



Article

Beringian Freshwater Mussel *Beringiana beringiana* (Unionidae) in Northeast Asia

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Abstract: The origin of the fauna of Beringia is a notable biogeographical puzzle. Large mussels of the genus *Beringiana* inhabit both Northeast Asia and the northwestern part of North America and thus provide an important model to investigate the paleobiogeography of Beringia and the past and current intercontinental species exchanges. Data on *Beringiana* distribution, morphology, genetics, and taxonomy are fragmentary or questionable. In this study, we summarized the data on its distribution in Northeast Asia, performed genetic analysis (*cox1*), and studied the variation in the shell morphology in samples from four isolated populations, including the putative sympatric species. Over ten large enclaves of *Beringiana* are currently known in Northeast Asia (east to the Verkhoyansk Range), mostly in the lower reaches of large rivers in northeastern Yakutia, Kamchatka, Magadan Oblast, and Khabarovsk Krai. These enclaves are far apart (several hundreds of kilometers) because the mussel is associated with muddy sand or pebbly sand bottom substrates and spreads through its glochidia, which are parasitic on the fish. Shell morphology can be highly variable even in a single population, overlapping the diagnoses of several *Beringiana* species (which are currently not recognized as valid). Our analysis of the *cox1* sequence in four populations identified all individuals as *B. beringiana*. We evaluated the possible current and probable Late Pleistocene–Early Holocene freshwater and marine pathways of *B. beringiana* dispersal through the area of former Beringia, including the current intercontinental migration of glochidia on fish.

Keywords: Beringia; genetic variation; conchological traits; glochidia; dispersal; phylogeography



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1. Introduction

Animal and plant taxa that are found in both Northeast Asia and the northwestern part of North America attract particular attention because these regions belong to ancient Beringia, where a land bridge existed to connect the two continents quite recently. The distribution and ecology of this group of organisms, known as Beringians, helps one to understand many issues in paleogeography and the genesis of flora and fauna in the region of past contacts between the two continents. The history of aquatic fauna of Beringia was recently reviewed in several publications [1–6].

The genus *Beringiana* Starobogatov in Zatravkin, 1983, comprises large mussels belonging to the family Unionidae. Its taxonomy and ecology are still under dispute. *Beringiana* is recognized as a Beringian species and is known to inhabit freshwater habitats on both continents. Its range in Asia includes Japan, the south of the Russian Far East, Sakhalin, Kamchatka, the Kuril Islands, and the basins of certain Arctic seas such as the Chukchi, East

Siberian, and probably the Laptev seas. These mollusks were also detected in the basins of a few rivers that flow into the Bering Sea and the Sea of Okhotsk. In North America, *Beringiana* is found in the basins of rivers that flow into the North Pacific.

The taxonomy of the genus *Beringiana* changed significantly over time, and there is still no consensus. As many as nine species were described based primarily on conchological traits, most of them from the Russian Far East, where multiple species were sometimes observed in the same water bodies. For instance, three sympatric species: *Beringiana beringiana* (Middendorff, 1851), *B. youkonensis* (Lea, 1867), and *B. kamchatica* Bogatov et Starobogatov, 2001, were found in the basins of the Kava and Ola rivers in Magadan Oblast [7,8]. In addition, *B. beringiana*, *B. youkonensis*, *B. kamchatica*, *B. derzhavini* Bogatov et Starobogatov, 2001, and *B. chershnevi* Bogatov et Starobogatov, 2001, were detected in various combinations in water bodies of the Kamchatka River basin [9].

After several revisions [10–12], over a dozen species from several synonymized genera (*Kunashiria* and *Arsenievinaia*) were included in the genus *Beringiana*. The number of species in the genus was reduced to four in recent genetic studies. Only one of the species, *B. beringiana*, is found in Russia, while the greatest diversity (all four species) is observed in Japan [13–15]. Bogatov [16] has compared the transversal contours of the shell in *B. beringiana* and isolated three “comparatory” subspecies and an intraspecific form: *B. b. beringiana*, *B. b. kamchatica*, *B. b. youkonensis*, and *B. b. f. compressa* (see [17,18] for comparatory method description).

For the southern part of the Russian Far East, there is abundant information on *B. beringiana* distribution, morphology, and DNA sequences, while much less is known on the northern part of the distribution [7–9,13–15,19–23].

Maps in the papers of Bolotov et al. [13] and Lopes-Lima et al. [14] depict the continuous distribution of *B. beringiana* in Yakutia river basins east of the Lena river, in Chukotka, Magadan oblast, and the north of the Khabarovsk krai. However, few *B. beringiana* samples are known from this region according to the literature and museum collections, and the respective river basins are far apart, separated by many hundreds of kilometers in many cases [8,9,24,25]. Moreover, DNA sequences of only two populations in Northeast Asia are available: one from a lake near the Belaya Gora village in the Indigirka River basin, and the other from the Bol’shaya River in Kamchatka [13,14]. *Beringiana* has a patchy distribution, so it makes sense to genotype more populations. New species might be found in island populations [26].

Based on this, we set the following objectives:

1. To summarize the available data on the *Beringiana* distribution in Northeast Asia east of the Verkhoyansk Range and the Okhota River basin;
2. To study conchological variation in *Beringiana*, including the cases of several species found in sympatry [7,8] and to study *cox1* variation in different morphs;
3. To analyze the possible *Beringiana* dispersion pathways given the high distances between its enclaves and, in particular, the distribution of the species on the two continents.

2. Materials and Methods

The study area included four localities in Northeast Asia. For two of them, this is the first report of *Beringiana*: the Medvezh’e Lake (Chukotka Autonomous Okrug, left bank area of the Anadyr River) and a lake near the Rezidentsiya village (Khabarovsk Krai, left bank area of the Kukhtuy River). For two other localities, *Beringiana* populations were reported earlier [7]: the Kava River basin with its Chukcha River tributary (system of the Chukcha, Malaya Chukcha, and Bezymyanka lakes) and the Ola River basin (Chistoe Lake).

B. beringiana is in the regional Red Data Book of Magadan Oblast and the Chukotka Autonomous District [8,22,24], so we examined only dead mussels that were washed up ashore after storms (Figure 1).

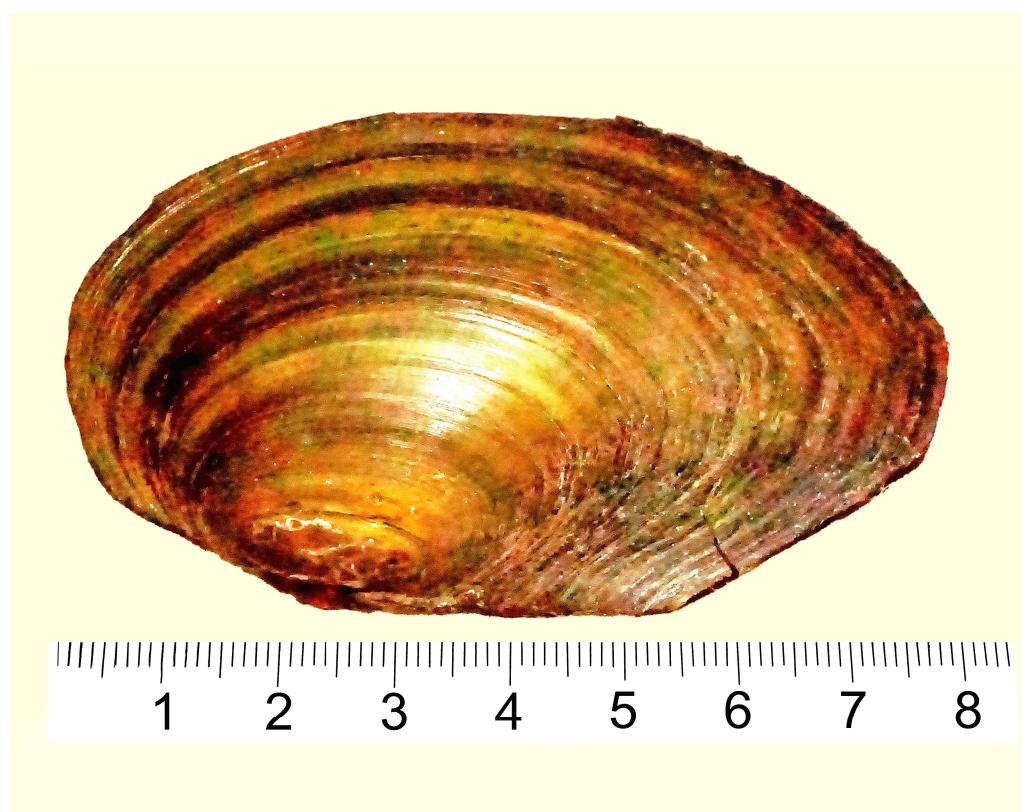


Figure 1. *Beringiana beringiana*. Magadan Oblast, Chukcha lake.

Genetic methods. Tissue samples for genetic testing were collected from well-preserved dead mussels. Tissue DNA isolation was successful in only eleven mussels (five from Chukcha Lake and two samples from each of the other three populations). DNA was isolated from soft tissue samples fixed with ethanol using BioSilica columns (Novosibirsk, Russia) according to a published protocol [27]. A fragment of the *cox1* mitochondrial gene was amplified with the universal primers LCOM and HCO [28] within project no. FWNR-2022-0022. DNA sequencing with BigDye 3.1 (Applied Biosystems, Waltham, Massachusetts, USA) was performed at the SB RAS Genomics Core Facility. The same primers were used for amplicon sequencing in both directions.

Sequencing data were analyzed and edited using Chromas 2.6.6 (<http://technelysium.com.au>; accessed on 10 February 2023). A haplotype network was constructed using the program Network 10.2.0.0 [29]. Molecular genetic indices (nucleotide and haplotype diversity, mismatch distribution) were calculated in Arlequin v.3.0 [30]. Maximum likelihood trees were built by RAxML v. 8.2.12 [31] with the GTRCAT model with 1000 bootstrap repetitions.

Shell morphology variation was studied in both live mussels, which were then returned to their water bodies, and dead ones collected on lake banks. In total, we examined 12 mussels near the village of Rezidentsiya, 31 in the Kava River basin, 18 in the Ola River basin, and 10 in the Anadyr River basin. Morphometric analysis was carried out as described in [16,19] using the identification keys of [9,10]. We measured the length (L), height (H), and convexity (B) of the shells; the distances between the apex (M) and the columella (N), and between the apex and the anterior margin of the shell (Lm).

***Beringiana* distribution map** in Northeast Asia was constructed using literature data, the collections of the Zoological Institute (Saint Petersburg), survey data, and original materials.

Statistical analysis was performed by standard methods using Statistica 10 for Windows. Values are reported as mean \pm SE. Comparison of morphological values was performed by the Mann–Whitney U-test. The level of significance was set at $p \leq 0.05$.

3. Results

3.1. Distribution

Data on the species distribution in Northeast Asia are summarized in Figure 2. We mapped all sites of *Beringiana* reports currently known in northeastern Yakutia, Chukotka, Kamchatka, Magadan Oblast, and northernmost Khabarovsk Krai, that is, an area east of the river Indigirka and Suntar-Khayata ranges.

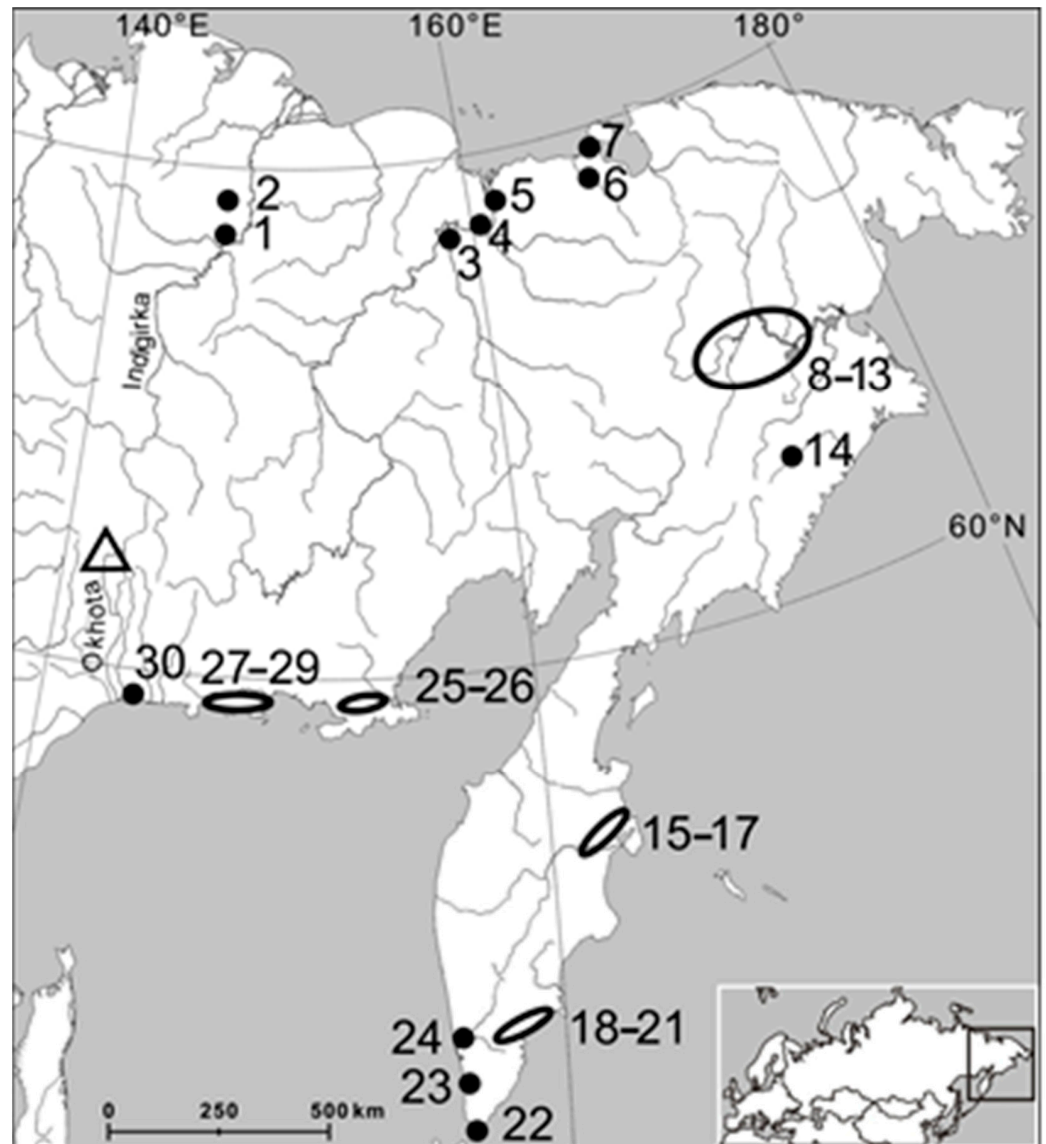


Figure 2. Detection sites (black dots and circles) currently known for mussels of the genus *Beringiana* in Northeast Asia. A bifurcation of the Del'kyu River is shown with a triangle. See Table S1 (References [32–36] are cited in the supplementary materials) for numerical designations.

3.2. Genetic Analysis

Cox1 sequences were obtained for 11 soft tissue samples of *Beringiana* mussels from four localities (Figure 3) and compared to GenBank sequences. All individuals were assigned to *B. beringiana*. All GenBank data available for the species were combined with our data, and a haplotype network was constructed for a pooled sample (Figure 4). In total, 11 haplotypes and 15 variable sites were observed in 39 sequences of the pooled sample. The majority (24 out of 39) sequences belonged to the same haplotype, while the other haplotypes were represented by 1 to 4 mussels each.

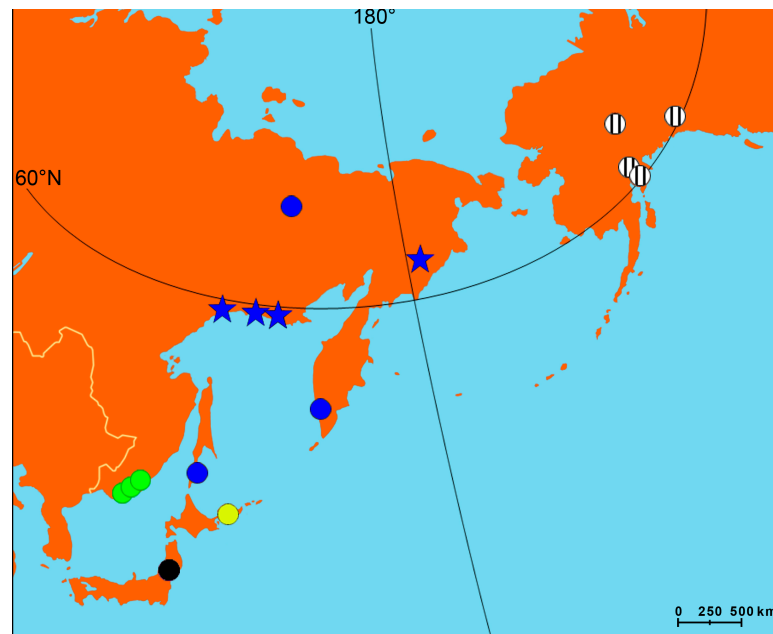


Figure 3. *Beringiana beringiana* populations with available *cox1* data. Circles, GenBank; stars, this study. See Figure 4 for color legend.

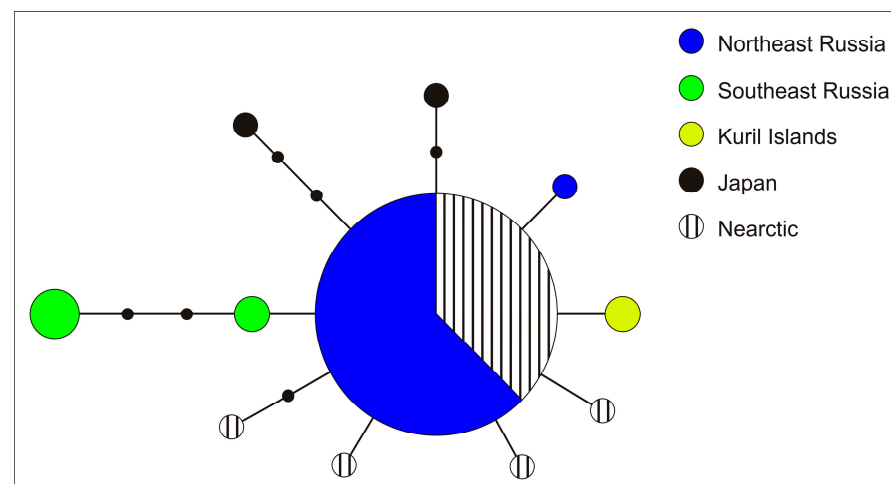


Figure 4. *Cox1* haplotype network of *B. beringiana*. Missing haplotypes are shown as dots.

Haplotype diversity for the whole dataset amounted to 0.6167 (SD, 0.0885), and nucleotide diversity was 0.002582 (SD, 0.00177). Both Tajima's D (-1.85995) and Fu's F_s (-5.06095) values were negative, with p -values of 0.012 and 0.004, respectively. For mismatch distribution, the observed frequency distribution and that expected under the population expansion model differed with borderline $p = 0.05$. Since southern haplotypes differed from northern ones, we calculated these indices for a dataset of 28 specimens that excluded the populations from Japan and Primorye. Tajima's D was -2.09646 (p -value = 0.00200) and Fu's F_s , -4.61217 (p -value $< 10^{-5}$). The observed mismatch distribution almost perfectly matched the expected one, with no statistical differences between the two distributions.

We constructed a phylogenetic tree for the available dataset of the four *Beringiana* species, *B. beringiana*, *B. japonica*, *B. fukuoharai*, and *B. gosannensis* (Figure 5). The datasets for the latter three species were taken from GenBank; all specimens were from various parts of the Japanese Archipelago. The monophyly of all four species was supported by bootstrap. Species identification of only one specimen was probably incorrect: accession LC519019 was submitted as *B. japonica*, while it was grouped together with *B. beringiana*.



Figure 5. Phylogenetic tree constructed using the maximum likelihood method for the *Beringiana* species. The tree is rooted at midpoint. Specimen names refer to GenBank accession or to our internal numbers. Numbers near branches indicate bootstrap support.

3.3. Conchological Analysis

Shell morphological traits used in the taxonomy of the genus *Beringiana* include not only descriptive characters (shape, umbo sculpture, nacre color, etc.) but also indices based on measurements and calculations. The following indices are most often used in identification keys [9,10]:

- The ratio of shell width (B) to shell height (H) characterizes the degree of prominence (a major trait) of the shell;
- The ratio of the distance between the apex (M) and nymph base (N) to the shell width (B);
- The ratio of the distance between the apex and the anterior margin (L_m) to the shell length (L);
- The ratio of the shell height (H) to the shell length (L) characterizes the general shape of the shell.

We calculated the main ratios used for species identification in the studied specimens. The results are summarized in Table 1. Figure 6 shows the variation in the B/H key diagnostic trait, which characterizes the degree of prominence of the shell.

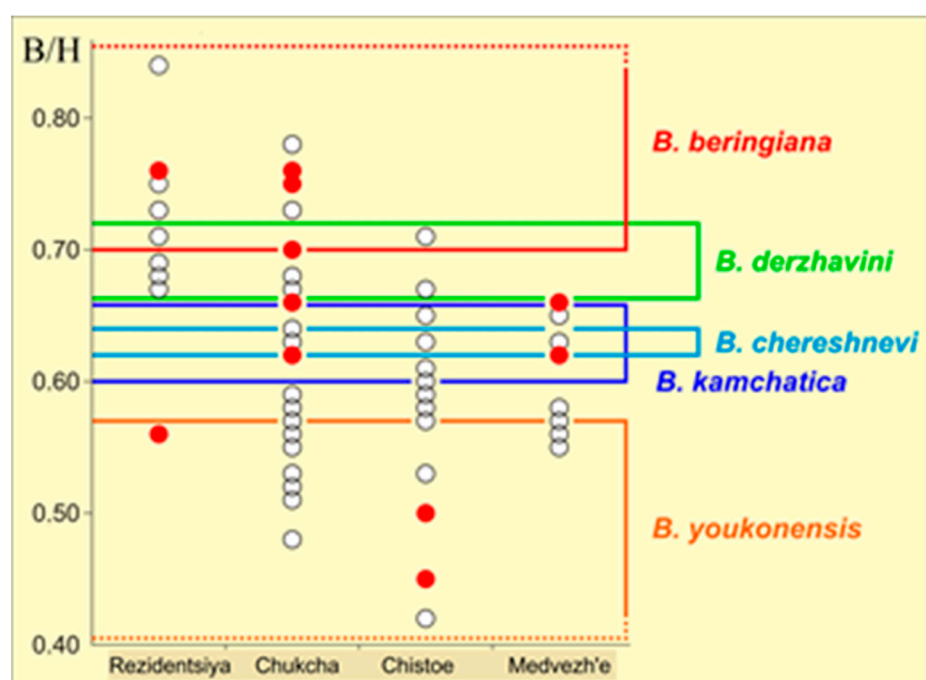
Based on the first trait $(M - N)/B$, the populations formed two groups, Rezidentsiya–Chukcha and Chistoe–Medvezh’e, with trait values being statistically similar within each of the groups and significantly different between the groups (U -test, $p = 0.001$).

A difference in L_m/L was observed only between the two western populations, Rezidentsiya and Chukcha (U -test, $p = 0.0003$).

The B/H ratio, which reflects the degree of prominence of the shell, was significantly higher in the Rezidentsiya population compared with the other populations (U -test, $p < 0.01$ in all cases) (Table 1).

Table 1. Mean values (mean \pm SEM) and coefficients of variation (Cv, %) of the main diagnostic conchological traits in the four *Beringiana* populations of Northeast Asia.

Population	Trait			
	$(M - N)/B$	L_m/L	B/H	H/L
Kukhtuy, n = 12	0.83 \pm 0.03 13.6	0.18 \pm 0.01 10.1	0.71 \pm 0.02 9.4	0.54 \pm 0.01 4.7
Chukcha, n = 31	0.82 \pm 0.02 14.5	0.22 \pm 0.01 13.9	0.63 \pm 0.01 13.2	0.60 \pm 0.01 5.5
Ola, n = 18	0.96 \pm 0.05 22.8	0.19 \pm 0.01 15.1	0.57 \pm 0.02 14.6	0.61 \pm 0.01 4.5
Anadyr, n = 10	0.96 \pm 0.04 12.8	0.20 \pm 0.01 15.0	0.61 \pm 0.01 6.7	0.57 \pm 0.01 6.4

**Figure 6.** Diagram of the B/H trait in the studied populations. Vertical axis, B/H value; horizontal axis, populations; colored frames indicate B/H values characteristic for the corresponding species. Individuals included in the genetic analysis are shown with red circles.

The H/L ratio varied from 0.51 to 0.64 in 97% of the shells examined, i.e., the shells were oval in shape according to Bogatov's [16] classification. Only two shells (3%) of the Chukcha population had higher values (0.65 and 0.66) and were consequently classified as ovate. Although the shell shape was the same in all populations, the easternmost (Medvezh'e) and westernmost (Rezidentsiya) populations differed in H/L from the populations of Magadan Oblast (U -test, $p < 0.01$ in both cases) (Table 1).

In each of the samples examined, the variation ranges of the traits were great and exceeded the respective ranges of several species described earlier. The mussels whose species identification was performed genetically in various populations were similarly found in the trait ranges of all the species described earlier (Figure 6).

4. Discussion

4.1. *Beringiana beringiana* Distribution in Northeast Asia

The published distribution maps of *B. beringiana* depict a continuous range in the Russian Far East [13]. However, the list of its findings (Figure 2) suggests that it occurs

as scattered enclaves, mostly associated with the lower reaches of large rivers (Indigirka, Kolyma, Anadyr, Kamchatka, and their tributaries). Reports of *B. beringiana* deep in the continent are rare. This species needs sandy or silty river beds, while rock beds prevail in Northeast Asia. Suitable habitats usually form in lower reaches, backwaters, or floodplain lakes.

B. beringiana is found in the middle and upper reaches only in rare cases (e.g., in the rivers Anadyr, Khatyrka, and Kava). These habitats are characterized by a low vertical drop, which results in vast floodplains with many distributaries and through-flowing lakes. This situation is characteristic of the middle reaches of the Anadyr River, in its part parallel to its tributary Mayn River (locations 8 and 9 in Figure 2), as well as in the basin of the mountainous Khatyrka River, where the floodplain Elergytkyn Lake is located in a vast intermountain depression (location 14 in Figure 2).

High population densities of *B. beringiana* are characteristic of many lakes belonging to the upper and middle basins of the Kava River (locations 27–29 in Figure 2). This territory lies in a vast glacier plain (40–60 km long and 120 km wide) covered by thick sand deposits. Low vertical drops and slow flow favor water heating [37]. *B. beringiana* was reported from five lakes in this region: Sbornoe, Chukcha, Malaya Chukcha, Bezmyanka, and Zaton, but we believe this list is not exhaustive. Bottom features are constant in through-flowing lakes even during floods, in contrast to backwaters. Due to these factors, the upstream basin of the Kava River probably has a population density of *B. beringiana* similar to other rivers in Northeast Asia.

Only two known *B. beringiana* populations in the region are found in large lakes, which are sources of the Ola River. One is Chistoe Lake, located in tundra (approximately 9×6.5 km, altitude 91 m) with a gray silt bottom and a substantial area of shallow depths with a sand or fine pebble bottom [37]. The other is the mountainous Kisi Lake (approximately 4×1.5 km, altitude 333 m), with the bottom formed by silt, rock grit, and rock fragments [38].

Based on our data collected in this study and the association of *B. beringiana* with certain bottom types, we believe it is far more widespread than is currently considered. Possible habitats in Chukotka may include the Velikaya and Tumanskaya rivers [24], Krasnoe Lake, and some other water bodies. *B. beringiana* may be found in many sites of the Kolyma River delta downstream of the Cherskii village because its shells are abundant in floodplain lakes and branches ([25]; S.P. Davydov, personal communication). In the lower reaches of the Indigirka River, shells of *B. beringiana* are not uncommon in floodplain lakes from the village of Belaya Gora to the Ozhogina River and Ozhogina Lake (S. Yu. Solomov, personal communication); *B. beringiana* is probably spread down to the river mouth.

Thus, although the range of *B. beringiana* spans approximately 10° of latitude ($59^\circ 30' - 69^\circ 30'$) from rivers of the Sea of Okhotsk to downstream regions of the Indigirka, Kolyma, and Anadyr rivers, it is highly fragmented and its populations are often several hundreds of kilometers apart.

4.2. Temperature of *B. beringiana* Habitats in Northeast Asia

The northeastern part of the *B. beringiana* range north to the 60th parallel is one of the coldest regions of Eurasia. Winter air temperatures are extremely low, and the climatic summer (a period when average daily air temperatures are higher than 15°C) is absent in many of its parts.

The differences between the duration of the ice-free period in the northernmost (lower reaches of the Rauchua River) and the southernmost (lower reaches of the Kukhtuy River) known *B. beringiana* localities exceed 50–60 days [39]. The average July water temperatures are similar throughout the region (ca. $10\text{--}12^\circ\text{C}$), up to 14°C only in the middle part of the Kolyma River basin [40]. However, *Beringiana* habitats stand out: they have average ice-free periods, but much higher summer water temperatures. No special studies were performed on the subjects, but we are aware that many of these locations are traditionally used for bathing.

We should note that *B. beringiana* is able to live in habitats heated by thermal springs. Derzhavin [41] reported a population from a warm river in Kamchatka near the Paratunka village, which even in late winter was hotter than 11 °C. In the major part of Northeastern Asia, these mollusks spend winter burrowing in bottom sediments at low positive temperatures.

Thus, although *B. beringiana* inhabits cold regions of Northeast Asia, it is confined to the warm and shallow water bodies in this region.

4.3. Genetic Studies

Our genetic analysis of four populations from Northeast Asia confirmed that they belong to the same species, *B. beringiana*. Genetic variation in *B. beringiana* is low, as is evident from the haplotype network (Figure 4), suggesting recent divergence of populations and their dispersal through the current range. The network corresponds to a classical star-like cluster [42], in which a central haplotype is usually considered ancestral and the others are thought to be its derivatives formed by accumulating substitutions. It is also possible to assume in our case that the large size of the central (“basic”) haplotype in the network is explained by the fact that more mussels were examined in samples from northern populations compared with southern ones. While the same haplotype is found in Northeast Asia, Sakhalin, and Alaska, various haplotypes are characteristic of Primorye, the Kuril Islands, and Japan. A center of genetic diversity of *B. beringiana* is likely to be in the south, but the available data on southern regions are insufficient for deciding whether the center should be sought on the continent or islands. This question will be resolved by extensive sampling.

Tajima’s D and Fu’s Fs measures were negative and deviated significantly from neutrality, supporting recent population expansion. However, mismatch distribution analysis for the total *B. beringiana* sample showed that the differences between the observed distributions and those expected for the population expansion model had p -value = 0.05, i.e., at the border of statistical significance. This was due to the specimens from the southern locations. For the sample of the northern populations (without Primorye and the Japanese archipelago), the observed mismatch profile almost perfectly fitted the distribution expected under the recent expansion model. Given the available data, we can state that the Northern Palearctic and Nearctic part of the distribution was colonized recently. However, as said above, there is still not enough data for the Southern Palearctic to infer the age of the populations and the genetic distances between them.

4.4. Morphological Variation

Highly variable shell morphology was observed in the four studied *B. beringiana* populations of Northeast Asia. Within-population variation was found to be very high, and the calculated index values fell out of the ranges accepted for the species in the literature earlier [9]. Significant differences in certain key morphological traits were detected even between neighboring populations that live in similar climatic and landscape conditions but are separated by a mountain ridge, as is the case with the populations of the Kukhtuy River basin on the shore of the Sea of Okhotsk (near the village of Rezidentsiya) and the Kava River basin. The ecological factors that determine the shell shape of *B. beringiana* are difficult to identify because only limited data are available on the environmental conditions of water bodies inhabited by the species in Northeastern Asia. Variation in external traits most likely explains why the sympatry of several species was reported earlier, for example, in the Kava and Ola basins of Magadan Oblast [24]. The variation range observed in the pooled sample from the four populations included all species ranges described in the literature (Figure 6).

Mussels randomly selected for genetic testing were assigned to different species (*B. beringiana*, *B. youkonensis*, *B. derzhavini*, *B. chereshevi*, and *B. kamchatica*) by the set of morphological traits. However, all of them were identified as *B. beringiana* by *cox1* sequence analysis. Our study thus confirmed that high conchological variation, which was reported

for the species more than 100 years ago [32,36] lacks taxonomic significance. A similar conclusion was made for freshwater pearl mussels of the genus *Margaritifera* [43,44].

High morphological diversity and ecological plasticity are characteristic of inhabitants of northern freshwaters but are often not accompanied by genetic differentiation (for a review, see [45]). Evidence for the phenotypic plasticity of shell morphology has been found in other species of Unionidae [46–49]. This factor possibly underlies the phenotypic diversity in *B. beringiana*, but experiments are problematic to perform on this protected species.

4.5. Freshwater Dispersal Pathways of *B. beringiana*

The mosaic distribution of *B. beringiana* populations across a vast territory (including two continents separated by a strait for 10–12 thousand years) and the identity of haplotypes throughout its range suggest a relatively recent dispersal history of this species. The current range of *B. beringiana* suggests that this species dispersed by means of ancient river basins that existed during ocean regression. To explain how the species range of Beringian fishes might have formed, Chereshev [50] and, more recently, Ager [51] proposed paleogeographic schemes of the hydrographic network of Northeastern Asia and a northwestern region of North America (Figure 7). They were based on the works of Soviet and American researchers, primarily, Baranova and Biske [52] and Hopkins [53]. The schemes suggest that the exposed shelf of the Chukchi Sea was drained by rivers of the Kolyma–Chukotka and Chukotka–Alaska complexes. Hopkins [53] believed that Merklin Lake existed in place of the current Bering Strait. The lake was fed by the rivers of Chukotka and Alaska and was drained into the Chukchi Sea. The northern part of the basins of Pacific rivers was drained by the Anadyr complex, paleo-Penzhina, rivers of Tauï Bay, and the Okhotsk group of rivers, while the American shore was drained by paleo-Yukon and paleo-Kuskokwim.

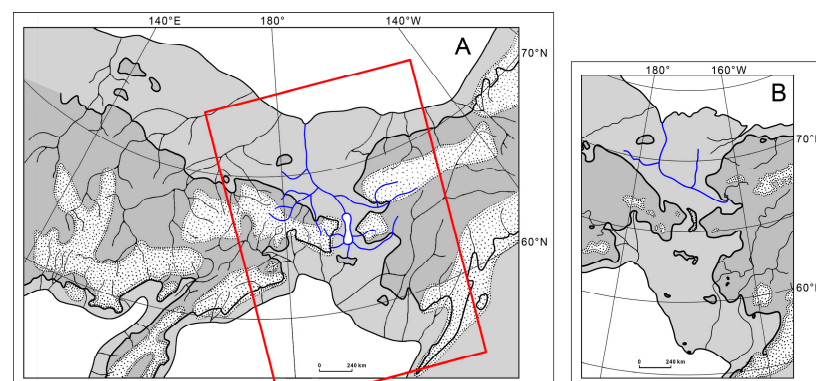


Figure 7. Hydrography of Beringia in the Late Pleistocene ocean regression: (A) after Chereshev [50] with changes; (B) after Ager [51]. Dark gray, modern land; light gray, land borders 20–18 thousand years BC; white dotted contours, glaciers; white background, open water; rivers draining both continents are shown in blue. The red frame is the position of Figure 7B.

Thus, during the global 100–120 m ocean regression in the Late Pleistocene, hydrobionts could have moved between Chukotka and Alaska through common streams on the exposed shelf.

Based on the schemes, the exchange of freshwater organisms (other than anadromous fish) was unlikely to occur between the mouth populations of Indigirka and Kolyma and between these populations and those of the Pacific coast in Northeast Asia in the Late Pleistocene. The mouth of paleo-Kolyma was far away from the mouth of a great stream that ran on the dry shelf of the Chukchi Sea and drained Chukotka and Alaska.

In Northeastern Asia, the gradual dispersal of *B. beringiana* along rivers is impeded by the lack of suitable bottom substrates. We believe that long-distance dispersal by means of glochidia is possible not only for anadromous salmon. Grayling, the most abundant fish in the upper reaches of local rivers, might also be among the hosts of *B. beringiana*

glochidia, and it could facilitate their dispersal between flatland watersheds observed in certain species. The Indigirka–Okhota–Kukhtuy river system might have been such a putative zoogeographical channel (Figure 2).

A bifurcation, which is extremely rare in global hydrology, is known for Del'kyu, one of the largest tributaries of Okhota [54]. Approximately 30 km away from its origin (62°08' N, 141°34' E; altitude 1400 m), Del'kyu separates into Del'kyu-Okhotskaya (the basin of the Sea of Okhotsk) and Del'kyu-Kuidusunskaya, which is a tributary of the Kuidusun River, which runs into Indigirka (the basin of the East Siberian Sea). The bifurcation region (see Figure 2) is freely passable for boats and certainly fish in years of medium water content [55].

A stream separates from Okhota on its left bank, 32 km away from its mouth, and runs into Khaibas, which is a right tributary of Kukhtuy. The stream ensures a continuous connection of downstream Indigirka with Okhota and Kukhtuy, thus eventually connecting the Pacific and the Arctic Ocean.

Pugachev [54] observed that ichthyofaunal exchange between Okhota and Indigirka is still possible now. Chereshev [56] (p. 62) did not mention the Del'kyu bifurcation but noted that a pathway from Indigirka through a drainage divide into Okhota and Kukhtuy of the basin of the Sea of Okhotsk was utilized in the spreading of the Siberian species *Phoxinus phoxinus*, *Ph. perenurus*, *Perca fluviatilis*, *Carassius carassius jacuticus*, *Nemacheilus toni*, *Exos lucius*, *Salvelinus neiva*, and *Thymallus arcticus pallasi*.

Beringiana beringiana populations are found in the downstream valley lakes of both Indigirka (near the village of Belaya Gora) and Kukhtuy (the village of Rezidentsiya), and their common origin is possible to assume in view of the above. The distance in a straight line between the populations is over 1000 km, and the mussel is so far unknown to inhabit other localities along the line, although its presence there in the past cannot be excluded.

The region of the Del'kyu bifurcation is in an area of recent glaciation and is in the immediate vicinity of the currently greatest mountain glaciers of Northeast Asia [57]. The Okhota–Indigirka continuous water system could apparently not act as a biogeographical channel until the glaciers had regressed [54] to their current level in the most highland part of the Suntar-Khayata Range.

The conclusion does not contradict the molecular genetic data on the genetic similarity of mussels from the downstream regions of Indigirka and Kukhtuy, or from other localities of the species range.

4.6. On the Possibility of *B. beringiana* Larva Dispersal with Fish across Seas

Since molecular data suggest that *Beringiana* populations from both continents diverged relatively recently, it is reasonable to investigate whether its larvae (glochidia) might spread through seas as parasites of migrating fish.

Eight host fish species are currently known for *Beringiana* glochidia [20]: the three-spined stickleback *Gasterosteus aculeatus* Linnaeus, 1758, the ninespine stickleback *Pungitius pungitius* (Linnaeus, 1758), the pond smelt *Hypomesus olidus* (Pallas, 1814), the coho salmon *Oncorhynchus kisutch* (Walbaum, 1792), the sockeye salmon *O. nerka* (Walbaum, 1792), the dolly varden *Salvelinus malma* (Walbaum, 1792), the white char *S. albus* Glubokovsky, 1977, and the whitespotted char *S. leucomaenis* (Pallas, 1814). All but one species (white char) are euryhaline, living both in rivers and marine waters, and could therefore be capable of transferring glochidia between distant river mouths through the sea.

It is unclear now how long it takes for *B. beringiana* glochidia to develop in host fish; glochidia are only known to infest fish in Kamchatka in July and August [58]. There are no data as to whether *B. beringiana* glochidia survive on gills in marine water. Glochidia of the freshwater pear mussel *Margaritifera margaritifera* remain viable on Atlantic salmon gills in the sea [59]. A spreading of *M. margaritifera* through the sea has been confirmed in a phylogenetic study [60]. Taken together, the above data indicate that dissemination of *B. beringiana* glochidia from one river basin to another through the sea on fish gills might be possible and needs investigation.

Significant distances separate *B. beringiana* populations inhabiting the mouths of large rivers. For example, the distances between the Indigirka and Kolyma mouths along the shoreline are over 500 km; between the Kolyma and Anadyr mouths, there is over 2000 km; and between the Anadyr and Khatyrka mouths, there is over 1000 km.

Distances of several hundred kilometers can be crossed by anadromous fish and probably within a reasonable time. Transcontinental migration (approximately 1700 km) from the Wulik River in Alaska to Anadyr in Chukotka is known for two dolly wardens (*Salvelinus malma*) [61]. According to Chereshev [50], quite intense fish exchange probably exists between *S. malma* populations of eastern Chukotka and Alaska.

No new haplotype was detected in addition to the known ones in our mtDNA analysis of four *B. beringiana* populations of Northeast Asia. Similar genetic characteristics were observed for the *B. beringiana* populations of the region (and other localities of the species range), supporting the idea of recent (Late Pleistocene–Early Holocene) colonization of Northeast Asia by the species. A similar conclusion has been reached in studies of modern fish distributions and paleogeographic reconstructions [62]. Molecular genetic studies have confirmed a recent spreading of certain fish phylogenetic lineages in Northeast Asia [63–67], although genetic data support the long-term existence of endemic salmonids in the El'gygytyn Lake of Chukotka [68,69].

5. Conclusions

At least 30 *B. beringiana* populations are currently known in Northeast Asia, and most of them inhabit river mouths that are often several hundred kilometers apart. The patchy distribution of *B. beringiana* is caused by its paleogeographic history, stringent requirements for muddy sand bottom substrates, and dispersal mode (through parasitic glochidia).

All *B. beringiana* populations throughout the distribution appear to be genetically similar, which supports the idea of recent Late Pleistocene–Early Holocene colonization of Northeast Asia. Moreover, we found that individuals assigned to different species showed no genetic differences, which supports a high conchological variation in *Beringiana* that does not have taxonomic consequences.

The geographical isolation of enclaves indicates that glochidia might be dispersed by fish for long distances, both in fresh and marine waters. The available literature data suggest the possibility of long-distance and rapid dispersal, including the transfer between continents.

We suggest that the «Indigirka–Okhota–Kukhtuy» river system might be an important biogeographic channel that connects the biotas of river basins of the two oceans, which warrants further studies of various hydrobionts inhabiting this region.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/w15203538/s1>, Table S1: Numerical designations used in Figure 2.

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