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SHORT NOTE

The first complete mitochondrial genomes of two species of charr, *Salvelinus boganidae* and *Salvelinus elgyticus,* from Lake El'gygytgyn (Chukotka)

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Abstract

Complete mitochondrial genomes are important molecular markers for understanding phylogeny of various species. Although recent studies on the complete mitochondrial genomes of salmonids have reached some success, information regarding charrs of the genus *Salvelinus* is still insufficient. To further investigate the phylogeny of *Salvelinus*, we sequenced the complete mitochondrial genomes of Boganida charr *Salvelinus boganidae* and smallmouth charr *Salvelinus elgyticus* from Lake El'gygytgyn (Chukotka) for the first time. The genome sequences are 16,654 bp for *S. elgyticus* and 16,655 bp for *S. boganidae*, and the gene arrangement, composition, and size are similar to the charr mitochondrial genomes published previously. Our results show the phylogenetic closeness of *S. boganidae* and *S. elgyticus* with Taranetz charr *Salvelinus taranetzi* and their origin from a common ancestor. Based on the complete mitochondrial genomes, we suggest that the origin of *S. boganidae* and *S. elgyticus* may result from a double invasion of the lake during postglacial periods by ancestral lineages of Taranetz charr.

Keywords Boganida charr · *Salvelinus boganidae* · Smallmouth charr · *Salvelinus elgyticus* · mtDNA · Phylogeny

Introduction

Salvelinus is one the most species-rich genera of salmonids (Salmoniformes: Salmonidae). Charrs manifest all biological traits that hamper the reconstruction of the phylogeny of the genus (high morphological and ecological variability, rapid radiation, introgressive hybridization, local adaptations) (Klemetsen 2010). This leads to an inaccurate determination of the species affiliation of individual populations and, as a result, can provide erroneous tree topologies and phylogenetic mistakes. Phylogenetic studies of narrow-ranged/endemic and disputed charr species would benefit significantly from accessing or sequencing the complete mitochondrial genomes of *Salvelinus* species (Balakirev et al. 2016a; Oleinik et al. 2019b, c, 2020a), since the original descriptions of most of them are exclusively based on morphological features. Among these are three charr species known in Lake El'gygytgyn: smallmouth charr *Salvelinus elgyticus* Viktorovsky et Glubokovsky 1981, Boganida charr *Salvelinus boganidae* Berg, 1926, and long-finned charr *Salvethymus svetovidovi* Chereshnev et Skopets 1990. *S. elgyticus* and *Sl. svetovidovi* are endemic to the lake (Chereshnev and Skopets 1990). These charr species can easily be distinguished based on morphology, including characters connected with ecological and trophic specialization (Chereshnev and Skopets 1993; Chereshnev et al. 2002). Based on the morphological analysis (Chereshnev and Skopets 1993), hybrid fish have not been observed in the lake. Molecular

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data (Osinov et al. 2015) also support that all three species are strongly reproductively isolated, and, at the present time, no hybridization has been documented between them. The peculiarity of the charr species community is associated with the specific features of the lake located in the Anadyr Plateau of Chukotka at an altitude of 490 m above sea level. Origin of the lake in the Pliocene (about 3.6 Mya) is attributed to a meteorite impact (Gurov and Gurova 1983) or to a gas explosion of endogenous nature (Bely 1993). Later on during the Pliocene, the lake might have not been frozen completely to the bottom but might have been repeatedly covered with ice for decades (Melles et al. 2012). Since under contemporary conditions charrs inhabit water bodies in which ice cover breaks up every year, it is difficult to suppose that fish could have survived the entire Pliocene in the lake (Esin and Markevich 2017).

There are different hypotheses that discuss the origin of charrs in Lake El'gygytgyn and their relationships within the genus *Salvelinus*. Morphological data (Viktorovsky et al. 1981; Chereshnev and Skopets 1993; Glubokovsky et al. 1993) suggest that the origin of the three species is connected with multiple invasions of the lake. General consensus is that the first invasion of *Sl. svetovidovi* ancestor occurred in the Pliocene, and the ancestor forms for *S. boganidae* and *S. elgyticus* invaded the lake during the Pleistocene. Some authors think that *S. boganidae* was the first to invade the lake (Viktorovsky et al. 1981; Chereshnev and Skopets 1993), while others think it was the ancestor of *S. elgyticus* (Glubokovsky et al. 1993). Later, molecular phylogenetic studies based on RFLP analysis of the ATPase6–NADH4L fragment of mtDNA (Radchenko 2003) and sequencing of the same 2162-bp fragment (Osinov and Volkov 2020) confirmed that the origin of *S. boganidae* and *S. elgyticus* in Lake El'gygytgyn relates to a double invasion. Their ancestors were represented by two glacial lineages of *S. taranetzi* (Oleinik et al. 2019a; Osinov and Volkov 2020). However, after Radchenko (2003) proposed the double invasion hypothesis, there was an additional discussion how two charr species got into the lake (Osinov et al. 2015; Osinov and Volkov 2020). Osinov et al. (2015) suggested that the appearance of two lacustrine charrs might be connected with the process of trophic and ecological differentiation following the sympatric speciation pattern. Based on their own phylogenetic analysis and estimation of the divergence time, the authors proposed that *S. boganidae* and *S. elgyticus* are young species that might have formed in the lake after the Last glacial maximum and the final opening of the Bering Strait (approximately 9000–10,000 years BP).

The discrepancy of views seems to be due to that the above studies analyzed different genes and different amounts of sequence data. In most studies, only about 400–3360 base pairs (bp) mitochondrial sequence data were used. At the same time, it was shown that complete mitochondrial genomes (mitogenomes) can provide adequate resolution of the controversial phylogenetic relationships of fish (Miya and Nishida 2015). Longer DNA sequences were also able to resolve the relationships of closely related species at the genus level. Analyses based on mitogenomes revealed recent divergences between morphologically and ecologically distinct whitefish of the genus *Coregonus* (Jacobsen et al. 2012), as well as the relationships of all species/subspecies of the freshwater eels of the genus *Anguilla* (Minegishi et al. 2005).

A revision of the relationships of all charr species of Lake El'gygytgyn community was the first objective of this study. We recently sequenced the mitogenomes of *Sl. svetovidovi* (Oleinik et al. 2019b) and *S. taranetzi* (Oleinik et al. 2019c). In this study, we have sequenced the mitogenomes of *S. boganidae* and *S. elgyticus* for the first time. We also investigated the relationships of *S. boganidae* and *S. elgyticus* to test two alternative hypotheses on their origins in Lake El'gygytgyn: (1) sympatric divergence based on trophic and biotopic specialization from an ancestral form; or (2) secondary contact of earlier allopatric populations. According to the first hypothesis, *S. boganidae* and *S. elgyticus* will form a well-supported clade in a phylogram. According to the second hypothesis, taxa that spread from separate refugia will successively diverge from the common ancestor stem or will be placed in different phylogenetic groups.

Materials and methods

For genetic analysis, two specimens, one specimen of *S. elgyticus* and one *S. boganidae,* from Lake El'gygytgyn (67°30′N/172°05′E) were collected by A.A. Semenchenko in the summer of 2017. An additional specimen of *S. elgyticus* was provided by O.A. Radchenko (Institute of Biological Problems of the North, FEB RAS). The fish specimens are stored in 96% ethanol in the collection of the Genetics Laboratory, A.V. Zhirmunsky National Scientific Center of Marine Biology, FEB RAS, Vladivostok, Russia (www.imb.dvo.ru).

Total genomic DNA was isolated from fin fragments using standard phenol–chloroform extraction and ethanol precipitation methods. The mitogenomes were amplified in six overlapping fragments using the Phusion High-Fidelity DNA Polymerase (Thermo Fisher Scientific). The primers (Online Resource 1) were designed based on public mitogenomes of salmonid fishes available in GenBank. PCRs were performed in a total volume of 20 µl containing 1× Phusion Green HF Buffer; 10 mM dNTPs (each); 0.5 µM forward and reverse primer (each); 0.02 U/µ and 50 ng of total DNA under the following profile: preheating at 98 °C for 1 min, followed by 35 cycles of denaturing at 98 °C for 10 s, annealing at 56–62 °C (depending on the primers) for

20 s, and elongation at 72 °C for 100 s. Amplification was completed with a final extension at 72 °C for 5 min. PCR products were tested by electrophoresis in 1% agarose gel.

Libraries were prepared using an Ion Plus Fragment Library Kit and unique adapters (Ion Xpress), preliminary fragmentation of PCR products was performed on a Covaris M220 ultrasonicator. Libraries were sequenced on the Ion S5 platform (Thermo Fisher Scientific). Clean reads were assembled into contig with the Bowtie2 algorithm in Geneious R11 (http://www.geneious.com/). Our previously published mitogenome of *S. taranezi* (Oleinik et al. 2019c) was used as a reference for correct contig position and orientation. The total length of overlapped sequences obtained from different primers was at least 3746 bp (Online Resource 1). The expected length of the overlapped sequences between PCR fragments produced from different primers ranged from 130 to 1221 bp (including primer sequences). No mismatches in the overlapped sequences of the independent PCR products were found. Genome annotation was performed with Geneious, the new obtained mitogenomes were compared with the mitogenome of *Salvelinus malma* (NC037502). Finally, a physical map of *S. boganidae* and *S. elgyticus* mitogenomes was generated and uploaded to GenBank with accession numbers MK695623, MK695624, and MK695625.

To confirm the phylogenetic position of *S. elgyticus* and *S. boganidae*, 23 mitogenomes of representatives of the genus *Salvelinus* together with the mitogenomes of outgroups (*Parahucho*, *Salmo*) were obtained from the GenBank database (Table 1). Complete mitochondrial genomes were aligned with the MAFFT algorithm in Geneious. We further assessed the quality of our assembly by its consistency with other mitogenomes in the protein-, rRNA- and tRNA-coding regions. All positions containing gaps were eliminated from the dataset. We then identified the best-fitting nucleotide substitution model for this alignment using the Bayesian Information Criterion (BIC) in jModelTest 2 (Darriba et al. 2012). Nucleotide

Table 1 List of taxa (and Genbank accession numbers) included in this study

Species	Common name	Length (bp)	GenBank accession number	References
Salvelinus albus	White charr	16,653	KT266870	Balakirev et al. (2015)
Salvelinus albus	White charr	16,653	KT266871	Balakirev et al. (2015)
Salvelinus alpinus	Arctic charr	16,659	AF154851	Doiron et al. (2002)
Salvelinus alpinus alpinus	Arctic charr	16,657	MN957795	Oleinik et al. (2020b)
Salvelinus alpinus alpinus	Arctic charr	16,655	MN957796	Oleinik et al. (2020b)
Salvelinus alpinus alpinus	Arctic charr	16,655	MN957797	Oleinik et al. (2020b)
Salvelinus boganidae	Boganida charr	16,655	MK695623	This study
Salvelinus curilus	Southern asian Dolly Varden	16,654	KJ746619	Balakirev et al. (2016b)
Salvelinus curilus (*S. malma* sp.)	Southern asian Dolly Varden	16,652	NC037502	Yang et al. (2017)
Salvelinus elgyticus	Smallmouth charr	16,654	MK695624	This study
Salvelinus elgyticus	Smallmouth charr	16,654	MK695625	This study
Salvelinus fontinalis	Brook trout/Brook charr	16,624	NC000860	Doiron et al. (2002)
Salvelinus leucomaenis	Whitespotted charr	16,655	KF974451	Shedko (2016)
Salvelinus levanidovi	Levanidov's charr	16,624	MK695626	Oleinik et al. (2020a)
Salvelinus malma kuznetzovi	Stone charr	16,654	KU674351	Balakirev et al. (2016a)
Salvelinus malma kuznetzovi	Stone charr	16,654	KU674352	Balakirev et al. (2016a)
Salvelinus malma malma	Dolly Varden	16,654	KJ746618	Balakirev et al. (2016b)
Salvelinus namaycush	Lake trout	16,653	NC036392	Schroeter et al. (2020)
Salvelinus taranetzi	Taranetz charr	16,654	MK695630	Oleinik et al. (2019c)
Salvelinus taranetzi	Taranetz charr	16,654	MK695631	Oleinik et al. (2019c)
Salvethymus svetovidovi	Long-finned charr	16,655	MK695627	Oleinik et al. (2019b)
Salvethymus svetovidovi	Long-finned charr	16,655	MK695628	Oleinik et al. (2019b)
Salvethymus svetovidovi	Long-finned charr	16,655	MK695629	Oleinik et al. (2019b)
Salmo salar	Atlantic salmon	16,669	AF133701	Arnason et al. (1999)
Salmo trutta trutta	Brown trout	16,677	AM910409	Duc et al. (2007)
Parahucho perryi	Sakhalin taimen/Japanese huchen	16,652	KJ816315	Balakirev et al. (2014)
Parahucho perryi	Sakhalin taimen/Japanese huchen	16,653	KJ816316	Balakirev et al. (2014)

content, codon position, *p* distances, and average number of nucleotide substitutions per site between populations (D_{xy}) were calculated using DNASP 6 (Rozas et al. 2017) and MEGA X (Kumar et al. 2018). Gene polymorphism was calculated as a proportion of variable sites to the total gene length. The selected model (GTR + G + I) was used for a heuristic search for the best tree with Maximum Likelihood (ML), NeighborJoin (BioNJ) methods, and Bayesian Inference (BI) using MEGA X and MrBayes v.3.2 (Ronquist et al. 2019), respectively. Two independent runs were performed with random starting trees for BI analyses on the CIPRES science gateway portal (Miller et al. 2010). Each run was simultaneously run for 1,000,000 generations, with four Markov chains under default heating settings, with sampling every 100 generations. The first 25% of the generations were discarded as burn-in. The BI tree was considered to be reached since the average standard deviation of the split frequencies was below 0.01. Nodal support for the trees was evaluated with 100 or 1000 bootstrap pseudo replicates (BSs) of the data. FigTree v.1.4.2 (http://tree.bio.ed.ac.uk/software/figtree/) was employed for visualization of the phylogenetic tree.

As a preferable alternative to phylogenetic trees in cases where past hybridization between some species likely occurred, Neighbor-Net networks were constructed by the uncorrected *p* distance method implemented in SplitsTree4 v4.14.6 (Huson and Bryant 2006). Neighbor-Net networks are used to represent conflicting and ambiguous signals in a dataset (Huson and Bryant 2006). In such a network, parallel edges, rather than single branches, are used to represent the splits computed from the data. When the data correspond well with a tree, the method generalizes a network that is close to this tree.

Results and discussion

The length of the mitogenomes was 16,654 bp for *S. elgyticus* and 16,655 bp for *S. boganidae*. The genomic organization was identical to typical salmon mitogenomes, including two rRNA genes, 13 protein-coding genes, 22 tRNA genes, a light-strand replication origin (OL), and a control region (CR). Studies of complete sequences confirmed a typical vertebrate order of mitochondrial genes in all species of the genus *Salvelinus*. Like mitogenomes of other charrs (Balakirev et al. 2016a, b; Oleinik et al. 2019b), the overall base composition was 28.0% of A, 26.4% of T, 28.6% of C, and 17.0% of G with a slight A + T bias (54.4%). We detected 12 single-nucleotide and no length differences between sequences *S. elgyticus* (MK695624, and MK695625); total sequence divergence (D_{xy}) was 0.0007 ± 0.0002. At the same time, 61 single-nucleotide substitutions and one length difference were found between sequences of *S. boganidae* (MK695623) and *S. elgyticus*. Only 45 substitutions were found in overall protein-coding sequences, and eight were detected in CR. Protein coding genes had a different degree of variability (Fig. 1), but variability of the NADH dehydrogenase subunit genes was highest for the three sequences (52.5% proportion of all variable sites).

The comparison of mitogenomes now obtained with other mitogenomes of related charrs available in GenBank supported that *S. elgyticus* and *S. boganidae* are part of the *Salvelinus* clade (Fig. 2). Lake charr species were phylogenetically positioned with other charrs, and the level of divergence (D_{xy}) between them and taxa within the phylogenetic group was in the range from 0.00186 ± 0.00074 to 0.044533 ± 0.00152. These values correspond to the level of intraspecific variability in the genus *Salvelinus* (Oleinik et al. 2015). The lowest sequence divergence ($D_{xy} = 0.00186 \pm 0.00074$ and $D_{xy} = 0.00306 \pm 0.00040$) was detected between the mitogenomes of *S. taranetzi*

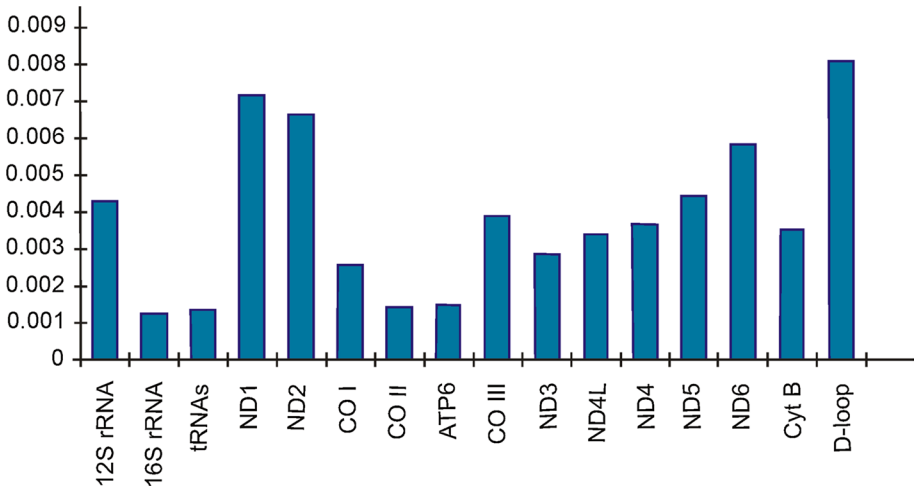

Fig. 1 Relative number of single-nucleotide substitutions between complete mitochondrial genomes of *S. elgyticus* (MK695624, and MK695625) and *S. boganidae* (MK695623)

Fig. 2 Phylogenetic tree constructed based on the comparison of complete mitochondrial genomes of *S. elgyticus* and *S. boganidae* and other GenBank representatives of charrs (genus *Salvelinus*). The tree is based on the GTR plus gamma plus invariant sites model of nucleotide substitution. Genbank accession numbers for all sequences are listed in the figure. The numbers at the nodes are bootstrap values (BSs) for BioNJ and ML trees, and Bayesian posterior probabilities (*PP*) for BI tree. *S. elgyticus* and *S. boganidae* are marked in bold

(MK695630, and MK695631) and our specimens of *S. boganidae* and *S. elgyticus*, respectively. A low level of sequence divergence was also detected between mitogenomes of *S. elgyticus* and *S. boganidae* ($D_{xy} = 0.00325 \pm 0.00040$). At the same time, specimens of *S. elgyticus* and *S. boganidae* showed very similar sequence divergence (0.01064 ± 0.00077 on average) from the mitogenome of Northern Dolly Varden *S. malma malma* and Arctic charr *Salvelinus alpinus*. Moreover, both *S. elgyticus* and *S. boganidae* showed an equal level of divergence from *Sl. svetovidovi* (0.01750 ± 0.00098 and 0.01699 ± 0.00104, respectively). These data support the result of Osinov et al. (2015) that the level of genetic divergence between *Sl. svetovidovi* and the two other species from Lake El'gygytgyn is substantially higher than between *S. elgyticus* and *S. boganidae*. The lack of a second mitogenome of *S. boganidae* cannot lead to a significant bias of final results, because available data on the variation of individual mtDNA regions indicate a very low genome diversity of the *S. boganidae* population from Lake El'gygytgyn (see Online Resource 2).

All phylogenetic trees of *Salvelinus* (BioNJ, ML and BI) constructed using mitogenomes had a similar topology

with very high statistical support in most nodes [greatest posterior probabilities ($PP = 1$) and highest bootstrap values (100% BPs)] and are interpreted in reference to the ML tree depicted in Fig. 2. Alternative variants are connected with the unstable position of branches of *Sl. svetovidovi* and *Salvelinus curilus* (syn. *S. malma krascheninnikovi*), as well as with the relationships between basal taxa. In our phylogenetic trees, *Salvelinus leucomaenis* (BioNJ, ML) or *Salvelinus levanidovi* (BI) are placed near the root after the *Salvelinus fontinalis* branch. However, the placement of *S. elgyticus* and *S. boganidae* in the phylogenetic trees is strictly defined (Fig. 2). *S. boganidae* and *S. taranetzi* are grouped together, and *S. elgyticus* is their sister branch. The formation of this cluster was highly statistically supported (100% BPs; $PP = 1$). The Neighbor-Net analysis produced a network with resolved phylogenetic relationships (Fig. 3a), and few conflicting signals within the genus *Salvelinus* likely resulting from past hybridization between some species, such as *S. taranetzi* and *S. boganidae*, but also between *S. elgyticus* and *S. boganidae* (Fig. 3b). The phylogenetic inference of the relationships between species is predominantly tree-like and consistent with all phylogenetic trees (BioNJ, ML and BI) in Fig. 2.

Current views on the phylogeny of charrs are based on the study of mtDNA CR variation (Brunner et al. 2001; Alekseyev et al. 2009; Yamamoto et al. 2014). Several phylogenetic groups have been identified that unite the closely related species of charrs (Arctic, Atlantic, Siberia, Acadia, Bering, Western Pacific, and Eastern Pacific). Previously, we also proposed to distinguish an independent Arctic phylogenetic group of Taranetz charr *S. taranetzi* (Oleinik et al. 2015), which includes Asian and North American charrs with Arctic group haplotypes. Our results show that specimens of *S. boganidae* and *S. elgyticus* belong to the Arctic group of *S. taranetzi*. The Neighbor-Net network supports the phylogenetic closeness of these taxa and their origin from a common ancestor.

The present phylogenetic analysis using mitogenomes supports relationships that correspond to the hypothesized origin of the three species with multiple invasions of Lake El'gygytgyn. The phylogeny shows a deep divergence between *Sl. svetovidovi* and sister group (*S. elgyticus*, *S. boganidae*, and *S. taranetzi*). As suggested previously (Chereshnev and Skopets 1990), the endemic *Sl. svetovidovi* was the first to invade the lake possibly immediately after it has emerged. Recently, the views on the origin of *Sl. svetovidovi* were revised. Not all researchers shared the opinion of Chereshnev et al. (2002) that *Sl. svetovidovi* is one of the most ancient salmonid taxa and is phylogenetically close to the common ancestor of charrs of the genus *Salvelinus*. Alternative hypotheses were put forward, thus necessitating a revision of the existing views on the ancient origin of *Salvethymus* (Alekseyev 2000; Osinov et al. 2015). Molecular data based on ten microsatellite loci and mtDNA sequences of the CR and cytochrome *b* gene (Osinov et al. 2015), cytochrome *b* and cytochrome *c* oxidase I genes (Crête-Lafrenière et al. 2012) as well as RAD-sequencing (Lecaudey et al. 2018) support the placement of *Salvethymus* within the genus *Salvelinus*. In the phylogeny based on the mitogenomes of charrs (Fig. 2), *Sl. svetovidovi* represents the latest branch that diverged after the basal group of species (*S. fontinalis*, *S. leucomaenis*, *S. levanidovi*, and *S. namaycush*). Therefore, our results are in agreement with previous molecular analyses (Osinov et al. 2015; Lecaudey et al. 2018) which suggested the inclusion of the genus *Salvethymus* in *Salvelinus*.

The present study clearly indicated a sister relationship between two charr species from Lake El'gygytgyn (*S. boganidae*, *S. elgyticus*) and *S. taranetzi* (Fig. 2), which now have a geographically isolated distribution. However, two charr species did not form a supported clade in the phylogram; *S. boganidae* was clustered with *S. taranetzi* from Chukotka, as some authors suggested previously (Osinov et al. 2015). We tested two alternative hypotheses regarding the origin of charrs in Lake El'gygytgyn. The evidence presented is most consistent with the conclusion that two temporally distinct colonization events of the ancestral lineages of Taranetz charr occurred in Lake El'gygytgyn during the postglacial periods. Despite the stability of topology, conflicting signal or alternative phylogenetic histories were detected within the Arctic phylogenetic group. Considering previous microsatellite-based genetic work on these species by Osinov et al. (2015), we suggest that reticulations detected by Neighbor-Net network revealed several signals of hybridization events. Phylogenetic network showed that past hybridization between *S. boganidae* and *S. elgyticus* is plausible, though hybrids between them are not observed (Chereshnev and Skopets 1993). *S. boganidae* also shows potential past hybridization with *S. taranetzi*. These species are allopatric and hybridization is difficult to explain based on the current geographic distributions. Introgressive hybridization between different lineages or species as a result of historical secondary contact has been well documented for *Salvelinus* species (Yamamoto et al. 2006, 2021; Lecaudey et al. 2018). However, the presence of parallel edges in the network does not imply hybridization, only the possibility of hybridization (Huson and Bryant 2006). The application of Neighbor-Net network becomes more challenging in situations to distinguish between separate events when one species is involved in hybridization with several species. It can also be challenging to distinguish past hybridization and incomplete lineage sorting between closely related species. Neighbor-Net, also like any phylogenetic method, is affected by sampling error (e.g., unknown closely related species involved in the hybridization not

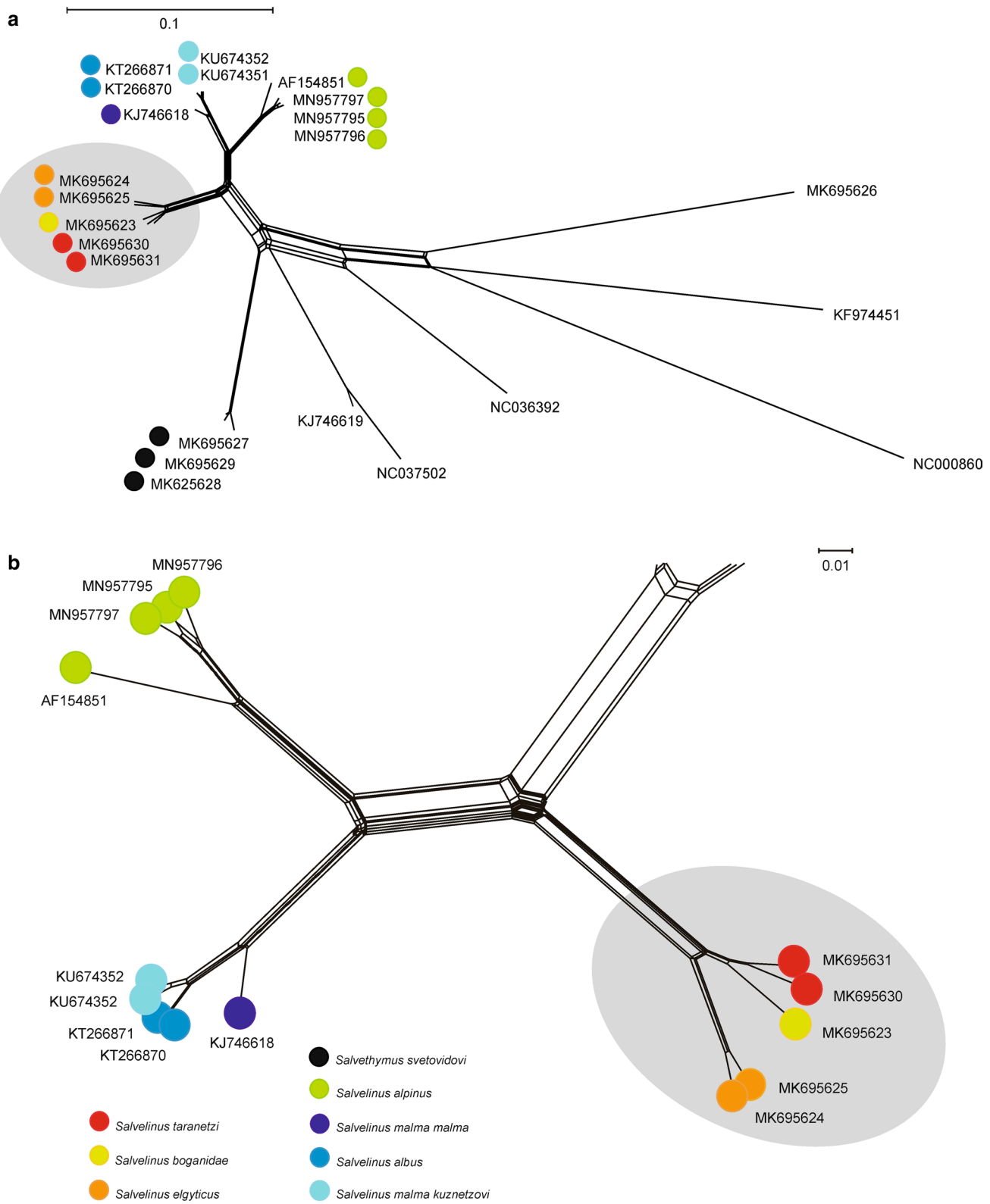

Fig. 3 **a** Phylogenetic Neighbor-Net network for complete mitochondrial genome sequences of representatives of charrs (genus *Salvelinus)* generated using SplitsTree4. Designations of charr taxa sequences: NC000860, *Salvelinus fontinalis*; NC036392, *Salvelinus namaycush*; MK695626, *Salvelinus levanidovi*; KF974451, *Salvelinus leucomaenis*; KJ746619 and NC037502, *Salvelinus curilus*. **b** Zoom of *S. elgyticus* and *S. boganidae* from this study in the Neighbor-Net network. Arctic phylogenetic group of *S. taranetzi* (sensu Oleinik et al. 2015) are shaded in the gray ellipse. The scale bar represents the nucleotide substitutions per site

included in dataset). Therefore, further detailed examinations are needed to test for hybridization suggested by the network using nuclear markers and a more detailed statistical analysis.

The findings of the present phylogenetic analysis are consistent with earlier studies based on mtDNA fragments (Crête-Lafrenière et al. 2012; Yamamoto et al. 2014; Oleinik et al. 2015; Osinov et al. 2015). Compared to phylogenetic trees in previous studies, the present phylogenetic tree based on the mitogenomes of charr species has become more robust and reliable. Earlier, it was shown that longer DNA sequences can provide adequate resolution of the higher-level relationships of fishes (Miya and Nishida 2015). Our research has also shown that the mitogenomes can provide a robust phylogenetic tree and resolve the relationships of closely related charr species.

Based on the morphological similarity, Boganida charr of Chukotka and Taimyr were assigned as the same species (Viktorovsky et al. 1981; Chereshnev et al. 2002). However, results of the mtDNA analysis indicate a plausible polyphyletic origin of Boganida charr allopatric populations (Radchenko 2003; Osinov et al. 2015). The morphological similarity of Boganida charr may in this case be a manifestation of parallelism, which is regarded as an independent acquisition of common features among closely related groups in the process of evolution (Osinov et al. 2015). The mitogenome of *S. boganidae* from the original description locality (Lake Boganidskoe, Khatanga River basin, Taimyr Peninsula) needs to be sequenced to fully resolve this contradiction. Until additional data are obtained, the mitogenome (GenBank accession number MK695623) represents only *S. boganidae* from Lake El'gygytgyn.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00300-021-02861-0.

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Author contributions AGO, LAS, and ADK conceived and designed the experiments. ADK, LAS, and AAS performed the experiments. AAS contributed new reagents and analytical tools. AGO and ADK analyzed and interpretation of the data. AGO, ADK, and LAS wrote the paper. All authors read and approved the final manuscript.

Declarations

Conflict of interest The authors declare that they have no conflict of interest. The authors declare no financial interest or benefit has arisen from the direct applications of this research. The research on mitochondrial genome sequencing was conducted at the Far Eastern Federal University, Vladivostok, Russia. The data analysis and manuscript preparation were conducted at the A.V. Zhirmunsky National Scientific Center of Marine Biology, Vladivostok, Russia.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving charr of the genus *Salvelinus* were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

Research involving human and animal participants This article does not contain any studies with human participants performed by any of the authors.

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