ABS ACTA BIOLOGICA SIBIRICA
A journal on the biodiversity of Siberia and the adjacent lands

Acta Biologica Sibirica 10: 1819–1834 (2024)
doi: 10.5281/zenodo.14565746
http://journal.asu.ru

RESEARCH ARTICLE

Branchinecta orientalis Sars, 1901 (Anostraca: Branchinectidae) in Onon-Torey lakes of the Trans-Baikal Territory

Petr V. Matafonov[1], Natalia M. Sukhikh[2, 3]

1 *Institute of Natural Resources, Ecology and Cryology SB RAS, Chita, Russia*
2 *Zoological Institute RAS, 1 Universitetskaya Embankment, Saint-Petersburg, 199034, Russia*
3 *A.N. Severtsov Institute of Ecology and Evolution, Leninsky Prospect 33, Moscow, 119071, Russia*

Corresponding author: Petr V. Matafonov (benthos@yandex.ru)

Academic editor: R. Yakovlev | Received 10 December 2024 | Accepted 24 December 2024 | Published 29 December 2024

http://zoobank.org/65E98E89-DD08-4985-B95D-AAF65FBB5077

Citation: Matafonov PV, Sukhikh NM (2024) *Branchinecta orientalis* Sars, 1901 (Anostraca: Branchinectidae) in Onon-Torey lakes of the Trans-Baikal Territory. Acta Biologica Sibirica 10: 1819–1834. https://doi.org/10.5281/zenodo.14565746

Abstract

The habitat of *Branchinecta orientalis* Sars, 1901 in the Onon-Torey lakes of the Trans-Baikal Territory (Russia) was established according to the results of molecular-phylogenetic analysis of individuals from Lakes Bain-Tsagan and Nozhiy. Mitochondrial 12SrRNA and CO1 sequences from Transbaikalia were integrated into the pool of Asian populations of *B. orientalis*. Both studied CO1 haplotypes turned out to be individual, although at a distance of two or three nucleotide substitutions from one of the most numerous Mongolian-Tibetan haplotypes. Materials on the morphology and abundance of *B. orientalis* in the lakes of Bain-Tsagan, Nozhiy and Tsagan-Nur are presented. The similarity of the basal segment of the second antennae of *B. orientalis* Sars male from Onontorean lakes and *Branchinecta minuta* was revealed. The authors substantiate the fallacy of previous indications of *Artemia salina* in the group of Torey lakes and the attribution of data on the abundance and functional indicators of this species for the 1980s.

Keywords

Branchinecta, Transbaikalia, Onon-Torey lakes, systematics, taxonomy

Introduction

Large Branchiopods are a relatively small group of ancient lower crustaceans, inhabiting mainly temporary reservoirs of arid and semiarid regions (Brendonk 2008). These organisms are typical for reservoirs with parameters unattractive to many other aquatic organisms (Zharov et al. 2020). In a number of aquatic ecosystems, in particular in drying and saline reservoirs, Branchiopods are the main component of zooplankton and zoobenthos, an important component of trophic chains and a food source for fish and birds. Some Branchiopods species are objects of industrial fishing or mass cultivation (Yabandeh 2017). The greatest diversity of the genus *Branchinecta* species has been recorded in the Nearctic, one species is known from Antarctica (Brendonck et all. 2008) and six species of this genus are known in the Palearctic, of which Arctic forms predominate in Russia (Alekseev 1995).

Branchinecta orientalis G.O. Sars, 1901 – is a widespread species known from Algeria (Beladjal and Amarouayache 2023), Mongolia (Sars 1901; Brtek 1984; Horn and Paul 2004; Alonso 2010; Marrone et al. 2015), the Himalayas (Manca and Mura 1997), Tibet (Deng et al. 2021), Iran (Atashbar et al. 2016), Europe (Petkovski 1991) and other regions of Eurasia. *B. orientalis* is used in the study of ways of the continents fauna formation (according to Williams 1991), it has been sufficiently well studied genetically (Lukić et al. 2021; Rogers and Aguilar 2020; Rodríguez–Flores et al. 2017) and considered an ideal example for testing hypotheses of Anostraca phylogeography (Rodríguez–Flores et al. 2017).

There is little information about *B. orientalis* in Russia – it was discovered only recently in Western Siberia (Pyatkova and Bezmaternykh 2024). In the Saratov region, the species has a protected status (Sergeeva et al. 2017). As for *Branchinecta* in the Transbaikal region, until now they were known only as remains of *Branchinecta* c.f. *paludosa* and eggs similar to those of *Branchinecta ferox* from the Pleistocene deposits of Lake Nozhiy (Zharov et al. 2020). At the same time, there are a number of publications about *Artemia salina* in the Onon-Torey lakes, where the species identification of the organisms raises doubts (Klishko and Balushkina 1991a, b, c).

Thus the aim of the work is to clarify information about the abundant Anostraca species inhabiting the Onon-Torey lakes and about the distribution of *B. orientalis* in Russia.

Materials and methods

Sample collection

The specimens were collected in 2014–2023, during the complex hydrobiological studies of Onon-Torey lakes located in the steppe zone in the south of the Trans–Baikal Territory near the junction of the borders of China, Mongolia and Russia (Fig.1, Table 1).

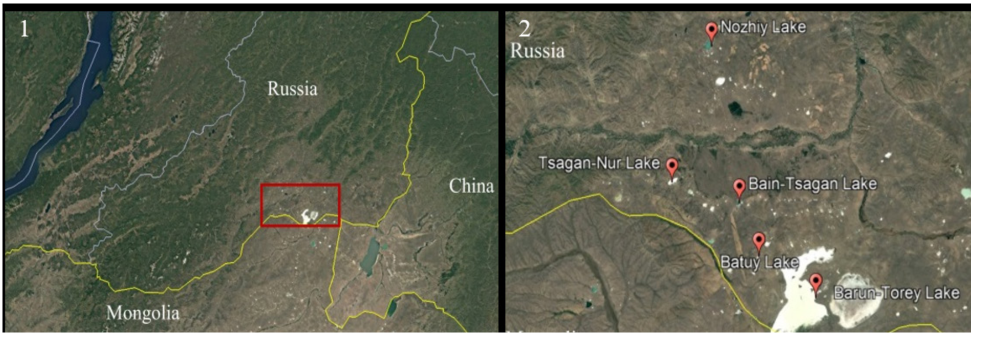

Figure 1. Location of the studied lakes. The map was produced using the Google Earth mapping application.

Table 1. *Branchinecta orientalis* studied with morphological and genetic methods

Studied locations	Coordinates	Date	Material studied with morphology	Material studied with genetics
Lake Bain-Tsagan	50°19′57″N, 115°6′17″E	22.07.2021; 18.08.2021 19.07.2023	2♂, 6♀ 1♂, 1♀ 8♂, 8♀	1♂, 1♀
Lake Batuy	50°9′57″N 115°15′18″E	07.08.2018	1♀	-
Lake Nozhiy	50°49′45″N, 114°48′59″E	21.07.2021	1♂, 1♀	1♂, 1♀
Lake Tsagan-Nur	50°22′4″N, 114°43′39″E	30.07.2014	2♂, 2♀	-

The lakes were in low-water – extremely low-water phases, while the mineralization of their waters did not exceed 16 g/l. *Branchinecta* samples for morphological and quantitative studies were collected in the coastal area of Lake Tsagan-Nur in July 2014, in lakes Bayn-Tsagan samples were collected in the coastal area on July 22, 2021 and July 19, 2023, in Lake Nozhiy – in the center of the lake on July 21, 2021. Quantitative samples were taken by the Petersen dredger (DH 0.025) in studies of lakes zoobenthos. Benthic samples were collected by the P.V. Matafonov. Specimens from Lake Batuy and 1♂ and 2♀ from Lake Tsagan-Nur provided by E.Y. Afonina (INREC SB RAS, Russia, Chita). All of this samples were fixed with formalin. Crustaceans for molecular genetic studies, were collected by P.V. Matafonov in Nozhiy and Bayn-Tsagan lakes on July 21 and 22, 2021, respectively. This samples were fixed with 96% ethanol.

Morphological analysis

Temporary pressure preparations of the specimens were made in water and water-glycerin solutions. Identification by morphological features was performed using taxonomic keys (Alekseev 1995; Alekseev 2010). The total length of specimens was measured from the anterior margin of the head to the posterior margin of the telson.

Specimens were photographed using CanonPowerShot A4000 IS digital camera, Xiaomi 12T PRO digital camera, Amscope microscope with Amscope MU800 digital camera, Zeiss Scope A1 microscope with AxioCam Zeiss Cc1 digital camera. Digital processing of the photographs was performed using the Amscope 3.7, Axiovision V 4.8.1, and Adobe Photoshop CS2.

All specimens from the Lakes Bain-Tsagan and Nozhiy and 1♂ from the Lake Tsagan-Nur were taken from the benthic samples of P. Matafonov, Institute of Natural Resources, Ecology and Cryology SB RAS. A specimen from the Lake Batuy and 1♂ and 2♀ from the Lake Tsagan-Nur were taken from the plankton samples of E.Y. Afonina and Institute of Natural Resources, Ecology and Cryology SB RAS.

DNA extraction, PCR, and sequencing

DNA was isolated from the limbs of 2♂ and 2♀ crustaceans using ExtractDNA Blood kits (Eurogen, Russia), following the manufacturer's instructions. Universal primers and reagents for PCR were used to amplify the target DNA fragments (Table 2) (Eurogen, Russia). The amplification program for all genes included the stage of heating the mixture to 95°C for 4 minutes; 35-40 cycles consisting of the following stages: melting of the matrix at 94°C for 15 seconds, annealing of primers at a specific temperature (Table 2) for 20 seconds, DNA synthesis at 72°C for 1 min; the elongation stage at 72°C for 4 minutes. Sequencing was performed on a 3500hL Applied Biosystems genetic analyzer in Eurogen, Russia (Table 1).

Table 2. Primers used in the studies

Molecular marker	Primer	Primer sequence (5'-3')	Annealing temperature, °C	Reference
12SrRNA	L13337-12S	YCTACTWTGYTACGACTTATCTC	57–60	Machida et al. 2002
	H13845-12S	GTGCCAGCAGCTGCGTTA		
COI	LCO-1490	GGTCAACAAATCATAAAGATATTGG	48–50	Folmer et al. 1994
	HCO-2198	TAAACTTCAGGGTGACCAAAAAATCA		

Molecular phylogenetic analysis

The nucleotide sequences were aligned in BioEdit program. Genetic distances were calculated using the Mega X program (Kumar et al. 2018). Support for branching nodes was evaluated using a bootstrap algorithm with 1000 replications. The analysis included our date and 92 *Branchinecta orientalis* CO1 gene region sequences available in GenBank from European countries, Baikal region, Tibet, Mongolia (LC469606, MW822916, MW822920, MW822922- MW822927, ON411462- ON411463, LT821325- LT821333, OK047196- OK047268). There are also 8 sequences of the genetically closest branchipod species: *Branchinecta hiberna* (MF037647-MF037649) and *Branchinecta ferox* (LT821334- LT821337; OK047195). The DNA sequences of the 12SrRNA gene site for branchinects are significantly smaller, only one *B. orientalis* sequence (Turkey) MT010686 was found, sequences of other species of the studied genus were used for comparison, the numbers and species names for which are shown on the phylogenetic tree.

Results

Crustaceans of the genus *Branchinecta* inhabit the entire water column in the studied lakes and were found in the benthic samples from Lake Tsagan-Nur in 2014 (Fig. 2). Initially they were identified by morphological features using Russian keys (Alekseev 1995) as *Branchinecta* sp. (*minuta* Smirnov, 1948). All males from this and other lakes examined by us have a well-marked tubercle-shaped formation on the inner edge of the basal segment of the antennae, covered with numerous and very small spikes (Figs 3, 4, 5). In addition, there is a well-marked long plate-shaped formation on the inner side of the basal segment of the antennae, also covered with numerous and very small spikes (Figs 3, 4, 5). Cercopods bear plumose setae on medial and lateral margins (Fig. 6). Gonopod has proximal lobe overreaching the ventrolateral spine (Fig. 7).

Females from the surveyed lakes (Fig. 2) had the same omission of the outer and inner edges of the cercopods (Fig. 8). Antenna in the distal part bears hairs along the inner edge (Fig. 9).

The size structure of the *Branchinecta* population from Lake Bain-Tsagan on July 19, 2023 was dominated by immature individuals with rudiments of gonads, the length of males was 12.8±0.34 mm (M±SE, n=8), females – 12.4±0.25 mm (n=8). The weight of the individuals varied from 12 to 25 mg. On July 22 in 2021, adults prevailed. The length of the females was 27.5±0.78 mm (n=6), the length of the males reached 26 mm (n=2). The individual weight of females was 131±8 mg (n=6) and reached 152 mg, the individual weight of males reached 116 mg (n=2). In Lake Tsagan-Nur, the size of males varied from 27 to 30.5 mm, the length of females reached 21.5 mm. The individual weight of crustaceans in Nozhiy Lake in 2021 reached 152 mg, its average value was 95 mg.

The abundance crustaceans of the genus *Branchinecta* at their habitats in lakes Tsagan-Nur, Nozhiy and Bayn-Tsagan did not exceed 640 specimens/m^2, however, the biomass due to the large size of individuals was high – 7.36-9.72 g/m^2 (n=3), and the proportion by biomass in the benthic invertebrates samples varied from 18 to 100%.

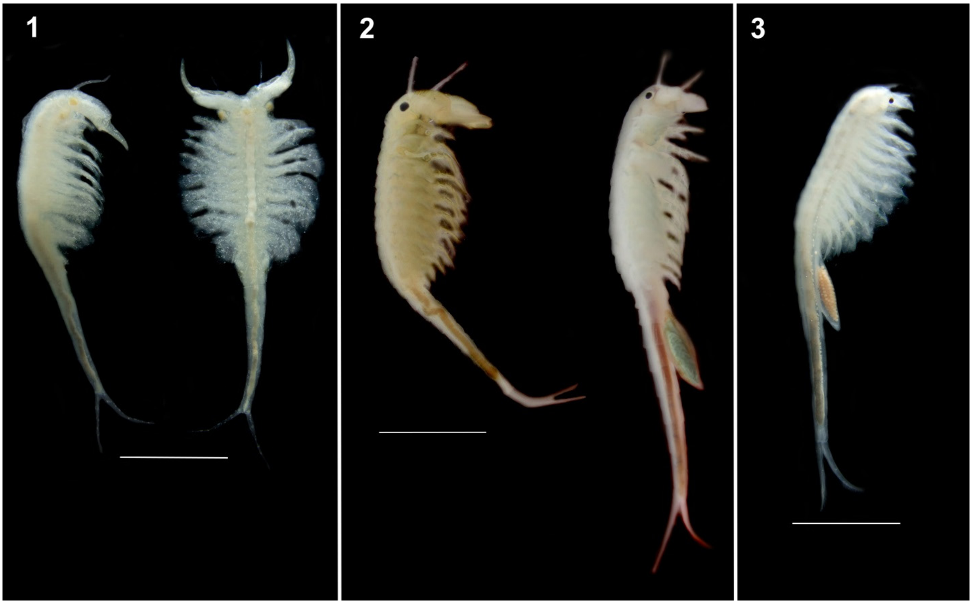

Figure 2. General *Branchinecta orientalis* view. **1** – male, lateral (left) and ventral (right side) view (Lake Tsagan-Nur), **2** – male (left side) and female (right side) (Lake Bain-Tsagan, 18.08.2021, alive specimens), **3** – female (Lake Batuy). Scale bars: 10 mm.

Figure 3. *Branchinecta orientalis* male head. **1** – ventral view (Lake Tsagan-Nur); **2** – ventral view (Lake Nozhiy); **3** – ventro-lateral view (Lake Bain-Tsagan, 18.08.21, alive specimen). The arrows indicate the tubercle and lamellar appendage. The arrow shows the lamellar appendage. Scale bars: 1 mm.

As a result of crustacean genetic studies, 2 DNA sequences of the 12SrRNA gene site (PQ804779-PQ804780) and 2 DNA sequences of the CO1 gene site were obtained (PQ810797-PQ810798), per one sequence of one gene from each Bain-

Tsagan and Nozhiy lakes. The resulting nucleotide sequences were entered into the GenBank database. The genetic differences between the obtained DNA sequences were minimal: 1 nucleotide for the CO1 gene region and 4 nucleotides for the 12Sr-RNA gene region.

According to GenBank data using the BLAST algorithm, all the sequences of 12SrRNA and CO1 of Transbaikal crustaceans obtained by us were identified as *Branchinecta orientalis*. This is shown by the haplotype network based on the CO1 gene (Fig. 10) and the phylogenetic 12S tree by the authors (Fig. 11).

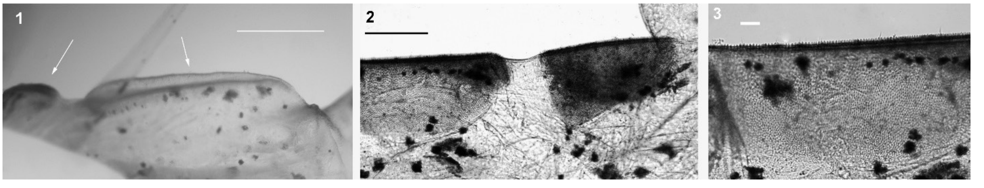

Figure 4. *Branchinecta orientalis* male second antenna (Lake Tsagan-Nur). **1** – tubercle-shaped formation (left side) and lamellar appendage, scale bar: 1 mm; **2** – tubercle-shaped formation (right) and lamellar appendage (left, part), scale bar: 0.25 mm; **3** – small spikes on the lamellar appendage, scale bar: 0.05 mm.

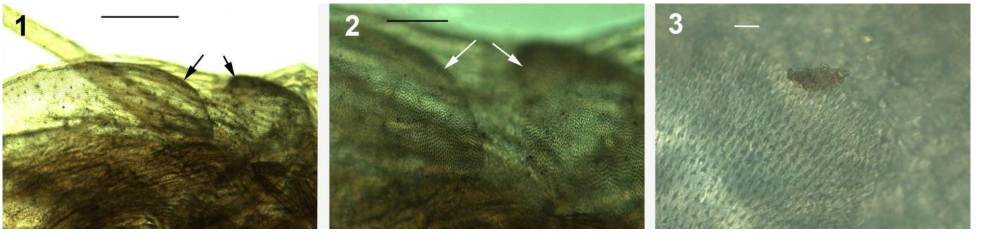

Figure 5. *Branchinecta orientalis* male second antenna (Lake Nozhiy). **1** – lamellar appendage (left side) and tubercle (right side), scale bar: 0.5 mm; **2** – tubercle (right side) and lamellar appendage (left side), scale bar: 0.2 mm; **3** – numerous small spikes on the lamellar appendage, scale bar: 0.02 mm. The arrows indicate the tubercle and lamellar appendage.

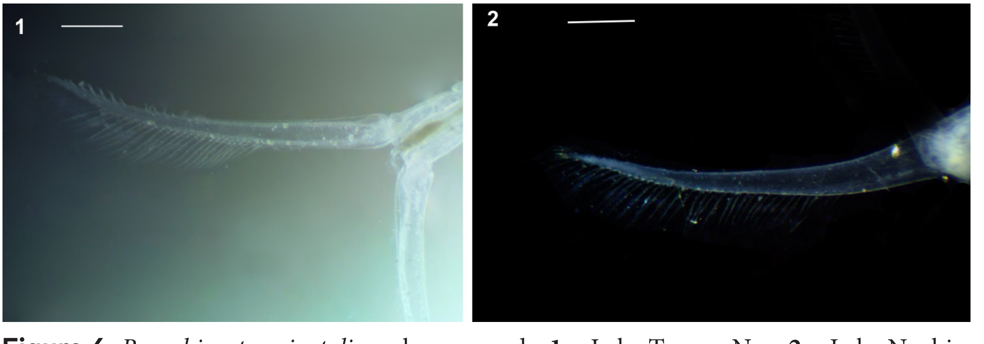

Figure 6. *Branchinecta orientalis* male cercopods. **1** – Lake Tsagan-Nur; **2** – Lake Nozhiy. Scale bars: 1 mm.

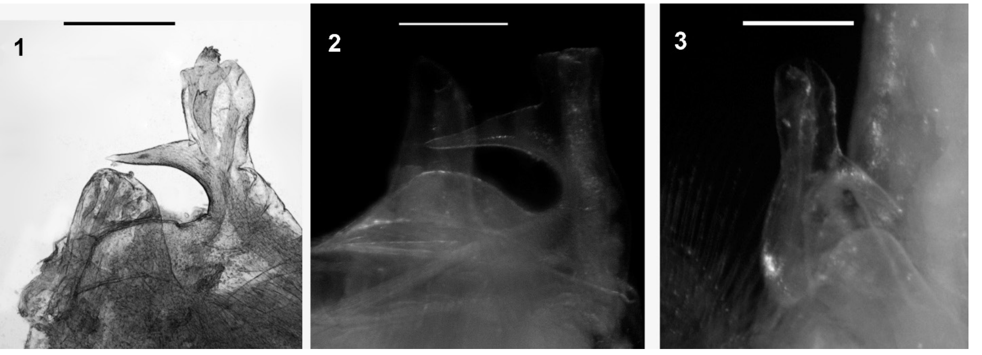

Figure 7. *Branchinecta orientalis* gonopods, ventral view. **1** – Lake Bain-Tsagan (22.07.21); **2** – Lake Nozhiy; **3** – Lake Tsagan-Nur. Scale bars: 0.5 mm.

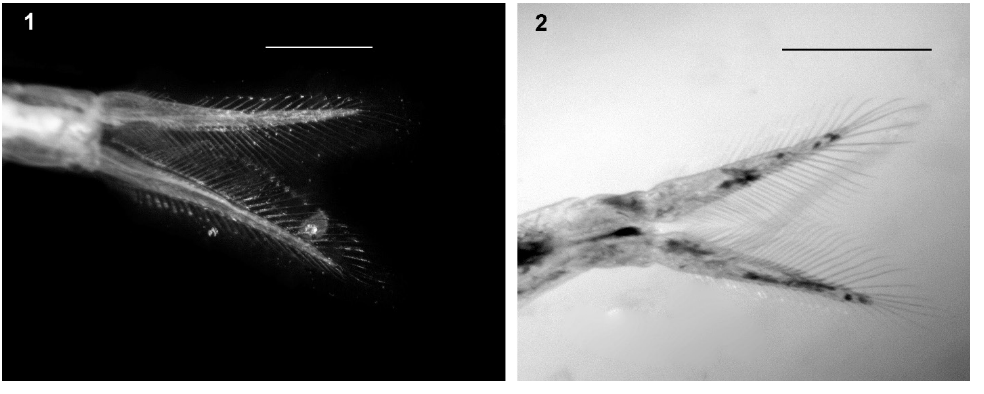

Figure 8. *Branchinecta orientalis* female cercopods. **1** – Lake Nozhiy. **2** – Lake Tsagan-Nur. Scale bars: 1 mm.

Figure 9. *Branchinecta orientalis* female second antenna. **1** – Lake Nozhiy, scale bar: 0.2 mm. **2** – Lake Nozhiy, scale bar: 0.05 mm. **3** – Lake Tsagan-Nur, scale bar: 0.1 mm.

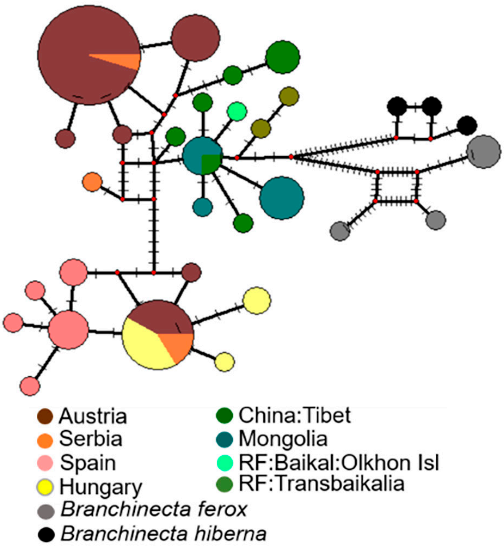

Figure 10. Median-joining network of haplotypes of *Branchinecta orientalis*, built with 102 nucleotide sequences of the CO1part of gene. The lines indicate the number of mutations between haplotypes. The smallest rings correspond to the single crustacean haplotype; the biggest ring corresponds to 40 crustaceans with the same haplotype.

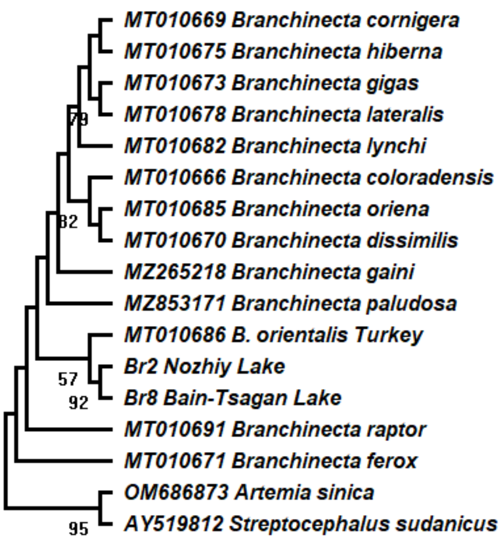

Figure 11. Maximum Parsimony phylogenetic tree based on sequences of the mitochondrial 12SrRNA gene region of *Branchinecta* species. Numbers at the nodes are bootstrap values.

Discussion

The findings of *B. orientalis* in the reservoirs of the Trans-Baikal Territory, established by the results of molecular phylogenetic analysis, is expected, since the species has a wide distribution in Mongolia near the lakes studied by us (Horn and Paul 2004). The recent phylogenetic analysis using the CO1 gene site of the *B. orientalis* species revealed the presence of two genetic lines: European and mixed-Asian-European (Lukić et al. 2021). The last line is divided into 2 corresponding clusters - European and Asian. Our sequences from two lakes of Transbaikalia were expectedly integrated into the pool of sequences of Asian populations, while both studied haplotypes turned out to be individual, although at a distance of two- three (CO1) nucleotide substitutions from one of the most numerous Mongolian-Tibetan haplotypes.

It should be noted that the identification of *B. orientalis* from the Onon-Torey lakes by morphological features is associated, in our opinion, with difficulties. The taxonomy and phylogeny of Anostraca species is based on the structural features of the second antennae and genitalia of males (Brendonk et al. 2008). One of the important diagnostic features in the identification of species of the genus *Branchinecta* is the presence of an outgrowth or lamellar appendage on the basal segment of the second antennae of males (Alekseev 1995; Alekseev 2010). According to this feature, *B. orientalis* from the Onon-Torey lakes shows similarities with *B. minuta*. In the original description of *B. minuta* Smirnov (1948) pointed out in this species "on the inner edge of the basal segment, at the base there is a gentle tubercle-like formation covered with numerous and very small spikes". In addition, there is a long lamellar formation on the same segment, which attaches to the inner side of the segment and is obliquely directed to the dorsal surface, where it ends near the end of the segment. This plate is armed with numerous small spikes along the edge" (Smirnov 1948). According to Smirnov (1948), a lamellar outgrowth on the inner side of the basal segment of the posterior antennae of the *B. minuta* male "has a shape that has not been observed so far in *Branchinecta* species." Nevertheless, he suggested (Smirnov 1948) a possible identity on this basis of *B. minuta* with the described *Branchipus ferox* f. *aestivalis* Daday, 1890. Since Daday de Dees (1910) indicated *Branchipus ferox* f. *aestivalis* as a synonym of *Branchinecta orientalis*, apparently, our data are consistent with the assumption of Smirnov (1948) about the similarity of *B. minuta* and *Branchipus ferox* f. *aestivalis*. The similarity of *B. minuta* and individuals of *B. orientalis* from the Pamirs in the two-division of preepipodites, indicated by Smirnov (1948), can also show the proximity of these species. Perhaps the small average sizes of females and males (8.4-8.8 mm) at the time of their entry into the reproductive phase in some reservoirs of the Saratov region (Sergeeva et al. 2017) also deserve attention in this regard.

In 1987, Akatova (Akatova 1987), referring to Brtek (1984) and recognizing the structure of the penis as the most reliable sign, noted difference between *B. minuta* from *B. ferox* and *B. orientalis* primarily in the armament of the thoracic segments of the female and the presence of a comb-shaped outgrowth on the basal segment of the antenna, covered with spikes throughout on the surface, and along the edge – with cone-shaped teeth. In the Russian identification keys (Alekseev 1995; Alekseev 2010) figures *B. orientalis* by G.O. Sars are used, where the lamellar appendage is not shown. Indeed, according to the description of *B. orientalis* by Sars (1901) and in Daday de Deés (1910), lamellar outgrowths on the basal segment of the males antennae are absent on the figures. In the figures of *B. orientalis* from Tibet (Deng et al. 2021), there is no spike-covered plate on the second antennae of the male. A male *B. orientalis* from Western Siberia (Pyatkova and Bezmaternykh 2024) has a distinct lamellar formation on the basal segment of the second antennae in addition to the tubercle. The figures of *B. orientalis* from Europe (Petkovski 1991) and Algeria (Beladjal and Amarouayache 2023) show very small spikes along the inner edge of the basal segment of the second antennae of males. In the identification key Branchiopoda of the Palearctic (Rogers et al. 2019), the presence of tiny spines distinguishes *B. ferox*, *B. orientalis* and *B. minuta* from other species. In our opinion, the basal segment of the *B. orientalis* males antennae from the Onon-Torey lakes has a lamellar appendage covered with spikes and corresponds to its description and *B. minuta* image by Smirnov (Smirnov 1948). Further identification of this group *Branchinecta* species occurs according to the shape of the male gonopod (Rogers et al. 2019) – according to this feature, *Branchinecta* from the Onon-Torey lakes belongs to *B. orientalis*.

The attention to *B. orientalis* in the Onon-Torey lakes is also due to doubts about the accuracy of the identification of Anostraca in these lakes in the 1980s. According to previous studies (Klishko and Balushkina 1991a, b, c), in the lakes Barun-Torey, Zun-Torey and Bayn-Tsagan, the basis of their zoobenthos in some periods of the low-water 1980s consisted *A. salina*. Although our research was carried out in extremely low-water years and *Artemia* has not been detected in Lakes Bayn-Tsagan and Barun-Torey. A number of circumstances make it possible to doubt the accuracy of the identification of Anostraca. Optimal conditions for *A. salina* are observed in the mineralization range of 71-150 g/l (Litvinenko et al. 2013). In Mongolia, *A. salina* inhabits reservoirs with a mineralization of more than 15 g/l, whereas reservoirs with a mineralization of approximately less than 13 g/l are inhabited by *B. orientalis* (Alonso 2010). The mineralization of waters in lakes Barun-Torey and Bayn-Tsagan in the 1980s was below 15 g/l and amounted to 3.4-5.7 g/l (Strizhova and Orlik 1991a, b), which corresponds to the habitat conditions of *B. orientalis*, but not *A. salina*. The individual mass of organisms was up to 45-114 mg in the Torey lakes (Klishko and Balushkina 1991a, b, c), whereas according to our data, the individual mass of adult *A. salina* males and females reaches not more than 13 mg. Against this background, the individual mass of *B. orientalis* corresponds to the indicated average values of the individual mass of *A. salina* in the Torey lakes (Klishko and Balushkina 1991a, b, c). This suggests that information on the abundance and production indicators of *A. salina* in the Torey lakes (Klishko and Balushkina 1991a, b, c) belong to *B. orientalis*. When studying the reservoirs of Mongolia, cases of erroneous identification of large Branchiopods were pointed out (Naganava and Zagas 2002). The case of *B. orientalis* from the Torey lakes is also one of the examples of errors in their identification and indicates insufficient attention to these rather large and massive representatives of the fauna of shallow steppe lakes.

The appearance of *B. orientalis* corresponds to an extremely arid phase of the climate and a "branchinect" phase in the functioning of the Onon-Torey lakes, characterized by extremely low water levels and increased mineralization. In high-water years, *B. orientalis* is probably disappears from the fauna of lakes and remains in resting eggs. Thus, with a decrease in the water level in Lake Bain-Tsagan in 2014, we noted the disappearance of fish and the dominance of *Gammarus lacustris* even in the water column. During this period, fairy shrimp *Branchinecta* were not found in samples even with a detailed study of the lake. With a further decrease in the lake level, *Gammarus* is replaced by *B. orientalis*. Similarly, apparently, in Lake Nozhiy – in high–water years, the lake has a depth of up to six meters and is inhabited by fish, whereas in the "branchinect" phase in 2021, the depth of the lake reached only 1.5 m and was fishless. According to visual assessment, in the largest lake of the basin of the Torey lakes – Lake Barun-Torey *B. orientalis* was quite numerous in the water column of the shallow zone of the lake in the initial phase of filling the lake in 2023.

Lakes Barun-Torey and Zun-Torey are included in the Daursky International Nature Reserve, therefore, clarification of information about the massive Anostraca in the Onon-Torey Lakes is necessary to understand the role of aquatic biota in the nutrition of protected bird species, as well as to identify patterns of changes in lake ecosystems in various phases of climate.

Conclusion

Thus, the populations of branchipods studied by us from the lakes of Transbaikalia Nozhiy and Bain-Tsagan, according to molecular genetic analysis, turned out to be representatives of *B. orientalis*, and not *A. salina*, as previously thought. According to morphological features, given in the Rogers (2019) identification key, the studied populations are also defined as *B. orientalis*, although the lamellar appendages of the males second antennae basal segment according to Smirnov (1948), are similar to those in *B. minuta*.

The lack of research on *B. minuta*, as well as lack of its DNA sequences in the Genbank with a large number of *B. orientalis* sequences, including from areas intersecting with the range of *B. minuta*, together with the ambiguity of the species identification of the populations studied by us from Transbaikalia indicate difficulties with the taxonomic definition of *B. minuta* and *B. orientalis* species among specialists. Further research of the group with the including of nuclear genes in the genetic analysis, the study of the *B. minuta* species from the type locality using molecular-genetic and morphological methods, as well as the expansion of the number of studied populations of the species will allow solving the issues raised in the future.

Taking into account the results of previous studies (Klishko and Balushkina 1991a, b, c), it can be noted that *B. orientalis* is one of the main components of ecosystems in a number of Onon-Torey lakes and an indicator of their "branchinect" functional phase in extremely low-water years.

Acknowledgement

We thank E.Y. Afonina for the specimens from Lake Tsagan-Nur and Batuy. Genetic studies were done at the Taxon Centre of ZIN RAS. Sequencing was done at Eurogen (Moscow).

B. orientalis sampling in the Nozhiy and Bayn Tsagan lakes were carried out with the support of the Trans-Baikal regional branch of the NGO "Russian Geographical Society". Genetic part of the work was performed in the Core Facilities Centre "Taxon" ZIN RAS and was supported by P.V. Matafonov and sequencing was performed in Evrogen Joint Stock Company (Moscow) and was supported by the Russian Science Foundation N 22-14-00258. The morphological analysis and discussion of the results obtained were carried out according to the Program of Fundamental Scientific research of the Siberian Branch of the Russian Academy of Sciences "Geoecology of aquatic ecosystems of Transbaikalia in the conditions of modern climate and technogenesis, basic approaches to the rational use of waters and their biological resources" (state registration No. 121032200070-2).

The contribution of the authors. Research concept, identification of *Branchinecta* sp. (*minuta*?), morphological analysis, discussion of all results, P.V.M.; DNA isolation, PCR, sequencing, molecular phylogenetic analysis and discussion of these results, identification of *B. orientalis*, N.M.S.

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