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EXPERIMENTAL ARTICLES

Colorless Sulfur Bacteria *Thioploca* from Different Sites in Lake Baikal

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Abstract—The colorless sulfur bacteria *Thioploca* spp. found in Lake Baikal are probably a marker for the influx of subterranean mineralized fluids. Bacteria act as a biological filter; by consuming sulfide in their metabolism, they detoxicate it and maintain the purity of Lake Baikal's water. The bacteria were investigated by various techniques. According to analysis of the 16S rRNA gene fragment, *Thioploca* sp. from Frolikha Bay, Baikal belongs to the clade of freshwater species found in Lake Biwa and Lake Constance; it is most closely related to *Thioploca ingrica.*

Key words: Thioploca, Lake Baikal, bottom sediments, colorless sulfur bacteria, phylogeny.

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Colorless sulfur bacteria of the genus *Thioploca* have long attracted the attention of many researchers [1–3]. In marine ecosystems, these large organisms form bacterial mats with a high biomass [2].

Thioploca was also found in a number of freshwater lakes: Lake Constance (Germany) [3], Lake Baikal (Russia) [4], Lake Biwa (Japan) [5], and Lake Ontario (Canada) [6]. Both the individual filaments and the common sheath of freshwater *Thioploca* are smaller than in marine species. Some *Thioploca* were found to be capable of intracellular nitrate accumulation [7, 8].

The species affiliation of colorless sulfur bacteria, including *Thioploca*, is based on their physiological characteristics and trichome diameter [9]. The recent data on the 16S rRNA gene structure support the usability of these criteria for species identification [8, 10]. In some mixed communities of colorless sulfur bacteria, however, morphologically similar *Beggiatoa* species were observed, which differed in the 16S rRNA gene structure [11].

Three species of these colorless sulfur bacteria are known in freshwater environments: *Thioploca schmidlei* [3], *T. ingrica* [5, 6, 8, 9], and *T. minima* [9, 12, 13]. *T. ingrica* was found in Lakes Ontario, Constance, and Biwa; *T. minima* was revealed in Lake Erie. The species were identified based on their trichome diameter.

T. schmidlei was revealed in the deep part of the Frolikha Bay, Lake Baikal in 1994 [4]. After 2003, new habitats for colorless sulfur bacteria *Thioploca* were discovered, including the estuaries of the Selenga and Barguzin rivers. The morphological analysis of *Thioploca* spp. filaments from different regions of Lake Baikal revealed several different morphotypes.

The goal of the present work was thorough investigation of the morphology of the Lake Baikal *Thioploca* and of the physicochemical conditions of their habitats, as well as analysis of the phylogenetic position of one of these bacteria from the vicinity of an underwater spring in the Frolikha Bay, Lake Baikal.

MATERIALS AND METHODS

Source of isolation. The *Thioploca*-containing bottom sediments from Lake Baikal were collected in late August–early September 2003 and in June 2005 using sample collectors (Okean grab, benthic tube) during the Vereshchagin research vessel expeditions. *Thioploca* spp. were revealed in the deep (403 m) and coastal (125 m) parts of the Frolikha Bay, in the Selenga estuary, and in the Barguzin Bay. Due to their white coloration and long filaments (sometimes up to 2 cm), they were easily recognizable in the samples.

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Analysis of Bottom sediments. The physicochemical characteristics of the *Thioploca*-containing sediments were determined as described in [14, 15]. Sulfide was determined with dimethyl-*p*-phenylenediamine in pore water obtained under argon [16].

Morphological characteristics. The samples from the Frolikha Bay, Selenga estuary, and Barguzin Bay were immediately fixed with glutaraldehyde. The morphological parameters were determined in the laboratory under an Olympus (Japan) epifluorescence microscope at various magnifications. The following morphological characteristics of *Thioploca* from various biotopes were analyzed: inner and outer diameter of the sheath, diameter of individual trichomes, and cell length and width. The results are presented in Table 1.

The variation rows for the morphological parameters of bacteria from four regions were analyzed statistically with the Microsoft Excel 2002 software package.

Phylogenetic analysis. *Thioploca* sp. filaments were collected under a dissection microscope by means of a needle and washed with sterile water; a portion of this material was then fixed with 2% glutaraldehyde, while another portion was used for DNA isolation.

DNA isolation, amplification, cloning, and sequencing were carried out as described by Teske [17]. The sequences (699 bp) are deposited in GenBank, accession no. DQ338566.

RESULTS

Physicochemical characterization of the *Thioploca* habitats. Characteristics of the *Thioploca*-containing sediments from the vicinity of an underwater spring in the Frolikha Bay, Lake Baikal (the site of seeping of more mineralized subterranean waters) [4, 14, 17] are presented in Table 2. The parameters of *Thioploca*-containing sediments at different depths (from 14 to 400 m) in the Barguzin and Selenga estuaries are also listed. The distribution of these bacteria in the near-estuarine sediments is patchy; although local fields (up to 10 m in diameter) were formed, not all the areas of the bays were covered. In all the habitats, the sediment surface was reduced; the redox potential (–152 to –390 mV) corresponded to anaerobic or microaerobic conditions. However, oxygen concentration was relatively high (275 μM) several centimeters from the bottom; the average value for Lake Baikal water is 331.25 μM. The lowest oxygen content (57.8 μM) was detected in the Selenga shallows at the bottom; it was below 10% of the saturation level for this depth. In some samples, a thin (1–2 mm) oxidized layer was observed. The pH values of the sediments varied within a narrow range, from 6.86 to 7.52.

The chemical composition of the pore waters of *Thioploca*-containing sediments was determined with a step of 2 cm. The vertical distribution of sulfate and chloride ions in the sites where *Thioploca* was present differed from their distribution at background stations (Fig. 1), indicating the influx of subterranean fluids. In some horizons of the cores with *Thioploca* spp., higher concentrations of sulfate and chloride ions were revealed than in other regions of Baikal; the differences reached one to two orders of magnitude. The highest fluctuations in anion concentration with depth were recorded in the vicinity of the underwater hydrothermal spring in the Frolikha Bay (125 m). The highest content of sulfate and chloride ions (Fig. 1b) were 755.21 and 534.29 μM, respectively. In the deep part of the Frolikha Bay (403 m), chlorine concentrations exceeded those in the lake water only at the surface and at 17-cm depth (145.1 and 126.2 μM, respectively) (Fig. 1c). High sulfate content (21–796 μM) was observed in the Barguzin Bay (Fig 1d). In the Selenga shallows, the concentrations of sulfate and chlorine anions were generally close to the values in Lake Baikal's background sites (Fig. 1a, d); at 16–18 cm, however (below the zone of colorless sulfur bacteria), elevated concentrations of chlorine ions were found (102.9 μM). The elevated content of sulfate and chloride ions in Baikal sediments result from discharge of deep, more mineralized fluids [15, 18, 19]. Their high concentrations were revealed in the vicinity of the hydrothermal spring in the Frolikha Bay and around the mud volcanoes and natural oil manifestations. In the regions with undisturbed sedimentation, pore water inherits the composition of the lake water with low mineralization [20], a sulfate content not above 52 μM, and chloride content of 11 μM [21]. Our data demonstrate that in the zones of *Thioploca* development mineralized fluids enriched with either sulfate, chloride, or both, are discharged.

In the pore water of *Thioploca* habitats, nitrates were found; their concentration was usually below the detection limit. Nitrates were detected only in 4% of 313 pore water samples from different parts of Lake Baikal collected after 2003. Their maximal concentration did not exceed 560 μM. In 1997, nitrates were not detected in the Frolikha Bay sediments. In 2003, their concentration in the Selenga shallows, Barguzin Bay, and Frolikha Bay was 19.4, up to 500, and 19.4 μM, respectively in the *Thioploca*-containing zone and below.

Sulfide was revealed only in the deep part of the Frolikha Bay in individual samples and at low concentrations (the maximal value was 2.35 μM) (Table 2).

Morphological characterization of *Thioploca* spp. from different regions in Lake Baikal. The colorless sulfur bacteria obtained from the samples form a common sheath containing from 2 to 21 filaments. The terminal cells of the filaments are tapered or rounded (Fig. 2a). Sulfur globules are present within the cells, along the cell periphery. The vacuoles occupy a significant part of the cell (Fig. 2b). Nitrates are accumulated within the vacuoles. Individual bacterial filaments are capable of moving independently within the sheath. In the sediments, mainly from the Frolikha Bay, a number

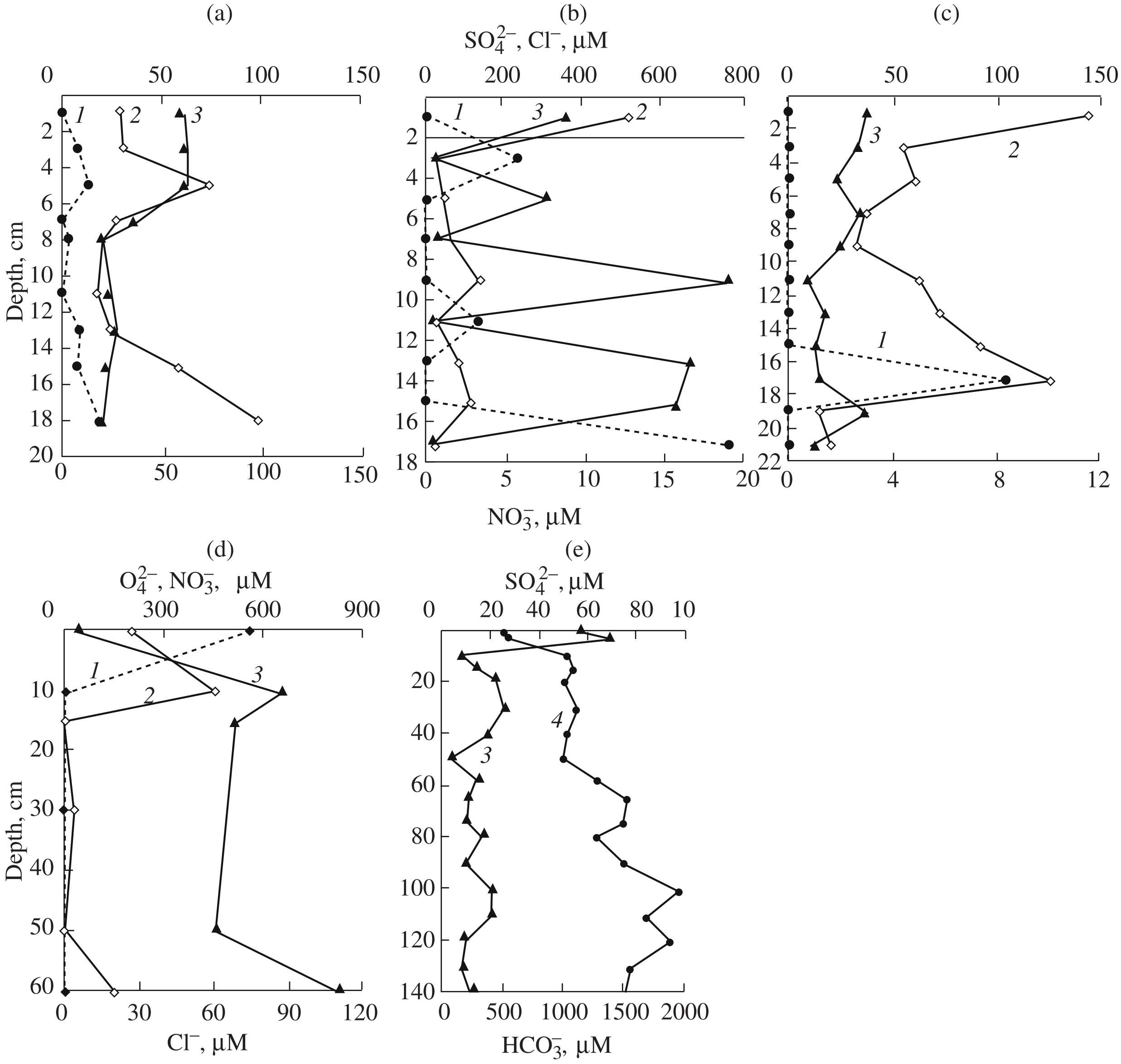

Fig. 1. Anion concentrations in bottom sediments: a, Selenga shallows, 14 m; b, Frolikha Bay, 125 m; c, Frolikha Bay, 403 m; d, Barguzin Bay, 200 m; e, background station Southern Baikal, 1300 m. Nitrate (*1*), chloride (*2*), sulfate (*3*), hydrocarbonate (*4*). For plates a, b, and c: Y axes, sediment depth, cm; upper X axes, sulfate and chloride concentrations; lower X axes, nitrate concentration. For plate d: Y axis, sediment depth, cm; upper X axis, sulfate and nitrate concentrations; lower X axis, chloride concentration. For plate d: Y axis, sediment depth, cm; upper X axis, sulfate concentration; lower X axis, hydrocarbonate concentration.

of long colorless *Thioploca* filaments with adjoining smaller filaments were found. Short filaments were located both on the surface and inside the lipopolysaccharide sheaths. Most of the short filaments contained no sulfur granules. Some of the *Thioploca* had two to three filaments covered with a thin and transparent sheath. Inside these cells, vacuoles and sulfur inclusions were clearly visible. The trichomes in the sediments were oriented vertically. Their highest content was found in the upper sediment layer (2 cm). The depth of bacterial penetration into the sediments in the Frolikha Bay, Selenga shallows, and Barguzin Bay was 19, 6, and 5 cm, respectively.

Thioploca spp. from different regions of Lake Baikal had two ranges of filament diameter, 2.0–4.5 µm (characteristic of *T. ingrica*) and 5.0–10.7 µm (characteristic of *T. schmidlei* according to classification [9, 13]). The presence of two morphotypes of different sizes was statistically confirmed (Table 1, *n* = 2306 measurements). Bacteria from the Barguzin Bay were the most variable morphologically; the coefficient of variation for the sheath internal diameter, trichome diameter, and cell length was 66, 37, and 47%, respectively. The morphological characteristics of the Frolikha Bay bacteria varied less (Table 1). Similar to the Barguzin Bay, two types of filament diameter charac-

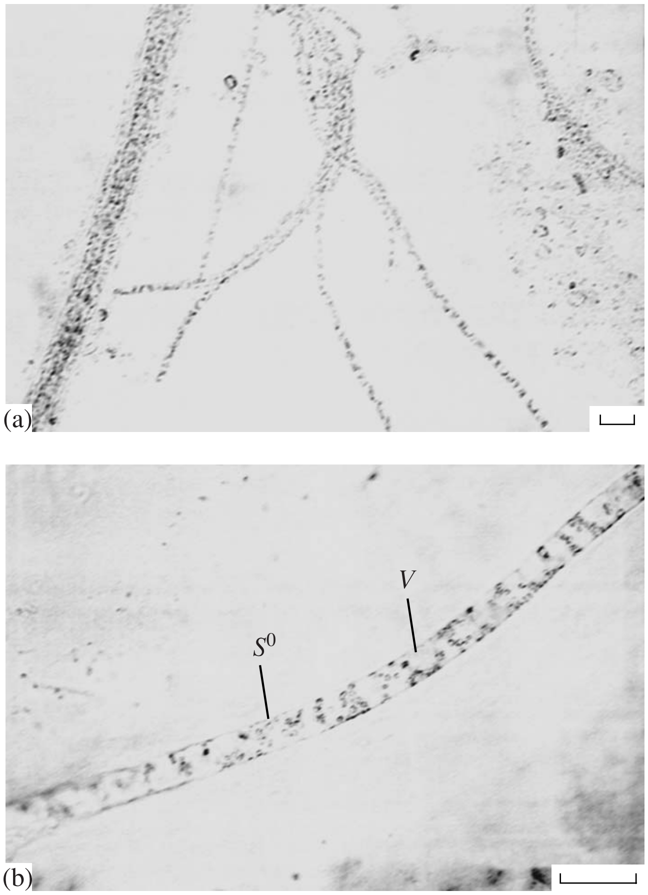

Fig. 2. a, *Thioploca* filaments; tapered ends of individual filaments are visible. Two or more filaments were present in a sheath. b, Individual *Thioploca* filament; sulfur globules (S^0) and vacuoles (V) are visible. Scale bar, 10 μm.

teristic for *T. ingrica* and *T. schmidlei* were found in the Frolikha Bay (Fig. 3a). In 2003, bacteria from the Frolikha Bay had the greatest trichome diameter (5.0 μm) and the highest number of filaments per sheath (13) (Table 1). In 1997, *Thioploca* filaments of even greater diameter were observed. The number of filaments per sheath reached 21.

Bacteria from the Selenga shallows were the least variable in morphology; the filament diameters follow the typical Gaussian distribution pattern. Thus, one morphotype (*T. ingrica*) was present only in the Selenga shallows (Fig. 3b).

In other regions of Lake Baikal, the *Thioploca* community of different dimensions is evident; it contains at least two morphotypes. In the Barguzin Bay (Fig. 3a) and the deep part of the Frolikha Bay (Fig. 3c), 77 and 71% of the *Thioploca* sheaths contained filaments of 1–4.5 μm in diameter characteristic of the species *T. ingrica.* In the coastal part of the Frolikha Bay (Fig. 3d), most of the population (69%) consisted of larger filaments (5–11 μm in diameter) characteristic of *T. schmidlei.*

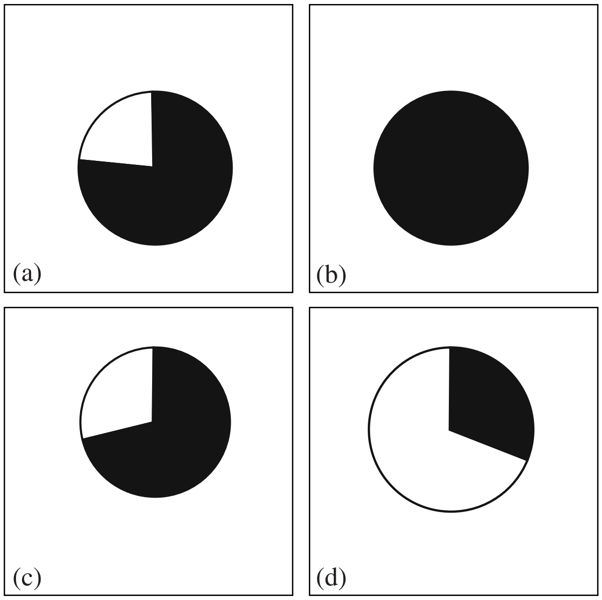

Fig. 3. Content of the *Thioploca* filaments of different diameter in Baikal sites. a, Barguzin Bay, 23% filaments with 5.0–11.0 μm diameter (light sector), 77% filaments with 1.0–4.5 μm diameter (shaded sector); b, Selenga shallows; 100% filaments with 1.0–4.5 μm diameter; c, Frolikha Bay, 403 m, 29% filaments with 5.0–11.0 μm diameter (light sector), 71% filaments with 1.0–4.5 μm diameter (shaded sector); d, Frolikha Bay, 125 m, 69% filaments with 5.0–11.0 μm diameter (light sector), 31% filaments with 1.0–4.5 μm diameter (shaded sector).

In order to confirm our conclusions on the morphological classification of one of the *Thioploca* sp. samples from the deep part of the Frolikha Bay as *T. ingrica*, the nucleotide sequence for the 16S rRNA gene was analyzed. Experiments on DNA isolation from *Thioploca* cells were carried out with all the populations under study; however, nucleotide sequences of colorless sulfur bacteria have been presently obtained only for the deep part of the Frolikha Bay. Phylogenetic analysis of this sequence demonstrated that the analyzed *Thioploca* sp. morphotype (average filament diameter 4.0 μm) fits into the clade of freshwater species and is most closely related to *Thioploca ingrica*, together with those isolated from Lakes Biwa and Constance (Fig. 4). As was noted in [8], these freshwater bacteria formed a clade different from marine *Thioploca* and *Beggiatoa.* On the phylogenetic tree, the 16S rRNA gene sequence of the *Thioploca* from the deep part of the Frolikha Bay occupies an intermediate position between the relevant *Thioploca* sequences from Lakes Biwa and Constance; the difference in the investigated fragments are one nucleotide. We also investigated the 16S rRNA gene sequence of a different-size *Thioploca* population from the deep part of the Frolikha Bay. High similarity (99.1%) with freshwater *T. ingrica* was revealed.

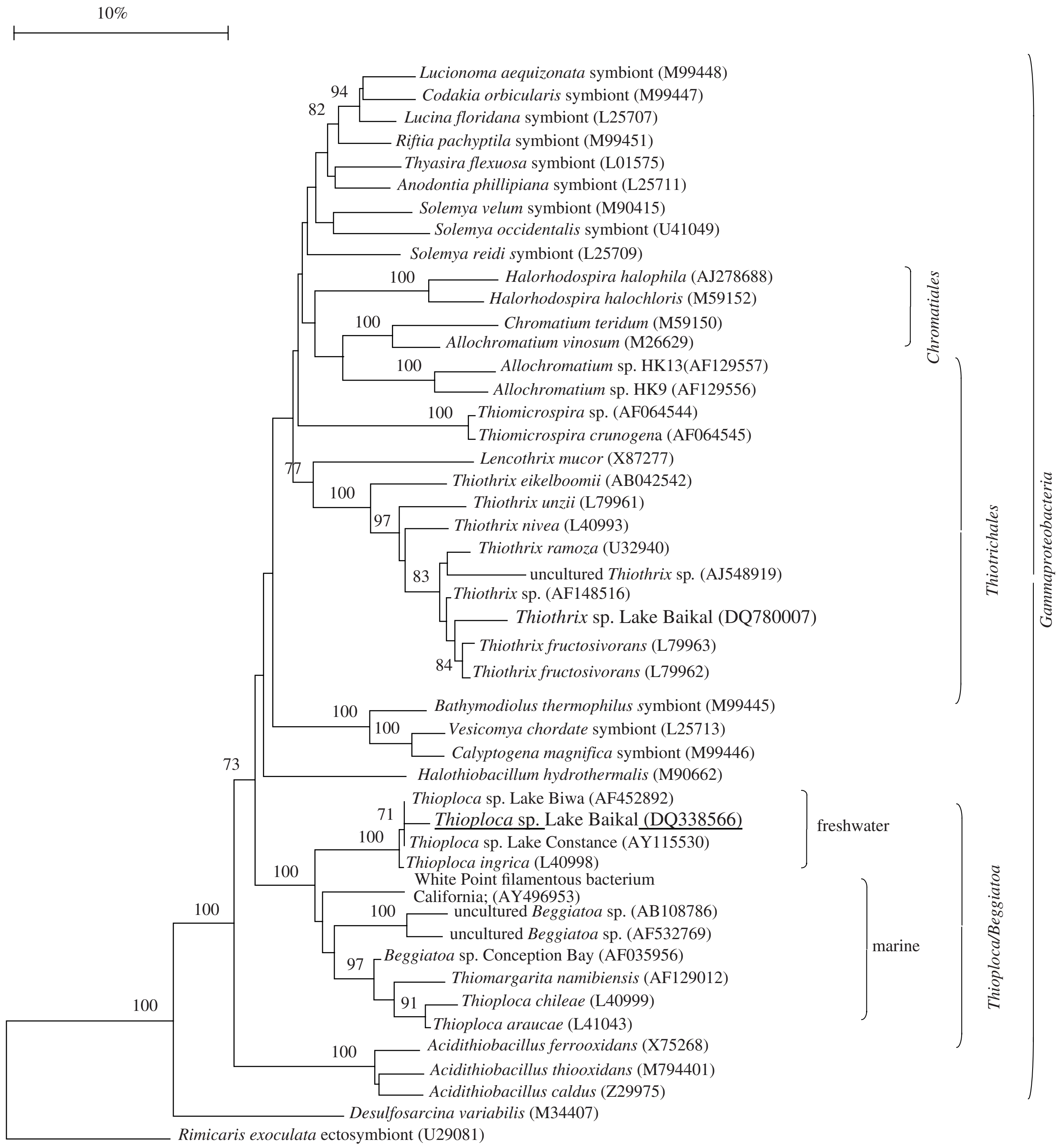

Fig. 4. Phylogenetic tree for *Thioploca* from the Frolikha Bay, Lake Baikal constructed using neighbor-joining analysis of 16S rRNA gene sequences. The Baikal *Thioploca* sequence is underlined, other sequences were obtained from the databases. Bootstrap values above 70% are displayed. The scale represents 0.1 nucleotide substitutions per site.

DISCUSSION

The bottom sediments inhabited by *Thioploca* have low contents of H_2S and O_2. In the zone of development for these bacteria, sulfide is often not determined analytically; however, the presence of sulfur in *Thioploca* spp. cells suggests its diffusion from underlying bottom sediments. Since sulfate reduction in the lake sediments is limited by low sulfate concentrations, sulfide formation in Lake Baikal can not be significant [22]. Elevated content of this ion in bottom sediments was observed only in the discharge zones of subterranean fluids [15, 21, 23]. In these regions, a low redox potential is

Table 1. Morphological parameters of the colorless sulfur bacteria *Thioploca* from different regions in Lake Baikal

Baikal regions	Filaments per sheath		Sheath diameter		Bundle diameter, μm						Trichome diameter, μm						Cell length, μm					
	Min.	Max.	Min.	Max.	Min.	Max.	x	σ^2	v	n	Min.	Max.	x	σ^2	v	n	Min.	Max.	x	σ^2	v	n
Selenga shallows, 14 m	2	7	21.5	89.1	2.7	27.7	10.5	32.4	54.3	340	1.5	4.2	2.8	0.26	18.2	387	1.0	5.7	2.7	0.6	29.3	536
Frolikha Bay, 125 m	1	13	10.4	65.3	5.2	45.5	16.6	72.2	55.4	280	2.2	10.7	5.0	1.6	25.2	363	1.37	11.1	4.1	3.1	42.9	444
Frolikha Bay, 403 m	2	13	10.8	124.6	2.5	47.3	18.4	125.5	63.6	333	1.6	7.4	4.0	1.2	27.6	465	1.2	8.9	3.3	1.5	37.2	441
Barguzin Bay, 200 m	2	7	234.0	233.4	3.9	56.4	12.5	63.6	65.6	333	1.4	9.4	3.7	1.8	36.5	1090	1.0	11.9	3.9	3.4	47.1	721
Frolikha Bay*, 400 m (data of 1991)	–	–	–	–	–	–	–	–		–	6.5	10.5	7.5	–		–	–	–	–	–		–
Frolikha Bay, 405 m (data of 1997)	1	21	100.0	200.0	15.0	50.0	–	–		–	2.5	5.0	–	–		–	–	–	–	–		–
Frolikha Bay, 32 m (data of 1997)	1	3	17.0	28.0	17.0	28.0	–	–		–	2.0	4.3	–	–		–	–	–	–			–

Note: x is the average value; σ^2 is the standard deviation; v is the coefficient of variation; n is the number of measurements; "–" stands for not determined.

* The 1991 samples were obtained by manned submersibles [4].

Table 2. Physicochemical characteristics of the sediments containing colorless sulfur bacteria *Thioploca*

Physicochemical parameters	Baikal regions			
	Selenga shallows, 14 m	Frolikha Bay, 125 m	Frolikha Bay, 403 m	Barguzin Bay, 200 m
pH	6.86–7.08	7.08–7.26	7.00–7.52	7.14
Eh, mV	–258…–323	–227…–390	–152…–201	–181
T, C°	–	9.0	–	8.1
Oxygen concentration in the near-bottom water, µM	57.8	275.0	283.1	279.1
Sulfide concentration, µM	–	Bd	0–2.35	Bd

Note: "–" stands for not determined; Bd, below detection limit.

detected (Eh from –152 to –390 mV) and microaerobic conditions are established. In the Frolikha Bay, as well as in the Selenga and Barguzin estuaries where organic matter is actively decomposed, colorless sulfur bacteria of the genus *Thioploca* were revealed only in the local zones of discharge for mineralized deep fluids, usually enriched with chloride and/or sulfate ions [14]. This may be the reason for the patchiness of *Thioploca* bacterial mats in the investigated areas.

According to the data in [9, 13, 24], oxygen influences the development of *Thioploca.* Differences of the oxygen regime were observed in the near-bottom zone of Lake Baikal where these bacteria dwell. In the Selenga shallows, oxygen content in the near-bottom zone was below 10% of saturation. The population was uniform in size and contained one morphotype. Bacteria in these sediments occurred to the depth of 6 cm; trichome size, sheath size, and cell length were lower than in other regions. The conditions of the near-bottom layer in the Selenga shallows (low oxygen content) possibly limit the growth of sulfur bacteria. In the Frolikha Bay and Barguzin Bay, oxygen content in the near-bottom zone was relatively high; bacteria with trichomes of at least two morphotypes were revealed there. However, the redox values of the surface sediment layer inhabited by *Thioploca* correspond to microaerobic conditions.

The known Lake Baikal *Thioploca* have less trichomes per sheath and are more variable in size than other freshwater forms [8]. This is probably the result of different intensity of deep fluid influx, which is the major factor limiting these organisms in Lake Baikal.

Only one species of colorless sulfur bacteria is found in freshwater environments [5, 6, 8]. *T. ingrica* is the most widespread species found in practically all investigated freshwater lakes. The species *T. schmidlei* was described earlier, in 1907, from Lake Constance [3]. This species is presently not found in this lake by its morphological characteristics or by its 16S rRNA gene structure. Recent research revealed only the presence of *T. ingrica* [8].

In 1991, the colorless sulfur bacteria *Thioploca* isolated from the sediments in the Frolikha Bay hydrothermal vent were identified as *T. schmidlei* by their morphological characteristics [4]. Our present data on *Thioploca* morphology in different biotopes of Lake Baikal indicate the presence of at least two morphotypes. Sulfur bacteria with the filament diameter characteristic of *T. ingrica* (1.0–4.5 µm) constitute the majority of the population in the deep parts of the Frolikha Bay and the Barguzin Bay (71 and 77%) and the whole population of the Selenga shallows (100%). Only in the shallow part of the Frolikha Bay most of the population (69%) had the filaments of diameter characteristic for *T. schmidlei* (5.0–11.0 µm). All sulfur bacterial morphotypes contained intracellular sulfur granules and big vacuoles. The presence of common sheaths in short *Thioploca* filaments containing no sulfur globules suggests intense growth of this organism during the sampling period. Existence of two morphotypes of colorless sulfur bacteria *Thioploca* is therefore insufficient to consider them different species. Determination of their exact phylogenetic state requires further research in the structure of 16S rRNA genes in *Thioploca* from different biotopes. Apart from their geographical remoteness, *Thioploca* from Lakes Biwa, Constance, and Baikal have the same morphological and genetic characteristics [8, 14]. The similarity is 99.9%. Our data are insufficient to determine whether one or two *Thioploca* species inhabit Lake Baikal, and 16S rRNA gene analysis of different morphotypes is required for this purpose. However, our results for the 16S rRNA gene sequence of sulfur bacteria from the deep part of the Frolikha Bay are not different from the similar sequences of known freshwater species. They may therefore be classified as a widespread freshwater species *T. ingrica.* The morphological variability of colorless sulfur bacteria in different regions results probably from the rate of sulfide supply with fluids and the presence of metabolically necessary carbon. Development of colorless sulfur bacteria in the regions of discharge of underwater mineralized fluids suggests their application as biomarkers to reveal these zones in the lake. In such regions, *Thioploca* may act in these regions as a biological filter providing sulfide detoxification and may thus maintain the purity of Lake Baikal water.

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