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EXPERIMENTAL ARTICLES

Analysis of the Bacterial Community Developing in the Course of *Sphagnum* Moss Decomposition

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Abstract—Slow degradation of organic matter in acidic *Sphagnum* peat bogs suggests a limited activity of organotrophic microorganisms. Monitoring of the *Sphagnum* debris decomposition in a laboratory simulation experiment showed that this process was accompanied by a shift in the water color to brownish due to accumulation of humic substances and by the development of a specific bacterial community with a density of 2.4×10^7 cells ml^{-1}. About half of these organisms are metabolically active and detectable with rRNA-specific oligonucleotide probes. Molecular identification of the components of this microbial community showed the numerical dominance of bacteria affiliated with the phyla *Alphaproteobacteria, Actinobacteria,* and *Planctomycetes.* The population sizes of the *Firmicutes* and *Bacteroidetes*, which are believed to be the main agents of bacterially-mediated decomposition in eutrophic wetlands, were low. The numbers of planctomycetes increased at the final stage of *Sphagnum* decomposition. The representative isolates of the *Alphaproteobacteria* were able to utilize galacturonic acid, the only low-molecular-weight organic compound detected in the water samples; the representatives of the *Planctomycetes* were able to decompose some heteropolysaccharides, which points to the possible functional role of these groups of microorganisms in the community under study. Thus, the composition of the bacterial community responsible for *Sphagnum* decomposition in acidic and low-mineral oligotrophic conditions seems to be fundamentally different from that of the bacterial community which decomposes plant debris in eutrophic ecosystems at neutral pH.

Key words: microbially mediated decomposition of *Sphagnum* debris, bacterial community, molecular in situ identification of bacteria, the *Alphaproteobacteria*, the *Planctomycetes.*

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Sphagnum-dominated peat bogs are among the most extensive terrestrial ecosystems in Russia and some other countries of the northern hemisphere [1, 2]. They represent a significant carbon store [2, 3]. Another global function of *Sphagnum* peat bogs which directly affects the future of mankind is associated with their role as one of the largest reservoirs of fresh water on our planet. Wetlands are usually located within water catchment areas and therefore determine the hydrological cycles of rivers. The microbiological processes that occur in these environments determine the chemical composition of the water [4]. Among these processes, microbial decomposition of the biomass of *Sphagnum* mosses, the main constituent of the phytocenoses of northern ombrotrophic peat bogs, is the key one.

The class *Sphagnopsida* includes one family (*Sphagnaceae*) with a single genus (*Sphagnum*) which comprises approximately 250 species [5]. In oligotrophic bogs, *Sphagnum* mosses play a key role both in the processes of production and in those of degradation and accumulation of organic matter. In these ecosystems, slow decomposition of organic debris is the main cause of organic matter accumulation in peat deposits [6–8]; since *Sphagnum* mosses are the main producers in the *Sphagnum* peat bog phytocenoses, they exert the main influence on the composition of bog peat. It has been shown that the rate of degradation was much lower for peat composed mainly of *Sphagnum* moss than for peat formed from vascular plant debris [9, 10]. This phenomenon can be attributed to the unique properties and chemical structure of *Sphagnum* mosses. The *Sphagnum* cell walls include polyuronic acids; uronic acids are therefore predominant both in the excretion products of live plants and in the products of *Sphagnum* degradation; their high cation-exchange capacity causes acidification of peat and bog water [11, 12]. There are indications that uronic acids are able to inactivate some enzymes catalyzing the processes of microbial transformation of organic matter [13]. Sphagnum acids (or sphagnols), high-molecular-weight phenolic glycosides with antimicrobial activity, are another important group of secondary *Sphagnum* metabolites [13–15]. Since the process of organic matter destruction is inhibited in these environments, *Sphagnum* bogs can be considered

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Table 1. Physicochemical properties of water from Obukhovskoe bog

Parameters	August, 2004	May, 2005
pH	3.64	4.40
Water color*	850	550
POC**	147.3	183.8
Ion content, mg/l		
HCO_3^-	0	0
Cl^-	6.36	6.41
SO_4^{2-}	–	2.65
Ca^{2+}	1.96	5.05
Mg^{2+}	0.51	1.37
Na^+	0.58	0.44
K^+	0.52	1.13
Σ of ions	9.93	17.05

Notes: * Degrees of the platinum-cobalt scale.
** Permanganate oxidation capacity.

an extreme habitat, and the microorganisms inhabiting these ecosystems should be assigned to extremophiles. The application of molecular techniques enabled us to demonstrate that the prokaryotic component of *Sphagnum* peat bogs is quite unique. Bacteria belonging to the phylogenetic groups *Alphaproteobacteria, Acidobacteria, Actinobacteria, Verrucomicrobia*, and *Planctomycetes* are its main constituents [17–19].

Microfungi have been convincingly demonstrated to decompose the *Sphagnum* phytomass [16]; however, the role of bacteria in this process is poorly understood. It is still unknown which of the above-mentioned groups of bacteria are involved in the degradation of *Sphagnum*-derived organic matter. The goal of the present work was therefore to study the population dynamics and the composition of the bacterial community which develops in the course of microbial decomposition of *Sphagnum* mosses, and to reveal the functional role of the representative components of this community.

MATERIALS AND METHODS

Sampling and performance of a model experiment. In our studies, we used *Sphagnum* peat and water samples collected in May, 2005 from the ombrotrophic peat bog Obukhovskoe of the Mologo-Sheksninskii water catchment area in Yaroslavl oblast (57° N, 39° E). In the studied area, *Sphagnum* peat bogs in watersheds predominate; the bog bryoflora is represented by more than 27 species of *Sphagnum* moss [20]. In Obukhovskoe bog, *Sphagnum angustifolium* (with occasional *Sph. magellanicum* and *Sph. fuscum, Oxicoccus* sp., and *Vaccinium* sp.) dominated in the plant community of the bog. The peat thickness was approx. 3 m. The pH of the bog water is 4.4 and the conductivity was 30 μS/cm. The data on the hydrochemical composition of the Obukhovskoe bog are presented in Table 1. The peat profile consisted of the following layers: a photosynthetically active green *Sphagnum* moss layer (5–6 cm); a layer of whitish, chlorophyll-free plant parts (20 cm); and the underlying brown layer of decomposed peat.

To perform the laboratory experiment, stems of the whitish parts of *Sphagnum* plants were used. Portions (20 g) of peat material were cut into small fragments (2–5 cm) and transferred into sterile bags made of nylon gauze. Each bag was then placed in a 500-ml serum vial with 100 ml of bog water so that the water covered the bag completely. The vials were sealed with air-permeable film to prevent water evaporation and incubated at 20°C for three months. The rates of the microbiological processes involved in *Sphagnum* decomposition were estimated from the rate of CO_2 accumulation in the gas phase. Water samples were taken at regular intervals in order to determine the pH, color, and conductivity of the water, as well as the content of organic humic compounds and low-molecular-weight metabolites (see below). To study the structure of the bacterial community by fluorescent in situ hybridization, aliquots of each sample were fixed by addition of 100% ethanol (1 : 1) and stored at –20°C until use.

Analytical methods. The color of bog water was determined from absorption coefficients measured on a Specol spectrophotometer (Carl Zeiss, GDR) at 420 nm. The water conductivity was determined with a portable TDS4 conductometer (Trans Instruments, Singapore). The rate of CO_2 production was measured with an Infralit-4 infrared gas analyzer (GDR). The vials were hermetically sealed with silicon stoppers and incubated for one day; the increase in the CO_2 concentration in the gas phase during 1-h exposure was then determined. Analysis of the content of organic humic compounds in the microcosm water was performed by exclusion chromatography on an Agilent 1100 chromatograph (Agilent Technologies, United States) equipped with a diode-matrix spectral detector (scanning wavelength 450 nm) and a G3000SW column (60 × 7.5 mm; Tosoh Bioscience, United States). The carrier was TSK-GEL; 0.1 M Na-phosphate buffer (pH 7) with 0.1% SDS was used as the eluent; the flow rate was 0.75 ml/min; and the sample volume was 100 μl. Analysis of low-molecular-weight metabolites was carried out on a Staier high-pressure chromatograph (Russia) equipped with a refractometer detector. The separation was carried out on an Aminex HPX-87H column (BioRad, United States) designed

for organic acids and alcohols; 5 mM H_2SO_4 was used as an eluent.

Enumeration and in situ identification of *Bacteria* community composition. Identification of the main components of the bacterial community developing in the course of *Sphagnum* decomposition was carried out by means of in situ hybridization with rRNA-specific fluorescent oligonucleotide probes (FISH). Suspensions of the fixed samples (5–10 μl) were applied to gelatin-coated (0.1% wt./vol/) Teflon-laminated slides (MAGV, Germany) with eight wells for independent positioning of the samples. The specimen samples were air-dried for 12–24 h and dehydrated by successive passages through an ethanol series (50%, 80%, and 100%). The set of Cy3-labelled oligonucleotide probes applied in this study included the probes with reported group specificity for the domain *Bacteria* (EUB338-mix) as well as for some phylogenetic groups within this domain, i.e. *Alphaproteobacteria* (ALF1b + ALF968), *Betaproteobacteria* (BET42a), *Gammaproteobacteria* (GAM42a), *Bacteroidetes* (CF319a + CFB560), *Firmicutes* (LGC354A + LGC354B + LGC354C), *Actinobacteria* (HGC69a), and *Planctomycetes* (PLA46 + PLA886). The nucleotide sequences of these probes, as well as the hybridization conditions, were previously described in [17–19]. After hybridization, the slides were additionally stained for 5 min with a 0.5 μM solution of the DNA-specific fluorescent dye DAPI (4',6'-diamidino-2-phenylindole), rinsed with distilled water, and dried. The slides were examined under a Zeiss Axioplan 2 epifluorescence microscope (Jena, Germany) equipped with Zeiss 20 and Zeiss 02 light filters for the Cy3-labeled probes and DAPI, respectively. The numbers of target microorganisms in the samples were determined by counting the cells hybridized with the relevant probes in 100 fields of view with subsequent calculation of bacterial numbers per ml of microcosm water. Microsoft Excel 2000 was used for statistical analysis of the results.

Development of probes for specific detection of *Chitinophaga arvensicola* isolated from *Sphagnum* peat bogs. For enumeration of the representatives of the phylum *Bacteroidetes*, apart from the above-mentioned probes CF319a and CFB560, a new oligonucleotide probe, Chit1004 (5'-GACACCTTTCAGCATCAG-3'), was used. It was designed for detection of the gliding *Cytophaga*-like bacteria capable of degrading various heteropolysaccharides. We had previously isolated these organisms from a number of *Sphagnum* peat bogs and identified them as *Chitinophaga arvensicola* [21]. Since these bacteria were targeted neither with CF319a nor with CFB560, the development of this novel probe was imperative. The search for unique nucleotide sequence regions within 16S rRNA of *C. arvensicola* was performed by using the Probe Design function implemented in the ARB software package (http://www.arb-home.de). The specificity of the new probe was tested using the Probe Match Tool of the Ribosomal Database Project. Strain *Flexibacter japonensis* DSM 13484, whose 16S rRNA gene sequences have the minimum number of mismatches with the target sequence of the new probe, was used as a negative control. The desired probe specificity was achieved at a 20% formamide concentration in the hybridization buffer.

The study of the representative isolates. The isolate PLO1 was obtained by spread plating of a water aliquot from the microcosm of decomposing *Sphagnum* on the complex organic agar medium R2A (pH 5.8) (Difco, France) diluted tenfold. The primary identification of the isolate was performed by hybridization with a set of probes specific for various phylogenetic groups of bacteria. The final identification included the determination of the partial 16S rRNA gene sequence of this isolate. Utilization of galacturonic acid by strain PLO1 as a carbon and energy source was studied on the following medium (g/l): KH_2PO_4, 0.1; $MgSO_4 \cdot 7H_2O$, 0.05; $(NH_4)_2SO_4$, 0.1; $CaCl_2 \cdot 2H_2O$, 0.01; Hutner's basal salt solution [22], 20; sodium galacturonate (Fluka), 0.1; yeast extract, 0.05; pH 5.8. The suspension optical density (OD_{600}), pH, and galacturonate concentration were determined on a Staier high pressure chromatograph (Russia).

The new planctomycete strain MOB10, which was used in the present work, was previously isolated by us from peat sampled from Obukhovskoe bog [19]. The capacity of this bacterium for utilization of galacturonic acid was checked in the same manner as in the case of isolate PLO1. The range of the polymeric substrates utilized by strain MOB10 was studied on the above-mentioned medium supplemented with individual compounds as carbon and energy sources (0.05%). The growth rate of the culture was estimated from the dynamics of CO_2 accumulation in the gas phase.

RESULTS AND DISCUSSION

Monitoring of microbial decomposition of *Sphagnum* moss. Development of brown coloration of bog water caused by the accumulation of humic organic compounds, as well as increased rates of the microcosm respiration induced by addition of the *Sphagnum* phytomass (Fig. 1a) indicated the transformation of *Sphagnum* moss organic matter. During the first month of incubation, the water conductivity increased from 30 to 70 μS and then remained stable throughout the experiment (Fig. 1c). The pH value of the water increased in the course of *Sphagnum* decomposition; after 100 days of incubation, it was 4.8–5.0 (Fig. 1b). Such a pH rise with increased degradation of plant debris is characteristic of the profile of *Sphagnum* peat bogs. Analysis of the water samples for the presence of organic acids and alcohols did not reveal their accumulation in the course of *Sphagnum* decomposition. The

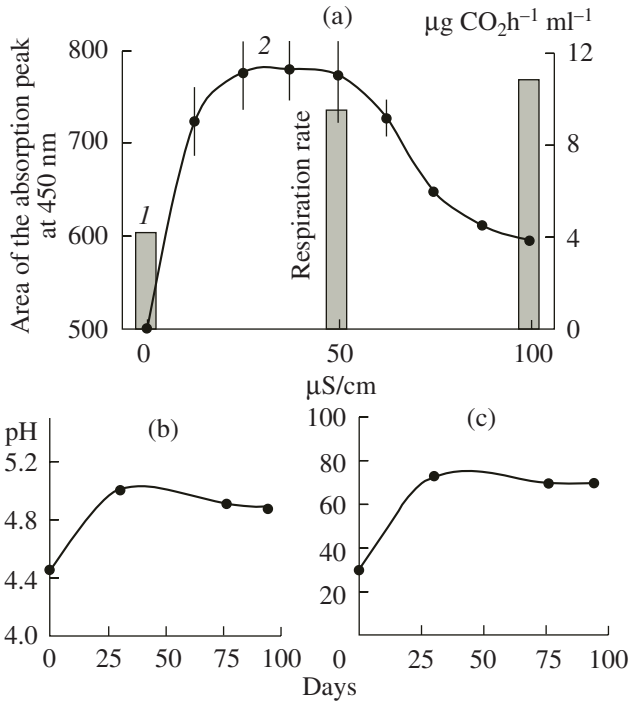

Fig. 1. (a) Dynamics of accumulation of humic organic compounds in bog water (bars, *1*) and the microcosm respiration rate (curve, *2*) in the course of *Sphagnum* decomposition. Dynamics of pH (b) and conductivity (c) of bog water.

absence of these compounds indicates their rapid utilization by the microbial community. Galacturonic acid, a product of decomposition of *Sphagnum* cell walls, was the only low-molecular-weight compound detected in the water. At the beginning of the experiment, its concentration was below the detection limit; it increased up to 0.032 mM by day 40 of incubation and then dropped to 0.018 mM by day 90 of incubation.

In water samples, the total numbers of microbial cells determined by DAPI staining increased from 1.8×10^7 cells ml^{-1} at the early stages of the experiment to 2.4×10^7 cell ml^{-1} by day 40 of incubation and then decreased to 2.1×10^7 cells ml^{-1} by the end of the experiment (Table 2). The respiration dynamics of the microbial community was similar (Fig. 1a). The dynamics of the respiration rates and the total number of microbial cells indicated low rates of microbialy mediated destruction of *Sphagnum*, without the pronounced burst of microbial growth commonly observed during degradation of herb debris.

The component structure of the bacterial community developing in the course of *Sphagnum* decomposition. At least 50% of the microbial cells detected in the water samples by DAPI staining were detected by hybridization with EUB338-mix, a mixture of three oligonucleotide probes which is specific for all *Bacteria* (Table 2). For a freshwater ecosystem, this is a relatively high detection index pointing to the active metabolic status of at least half of the microbial cells in the community. Further identification and quantitative assessment of these metabolically active components of the community were carried out using a set of group-specific oligonucleotide probes for the major phylogenetic groups of the domain *Bacteria*, as well as for some classes of the *Proteobacteria* (Table 2). The data shown in Fig. 2 demonstrate large changes in the component structure of the bacterial community during *Sphagnum* decomposition. Members of the *Alpha-* and *Betaproteobacteria*, as well as of the *Bacteroidetes* and

Table 2. The numbers and the component structure of the bacterial community developing in bog water in the course of *Sphagnum* decomposition

Incubation time, days	Bacterial numbers ($N \times 10^6$ cells ml^{-1} water)									
	Total number of cells	*Bacteria*	Detection with 16S rRNA-targeted oligonucleotide probes with reported specificity for certain phylogenetic groups within the domain *Bacteria*							
	DAPI staining	EUB338 mix	ALF1b + ALF968	BET42a	GAM42a	PLA46 + PLA 886	HGC69a	LGC354ABC	CF319a + CFB560	Chit1004
1	18.30 ± 1.70	9.16 ± 1.90	1.71 ± 0.28	2.4 ± 0.70	0.28 ± 0.08	0.31 ± 0.22	1.54 ± 0.32	0.01 ± 0.00	1.19 ± 0.39	0.67 ± 0.21
40	23.60 ± 2.56	11.60 ± 1.34	4.91 ± 0.78	0.65 ± 0.18	0.17 ± 0.07	0.77 ± 0.23	1.07 ± 0.16	0.05 ± 0.03	0.20 ± 0.09	0.27 ± 0.15
90	20.80 ± 2.27	12.6 ± 2.62	0.71 ± 0.20	0.17 ± 0.07	0.31 ± 0.12	0.85 ± 0.12	1.79 ± 0.44	0.02 ± 0.02	0.16 ± 0.07	0.19 ± 0.15

Actinobacteria were the main components of the initial community. During further incubation, the proportions of *Betaproteobacteria* and *Bacteroidetes* decreased sharply; by the end of incubation, they were minor components of the community. Microbial activity peaked on the 40th day of incubation mainly due to the active growth of *Alphaproteobacteria*; the number of these microorganisms increased threefold during this period as compared to the beginning of the experiment. In the course of the experiment, *Actinobacteria* were an important component of the community. Their numbers varied insignificantly and comprised 10–20% of the total number of identified bacteria. At the final stage of succession, actinobacteria were predominant; this fact can be attributed to their ability to decompose a number of slowly degraded biopolymers. For example, we have demonstrated that the members of the phylum *Actinobacteria* play a leading role in the aerobic processes of cellulose destruction in *Sphagnum* bogs [23]. The population density of planctomycetes increased steadily during incubation; by day 90, they comprised up to 7% of the total cell count. It is noteworthy that the members of the phylogenetic group *Firmicutes*, which includes bacilli, were virtually absent from the community developing in the course of *Sphagnum* decomposition. The numbers of their vegetative cells did not exceed 5×10^4 cells ml^{-1}. On the whole, the proportion of bacteria identified with oligonucleotide probes was high at the early stages of *Sphagnum* destruction (89 and 94% of the total number of bacterial cells detected with EUB338-mix at the beginning of the experiment and on day 40 of incubation, respectively). However, this proportion decreased to 34% at the final stage of succession. This fact suggests that the community includes bacteria that cannot be identified with the set of probes applied in the present work.

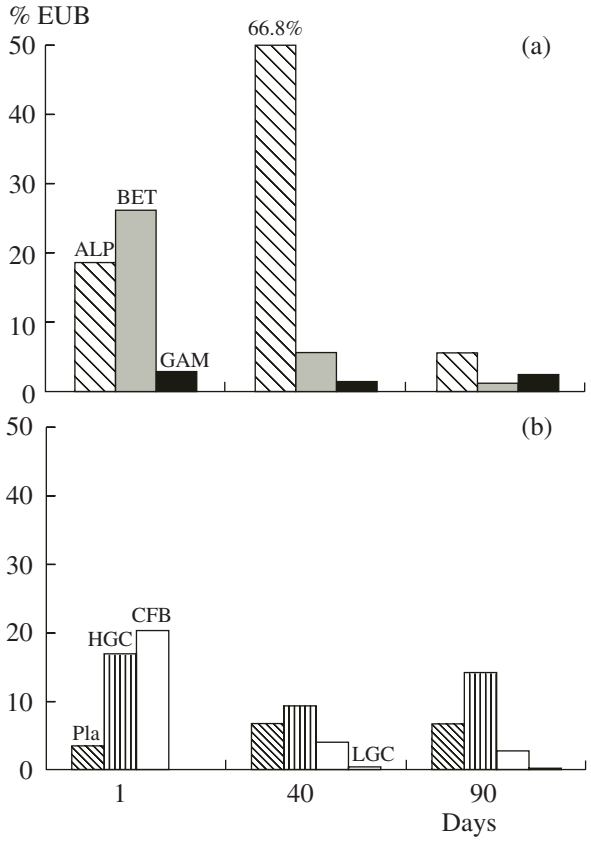

Fig. 2. Changes in the proportions of various phyla of bacteria in the total number of cells detected in bog water with the probe EUB338-mix (%) at various stages of *Sphagnum* degradation: (a), various classes of the *Proteobacteria*: *Alphaproteobacteria* (ALP), *Betaproteobacteria* (BET), and *Gammaproteobacteria* (GAM); (b), phylogenetic groups of *Planctomycetes* (Pla), *Actinobacteria* (HGC), *Bacteroidetes* (CFB), and *Firmicutes* (LGC).

Application of a novel probe for specific detection of *Chitinophaga arvensicola*. Gliding bacteria with long cells which become fragmented in old cultures have been studied by us and affiliated with the recently described taxon *C. arvensicola* [21]. They are an example of bacteria inhabiting *Sphagnum* bogs which cannot be identified with existing oligonucleotide probes. Although they belong to the phylogenetic group *Bacteroidetes*, they cannot be detected with the oligonucleotide probes CF319a and CFB560 which are commonly used for detection of the microorganisms belonging to this group. At the same time, they are able to degrade some heteropolysaccharides; this fact suggests that they may be involved in the transformation of *Sphagnum* organic matter. To detect *C. arvensicola* cells in the studied bacterial community, we have designed the new species-specific probe Chit1004 targeting these bacteria (see Materials and Methods). The application of this probe has enabled us to easily visualize the targeted microorganisms in microbial landscapes (Fig. 3b), as well as to estimate their cell numbers, which varied from 1.9 to 6.7 $\times$ 10^5 cells ml^{-1} (Table 2). This relatively low population density is quite comparable with that revealed by the combined application of the oligonucleotide probes CF319a and CFB560 (Fig. 3a). Thus, in the studied samples, *C. arvensicola* comprised nearly half of the total number of the representatives of the phylum *Bacteroidetes.* The sharp decrease in the population density of *C. arvensicola* in the course of *Sphagnum* decomposition can be due to the rapid exhaustion of the available pool of substrates (heteropolysaccharides) and to the inability of these microorganisms to utilize difficult-to-degrade polymers, such as cellulose. A similar population dynamics was recorded in the case of other representatives of the *Bacteroidetes*, which attests to the similarity of their metabolic potential with that of *C. arvensicola*, as well as to the fact that the functional role of these bacteria is less important at the stage of decomposition of difficult-to-degrade polymers.

Metabolic potential of the representative isolate of the *Alphaproteobacteria*. The water aliquots from the studied microcosm were spread plated on tenfold

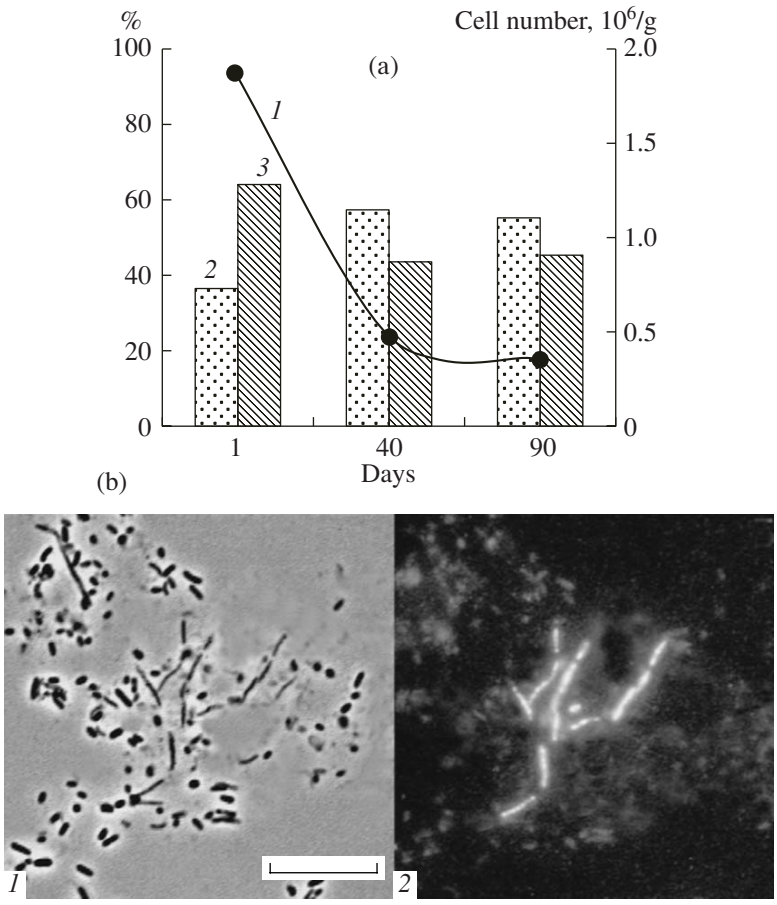

Fig. 3. (a), dynamics of the total number of *Bacteroidetes* cells (*1*) and the proportion of the cells detected with the new oligonucleotide probe Chit1004 (*2*) and the probes CF319a + CFB560 (*3*) in the microcosm with decomposing *Sphagnum* moss. (b), in situ detection of *Chitinophaga arvensicola* cells in the microbial community developing on day 40 of *Sphagnum* decomposition: (*1*) phase contrast; (*2*) fluorescence microphotograph showing hybridization with the Cy3-labeled probe Chit1004. Scale bar, 10 μm.

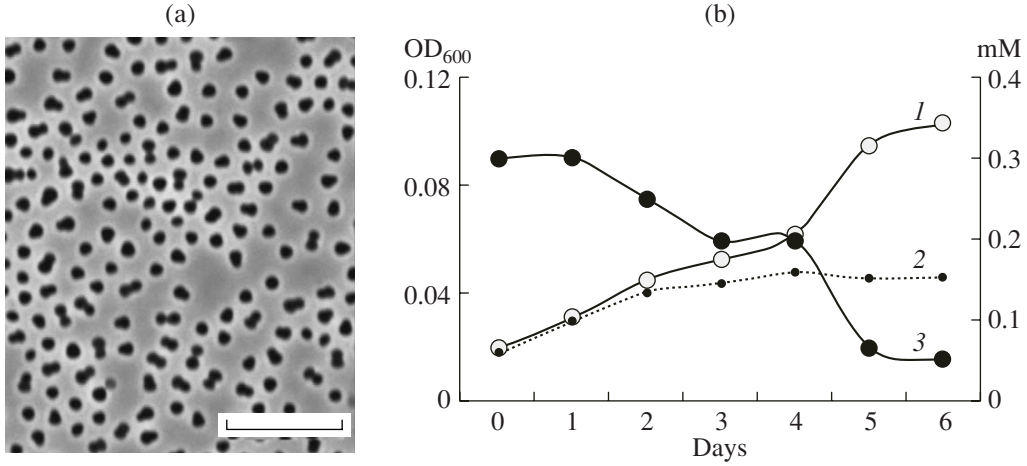

Fig. 4. (a), cell morphology of the alphaproteobacterial strain PLO1 isolated from the microcosm with decomposing *Sphagnum* moss. Scale bar, 10 μm. (b), the growth dynamics of strain PLO1 on the medium with sodium galacturonate: (*1*) optical density of the culture on the medium with sodium galacturonate; (*2*) control without a carbon source; (*3*) dynamics of the decrease in the substrate content.

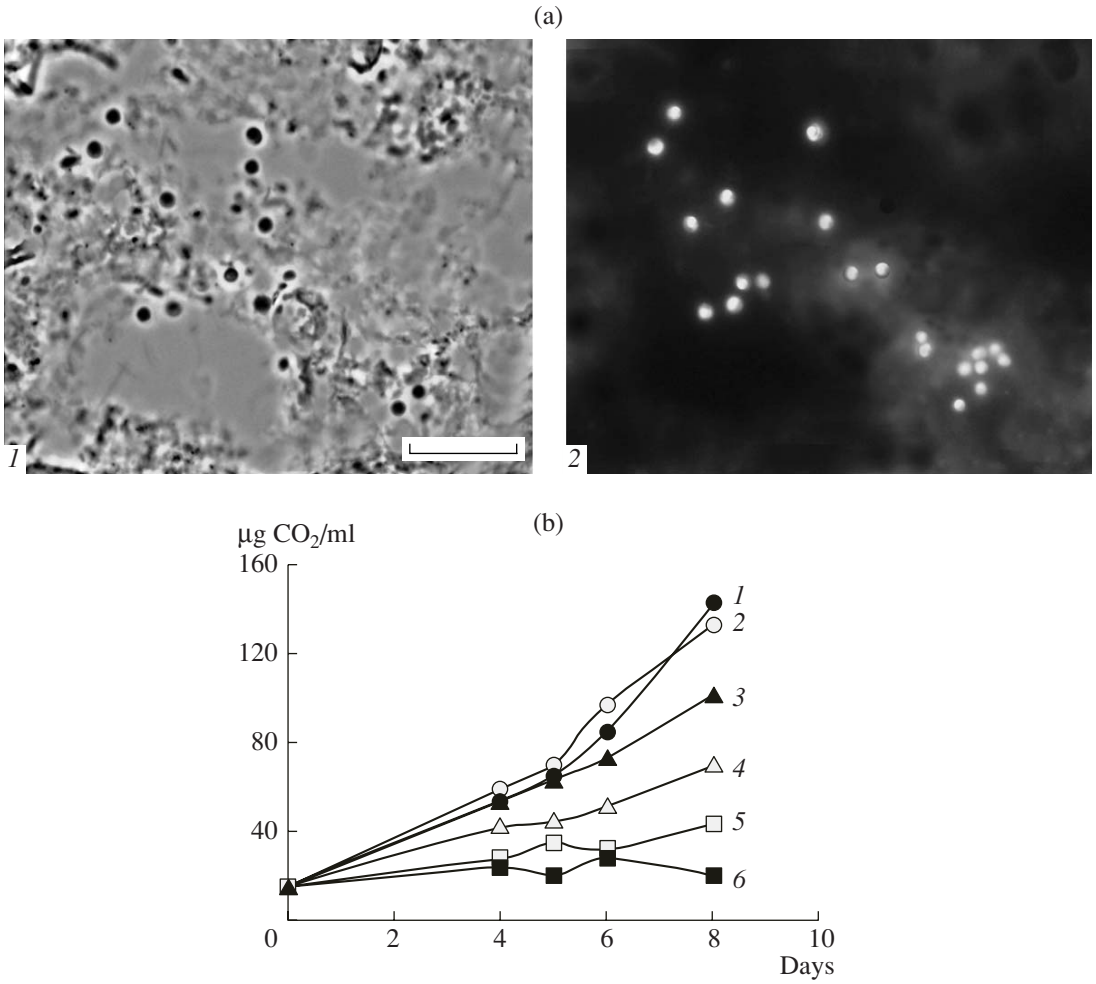

Fig. 5. (a), detection of *Planctomycetes* cells in the microbial community of the microcosm with decomposing *Sphagnum* moss (day 40 of incubation): (*1*) phase contrast; (*2*) fluorescence microphotograph showing hybridization with the Cy3-labeled probes PLA46 + PLA 886. (b), the growth of strain MOB10 on the media with various polymeric substrates: (*1*) N-acetyl-D-glucosamine; (*2*) glucose; (*3*) laminarin; (*4*) xylan; (*5*) casein; (*6*) control.

diluted complex organic medium R2A. A number of pure bacterial cultures were thus obtained. The screening of these isolates by hybridization with rRNA-specific oligonucleotide probes showed that most of them belong to the phylogenetic group *Alphaproteobacteria.* Strain PLO1, with the cells of characteristic shape, was among the predominant ones according to the results of plate growth experiments (Fig. 4a). More complete identification of this isolate by the determination of a partial 16S rRNA gene sequence (about 400 bp) has shown a 99% sequence similarity with a member of the recently described genus *Kaistia* [24], *Kaistia granuli".* The study of the metabolic potential of strain PLO1 has demonstrated its ability to utilize galacturonic acid as a growth substrate (Fig. 4b), which is a characteristic trait of a limited number of bacteria. Hence, it seems likely that utilization of uronic acids released from decomposing *Sphagnum* cell walls is the function of these microorganisms in the studied microcosm.

Metabolic potential of the representative isolate of the *Planctomycetes*. Members of the phylum *Planctomycetes* were a permanent component of the studied microbial community (Fig. 5a). Their numbers increased in the course of succession; by day 90 of the incubation, they were one of the predominant groups of microorganisms. Strain MOB10, which we had previously isolated from Obukhovskoe bog [19], has the morphology typical of the planctomycetes present in the investigated samples; this strain was selected to elucidate the possible function of these microorganisms in the community. This isolate utilizes some sugars, organic acids, and N-acetyl-D-glucosamine as growth substrates. Contrary to the above-described representative of the *Alphaproteobacteria*, strain MOB10 was found to be unable to grow on galacturonate. At the same time, strain MOB10 grew actively on media containing such heteropolysaccharides as xylan and laminarin; however, it was unable to grow on media containing such

difficult-to-degrade biopolymers as cellulose, chitin, or chitosan (Fig. 5b).

Thus, the present study has shown that the composition of the bacterial community involved in the process of transformation of organic compounds of *Sphagnum* moss is quite specific and undergoes fundamental transformations at the various stages of *Sphagnum* degradation. The representatives of the phylogenetic groups *Bacteroidetes* and *Firmicutes*, which are the main agents responsible for bacterial destruction of plant remains in eutrophic habitats with neutral pH, do not play any significant role in the process of *Sphagnum* decomposition. Representatives of the phyla *Alphaproteobacteria, Actinobacteria*, and *Planctomycetes* play the key role in *Sphagnum* biodegradation. Alphaproteobacteria are able to assimilate uronic acids released from decomposing *Sphagnum* cell walls; these microorganisms predominate at the early stages of succession. On the contrary, actinobacteria and planctomycetes dominated at the late stages of succession; their functional role in the process of organic matter transformation in acidic *Sphagnum* bogs consists in the degradation of polymer compounds of *Sphagnum* phytomass.

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