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Biological potential of cultivated microbiota of bryophytes from the different biotopes of the maritime Antarctic

Olha Maslovska[1], Solomiia Komplikevych[1], Laslo Uliganets[1], Iryna Vronska[1], Taras Peretyatko[1, 2], Ivan Parnikoza[2, 3], Svitlana Hnatush[1, *]

[1] Ivan Franko National University of Lviv, Lviv, 79005, Ukraine
[2] State Institution National Antarctic Scientific Center, Ministry of Education and Science of Ukraine, Kyiv, 01601, Ukraine
[3] National Historical and Architectural Museum "Kyiv Fortress", Kyiv, 01133, Ukraine

*** Corresponding author:** svitlana.hnatush@lnu.edu.ua

Abstract. Antarctic substrates are inhabited by microorganisms resistant to environmental factors. Since large areas of soil worldwide are saline and contaminated with metals, which limit plant growth, it is important to isolate plant growth-promoting bacteria that are resistant to environmental factors. The aim of this study was to isolate copiotrophic, oligotrophic, oligonitrophilic, phosphate-, and zinc-solubilising bacteria, and to determine their properties, including enzymatic activity, the ability to produce auxins and siderophores, and growth under the influence of heavy metals and NaCl. The research material consisted of samples of short moss turf and cushion subformation with *Andreaea depressinervis* or *Andreaea regularis*, bryophyte carpet and mat subformation dominated by *Ceratodon purpureus* or *Sanionia georgicouncinata* and tall moss turf subformation (moss bank) fragments dominated by *Polytrichum strictum* or *Chorisodontium aciphyllum*, collected from biotopes of the maritime Antarctic. The cultivated microbiota of bryophytes of short moss turf and cushion subformation, bryophyte carpet and mat subformation, and tall moss turf subformation (moss banks) differed in the number of detected microbial groups and their enumeration. Copiotrophs and oligotrophs dominated the bacterial community structure of most samples, but oligonitrophyles prevailed in the short moss turf and cushion subformation fragments with *An. depressinervis*. Bacteria isolated from samples of bryophyte carpet and mat subformation with dominance of *San. georgicouncinata* are characterised by a wider range of properties – amylase, protease, cellulase, and lipase activities, and the ability to solubilise ZnO and $Ca_3(PO_4)_2$. All bacterial isolates synthesised auxin-like compounds (up to 11.8 μg · ml^{-1}). Most of them produced siderophores. The isolated bacteria possess a range of adaptive properties, including the ability to grow over a wide temperature range (+4...+42 °C), high salt tolerance (up to 10.0% NaCl), and resistance to heavy metals (Mn^{2+}, Fe^{2+}, Cu^{2+}, Cd^{2+}, Co^{2+}, and $Cr_2O_7^{2-}$). Based on 16S rRNA gene sequencing, *Bacillus* sp. Sg840, *Pseudomonas* sp. S135, and *Sporosarcina* sp. S371 were identified. The identified properties and tolerance to environmental factors characterise the plant growth-promoting potential of bacteria isolated from Antarctic bryophyte subformations.

Keywords: *Andreaea, Bacillus, Polytrichum, Pseudomonas, Sanionia, Sporosarcina*

1 Introduction

Antarctic biota functions under the combined influence of extreme environmental factors, including low temperatures, strong winds, high salinity, limited water availability, and a shortage of micro- and macronutrients *etc.* (O'Brien et al., 2004; Yerkhova et al., 2022; Kovalenko et al., 2025). Despite these limitations, Antarctic terrestrial ecosystems are characterised by a high degree of adaptation of organisms to adverse environmental conditions. In the ice-free areas of Antarctica, bryophytes and lichens form microhabitats that serve as habitats for a variety of microbial communities. Together, these organisms play a key role in driving biogeochemical processes, sustaining ecosystem function, and enhancing their resilience to the extreme environmental conditions of Antarctica (Anderson et al., 2024; Zhang et al., 2025).

The adaptive potential of mosses and lichens is largely linked not only to their own physiological characteristics but also to complex interactions with their microbiota (Cho et al., 2020; Carrell et al., 2022; Živković et al., 2025). Bacterial communities associated with mosses play a role in key biogeochemical processes, particularly the fixation of atmospheric nitrogen (DeLuca et al., 2002; Warshan et al., 2016; Holland-Moritz et al., 2021), oxidise methane (Kip et al., 2010; Holland-Moritz et al., 2021), and promote the decomposition of organic matter in peatlands. The metagenome of *Sanionia uncinata* (Hedw.) Loeske was studied (Bones et al., 2026), as well as the influence of environmental factors on the microbiome of the tall moss turf subformation (moss banks) (Prekrasna-Kviatkovska et al., 2024), as well as changes in the microbiota during the formation of so-called "fairy rings" – concentric zones of darkening and moss die-off (Choi et al., 2026). The composition of the moss microbiome is often specific to the host plant, although it is also influenced by environmental factors, particularly temperature and substrate acidity *etc.* (Holland-Moritz et al., 2021).

Bacteria associated with mosses can stimulate the growth of other plants. In particular, isolates derived from the fairy ring of *San. uncinata* exhibited plant growth-promoting activity toward *Arabidopsis thaliana* (L.) Heynh. (Choi et al., 2026). Bacteria isolated from *Hypnum plumaeforme* Wilson stimulate barley growth (Park et al., 2025).

It is well known that plant growth-promoting bacteria can improve the availability of nitrogen, which is why oligonitrotrophylic microorganisms are often among the target groups for the isolation of plant growth-promoting microorganisms (Grzyb et al., 2021; Styczynski et al., 2022). In addition, the hydrolytic enzymes they synthesise – cellulases, amylases, proteases, and others – participate in the mineralisation of organic polymers, thereby providing accessible sources of carbon and nutrients for plants (Sritongon et al., 2023).

No less important is the study of microorganisms capable of solubilising hard-to-access mineral compounds. Phosphorus and zinc are among the elements whose deficiency often limits plant growth, especially under extreme environmental conditions. Phosphate-solubilising bacteria convert insoluble phosphates into forms that are available for plant uptake (Ramos Cabrera et al., 2024), while zinc-solubilising microorganisms increase the availability of zinc, an essential trace element involved in the functioning of numerous enzymatic systems (Singh et al., 2024).

Screening for strains with plant growth-promoting traits is conducted among various groups of microorganisms. Copiotrophic microorganisms predominate under conditions of relatively high organic compound availability, grow rapidly, and actively participate in the transformation of organic matter (Couso et al., 2023). In contrast, oligotrophic forms can sustain life at low substrate concentrations, which is particularly important for Antarctic terrestrial ecosystems, where available carbon and nutrient sources are limited (Couso et al., 2023).

Given the environmental changes caused by human activities, the isolation of halotolerant, metal-resistant, and plant growth-promoting bacteria and the study of their properties are of both theoretical and practical importance. Microorganisms

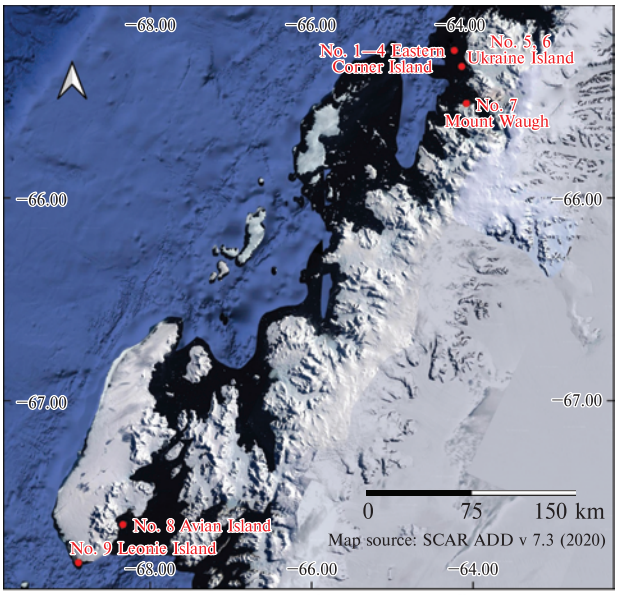

Figure 1. Map of sampling sites in maritime Antarctica

from Antarctic ecosystems, which are adapted to numerous stress factors – including heavy metal compounds and NaCl (Zhang et al., 2025; Lehosmaa et al., 2025), as such isolates are potentially suitable for use in bioremediation technologies and for enhancing plant productivity on saline or heavy-metal-contaminated soils.

In this study, from samples of various Antarctic bryophytes inhabiting environments with distinct conditions – rocks or more humid areas – and forming complex interspecific communities, copiotrophic, oligotrophic, oligonitrophilic, phosphate- and zinc-solubilising microorganisms were isolated, and the properties of the isolates were determined, including their enzymatic activities, ability to produce auxins and siderophores, and growth under the influence of heavy metal compounds and NaCl.

2 Materials and methods

The research material consisted of bryophyte samples collected during the 28th Ukrainian Antarctic Expedition (2023/24) from various sites (Fig. 1, Table 1). For this study, bryophytes from various communites characterised by high resilience to Antarctic conditions were selected (Prather et al., 2019; Perera-Castro et al., 2020).

The above-ground parts of the bryophytes, and the rhizosphere with substrate under the bryophytes were collected and analysed separately. For this, 4 different points were selected on the community. Using a disinfected knife/spatula, the samples were transferred to a sterile double parchment bag. Before each sample was taken, the tools were disinfected. After collection, the samples (in a closed bag) were dried for several days at room temperature (until traces of moisture on the bag disappeared), protected from direct sunlight. After collection, the moisture status of the bags was constantly monitored to prevent dampness. All samples were stored and transported at 4 °C with minimal humidity. All bryophytes were determined according to keys (Ochyra et al., 2008), and vouchers of all species were deposited in the bryophyte herbarium (KRAM B) of the Institute of Botany of Polish Academy of Science (Kraków, Poland).

Surface sterilisation of the above-ground parts of bryophyte samples was carried out using a modified method described by Barra et al. (2016) and by Prekrasna et al. (2021). This involves washing the plant in sterile distilled water, then in a 70% ethanol solution, and further in a 5.6% sodium hypochlorite solution. The water from the last rinse was inoculated into tryptic soy agar (TSA, Merck, Millipore) and R2A (Merck, Millipore) media to assess sterility. Next, the plants were crushed, serial dilutions were prepared in 0.9% NaCl, and the dilutions were sown on nutrient media.

To 1,0 g of samples of the rhizosphere zone and substrate from under the bryophytes, 9 ml of 0.9% NaCl solution was added. The resulting suspension was thoroughly mixed and incubated for 20 min, after which it was shaken again, diluted, and 0.1 ml of the obtained suspension was sown onto the culture media.

Copiotrophic microorganisms were isolated on TSA, oligotrophic microorganisms on R2A,

Table 1. Locations of moss and moss bank sampling sites of maritime Antarctica and isolated bacteria

Marking on the map	Location*	Coordinates	Short description of the sample**	Isolates of bacteria
№ 1	Argentine Islands, Eastern Corner Island	65.245000 S, 64.233400 W	Bryophyte carpet and mat subformation, *Ceratodon purpureus* (Hedw.) Brid. (the aboveground part, rhizosphere, and substrate from under the moss)	Cp824, Cp825, Cp826
№ 2	Argentine Islands, Eastern Corner Island	65.244967 S, 64.23333 W	Bryophyte carpet and mat subformation, *Sanionia georgicouncinata* (Müll. Hal.) Ochyra & Hedenäs (the aboveground part, rhizosphere, and substrate from under the moss)	Sg840, Sg841, Sg842, Sg845, Sg861
№ 3	Argentine Islands, Eastern Corner Island	65.244933 S, 64.233300 W	Tall moss turf subformation, moss bank fragment dominated by *Polytrichum strictum* Brid., with the addition of *Cephaloziella varians* (Gottsche) Steph. and *Pohlia nutans* (Hedw.) Lindb. (the above-ground part, rhizosphere, and substrate from under the bryophytes)	MB832, MB833, MB834, MB835
№ 4	Argentine Islands, Eastern Corner Island	65.245017 S, 64.233267 W	Tall moss turf subformation, the moss bank fragment dominated by *Chorisodontium aciphyllum* (Hook. f. & Wilson) Broth., with the addition of *Pohlia nutans*, *Cephaloziella varians* (the above-ground part, rhizosphere, and substrate from under the bryophytes)	MB800, MB801
№ 5	Berthellot Islands, Ukraine Island	65.328033 S, 64.141117 W	Short moss turf and cushion subformation, *Andreaea depressinervis* Cardot	Ad847, Ad857, Ad859
№ 6	Berthellot Islands, Ukraine Island	65.327950 S, 64.140833W	Tall moss turf subformation, moss bank, fragment dominated by *Polytrichum strictum,* with the addition of *Cephaloziella varians, Pohlia nutans*, *Sanionia georgicouncinata* (the aboveground part, rhizosphere, and substrate from under the bryophytes)	MB813, MB814, MB815
№ 7	Graham Coast, Mount Waugh	65.518367 S, 64.083817 W	Short moss turf and cushion subformation, *Andreaea regularis* Müll. Hal.	Ar806, Ar807, Ar808
№8	Marguerite Bay, Avian Island	67.772609 S, 68.889831 W	Bryophyte carpet and mat subformation, *Sanionia georgicouncinata* (the above-ground part, rhizosphere, and substrate from under the moss)	S135, S152, S153, S167, S371, S376
№9	Marguerite Bay, Leonie Island	67.593549 S, 68.338234 W	Bryophyte carpet and mat subformation, *Bryum pseudotriquetrum* (Hedw.) G. Gaertn., B. Mey. & Scherb. (above-ground part)	Bp140, Bp141, Bp142

* Toponyms of the Argentine Islands-Kyiv Peninsula region provided according to Yevchun et al. (2021).
** Bryophyta species names and communities provided according to Ochyra et al. (2008).

oligonitrophilic microorganisms on Ashby's medium (Ashby, 1907), microorganisms that solubilise $Ca_3(PO_4)_2$ – on Pikovska's medium (Nautiyal, 1999), microorganisms capable of solubilising ZnO – on MSM medium with 0.1% ZnO (Bhakat et al., 2021). The cultures were grown for 7–10 days under aerobic conditions at 20 ± 2 °C.

The moisture content was determined by the weight method. The samples were dried for 5 hours at 105 °C until a constant mass was achieved. The hygroscopic moisture content in the samples was determined using the formula:

$$\% \text{ hygroscopic moisture} = (a \times 100)/b,$$

where a is the mass of the dry sample and b is the mass of the wet sample.

To identify isolates Sg840, S135, and S371, we sequenced the 16S rRNA gene as described previously (Maslovska et al., 2024). The 16S rRNA gene sequences of these isolates were deposited in GenBank under the accession numbers PX482618.1, PX482615.1, and PX482610.1. Pairwise alignment of the obtained nucleotide sequences with the GenBank database sequences was performed using the BLASTN service. The phylogenetic tree was constructed in MEGA 12 (Kumar et al., 2024) using the Kimura 2-parameter model (Kimura, 1980).

The morphological features of microorganisms (cell shape, size, spore formation, and determination of the structural organisation of the cell wall after Gram staining) were studied using light microscopy methods (Carl Zeiss Axio Lab.A1 binocular microscope and an Olympus IX73 inverted microscope with a DP-74 digital camera).

The ability of bacteria to form endospores was detected by the Peshkov–Trujillo method and by pasteurisation of cell suspensions (80 ± 1 °C, 15 min), followed by cultivation for 7 days at 20 ± 2 °C. Spore-forming bacteria were able to grow after pasteurisation (Hudz' et al., 2014).

Bacterial motility was assessed by observing chemotactic spread in semi-solid TSA (0.2% agar) columns after incubation for 7 days at 20 ± 2 °C.

The respiratory requirements of the isolates were determined using fluid thioglycollate medium (Merck, Millipore, Cat. No 1.08191.0500).

Catalase activity was assessed by the presence of effervescence upon the addition of 10% H_2O_2 (Arenas et al., 2014; Hudz' et al., 2014). Oxidase Activity was evaluated using Bactident® Oxidase test strips (Merck, Millipore, Cat. No 1.00181.0002).

The capacity for nitrate reduction was tested in tryptic soy broth (Merck, Millipore, Cat. No 1.05459.0500) enriched with 0.2% KNO_3. After 7 days of cultivation, the presence of residual nitrates was verified using diphenylamine and sulfuric acid, while nitrite accumulation was monitored with Griess reagent (Merck, Millipore, Cat. No 1.09023.0500). Additionally, denitrification was confirmed by the presence of N_2 gas in Durham tubes (Hudz' et al., 2014).

The proteolytic activity of the studied isolates was assessed by their ability to liquefy gelatin during growth in a column of tryptic soy broth with gelatin (12.5%). The bacteria were cultured at room temperature for 14 days. Gelatin liquefaction or the absence of this feature was assessed visually (Hudz' et al., 2014).

To determine the ability of isolates to synthesise hydrolytic enzymes, bacteria were inoculated on a medium containing carboxymethylcellulose (Ahmed et al., 2018), starch-ammonia agar (Hudz' et al., 2014), MSM medium with 0.1% ZnO (Bhakat et al., 2021), and medium with Tween-20 (Hudz' et al., 2014). The cultures were grown at 20 ± 1 °C for 7–10 days. The ability to synthesise lipases on a medium containing Tween-20 was assessed by the formation of calcium salts of fatty acid crystals around bacterial colonies and by the solubilisation of ZnO, as indicated by the transparent zone around the colonies. The ability to hydrolyse starch and cellulose was assessed after applying Lugol's solution (Gohel et al., 2014). The hydrolysis index was determined using the formula IE = (A–B)/B, where A is the diameter of the hydrolysis zone of cellulose, starch, or Tween-20; B is the diameter of the bacterial colony, mm.

Urease activity was detected after sowing bacteria into Urea Agar Medium (Himedia, SKU GM112A). Bacteria were grown for 3–5 days at 20 ± 2 °C. Enzymatic activity was shown by the colour change in the medium.

To determine the quantitative content of siderophores, we used the method described in the work by Arora & Verma (2017). The optical density of the reaction mixtures was determined spectrophotometrically (λ = 630 nm). The siderophore content was determined from optical density values and expressed in conventional units (SU) using the formula SU = [(Ar − As)/Ar] × 100, where Ar is the optical density of the control sample, and As is the optical density of the test sample.

To study the ability of microorganisms to synthesise auxin-like compounds, a method using Salkowski's reagent (0.5 M $FeCl_3 \cdot 6H_2O$ in 35% $HClO_4$), which reacts with them to produce a red colour, was used (Gang et al., 2019). The optical density of the reaction mixtures obtained was determined spectrophotometrically (λ = 536 nm). The content of auxin-like compounds was determined using a calibration curve constructed using a solution of indolyl-3-acetic acid containing 1–25 μg · ml^{-1} of this compound.

To assess the sensitivity of bacterial isolates to different temperatures (4, 8, 16, 20, 28, 37, 42 °C), a three-day-old culture was inoculated onto TSA using the streak method. The cultures were grown for 5–14 days.

To determine the tolerance of isolates to NaCl, TSA with different concentrations of NaCl (2.0, 5.0, 7.5, 10.0, 15.0 %) was used. A three-day-old bacterial culture was sown using the streak method. The cultures were grown at 20 ± 1 °C for 5–14 days.

The growth of bacterial isolates under the influence of heavy metals was studied using TSA supplemented with $MnCl_2 \cdot 4H_2O$ (1.0–20.0 mM), $FeSO_4 \cdot 7H_2O$ (0.5–20.0 mM), $CoCl_2 \cdot 6H_2O$ (0.5–5.0 mM), $CdCl_2 \cdot 2.5H_2O$ (0.2–500 μM), $CuCl_2 \cdot 2H_2O$ (1.0–6.0 mM), or $K_2Cr_2O_7$ (0.1–10.0 mM) after sterilisation. The bacteria were grown for three to five days at a temperature of 20 ± 2 °C. The medium without heavy metal compounds was used as a control.

To evaluate the utilisation of different carbon sources by microorganisms, we used Hugh Leifson medium, replacing glucose with other carbon sources. The medium was inoculated into the column, and half of the tubes were filled with sterile vaseline oil. The bacteria were cultivated at 20 ± 2 °C for 3–5 days. Bacterial growth, changes in the medium color (acid formation), and gas production under aerobic and anaerobic conditions were evaluated.

Statistical analysis of research results was performed in Microsoft Excel 2021, and graphs were generated in OriginPro 8.5. The results are presented as the arithmetic mean (M) and the standard deviation (SD).

3 Results

3.1. The enumeration of microorganisms of different groups in bryophyte samples of different communities

During the study of the cultivated microbiota of bryophytes, the focus was on enumerating copiotrophic, oligotrophic, and oligonitrophilic microorganisms, as well as those that solubilise $Ca_3(PO_4)_2$ or ZnO.

The number and diversity of culturable microorganisms in samples of the driest-biotops mosses *An. depressinervis* (Ukraine Island) and *An. regularis* (Mount Waugh) varied (Fig. 2). In the sample of *An. depressinervis*, copiotrophic, oligotrophic microorganisms, microorganisms that solubilise $Ca_3(PO_4)_2$, oligonitrophilic microorganisms, and microorganisms capable of solubilising ZnO were found. Unlike other mosses studied in the work, oligonitrophilic microorganisms were the most numerous group of microorganisms in the *An. depressinervis* sample. Only copiotrophic and oligotrophic microorganisms were found in the sample of *An. regularis*. Unlike the *An. depressinervis* moss sample, in the *An. regularis* sample, the amount of copiotrophic microorganisms was 53% higher than that of oligotrophic microorganisms.

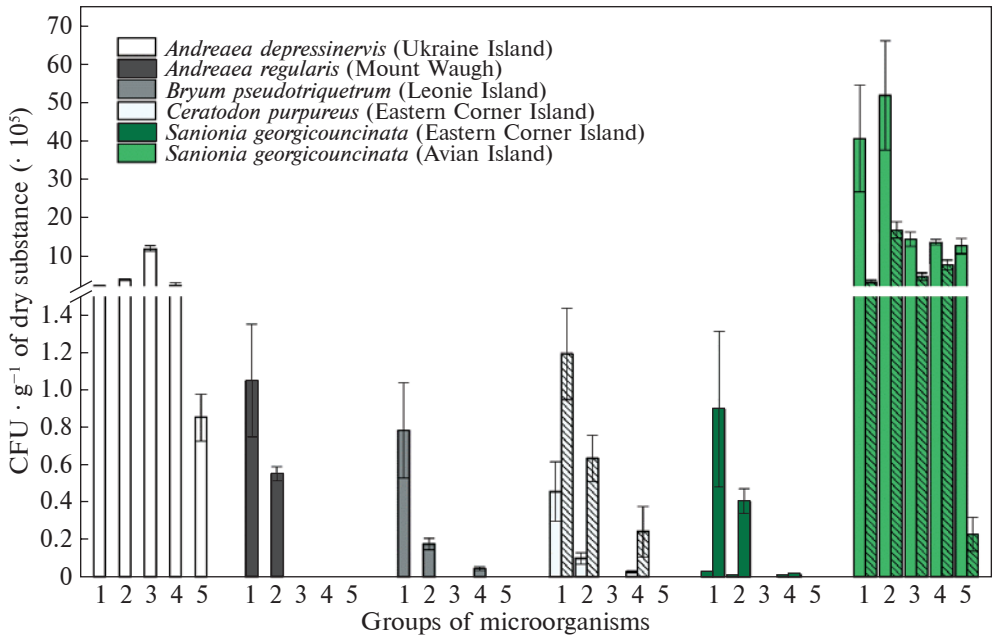

Figure 2. Enumeration of different groups of microorganisms in bryophyte samples from different sites of the maritime Antarctic (1 – copiotrophic microorganisms; 2 – oligotrophic microorganisms; 3 – oligonitrophilic microorganisms; 4 – $Ca_3(PO_4)_2$-solubilising microorganisms; 5 – ZnO-solubilising microorganisms; columns without shading – above-ground part of moss, shaded columns – rhizosphere and substrate under the moss; M ± SD, n = 3)

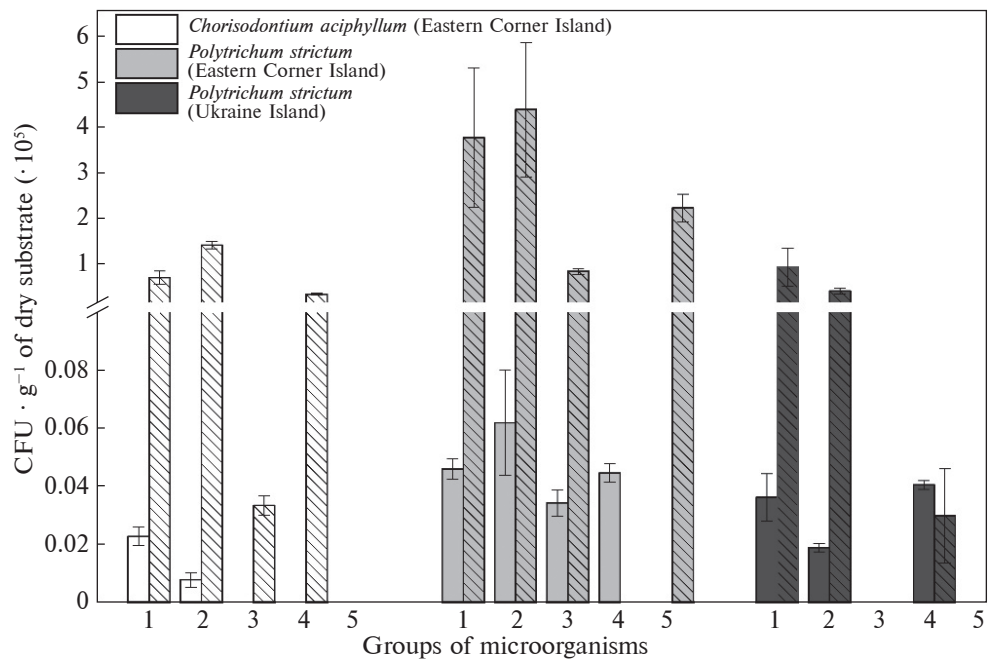

Figure 3. The enumeration of microorganisms of different groups in samples of tall moss turf subformation from different biotopes of the maritime Antarctic (1 – copiotrophic microorganisms; 2 – oligotrophic microorganisms; 3 – oligonitrophilic microorganisms; 4 – $Ca_3(PO_4)_2$-solubilising microorganisms; 5 – ZnO-solubilising microorganisms, columns without shading – above-ground part of moss, shaded columns – rhizosphere and substrate under the moss; M ± SD, n = 3)

Three groups of microorganisms were identified in samples of the above-ground part of *B. pseudotriquetrum* (Leonie Island): copiotrophs, oligotrophs, and $Ca_3(PO_4)_2$ solubilisers. The most numerous group of microorganisms in the *Cer. purpureus* samples was copiotrophic microorganisms, while oligotrophic microorganisms were less numerous. The enumeration of microorganisms that solubilise ZnO in samples of these two mosses was the lowest.

The number of microorganism groups identified and their enumeration in samples of the above-ground part of *Cer. purpureus* (Eastern Corner Island) did not differ a lot from those in the above-ground part of *B. pseudotriquetrum* (Leonie Island) moss. The same groups of microorganisms were identified in the rhizosphere and the substrate under *Cer. purpureus*, but their amounts were 2.6–9.1 times higher than in the above-ground part of this moss.

There was a difference in the enumeration and number of identified groups in the *San. georgicouncinata* samples collected from Eastern Corner Island and Avian Island. The most numerous group of microorganisms in the Eastern Corner Island sample was copiotrophic microorganisms, slightly less numerous were oligotrophic microorganisms, and the least numerous (~1500 CFU · g^{-1} of dry substrate) were microorganisms that solubilise $Ca_3(PO_4)_2$. The enumeration of copiotrophic and oligotrophic microorganisms in the rhizosphere and substrate beneath *San. georgicouncinata* was higher than that in the above-ground part of the moss. The culturable microbiota of the above-ground part of the moss from Avian Island was the most numerous compared to the enumeration of microorganisms in the Eastern Corner Island sample and in the samples of other bryophytes studied in the work. All five groups of microorganisms studied were found in this sample. The most numerous microorganisms were copio- and oligotrophic. Other groups were slightly less numerous. Oligotrophic microorganisms were the most numerous in the rhizophere and moss substrate. The copiotrophic, oligonitrophilic, and $Ca_3(PO_4)_2$-solubilising microorganisms ranged from 4.6 to 16.7 · 10^5 CFU · g^{-1} of dry substrate. The smallest enumeration was found for the ZnO-solubilising microorganisms.

In the above-ground part of *Ch. aciphyllum*-dominated fragment of tall moss turf subformation (Eastern Corner Island), only copiotrophic and oligotrophic microorganisms were detected (Fig. 3). Their enumeration in the sample was lower than in the above-ground part of moss bank samples, where *Pol. strictum* dominated. No microorganisms capable of solubilising ZnO were detected in the rhizosphere or in the substrate from under this moss bank. The enumeration of microorganisms in the rhizosphere and substrate beneath the *Ch. aciphyllum* tall moss turf subformation ranged from 3.3 to 14.1 · 10^4 CFU · g^{-1} of dry substrate.

Two *Pol. strictum* samples from Eastern Corner Island and Ukraine Island were studied. These samples differed in the presence of *San. georgicouncinata*. The groups of microorganisms we identified, and their enumeration, also differed. The most numerous group of microorganisms in moss bank fragments samples, dominated by *Pol. strictum*, containing *Ceph. varians* and *Poh. nutans* (Eastern Corner Island), was oligotrophic microorganisms, occurring both in the above-ground part and in the substrate. Copiotrophic, oligotrophic, and microorganisms that solubilise $Ca_3(PO_4)_2$ were less numerous. No microorganisms capable of solubilising ZnO were detected in the above-ground part, whereas in rhizosphere and substrate samples from beneath the moss bank, the enumeration was 2.2 ± 0.3 · 10^5 CFU · g^{-1} of dry substrate. In samples from the above-ground part of the moss bank, where, in addition to *Pol. strictum, Ceph. varians,* and *Poh. nutans*, there was also *San. georgicouncinata* (Ukraine Island), only three groups of microorganisms were found: copiotrophic, oligotrophic, and microorganisms capable of solubilising $Ca_3(PO_4)_2$. Unlike the moss bank without *San. georgicouncinata*, the most numerous here were copiotrophic microorganisms and microorganisms capable of solubilising $Ca_3(PO_4)_2$, while oligonitrophilic microorganisms were not

Table 2. Properties of bacterial isolates from bryophyte samples of different communities

Isolate	Ability to grow in the Ashby's medium	Protease activity	Hydrolysis index of				Synthesis of	
			starch	cellulose	Tween-20	ZnO	siderophores, SU	auxin-like compounds, $\mu g \cdot mL^{-1}$
Andreaea depressinervis (Ukraine Island)								
Ad847	−	−	0	0	2.02 ± 0.2	0	0	1.45 ± 0.21
Ad857	+	−	0	0	0	0	1.48 ± 0.27	1.70 ± 0.18
Ad859	+	+	0	0	2.12 ± 0.24	0	0.16 ± 0.11	3.94 ± 0.17
Andreaea regularis (Mount Waugh)								
Ar806	−	−	0	0	0	0	2.22 ± 0.34	3.48 ± 0.23
Ar807	−	+	0	0	0	0	4.65 ± 0.38	3.09 ± 0.29
Ar808	+	−	0	0	0.39 ± 0.09	0	0	2.73 ± 0.22
Ceratodon purpureus (Eastern Corner Island)								
Cp824	−	−	0	0	0	0	3.50 ± 0.26	0.61 ± 0.27
Cp825	−	−	0	0	1.0 ± 0.24	0	3.66 ± 0.27	9.91 ± 0.31
Cp826	−	+	5.91 ± 1.73	3.71 ± 0.41	0	3.19 ± 0.58	0	1.80 ± 0.26
Bryum pseudotriquetrum (Leonie Island)								
Bp140	−	−	0	0	2.89 ± 0.52	0	0	2.90 ± 0.67
Bp141	−	+	0	0	0.5 ± 0.01	0	0	1.50 ± 0.27
Bp142	−	−	0	0	0	0	0	1.25 ± 0.45
Sanionia georgicouncinata (Eastern Corner Island)								
Sg840	+	+	2.67 ± 0.22	0	1.29 ± 0.55	2.34 ± 0,15	83.80 ± 3.70	3.21 ± 0.28
Sg841	−	+	1.70 ± 0.24	3.67 ± 0.31	0.83 ± 0.14	0	0	1.46 ± 0.29
Sg842	−	+	2.64 ± 0.33	9.99 ± 1.63	0.43 ± 0.10	4.38 ± 0.46	0	2.84 ± 0.37
Sg845	+	+	2.17 ± 0.50	1.01 ± 0.18	2.08 ± 0.80	0	18.13 ± 4.19	2.44 ± 0.23
Sg861	−	+	1.27 ± 0.74	3.10 ± 0.03	0.60 ± 0.22	0	0.17 ± 0.06	2.46 ± 0.26
Sanionia georgicouncinata (Avian Island) the above-ground part								
S135	−	+	9.50 ± 3.81	1.87 ± 0.92	4.86 ± 0.41	2.51 ± 0.46	30.34 ± 4.32	7.84 ± 0.53
S152	−	−	0	2.73 ± 1.41	5.43 ± 0.61	1.33 ± 0.74	28.08 ± 2.13	8.93 ± 0.95
S153	−	−	0	0	6.44 ± 0.27	3.02 ± 1.02	26.45 ± 3.40	8.03 ± 1.88
S167	−	+	0	0	5.36 ± 0.87	1.41 ± 0.34	26.44 ± 1.95	9.16 ± 2.94
sample of the rhizosphere and substrate from under moss								
S371	−	−	0	0	0	0	60.59 ± 2.27	3.43 ± 0.75
S376	−	−	0	2.60 ± 0.51	1.25 ± 0.58	0	42.06 ± 3.50	2.56 ± 0.63
Chorisodontium aciphyllum (Eastern Corner Island)								
MB800	−	−	0	0	0	0	1.30 ± 0.20	2.94 ± 0.29
MB801	+	−	0	0	0	0	0	9.74 ± 0.45

End of Table 2

Isolate	Ability to grow in the Ashby's medium	Protease activity	Hydrolysis index of				Synthesis of	
			starch	cellulose	Tween-20	ZnO	siderophores, SU	auxin-like compounds, $\mu g \cdot mL^{-1}$
Polytrichum strictum (Eastern Corner Island)								
MB832	−	−	0	0	5.67 ± 0.78	0	4.45 ± 0.36	2.02 ± 0.20
MB833	+	−	0	0	0.42 ± 0.04	0	0	2.68 ± 0.28
MB834	+	−	0	0	0.96 ± 0.15	0	0	11.80 ± 0.34
MB835	+	−	0	0	0	0	1.67 ± 0.18	3.32 ± 0.24
Polytrichum strictum (Ukraine Island)								
MB813	+	−	0	0	0	0	1.31 ± 0.17	5.80 ± 0.22
MB814	−	+	3.38 ± 0.60	3.77 ± 0.43	1.86 ± 0.16	4.93 ± 0.8	0	6.42 ± 0.94
MB815	+	−	0	0	0.43 ± 0.14	0	0	4.55 ± 0.31

Note: "−" − no feature detected, "+" − feature detected.

detected. Only these three groups of microorganisms were also detected in the rhizosphere and substrate beneath the *Pol. strictum* tall moss turf subformation (Ukraine Island). Copiotrophic and oligotrophic microorganisms were the most abundant in the samples from the underground portion.

3.2 Properties of bacterial isolates

From moss samples collected at various locations in Antarctica, we obtained 400 bacterial isolates with distinct colony morphologies. A preliminary screening was carried out on the isolates. Considering the morphology of the colonies and cells, their ability to grow consistently on various synthetic media, and their origin from different substrates, 32 isolates (Table 1) were selected for further study.

The studied bacterial isolates from *An. depressinervis* and *An. regularis* mosses did not produce amylase and cellulase, nor were they capable of solubilising ZnO. Only some synthesised lipases and proteases, and some were capable of growing in Ashby's medium (Table 2).

Bacterial isolates from *C. purpureus* differed in their properties. The Cp824 bacterial isolate did not exhibit any of the studied characteristics. The Cp825 isolate synthesised only lipases. The Cp826 isolate synthesised proteases, amylases, cellulases, and solubilised ZnO. Most bacterial isolates with hydrolytic properties were isolated from *San. georgicouncinata*. All of them produced amylases and lipases; all except isolate Sg840 produced cellulases. From this set of bacterial isolates, only two were able to grow in Ashby's medium (Sg840 and Sg845) and solubilised ZnO (Sg840 and Sg842).

Bacterial isolates from the above-ground part of *San. georgicouncinata* (Avian Island) solubilised ZnO and synthesised lipases. Only two bacterial isolates synthesised cellulases. The most active was isolate S135, which exhibited protease, amylase, cellulase, and lipase activities and solubilised ZnO.

Bacterial isolates from moss bank fragment did not synthesise hydrolytic enzymes, except for lipases. The exception was bacterial isolate MB814, isolated from the moss bank formed by *Pol. strictum*, that contained *Ceph. varians*, *Poh. nutans*, and *San. georgicouncinata* (Ukraine Island).

The highest content of siderophores was found in the culture medium of bacteria isolated from

Table 3. Growth of bacterial isolates under the influence of different temperatures and NaCl

Isolate	Temperature, °C							NaCl, %					
	4 ± 1	8 ± 1	16 ± 1	20 ± 1	28 ± 1	37 ± 1	42 ± 1	0	2.0	5.0	7.5	10.0	15.0
Andreaea depressinervis (Ukraine Island)													
Ad847	+	+	+	+	+	−	−	+	+	+	+	−	−
Ad857	−	−	+	+	+	−	−	+	−	−	−	−	−
Ad859	−	−	+	+	+	−	−	+	+	−	−	−	−
Andreaea regularis (Mount Waugh)													
Ar806	+	+	+	+	+	−	−	+	+	±	±	−	−
Ar807	−	−	+	+	+	−	−	+	+	−	−	−	−
Ar808	+	+	+	+	+	−	−	+	+	+	+	−	−
Ceratodon purpureus (Eastern Corner Island)													
Cp824	+	+	+	+	+	−	−	+	+	−	−	−	−
Cp825	−	−	+	+	+	−	−	+	+	−	−	−	−
Cp826	−	+	+	+	+	+	+	+	+	+	+	+	−
Bryum pseudotriquetrum (Leonie Island)													
Bp140	+	+	+	+	+	−	−	+	+	+	+	+	−
Bp141	+	+	+	+	+	−	−	+	+	−	−	−	−
Bp142	+	+	+	+	+	−	−	+	+	−	−	−	−
Sanionia georgicouncinata (Eastern Corner Island)													
Sg840	−	±	+	+	+	+	+	+	+	+	+	+	−
Sg841	−	−	+	+	+	+	+	+	+	+	+	+	−
Sg842	−	−	+	+	+	+	+	+	+	+	+	+	−
Sg845	−	±	+	+	+	+	+	+	+	+	+	+	−
Sg861	−	−	+	+	+	+	+	+	+	+	+	+	−
Sanionia georgicouncinata (Avian Island) the above-ground part													
S135	+	+	+	+	+	−	−	+	+	+	+	+	−
S152	+	+	+	+	+	−	−	+	+	+	+	−	−
S153	+	+	+	+	+	−	−	+	+	+	+	+	−
S167	+	+	+	+	+	−	−	+	+	+	+	−	−
sample of the rhizosphere and substrate from under the moss													
S371	+	+	+	+	+	−	−	+	+	+	+	+	−
S376	+	+	+	+	+	−	−	+	+	+	+	−	−
Chorisodontium aciphyllum (Eastern Corner Island)													
MB800	−	−	+	+	+	+	−	+	+	+	−	−	−
MB801	+	+	+	+	+	−	−	+	+	+	+	−	−

End of Table 3

Isolate	Temperature, °C							NaCl, %					
	4 ± 1	8 ± 1	16 ± 1	20 ± 1	28 ± 1	37 ± 1	42 ± 1	0	2.0	5.0	7.5	10.0	15.0
Polytrichum strictum (Eastern Corner Island)													
MB832	−	−	+	+	+	−	−	+	+	−	−	−	−
MB833	+	+	+	+	+	+	−	+	+	+	+	−	−
MB834	+	+	+	+	+	−	−	+	+	−	−	−	−
MB835	−	−	+	+	+	+	−	+	+	−	−	−	−
Polytrichum strictum (Ukraine Island)													
MB813	+	+	+	+	+	−	−	+	+	+	+	−	−
MB814	−	−	+	+	+	+	+	+	+	+	+	+	−
MB815	+	+	+	+	+	−	−	+	+	+	−	−	−

Note: "−" − no growth detected, "+" − growth detected, "±" − weak growth.

S. georgicouncinata (Eastern Corner Island), the above-ground part of *San. georgicouncinata* (Avian Island), and a sample of the rhizosphere of *San. georgicouncinata* and substrate from under the moss (Avian Island) (Table 2). Bacterial isolates from the mosses *An. depressinervis* and *An. regularis* produced slightly fewer siderophores. Only four bacterial isolates from moss banks synthesised siderophores, but their content was lower than that found in the culture medium of bacterial isolates from mosses of the genera *Sanionia* and *Andreaea*.

Most of the studied bacterial isolates synthesised auxin-like compounds (Table 2). The leaders in the synthesis of auxin-like compounds were bacteria from moss banks, *Cer. purpureus,* and the above-ground part of *San. georgicouncinata* (Avian Island). Bacteria isolated from mosses *An. depressinervis*, *An. regularis*, and *San. georgicouncinata* (Eastern Corner Island) synthesised average amounts of auxin-like compounds among the studied set of bacteria.

The isolated bacteria from bryophytes of different communities in their ability to grow at different temperatures (Table 3). Bacterial isolates from mosses *An. depressinervis*, *An. regularis*, two of three isolates from mosses *Cer. purpureus*, *B. pseudotriquetrum*, the above-ground part of *San. georgicouncinata* (Avian Island), and a sample of the rhizosphere and substrate from under the moss *San. georgicouncinata* (Eastern Corner Island) grew in a temperature range from 4 ± 1 to 28± 1 °C. A distinctive feature of bacterial isolates from *San. georgicouncinata* (Avian Island) was their ability to grow in a temperature range from 16± 1 to 42± 1 °C. From moss banks there was obtained the bacterial isolate MB832 that grew in a fairly narrow temperature range − from 16 ± 1 to 28 ± 1 °C, as well as bacteria that grew at 4−28 °C, 4−37 °C, or 16−37 °C. All bacterial isolates from *San. georgicouncinata* (Eastern Corner Island) were able to grow in the presence of 10% NaCl. Some bacterial isolates from *San. georgicouncinata* moss samples (Avian Island) showed the same tolerance. Bacterial isolates from other bryophytes were less tolerant to NaCl.

The ability of bacterial isolates from *San. georgicouncinata* moss samples to grow in the presence of NaCl prompted us to examine their tolerance to heavy metal compounds (Table 4).

Bacterial isolates from *San. georgicouncinata* (Avian Island) grew at higher concentrations of $FeSO_4 \cdot 7H_2O$, $CuCl_2 \cdot 2H_2O$, $CdCl_2 \cdot 2.5H_2O$,

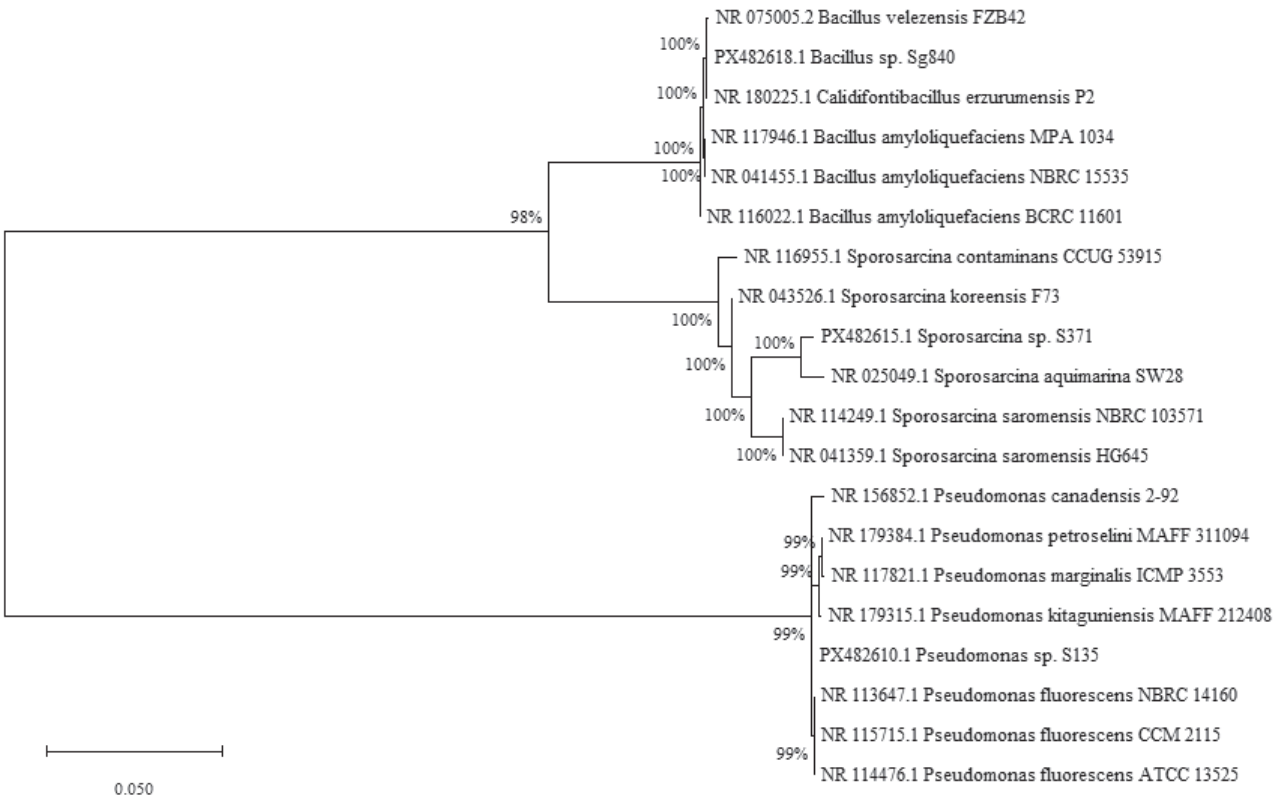

Figure 4. Phylogenetic reconstruction with the highest log likelihood using the maximum likelihood method based on the Kimura 2-parameter model of the 16S rRNA gene of isolates Sg840, S135, and S371, and their closest relatives

and $CoCl_2 \cdot 6H_2O$, compared to bacterial isolates from *San. georgicouncinata* (Eastern Corner Island).

All bacterial isolates from *San. georgicouncinata* (Eastern Corner Island) grew under the influence of 2.0 mM $FeSO_4 \cdot 7H_2O$, 0.5 mM $CuCl_2 \cdot 2H_2O$, and 0.01 mM $CdCl_2 \cdot 2.5H_2O$. The most tolerant to $MnCl_2 \cdot 4H_2O$ was the Sg840 bacterial isolate, which grew in the presence of 20.0 mM $MnCl_2 \cdot 4H_2O$ in the medium. Isolate Sg842 grew in the presence of 0.5 mM $CoCl_2 \cdot 6H_2O$, while the remaining bacterial isolates from *San. georgicouncinata* (Eastern Corner Island) grew at 1.0 mM metal salt. Isolate Sg842 was also more sensitive to $K_2Cr_2O_7$ than other bacterial isolates from *San. georgicouncinata* (Eastern Corner Island).

In terms of psychrotolerance, hydrolytic activity, the ability to grow in the presence of various heavy metals, and the ability to synthesise siderophores and auxin-like compounds for further work, the following isolates were selected: Sg840 (from the above-ground part of *San. georgicouncinata* (Eastern Corner Island)), S135 (from the above-ground part of *San. georgicouncinata* (Avian Island)), and S371 (from a sample of the rhizosphere and substrate from under *San. georgicouncinata* (Avian Island)).

The nucleotide sequence of the 16S rRNA gene of isolate Sg840 is characterised by a high identity value to the 16S rRNA gene sequence of *Bacillus velezensis* FZB42 (99.79%, query cover 100%), *Bacillus amyloliquefaciens* MPA 1034, *Bacillus velezensis* CBMB205, and *Bacillus amyloliquefaciens* NBRC 15535 (99.71%, 100% query cover), and *Calidifontibacillus erzurumensis* P2 (99.93%, query cover 99%) (Table 5). Phylogenetic recon-

struction (Fig. 4) confirmed the phylogenetic relationship of isolate Sg840 with other representatives of the *Bacillus* genus; therefore, it was identified as *Bacillus* sp. Sg840. When grown on TSA, these bacteria form large, convex, matte colonies that are milky white, with an entire margin, 5–7 mm in diameter, and a smooth surface. *Bacillus* sp. Sg840 cells are Gram-positive, solitary, motile rods that form centrally located spores. Catalase-negative, oxidase-positive. They grow at temperatures between +8 and +42 °C. Aerobes. They reduce nitrates to nitrites and grow in the Ashby's medium. They have amylase, protease, and lipase activity. Form siderophores. No urease activity is detected. They ferment rhamnose, sucrose, lactose, raffinose, inositol, and sorbitol to form acid (Table 6). Glucose, fructose, galactose, and arabinose are not used as carbon sources. Grow in medium with 20.0 mM $MnCl_2 \cdot 4H_2O$, 2.0 mM $FeSO_4 \cdot 7H_2O$, 10.0 μM $CdCl_2 \cdot 2.5H_2O$, 1.0 mM $CoCl_2 \cdot 6H_2O$, 1.0 mM $K_2Cr_2O_7$, or 10.0 % NaCl.

The nucleotide sequence of the 16S rRNA gene of isolate S135 is characterised by a high identity value to the 16S rRNA gene sequence of *Pseudomonas fluorescens* strains NBRC 14160, CCM 2115 and ATCC 13525 (99.93%), and to *Pseudomonas canadensis* 2-92, *Pseudomonas petroselini* MAFF 311094, and *Pseudomonas kitaguniensis* MAFF 212408 (99.64%). Phylogenetic reconstruction (see Fig. 4) confirmed the phylogenetic similarity of isolate S135 to other representatives of the genus *Pseudomonas*; therefore, it was identified

Table 4. Growth of bacterial isolates from mosses under the influence of different concentrations of heavy metal compounds

Isolate	Salt concentration*, mM																	
	$MnCl_2$			$FeSO_4$			$CuCl_2$			$CdCl_2$			$CoCl_2$			$K_2Cr_2O_7$		
	5.0	15.0	20.0	0.5	2.0	7.5	0.5	1.0	2.0	0.01	0.1	0.5	0.5	1.0	2.0	0.1	0.5	1.0
Sanionia georgicouncinata (Eastern Corner Island)																		
Sg840	+	+	+	+	+	–	+	–	–	+	–	–	+	+	–	+	+	+
Sg841	+	+	–	+	+	–	+	–	–	+	–	–	+	+	–	+	+	+
Sg842	+	+	–	+	+	–	+	–	–	+	–	–	+	–	–	+	–	–
Sg845	+	–	–	+	+	–	+	–	–	+	–	–	+	+	–	+	+	+
Sg861	+	+	–	+	+	–	+	–	–	+	–	–	+	+	–	+	+	+
Sanionia georgicouncinata (Avian Island) the above-ground part																		
S135	+	+	+	+	+	+	+	+	–	+	+	+	+	+	+	+	+	+
S152	+	+	+	+	+	+	+	+	–	+	+	+	+	+	+	+	+	–
S153	+	+	+	+	+	+	+	+	–	+	+	+	+	+	–	+	+	–
S167	+	+	+	+	+	–	+	+	–	+	+	+	+	+	–	+	+	+
sample of the rhizosphere and substrate from under the moss																		
S371	+	+	+	+	+	–	+	–	–	+	–	–	+	+	–	+	+	+
S376	–	–	–	+	+	–	+	–	–	+	–	–	+	–	–	+	–	–

Note: * – the following crystal hydrates were used in the work: $MnCl_2 \cdot 4H_2O$, $FeSO_4 \cdot 7H_2O$, $CuCl_2 \cdot 2H_2O$, $CdCl_2 \cdot 2.5H_2O$, $CoCl_2 \cdot 6H_2O$; «+» – growth detected, «–» – no growth detected.

Table 5. Nearest neighbors of identified strains isolated from samples of *Sanionia georgicouncinata*

Strain	Next relatives	% identity	Query Cover, %
Sg840*	*Bacillus velezensis* FZB42	99.79	100
	Bacillus amyloliquefaciens MPA 1034	99.71	100
	Bacillus velezensis CBMB205	99.71	100
	Bacillus amyloliquefaciens NBRC 15535	99.71	100
	Calidifontibacillus erzurumensis P2	99.93	99
	Bacillus amyloliquefaciens BCRC 11601	99.64	100
S135**	*Pseudomonas fluorescens* NBRC 14160	99.93	100
	Pseudomonas fluorescens CCM 2115,	99.93	100
	Pseudomonas fluorescens ATCC 13525	99.93	100
	Pseudomonas canadensis 2-92	99.64	100
	Pseudomonas petroselini MAFF 311094	99.64	100
	Pseudomonas kitaguniensis MAFF 212408	99.64	100
	Pseudomonas marginalis ICMP 3553	99.57	100
S371***	*Sporosarcina aquimarina* SW28	98.73	100
	Sporosarcina contaminans CCUG 53915	97.53	100
	Sporosarcina saromensis NBRC 103571	97.46	100
	Sporosarcina koreensis F73	97.46	100
	Sporosarcina saromensis HG645	97.39	100

* Isolated from Eastern Corner Island.
** Isolated from the above-ground part of the moss (Avian Island).
*** Isolated from a sample of the rhizosphere and substrate from under the moss (Avian Island).

Table 6. The use of different carbon sources by bacterial strains from *Sanionia georgicouncinata*

Source of carbon	*Bacillus* sp. Sg840*		*Pseudomonas* sp. S135**		*Sporosarcina* sp. S371***	
	aerobic	anaerobic	aerobic	anaerobic	aerobic	anaerobic
Glucose	–	–	+ A	+ A	+	–
Fructose	–	–	+ A	+ A	–	–
Galactose	–	–	+ A	+ A	–	–
Mannose	+	+	+ A	+ A	–	–
Arabinose	–	–	+ A	+ A	–	–
Rhamnose	+	+ A	+	+	–	–
Maltose	+	–	+	+	–	–
Sucrose	+ A	+	+	+	+	+
Lactose	+ A	–	+ A	+	+	+
Raffinose	+ A	+	+	+	+	+
Inositol	+ A	+	+ A	+ A	+	+ A
Sorbitol	+ A	–	+ A	+ A	+	+

Note: "–" – no growth detected, "+" – growth detected, A – acid formation; * – isolated from Eastern Corner Island; ** – isolated from the above-ground part of the moss (Avian Island); *** – isolated from sample of the rhizosphere and substrate from under the moss (Avian Island).

as *Pseudomonas* sp. S135. When grown on TSA, these bacteria form large (5–7 mm) convex, matte, milky-colored colonies with a smooth surface. Gram-negative, non-motile, rod-shaped bacteria. Catalase- and oxidase-positive. Aerobes. Grow at +4...+28 °C. Not capable of growing in the Ashby's medium, do not reduce nitrates. No urease activity is detected. They produce siderophores and exhibit protease and cellulase activities. They are capable of solubilising ZnO. Glucose, fructose, galactose, mannose, arabinose, lactose, inositol, and sorbitol are fermented with the formation of acid (Table 6). *Pseudomonas* sp. S135 are able to grow in medium with 20.0 mM $MnCl_2 \cdot 4H_2O$, 10.0 mM $FeSO_4 \cdot 7H_2O$, 1.0 mM $CuCl_2 \cdot 2H_2O$, 0.5 mM $CdCl_2 \cdot 2.5H_2O$, 2.0 mM $CoCl_2 \cdot 6H_2O$, and 1.0 mM $K_2Cr_2O_7$. Able to grow in medium with 10.0 % NaCl.

The nucleotide sequence of the 16S rRNA gene of isolate S371 is characterised by a high degree of identity with the 16S rRNA gene sequence of the *Sporosarcina aquimarina* SW28 (98.73%). The nucleotide sequence identity of the 16S rRNA gene of other representatives of the genus *Sporosarcina* relative to the isolate S371 did not exceed 98% (see Table 5). Phylogenetic reconstruction (Fig. 4) confirmed the phylogenetic relationship of isolate S371 with other representatives of the genus *Sporosarcina*; therefore, it was identified as *Sporosarcina* sp. S371. When grown on TSA, these bacteria form large (5–7 mm) light-orange, smooth-surfaced colonies. Gram-positive, spore-forming, slow-moving rods with rounded edges. Catalase-positive, oxidase-negative. Aerobes. Grow at +4... +42 °C. Bacteria are not capable of growing in the Ashby's medium and do not reduce nitrates. Gelatin is not liquefied. No urease activity is detected. Form siderophores, able to solubilise ZnO. Glucose, sucrose, lactose, raffinose, inositol (fermented to form acid), and sorbitol are used as carbon sources. *Sporosarcina* sp. S371 grow in medium with 20.0 mM $MnCl_2 \cdot 4H_2O$, 2.0 mM $FeSO_4 \cdot 7H_2O$, 10.0 μM $CdCl_2 \cdot 2.5H_2O$, 1.0 mM $CoCl_2 \cdot 6H_2O$, and 1.0 mM $K_2Cr_2O_7$. Able to grow in medium with 10.0% NaCl.

4 Discussion

This study analyses the enumeration of various groups of culturable microorganisms in bryophytes communities from environments with different conditions – rocks or more humid areas – that form complex interspecific complexes, particularly with lichens. The cultured microbiota of different bryophytes collected from various sites in the maritime Antarctic differed in the number of microbial groups identified and in their enumeration. The highest enumeration of cultured microorganisms were observed in the *San. georgicouncinata* samples. During the study, in *San. georgicouncinata* samples all the studied groups of bacteria were detected – copiotrophic, oligotrophic, and oligonitrophilic bacteria – as well as microorganisms capable of solubilising calcium phosphates and zinc oxide. The bacterial isolates obtained from these samples were characterised by a number of studied properties. The bacterial isolates from *S. georgicouncinata* synthesised various enzymes, siderophores, and auxin-like compounds, and were resistant to NaCl and heavy metal compounds.

At the same time, *An. depressinervis*, *An. regularis*, and moss banks fragments were characterised by lower enumeration of certain groups of microorganisms. These differences may be due to variations in the physical and chemical conditions of the microenvironment, moisture availability, and the physiological characteristics of the host plants which requires further comprehensive biological and chemical studies. The quantity of culturable microorganisms in the above-ground part of bryophyte cover were lower compared to the enumerations of culturable microorganisms in samples of rhizosphere and substrate under a bryophyte community possibly due to the fact that the above-ground parts of the bryophytes are exposed to environmental factors, and in the case of partial coverage of the moss bank with snow, the external parts of the mosses exposed to the wind and poorly covered with snow die off (Parnikoza et al., 2018). In addition to environ-

mental factors, physiological differences within a single plant – specifically, differences among various tissues along the moss gametophyte – can also influence the abundance and diversity of microorganisms. The moss gametophyte can be divided along a vertical gradient into two distinct parts: the live "green" part and the lower "brown" part, which differ in microbial diversity, composition, and the functional potential of their microbial communities. The green part contains photosynthetically active and/or nitrogen-fixing bacteria. The brown part has been studied much less, although it is an important source of nutrients for certain groups of microorganisms (Ishak et al., 2024). The observed differences in the enumeration of copiotrophic, oligotrophic, oligonitrophilic, phosphate- and zinc-solubilising microorganisms do not reflect the characteristics of the entire microbiome of the mosses studied in this work, but only those of the microorganisms that grew consistently on synthetic media.

Bacterial isolates from the above-ground parts of the moss banks studied mostly grew in the nitrogen-free medium, showed no hydrolytic activity other than lipase, and were unable to solubilise ZnO. However, these bacterial isolates, as all others studied in the work, were capable of synthesising auxin-like compounds. It is known that plant growth and adaptation to the environment are mediated by phytohormones. Auxin (indole-3-acetic acid) is a key regulator of plant ontogenesis and adaptation to abiotic stresses, such as low temperatures, drought, salinity, and heavy metal exposure. It acts as a central integrator of hormonal networks, interacting with abscisic, jasmonic, and salicylic acids and other phytohormones to precisely coordinate adaptive responses (Abdel Latef et al., 2021; Cackett et al., 2022; Musazade et al., 2025). In various plants, exogenous auxin application has been shown to mitigate stress from drought, salinity, heavy metals, and extreme temperatures (Musazade et al., 2025).

Most of the isolates obtained from these samples were characterised by traits that can be considered adaptations to the extreme conditions of Antarctica. First and foremost, this concerns the ability to grow over a wide temperature range, tolerance to high concentrations of NaCl, resistance to heavy metal compounds, and the synthesis of compounds potentially involved in interactions with the host plant as discussed by Styczynski et al. (2022), Ramasamy et al. (2023), Maslovska et al. (2024). The ability of all isolates to grow at temperatures ranging from +16 to +28 °C, and of some of them at +37 °C and +42 °C, is likely due to the broad ecological tolerance of these isolates, shaped by the characteristics of the Antarctic environment and the microenvironment created by these mosses. This result is consistent with current understanding of the temperature regime within the moss canopy, where temperatures can reach +20–30 °C and sometimes exceed +40 °C (Perera-Castro et al., 2020; Yin et al., 2023).

The high tolerance of the isolates to NaCl (up to 10.0%) may result from adaptation not only to aerosol transport of sea salts but also to the effects of freeze-concentration. When water freezes in moss tissues, the concentration of dissolved salts in the residual liquid phase increases rapidly, creating conditions of extreme osmotic pressure (Osborne et al., 2020; Romero-Perez et al., 2023).

Antarctic terrestrial ecosystems are characterised by natural heterogeneity in metal content, which is determined by the mineralogical composition of rocks (Nędzarek et al., 2014), weathering processes (Vašinka et al., 2020), marine aerosol transport (Shuhui et al., 2015), the activities of seabirds and marine mammals (Castro et al., 2021), as well as local anthropogenic impacts in the areas of research stations (Darham et al., 2023). Therefore, Antarctic microorganisms may be adapted to both deficiencies and elevated concentrations of certain metals. The concentration ranges we selected for Mn, Fe, Co, Cd, Cu, and Cr exceed their natural concentrations in Antarctic soils (Castro et al., 2021; Lin, et al., 2021; Komplikevych et al., 2022; Bhakta et al., 2022), which makes it possible to assess not only

the isolates' environmental tolerance but also their potential for survival under conditions of anthropogenic stress and their possible use in bioremediation technologies. It was found that all bacterial isolates studied, isolated from Antarctic mosses and associated substrates, exhibited a certain level of tolerance to heavy metal compounds. The ability of bacteria to grow in the presence of elevated metal concentrations may be a result of adaptation to Antarctic environmental conditions, where microorganisms are constantly exposed to a complex of stress factors, including low temperatures, high levels of ultraviolet radiation, periodic water shortages, and osmotic fluctuations (Coppola et al., 2023). It is known that many mechanisms of the cellular response to various types of stress are nonspecific and may confer cross-resistance to several adverse factors simultaneously (Jomova et al., 2012; Maslovska et al., 2023; Rapacka-Zdonczyk, 2026).

Various plant growth-promoting microorganisms have been isolated from Antarctic plants, which, in addition to stimulating the growth of Antarctic plants, can also positively affect crops (Choi et al., 2026) or can provide biological control (Iungin et al., 2024). Among the bacterial isolates we isolated from moss subformations, we selected *Bacillus* sp. Sg840, *Pseudomonas* sp. S135, and *Sporosarcina* sp. S371, which were halotolerant, grew on media containing heavy metal compounds, and exhibited properties that can be considered plant growth-promoting.

The bacteria *Bacillus* sp. Sg840 (isolated from *San. georgicouncinata* (Eastern Corner Island)) and *Pseudomonas* sp. S135 (from the above-ground part of *San. georgicouncinata* (Avian Island)) exhibited several characteristics that could be considered plant growth-promoting. They synthesised auxin-like compounds and siderophores, solubilised ZnO, and synthesised hydrolytic enzymes, *etc.* The synthesis of siderophores by bacteria provides plants with accessible iron compounds and enables biocontrol of phytopathogens by creating a local iron-deficient environment (Lemanceau et al., 2009; Sayyed et al., 2012; Aznar et al., 2014). The ability of selected bacterial strains to utilise various carbon sources (monosaccharides, disaccharides, trisaccharides, polysaccharides, and alcohols) ensures their competitive ability to meet trophic needs. The ability to produce acids during the breakdown of carbon sources is considered in the context of biocontrol of phytopathogens (de Werra et al., 2009; Seo et al., 2019) and as a method for solubilising salts of essential elements (Vyas & Gulati, 2009; Mumtaz et al., 2019). We assume that such a complex of properties can be used to stimulate the growth of mosses from which they were isolated by improving the availability of certain elements for plant nutrition, biocontrol of phytopathogens, and regulation of plant responses to stress factors.

According to the phylogenetic analysis, the 16S rRNA gene sequence of *Pseudomonas* sp. S135 forms a single clade with *Ps. fluorescens* strains. Some strains of *Ps. fluorescens* are used as seed inoculants for various crops to improve growth parameters and increase yields. These bacteria quickly colonise the roots of potatoes, radishes, and sugar beets, significantly increasing the yield of these plants (Mehmood et al., 2023).

In previous studies of the rhizosphere of *Deschampsia antarctica* É. Desv. from King George Island, we isolated *Bacillus* sp. RT1 (later *Bacillus* sp. IMV B-8128) (Maslovska et al., 2024), which stimulated the growth of spring wheat. According to phylogenetic analysis of the 16S rRNA gene, *Bacillus* sp. IMV B-8128, like *Bacillus* sp. Sg840, was closely related to *Bac. velezensis* CBMB205 and *Bac. amyloliquefaciens* MPA 1034. *Bac. velezensis* strains are considered model Gram-positive plant growth-promoting bacteria capable of biocontrol of pathogens (Fan et al., 2018). *Bac. amyloliquefaciens* is a rhizobacterium that promotes plant growth and is used as an environmentally friendly biofertiliser and biological control agent (Luo et al., 2022). Work was started on studying the effect of bacterial isolates derived from Antarctic mosses on seed germination, morphometric parameters, and chlorophyll content in the spring wheat variety Tubalt (Hnatush et al., 2026).

Sporosarcina sp. S371 was isolated from a sample containing rhizosphere and substrate from under *San. georgicouncinata* (Avian Island). Apart from the synthesis of auxin-like compounds and siderophores, these bacteria did not exhibit any other plant growth-promoting traits. However, they were able to grow in the presence of NaCl and heavy metal compounds. Information on the plant growth-promoting traits of bacteria of the genus *Sporosarcina* is limited. Improved growth of *Bacopa monnieri* (L.) Pennell, *Eupatorium triplinerve* Vahl, *Excoecaria agallocha* L., and *Avicennia marina* (Forssk.) Vierh. has been observed following bacterisation with *S. aquimarina* SjAM16103, isolated from the pneumatophores of *Av. marina* (Janarthine & Eganathan, 2012). There are also reports of stimulating garlic (*Allium sativum* L.) growth with *Sporosarcina globispora* EU-GRN-46 bacteria from the Himalayan Region of Kinnaur (Negi et al., 2025).

Thus, Antarctic mosses serve as a reservoir of culturable bacteria that combine adaptation to a complex of extreme environmental factors with characteristics typical of plant growth-promoting microorganisms. The identified isolates may be of interest both as model organisms for studying the mechanisms of microbial adaptation to polar conditions and as potential biotechnological agents for use under conditions of salt, temperature, or metal-induced stress. Therefore, there is great potential and relevance in studying the microbiota of Antarctic mosses and their subformations.

5 Conclusions

The cultivated microbiota of short moss turf and cushion subformation, bryophyte carpet and mat subformation, and tall moss turf subformation (moss banks), collected from various islands of the maritime Antarctic, differed in the enumeration of copiotrophic, oligotrophic, and oligonitrophilic, zinc- and phosphate-solubilising microorganisms. Copiotrophs and oligotrophs dominated in most samples, but oligonitrophyles prevailed in the *An. depressinervis* sample. The results obtained reflect only the cultured fraction of the microbiota of the studied mosses and do not represent the full diversity of their microbiome. The widest range of functional properties was found in bacterial isolates obtained from *Sanionia georgicouncinata*. They were characterised by the activity of hydrolytic enzymes (amylases, proteases, cellulases, and lipases), the ability to solubilise ZnO and $Ca_3(PO_4)_2$. All isolates studied synthesised auxin-like compounds, most of them siderophores. The isolated bacterial strains possess a range of adaptive properties, including the ability to grow over a wide temperature range (+4...+42 °C), high salt tolerance (up to 10.0% NaCl), and resistance to heavy metal compounds (Mn^{2+}, Fe^{2+}, Cu^{2+}, Cd^{2+}, Co^{2+}, and $Cr_2O_7^{2-}$). Based on the results of 16S rRNA gene sequencing, *Bacillus* sp. Sg840, *Pseudomonas* sp. S135 and *Sporosarcina* sp. S371 were identified. The identified set of properties and tolerance to environmental factors characterises the plant growth-promoting potential of bacteria isolated from Antarctic moss subformations.

Data availability. The authors declare that the data supporting the findings of this study are available within the paper. Other relevant data supporting the findings of this study are available from the corresponding author upon request. Sequencing data were deposited in the NCBI database.

Author contributions. Idea, conceptualisation: O. M., S. K., S. H. Data preparation and processing: O. M., S. K., S. H. Research: O. M., S. K., L. U., I. V., T. P., S. H. Visualisation: O. M., S. K., T. P. Samples collection: T. P., I. P. Drafting and redaction of the manuscript: O. M., S. K., T. P., I. P., S. H.

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Біологічний потенціал культивованої мікробіоти мохоподібних з різних біотопів морської Антарктики

Ольга Масловська[1], Соломія Комплікевич[1], Ласло Уліганець[1], Ірина Вронська[1], Тарас Перетятко[1, 2], Іван Парнікоза[2, 3], Світлана Гнатуш[1, *]

[1] Львівський національний університет імені Івана Франка, м. Львів, 79005, Україна
[2] Державна установа Національний антарктичний науковий центр, МОН України, м. Київ, 01601, Україна
[3] Національний історико-архітектурний музей «Київська фортеця», м. Київ, 01133, Україна

*** Автор для кореспонденції:** svitlana.hnatush@lnu.edu.ua

Реферат. Антактичні субстрати населені мікроорганізмами, стійкими до впливу факторів довкілля. Оскільки значні площі ґрунтів у всьому світі є засоленими та забрудненими металами, що обмежує ріст рослин, важливо виділити стійкі до впливу чинників середовища фітостимулювальні бактерії. Метою дослідження було виділення копіотрофних, оліготрофних, олігонітрофільних бактерій, а також фосфат- та цинксолюбілізувальних бактерій і визначення їхніх властивостей, зокрема ферментативних, здатності до синтезу ауксинів та сидерофорів, а також росту за впливу важких металів і NaCl. Матеріалом для дослідження були зразки мохоподібних з субформації мохів, які формують неглибокий торф та куртини: *Andreaea depressinervis* або *Andreaea regularis*; угруповання килимових мохів з домінуванням *Ceratodon purpureus* або *Sanionia georgicouncinata* та фрагментів угруповання торф'янистих мохів (мохові банки) з домінуванням *Polytrichum strictum* або *Chorisodontium aciphyllum*, зібраних з різних біотопів морської Антарктики. Культивована мікробіота субформацій мохів, а також мохових банків відрізнялася за кількістю виявлених груп мікроорганізмів і їхньою чисельністю. У структурі бактеріальних угруповань більшості зразків домінували копіотрофи та оліготрофи, проте у зразку *An. depressinervis* переважали олігонітрофіли. Бактерії, виділені зі зразків субформації мохів, які формують неглибокий торф та куртини з домінуванням *San. georgicouncinata*, характеризувалися амілазною, протеазною, целюлазною, ліпазною активностями, здатністю солюбілізувати ZnO і $Ca_3(PO_4)_2$. Усі досліджені ізоляти синтезували ауксиноподібні сполуки (до 11,8 мкг · $мл^{-1}$), більшість – сидерофори. Виявлено адаптивні властивості ізолятів: здатність до росту в широкому температурному діапазоні (від +4 до +42 °C), високу галотолерантність (до 10,0% NaCl) та резистентність до важких металів (Mn^{2+}, Fe^{2+}, Cu^{2+}, Cd^{2+}, Co^{2+} і $Cr_2O_7^{2-}$). За результатами сиквенування гена 16S рРНК ідентифіковано *Bacillus* sp. Sg840, *Pseudomonas* sp. S135 та *Sporosarcina* sp. S371. Виявлені властивості та стійкість до факторів навколишнього середовища характеризують фітостимулювальний потенціал бактерій, виділених із субформацій антарктичних мохоподібних.

Ключові слова: *Andreaea*, *Bacillus*, *Polytrichum*, *Pseudomonas*, *Sanionia*, *Sporosarcina*