

Article

Mitochondrial Lineage Diversity and Phylogeography of *Daphnia* (*Daphnia*) (Crustacea: Cladocera) in North-East Russia

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Abstract: The variability of the 12S gene fragment of the mtDNA for taxa belonging to subgenus *Daphnia* (*Daphnia*) O.F. Müller, 1776 (Crustacea: Cladocera) in NE Russia is studied, and their phylogenetic analysis performed. We identified (based both on morphological and molecular data) nine species belonging to four species complexes, namely: (A) *D. longispina* s.l.: (1) *D. longispina* O.F. Müller, 1776; (2) *D. dentifera* Forbes, 1893; (3) *D. galeata* Sars, 1864; (4) *D. umbra* Taylor, Hebert et Colbourne, 1996; (B) *D. cristata* s.l.: (5) *D. cristata* Sars, 1862; (6) *D. longiremis* Sars, 1862; (C) *D. curvirostris* s.l.: (7) *D. curvirostris* Eylmann, 1887; (D) *D. pulex* s.l.: (8) *D. pulex* Leydig, 1860; (9) *D. middendorffiana* Fischer, 1851. Rare arcto-mountainous taxon *D. umbra* was found in the mountains of the Sakha (Yakutia) Republic for the first time. Species diversity in NE Asia is relatively low, and the most revealed taxa are trans-Beringian. We also performed a phylogeographic analysis of *D. dentifera* and *D. pulex* s.l., the two most common species in NE Russia. Our new data allow us to assume that the daphniids of NE Asia have undergone various evolutionary scenarios during the Pleistocene period: survival is within some local refugia, and re-colonization from these areas and from North America through the Beringian land bridge, etc. We agree with previous authors who revealed that the patterns in the studied species groups are relatively recent (of Late Pleistocene or even Holocene age), although the main phylogenetic daphniid lineages (mainly congruent with the biological species) are very old. Our results provide convincing evidence for the hypothesis that NE Russia is a very important source of modern haplotypic diversity for the cladocerans.

Keywords: *Daphnia*; species diversity; 12S gene; phylogeography; evolution history; subarctic; Beringian zone; Russia

1. Introduction

The biodiversity in continental waters has undergone intensive studies recently, i.e., due to an understanding of the need for its conservation and its dramatic decline due to human activity [1,2]. It is obvious that we need to “enhance the taxonomic, ecological and genomic knowledge of freshwater organisms to increase the efficient monitoring across organismal groups and geographical areas” [3]. However, there still are large regions with

inadequately studied freshwater biodiversity due to their remoteness and low human population, which, as a result, are almost non-transformed by man to date. Arctic and subarctic zones are among such regions, and it is well-known that their continental water bodies (as well as communities of organisms inhabiting them) are fragile and especially vulnerable to harmful human impacts [4,5].

The biodiversity in the arctic–subarctic hydrobionts is relatively low compared to other regions [4,6]. An especially interesting portion of the arctic–subarctic is the Beringian zone, which has had a very important role in the history of the freshwater ecosystems of Eurasia and North America. In the geological history of the Earth, the two continents were interconnected several times by a wide land bridge, Beringia [7,8]. The Beringian region has a special role in the zoogeography of different animal groups [9,10], i.e., because it served as a refugium for terrestrial and freshwater fauna during the coldest phases of the Pleistocene [11,12]. Note that the Beringian region is bound to the east by the Mackenzie River in Canada and in the west by the Lena River in Russia; therefore, all of NE Siberia belongs to this zone.

Water fleas (Crustacea: Cladocera) are dominant in the different types of continental water bodies in all climatic zones [13]. The recent intensification of such works in NE Asia is explained by the influence of global climate changes and anthropogenic impacts on high altitude ecosystems. However, all such investigations are based on the morphological analysis only [14–24]. Several recent investigations have demonstrated a special significance of the Beringian region in the cladoceran phylogeography, i.e., as a center of dispersion of some taxa through the whole of Eastern Asia [25–27]. Additionally, the region is populated by endemic taxa [28] and very locally distributed phylogroups of widely distributed taxa [25,26]. Moreover, a trans-Beringian distribution is demonstrated for several cladoceran taxa or phylogroups [29,30]. Some endemic phylogroups revealed by molecular biologists still are waiting for their formal description as new species [29,31,32].

Usually, the genus *Daphnia* O.F. Müller is among the best studied freshwater microfaunal groups in the world and a model group for the study of biogeographic patterns [33–36]. Several taxa were studied in detail in east Beringia [37,38]. However, despite the importance of the genus, our knowledge of the exact species composition, genetic diversity and phylogeography of its representatives in NE Russia are rather intuitive and inadequate. Populations from several species groups such as *D. pulex* [39–41], *D. magna* [27] and *D. curvirostris* [26,42] were analyzed in the course of previous trans-Holarctic studies, but west Beringia was never an object of study of the genus diversity based on molecular phylogenetic methods.

The aims of this study are: (1) to investigate the species diversity of *Daphnia* from different water bodies of NE Russia (Beringian zone); (2) to reconstruct the phylogenetic relationship between the species; (3) to provide preliminary data on their demographic history. We expect that our study will contribute to a more complete understanding of the specific and haplotype *Daphnia* diversity and distributions across the whole northern portion of the Holarctic.

2. Materials and Methods

2.1. Ethic Statement

Field collection on public property in Russia does not require permissions. Verbal permission to collect in private farm ponds was obtained from local owners. Sampling in the natural reserves of Russia was conducted with special permission of their directors (A.L. Strelnikov, Komandorsky State Natural Reserve; T.I. Shpilenok, Kronotsky Biosphere Reserve).

2.2. Sampling and Used Material

Zooplankton samples were collected using the Apstein-type plankton net (125 µm mesh size) during summer seasons of 2017–2020. Immediately after collection, the samples were fixed by 96% ethanol and stored at −20 °C. Different water bodies were situated mainly

in the Russian part of the arctic–subarctic zone, mostly from the Beringian region: Bering Island, Kamchatka Peninsula, Chukotka Peninsula, Magadan region and Sakha (Yakutia) Republic (Figure 1, Table S1). *Daphnia* specimens were identified to species level according to modern keys [43].

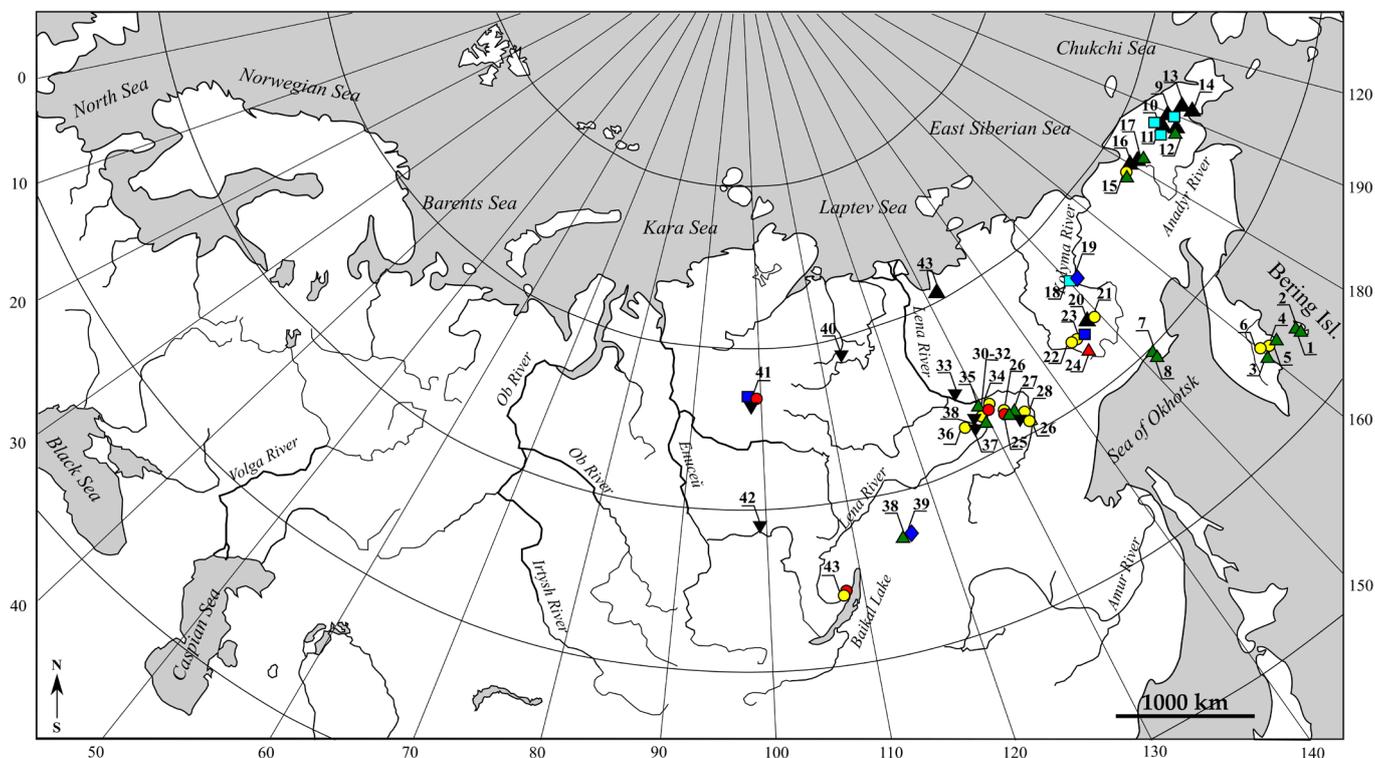


Figure 1. Map of the *Daphnia* sampling localities and species distribution in the water bodies of Russian part of the arctic–subarctic zone; red circle—*D. longispina* s.str., yellow circle—*D. dentifera*, upside black triangle—*D. galeata*, red triangle—*D. umbra*, blue square—*D. cristata*, turquois square—*D. longiremis*, blue diamond—*D. curvirostris*, black triangle—*D. middendorffiana*, green triangle—*D. pulex*. Numbers of sampling sites correspond to Table S1.

2.3. DNA Sequencing

Previous to DNA extraction, each *Daphnia* specimen was photographed in lateral view using an Altami microscope (Altami, Russia, under 4× and 10× magnification) in order to document its body and head shape. Genomic DNA was extracted with a 5% suspension of Chelex 100 resin (Bio-Rad, Hercules, CA, USA) from single ethanol-preserved *Daphnia* specimen. Two to twelve individuals per population were selected for mitochondrial DNA analysis. Fragment of the 12S ribosomal RNA of the mtDNA were amplified for each specimen. The PCR conditions and protocols were identical to those used by Zuykova et al. [44,45]. The PCR products were separated on 1% agarose (low EEO standard agarose, BIOZYM, Moscow, Russia) with ethidium bromide and photographed under UV light. The amplified products were purified using a kit from BIOSILICA (Novosibirsk, Russia) and the samples were sequenced in both the forward and reverse direction at the company “Syntol” (Moscow, Russia). The nucleotide sequences were automatically aligned using the ClustalW v.2.0 [46] and MAFFT v.7 algorithms [47] and then manually edited with BioEdit v.7.0 [48] when it was necessary. Total of 159 nucleotide sequences of 567–572 bp fragment of the 12S gene were newly obtained and were deposited into the GenBank database according to revealed haplotypes under accession numbers OL333450–OL333526, OL333529–OL333532 and ON713422 (Table S1).

2.4. Phylogenetic Analyses

Reconstruction of the phylogenetic relationships based on the fragment of the 12S gene of the mtDNA between the *Daphnia* species from the water bodies of NE Siberia included three stages. First, we needed to identify their position in the general subgenus phylogeny (i.e., within *D. longispina* and *D. pulex* complexes). For this, we used both original and NCBI GenBank sequences. Second, it was necessary to assess the 12S phylogeny for each complex separately to obtain more suitable schemes (i.e., because particular substitution models could be different from a general model). The *D. cristata*–*longiremis* group was used as an outgroup for the *D. longispina* complex, while *D. ambigua* sequences were used as an outgroup for the *D. pulex* complex. Third, we tried to detect relationships between haplotypes among widespread *Daphnia* species, which were most common in water bodies of NE Russia. In this analysis the additional 12S sequences of *D. dentifera* were involved. In sum, 194 sequences from the NCBI GenBank database were used (see Table S2).

The best fitting models of nucleotide substitution for the 12S dataset were selected in jModelTest v.2.1.7 based on the likelihood scores for 88 different models and under the Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC) [49,50]. The best models were Tamura 3-parameter with invariant sites and gamma distribution (T92+I+G, $\gamma = 0.308$; Tamura, 1992) and general time reversible with invariant sites and gamma distribution (GTR+I+G, $\gamma = 0.610$; [51]). The phylogenetic trees based on the 12S dataset were reconstructed in MEGA v.7.0.26 using the maximum likelihood (ML) algorithm with pairwise deletion of the gaps and missing sites [52]. One thousand bootstrap replicates were run to assess the statistical support for the tree nodes [53].

Bayesian analysis was performed with MrBayes v.3.2 [54] under the GTR+I+G model. Two simultaneous runs with four Markov chains each were run for 1×10^6 generations and sampled every 500 generations. The first 25% of generations were discarded as burn-in. Convergence of runs was assessed by examination of the average standard deviation of split frequencies and the potential scale reduction factor. In addition, a stationarity was confirmed by examining posterior probability, log likelihood, and all model parameters by the effective sample sizes (ESS > 500) and trace plots of MCMC output in the program Tracer v.1.7 [55]. The 12S datasets for the *D. longispina* and *D. pulex* complexes were tested for redundancy and saturation and were collapsed into haplotypes using METAPIGA v.3.01 [56]. In addition, the circular trees using SeaView v.5.05 [57] were constructed for the *D. dentifera* and *D. pulex*–*D. middendorffiana*.

The haplotype networks were constructed by the median-joining method (MJ) [58] using Network v.5.0 (available on www.fluxus-engineering.com, accessed on 1 May 2022) based on the 12S sequences for widespread species in water bodies of NE Russia *D. dentifera*, *D. pulex* and *D. middendorffiana*.

Based on the phylogenetic reconstruction and the haplotype networks, unique haplotypes of *Daphnia* from NE Russia only were identified.

Evolutionary distances (uncorrected *p*-distances) were estimated among and between *Daphnia* species in MEGA v.7.0.26 [52]. This analysis was carried out for all *Daphnia* species, including sequences, obtained from the GenBank database. The mitochondrial DNA polymorphism for the studied species and clades of *D. longispina* s.str. was estimated for 12S dataset, which consists of only original nucleotide sequences; the following parameters were calculated: the number of haplotypes (*h*), number of segregating sites (*S*), haplotype diversity (H_d) and nucleotide diversity (π) using DnaSP v.5.10 [59]. The neutrality tests of Fu's F_S [60] and Tajima's *D* [61] were performed with Arlequin v.3.5.2.2 [62] to investigate the historical population demographics in water bodies of NE Russia and test whether the sequences conformed to the expectations of neutrality. The significance of these tests was proved using the coalescent simulation with 1000 permutations.

3. Results

3.1. Mitochondrial Phylogeny and Haplotypes Distribution

Nine species were identified morphologically in the water bodies of NE Siberia belonging to the subgenus *Daphnia* (*Daphnia*) O.F. Müller, 1776, namely:

- (1) *D. longispina* O.F. Müller, 1776 s.str.;
- (2) *D. dentifera* Forbes, 1893;
- (3) *D. galeata* Sars, 1863;
- (4) *D. umbra* Taylor, Hebert & Colbourne, 1996;
- (5) *D. curvirostris* Eylmann, 1887;
- (6) *D. cristata* Sars, 1862;
- (7) *D. longiremis* Sars, 1862;
- (8) *D. middendorffiana* Fischer, 1851;
- (9) *D. pulex* Leydig, 1860 s.l.

The most common and widespread species were *D. dentifera*, *D. middendorffiana* and *D. pulex* s.l.

The function of Figure 2 is to demonstrate the position of the original sequences in the general tree of *Daphnia* (*Daphnia*) based on the original and the GenBank data, therefore we do not discuss such phylogeny as it is identical to that previously obtained by many authors [33,45]. The tree topologies are identical in both analyses. According to BI and ML analyses, all new 12S sequences from NE Russia were also clearly subdivided into nine large clusters corresponding well to the morphological species. All 12S sequences (original and GenBank) form two large, well-supported monophyletic clusters corresponding to the *D. longispina* and *D. pulex* complexes; separate trees for each complex are represented in Figure 3A,B.

There are divergent mitochondrial lineages (subclades) within all specific clades with branch support up to 100%, except for *D. cristata* and *D. longiremis* that are represented by few sequences. Conventionally, the *D. longispina* sequences form two well-supported subclades, “Siberian” (A) and “European” (B); all new haplotypes from Yakutia and Evenkiya belong to the “Siberian” one (Figure 3A). Several earlier derived subclades are found within the *D. dentifera* cluster consisting of the haplotypes from the Kamchatka Peninsula and Sakha (Yakutia) Republic. Within *D. galeata*, the divergent subclades are formed by the haplotypes from the water bodies of Yakutia and Irkutsk Area. The haplotypes of *D. umbra* from a single lake in Sakha (Yakutia) Republic also form a well-supported distinct subclade (Figure 3A). The 12S haplotypes of *D. curvirostris* s.str. are divided into two divergent subclades consisting of the haplotypes from Yakutia and the Novosibirsk region, and Tuva Republic.

In the tree of the *D. pulex* complex, *D. pulex* s.lat. sequences are grouped into four large subclades, LI–LIII plus *D. cf. pulex* from Japan. (Figure 3B). Note that the *D. pulicaria* GenBank sequences have an unclear position in the 12S phylogenies; moreover, the specimens of *D. pulicaria* AY626355 from Germany and *D. pulex* JN903685 from Russia (Chany Lake) are combined into a distinct subclade associated with the *D. middendorffiana* specific cluster (Figure 3B). *D. middendorffiana* is represented by two subclades, with one of them endemic to the Sakha (Yakutia) Republic, while the second is widely distributed in the subarctic of Eurasia. Such taxa as *D. obtusa*, *D. parvula*, *D. izpodvala* and *D. ambigua* are not found in the region.

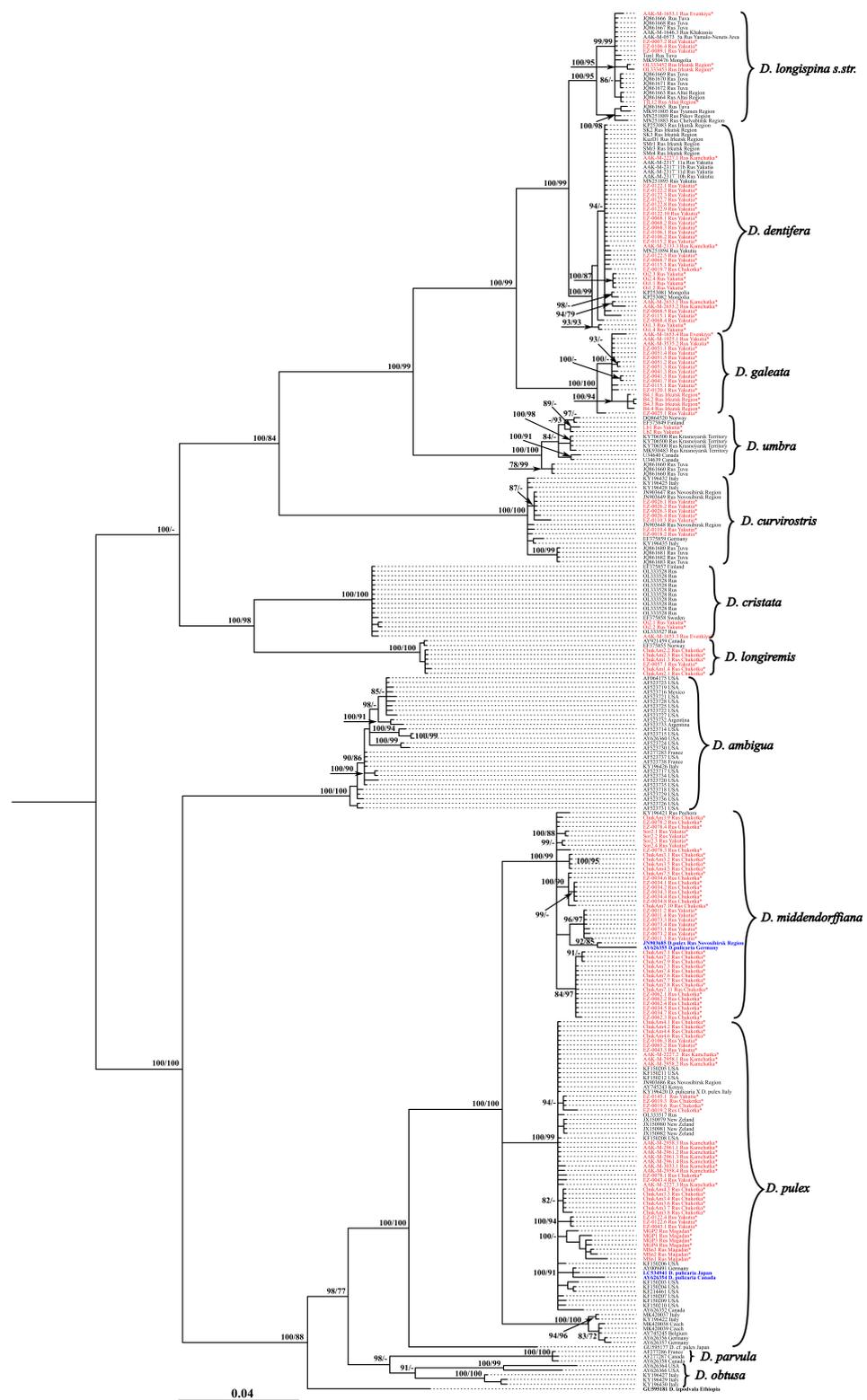


Figure 2. Bayesian phylogenetic tree for the *Daphnia* species based on the 125 sequences (original and obtained from the GenBank database, Table S2). Bayesian posterior probabilities BI and bootstrap values from ML analysis above 72% expressed as a percentage are indicated for each significant node; red *—new nucleotide sequences; blue—ambiguous specific status of the GenBank sequences. Scale is given in expected substitutions per site.

The 12S circular phylogenetic tree of *D. dentifera* (the most widespread species) confirms that all 12S haplotypes are subdivided into four haplogroups: I (Japan–USA); II (Japan–China–USA), III (Russia–Mongolia) and IV (Japan–Canada, USA) (Figure 4A). Remarkably, no 12S haplotypes of *D. dentifera* within Russia–Mongolia and Japan–China (Tibet)–North America were found, while three clades had a trans-Beringian distribution. The 12S haplotypes forming subclade IV (Japan–USA–Canada) are closely related to those distributed in Kamchatka (the Beringian region) and the Baikal basin (Figure 4B). The central 12S haplotype of clade III (H1) occurs in eastern Siberia (Yakutia and the Baikal basin) and Kamchatka, while clade IV also has a central haplotype present in the USA and Canada but absent in Japan (Figure 4B). Note that unique regional haplotypes of *D. dentifera* are found in Yakutia, Mongolia and Chukotka.

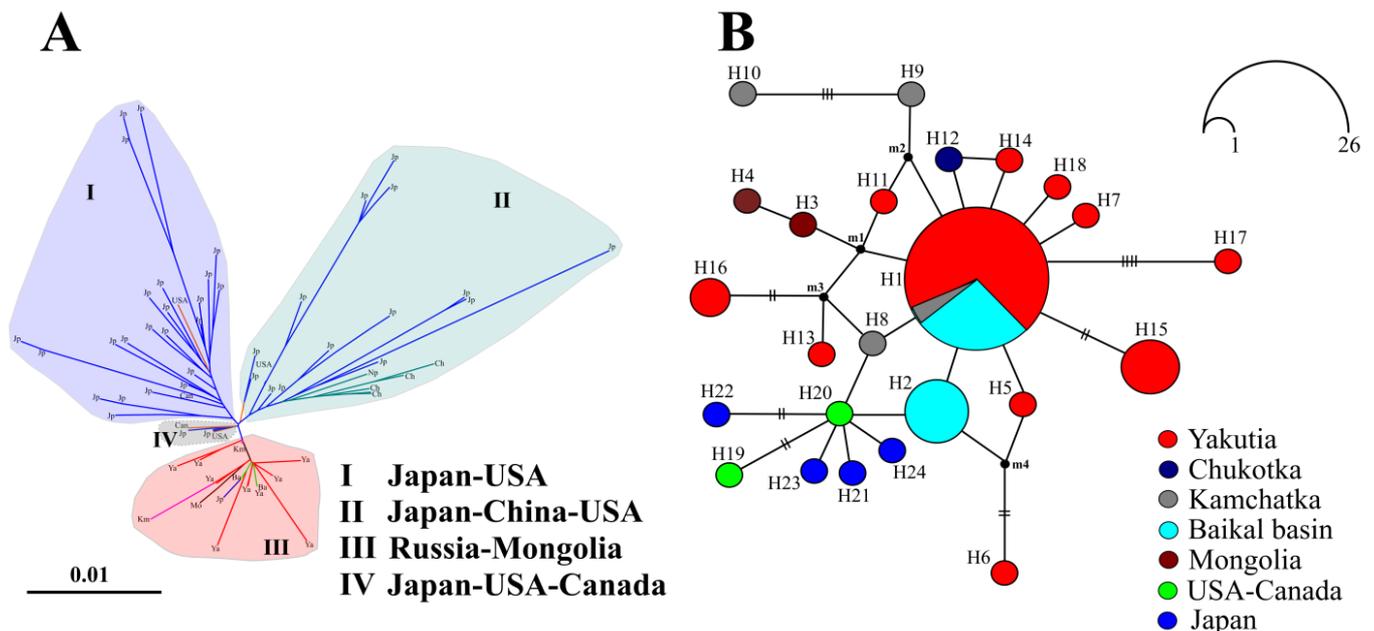


Figure 4. Phylogenetic tree for *Daphnia dentifera* reconstructed based on original and obtained from the GenBank database 12S haplotypes (A) and median-joining network for the clades III and IV (B). The scale is given in expected substitutions per site.

Similarly, the 12S circular phylogenetic tree of *D. middendorffiana*–*D. pulex* (Figure 5A) reveals four haplogroups: *D. middendorffiana* (Dm) and three others comprised of the *D. pulex* haplotypes (Dp_I, Dp_II, Dp_III). Several ambiguous 12S sequences of *D. pulex* and *D. pulicaria* belong to the divergent mitochondrial lineages II and III (Figure 2). The 12S median-joining network of the *D. pulex* haplogroup Dp_II has a very characteristic star-like pattern with the central haplotype H16, which occurs in the Russian part of the arctic–subarctic zone (Kamchatka, Chukotka, Yakutia), western Siberia, Western Europe, the USA and even Africa (Figure 5B). The haplotypes from New Zealand and the USA are closely related with the central haplotype. However, the haplotypes from the Magadan Area (H14, H16–H20), which is an adjacent region to Kamchatka and Chukotka, form a distant haplogroup; also, the haplotype H15 in this area is a very specific one.

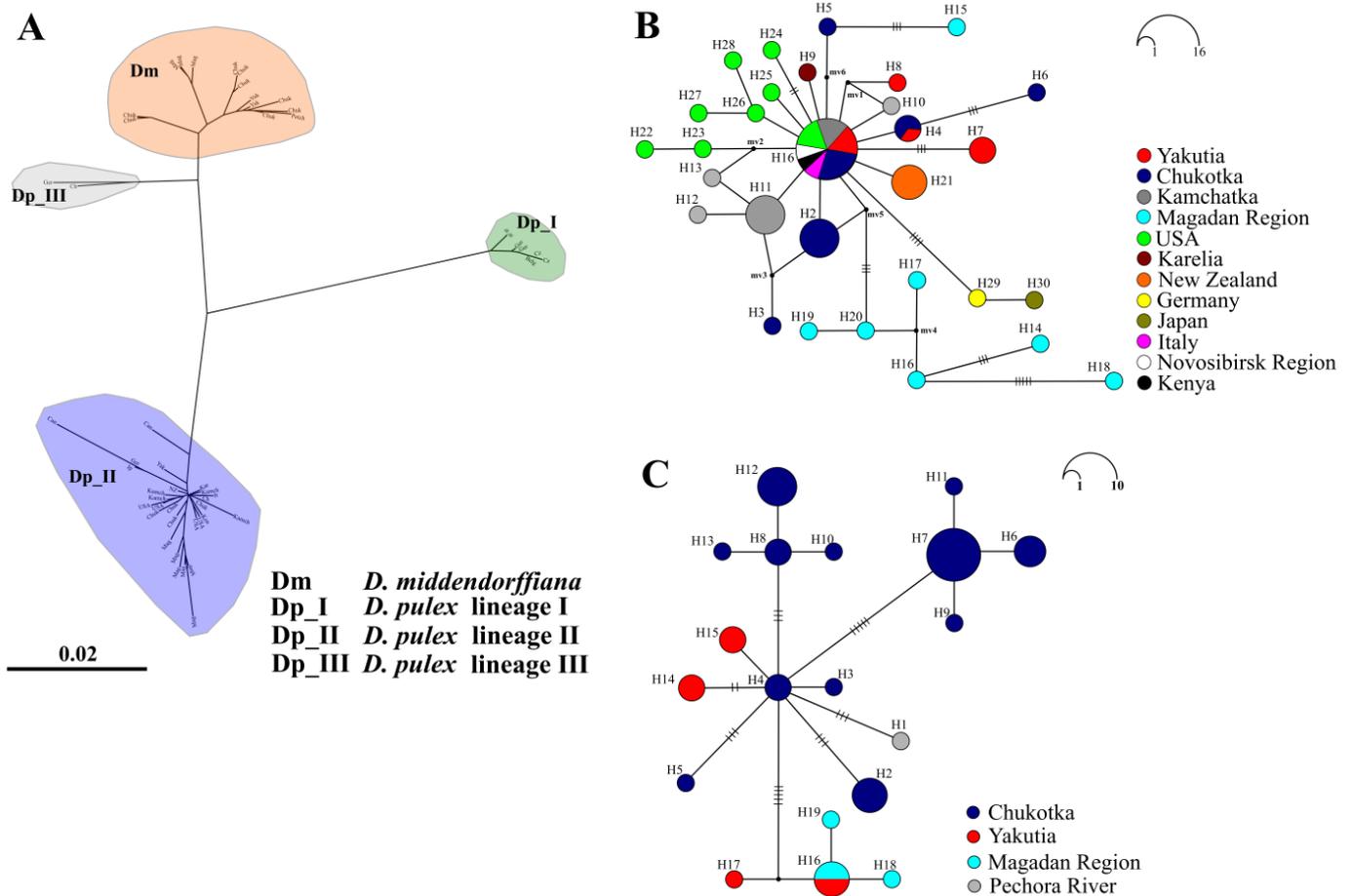


Figure 5. Phylogenetic tree for species of the *Daphnia pulex* complex reconstructed based on original and obtained from the GenBank database 12S haplotypes (A); median-joining networks for Dp_II clade (B) and *D. middendorffiana* clade (C). The scale is given in expected substitutions per site.

The median-joining network of *D. middendorffiana* (Dm) haplotypes is more reticulated: the haplotypes are subdivided into four groups with central haplotypes H4, H6, H7 and H8 (Figure 5C). Two groups exclusively consist of the haplotypes from Chukotka; the third group is formed by the haplotypes from Chukotka, Yakutia and the Pechora River (H1, KY196421), and the central haplotype is found in Chukotka only. The fourth group consists of the haplotypes from Yakutia and the Magadan area (Figure 5C).

3.2. Mitochondrial Polymorphism, Evolutionary Distances and Neutrality Tests

Evolutionary divergence (under uncorrected *p*-distances over the 12S sequence pairs) within and between studied *Daphnia* species belonging to different specific complexes is high (up to 24.1%, *D. pulex* LIII–*D. dentifera*, Table 1). *P*-distances between species within each complex are smaller, 2.0–7.8% in the *D. longispina* complex) and 3.2–17.2% in the *D. pulex* complex. In regards to certain species, the highest values for *p*-distances are found in *D. obtusa*—6.3% (Table 1). The highest values are also registered for such species and mitochondrial lineages as *D. curvirostris* (0.9%), *D. pulex* LIII (1.0%), *D. umbra* (1.1%), *D. middendorffiana* (1.2%), *D. ambigua* (1.3%) and *D. pulex* LII (1.9%). Evolutionary divergence within *D. cristata* and *D. longiremis* is the lowest—0.1%.

Table 1. Evolutionary divergence over sequence pairs within and between *Daphnia* species (below the diagonal—uncorrected *p*-distances, %; above the diagonal—standard error estimates) based on the full 12S dataset (original sequences plus GenBank). The analysis involved 295 nucleotide sequences. Note: 1—*D. longispina* s.str. “Siberian” clade A; 2—*D. longispina* s.str. “European” clade B; 3—*D. dentifera*; 4—*D. galeata*; 5—*D. umbra*; 6—*D. curvirostris*; 7—*D. cristata*; 8—*D. longiremis*; 9—*D. middendorffiana*; 10—*D. pulex* LIII; 11—*D. pulex* LI; 12—*D. pulex* LII; 13—*D. parvula*; 14—*D. obtusa*; 15—*D. ambigua*.

Within Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
1	0.3 ± 0.1		0.5	0.7	1.0	1.3	1.5	1.5	1.5	1.6	1.6	1.6	1.7	1.6	1.5	1.6
2	0.7 ± 0.2	2.0		0.7	1.0	1.2	1.5	1.5	1.5	1.6	1.6	1.6	1.7	1.6	1.5	1.6
3	0.3 ± 0.1	3.5	3.5		1.1	1.2	1.5	1.5	1.6	1.6	1.6	1.6	1.7	1.6	1.5	1.6
4	0.6 ± 0.2	7.1	7.9	7.8		1.3	1.6	1.5	1.5	1.6	1.6	1.6	1.7	1.7	1.5	1.6
5	1.1 ± 0.3	12.7	12.9	12.4	13.3		1.4	1.6	1.6	1.6	1.6	1.6	1.7	1.7	1.6	1.6
6	0.9 ± 0.2	18.2	17.7	18.1	18.6	18.2		1.6	1.6	1.6	1.6	1.6	1.7	1.7	1.5	1.6
7	0.1 ± 0.1	17.3	17.8	17.6	17.1	18.5	18.2		1.3	1.6	1.5	1.6	1.6	1.6	1.4	1.4
8	0.1 ± 0.1	18.8	18.5	19.4	18.1	18.9	19.2	11.9		1.6	1.6	1.6	1.6	1.6	1.5	1.6
9	1.2 ± 0.2	22.3	22.7	22.6	21.6	21.2	21.7	19.8	19.3		0.9	1.0	0.6	1.4	1.2	1.4
10	1.0 ± 0.1	23.0	23.7	23.1	22.2	21.7	22.7	19.5	20.7	5.9		1.0	0.6	1.4	1.3	1.4
11	0.4 ± 0.2	23.1	23.6	23.1	22.5	22.6	22.7	19.8	20.7	7.4	6.9		0.9	1.3	1.3	1.5
12	1.9 ± 0.5	23.8	24.3	24.1	22.4	22.1	23.0	21.1	20.3	3.2	6.2	7.6		1.5	1.2	1.4
13	0.2 ± 0.2	22.7	23.1	23.1	23.8	24.1	21.3	20.5	20.0	14.0	14.3	12.6	15.0		1.3	1.4
14	6.3 ± 0.7	22.0	22.2	22.2	21.7	22.5	19.1	18.1	18.7	12.7	13.0	13.1	13.4	11.8		1.5
15	1.3 ± 0.2	21.5	22.1	22.7	22.5	21.7	21.7	18.1	20.2	14.9	16.2	17.1	16.1	17.2	16.1	

The level of polymorphism based on the fragment of the 12S gene of the mtDNA was different for the studied *Daphnia* species. Only one species is characterized by the relatively low level of genetic polymorphism—*D. cristata* (Table 2). All studied species except for the abovementioned and *D. longiremis* have a large number of the haplotypes (*h*) and polymorphic sites (*S*). The highest haplotype diversity (H_d) and nucleotide diversity (π) values are found in the “European” clades of *D. longispina* s.str., *D. galeata*, *D. umbra*, *D. curvirostris*, *D. middendorffiana* and *D. pulex*. The “Siberian” clades of *D. longispina* s.str., *D. dentifera* and *D. longiremis* are characterized by relatively high H_d values at lower π values (Table 2).

Table 2. Polymorphism of the 12S gene fragment of mtDNA for *Daphnia* species and neutrality tests based on original sequences only. Note: *n*—number of sequences used; *S*—polymorphic (segregating) sites; *h*—number of haplotypes; H_d —haplotype (gene) diversity; π —nucleotide diversity; st.d.—standard deviation; * *p* < 0.05, *** *p* < 0.001.

Species	<i>n</i>	<i>h</i>	<i>S</i>	$H_d \pm \text{st.d.}$	$\pi \pm \text{st.d.}$	Tajima’s <i>D</i>	Fu’s F_S
<i>D. longispina</i> s.str. clade A	20	8	10	0.805 ± 0.070	0.0029 ± 0.0007	−1.421	−2.851 *
<i>D. longispina</i> s.str. clade B	4	4	8	1.000 ± 0.177	0.0073 ± 0.0016	−0.446	−0.768
<i>D. dentifera</i>	45	16	22	0.665 ± 0.080	0.0032 ± 0.0006	−2.087 **	−9.913 **
<i>D. galeata</i>	18	11	20	0.915 ± 0.050	0.0064 ± 0.0011	−1.462	−3.550 *
<i>D. umbra</i>	9	5	12	0.833 ± 0.098	0.0095 ± 0.0013	1.045	1.386
<i>D. curvirostris</i>	15	8	21	0.848 ± 0.071	0.0103 ± 0.0016	−0.377	0.278
<i>D. cristata</i>	16	5	4	0.533 ± 0.142	0.0011 ± 0.0003	0	1.061
<i>D. longiremis</i>	8	3	2	0.607 ± 0.164	0.0012 ± 0.0004	1.826	13.378
<i>D. middendorffiana</i>	43	17	34	0.907 ± 0.029	0.0115 ± 0.0006	−0.113	−0.047
<i>D. pulex</i>	73	40	130	0.941 ± 0.019	0.0231 ± 0.0045	−2.293 **	−5.486 **

Most of the studied *Daphnia* species are characterized by negative values of Tajima’s *D* and Fu’s F_S tests (Table 2). Positive (but insignificant) values of Fu’s F_S test are registered for *D. cristata* and *D. longiremis*. The significant negative values for both neutrality tests are

found in *D. dentifera* and *D. pulex*, and for Fu's F_S for the "Siberian" clade of *D. longispina* s.str. and *D. galeata* (Table 2).

4. Discussion

4.1. Comments of Revealed Species and Phylogroups

Most species of *D. longispina* s.l. are well-known from the region (see above). *D. longispina* s.str. haplotypes from Eurasia are clearly divided into two clades—A ("Siberian") and B ("European") with different evolutionary histories [38,63]. As was expected, clade B is absent in NE Russia. However, our previous conclusion that the distribution of the "Siberian" clade A in the eastern direction is limited to the basin of the Yenisei River is now thrown into doubt by our results as few populations of this clade were noted in the Sakha (Yakutia) Republic. However, the finding of a single haplotype here may be evidence of recent dispersion or incidental drift.

In contrast, *D. dentifera* haplotypes are widespread in the water bodies of the north-eastern part of Russia, from Kamchatka to the western portion of the Sakha (Yakutia) Republic, and some of them are divergent mitochondrial lineages. In addition, the coexistence of *D. longispina* s.str. (haplotypes of the "Siberian" clade A) and *D. dentifera* is detected in two water bodies (Lake Baikal basin and Central Yakutia). Thus, our assumption that the Baikal region and Yakutia could be a contact zone of two vicariant species, *D. longispina* s.str. and *D. dentifera* [63], is confirmed by these data.

The most studied *D. galeata* haplotypes belong to a widely distributed clade in Eurasia, and such haplotypes are common in NE Siberia. Within this cluster, specific mitochondrial lineages are detected in the water bodies of Yakutia, Evenkiya and the Irkutsk area. Two earlier derived deeply divergent haplogroups are found: the first is from Tuva (Central Siberia) and was already recorded by Zuykova et al. [44,64]; the second one is a newly found basal lineage of *D. galeata* s.lat. from the Sakha (Yakutia) Republic. Its status must be specially checked as it could represent a separate biological species, endemic to eastern Siberia.

D. umbra from Vorota Lake (located at 1109 m.a.s.l. in the Sakha (Yakutia) Republic represents an interesting new record. This species was detected in the Canadian and European arctic–subarctic, the western portion of eastern Siberia [63], the mountains of Kamchatka Peninsula and the mountains of south Siberia [65]. Our finding confirms the ideas of its arcto-mountainous distribution, covering all the arctic–subarctic regions of the Holarctic (although being rare in all of this huge territory). This finding also supports our hypothesis of a strong effect of the Pleistocene glaciation on populations of this species [45]. Most probably, this species was distributed on the entire territory of the northern Holarctic and differentiated during the pre-Pleistocene epoch. A similar hypothesis was proposed for its sister species, *D. lacustris* [66]. Deeply divergent mitochondrial lineages within the *D. umbra* (clearly seen in the 12S tree, see Figure 3A) are consistent with the idea of the long-term isolation of separate populations in some Pleistocene glacial refugia, i.e., in the mountain valleys [45].

We did not discuss *D. curvirostris* here as it was revised in detail previously [26,42], and the resolution of our tree is strongly lower than that in the two aforementioned publications.

Closely related species *D. cristata* and *D. longiremis* are also detected in the north-eastern part of Russia (Chukotka and Yakutia), but only few sequences were obtained and a further study of these taxa is necessary for adequate conclusions.

As mentioned above, species of the *D. pulex* complex are widely distributed in the arctic–subarctic water bodies of Eurasia and North America. *D. middendorffiana* and *D. pulex* are investigated studied using molecular genetic methods [40,41,67–71]. The analysis of the variability of the mitochondrial DNA gene fragments (COI, ND4 and ND5) within the *D. pulex* complex allow the detection of four to 12 deeply divergent lineages, which were characterized by different demographic histories and origins [41]. Moreover, the phylogenies reconstructed in these studies [41,67] are similar to the 12S phylogeny that is obtained above.

Generally, all studied *D. pulex*-like haplotypes are separated into three large distinct mitochondrial subclades, supporting the earlier hypothesis that this taxon includes several closely related species [43]. However, only a single large clade LII is detected in NE Siberia, the 12S haplotypes belonging to it are widely distributed in water bodies here. This clade is congruent with the “panarctic *D. pulex*” of Crease et al. [41] detected based on the mitochondrial ND5 gene; the latter authors have already reported this clade from this region. In reality, the “panarctic *D. pulex*” of Crease et al. [41] is a very widely distributed mitochondrial phylogroup rather than a biological species. Based on our data, we also cannot discuss a possible hybrid status of some of our specimens and/or populations. Several specimens of *D. pulex* and *D. pulicaria* from the GenBank have ambiguous specific status. Our assumption is based on their uncertain and unclear positions in phylogenetic trees. In particular, it should be noted that two specimens of *D. pulicaria* from Canada (AY626354) and Japan (LC534941) are associated with the *D. pulex* LII mitochondrial clade, which also includes 12S haplotypes from Kamchatka, Chukotka, Yakutia; as well as *D. pulex* from Russia (JN913685) and *D. pulicaria* from Germany (AY626355), which formed a distinct subclade within *D. middendorffiana* clade on the common phylogenetic tree. All the studied populations have a *pulex*-like morphology, but real specific status of each population must be checked with this based on nuclear genes.

D. middendorffiana is very common in the water bodies of Chukotka and Yakutia and several divergent mitochondrial lineages were found within this specific cluster. This fact suggests that this taxon (in common with *D. pulex*) is also actually a mix of species and needs careful taxonomic revision.

In toto, we reveal nine morphospecies of *Daphnia* (*Daphnia*) in NE Russia. This number is lower than in more southern regions, like Southern Europe [72], South Siberia [63] and, especially, the Far Eastern endemic zone [26]. The following taxa are very common taxa in Northern Eurasia, but not found in our study: *D. cucullata* Sars, 1862; *D. obtusa* Kurz, 1874; *D. pulicaria* Forbes, 1893. Note that these species were also not recorded by the morphological methods from Chukotka Peninsula [15], Central Yakutia [20], the northern portion of Yakutia [73], Bering Island [21] and neighboring regions.

Such daphniid poorness may be explained by harsh climatic conditions in the arctic and subarctic zones, which occupy a significant portion of the studied territory. Therefore species diversity of the arctic–subarctic crustaceans is depleted. Most researchers note that cladocerans have an advantage in colonizing new water bodies compared to copepods, but at the same time they are more sensitive to low temperatures and also more abundant in warmer water bodies [74–77].

D. cristata, *D. longiremis*, *D. middendorffiana* and *D. pulex* are most common in the arctic–subarctic water bodies [14,22,23,73,78,79]. *D. cucullata* is detected in the Western Arctic only [80–82]. *D. curvirostris* is relatively common in Central Yakutia, but rare in more northern and eastern regions, while it was common there during some phases of the Pleistocene [83].

Note that the arctic and subarctic water bodies of Canada are characterized by similar specific diversity of *Daphnia*; however, additionally, *D. rosea* Sars, 1862, *D. ambigua* Scourfield, 1947, *D. schoedleri* Leydig, 1860 were found there [74]. If we consider that the first taxon in the author’s understanding is a synonym of *D. dentifera*. and the last one is a junior synonym of *D. pulex* s.lat. [43], then the high degree of similarity of the daphniids fauna on both sides of the Bering Strait is obvious. In reality, most revealed species have a trans-Beringian distribution, with *D. longispina* absent in North America [38] and *D. curvirostris* present only in a few localities in its NW corner [42].

No endemic *Daphnia* taxa are present in NE Siberia in contrast to South Siberia [63] and the Amur basin [43], although numerous local endemic phylloclades and haplotypes are detected.

4.2. Demographic History: Preliminary Data on Mitochondrial DNA

A combination of genetic polymorphism indexes and neutrality test values allows us to reconstruct a demographic history of some *Daphnia* species in the studied region. We found that the mitochondrial 12S gene demonstrates high values of H_d at high values of π in the most *Daphnia* species from the NE Russia. As a rule, such a combination supports a mixing of historically heterogeneous and geographically differentiated *Daphnia* populations and the existence of a large stable population [84]. However, the exact phylogeographic patterns are somewhat different in different taxa.

To date, it should be recognized that the area of haplotype distribution of the “Siberian” clade of *D. longispina* s.str. extends in a northeastern direction from the Yenisei River basin to Central Yakutia and the Baikal Lake basin, where this species coexists with the vicariant *D. dentifera*. However, such findings did not change an earlier proposed scheme for the explanation of the *D. longispina*–*dentifera* complex in Eurasia, including the influence of the Pleistocene glaciation on its geographic history. No shared haplotypes of *D. dentifera* in NE Russia and Mongolia vs. Japan and North America were found. Similarly, no shared haplotype was found in the previous studies of the *D. dentifera* populations, but a lot of unique haplotypes and distinct mitochondrial lineages were detected within this species [38, 85,86]. We revealed a central 12S haplotype H1 occurring in Baikal Lake basin, Yakutia and Kamchatka. Based on the aforementioned and published data [85–87], *D. dentifera* needs to be designated as an arcto-mountain taxon. Previously, we speculated that this species was widespread throughout northeast Asia in a pre-Pleistocene time, and during the cold phases of the Pleistocene survived in some periglacial refugia [63,65] similar to *D. umbra* [45]. The northeast *D. dentifera* populations may have undergone a “bottleneck” event with subsequent spatial expansions. What this indicates is the star-like 12S haplotype network and the significant negative values of Tajima’s D and Fu’s F_s tests. Most likely, a secondary contact happened between different mitochondrial lineages of this species, which is indicated by the existence of intermediate clade IV (Figure 3A,B) closely related with the Japanese–North American and Russian–Mongolian clades. Thus, with an increase in the number of populations of *D. dentifera* from NE Russia the level of genetic polymorphism changed, essentially in comparison with previously data [63].

Taking into consideration the highest values of H_d and π in the “European” clade of *D. longispina* s.str., *D. galeata*, *D. umbra*, *D. middendorffiana* and *D. pulex*, we believe that these species were subjected to mixing of historically heterogeneous populations and distinct mitochondrial lineages, presumably having different origins. Statistically significant negative values of neutrality tests [60,61] for the “Siberian” clade of *D. longispina* s.str., *D. dentifera*, *D. galeata* and *D. pulex* more likely argue for a recent post-glacial colonization of the studied region. Likewise, for other species under consideration, the neutrality tests possess negative, but insignificant, values. However, we believe that this also indicates their post-glacial colonization as previously noted [63]. The presence of a large number of divergent mitochondrial lineages within different species of *Daphnia* also justifies this assumption.

A well-recognizable star-like shape with central haplotype H16 in the *D. pulex* clade Dp_II suggest a rapid expansion of this group. Crease at al. [41] concluded that the Panarctic *D. pulex* clade (widely distributed over Holarctic) experienced a great spatial expansion in the Holarctic between 8800 and 22,000 years BP, after the last glacial maximum. There is some discord between our data and the published data related to the *D. pulex* complex, especially for *D. pulicaria* delimitation (in particular, H_d and π values indicate mixing lineages or different species), but we agree with a very recent (late Pleistocene–Holocene) differentiation of this large clade and its rapid colonization of the Holarctic. Unfortunately, we expect that the phylogeographic results on this very usual and easily dispersed taxon may be strongly affected by recent anthropogenic long-distance transitions [88], which were detected many times for the *D. pulex* group [89–91]. Interpretation of the dispersion pattern through the world is difficult for this clade, as the central haplotype H16 (Figure 5B) (found in NE Siberia) may be the result of anthropogenic introductions in some countries

(such as Kenya). In reality, all populations of this clade in the southern hemisphere could have an anthropogenic origin [41].

The network of *D. middendorffiana* is represented by four subclusters subdivided by 3–5 substitutions, with Chukotka being the center of haplotypic diversity (Figure 5C). In the case of the central haplotype cluster H4, we propose a colonization of Yakutia from Chukotka. However, to date, we cannot definitively say whether Chukotka is a dispersion center from a separate refugium, or a bridge for the colonization of NE Russia from North America. It is known that the *D. middendorffiana*–*tenebrosa* group has several clades in North America, but no 12S dataset exists for it. In any case, our preliminary data also provide further evidences of a cryptic diversity within the *D. middendorffiana* and *D. pulex* groups.

5. Conclusions

In general, our data on mitochondrial phylogeny and the distribution of the *Daphnia* species in NE Russia are concordant with the published results, and suggest a more complete understanding of the diversity and distribution of the daphniid taxa across the northern Holarctic. Our new data allow us to assume that the daphniids of NE Russia have undergone various evolutionary scenarios during the Pleistocene period: survival in some local refugia, followed by re-colonization from them plus from North America through the Beringian land bridge, etc. All revealed patterns are relatively recent (of Late Pleistocene or Holocene age) as compared to more southern territories within East Asia, although main phylogenetic daphniid lineages (mainly congruent with the biological species) are very old [26,33]. Species diversity in NE Russia is relatively low and most taxa are trans-Beringian. However, our results provide convincing evidence for the hypothesis that NE Russia is a very important source of modern haplotype diversity for the Cladocera [63]. The newly obtained data confirm our previously assumption about the different regimes of natural selection on different *Daphnia* species inhabiting the same territory [63].

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/w14121946/s1>, Table S1: List of the 12S mitochondrial DNA sequences for *Daphnia* species used in this study; Table S2: List of the 12S mitochondrial DNA sequences obtained from the GenBank database for studied *Daphnia* species.

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