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EXPERIMENTAL ARTICLES

Bacteriophages in Arctic and Antarctic Low-Temperature Systems

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Abstract—Comparative analysis of the presence of bacteriophages was carried out for the water column of a permanently ice-covered, extremely oligotrophic Lake Untersee (East Antarctica) and the ancient ice wedge of the Mamontova Gora outcrop (Aldan River, Central Yakutia). Microscopy revealed bacteriophages in the Mamontova Gora ice samples and in the lysates of the pure cultures of phage-sensitive bacteria isolated from the same samples. Bacteriophages isolated from these cultures were filamentous and interacted with bacteria as moderate (lysogenic) phages. A similar filamentous bacteriophage was isolated from the Lake Untersee water column. The highest morphological diversity of bacteriophages was revealed by microscopy in the oxic Lake Untersee water column in the chemocline zone (70–76 m) and in the sulfide layer (85 m). Detection of similar filamentous bacteriophages in a relic ice sample and in the samples from Antarctic Lake Untersee indicate wide occurrence of bacteriophages and lysogeny in microbial communities of low-temperature ecosystems.

Keywords: bacteriophages, phage-sensitive bacteria, lysogeny, ice wedge, ice-covered Antarctic lakes

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Biogeochemical activity of microbial communities in low-temperature Arctic and Antarctic ecosystems has recently been of interest. Special attention is paid to high-latitude lakes (both permanently ice-covered and debacling ones), glaciers, subglacier deposits, ground ice, and permafrost rocks. The presence of microbial communities of diverse composition in these ecosystems indicates high survival potential and possible restoration of the biological activity of the microorganisms involved.

Microbial viruses (bacteriophages) are an integral part of microbial communities. The phage component of microbial communities of glacial and subglacial polar ecosystems is therefore a subject of special attention. Bacteriophages were shown to play a key role in the regulation of the composition and abundance of microbial communities in ice-covered Antarctic lakes with extremely low nutrient concentrations (Säwström et al., 2008). Phage-induced lysis of bacterioplankton results in the return of organic compounds to the pool of dissolved organic matter required to sustain microbial viability and physiological activity. The numbers of viral particles in the water column of Antarctic lakes correlate with the numbers of bacterioplankton (in these lakes virioplankton is mostly represented by bacteriophages). The values of virioplankton abundance in these lakes determined as numbers of virus-like particles (vlp) vary from 10^6 to10^7 vlp/ L (Säwström et al., 2008).

In the meromictic lakes Bonney and Fryxell (Dry Valleys), as well as in Ace Lake (Vestfold Hills), higher numbers of viral particles were detected in the chemocline layer, which correlated with higher bacterioplankton abundance caused by elevated concentrations of dissolved organic carbon, phosphorus, and nitrogen in this zone (Lisle and Priscu, 2004). Limitation by these nutrient sources may, in turn, have an indirect effect on production of viral particles by affecting the metabolic activity of bacterial hosts (Weinbauer, 2004). Insufficient phosphorus content is a factor considerably limiting bacterial growth in oligotrophic lakes of the polar areas (Dore and Priscu, 2001; Säwström et al., 2007). Viruses are probably more sensitive to phosphorus limitation than to nitrogen deficiency, since changes in the phosphate status of the water may be directly associated with production of viral particles (Lymer and Vrede, 2006). Detection of phosphate-induced starvation genes (Rohwer et al., 2000) confirms the role of phosphates for productive viral activity in aquatic ecosystems. Phosphate concentration in the medium is considered one of the possible factors responsible for the switching between the lytic and lysogenic cycles in viral particles (Wilson and Mann, 1997).

Recent research showed the level of bacterial lysogenic response in planktonic communities to depend primarily on the trophic status of aquatic ecosystems, while the role of temperature in development of the lysogenic state in bacteria is less important (Weinbauer, 2004). The highest share of lysogenic forms of bacteria was revealed in extremely oligotrophic Antarctic lakes and in cryoconite holes of glacial Arctic systems (Säwström et al., 2008). This is confirmed by the results of the authors of the present work on detection of a temperate bacteriophage in bacterial host cells from water samples of an extremely oligotrophic Antarctic Lake Untersee (Filippova et al., 2013).

Polar ecosystems, including the glacial ones, are characterized by both high levels of viral infection in bacterial community and low species specificity of the phages to bacterial host cells (Säwström et al., 2008). These characteristics of the viral component may play a key role in the survival strategy of microbial communities in extreme conditions of polar ecosystems.

Unlike aquatic ecosystems, the information on viral particles detected in polar frozen soils and permafrost rocks is scarce (Meiring et al., 2012; Legendre et al., 2013). Model experiments revealed the crucial role of the phage component in development of the structure of microbial communities in Arctic frozen soils (Allen et al., 2010). Isolation of lysogenic psychrophilic bacteria *Psychrobacter* spp. containing a temperate phage Psymv2 from the McMurdo Dry Valleys, Eastern Antarctica, was recently reported (Meiring et al., 2012). Arctic and Antarctic permafrost is presently considered a reservoir for various forms of microorganisms, including those adapted to cold conditions and able to return to growth and proliferation after thawing of the frozen rocks. Lysogenization of bacterial cells by moderate phages may result in their decreased metabolic activity due to the ability of the prophages to encode repressor proteins and transcription regulators suppressing the "unnecessary" metabolic processes. This may be one of the mechanisms responsible for the preservation of bacterial viability (Paul, 2008). The controlling function of the viral component in microbial communities is presently considered an important part of microbial biogeochemical processes.

The goal of the present work was to reveal bacteriophages in extremely low-temperature Arctic and Antarctic ecosystems.

MATERIALS AND METHODS

The subjects of research were the permanently ice-covered Lake Untersee (East Antarctica, 2011–2012) and the ancient ice wedge from the Mamontova Gora outcrop (Central Yakutia). Samples from the lake were collected along the depth profile of the water column (4–98 m). The samples were transported in heat-insulating containers and stored at 5°C. Ice blocks (40 × 20 × 20 cm) were cut out of the ice wedge outcropping at Mamontova Gora and stored in sterile plastic bags. Ice samples were transported in heat-insulating containers with coolants at –20°C. In the laboratory, ice samples were stored at the temperatures from –15 to –18°C.

Material for analysis was taken aseptically from the central part of the ice blocks. The preparations of lake water and molten ice were applied to formvar-coated grids, contrasted with 2% phosphotungstic acid (Biryuzova et al., 1963) and examined under a JEM-100CXII electron microscope (JEOL, Japan).

Enrichment of the phage component of the ice sample was carried out in an enrichment culture obtained by inoculating 50 mL of liquid ISP1 medium (Difco) (Shirling and Gottlieb, 1966) with 5 mL of molten ice with incubation for two to five days. The cell mass was then separated by centrifugation at 5000 *g* for 15 min on a Mini Spin centrifuge (Germany) with subsequent filtration through 0.45-μm porous membranes (MS® CASyringeFilter). The filtrate was used to prepare the preparations for electron microscopy.

For detection of bacteriophages, colonies of aerobic heterotrophic bacteria isolated from ice wedge samples were used. A standard set of nutrient media was used: CP1 with glucose, starch-and-ammonia medium, synthetic medium with chitin (Valagurova et al., 2003), ISP1 (liquid and with 2% Difco agar), and ISP3 (Difco) with 0.25% yeast extract (Difco). The samples were inoculated in three repeats and incubated at 20 and 28°C for 5 to 10 days. The isolates were maintained on solid ISP1 and ISP3 media with yeast extract. Cell morphology of the isolates was studied under an Axioplan phase contrast microscope (Carl Zeiss, Germany). The zones of growth suppression (plaques) in the colonies of phage-sensitive bacteria in the area of active growth were examined visually and by phase microscopy. The viral content of the plaques was analyzed by electron microscopy. The colonies of phage-sensitive bacteria were isolated and maintained on solid ISP1 and ISP3 media with yeast extract.

To accumulate the virus material, phage-sensitive bacterial cultures were grown in liquid ISP1 medium for five days at 28°C with shaking at 180 rpm. The culture liquid was centrifuged for 10 min at 5000 *g*. For more complete precipitation of bacterial cells, the supernatant was centrifuged again under the same conditions. The presence of phage particles in the supernatant was confirmed by electron microscopy. To obtain phage suspensions, the supernatant was filtered through a 0.45-μm polycarbonate membrane (Nuclepore, United States).

Lytic activity of the phages was determined using the drop test procedure based on agar layers, according to the standard technique (Karlson, 2012). Lytic

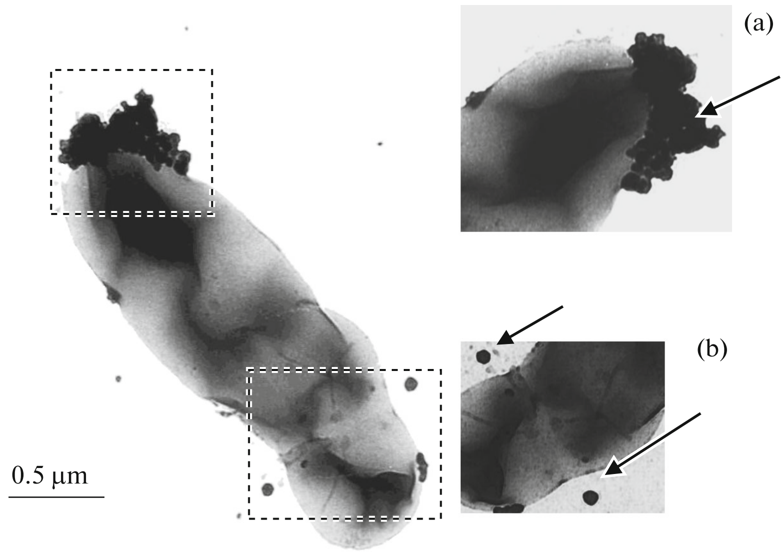

Fig. 1. Icosahedral virus-like particles; their adsorption on the cell surface: part of the cell with adsorbed virus-like particles (arrow) (a) and free virus-like particles (b). Lake Untersee, 4 m depth.

action of the phage suspension was determined using *Paenibacillus* sp. U14-9 as the indicator culture.

RESULTS

Lake Untersee is located in Antarctica, 71°20′ S, 13°45′ W, in the interior of the Gruber Mountains of central Queen Maud Land. This extremely oligotrophic lake is situated 563 m above the sea level and is the largest surface lake in East Antarctica (11.4 km^2). The lake consists of two parts. The larger one, with the depth of 160 m, is adjacent to the Anuchin Glacier and is separated from the smaller, southwestern part of the lake with 100-m depth by a ridge (50 m high). Water temperature of the deep part of the lake is almost constant along the profile (0 to 5°C). Oxygen concentration in the oxic part of the lake (0–70 m) is high, up to 200% saturation; oxygen content in the transition zone (64–79 m) was from 160 to 0%, while below 80–98 m the water column was anoxic. High pH of the water (10.2–6.9) is evidence of erosion of the mostly anorthosite rocks of the lake basin (Andersen et al., 2011).

Virus-like particles were detected in all layers of the Lake Untersee stratified water column. In the upper layers, within the mixolimnion zone (4 m depth), free virus-like particles of icosahedral shape were observed, as well as their adsorption on the surface of microbial cells (Fig. 1). The highest morphological diversity of virioplankton was observed in the chemo/oxycline zone at the depth of 70 to 72 m (Fig. 2) and in the anoxic zone (85 m). Electron microscopy was used to reveal the interaction of virus-like particles with the host cells (Fig. 3). The morphotypes of icosahedral, caudate, and filamentous particles were detected in the water samples collected below the chemocline, in the anoxic part of the water column (85–90 m), and in the hypolimnion (98 m) (Fig. 4).

Mamontova Gora is one of the best-known outcroppings of ancient (25–40 ka) syngenetic deposits of ice wedge in Central Yakutia. It is located at the left shore of the Aldan River, 500 km from its estuary. At this site, the river exposes Neogene–Pleistocene alluvial deposits (16 Ma to several ka), characterizing all the periods of Pleistocene glaciations. In the profile of the 50-m Mamontova Gora terrace, upper Quaternary deposits with ice wedge are especially pronounced. Ice wedge deposits are 7 to 10 m thick.

Electron microscopy of ice samples revealed virus-like particles of various morphology (Fig. 5). Bacteriophages were also revealed by enrichment for the phage component in enrichment cultures of microorganisms from the ice samples. This procedure resulted in detection of two more morphotypes of caudate phages and of filamentous phages (Fig. 6).

For detection of lysogenic bacterial forms in the aerobic heterotrophic component of the Mamontova Gora relic ice communities, melted samples of ice wedge were plated on solid media. Colonies of phage-sensitive bacteria were revealed. These colonies exhibited sterile spots (plaques), which became more numerous with increasing age. Electron microscopy of the material collected from these plaques and of the phage lysates of phage-sensitive bacterial isolates revealed the presence of filamentous phages (Fig. 7). According to drop tests, the filamentous phage isolate exhibited low lytic activity. The presence of turbid plaques, indicating incomplete lysis of the sensitive bacteria, was observed on the lawn of the indicator

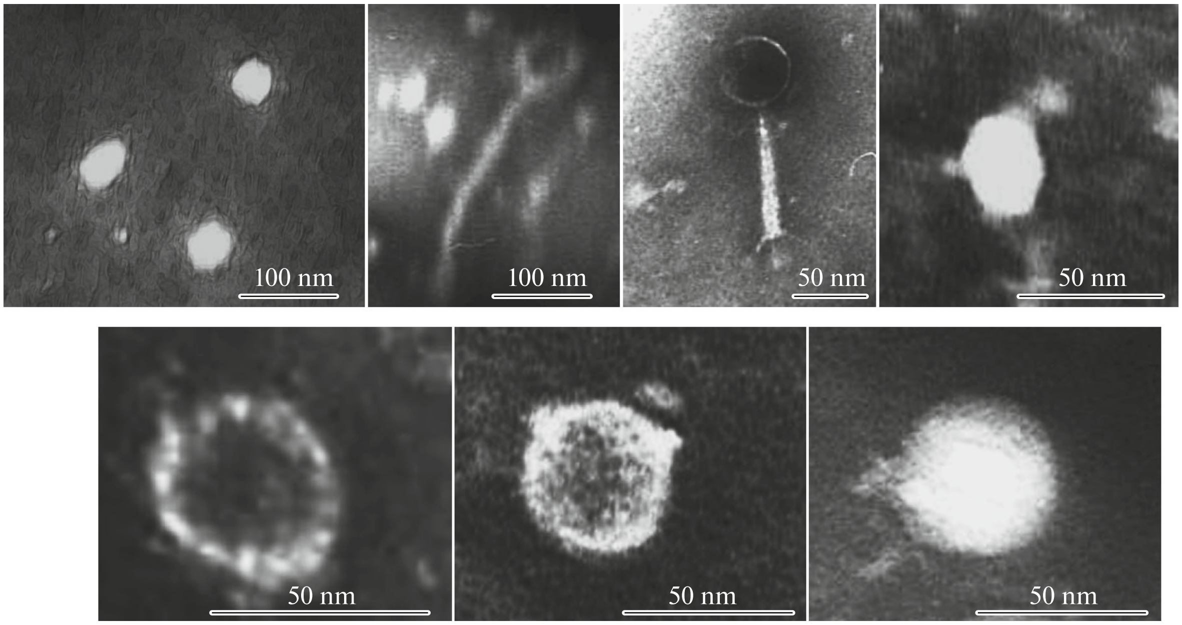

Fig. 2. Morphological diversity of virus-like particles in the samples from Lake Untersee chemocline (70–80 m).

culture *Paenibacillus* sp. U14-9 only when concentrated phage suspensions were applied.

DISCUSSION

This work provided comparative experimental data on the presence and morphological diversity of bacteriophages in extreme low-temperature environments: water column of an ultra-oligotrophic, ice-covered Antarctic Lake Untersee and ancient ice wedge from the Mamontova Gora outcropping (Yakutia, Russia).

Permanently ice-covered continental Antarctic lakes belong to the type of subglacial systems (Hodson et al., 2008) where unique ecosystems are formed due to the activity of microbial communities. In spite of considerable diversity and significant differences, these continental water bodies share certain features: (1) permanence of the ice cover for many millennia; (2) stability of the physicochemical parameters of the water column; and (3) predominance of microbial communities (Wharton et al., 1994). The values of the rates of the major biogeochemical processes in ultra-oligotrophic water columns of Antarctic subglacial

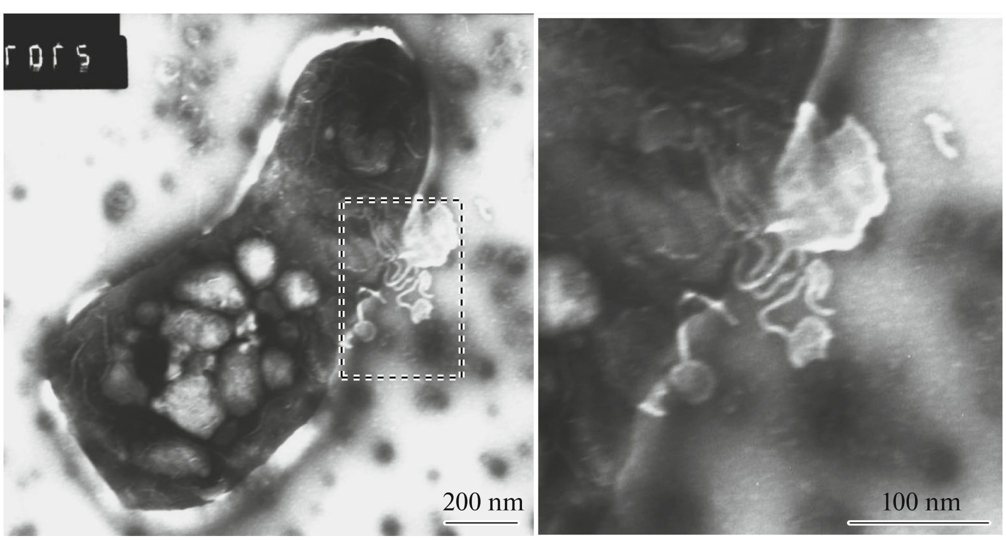

Fig. 3. Interaction of virus-like particles with a host cell: cell fragment with virus-like particles. Lake Untersee, 80 m.

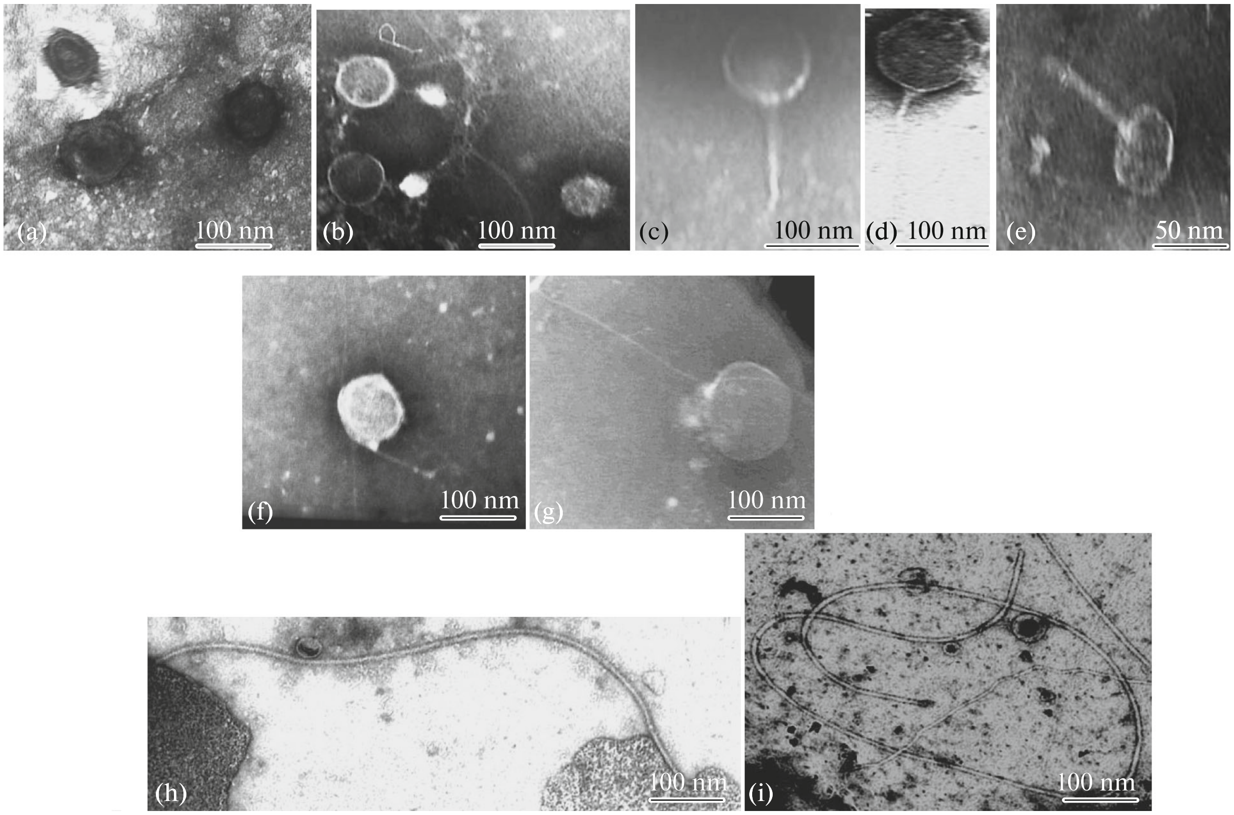

Fig. 4. Morphotypes of virus-like particles from Lake Untersee anoxic water column: icosahedral ((a) 85 m); caudate at 85 (b–e) and 90 m (f, g); and filamentous ((h, i) 90 and 98 m).

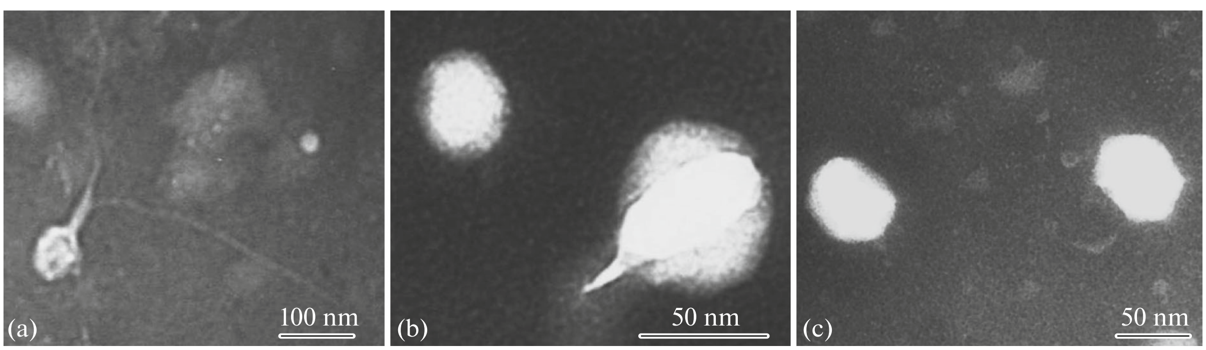

Fig. 5. Virus-like particles in the molten ice wedge sample, Mamontova Gora outcropping: particle with two filamentous projections (a), particle with a short conical projection (b), and icosahedral particles (c).

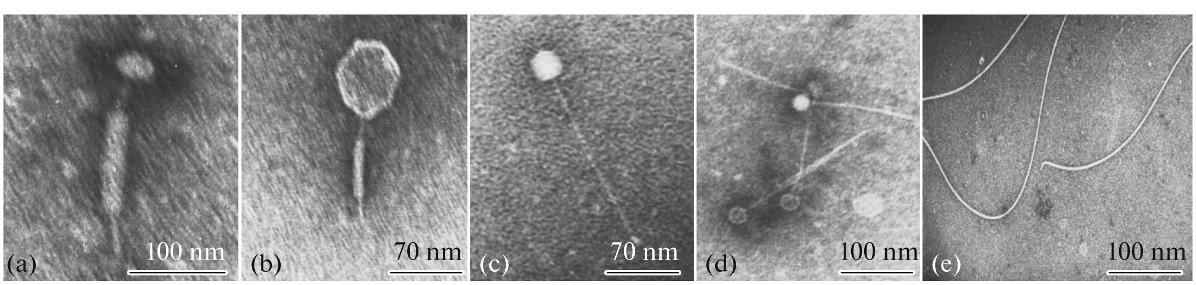

Fig. 6. Morphotypes of caudate and filamentous phages from the enrichment culture inoculated with ice wedge samples: with contractile sheaths of the projections (a, b); with long projections (c, d); and filamentous (e).

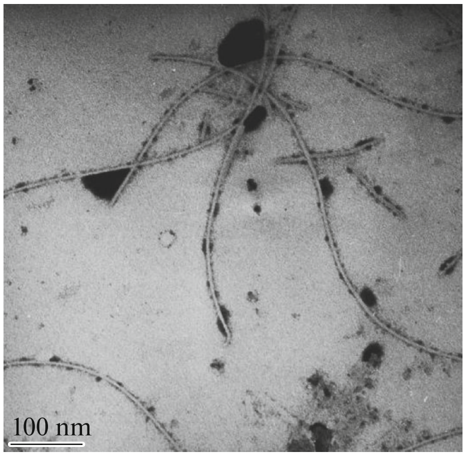

Fig. 7. Filamentous phages from plaques on the colonies of a phage-sensitive bacterium isolated from Mamontova Gora ice wedge.

lakes indicate the physiological potential of microbial communities for the maintenance of complexly coupled carbon and sulfur cycles (Gal'chenko, 1994).

Our study of virioplankton from the Lake Untersee stratified water column revealed the highest morphological diversity of virus-like particles to occur in the chemocline zone (70–72 m deep) and in the anoxic zone at the depth of 85 m. Virioplankton diversity revealed in these layers results probably from an elevated abundance of bacterioplankton, which is diverse in species composition and exhibits metabolic activity (Gal'chenko, 1994; Säwström et al., 2008). Inside the chemocline and in the layers of the water column close to this zone, narrow niches are known to exist, in which vertical variations of the concentrations of oxygen and organic carbon may provide conditions for both autotrophic and heterotrophic growth of microorganisms with different tolerances to oxygen (Hamilton et al., 2014). Diversity of conditions may promote increased diversity of bacterioplankton communities, which may in turn result in diversity of the forms and types of viral particles. As for the ecological aspect of the specificity of bacteriophages in various aquatic systems, this issue remains insufficiently clear. Multivalence of bacteriophages in oligotrophic aquatic environment due to low bacterioplankton levels was hypothesized (Wommack and Colwell, 2000). Stratification of the water column of Antarctic ice-covered lakes provides, however, for existence, apart from multivalent, of specific bacteriophages capable of infecting specific groups of microorganisms physiologically adapted to different layers within these water bodies (Säwström et al., 2008).

Filamentous virus-like particles were revealed in the anoxic zone of Lake Untersee (90–98 m deep). Previously, we reported detection of filamentous phages in the cells of a phage-sensitive bacterium isolated from the chemocline zone of the lake, 70 m deep (Filippova et al., 2013). Filamentous phages belong to the temperate (lysogenic) type. Due to the difficulty of identification of filamentous phages caused by their low lytic activity, information on their diversity and specificity is scarce. While filamentous phages are known to infect mostly gram-negative bacteria, infection of some gram-positive bacteria was also reported (Rakonjac et al., 2012). Filamentous phage infection is common among bacteria *Pseudoalteromonas* spp., which are predominant in the microbial community of Arctic brine ice. Filamentous phages were hypothesized to promote survival of these bacteria, acting as the regulators of growth rate, cytoplasm density, and tolerance to NaCl and H_2O_2 (Yu et al., 2015).

Detection of lysogenic phages in the viral community of the Lake Untersee water column indicated wide occurrence of lysogeny among bacterioplankton. Apart from extremely oligotrophic conditions in lake water, low content of soluble phosphorus may favor the lysogenic state of the phages in this microbial community (Andersen et al., 2011), since phosphorus is known to play an indirect important role in phage reproduction (Lymer and Vrede, 2006).

Unlike the ecosystem of Antarctic subglacial Lake Untersee, the ancient ice wedge of the Mamontova Gora outcropping are probably simply a reservoir of microorganisms, which arrived there from the ancient environment. Many of them are able to restore their physiological and proliferative activity after ice thawing (Katayama et al., 2007, Filippova et al., 2014). Conditions in the ancient cryolithozone may provide conditions for the preservation of microbial cells and their cellular structures (organelles). Apart from ice crystals, air and organic and mineral inclusions are the major components responsible for the structure of ice wedge. Most varieties of ice wedge are known to have low mineralization, which is close to the values for low-mineral surface water and atmospheric precipitation. Most organic and mineral matter is present in ice wedges as colloid compounds and coagulated particles (Ershov, 2002), which provides for the preservation of intact biological structures (Zvyagintsev, 1987). The presence of viable microflora in permafrost rocks implies the possibility of preservation of viral particles and restoration of their activity.

Direct electron microscopy of an ice wedge sample (25–40 ka) revealed at least two to three morphotypes of virus-like particles. Emergence of viral particles in the sample may result from lysis of some bacterial cells and phage release as a result of ice thawing. Reactivation of free viral particles adsorbed on organo-mineral inclusions within ice wedge crystals is also a plausible possibility. In filtrates of enrichment cultures of microorganisms from ice samples, other morphotypes of virus-like particles were revealed. Application of yeast extract-containing nutrient broth for enrichment cultures promoted the restoration of both bacterial physiological activity and the lytic activity of the phages and phage proliferation (Karlson, 2012). Under conditions of preservation in permafrost ice rocks, bacterial cells in an anabiotic state may contain prophages capable of reactivation on the restoration of the physiological activity of their host cells. Prolonged starvation of bacterial cells is known to promote the lysogenic state of bacteriophages (Wommack and Colwell, 2000). Detection of virus-like particles of different shape in ancient ice wedge samples, as well as direct isolation of a lysogenic bacterial form and a temperate phage capable of reproduction, demonstrate the possibility of preservation of viral particles in permafrost ice wedge. Interestingly, in the case of lysogenic forms of some pathogenic bacteria, freezing–thawing, which is typical of permafrost deposits, was shown to preserve the viability of viral particles as prophages and even to increase their infective activity (Rogers et al., 2004).

Detection of morphological diversity of viral particles in extreme low-temperature environments (the ecosystem of an ice-covered, ultra-oligotrophic Antarctic Lake Untersee and relict Arctic ice wedge) indicates that these organisms play an important role in bacterial communities of such systems, primarily by increasing their adaptive potential under extreme conditions. As the agents transferring genetic material between different groups of bacteria, phages maintain the stability of the lake biota as a whole, acting as regulators of bacterial communities in different layers of the stratified water column and providing for their interaction. In the case of preservation in ice wedge, viral particles as prophages increase the overall physiological potential of potentially viable microflora.

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