov et al., 2020; Klishko et al., 2017; Zhadin, 1952) as well as some shell images available from the MUSSELp online database (Graf and Cummings, 2021b). The museum specimens represented by dried shells were identified based on conchological features (shell shape and proportions, shell surface sculpture and coloration, and the hinge structure). The identity of some individuals collected by us in the field was confirmed utilizing molecular methods.

The *COI* gene sequences were generated, sequence alignments were processed and joined as described in our previous work (Bolotov et al., 2020; Tomilova et al., 2019). Additional sequences were obtained from the NCBI's GenBank. To assess the phylogeographic relationship between haplotypes of *Unio pictorum* and *U. tumidus* Philipsson in Retzius, 1788, we applied a network-based approach using Network v. 4.6.1.3 software (Bandelt et al., 1999). The information on *COI* sequences used in the analyses is given in Supplementary Table 1.

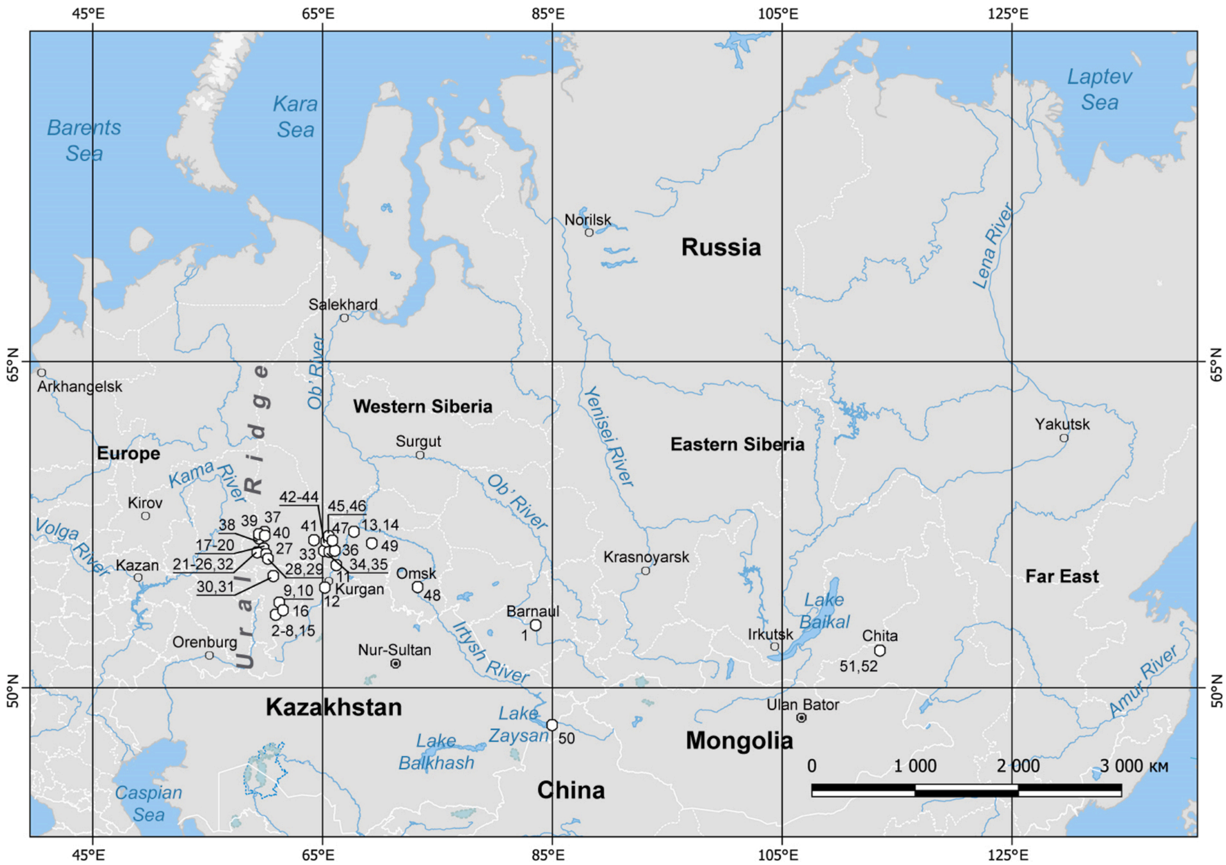

Fig. 1. Map of *Unio* spp. occurrences in the Urals, Siberia, and Eastern Kazakhstan. Numbers indicate the localities, which correspond to those in Table 1. The map was developed using QGIS software (https://qgis.org/) with a topographic base from Natural Earth Free Vector and Raster Map Data (www.naturalearthdata.com). (Map: Evgeny S. Babushkin).

3. Results

3.1. Historical records of Unio mussels in Siberia

Despite Zhadin's (1952) claim that the genus *Unio* is distributed in the USSR westward of the Urals and does not enter the territory of Western Siberia, the presence of this genus in the Ob' Basin was at least twice mentioned in malacological literature before 1952. First, the German malacologist Eduard von Martens listed two species of *Unio* (*Unio tumidus* Retzius in Philippson, 1788 and *U. crassus* Retzius in Philippson, 1788) from Barnaul, a city in the southeast part of Western Siberia. These mollusks were represented in a malacological collection brought to Europe by the Altai expedition headed by Alexander von Humboldt, which took place in 1829. The route of the expedition passed through European Russia, the Middle Urals, the south of Western Siberia, and the Altai Mountains (Vinarski, 2010). The main body of this collection is housed in the Natural History Museum of Berlin, Germany; a few samples are kept in ZIN (Vinarski, 2016).

In the ZIN collection, there is a sample (Fig. 2) consisting of two valves of *Unio tumidus*, labeled as "Ob' River at Barnaul" ("Ob bei Barnaul" in German). Martens (1875) added this species to his list of Siberian malacofauna, but doubted the geographical location of the sample. He noted that specimens of *Unio* with the label "Barnaul", examined by him in the Berlin Museum, "are all poorly preserved, heavily worn, apparently obtained from second hand, or found dead or abraded, so their origin must be confirmed" (von Martens, 1875: 96). In contrast to the shell material described by Martens (1875), specimens of the part of this sample kept in ZIN are quite well preserved, except for the strongly worn umbones, and their belonging to the genus *Unio* rises no doubt. These probably belonged to the part of the collection that was left in Russia and was once sent to the Swedish malacologist Carl Agardh Westerlund for identification (see Vinarski, 2010 for details). Most likely, Martens never worked with these specimens, and the initial identification, later confirmed by Westerlund, was made by an unknown person.

This still remains the only find of the species in the waterbodies of the Russian part of Altai. According to the most recent faunal surveys, *Anodonta anatina* is the sole representative of the family occurring in the vicinities of Barnaul (Kuzmenkin, 2015, 2013), and it cannot be ruled out that the shells labeled as found in Barnaul were, in fact, collected in another site, possibly in the Black Irtysh River basin (see below).

Martens' record of *Unio crassus* from Siberia remains more mysterious. We were unable to find this species either in ZIN or in other available mussel collections made in Asiatic Russia (see below), and the presence of this species in Siberia has not been confirmed by recent studies (e.g., Bolotov et al., 2020). During this study, we found 3 valves of *U. crassus* in a sample collected from the pond of the Tagil River (No. 37, see Fig. 1 and Table 1), which belongs hydrographically to the Ob' River basin but is situated on the eastern slope of the Ural Ridge, not in Siberia in the commonly accepted definition of this geographic region. This record is the easternmost verified location of the globally threatened species *U. crassus* known to date.

The next record of *Unio* mussels from the Ob' river basin was published by Alan Mozley, an American malacologist, who studied the malacofauna of Siberia in 1932 and 1933 (Vinarski, 2020). In his monograph on the Siberian continental mollusks, Mozley (1936: 651) asserted he had collected "a species of *Unio*" in the river Tom' (Tomsk Region, the east part of Western Siberia) but, unfortunately, these "specimens were stolen by some hungry natives" and probably eaten by them. The cause of this was the great famine in Siberia that took place

Table 1
List of *Unio* localities in Russia and Kazakhstan east of the Ural Ridge. The numbers of localities in the table correspond to those in the map (Fig. 1).

No	Species	Locality and sample data	Coordinates		Reference
			Latitude	Longitude	
?Ob' River basin: Altai Region, Russia					
1	*Unio tumidus*	?Barnaul, 1 specimen, 1829, A. von Humboldt expedition leg. [coll. ZIN]	53.3728?	83.7318?	von Martens, 1875; This study
Tobol River basin: Chelyabinsk, Kurgan & Tyumen regions, Russia					
2	*U. pictorum*	Uy River, 3 specimens, 22.06.2002, Belyaev leg. [coll. IPAE, No. 8110]	54.1167	61.1000	This study
3	*U. pictorum*	Uy River, 22 specimens, June 2005, Chashchin & Chashchina leg. [coll. LMBI]	54.0779	60.3936	Andreyeva et al., 2009
4	*U. pictorum*	Uy River, 3 specimens, 25.07.2005, Belyaev leg. [coll. IPAE, No. 11,080]	54.1000	61.1333	This study
5	*U. pictorum*	Uy River, 3 specimens, 04.08.2005, Erokhin leg. [coll. IPAE, No. 11,695]	54.0333	60.9167	This study
6	*U. pictorum*	Uy River, 1 specimen, August 2005, Kosintsev leg. [coll. IPAE, No. 11,547]	54.3333	60.0000	This study
7	*U. pictorum*	Uy River, 1 specimen, 24.07.2007, Koporikov & Chertykovtsev leg. [coll. IPAE, No. 13,335]	54.0286	61.7643	This study
8	*U. pictorum*	Uy River, 1 specimen, 27.07.2007, Koporikov & Chertykovtsev leg. [coll. IPAE, No. 13,342]	54.0667	61.5000	This study
9	*U. pictorum*	Yuzhnoural'skoye Reservoir, 5 specimens, 28.05.2007, Grebennikov leg. [coll. IPAE, No. 12,378]	54.4833	61.2500	This study
10	*U. pictorum*	Yuzhnoural'skoye Reservoir, 12 specimens, 17.07.2009, Grebennikov leg. [coll. IPAE, No. 17,304]	54.4833	61.2500	This study
11	*U. pictorum*	Tobol River, 1 specimen, June 2007, Stolbov leg. [coll. BITSU]	56.5175	66.3948	Stolbov and Voronova, 2019
12	*U. pictorum*	Tobol River, 3 specimens, 05.10.2007, Belyaev leg. [coll. IPAE, No. 13,308]	55.1623	65.1882	Vinarski et al., 2015
13	*U. pictorum*	Tobol River, 1 specimen, 27.08.2010, Erokhin leg., [coll. IPAE, No. 14,537]	58.0058	68.0426	Vinarski et al., 2015
14	*U. pictorum*	Tobol River, 4 specimens, 14.09.2012, Kosintsev leg. [coll. IPAE, No. 16,178]	58.0058	68.0426	This study
15	*U. tumidus*	Uy River, 1 specimen, 25.07.2005, Belyaev leg. [coll. IPAE, No. 11,080]	54.1000	61.1333	This study
16	*U. tumidus*	Uvel'ka River, 1 specimen, July 2005, Chashchin & Chashchina leg. [coll. LMBI]	54.0884	61.5069	Andreyeva et al., 2009
Iset River basin: Sverdlovsk & Chelyabinsk regions, Russia					
17	*U. pictorum*	Lake Isetskoye, 3 specimens, 03.08.1998, Pankratev leg. [coll. IPAE, No. 3859]	57.0167	60.4667	Khokhutkin et al., 2003
18	*U. pictorum*	Lake Isetskoye, 7 specimens, 20.07.2000, Pankratev leg. [coll. IPAE, No. 4929]	57.0002	60.4601	Khokhutkin et al., 2003
19	*U. pictorum*	Lake Isetskoye, 3 specimens, 09.07.2002, Erokhin leg. [coll. IPAE, No. 11,619]	56.9611	60.4039	This study
20	*U. pictorum*	Lake Isetskoye, 1 specimen, 07.10.2004, Erokhin leg. [coll. IPAE, No. 6431]	57.0333	60.4333	This study
21	*U. pictorum*	Verkh-Isetsky Pond, 73 specimens, 05.04.1998, Erokhin leg. [coll. IPAE, No. 10832, 10,834]	56.8652	60.5000	This study
22	*U. pictorum*	Verkh-Isetsky Pond, 3 specimens, 12.04.2003, Ermakov leg. [coll. IPAE, No. 13,955]	56.8500	60.5000	This study
23	*U. pictorum*	Verkh-Isetsky Pond, 58 specimens, 20.06.2003, Borisov leg. [coll. IPAE, No. 10625, 10627, 12,307]	56.8410	60.5237	This study
24	*U. pictorum*	Verkh-Isetsky Pond, 15 specimens, 21.06.2003, Borisov leg. [coll. IPAE, No. 11795, 12,303]	56.8500	60.5167	This study
25	*U. pictorum*	Verkh-Isetsky Pond, 42 specimens, 14.07.2004, Borisov leg. [coll. IPAE, No. 6404, 10,609]	56.8410	60.5237	This study
26	*U. pictorum*	Verkh-Isetsky Pond, 1 specimen, Lugas'kov leg. [coll. IPAE, No., 7835]	56.8333	60.5333	This study
27	*U. pictorum*	Gorodskoy Pond, 16 specimens, 05.11.2007, Erokhin leg. [coll. IPAE, No. 13,332]	56.8474	60.5869	This study
28	*U. pictorum*	Nizhne-Isetsky Pond, 3 specimens, 14.06.2000, Stepanov leg. [coll. IPAE, No. 4858]	56.7588	60.7000	Khokhutkin et al., 2003
29	*U. pictorum*	Nizhne-Isetsky Pond, 3 specimens, 12.09.2000, Stepanov leg. [coll. IPAE, No. 5037]	56.7588	60.7000	Khokhutkin et al., 2003
30	*U. pictorum*	Lake Kirety, 18 specimens, 11.10.2003, Erokhin leg. [coll. IPAE, No. 11,296]	55.9333	60.7667	This study
31	*U. pictorum*	Lake Kirety, 5 specimens, 06.07.2004, Erokhin leg. [coll. IPAE, No. 6414]	55.9333	60.7667	This study
32	*Unio* sp. indet.	Verkh-Isetsky Pond, 1 specimen, 20.09.2000, Erokhin leg. [coll. IPAE, No. 4853]	56.8667	60.4500	Khokhutkin et al., 2003
Pyshma River basin: Tyumen Region, Russia					
33	*U. pictorum*	Balda River, 1 specimen, 11.06.2019, Stolbov leg. [coll. BITSU]	56.9537	65.1905	This study
34	*U. pictorum*	Takhtym oxbow, 17 specimens, 14.06.2018, Stolbov leg. [coll. BITSU]	56.9308	65.5629	Stolbov and Voronova, 2019
35	*U. pictorum*	Takhtym oxbow, 10(5*) specimens, 18.06.2020, Babushkin & Stolbov leg. [coll. RMBH biv1107/7, 8, 10, 11, 14 and MCB]	56.9311	65.5593	This study
36	*U. pictorum*	Pyshma River, 2 specimens, June–August 2016, Voronova leg. [coll. BITSU]	56.9596	65.8042	Stolbov and Voronova, 2019
Tura River basin: Sverdlovsk & Tyumen regions, Russia					
37	*U. crassus*	Pond of Tagil River, 3 specimens, 09.07.2006, unknown students leg. [coll. IPAE, No. 19,485]	57.8000	60.0167	This study
38	*U. pictorum*	Verkhne-Tagilskoye Reservoir, 8 specimens, 23.05.2005, Talnishnikh leg. [coll. BITSU]	57.3779	59.9641	This study
39	*U. pictorum*	Svistukha River, 1 specimen, 19.07.2010, Tsybina leg. [coll. IPAE, No. 19,467]	57.7003	59.8745	This study
40	*U. pictorum*	An unknown water body in Kirovgrad town, 3 specimens, 14.08.2002, Stepanov leg. [coll. IPAE, No. 8112]	57.4333	60.0833	This study
41	*U. pictorum*	Nitsa River, 5 specimens, 17.09.2017, Stolbov leg. [coll. BITSU]	57.4785	64.5310	Stolbov and Voronova, 2019
42	*U. pictorum*	Tura River, 15 specimens, 24.09.2018, Kuzmin leg. [coll. BITSU]	57.1710	65.5158	This study
43	*U. pictorum*	Tura River, 11 specimens, June–August 2016, Voronova leg. [coll. BITSU]	57.1603	65.6000	Stolbov and Voronova, 2019
44	*U. pictorum*	Tura River, 10(2*) specimens, 18.06.2020, Babushkin & Stolbov leg. [coll. RMBH, No. biv1104/1 & 2 and MCB]	57.1603	65.6000	This study
45	*U. pictorum*	Lake Krugloye, 2 specimens, June–August 2016, Voronova leg. [coll. BITSU]	57.1634	65.6145	Stolbov and Voronova, 2019
46	*U. pictorum*	Lake Krugloye, 1* specimen, 18.06.2020, Babushkin & Stolbov leg. [coll. RMBH, No. biv1105/3]	57.1634	65.6145	This study
47	*U. pictorum*	Channel from Lake Krugloye, 7(2*) specimens, 18.06.2020, Babushkin & Stolbov leg. [coll. RMBH, No. biv1106/4 & 5 and MCB]	57.1632	65.6313	This study
Irtysh River basin: Omsk & Tyumen regions, Russia					
48	*U. pictorum*	Irtysh River Channel, 5 specimens, 15.10.2014, Vinarski leg. [coll. LMBI, No. 20-147]	55.1420	73.1600	This study
49	*U. pictorum*	Vagai River, 2 specimens, 20.08.2020, Kosintsev & Gimranov leg. [coll. IPAE, No. 24,256]	57.2931	69.1039	This study
Black Irtysh River basin: East Kazakhstan Region, Kazakhstan					
50	*U. tumidus*	Black Irtysh River, 3* specimens, 14.07.2018, Vinarski leg. [coll. RMBH]	47.9000	84.9000	Bolotov et al., 2020; This study
Amur River basin: Transbaikal Region, Russia**					
51	*U. pictorum*	Lake Kenon, numerous (8*) specimens, Klishko leg. [coll. INREC]	52.0486	113.3726	Klishko et al., 2017
52	***U. tumidus*	Lake Kenon, numerous specimens, Klishko leg. [coll. INREC]	52.0486	113.3726	Klishko et al., 2017

INREC – Collection of the Institute of Natural Resources, Ecology and Cryology, Russian Academy of Sciences, Siberian Branch, Chita, Russia; for other abbreviations see 2 Material and methods.

* The DNA sequences obtained from these specimens were used in the haplotype network analyses, see Figs. 5, 6, and Supplementary Table 1.

** Occurrences of *U. crassus* from Lake Kenon (Klishko et al., 2017) were based on erroneous identification and belong to *U. tumidus* (see Bolotov et al., 2020). Information on Lake Kenon is given after Klishko et al., 2017.

Fig. 2. Two valves of *Unio tumidus* labeled “Ob’ River at Barnaul” from Humboldt expedition, ZIN collection (No. 1, see Fig. 1 and Table 1). Scale bar =1 cm. (Photos: Maxim V. Vinarski).

between 1932 and 1934 (see Vinarski, 2020 for details). Notably, that, though the malacofauna of the Tom’ River basin was studied intensively in the 1950–1970 s (Ioganzen, 1951; Ioganzen and Novikov, 1971, 1969; Novikov, 1971), no record of this genus was published in these decades. Therefore, despite the great zoogeographic significance of Mozley’s find, it is impossible to verify its reliability.

3.2. Analysis of available museum collections

Among museum collections, examined by us during this study, that of ZIN contains numerous lots of *Unio* mussels collected in the 19th – first half of the 20th centuries from the rivers of the Volga-Kama basin (Belaya, Bisert, Irgizla, Sylva, Ural, and Ufa). Though all these basins are geographically close to Western Siberia, they do not belong to the Ob’ River basin. The significance of these samples is that they indicate a possible source of introduction of *Unio* mussels to Siberia through interconnections of the upper courses of the Volga-Kama and Ob’ river basin (see Andreyeva et al., 2009 for discussion). The only ZIN lot containing *Unio* from Asiatic Russia is that was collected by the Humboldt expedition and discussed above.

IPAE and BITSU collections, on the other hand, hold a relatively large number of *Unio* samples originating from the eastern slope of the Ural Ridge and Siberia, which, alongside our own findings, enable us to map the current distribution of this genus in the Ob’ River basin (see Fig. 1; Table 1). The vast majority of the IPAE samples were made within the boundaries of the Ural mountainous country i.e., their sampling sites are located relatively close to the watershed between the Volga-Kama and Ob’ river basins. It is noteworthy that all these occurrences were recorded quite recently. The first reliable recordings of *Unio* in waterbodies of the eastern slope of the Ural Ridge were made in the second half of the 1990s; no earlier samples from this area are kept in IPAE. Based on conchological traits, one can identify the shells as belonging to three species – *Unio pictorum, U. tumidus*, and *U. crassus* (Fig. 3; Table 1), the first of which is more abundant and is of broader distribution in Western Siberia.

BITSU collection holds a series of samples of *Unio* mussels collected in the course of the last two decades by the Institute’s employees from the basins of the left tributaries of the Irtysh River situated within the Tyumen and Sverdlovsk regions. An examination of this small collection revealed nine new occurrences of *U. pictorum* in the Ob’ River basin (see Fig. 1; Table 1). The most recent finds of 2017–2019 were made in rivers and oxbows of the Western Siberian Plain, already outside the Ural mountainous country.

3.3. DNA-barcoding and phylogeography of Siberian Unio

Our molecular analysis has confirmed the presence of at least two species of the genus *Unio* in the Siberian waterbodies. *Unio pictorum* has been identified in samples collected from the Tobol River basin, whereas *U. tumidus* was found in a sample from the upper reaches of the Irtysh River basin (Black Irtysh) (Fig. 4).

Unio pictorum from the Tobol River basin shared a single haplotype previously found in populations of European Russia (Fig. 5), namely in the Voronezh (Don River), Astrakhan (Volga River), Saratov (Khoper River, Don River basin), Novgorod (Volkhov River), and Arkhangelsk (Severnaya Dvina River) regions.

In the upper reaches of the Irtysh River basin two haplotypes of *U. tumidus* were found (Fig. 6), one of which is unique and has three

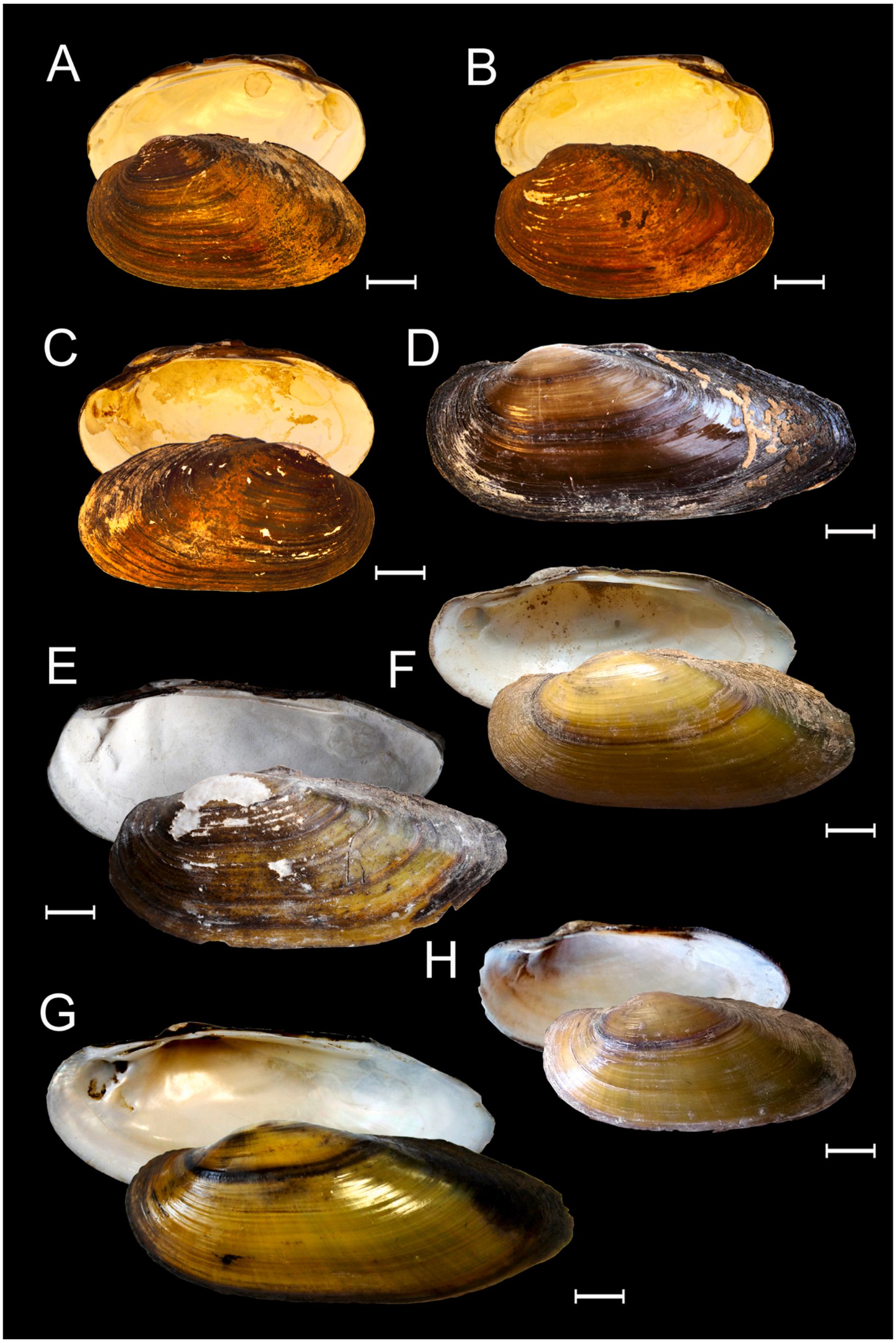

Fig. 3. Shells of *Unio* species from the Ob' River basin. (**A–C**) *Unio crassus*, 09.07.2006, Pond of Tagil River, Sverdlovsk Region (No. 37). (**D**) *U. pictorum*, 03.08.1998, Lake Isetskoye, Sverdlovsk Region (No. 17). (**E**) *U. pictorum*, 05.04.1998, Verkh-Isetsky pond, Sverdlovsk Region (No. 21). (**F**) *U. pictorum*, 14.09.2012, Tobol River, Tyumen Region (No. 14). (**G**) *U. pictorum*, 17.09.2017, Nitsa River, Tyumen Region (No. 41). (**H**) *U. pictorum*, 20.08.2020, Vagai River, Tyumen Region (No. 49). The numbers of localities correspond to those in Fig. 1 and Table 1. Scale bars =1 cm. (Photos: Evgeny S. Babushkin [A–F, H] and Vitaly A. Stolbov [G]).

nucleotide substitutions in comparison to the rest of the haplotypes obtained by us and available from the public databases. The second haplotype of *U. tumidus* from the Black Irtysh is identical to that of the samples collected from the Ural River in West Kazakhstan and European Russia (see Fig. 6), namely in the Perm (Iren' River), Saratov (Khoper River, Don River basin), Voronezh (Don and Khoper rivers), Bashkortostan (Belaya River), Astrakhan (Volga River), Kaluga (Oka River), and Krasnodar (Beysuzhek Levyi River) regions.

4. Discussion

Our integrative taxonomic analysis has revealed the presence of two *Unio* species in waterbodies of Siberia, earlier suggested by Andreyeva et al. (2009) based on examination of dead empty shells. Using the DNA sequencing approach, *Unio pictorum* was identified in samples originating from the floodplain waterbodies and rivers flowing from the Urals into the Tobol River, the largest tributary of the Irtysh River. *U. tumidus* was found in samples from the Black Irtysh, the upper course of the Irtysh River basin in East Kazakhstan. In Eastern Siberia, both species were previously registered in Lake Kenon, in the Upper Amur

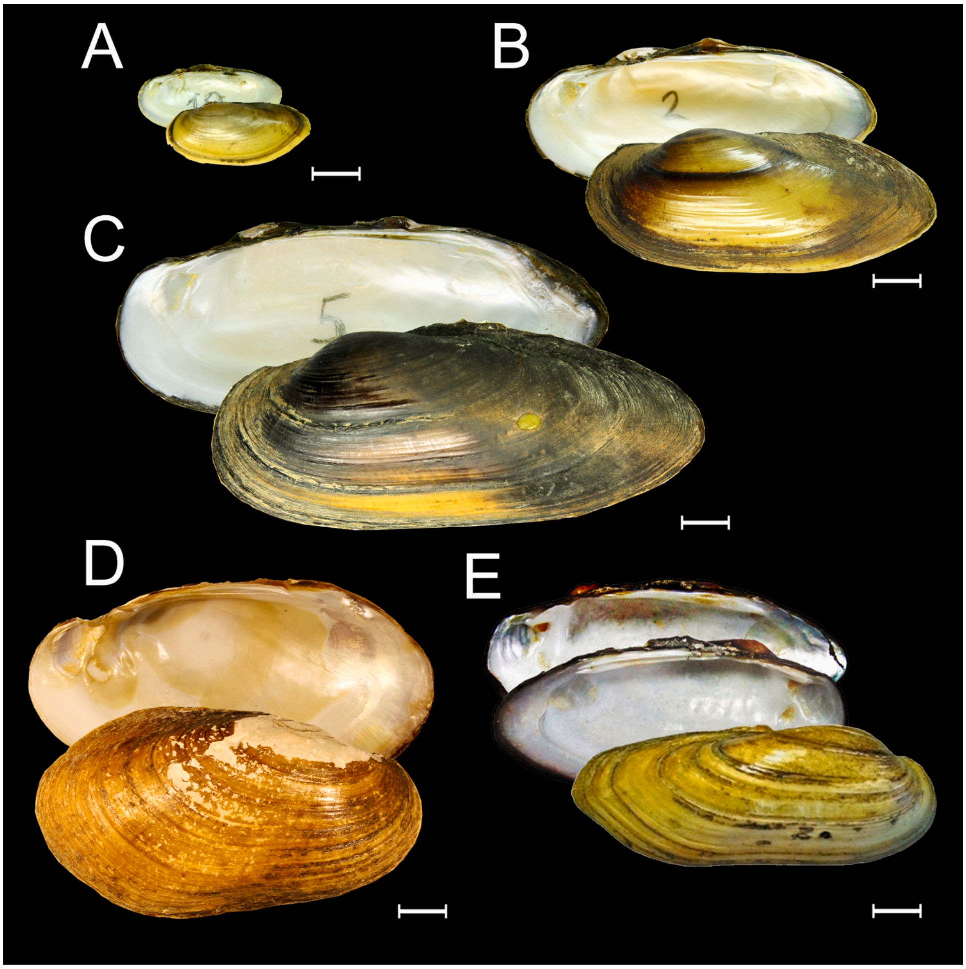

Fig. 4. Shells of sequenced specimens that were used in the haplotype network analyses (see Figs. 5,6, Table 1, and Supplementary Table 1). (**A**) *Unio pictorum*, 18.06.2020, Takhtym oxbow of Pyshma River, Tyumen Region, Russia (No. 35). (**B**) *U. pictorum*, 18.06.2020, Tura River, Tyumen Region, Russia (No. 44). (**C**) *U. pictorum*, 18.06.2020, Channel from Lake Krugloye, Tyumen Region, Russia (No. 47). (**D**) *U. tumidus*, Black Irtysh River, East Kazakhstan Region, Kazakhstan (No. 50). (**E**) *U. pictorum*, Lake Kenon, Transbaikal Region, Russia (No. 52). The numbers of localities correspond to those in Fig. 1 and Table 1. Scale bars =1 cm. (Photos: Alena A. Tomilova [A–C] and Maxim V. Vinarski [D]; E – after Klishko et al., 2017 with changes).

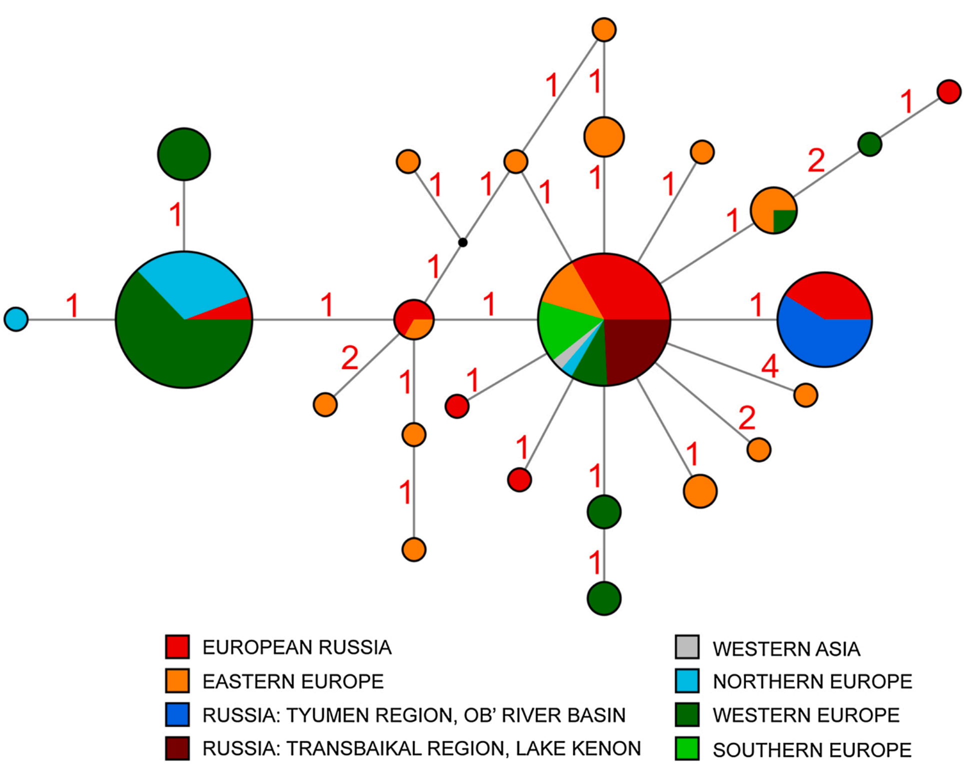

Fig. 5. Median-joining network of *Unio pictorum* based on the *COI* gene sequences (N = 120). The red numbers near branches indicate the numbers of nucleotide substitutions between haplotypes. The size of circles corresponds to the number of available sequences for each haplotype (smallest circle = 1 sequence, largest circles from left to right = 35, 33 and 17 sequences respectively). (Network: Alexander V. Kondakov) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

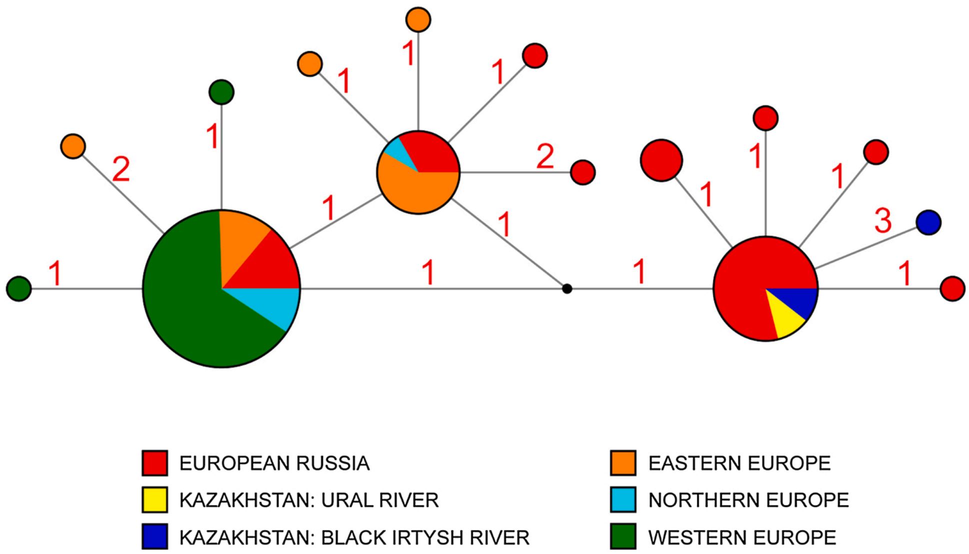

Fig. 6. Median-joining network of *Unio tumidus* based on the *COI* gene sequences ($N = 88$). The red numbers near branches indicate the numbers of nucleotide substitutions between haplotypes. The size of circles corresponds to the number of available sequences for each haplotype (smallest circle = 1 sequence, largest circles from left to right = 43, 12 and 19 sequences respectively). (Network: Alexander V. Kondakov) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

River basin in Transbaikalia (Klishko et al., 2017 and our unpublished data).

4.1. *Unio* in the Upper Irtysh River basin

The most unexpected result of our study was the identification of a unique *U. tumidus* haplotype in a sample from the Black Irtysh River, East Kazakhstan. This haplotype differs from other known haplotypes of this species by three nucleotide substitutions, which suggests its probable relict origin.

According to paleontological and paleogeographic information, the genus *Unio* could penetrate Siberia from Europe in the Neogene, after the disappearance of the Turgai Strait that once separated Europe from Northern Asia. The dispersal of this genus was a part of the replacement processes of the native endemic malacofauna of Western Siberia with the boreal European faunal complex of freshwater Mollusca (Starobogatov, 1986, 1970; Zykin, 2012, 1979). By the beginning of the Pliocene, the freshwater malacofauna of Western Siberia already contained a significant portion of genera and species migrated from Europe, whereas the share of taxa of Asian (Sino-Indian) origin had been steadily declining (Starobogatov, 1986, 1970; Zykin, 2012). The oldest known fossil remains of the genus *Unio* in Western Siberia and Kazakhstan are dated back to the Late Miocene (Zykin, 2012, 1979). In the Pleistocene, the range of this genus in Siberia extended eastward to the Baikal Lake Region (Popova, 1981), i.e., *Unio* mussels were widely distributed throughout Southern Siberia, and this epoch was the time of the greatest expansion of the genus in Asia.

The finding of a unique haplotype of *U. tumidus* in the Black Irtysh River may indicate the existence of a certain refugium, in the territory of modern East Kazakhstan, where these mussels might have survived during the Pliocene-Pleistocene climatic perturbations. Indeed, considering the mean *COI* substitution rate in the family Unionidae (Froufe et al., 2016; Zieritz et al., 2020), we roughly calculated that the accumulation of three nucleotide substitutions in this gene fragment would require at least 1.5 million years (95 % CI: 1.0–2.1 million years). Consequently, the divergence of the haplotypes that took place in the Pleistocene confirms the above hypothesis and indicates that the Black Irtysh unique haplotype of *Unio tumidus* has a relict origin. The available paleontological data does not contradict this assumption. Fossil remains of *U. tumidus* were found in the Pleistocene deposits of the Angara River Region in Eastern Siberia (Popova, 1981). In Western Siberia, some albeit doubtful records of *U. tumidus* from the Early Pleistocene deposits are known (Nikolayev, 1938). Though Maderni (1990) disputed the correctness of the species identification made by Nikolayev (1938), he described a few species and subspecies of *Unio*, which may be ancestral or sister for it, from the Early and Middle Pleistocene of Siberia and Central Kazakhstan. One cannot exclude that some of these taxa may, in reality, be conspecific with *U. tumidus* since their conchological features, as they were described and illustrated by Maderni (1990), are very close to the morphology of the latter species. For instance, the subspecies *Unio hybrida multus* Maderni, 1990, from the Early Pleistocene of Northern Kazakhstan, belongs to an extinct species (*Unio hybrida* Bogachev, 1961), which was described as a product of assumed hybridization between *U. pictorum* and *U. tumidus* demonstrating a mixture of morphological features characteristic for both species (Bogachev, 1961). Taking into account the high morphological variability of *Unio* species and the lack of data on their hybridization, we could assume that this fossil "hybrid" belongs to *U. tumidus*.

The hypothesis of a putative refugium in the upper courses of the Irtysh River allows us to explain the origin of *U. tumidus* sample studied by Martens. The label "Barnaul" may indicate not the sampling site but the place of keeping the material. The collection of the so-called Mining Museum (Gornyi Muzey) in Barnaul, which was headed by Friedrich August von Gebler, a prominent Russian naturalist of German origin (see Vinarski, 2010,), contained specimens of shells collected in various parts of the Altay Mts. and adjacent areas. At least one species of freshwater mollusks, *Radix gebleri* (von Middendorff, 1851), which type locality was stated as "Barnaul" (von Middendorff, 1851), is, actually, an endemic to Lake Zaysan in East Kazakhstan, a lake to which the Black Irtysh is emptied (see Vinarski, 2009 for details). It is reasonable to suggest that *Unio* shells brought back to Europe by the Humboldt expedition were collected somewhere in the Black Irtysh Basin, not in vicinities of Barnaul, and were donated by Gebler to von Humboldt and his colleagues when they meet in Barnaul in 1829. Though we have no direct evidence of this fact, such an assumption fits all known data and, if right, gives another support for the existence of a relic population of *U. tumidus* in the upper courses of the Irtysh River basin.

Another haplotype of *U. tumidus* from the Black Irtysh River is identical to that found in the samples collected from West Kazakhstan and European Russia. Considering the geography of dispersal and the presence of new haplotypes in the samples from European Russia, which appears a result of the long-term presence of this species in the territory, it is highly likely that the discussed haplotype *U. tumidus* is of European origin. We could assume that it was transferred to the Irtysh River basin by humans, most likely during the repeated stocking of reservoirs of the Upper Irtysh in the last half of the 20th century (Devyatkov, 2013, 2009). The parasitic larvae (glochidia) of freshwater mussels might have been brought to the Bukhtarma Reservoir with their host fishes. Several species of alien crustaceans as well as three other non-indigenous species of freshwater mollusks, *Viviparus viviparus* (Linnaeus, 1758), *Lithoglyphus naticoides* (Pfeiffer, 1828), and *Borysthenia naticina* (Menke, 1830), have been registered from this reservoir (Yanygina, 2016), which makes it a regional hotspot of alien diversity in Kazakhstan. The three species of invasive mollusks listed above seemingly reached there as a result of unintentional introductions.

Currently, *Unio* mussels are widespread in the Bukhtarma Reservoir and, though they are absent from the two other large reservoirs of the Upper Irtysh, the Ust-Kamenogorsk and Shulbinsk reservoirs (Devyatkov, 2011, 2010, 2009; Yanygina, 2016), were recently found downstream in a channel of the Irtysh River near Omsk City and upstream in the Black Irtysh River (see Fig. 1; Table 1).

4.2. An ongoing invasion of Unio from Europe?

Unio pictorum from the Tobol River basin share a single haplotype previously found in populations of this species in European Russia. Probably, the species entered the Irtysh River basin via water connections with the European riverine systems, most likely the Volga-Kama River basin (Andreyeva et al., 2009).

We cannot report here any evidence of the direct human involvement in the dispersal of *Unio* mussels eastward of the Ural Ridge; most likely, the mollusks are being spread using fish as hosts of their glochidia. The upper reaches of the Kama and Ural basins and the western tributaries of the Irtysh River are located in close proximity, their natural connections are quite likely, especially during periods of floods; in addition, there are canals that connect the Volga-Kama basin with the Ob'-Irtysh basin (Korlyakov and Nokhrin, 2014). However, the river basins probably had connections even before these canals were built in the first part of the 20th century. Several instances of the relatively recent dispersal of fishes across the Ural Ridge from Europe to Siberia are known (Makhrov et al., 2021; Schtylko, 1934).

If the idea of the almost complete Pleistocene extinction of the genus *Unio* in Siberia is correct, then this species should be considered as an alien to the modern Siberian malacofauna. The findings of *U. pictorum* in the Irtysh River basin may be thus viewed as a natural recovery of its former, pre-Holocene, range. Similarly, the recent dispersal of the common river snail, *Viviparus viviparus*, which became extinct in Siberia in the Pleistocene (Maderni, 1974; Zykin, 2012, 1979), throughout the southern part of Western Siberia (Babushkin and Vinarski, 2017; Vinarski et al., 2015; Yanygina, 2020, 2012) may be viewed as its former range recovery. However, in contrast to *Unio* mussels, the ongoing dispersal of this snail has been made possible exclusively by means of human activity (Vinarski et al., 2015; Yanygina, 2020); we have no confirmation of the natural crossing of the Europe-Asia boundary by this species.

The results of the current study demonstrate that we are observing a gradual northward and eastward spread of *U. pictorum*, from the eastern slope of the Ural Ridge (Andreyeva et al., 2009) to the lower reaches of the Tobol River basin and beyond, which took place over the past three decades. Some species of fish have earlier passed the same way (Makhrov et al., 2021; Schtylko, 1934), which might have facilitated the dispersal of the parasitic larval stages of the unionid mussels. This is precisely that migratory “route” along which in the Pleistocene-Holocene and, probably, in earlier epochs, numerous freshwater mollusk species of European origin penetrated Siberia (Starobogatov, 1970).

The rate of the current range extension of *U. pictorum* in Northern Asia seems to be very fast. Indeed, while in the mid-1990s all known localities were limited to near-watershed areas on the territory of the Ural Highland, in 2005–2010 several localities of these mussels were discovered in the rivers of the West Siberian Plain (Tobol River basin). In 2020, we discovered a large naturalized population of *U. pictorum* in the lower course of the Tobol River basin (No. 35, 44, and 47 in Table 1 and Fig. 1). In these sites, the mussels were represented by individuals of different sizes and ages, juveniles predominated, the aggregations reached several dozen individuals per square meter, and numerous empty shells were found on the shore. It has shown that the mussels find favorable life conditions in the waterbodies and watercourses of the middle part of the Irtysh River basin, and, probably, the press of predators and competitors is greatly relaxed or even absent here. We highly expect the further fast expansion of *U. pictorum* and, perhaps, *U. tumidus*, throughout the southern part of Western Siberia.

The natural sources of migration of the mussels are the Volga-Kama River basin and, possibly, the Ural River basin, which are inhabited by three species of the genus *Unio* (Bolotov et al., 2020; Pirogov et al., 1994; Zhadin, 1938). From the zoogeographic point of view, the South Urals and, especially, the Middle Ural Ridge do not act as an effective geographic barrier preventing the dispersal of mollusks. These mountains are not very high (usually up to 1000 m), and in some places, the upper reaches of the rivers belonging to the Volga-Kama and Ob' basins can merge, so that aquatic animals obtain the physical ability to move from one basin to another. This is especially easy for the unionid mussels using the parasitic larval stage as the means of their dispersal. Fish, being actively distributed organisms and also restoring the once lost parts of their former ranges in Siberia (Makhrov et al., 2021), can serve as agents ensuring efficient transfer of glochidia from one river basin to another. This makes it possible to understand the mechanisms of the appearance of unionids in the uppermost parts of the rivers flowing from the Ural Ridge to the East, and their further dispersal downstream to the West Siberian Plain.

4.3. Unio mussels in Transbaikalia

Another haplotype of *U. pictorum*, widespread in European Russia, Western and Southern Europe, and Western Asia, was found in the Lake Kenon of Transbaikalia (see Fig. 1; Table 1). The presence of *U. tumidus* in Transbaikalia was also pre-confirmed by our molecular genetic data, although this species was recorded at the larval stage only (Bolotov et al., 2020). In particular, a *COI* sequence (GenBank accession No. MK603940) was generated from a glochidium collected on the gills of Sharp-Snouted Lenok *Brachymystax lenok* (Pallas, 1773) from the Ingoda River, close to Lake Kenon. Along with the limited distribution and the remoteness from the native ranges, these facts indicate the establishment of these species in Transbaikalia (Upper Amur River basin), resulting from their intentional or unintentional introduction, most probably with introduced host fish. Despite the presence of *U. tumidus* shells in the Pleistocene deposits of the Baikal Lake area (Popova, 1981), we lack any evidence that the Lake Kenon mussels originate from a relic population that survived in a certain refugium.

Our conclusion about the very recent and fast dispersal of *Unio* mussels across the Ural Ridge from Europe to Siberia sheds light on the almost complete absence of specimens of this genus from the Ob' Basin in the largest malacological repositories of Russia and their recent "sudden" appearance in the collections. It remains inexplicable why these mollusks could not disperse to the West Siberian Plain in former times, since the connection of the Volga-Kama and Ob' basins, most likely, arose much earlier than the artificial channels connected them (e.g., Levin et al., 2017; Tomilova et al., 2020), which took place only in the first part of the 20th century.

An alternative assumption explaining the absence of information on the existence of *Unio* freshwater mussels in Siberia by their extreme rarity, combined with an insufficient sampling effort during the last centuries, looks unconvincing and, in our opinion, is unlikely. It is highly improbable that these large and conspicuous bivalves would go totally unnoticed by the prominent researchers of the Ob' Basin malacofauna. Therefore, even if the western parts of the Ob' Basin, situated on the eastern slope of the Ural Ridge, have long been inhabited by *Unio* mussels which remained overlooked until recently, their very recent dispersal to the West Siberian Plain can be considered a firmly established fact.

5. Conclusions

Since the end of the 19th century, two freshwater mussel species of the genus *Unio* (*U. pictorum* and *U. tumidus*) have been repeatedly recorded in Ob' River basin, and these finds are confirmed both morphologically and genetically. In the course of this study, the number of known occurrences of these mussels in the waterbodies of Asiatic Russia and Kazakhstan has drastically increased, and the third species, globally endangered *U. crassus*, was found in the Ob' River basin. It is reasonable to conclude that we are currently observing the ongoing recovery process of *Unio* former (North Asiatic) range's part. The origin of invasive freshwater mussels in Lake Kenon (Transbaikalia), as well as the presence of a European haplotype of *U. tumidus* in the Upper Irtysh basin, should, most likely, be explained by human-mediated introductions. Conversely, in the lower courses of the Irtysh Basin, we probably observe the continuing natural expansion of *U. pictorum* from the Volga-Kama basin, occurring without direct human participation. The unique *U. tumidus* haplotype from the Upper Irtysh is probably of relic origin, which may indicate the presence of a Pleistocene refugium in this area. Recently, Tomilova et al. (2020) demonstrated the significant role of refugia in the formation of the current ranges of unionid mussels, as exemplified by the Duck Mussel *A. anatina*.

As a consequence of natural environmental changes and increased human activity during the last century, several genera of freshwater Mollusca that previously inhabited Western Siberia, but went completely extinct in the Pleistocene, have started to recover the North Asiatic part of their former ranges. There are at least four alien mollusk genera of European origin (*Unio*, *Viviparus*, *Borysthenia*, and *Lithoglyphus*) in the Bukhtarma Reservoir alone (Devyatkov, 2013, 2009; Yanygina, 2016; our data). The case of *Unio* is, however, exceptional, since the recovery of its lost range in Siberia goes not exclusively with the humans' help but also involves the natural mechanisms of dispersal and range extension.

Author statement

Evgeny S. Babushkin: Conceptualization, Methodology, Software, Investigation, Resources, Writing - Original Draft, Visualization, Project administration, Funding acquisition.

Maxim V. Vinarski: Conceptualization, Methodology, Investigation, Resources, Writing - Review & Editing, Visualization, Funding acquisition.

Alexander V. Kondakov: Methodology, Software, Validation, Formal analysis, Investigation, Visualization.

Alena A. Tomilova: Methodology, Investigation, Visualization.

Maxim E. Grebennikov: Investigation.

Vitaly A. Stolbov: Investigation, Resources, Visualization.

Ivan N. Bolotov: Conceptualization, Methodology, Validation, Resources, Writing - Review & Editing.

Funding

The fieldwork, literature review, and examination of museum collections were supported by the Russian Foundation for Basic Research [project 19-04-00270], Russian Foundation for Basic Research, and Tyumen Region [project 20-44-720008], and the Department of Education and Youth Policy of the Khanty-Mansiysk Autonomous Okrug–Yugra. The molecular analyses were supported by the Russian Science Foundation [project 19-14-00066]. Open Access to the article was supported by the Russian Foundation for Basic Research and Tyumen Region [project 20-44-720008].

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

The authors are grateful to the curators of the malacological collections examined during our work: P.V. Kiyashko, L.L. Yarokhnovich (ZIN), and N.G. Erokhin (IPAE), for their invaluable help. We also grateful to the editor and referees for their valuable comments that helped us to improve the earlier version of the manuscript.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.limno.2021.125903.

References

Andreyeva, S.I., Vinarski, M.V., Karimov, A.V., 2009. The first record of *Unio* species (Bivalvia: Unionidae) in the Irtysh River basin (Western Siberia, Russia). Mollusca 27, 87–91.

Araujo, R., Buckley, D., Nagel, K.-O., García-Jiménez, R., Machordom, A., 2018. Species boundaries, geographic distribution and evolutionary history of the Western Palaearctic freshwater mussels *Unio* (Bivalvia: Unionidae). Zool. J. Linn. Soc. 182, 275–299. https://doi.org/10.1093/zoolinnean/zlx039.

Babushkin, E.S., Vinarski, M.V., 2017. First finding of the freshwater mollusc *Viviparus viviparus* (Linnaeus, 1758) in the River Tura (the Tyumen Region). Fauna Urala i Sibiri. 1, 19–24 (in Russian).

Bandelt, H.J., Forster, P., Rohl, A., 1999. Median-joining networks for inferring intraspecific phylogenies. Mol. Biol. Evol. 16, 37–48. https://doi.org/10.1093/oxfordjournals.molbev.a026036.

Bogachev, V.V., 1961. Materials to the History of Freshwater Fauna of Eurasia. Academy of Science of USSR, Kiev (in Russian).

Bogachev, V.V., 1966. The great unionid extinction in Siberia. Quat. Study Comm. Bull. 32, 96–99 (in Russian).

Bogan, A.E., 2008. Global diversity of freshwater mussels (Mollusca: Bivalvia) in freshwater. Hydrobiologia 595, 139–147. https://doi.org/10.1007/s10750-007-9011-7.

Bogan, A.E., Roe, K.J., 2008. Freshwater bivalve (Unioniformes) diversity, systematics, and evolution: status and future directions. J. North Am. Benthol. Soc. 27, 349–369. https://doi.org/10.1899/07-069.1.

Bolotov, I.N., Kondakov, A.V., Konopleva, E.S., Vikhrev, I.V., Aksenova, O.V., Aksenov, A.S., Bespalaya, Y.V., Borovskoy, A.V., Danilov, P.P., Dvoryankin, G.A., Gofarov, M.Y., Kabakov, M.B., Klishko, O.K., Kolosova, Y.S., Lyubas, A.A., Novoselov, A.P., Palatov, D.M., Savvinov, G.N., Solomonov, N.M., Spitsyn, V.M., Sokolova, S.E., Tomilova, A.A., Froufe, E., Bogan, A.E., Lopes-Lima, M., Makhrov, A. A., Vinarski, M.V., 2020. Integrative taxonomy, biogeography and conservation of freshwater mussels (Unionidae) in Russia. Sci. Rep. 10 https://doi.org/10.1038/s41598-020-59867-7.

Devyatkov, V.I., 2009. Macrozoobenthos. In: Bazhenova, O.P. (Ed.), Successions of the Bukhtarma Reservoir Biocenoses. Omsk State Agricultural University, Omsk, pp. 95–119 (in Russian).

Devyatkov, V.I., 2010. Macrozoobenthos of Shulbinsk reservoir. Selevinia, pp. 107–111 (in Russian).

Devyatkov, V.I., 2011. Macrozoobenthos of Ust-Kamenogorsk reservoir. Selevinia, pp. 53–57 (in Russian).

Devyatkov, V.I., 2013. Macrozoobenthos of Bukhtarma reservoir in 2005–2009. Selevinia 21, 43–48 (in Russian).

Ferreira-Rodríguez, N., Akiyama, Y.B., Aksenova, O.V., Araujo, R., Christopher Barnhart, M., Bespalaya, Y.V., Bogan, A.E., Bolotov, I.N., Budha, P.B., Clavijo, C., Clearwater, S.J., Darrigran, G., Do, V.T., Douda, K., Froufe, E., Gumpinger, C., Henrikson, L., Humphrey, C.L., Johnson, N.A., Klishko, O., Klunzinger, M.W., Kovitvadhi, S., Kovitvadhi, U., Lajtner, J., Lopes-Lima, M., Moorkens, E.A., Nagayama, S., Nagel, K.-O., Nakano, M., Negishi, J.N., Ondina, P., Oulasvirta, P., Prié, V., Riccardi, N., Rudzīte, M., Sheldon, F., Sousa, R., Strayer, D.L., Takeuchi, M., Taskinen, J., Teixeira, A., Tiemann, J.S., Urbańska, M., Varandas, S., Vinarski, M.V., Wicklow, B.J., Zając, T., Vaughn, C.C., 2019. Research priorities for freshwater mussel conservation assessment. Biol. Conserv. 231, 77–87. https://doi.org/10.1016/j.biocon.2019.01.002.

Froufe, E., Gonçalves, D.V., Teixeira, A., Sousa, R., Varandas, S., Ghamizi, M., Zieritz, A., Lopes-Lima, M., 2016. Who lives where? Molecular and morphometric analyses clarify which *Unio* species (Unionida, Mollusca) inhabit the southwestern Palearctic. Org. Divers. Evol. 16, 597–611. https://doi.org/10.1007/s13127-016-0262-x.

Graf, D.L., Cummings, K.S., 2019. Unionidae Rafinesque, 1820 and the General unionida. In: Lydeard, Ch, Cummings, K.S. (Eds.), Freshwater Mollusks of the World. John Hopkins University Press, Baltimore, pp. 202–209.

Graf, D.L., Cummings, K.S., 2021a. A 'big data' approach to global freshwater mussel diversity (Bivalvia: Unionoida), with an updated checklist of genera and species. J. Mollus. Stud. 87 https://doi.org/10.1093/mollus/eyaa034.

Graf, D.L., Cummings, K.S., 2021b. The Freshwater mussels (Unionoida) of the world (and other less consequential bivalves). MUSSEL Project Web Site [WWW Document]. URL http://mussel-project.uwsp.edu/ (Accessed 2.26.21).

Ioganzen, B.G., 1951. Freshwater mollusks in the vicinity of Tomsk. Proc. Tomsk. State Univ. Control. Syst. Radioelectron. 115, 291–302 (in Russian).
Ioganzen, B.G., Novikov, E.A., 1969. To the Study of Freshwater Mollusks in the Middle Ob' Basin, in: Problems of Siberian Malacology. Tomsk State University, Tomsk, pp. 39–43 (in Russian).
Ioganzen, B.G., Novikov, E.A., 1971. Freshwater mollusks from the middle Ob' waterbodies. Ecological Problems, pp. 47–52. Tomsk (in Russian).
Khokhutkin, I.M., Erokhin, N.G., Grebennikov, M.E., 2003. Mollusks: Biodiversity, Ecology (Catalogs of the Collection of the Zoological Museum of the Institute of Plant and Animal Ecology, Ural Branch of the Russian Academy of Sciences). Ural Branch of the RAS, Yekaterinburg (in Russian).
Klishko, O., Lopes-Lima, M., Froufe, E., Bogan, A., Vasiliev, L., Yanovich, L., 2017. Taxonomic reassessment of the freshwater mussel genus *Unio* (Bivalvia: Unionidae) in Russia and Ukraine based on morphological and molecular data. Zootaxa 4286, 93. https://doi.org/10.11646/zootaxa.4286.1.4.
Korlyakov, K.A., Nokhrin, D.Y., 2014. Trends in the emergence of the Volga-Ob' invasion corridor. Bull. Counc. Young Sci. Spec. Chelyabinsk Reg. 2, 19–38 (in Russian).
Kuzmenkin, D.V., 2013. The habitat distribution of freshwater mollusks in the plain part of upper Ob' basin. Bull. Altai State Univ. 3–1, 80–85 (in Russian).
Kuzmenkin, D.V., 2015. Ecological and Faunal Characteristics of Freshwater Mollusks in the Upper Ob' River Basin. PhD Thesis. Tomsk State University (in Russian).
Levin, B.A., Simonov, E.P., Ermakov, O.A., Levina, M.A., Interesova, E.A., Kovalchuk, O. M., Malinina, Y.A., Mamilov, N.S., Mustafayev, N.J., Pilin, D.V., Pozdeev, I.V., Prostakov, N.I., Roubenyan, H.R., Titov, S.V., Vekhov, D.A., 2017. Phylogeny and phylogeography of the roaches, genus *Rutilus* (Cyprinidae), at the Eastern part of its range as inferred from mtDNA analysis. Hydrobiologia 788, 33–46. https://doi.org/10.1007/s10750-016-2984-3.
Lindholm, W.A., 1932a. Freshwater Mollusks From Pliocene Sediments Along the Irtysh. Geolrazvedgiz, Leningrad, Moscow (in Russian).
Lindholm, W.A., 1932b. Mollusks From the Middle Pliocene Freshwater Deposits of Southwestern Siberia. Geolrazvedgiz, Leningrad, Moscow (in Russian).
Lopes-Lima, M., Sousa, R., Geist, J., Aldridge, D.C., Araujo, R., Bergengren, J., Bespalaya, Y., Bódis, E., Burlakova, L., Van Damme, D., Douda, K., Froufe, E., Georgiev, D., Gumpinger, C., Karatayev, A., Kebapçi, Ü., Killeen, I., Lajtner, J., Larsen, B.M., Lauceri, R., Legakis, A., Lois, S., Lundberg, S., Moorkens, E., Motte, G., Nagel, K.-O., Ondina, P., Outeiro, A., Paunovic, M., Prié, V., von Proschwitz, T., Riccardi, N., Rudzīte, M., Rudzītis, M., Scheder, C., Seddon, M., Şereflişan, H., Simić, V., Sokolova, S., Stoeckl, K., Taskinen, J., Teixeira, A., Thielen, F., Trichkova, T., Varandas, S., Vicentini, H., Zajac, K., Zajac, T., Zogaris, S., 2017. Conservation status of freshwater mussels in Europe: state of the art and future challenges. Biol. Rev. 92, 572–607. https://doi.org/10.1111/brv.12244.
Lopes-Lima, M., Burlakova, L.E., Karatayev, A.Y., Mehler, K., Seddon, M., Sousa, R., 2018. Conservation of freshwater bivalves at the global scale: diversity, threats and research needs. Hydrobiologia 810, 1–14. https://doi.org/10.1007/s10750-017-3486-7.
Maderni, U.N., 1974. On the most probable causes of the extinction of viviparids and unionids in Kazakhstan and Western siberia. Biostratigraficheskiy Sbornik, pp. 185–191. Leningrad (in Russian).
Maderni, U.N., 1990. Mollusks of the Continental Cenozoic of the Turgai Trough and Adjacent Regions. Nedra, Leningrad (in Russian).
Makhrov, A.A., Vinarski, M.V., Gofarov, M.Y., Dvoryankin, G.A., Novoselov, A.P., Bolotov, I.N., 2021. Faunal exchanges between the basins of the Arctic Ocean and the Caspian Sea: their history and current processes. Biol. Bull. 48, 28–42. https://doi.org/10.1134/S1062359021070190.
Mozley, A., 1936. The freshwater and terrestrial Mollusca of Northern Asia. Trans. R. Soc. Edinb. Earth Sci. 58, 605–695.
Nikolayev, V.A., 1938. Some new data on the fauna of Unionidae of the West Siberian Plain. Vestn. Zapadn. Geol. tresta 1, 25–31 (in Russian).
Novikov, E.A., 1971. Freshwater Mollusks in the Middle Reaches of the Ob River Basin. PhD Thesis. Tomsk State University (in Russian).
Pirogov, V.V., Tarasov, A.G., Kazantseva, S.Z., 1994. Malacofauna of typical waterbodies of the middle and lower Ural River. Ruthenica Russ. Malacol. J. 4, 61–65.
Popova, S.M., 1981. The Cenozoic Continental Malacofauna of Southern Siberia and Adjacent Territories. Nauka, Moscow (in Russian).
Schtylko, B.A., 1934. Neogene fauna of fresh-water fishes from Western Siberia. Transactions of the United Geological and Prospecting Service of USSR, pp. 1–108. Leningrad, Moscow, Novosibirsk (in Russian).
Starobogatov, Y.I., 1970. Molluscan Fauna and Zoogeographic Zonation of Continental Freshwater Bodies of the World. Nauka, Leningrad (in Russian).
Starobogatov, Y.I., 1986. The fauna of lakes as the source of information on their history. General Peculiarities of the Origin and Evolution of Lakes. Nauka, Leningrad, pp. 33–50 (in Russian).
Starobogatov, Y.I., Prozorova, L.A., Bogatov, V.V., Sayenko, E.M., 2004. Mollusks. In: Tsalolikhin, S.Y. (Ed.), Key to Freshwater Invertebrates of Russia and Adjacent Lands. Nauka, Saint-Petersburg, pp. 6–492 (in Russian).
Stolbov, V.A., Voronova, K.P., 2019. The infestation of mussels (Bivalvia: unionidae) by water mites of the genus *Unionicola* (Acari: Hydrachnidia: Unionicolidae) in water bodies of the south of Western Siberia. Parazitologiya 53, 220–229. https://doi.org/10.1134/S0031184719030049 (in Russian).
Tomilova, A.A., Kondakov, A.V., Kisil, O.Y., 2019. Usage of transcribed spacers ITS1 and ITS2 for identification of freshwater mussels of the genera *Anodonta* and *Pseudoanodonta* (Bivalvia: Unionidae: Anodontinae). Zh. Obshch. Biol. 80, 364–371. https://doi.org/10.1134/S0044459619050075 (in Russian).
Tomilova, A.A., Lyubas, A.A., Kondakov, A.V., Vikhrev, I.V., Gofarov, M.Y., Kolosova, Y. S., Vinarski, M.V., Palatov, D.M., Bolotov, I.N., 2020. Evidence for plio-pleistocene duck mussel refugia in the Azov Sea River Basins. Diversity 12, 118. https://doi.org/10.3390/d12030118.
Vinarski, M.V., 2009. The taxonomic status of *Limnaeus gebleri* Middendorff, 1851 (Gastropoda: Pulmonata: Lymnaeidae). Mollusca 27, 149–156.
Vinarski, M.V., 2010. A historical outline of study of Siberian freshwater malacofauna (end of XVIII – middle of XX centuries). Ruthenica Russ. Malacol. J. 20, 45–67 (in Russian).
Vinarski, M.V., 2016. Eduard von Martens's contribution to the knowledge of the Russian continental malacofauna (with examination of type materials of aquatic species accepted by Russian taxonomists). Ruthenica Russ. Malacol. J. 26, 1–16.
Vinarski, M.V., 2020. Alan Mozley: an american malacologist in Siberia (1932–1933). Folia Malacol. 28, 326–336. https://doi.org/10.12657/folmal.028.022.
Vinarski, M.V., Andreev, N.I., Andreeva, S.I., Kazantsev, I.E., Karimov, A.V., Lazutkina, E.A., 2015. Alien mollusk species in the aquatic ecosystems of Western Siberia: a review. Russ. J. Biol. Invasions 6, 137–147. https://doi.org/10.1134/S2075111715030078.
von Martens, E., 1875. Russische und sibirische conchylien von Ehrenberg gesammelt. Sitzungsberichte Der Gesellschaft Naturforschender Freunde Zu Berlin, pp. 88–96.
von Middendorff, A.Th, 1851. Mollusks. In: von Middendorff, A.Th (Ed.), Reise in Der äussersten Norden Und Osten Sibiriens Während Der Jahre 1843 Und 1844. Saint-Petersburg: Kaiserlich Akademie Der Wissenschaften, 2, pp. 163–465 (1).
Yanygina, L.V., 2012. The role of *Viviparus viviparus* (L.) (Gastropoda, Viviparidae) in formation of macrozoobenthos communities in the Novosibirsk Reservoir. Russ. J. Biol. Invasions 3, 64–70. https://doi.org/10.1134/S2075111712010146.
Yanygina, L.V., 2016. Regional features of alien macroinvertebrate invasion into the water ecosystems of the Ob River basin. Contemp. Probl. Ecol. 9, 384–390. https://doi.org/10.1134/S1995425516030161.
Yanygina, L.V., 2020. Community-level effects of a *Viviparus viviparus* L. (Gastropoda, Viviparidae) invasion in the Novosibirsk reservoir. Limnology 21, 165–171. https://doi.org/10.1007/s10201-019-00580-4.
Zhadin, V.I., 1938. Family Unionidae, in: Fauna of USSR. Mollusks. USSR Academy of Sciences, Moscow, Leningrad, pp. 1–170 (in Russian).
Zhadin, V.I., 1952. Mollusks of fresh and brackish waters of the USSR. Keys to the Fauna of the USSR Published by the Zoological Institute of the USSR Academy of Sciences. Leningrad, Moscow, pp. 1–376 (in Russian).
Zieritz, A., Froufe, E., Bolotov, I., Gonçalves, D.V., Aldridge, D.C., Bogan, A.E., Gan, H. M., Gomes-Dos-Santos, A., Sousa, R., Teixeira, A., Varandas, S., Zanatta, D., Lopes-Lima, M., 2020. Mitogenomic phylogeny and fossil-calibrated mutation rates for all F- and M-type mtDNA genes of the largest freshwater mussel family, the Unionidae (Bivalvia). Zool. J. Linnean Soc. https://doi.org/10.1093/zoolinnean/zlaa153 zlaa153.
Zykin, V.S., 1979. Stratigraphy and the Pliocene Unionids of the South of the West Siberian Plain. Nauka, Novosibirsk (in Russian).
Zykin, V.S., 2012. Stratigraphy and evolution of the natural environment and climate in the Late Cenozoic of the south of Western Siberia. Geo, Novosibirsk (in Russian).